GRASSHOPPER ECOLOGY AND CONSERVATION IN THE NAMA-KAROO

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A thesis submitted for the degree of Doctor of Philosophy

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I dedicate this dissertation to my great grand mother

ABAYNESH DEGEFU

whose model life of high moral values and hard work continues to influence me tremendously.

STATEMENT BY CANDIDATE

I declare that this thesis is my own original work. Where use has been made of the work of others, it has been duly acknowledged in the text. I have not submitted this material, either whole or in part, for a degree at this or any other institution.

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ABSTRACT

This study was undertaken in the Karoo, a semi-arid grazing land in South Africa, to elucidate the interaction between grasshopper assemblages and various aspects of the Karoo landscape. It falls into four sections, the first of which was a three-year study which was undertaken on and around a prominent South African mesa to determine its role as an elevational conservation refugium for grasshoppers in a sea of grazed flatlands (Chapter 2). The number of grasshopper species and individuals on the summit, slopes and flatlands varied significantly, in relation to measured environmental variables. The summit, through inaccessibility to livestock grazing, was effectively a conservation refugium for one grasshopper species, *Orthochtha dasycnemis*. There was no significant difference in species richness between years of sampling, although there were significant variations in grasshopper abundance between years. The difference in rainfall between years was significant and appeared to be the key factor influencing grasshopper population dynamics. This clearly shows that a mesa can act as a conservation island and refugium supporting an insect assemblage that would be otherwise altered by heavy livestock grazing on the surrounding flatlands. This summit assemblage is strongly linked with that on the slopes and below, and is determined not so much by an island effect per se, but by low grazing intensity and associated soil and vegetation structure.

The second part of the study focussed on the interaction between grasshopper assemblage response and three hill sizes at a regional scale (Chapter 3). Small hills contained a significantly higher grasshopper species richness and abundance than medium and large hills. There were significantly higher number of small-sized grasshopper species and individuals than medium and large-sized ones. Flatlands surrounding small hills had significantly higher grasshopper species richness and abundance than those surrounding medium and large hills. The slopes of the three hill sizes did not show significant difference in species richness and abundance. There was no significant variation between the summits of the three hill sizes in species richness but they varied in grasshopper abundance. The summits of small hills had significantly higher grasshopper abundance than the summits of medium and large hills.

Detrended Correspondence Analysis showed two clear grouping of sampling site and grasshopper species. While the flatlands of small hills formed a separate assemblage of several grasshopper species, slopes and summits of all hills formed another clump of few grasshopper species. Canonical Correspondence Analysis revealed that flaltands surrounding small hills occurred along increasing gradients of shrub cover whereas those surrounding medium and large hills occurred along increasing gradients of grass cover, vegetation density and greenness of grasses. Slopes and summits of all hill sizes occurred along increasing gradients of rock cover, cragginess, grass height and soil temperature. Patterns of grasshopper dominance were markedly variable among sites. There were low dominance patterns on flatlands of small hills where most species were rare. The distributional patterns varied of higher taxonomic groups varied among the three hill sizes. Small hills contained species from four families and nine subfamilies, but medium and large hills had only members of Acrididae in five subfamilies. About 50 % of the total grasshopper abundance were associated with small hills. The study revealed the patterns of grasshopper assemblages at regional scale, and showed that variability in hill sizes across the Karoo has marked role in grasshopper conservation, and that grasshoppers interact differentially with variable hill sizes across the Karoo.

The third part of the study was undertaken at twelve grassland sites in the Mountain Zebra National Park (MZNP) and the surrounding farms to assess changes in grasshopper assemblages to grazing by indigenous mammals inside the park in comparison with grazing by domestic cattle outside (Chapter 4). The MZNP has been restored from cattle-grazed farmland to indigenous mammal parkland for 62 years. The number of grasshopper species and families inside the park was not significantly different from outside the park, but the number of individuals inside the park was significantly higher.

Multivariate statistics did not reveal any strong site groupings based on simple inside/outside comparisons, but there were clear groupings of sites based on vegetation characteristics and other environmental variables. The park boundary, therefore, does not significantly determine grasshopper assemblages, although intensity of grazing does. The indigenous mammals inside the park had the same effect as the domestic cattle outside, and it was the level of defoliation and trampling that was important rather than type of mammal. Very intensive livestock grazing and trampling leads to bush encroachment and reduction in cover and/or disappearance of several grass species. In response to this pressure, grasshopper populations dropped, with localized extirpation of some species. Vegetation composition and structure showed a significant influence on grasshopper assemblages, particularly grass height and percentage cover. The MZNP is thus a localized area of elevated grasshopper abundance in comparison with the surrounding farm landscape, and presumably represents a situation prior to the current, intensive farming activities. Such elevated grasshopper abundances are important for maintaining soil quality and hence ecological integrity of this landscape which is poor in organics and nitrogen.

The significantly lower population of grasshoppers on the surrounding farms, with local extirpation of some species also suggests that the MZNP could be viewed as a local centre to which species with higher capacity for mobility may seek refugia from anthropogenic pressures. Hence the MZNP serves as a reference showing the difference between restored-through-natural-succession and anthropogenically-disturbed habitats, and compares desirable with undesirable ecosystem changes for herbivorous invertebrates such as grasshoppers.

The fourth part of the study was on grasshopper assemblage response to seasonal grazing (including summer, winter, spring and autumn grazing), rotational grazing, continuous resting and continuous grazing at a long-term experimental site (Chapter 5). Rotationally-grazed sites supported the highest number of grasshopper species and abundance, while continuously-grazed sites had the lowest. Cluster analysis revealed that spring-grazed and winter-grazed sites were the most similar, with continuously-rested sites being the next most similar to these. Rotationally-grazed sites showed the lowest similarity to the rest of the sites. DCA showed clear groupings of sites and grasshopper species, with most species associated with rotationally grazed sites. Continuously-grazed sites had a different grasshopper assemblage. CCA showed that the assemblages followed definite gradients of measured environmental variables. Rotationally-grazed sites occurred along gradients of increasing bare ground, while continuously-grazed and summer-grazed sites occurred along increasing gradients of shrub cover and soil temperature. Spring-grazed, autumn-grazed, winter-grazed and rotationally-grazed sites were characterized by high vegetation density. Grasshopper dominance patterns were very different at different sites. Summer-grazed sites had the highest percent dominance (40%) by *Picnodictya flavipes,* while winter-grazed sites showed higher percent dominance (32%) by *Pseudogmothela* sp. The significance of variable grazing management systems for maintaining floral and grasshopper diversity is discussed. It is recommended that rotational grazing in this arid system is most suited to maintaining plant and insect diversity.

These four parts in this study all clearly showed that grasshoppers interact with the landscape in a way that their assemblage patterns are dictated by patch as well as by regional dynamics. Topography in particular contributes significantly to biodiversity patterns at the spatial scale of landscape. But these patterns are also strongly determined by differential grazing pressures from domestic livestock which in turn interact with the various topographical features. These findings enable recommendations to be made on optimal grazing regimes relative to the hilly features of the landscape. The results also show that restoration which incorporates low-pressure grazing regimes and which takes cognizance of topographical features can maintain grasshopper abundance and diversity in the long term.

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CHAPTER ONE

General Introduction

1.1. Geography of the Karoo

The Karoo region (Fig 1.1) occupies more than 400,000 km ^{2} (Cowling, 1986) and, covers approximately 30 % of South Africa's land surface (Rutherford and Westfall, 1986). It encompasses a wide variety of physical environmental features, and is characterized by dwarf shrubland vegetation which typifies much of the semi-arid rangeland of the southern Africa subcontinent (Dean et al., 1995). The Karoo, divided by Rutherford and Westfall (1986) into the winter rainfall Succulent Karoo biome and the summer-rainfall Nama-Karoo biome, contributes to the Gross Domestic Product of South Africa through a profitable industry based on small livestock, mainly sheep (Botha et al., 1983; Cowling, 1986; Tainton et al., 1989; Du Toit, 1995, 1997, 1998 a, b).

Much of the Karoo is made up of sedimentary rocks of the Karoo Sequence (Visser, 1986). The region is a gently sloping plateaux at an elevation of 900-1200 m a.s.l., interrupted by emergent massifs, ranging in size from small rock outcrops to more extensive upland areas (Ellis and Lambrechts, 1986).

1.2. Climate of the Karoo

The Karoo is semi-arid to arid, and mean annual rainfall decreases westwards from about 500 mm in the eastern Karoo to less than 100 mm in the north-western Karoo (Venter et al., 1986). Rainfall seasonality also changes across the east-west gradient, from summer rainfall in the east, through between-season rainfall to winter-rainfall in the west (Dean et al., 1985). The annual increase of mean monthly rainfall across the Karoo shows a number

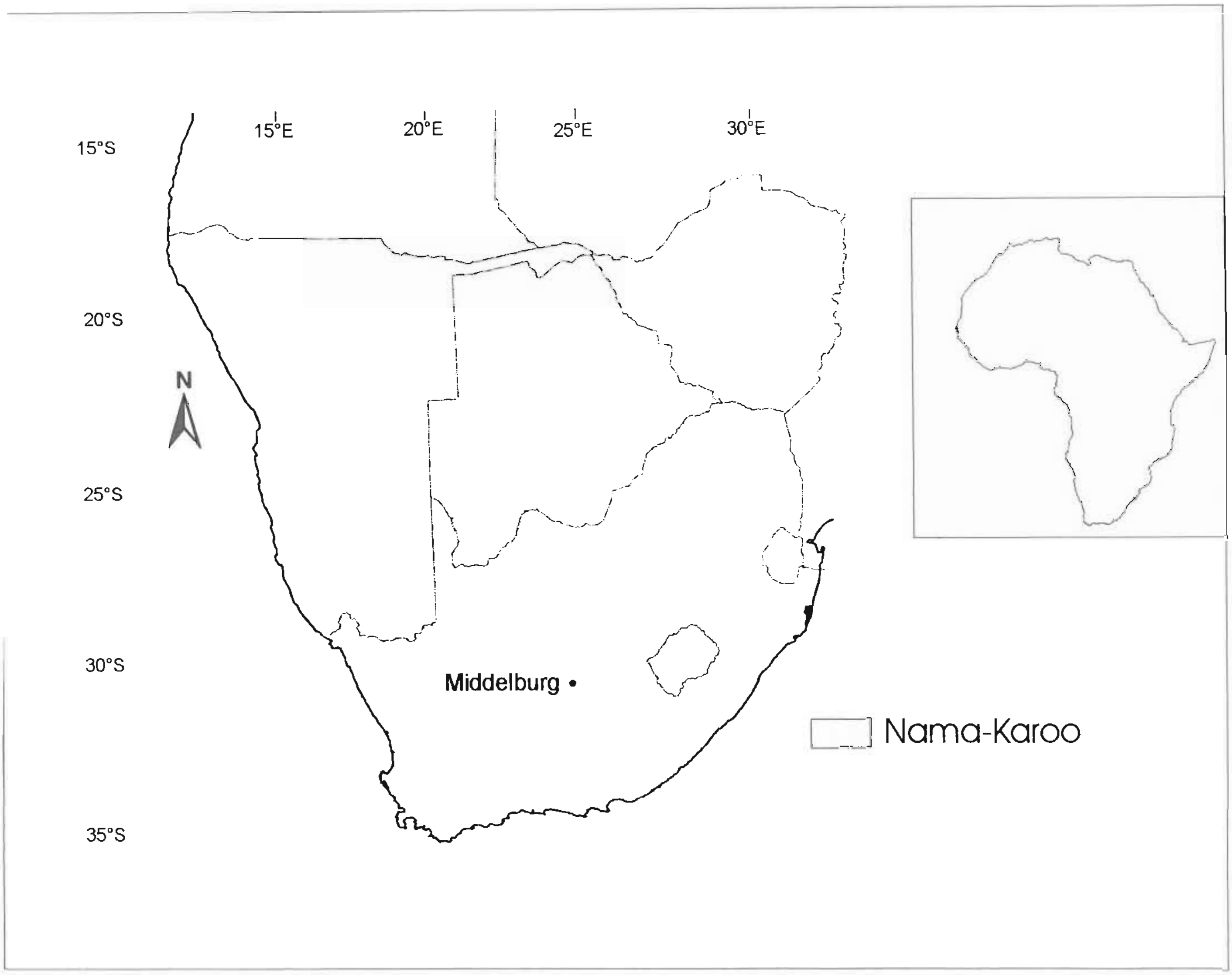

Figure .1.1 : Map illustrating the geographical position of the Nama - Karoo, with the sampling area of this thesis marked with a dot of distinct patterns. These rainfall patterns can be summarized in terms of three distinct parameters, namely, amplitude (high and low peaks), phase (a shift in winter - or summer - rainfall maxima or minima) and shape (a change of curve shape from the general parabolic curve to sinusoidal or aseasonal). Thus, within the Karoo, for the same given mean annual rainfall, there are a number of different possible combinations of rainfall distribution. Coupled to this variation are differences in reliability and intensity of rainfall (Desmet and Cowling, 1999). Prolonged droughts, defined in terms of a 12-month precipitation total below 60 % of the long-term mean (Venter et al., 1986), are typical for many parts of the Karoo (Booysen and Rowswell, 1983; Werger, 1986; Dean et al., 1995).

High temperature, low relative humidity and little to no cloud cover is characteristic of the Karoo, especially in the central areas which is a characteristic of arid climates generally (McGinnis, 1979; Desmet and Cowling, 1999). The annual changes of temperature in the region reflects both the coastal and continental pattern characteristic of southern Africa. Coastal areas along the west coast generally show a lag of one month in maximum and minimum temperatures, with February and August being the two extremes (Desmet and Cowling, 1999). Mean daily minimum temperatures in the region are highest along the west coast and increase equatorwards with the escarpment and high-lying areas of the plateau showing the coldest minimum temperatures (Schultze and McGee, 1978). In the Karoo, the lowest mean minimum temperatures are towards the centre of the subcontinent, and show the effect of both continentality and elevation (Werger, 1986). With the exception of the coastal and northern subtropical Namib Desert, the entire Karoo area falls within the line of 50 % probability of receiving frosts during winter (Schulze, 1997). High-lying areas of the escarpment and the central plateau are especially frost prone (Desmet and Cowling, 1999).

1.3. Geomorphology of the Karoo

The Karoo has always been subject to environmental changes, many of which have been reflections of major global events associated with continental drift and polar wandering, although intrinsic changes in climate are also apparent in the fossil record (Dean and Milton, 1999; Meadows and Watkeys, 1999). From a pedological perspective, the geomorphology of the Karoo can be broadly subdivided into two units. The western and northern areas are underlain by a 'basement complex' of Precambrian metamorphic rocks while the central and southern areas, are covered by Phanerozoic sediments intruded by dolerites. There is a wide variety of parent material in the Karoo ranging from ultramafic igneous rocks through to highly siliceous quartzites (Watkeys, 1999).

Superimposed on the geology are a number of land surfaces, the numbers, correlations and ages of which have been the subject of various conflicting interpretations (Partridge and Maud, 1987; Moon and Dordis, 1988; Gilchrist et al., 1994; Watkeys, 1999). Results emanating from numerous studies of the historical biogeography and palaeoenvironment of the Karoo depict change. This change in the characteristic climatic conditions is recorded in the fossil record, and inferred from contemporary biogeographical distribution, for the entire documented geological history of the Karoo. These changes have had major impacts on the biological communities throughout the passage of time, and a picture of the Karoo as a fundamentally dynamic entity emerges (Cowling and Hilton-Taylor, 1999; Meadows and Watkeys, 1999; Vernon, 1999).

The Karoo has been subject to long-term climatic fluctuation, with aridity consistently following more mesic conditions which, in turn, appear to be replaced once as a result of environmental circumstances which only came about, geologically speaking, relatively recently (Van Zinderen Bakker, 1978; Werger, 1978a; Vrba, 1985; Deacon and Lancaster, 1988; Bond and Richardson, 1990; Avery, 1992; Marker, 1995). It is only since the late Tertiary and throughout Quaternary that the essentially modern Karoo biota has flourished in the region. During that time, the climatic conditions appear to have continually fluctuated from arid and semi-arid to sub-humid and back again (Meadows and Watkeys, 1999; Cowling and Hilton-Taylor, 1999; Vernon, 1999; Desmet and Cowling, 1999).

1.4. Biodiversity of the Karoo

The south-western arid zone of Africa, which includes the Namib and Kalahari Deserts, and the succulent and Nama-Karoo biomes, is rich in plant and animal species, and in endemism (Vernon, 1999; Cowling and Hilton-Taylor, 1999). There are two extra-tropical areas that are recognized as extraordinary hotspots of plant diversity and endemism: the Mediterranean climate regions of South Africa and south-western Australia (Cowling et al., 1998). The Karoo is a third such region (Deacon et al., 1983; Ihlenfeldt, 1994; Cowling et al., 1996, 1998; Scott et al., 1997; Meadows and Watkeys, 1999; Cowling and Hilton-Taylor, 1999; Myers et al., 2000). The distribution of many animals, however, in this region is poorly known, and is further complicated by the presence of many undescribed species, particularly among the invertebrates (Vernon, 1999; Cowling and Hilton-Taylor, 1999; Myers et al., 2000). The invertebrates are probably the most compositionally important components of the fauna, but also the poorest-known group in the Nama-Karoo. This generalization is also important both in terms of pattern and process, as well as in the number of species, the number of individuals and their ecological adaptations. For example, the brown locust, *Locustana pardalina* (Acrididae) is one of the most important and characteristic animals of the Nama-Karoo and savanna biomes (Lea, 1968, 1969). During episodic irruptions, the locust is the most numerous animal in the Karoo. Its life history mirrors the patchily dispersed and temporally erratic occurrence of resources in the Karoo environment (Jago, 1987; Hanrahan, 1988; Hockey, 1988; Brown, 1989; Vernon, 1999).

From an agricultural perspective, it is best known for its periodic outbreaks of huge, migratory swarms, the damage it causes to crops, and the controversies surrounding its control (Jago, 1987; Boshoff, 1988; Hanrahan, 1988; Hockey, 1988; Lovegrove, 1999; Samways, 2000). From a biological perspective, the characteristics of its reproduction, emergence and polymorphism remain intriguing (Faure, 1932; Lea, 1964; Botha et al., 1974; Bouaichi et al., 1995).

1.5. Land-uses of the Karoo

The Karoo has a long history of utilization by hunter-gatherers and herders whose populations in the past always remained low, whose shifting settlements were unstable, and whose impact on the landscape was localized in space and time, like those of the indigenous and naturalized plants and animals on which they depended (Dean and Milton, 1999). Two hundred years ago, the Karoo was colonized by peoples of European origins, who brought with them agricultural traditions, livestock and crops more appropriate for a less stochastic mesic climate (Downing, 1978; Tainton et al.,1989; Dean and Milton, 1999). Settled agriculture dependent on underground water combined with ploughing of alluvial soils for dryland crops has since changed the structure and composition of Karoo habitats and biota (Roux and Vorster, 1983; Macdonald, 1989; Hoffman and Cowling, 1990 b; Milton and Hoffman, 1994; Dean and Macdonald, 1994; Dean and Milton, 1995; Steinschen et al., 1996). Ploughing lands to plant crops was a novelty in the Karoo ecosystem, and a largely unsuccessful experiment during the first 150 years of occupation (Macdonald, 1989; Dean and Milton, 1995).

Grazing by domestic livestock was thought to be sustainable in the Karoo and to be the best agricultural use of this arid region, but it, too, has associated problems. As a general rule the grasses (where they occur) provide much of the summer forage, whereas Karoo bushes normally provide the preferred grazing in winter (Roux, 1966). The Karoo is well suited to small stock (sheep and goats) except in inherently more grassy areas where cattle are the preferred livestock type (Tainton et al., 1989; Du Toit, 1996, 1997, 1998 a, b; Fynn and O'Connor, 2000). Indeed, woolled sheep have been the most important grazing animals since 1970 (Robert, 1981). More recently changed economic circumstances, and perhaps to an extent also the change in the composition of the vegetation, have led to an increase in the number of Angora goats and dual purpose sheep in the area (Tainton et al., 1989; Du Toit, 1995, 1997, 1998a,b)

1.6. Grazing and landscape productivity in the Karoo

The productivity of natural ecosystem is determined by the temporal and spatial availability, transfer and cycling of water, nutrients and energy, all processes that are influenced by the abundance and composition of species present (McNaughton, 1993; Walker, 1995;

Landsberg et al., 1999). Changes in the primary productivity of semi-arid rangeland have been shown to accompany changes in the species composition of the vegetation (Illius and O'Connor, 1999). Changes in primary production and species composition are related. Where the effect of grazing on species composition is more extreme, primary production can be reduced by up to 40 % (Acocks, 1955; Downing, 1978; Louda, 1982; Roux and Vorster, 1983; Schofield and Bucher, 1986; Liljelund et al., 1988; Westoby et al., 1989; Friedel et al., 1990; Milton and Dean, 1990; O´Connor, 1991; Milchunas and Launoth, 1993; Milton, 1994).

At the scale of the landscape, there are usually clear linkages between productivity and landscape diversity. In semi-arid environments, the pattern of distribution and concentration of water and organic litter produces patches. These patterns are reinforced and facilitated by feedbacks from the growth of plants, and the activities of a range of organisms including livestock (Tongway and Ludwig, 1990; Coughenour, 1991; James et al., 1995; Landsberg et al., 1999). If landscape patchiness breaks down, there is little to impede the overland flow of water and nutrients away from the system, instead of their deposition on a local scale. The consequences include loss of plant species that rely on fine-scale redistribution of water and nutrients, loss of plant and animal species that rely on associated habitat features, and sometimes, invasion by different species more able to cope with a more coarsely - patterned landscapes. Thus, landscape diversity is a primary basis for pastoral and ecological sustainability of the ecosystem (Burel, 1988; Burel and Bandry, 1990; Verboom and van Apeldon, 1990; Milton and Dean 1990; Bunce and Jongman, 1993; Dean and Macdonald 1994; Zonneveld, 1995; Chase, 1996; Landsberg et al., 1999; Samuel, 2001). The realization that rangeland grazing systems are characterized by variability, and not constancy, is a new paradigm that challenges traditional approaches of the classical view that grazing systems are in a state of equilibrium. In arid and semi-arid systems seasonal and annual climatic variation disrupts the stable equilibrium between animals and plants that would be expected to occur under constant conditions. Annual rainfall in semi-arid environments typically has a coefficient of variation greater than 30 %, with the result that coupling of animal and plant processes appear to be weak (Behnke and Scoones, 1993; Ellis and Swift, 1988; Owen-Smith, 1990; Behnke et al.,1993; Galvin and Ellis, 1996; Scoones, 1994; Illius and O'Connor, 1999;).

It would be difficult to find an African savanna or grassland that has not experienced an extended evolutionary history of mammalian herbivory, yet examples abound of plant communities transformed by livestock grazing. Some of the most dramatic transformations have occurred in semi-arid environments (O'Connor, 1985; Landsberg et al., 1999). Most species of livestock (sheep, cattle and goats) are predominantly grazing animals (Wilson and Hurrington, 1984). Grazing- related shifts from grass dominance to dominance by woody plants have been widely reported from arid and semi-arid grasslands and savannas around the world (Humphrey, 1987; Dick-Peddie, 1993; Archer 1995, 1996; Dougill and Trodd, 1999; Samuel et al., 2001). While other factors may be involved to a greater or lesser extent, the onset of bush encroachment (Taylor and Walker, 1978; Van Vegten, 1983; Bosch, 1989; Dougill and Trodd, 1999) by woody vegetation is frequently associated with intensification of grazing by livestock (Noy-meir and Walker, 1986; Westoby et al., 1989; Ringrose et al., 1990; Skarpe, 1990; Archer and Smeins, 1991; Briske, 1991; Perkins and Thomas, 1993 a, b; Milton et al., 1994; Ringrose et al., 1995; Landsberg et al., 1999). The main effects of livestock on individual plants act not so much through the animals eating the plants to local extinction, but more through the effects of grazing modifying the competitive abilities or recruitment success of one species relative to another (Crawley, 1983; Belsky, 1986; O'Connor and Pickett, 1992; Milton, 1994; Bullock, 1996; O'Connor, 1996; Moretto and Distel, 1999).

Since primary productivity is related to rainfall (Bell, 1982; O'Connor and Pickett, 1992), it follows that less productive arid regions would show the effects of overgrazing faster under higher stocking rates. The probability of overgrazing patches therefore appears to be greater for low than high rainfall regions (Steenbergh and Lowe, 1969; Jordaan and Nobel, 1982; Castellanos and Molina, 1990; O'Connor and Pickett, 1992; Esler and Phillips, 1994; Dean et al., 1995).

1.7. Orthoptera and landscape change

Orthoptera are well represented by individuals and species across the terrestrial biomes. Both the presence or absence and the density of local population of Orthoptera can change in response to long-term climatic shifts (Otte, 1976; Butlin et al., 1992; Kemp and Dennis, 1993; Kemp and Cigliano, 1994), elevation (Claridge and Singhrao, 1978; Sergeev, 1988, 1993; Dingle et al., 1990; Samways, 1990; Wachter et al.,1998), vegetational heterogeneity (Otte, 1976; Bergmann and Chaplin, 1992), and anthropogenic land modification (Bei-Bienko, 1970; Sergeev, 1987 a, b; Fielding and Brusven, 1993, a, b). Although particular biotopes may be characterized by a given orthopteran assemblage, they are determined in part by regional occurrence (Sergeev, 1992; Kemp, 1990 a), continental configuration (Otte, 1976) and preferences of orthoptera (Samways and Sergeev, 1997).

Mankind's modification of the landscape by means of linearization and geometrization is readily seen in hedges, fences, roads, canals and a mosaic of patchwork appearance (Samways and Sergeev, 1997). Each species and even each sex and developmental stage (Samways, 1994) may respond to the various landscape elements differently (With, 1994; Levin, 1992).The feeding habits and environmental requirements of exopterygota insects are similar in the young and adults. Yet the various life stages may be characterized by different responses to landscape form and pattern at the various spatial scales ranging from microsite to landscape element (Uvarov, 1977; Stabaev, 1972; Sergeev et al., 1988; Nagy, 1992; Samways and Sergeev, 1997). A modified landscape causes some species to increase in abundance and others to decrease. Their presence/absence patterning across the mosaics or patches/matrices also changes (Port and Thompson, 1980; Sobolev, 1990; Chambers, 1992; Muralirangan et al., 1993; Samways and Sergeev, 1997).

Some species apparently thrive on landscape disturbance, as opposed to fragmentation, providing it is neither too severe nor too frequent (Turner and Gardner, 1991). Species that respond positively to disturbance are mostly eurytopic (Samways and Sergeev, 1997). Disturbance can induce pest status in some species but cause a population decline in others (Lockwood and De Brey, 1990; Latchininsky, 1998; Foucart and Lecoq, 1998). Disturbances such as natural fires can precipitate outbreaks of species such as *Melanoplus sanguinipes* (Fielding and Brusven, 1993 a). Rehabilitation of annual grasslands by planting perennial grasses and shrubs and protecting endemic plant communities contribute to increasingly diverse grasshopper communities, with a lower proportion pest species (Devaux et al., 1983; Fielding and Brusven, 1993 b; Foucart and Lecoq, 1998).

1.8. Orthoptera in biodiversity

Orthoptera are a significant components of biodiversity, number of their species probably exceeding that of all vertebrates combined (Samways, 1997; Lockwood, 1998; Samways and Lockwood, 1998; Belovsky, 2000). Information on individual species worldwide is being collated under the auspices of the Orthoptera Species File (Otte, 1994a, b; 1995a, b)

Conservation of the vast majority of Orthoptera will depend principally on how landscapes are conserved, with management, or how they are preserved, without it. Their populations and species may then be viewed as functional, unnamed components of the ecosystems. Many of them will be ecologically redundant, i.e. their absence will not change substantially the physiognomy or processes of the host ecosystems (Samways, 1997). However, there are others that are keystone species (Quinn et al., 1993; Chase, 1996), especially in grasslands (Joern and Gaines, 1990; Kisebenedek, 1995; Chase, 1996). Ensuring survival of processes means maintaining as intact as possible as many large landscapes as possible (Samways, 1994, 1997; Bridgewater, 1996; Samways and Sergeev, 1997; Sergeev, 1998).

1.9. Conservation of Orthoptera

The taxonomic impediment, arising from not having all species of orthoptera described, is an important consideration in the conservation of Orthoptera, as with several other insect groups, especially in the tropics (Green, 1998). The perception impediment is significant both because a few Acrididae species are notorious agricultural pests which does not encourage support for their conservation (Samways, 1997; Samways and Lockwood, 1998; Lockwood, 1998). Yet among the Orthoptera are some of the most charismatic and threatened of insects. These pests may not be noxious throughout the whole of their range or even at all times (Jago, 1987; Nagy, 1992) and high population levels at one time do not preclude species extinction at another (Samways, 1989; Lockwood and De Brey, 1990). The order Orthoptera is relatively speciose and contains many flagship species (Otte, 1994 a, b; 1995 a, b). As an order it is also important in ecological processes (Lockwood, 1998). Investigation into the ecological values and conservation of Orthoptera is, thus, a necessary component of landscape conservation (Samways, 1997; Sergeev, 1998; Lockwood, 1998; Belovsky, 2000).

1.10. Objectives and organization of the thesis

The Karoo landscape is characteristically made up of low-lying flatlands and contrasting, prominent mesas. As grasshoppers are important native herbivores in this system, the first part of this study determined whether the most prominent mesa in the study area, standing out as a huge elevational island amidst the surrounding flatlands, is a conservation refugium for grasshoppers that are sensitive to heavy grazing disturbance on the flatlands. During this part of the study grasshopper population dynamics were investigated relative to 3-year inter-annual rainfall variation (Chapter 2).

The Karoo has variable topographies, with hills of different sizes. Grasshoppers are the dominant above-ground invertebrate herbivores in this ecosystem, yet no information exists on how these animals interact with these topographical features at the landscape scale. To address this issue, grasshopper behaviour and ecology were studied in relation to hills of different sizes (Chapter 3), including the large mesa studied in Chapter 2.

The Karoo is generally thought to be undergoing degradation from overstocking. The Mountain Zebra National Park is part of a long-term conservation and restoration plan designated as a park in 1937, to maintain a representative population of the Cape Mountain Zebra (*Equus zebra zebra*), and to conserve a spectrum of faunal and vegetation elements typical of the region. Prior to 1937, it was stocked with domestic livestock, but since then it has undergone over 60 years of restoration. A study was undertaken here to investigate how grasshopper assemblages, as significant herbivores in such systems, have responded to this long-term period of restoration, using the surrounding farms for comparison (Chapter 4).

Among grazing land management systems employed is the systematic variation of grazing cycles in space and time. The Grootfontein College of Agriculture at Middelberg has been running a field experiment for over 45 years which examines land management options for Karooveld and monitors long-term changes in vegetation. Treatments have included seasonal grazing, rotational grazing, continuous grazing and continuous resting. Although the effect of such grazing trials on the vegetation and soil dynamics have been assessed, there is no information on the response of grasshoppers to this long-term management experiment. This topic is addressed in Chapter 5.

The final chapter (Chapter 6) is a general comment and conclusions that weaves together the findings from each of the previous chapters and explores underlying general principles relating to grasshopper ecology, biodiversity and conservation in the broader context of Karoo ecosystems. It also highlights implications for future biodiversity assessment and conservation, thereby indicating areas for future research on the invertebrate fauna in the region.

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CHAPTER TWO

Conservation value of a large mesa for grasshoppers in South Africa

This chapter has been submitted for publication in *Biological Conservation*, and is in press. Slight editorial changes have been made to ensure continuity of the thesis.

2.1. Introduction

The landscape of the Karoo, a vast semi-arid region of South Africa, is punctuated by flat-topped mesas. While the surrounding flatlands are grazed by sheep and cattle, the summits are relatively ungrazed owing to absence of free water. The question that arises is: are these mesas conservation refugia in a sea of grazed flatlands ? (Mesas are large flat-topped hills capped by hard basalt and with vertical krantz and steep screes immediately around the base (Twidale, 1971).)

Grazing by domestic and wild megaherbivores can alter grasshopper assemblage and guild structure by altering the height, aerial cover, and species composition of the herbaceous stratum. Total grasshopper abundance, species richness and species diversity has been found to increase (Southwood and van Emden, 1967; Holmes et al., 1979) or decrease (Capinera and Sechrist, 1982; Quinn and Walgenbach, 1990) in response to grazing and mowing. Prendini et al. (1996) found that, in savannas, heavy grazing leads to a change in the guild structure of grasshoppers, but does not reduce grasshopper abundance and diversity overall. However, they pointed out that their investigation was made over short time (only 5 days) and that more comprehensive study was needed over a longer time since owing to the seasonality of Acridoidea, findings may vary over a single year, or between years with contrasting rainfall patterns. Indeed; Kemp (1992) found considerable turnover of species at a given site during the course of the summer. Grasshoppers are one of the few insect groups that can be consistently sampled across all terrain types (Gandar, 1982; Samways, 1990; Samways and Moore, 1991; Stewart, 1997). This study assesses the effects of topography and inter-annual variation in rainfall on grasshopper assemblages in the semi-arid Karoo of South Africa. Grasshoppers are sensitive indicators of landscape change, although they are not necessarily an umbrella taxon for all other taxa in biodiversity assessments (Lawton et al., 1998; Kotze and Samways, 1999). Here I present results of three years of sampling from 1998 to 2000. Mesas have become subjects of studies for testing hypotheses concerned with the regulation of biodiversity (Barthlott et al., 1993). The results are used to address the question of whether the isolated mesas, so characteristic of the central southern African landscape, are conservation refugia, and whether they might be considered as source habitats for restoring the surrounding, domestically-grazed area.

2.2. Materials and methods

2.2.1. Study area

The Karoo is a large semi-arid region with an approximate area of 420000 km^2 at ca.1200 m a.s.l. on the central plateau of South Africa. The landscape is characteristically punctuated by mesas. The land is utilized mainly for sheep farming and to a small extent for cattle farming. Rainfall is sparse and unpredictable (125-375 mm per annum) and temperatures range from a mean monthly minimum of 3° C to mean monthly maximum of 32 ° C. Vegetation composition varies widely, but consists primarily of widely spaced, small leafed, dwarf shrublets (60-80 cm). Grass is generally sparse in the western region of the Karoo, becoming more prominent towards the north-east.

The study area was in the Middelberg district, Eastern Cape Province. The largest mesa, 'Tafelberg' (maximum elevation at the summit ca. 1700 m a.s.l. and summit area of approximately 4 ^{2} km) represents a distinct "elevational island " (Begon et al., 1990) surrounded by a matrix of flatland (ca

1200 m a.s.l.) (Fig. 2.1) While the top of the mesa is ungrazed by livestock, owing to its physical inaccessibility and also absence of free water, some portion of the slope, the bottom and surrounding flatlands are regularly grazed.

2.2.2. Sampling sites

A transect of 100 m long and 5 m wide was considered as a single sampling unit. Six of these replicates constituted one site. There were five elevational categories: 1) flatlands (1200 m a.s.l.) 2) lower slope (1350 m a.s.l.) 3) mid-slope (1500 m a.s.l.) 4) upper slope (1650 m a.s.l.), and 5) summit (1700 m a.s.l.). In addition there were four aspects (NE, NW, SE, SW) representing highest, lowest, and two intermediate levels of insolation. This meant that the total number of sites was 20 (five elevations X four aspects). The distance between transects was 10 m to minimize sampling of grasshoppers twice (Kisebenedek, 1995). On the slope, each transect ran along the slope contour to maintain constant elevation. The sampling sites on the summit were 100 m inward from the edge of the steep scree. Sampling was done in April and May in 1998 and 1999 and January to May in 2000 starting after the area had received good rains and when vegetation growth was maximal, and discontinued when most of the adult grasshoppers were killed by the first frosts. Sampling for all aspects of this study was undertaken only on sunny days with <15 % cloud cover and when wind movement was minimal (<30 km hr^{-1}). The voucher collection is retained at the Invertebrate Conservation Research Centre in the University of Natal.

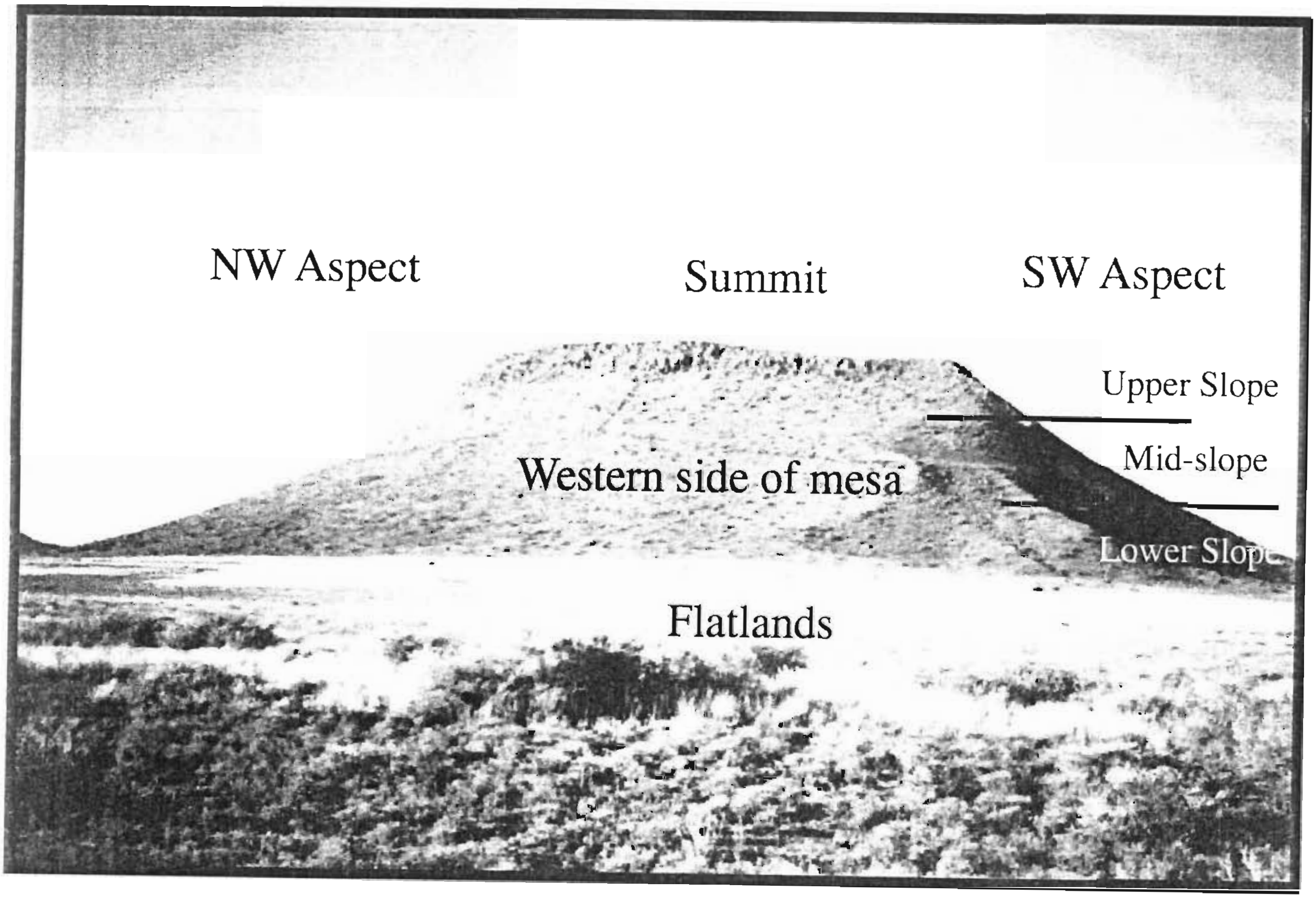


Fig. 2.1. Study area, illustrating the five elevational categories (Summit, Upper Slope, Mid-slope, Lower Slope and Flatlands) and two of the four aspects (North-West and South-West; The other two aspects on the farest side of the mesa are North-East and South-East). Note the sunlit NW aspect in comparison with the shady SW aspect.

2.2.3. Sampling methods

2.2.3.1. Grasshoppers

Extensive preliminary sampling of grasshoppers was done using a sweep net over one year prior to the quantitative sampling. Identification of the resident grasshopper species was done from a voucher collection. In addition, intensive familiarization was undertaken on the appearance (jizz) of each species in the field so that they were recognizable in the field with no or minimal error. Sampling of grasshoppers was then done visually, by making transect walks and counting them as they flushed. A transect was 100 m long and 5 m wide. This was replicated 6 times to constitute a sampling unit. This was supplemented with sweep netting to determine individuals that were still unfamiliar This method of visual recording was found in previous studies to be the most accurate and efficient means of documenting grasshopper species and abundances in the rugged African terrain (Samways, 1990; Chambers and Samways, 1998; Armstrong and van Hensbergen, 1999; Gebeyehu and Samways, 2001). Visual sampling has also been shown to be effective elsewhere (Kemp and Dennis, 1993; Kemp et al., 1989). Close-focus binoculars (Sigma-armada series 10 × 23 wp compact) were an essential recognition aid. Only adult individuals were counted.

2.2.3.2. Vegetation

The vegetation at each site was characterized by estimating percent basal cover for each plant species with 10 randomly placed $1 m^2$ quadrats (Daubenmire, 1965) along the lines of the transects where grasshoppers were sampled. Each quadrat was subdivided in to ten units of $10 cm^2$, and the relative proportion of grass, shrubs, rock and bare ground and percent greenness of the grasses was estimated. Average height of grasses was estimated by taking 30 random points in a transect and the tallest inflorescence was taken to give the maximum grass height. Surface soil temperature at a depth of 15 cm was measured in each quadrat using a soil thermometer inserted into a hole made at four random points in each quadrat and recorded after 5 minutes. This depth was selected because arid and semi-arid grasshopper species generally tend to lay their eggs between 11 cm and 15 cm (Popov, 1958; Braker, 1989).

2.2.4. Data analyses

Canonical Correspondence Analysis (CCA) revealed high correlation between maximum and average grass height, so the former was not included in the multivariate ordination. Detrended Correspondence Analyses (DCA) was used in preference over Correspondence Analysis to avoid the arch effect as recommended by ter Braak (1986) in which the second axis shows a systematic, often quadratic, relationship with the first axis. DCA uses a sites-and-species scores data matrix, and summarizes it such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. CCA was used to relate species and site scores to underlying environmental variables in which important environmental variables tend to be represented by longer arrows than less important environmental variables (ter Braak, 1986; ter Braak and Looman, 1995). All grasshopper abundance data were square-root transformed and all vegetation proportion data were log-transformed to maintain normality and to satisfy the requirements of ANOVA and the multivariate analyses. MINITAB and SPSS were used to undertake ANOVA. Tukey's family error test was used for mean separation. CANOCO version 4 (ter Braak and Smilauer, 1998) was used for multivariate analyses.

Recognizing the difficulties of interpretation arising from single diversity indices when parameters such as species richness, evenness and number of individuals and the area sampled are compounded (Ludwig and Reynolds, 1986; Curry, 1994), we used an alternative rank-abundance curves in which both species richness and evenness are graphically displayed. The curves are drawn such that the percentage abundance (dominance) is plotted against ranked species sequence (Ludwig and Reynolds, 1986; Curry, 1994).

2.3. Results

2.3.1. Elevation, environmental variables and grasshoppers

ANOVA showed that there were significant differences between the summit, slope and flatland sites with regard to environmental variables (Table 2.1). Grass cover was significantly higher on the summit compared to the slope and the flatlands, whereas bare ground cover was significantly higher on the flatlands than on the summit or on the slope. The slope and the flatlands did not show a significant difference in grass cover. Maximum and average grass heights were both significantly higher on the summit and slope compared to the flatland sites, but the slope and the summit did not show significant variation. Rock and shrub cover were significantly higher on the slope sites than at the summit and flatland sites, but the sites on the summit and on the flatlands did not vary significantly ($P>0.05$). Percentage greenness of grass was significantly higher at the summit sites than those on the slope and on the flatlands, although there was no significant difference between the slope and the flatlands (Table 2.1).

Table 2.1. ANOVA of the environmental variables on the summit, slope and flatlands of the Tafelberg mesa. Means followed by the same letter in a row are not significantly different at the 5 % level of significance.

Variable	Summit	Slope	Flatlands	*P*
Grass cover (%)	20.5b	41.0a	16.5b	<0.0001
Rock cover (%)	18.1b	18.5b	43.5a	<0.001
Shrub cover (%)	56.5a	27.2b	31.2b	<0.01
Bare ground (%)	5.0c	13.2a	8.7b	<0.0001
Grass max height (cm)	105a	68.7a	37b	<0.01
Grass avg height (cm)	79.2a	38.2a	13.2b	<0.01
Greenness of grass (%)	82a	52b	49b	<0.001

The flatland sites had a significantly higher number of grasshopper individuals compared to the summit and the slope, while the summit had a significantly higher number of grasshopper individuals than the slope. (F =103.5; P<0.0001; n = 20) (Fig. 2.2 a, b).

2.3.2. *Sampling years*

There was no significant difference in the number of grasshopper species between years of sampling (F = 1.06; P > 0.05; n = 60) but there was a significant difference between years in the number of grasshopper individuals. The highest number of individuals was in the year 2000, while the lowest number was in 1999 (F=3.67; P<0.05; n = 60) (Fig. 2.2 a, b).

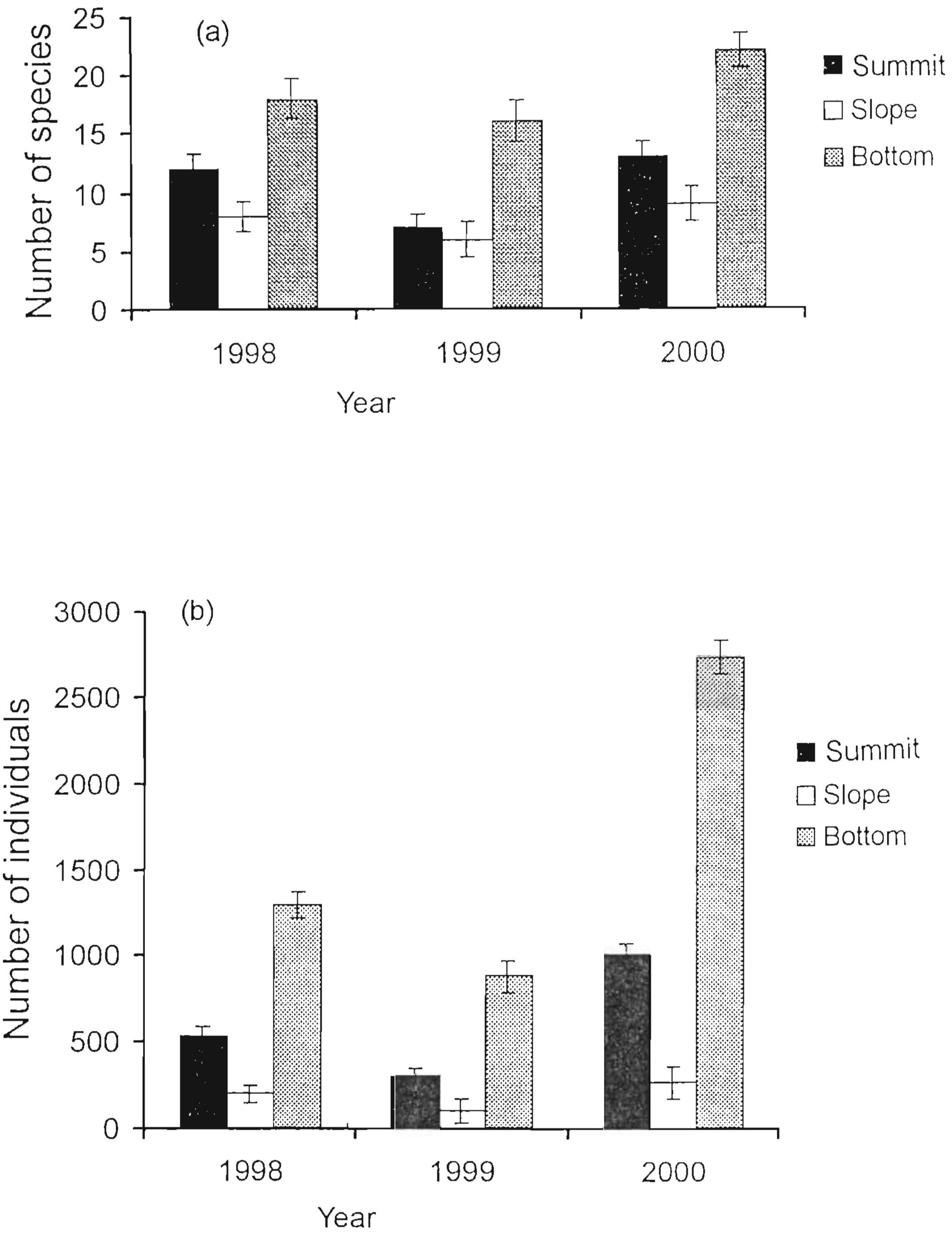


Fig. 2.2. Mean (±SE) number of grasshopper species (a) and individuals (b) across the three years on the summit, slope and flatlands of the Tafelberg mesa.

The mean monthly rainfall over the three years was markedly different, with 2000 receiving the highest rain and 1999 the least (Fig. 2.3).

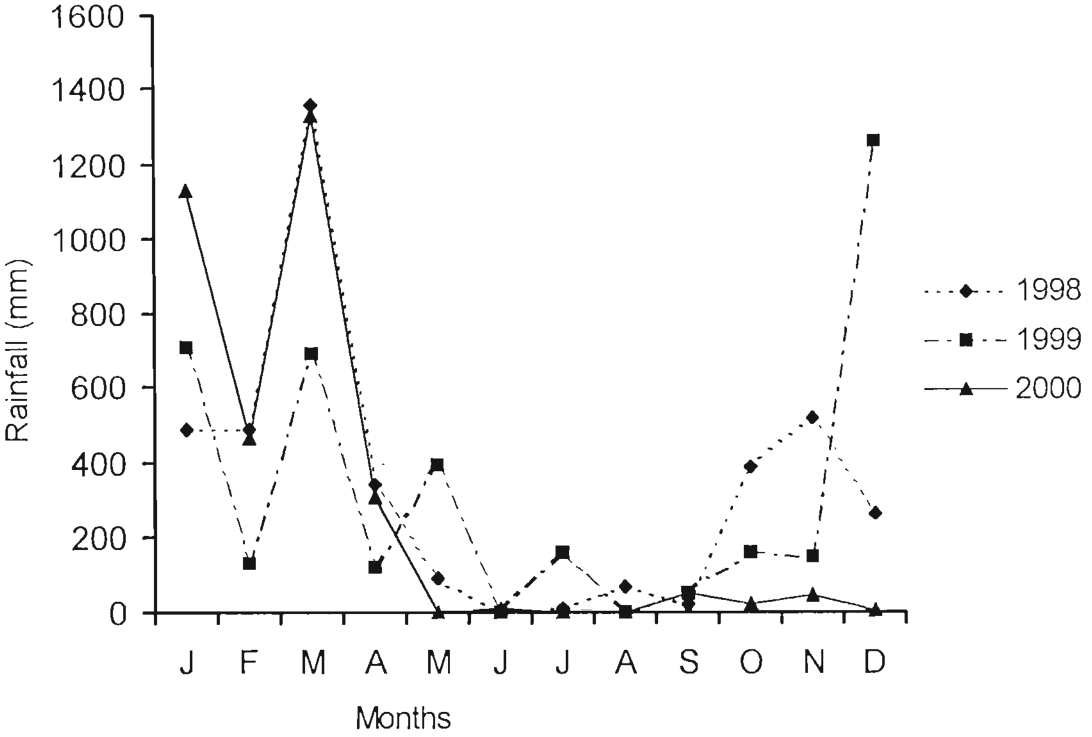
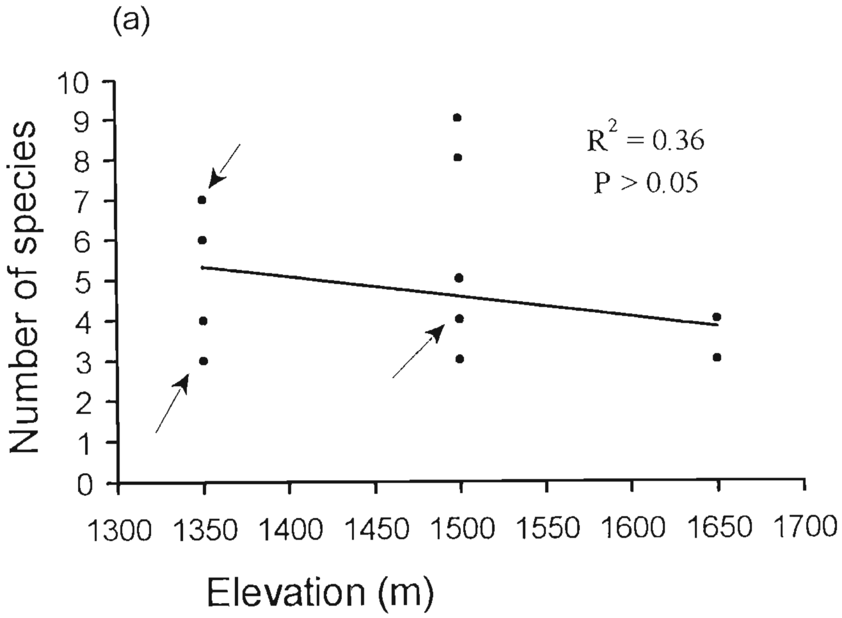


Fig. 2.3. Mean monthly rainfall (mm) from 1998-2000 recorded on a farm (ca. 3 km from Tafelberg mesa). Note that 1998 and 2000 had a similar trend from February-April and the high amount in December 1999 adds up to the amount in early 2000. This resulted in high vegetation growth over the subsequent months in 2000 until the onset of cold weather in June.

2.3.3. Slope gradient and aspect

The lower slope was the richest in grasshopper species richness but there was no significant difference between the middle and upper slope (Fig. 2.4a). In contrast, the number of grasshopper individuals varied significantly along the slope gradient, with a decline in grasshopper numbers with increasing slope (Fig. 2.4b).



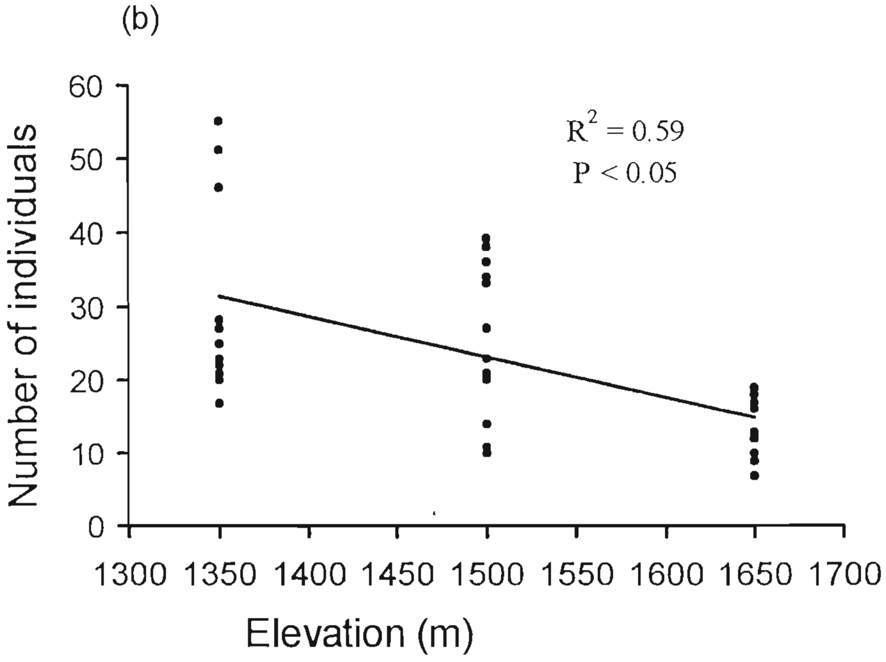


Fig. 2.4. Correlation between slope gradient and number of grasshopper species (a) and individuals (b) on the Tafelbeg mesa. Note that there were several overlapping points in the data on Fig. 2 (a) (indicated by arrows), and hence are represented by fewer circles compared to Figure 4 (b).

The four slope aspects also varied significantly in grasshopper species richness, with the SW and NW sides being richer than the SE and NE. There was also a significant difference among the slope aspects in the number of grasshopper individuals, with SW and SE supporting most individuals and NW the least. There was also a significant interaction between slope gradient and slope aspect both in grasshopper species richness (*F* = 14.95; *P*<0.001) and individuals (*F* = 19.95; *P*<0.001). The SE mid-slope had most species followed by the SW lower slope. Highest number of individuals were on the SW lower slope, followed by the SE middle slope (Table 2.2).

Table 2.2. Mean number of grasshopper species and individuals from slope aspect-by-gradient interaction from a two-way ANOVA. Means followed by the same letter across rows and columns are not significantly different at 5 % level of significance.

	Number of species			Number of individuals		
	Slope gradient			Slope gradient		
Aspect	Lower slope	Mid-slope	Upper slope	Lower slope	Mid-slope	Upper slope
NE	3.33d	3.67d	3.33d	25.33cd	30.67bc	9.67h
NW	6.67b	5.00c	3.33d	19.67def	11.67gh	11.33gh
SE	3.33d	3.67d	3.40d	25.00cd	36.33b	17.33ef
SW	6.67b	8.30a	3.67d	50.67a	23.33de	17.00fg
F	14.90			19.95		
P	<0.001			<0.001		

2.3.4. Detrended Correspondence Analysis (DCA)

The codes of the species used in the ordination are listed in Table 2.3.

Table 2.3. Grasshopper species recorded during this study. Species codes are those used in the multivariate analyses.

Family	Subfamily	Species	Code
Pamphagidae	Porthetinae	*Hoplolopha horrida* (Burmiester, 1838)	Hho
		Lamarkiana sp.	Las
Pyrgomorphidae		*Zonocerus elegans* (Thunberg, 1815)	Zel
Lentulidae	Lentulinae	*Lentula callani* Dirsh, 1956	Lca
Acrididae	Calliptaminae	*Sphodromerus gilli* (Uvarov, 1929)	Spg
		Acorypha pallidicornis (Stål , 1876)	Apa
	Euryphyminae	*Rhachitopis crassus* (Walker, 1870)	Rcr
		Euryphymus tuberculatus (Martinez, 1898)	Etu
		Calliptamulus hyalinus Uvarov, 1922	Chy
		Calliptamicus sp.	Csp
	Eyprepocnemidinae	*Heterachris* sp.	Hsp
	Cyrtacanthacridinae	*Cyrtacanthacris tatarica* (Linnaeus, 1758)	Cta
	Acridinae	*Acrida turrita* (Linnaeus, 1758)	Atu
		Truxalis burtti Dirsh, 1951	Tbu
		Orthochtha dasycnemis (Gerstaecker, 1869)	Oda
	Oedipodinae	*Locustana pardalina* (Walker, 1870)	Lpa
		Oedaleus nigrofasciatus (De Geer, 1773)	Oni
		Acrotylus insubricus (Scopoli, 1786)	Ain
		Sphingonotus scabriculcus (Stål, 1876)	Ssc
		Picnodictya flavipes (Miller, 1932)	Pfl
	Gomphocerinae	*Pseudogmothela* sp.	Psg
		Dnopherula crassipes (Uvarov, 1921)	Dcr
		Aulacobothrus dorsatus (I.Bolivar, 1912)	Ado
		Pnorisa squalus Stål, 1861	Psq
		Pseudoarcyptera sp.	Psa

The summit, slope and flatland sites fell into three distinctive clusters on the ordination plot (right, centre, and left sides respectively in Fig. 2.5.Species associated with the summit sites were: *Picnodictya flavipes*, *Lamarkiana* sp., *Scintharista saucia*, *Acrida turrita* and *Orthochtha dasycnemis*. Species associated with the flatland sites were *Oedaleus nigrofasciatus*, *Hoplolopha horrida*, *Acrotylus insubricus*, *Locustana pardalina*, *Dnopherula crassipes*, *Calliptamulus hyalinus* and *Aulacobothrus dorsatus*. Species associated with the slope were *Pnorisa squalus*, *Calliptamicus* sp., *Acorypha pallidicornis*, *Rhachitopis crassus*, *Cyrtacanthacris tatarica*, *Pseudoarcyptera* sp. and *Pseudogmothela* sp. Eigenvalues of the first two axes and the cumulative percentage variance according to the Monte Carlo tests are given in Table 2.4.

2.3.5. Canonical Correspondence Analysis (CCA)

Eigenvalues of the first two axes and the intraset correlations of the axes with environmental variables and the cumulative percentage variances according to the Monte Carlo tests are given in Table 2.4. The CCA biplot of grasshoppers species and environmental variables shows that the grasshopper assemblages followed gradients of certain environmental factors (Fig. 2.6). Grass cover and percentage greenness were highly correlated with the first (horizontal) CCA axis, while grass average height was highly correlated with the second (vertical) axis (Table 2.4). Accordingly, *O. dasycnemis*, and *Heterachris* sp. were associated with high grass cover, while *P. flavipes* and *D. crassipes* were associated with intermediate grass cover. *Sphodromerus gilli*, *P. squalus* and *R. crassus* were associated with low grass cover. *H. horrida* increased along an increasing gradient of greenness. Species at the top right corner of the ordination showed closer association with sites with more grass cover, coupled with greater grass height and % greenness. *Acrida turrita*, *O. nigrofasciatus* and *D. crassipes* were associated with intermediate bare ground cover and with increasing

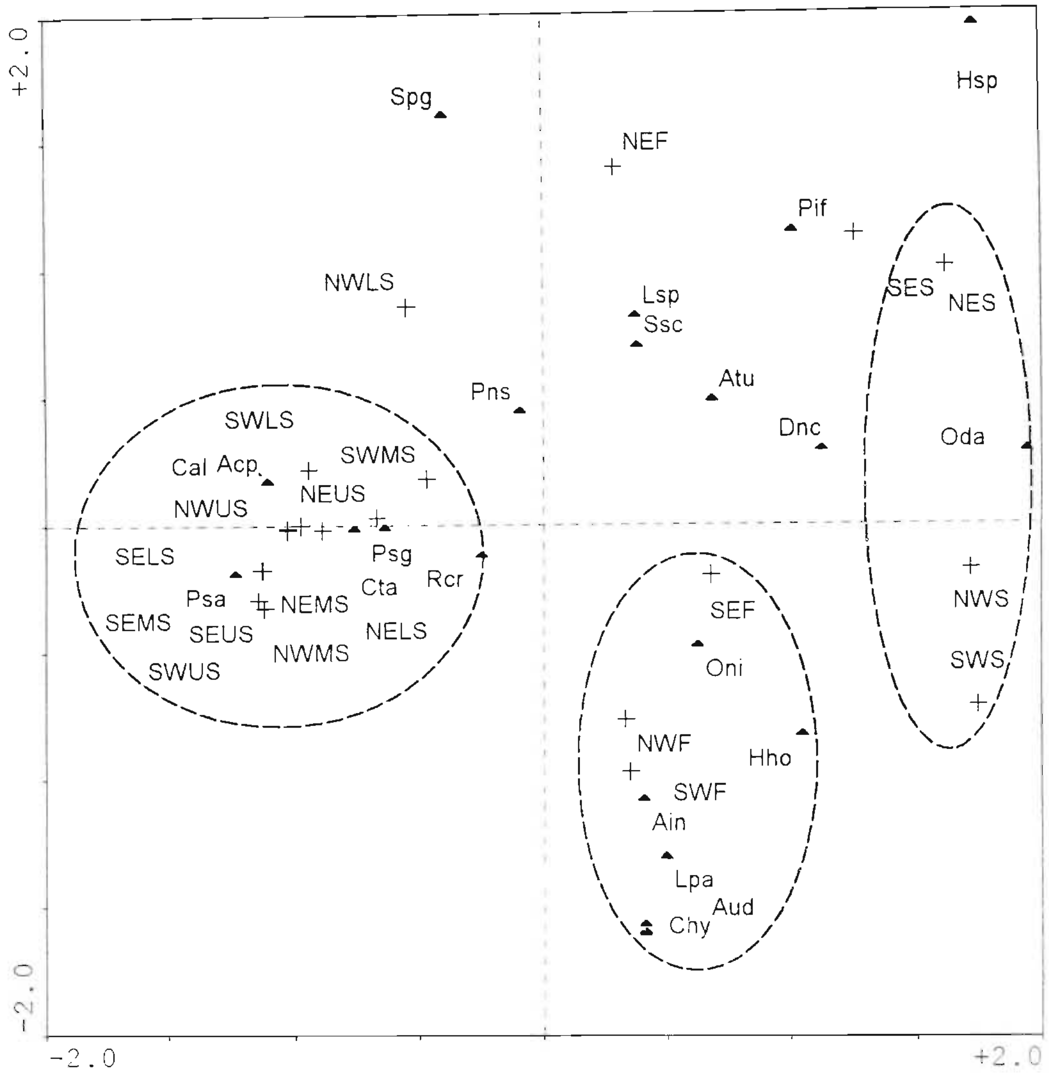


Fig. 2.5. DCA biplot of grasshopper species (▲) and sites (+). Axis 1 is horizontal and Axis 2 is vertical. Note that sites from a similar elevational position are closer together on the ordination (enclosed by ellipse). Species abbreviations are given in Table 2.3. Site abbreviations are: NES=north-east summit; NWS=north-west summit; SES=south-east summit; SWS=south-west summit; NEUS=north-east upper slope; NEMS=north-east mid-slope; NELS=north-east lower slope; NWUS=north-west upper slope; NWMS= north-west mid-slope; NWLS= north-west lower slope; SEUS= south-east upper slope; SEMS= south-east mid-slope; SELS= south-east lower slope; SWUS= south-west upper slope; SWMS= south-west mid-slope; SWLS= south-west lower slope; NEF= north-east flat; NWF= north-west flat; SEF= south-east flat; SWF= south-west flat.

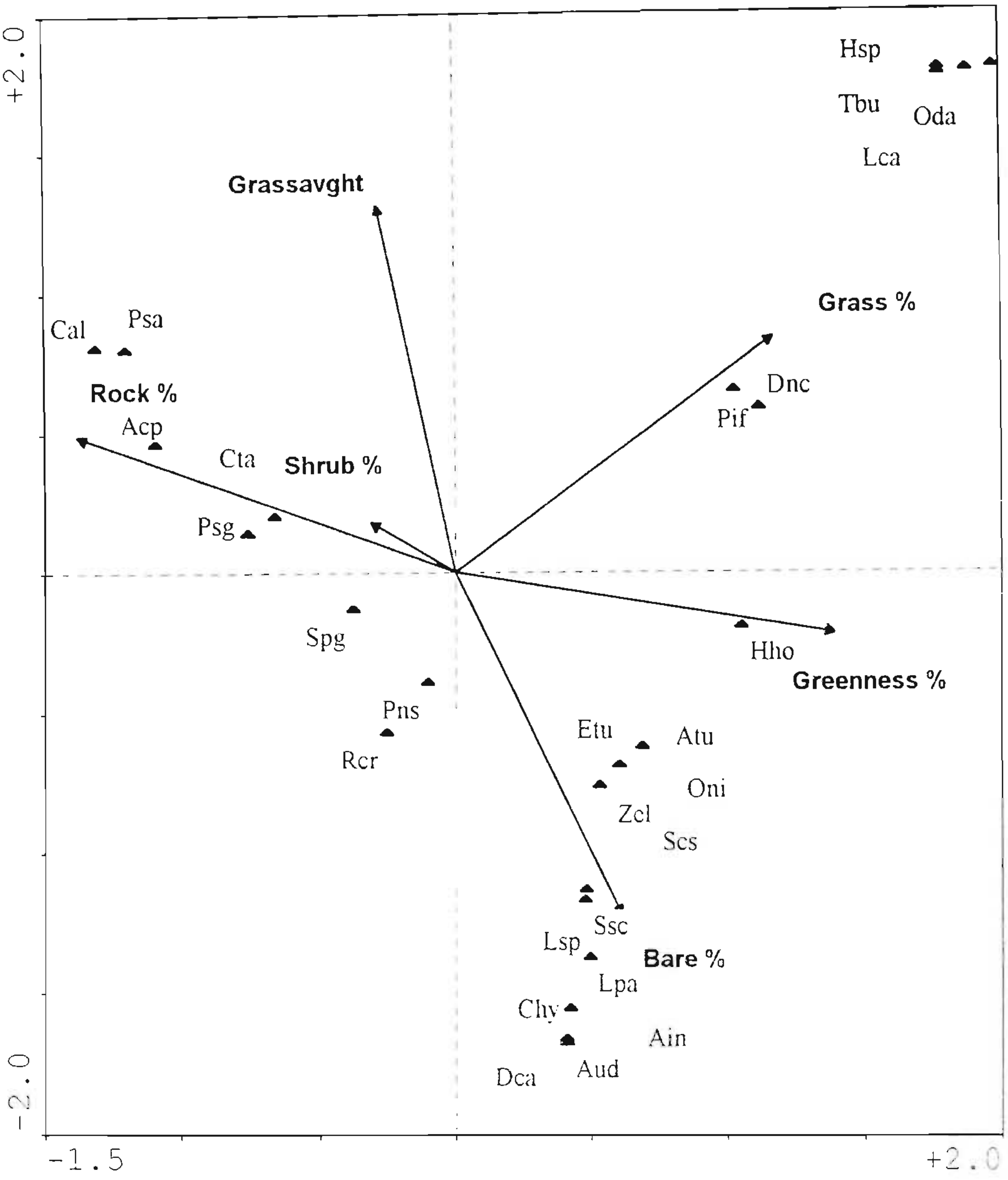


Fig. 2.6. CCA biplot of grasshopper species (▲) and environmental variables (arrows). Axis 1 is horizontal and Axis 2 is vertical. Species abbreviations are given in Table 2.3. Grassavght= Grass average height.

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gradient of greenness. A clear assemblage of species was also shown along an increasing gradient of bare ground including *Lamarkiana* sp., *S. saucia*, *L. pardalina* and *A. insubricus*. Another assemblage occurred with greater shrub cover and intermediate rock cover. The dominant species here are *C. tatarica* and *Pseudogmothela* sp., although shrub cover was the least important of all measured environmental variables as shown by the short arrow on the ordination (ter Braak 1986). *A. pallidicornis*, *Pseudoarcyptera* sp. and *C. hyalinus* were clearly associated with greater rock cover.

Table 2.4. Eigenvalues of DCA and CCA, and and intraset correlations between the first two axis of CCA and the environmental variables measured on the summit, slope and flatland sites of the Tafelberg mesa.

	DCA		CCA	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.68	0.29	0.66	0.46
Grass cover			0.72	0.55
Rock cover			-0.85	0.32
Shrub cover			-0.19	0.12
Bare ground			0.38	-0.81
Avg. grass height			-0.17	0.87
% greenness			0.86	-0.14

2.3.6. Grasshopper dominance patterns

A total of 3408 individuals in 27 species belonging to four families and nine sub-families were sampled (Table 2.4). When all the sites were combined, 66.6 % of the species had fewer than 50 individuals, 74 % had fewer than 100 individuals, 77 % had fewer than 250 individuals, and four species (14.8 %) had more than 300 individuals.

The six most abundant species were *O. nigrofasciatus*, *D. crassipes*, *C. tatarica*, *A. insubricus*, *A. pallidicornis* and *Pseudogmothela* sp. These six accounted for 82.2 % of the total number of individuals. The occurrence of the individual species varied across the 20 sampling sites. *C. tatarica* was the most habitat-tolerant species, occurring at 17 sites distributed on the summit, slope and bottom, followed by *Pseudogmothela* sp. which occurred at 14 sites, all of which were on the slope and at the bottom. *D. crassipes* occurred at ten sites situated across the summit, slope and bottom. *A. pallidicornis* occurred at ten sites, all of which were on the slope. Eighteen species (66.6 %) occurred in less than five sites, and four species (*Z. elegans*, *E. tuberculatus*, *T. burttii* and *S. saucia*) were the most habitat-restricted ones, occurring in only one site each. These species were also the rarest, represented by <10 individuals, except *Z. elegans* for which 18 individuals were counted.

Rank-abundance curves showed distinct patterns of dominance at the summit, slope and flatlands (Fig. 2.7). The summit was dominated by one species, *O. dasycnemis* (accounting for a third of individuals), another species, *D. crassipes*, occurred as sub-dominant contributing about 25 %, the remaining seven species each made up only 5 % or less. This dominant species occurred only at the summit, while the sub-dominant species occurred at all elevations. The slope was dominated by one

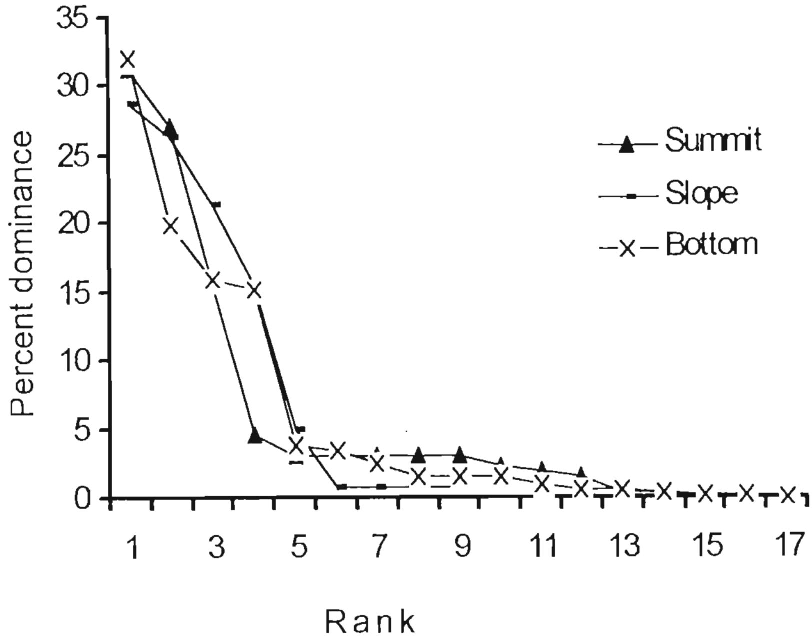

Fig. 2.7. Rank-abundance curves of grasshoppers on the summit, slope and flatlands of the Tafelberg mesa sampled from 1998-2000.

species, *A. pallidicornis*, which occurred only on the slope, and co-dominated by *C. tatarica* which was the most habitat-tolerant species, occurring across all the three elevational positions. The remaining species accounted for about 1 % of the total grasshopper abundance on the slope. The flatland sites were dominated by two species, *O. nigrofasciatus* (38 % of individuals) and *D. crassipes* (25 % of individuals). The majority of the species were rare, contributing between 1 and 2 % to the total abundance on the flatlands. Whereas very few individuals of *O. nigrofasciatus* were on the summit and slope sites, *D. crassipes* was represented by many individuals at the summit sites and few on the slopes.

The mean numbers of grasshopper species that occurred on the three elevations are shown in Fig. 2.8. Mean percentage of grasshopper species shared between the elevational categories varied. The highest number of shared species were between the slope and flatlands (33 %), followed by the summit and flatlands (29 %). Shared species between the summit and the slope, and between summit, slope and flaltands were 19 % each.

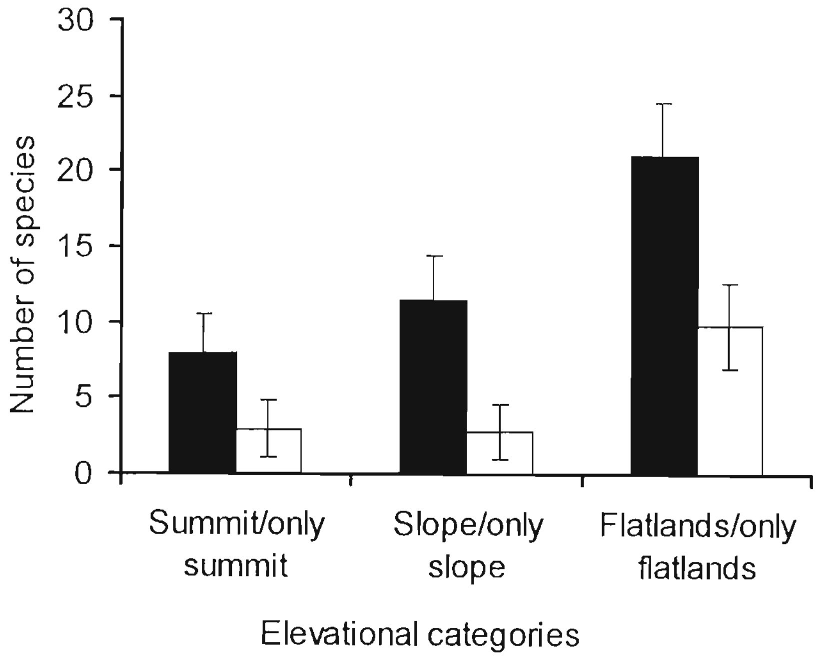

Fig. 2.8. Mean (±SE) number of grasshopper species on the summit / only the summit, the slope / only the slope, and the flatlands / only the flatlands, on and around the Tafelberg mesa.

2.4. Discussion

2.4.1. Environmental variables and grasshoppers

The variation in environmental variables follows a distinct pattern relative to elevation. The steepness of the slope, particularly with increasing elevation above the middle slope, coupled with lack of free-standing water, excludes sheep and cattle. This makes the mesa summit an exclosure. The dominant grass there, *Themeda triandra*, is highly palatable to domestic livestock and occurs sparsely on the slope, with almost none on the flatlands. Sheep and cattle reduce grass cover substantially and increase the proportion of bare ground. This, combined with hooves loosening rubble on the mid-slope, exposes the underlying rock and encourages the establishment of shrubs rather than grass. Similarly, on the flatlands, resistant shrubs such as *Acacia karoo* and *Pentzia incana,* become established. High % greenness of grass accompanies increased grass cover. More grasshopper species occurred on the flatlands compared to the summit or the slope. Several effects probably interplayed to produce this pattern, including more varied habitats lower down, greater area effect and greater chance for movement in adverse conditions.

2.4.2. Grasshopper population dynamics across sampling years

There were great differences in rainfall over the three years, which strongly influenced the grasshopper populations. Grasshopper densities are often correlated with the previous year's precipitation and temperature, and this relationship is used by pest managers to predict outbreaks (Rodell, 1977). Most grasshopper research emphasize that weather, acting through oviposition, egg development and juvenile survivorship, is the primary determinant of grasshopper population dynamics and distribution (Isely, 1937; Dempster, 1963; Uvarov, 1977). In this study, the sampling area received markedly different amounts of precipitation over the three years yet the number of grasshopper species remained unchanged. However, there was great variation in grasshopper abundance, indicating a clear and sensitive link between precipitation, vegetation and survivorship. Numerous accounts suggest that poor-quality food plants associated with extreme drought results in poor reproductive performance (Pickford, 1963; Chapman et al., 1979). The trend observed in this study was that grasshopper abundance was intermediate in 1998, crashed in 1999 but was markedly high in 2000, suggesting that a complex of factors affect grasshopper population dynamics in the Karoo.

2.4.3. Slope aspect and grasshoppers

Slope aspect also influenced the grasshopper assemblages and abundance patterns. While grasshopper species richness was significantly higher on the SW and NW slope, the number of individuals did not follow the same trend. The SE slope, although having fewer species, had many individuals as with the SW slope. Also, elevation had an interactive relation with aspect, adding further variation to the pattern of species richness and abundance. Aspect has a major effect on insolation (Samways, 1990; Schultze, 1975), and can lead to substantial thermal differences between faces of slopes receiving differential insolation. Chappell (1983) demonstrated that, as overheating is essentially impossible for montane and alpine grasshopper species, they consistently strive to expose their bodies to direct sunlight to maintain optimal body temperature required for their life activities. In contrast, grasshoppers in desert and semi-desert regions must continually strive to keep their body temperature as low as possible (Chappell, 1983). Grasshoppers in the Karoo are adapted to finding thermallyacceptable conditions mostly by moving from sunlit to shady microhabitats in the course of the day. Even the use of small patches can have significant effects. Uvarov (1977) noted that *Zonocerus variegatus* reduces body temperature from 50 °C to 40 °C by moving from the top to the bottom of large leaves.

2.4.4. Biotope preference and dominance patterns

The dominant species on the top of the mesa, *O. dasycnemis*, occurred only on the top. This species, although known to feed on soft and tough grasses, has unique association with tall and thick vegetation, coupled with high percentage greenness (Gandar, 1982; Gebeyehu and Samways, 2001). This narrow range of habitat preference for tall grasses with high greenness suggests that this species is also highly sensitive to disturbance by grazing, with the top of Tafelberg being a refugium for it. Moreover, its elongated body shape with its habit of resting along the long axis of the tall, green grasses appears to offer it good camouflage against predators, particularly from birds and lizards (Belovsky and Slade, 1993; Eterovick et al., 1997; Vitt et al., 2000). Indeed, for many grasshoppers, biotope preference results more from adaptive resemblance to their background than use of these habitats as food (Fogden and Fogden, 1974; Gandar, 1983; Gebeyehu and Samways, 2001). Interestingly, this species occurred at low elevations elsewhere, indicating that it is not elevation per se, but long grass that supports this species. In a study we carried out at a site only 90 km from the present study site, and on a similar elevation, to compare grasshopper assemblage patterns inside a reserve with indigenous mammals versus outside where domestic livestock graze, *O. dasycnemis* was found to be one of the dominant species. Nevertheless, it occurred only inside the reserve where level of defoliation and trampling were minimal, and the long and green grass blades offered it a suitable habitat (Gebeyehu and Samways, 2001). In contrast, *A. pallidicornis*, was not only the dominant species on the slope, but it occurred only there, being closely associated with rocks and mixed grasses.

O. nigrofasciatus, the most dominant species in the study area, is a mixed feeder on grasses and forbs (Gandar, 1982), and very responsive to variations in vegetation structure. Typically, it prefers a combination of grassy patches with bare ground, which attracts green and brown morphs of this species respectively. *A. insubricus* prefers bare patches, which is linked to its thermoregulatory behaviour of burrowing in the soil to avoid overheating (Chappell and Whitman, 1990). It avoids rock-dominated patches where it cannot do this.

Two of the six most abundant species, *C. tatarica* and *D. crassipes*, were widely distributed across all the three elevational categories. *C. tatarica* is a large species with a very strong flight, and had a more or less uniform distributional pattern across the different elevations. With (1994) demonstrated that large-sized species move over the landscape six times faster than their small-sized counterparts, and deduced that size makes a great difference in the way grasshoppers respond to scale of heterogeneity in the landscape. Perhaps, *C. tatarica*, a large and strong flier, might only perceive large patches in the landscape and hence move widely. *D. crassipes*, in contrast, is small, and was distributed across all elevations. Gandar (1982) reported that this species is widely distributed with respect to vegetation cover and height, although it avoids the extremes of very short and tall dense vegetation. Moreover, small size could be an added adaptive advantage to exploit different biotopes as reported by Joern and Gaines (1990). Kinvig (2001) in his study of grasshopper assemblages on the inselbergs of the Namib desert also reported that *D. crassipes* was the only species that showed a foot-to-hilltop distribution. The pattern shown by *D. crassipes* in this study could be linked to its small body size and darker body colour, both of which are associated with a wider habitat range, including variations in vegetation height and cover (Gandar, 1982; Joern and Gaines, 1990).

2.4.5. Implications for the grasshopper fauna as a whole

Depending on the degree of sensitivity of the resident grasshopper fauna in this area to the current system of land use and associated anthropogenic disturbance, there may be other grasshopper species that might respond like *O. dasycnemis* in the long-term. Indeed, just as we would not know when exactly this species was forced to retreat to the summit of the mesa as its only refugium, it will not be easy to predict how long it would be for other grasshopper species to start responding in a similar way. Perhaps those grasshopper species that are vagile might follow *O. dasycnemis*, but the impact on less mobile and brachypterous species, and those that are already rare might be more severe, probably leading to local extinction.

2.5. Conclusion

The Tafelberg mesa is effectively an island, and a conservation refugium for one grasshopper species that occurred only on the summit. Other grasshopper species also occurred on the summit, as well as on the slopes and the flatlands. If the mesa and the surrounding flatlands continue to be challenged by overgrazing, with associated defoliation and trampling, the summit would act as a refugium for various species, as its steep sides and lack of free water exclude livestock. This would presumably apply also to many other mesas across the Nama-Karoo, but further research is needed to have a clear understanding at a regional scale. Meanwhile, it is clear from this study and others in South Africa that the vertical dimension plays a major role in determining biodiversity spatial patterning. In effect, topography generates habitat heterogeneity, which, in turn, serves to maintain biodiversity. Although the mesa summit can act as a refugium, not all livestock pressure is harmful, since ungulates modify the vegetation structure and composition, and loosen the soil with their hooves, so providing optimal ecological requirements for certain grasshoppers. This appears to mimic the situation before settled farming when large herds of wild animals roamed the area. However, grazing must be moderated and be neither too little nor too extreme for grasshoppers, and possibly many other components of biodiversity, to survive in the long term.

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CHAPTER THREE

Regional scale interaction between grasshopper assemblage patterns and variability in hill sizes in the Karoo

This chapter has been submitted for publication. Slight editorial changes have been made to ensure continuity of the thesis.

3.1. Introduction

An understanding of pattern, its causes and consequences is central to understanding evolutionary processes such as speciation as well as ecological processes of succession, community development and the spread and persistence of a species (Wiens, 1976; Levin, 1989). The ability to translate fine-scale information across scales could facilitate the search for mechanistic explanations of broad-scale patterns, thus promoting a unification of pattern and process in ecology (With and Crist, 1995, 1996). Nevertheless each organism observes the environment on its own unique suite of scales of time and space (Levin, 1989). Indeed regional scaling is rarely explicit in population models in an effort to increase the generality of a given model (Collins and Glenn, 1997). However, results of tests of models regardless of their nature, will vary with spatial scale and type of organisms involved (Isawa and Roughgarden, 1986; Maurer, 1990; Hastings, 1991; Tokeshi, 1992; Collins and Glenn, 1997).

Since variability is not an absolute but only has meaning relative to a particular scale of observation, the problem is not to choose the correct scale of description, but rather to recognize that change is taking place on many scales, and that there are interactions among phenomena at different scales (Wiens, 1976; Levin, 1989). Factors influencing the proximate and physiological or behavioral state or the ultimate fitness of individuals exhibit discontinuities on many scales in time and space (Wiens, 1976). Furthermore, spatial patterning is expressed as both vertical and horizontal dimensions.

Small changes in the spatial patterning of resources can produce abrupt, sometimes dramatic, ecological responses and as such can be critical thresholds (Turner and Gardner, 1991; With, 1994). Critical thresholds occur particularly where the phenomenon of interest exhibits a nonlinear relationship with spatial scale, owing to shifts in the underlying process (es) at different scales or because new constraints govern the process at different scales (O'Neill et al., 1986; Kotliar and Wiens, 1990). Landscapes may exhibit critical thresholds in connectivity, often with serious ecological consequences (Gardner et al., 1987; Krummel et al., 1987; O'Neill et al., 1988). Critical threshold is the proportion of the landscape at which population shifts from a random to a clumped distribution (With and Crist, 1996).

Populations of small organisms with short generation are sensitive to short-term environmental fluctuations (Hutchinson, 1953; Hutchinson and MacArthur, 1959) and have greater potential for close tracking of environmental variation than is exhibited by populations of larger organisms (Margalef, 1969; Belovsky and Slade, 1995). They may thus be more responsive to physical features of their environment or patch. The patch structure of an environment is that which is recognized or relevant to the organism under consideration. Patchiness is thus organism-defined, and must be considered in terms of the perceptions of the organism rather than those of the investigator (Wiens, 1976; Levin, 1989; With and Crist, 1995, 1996; Collins and Glenn, 1997).

The Karoo landscape is characterized by a flatland matrix punctuated by hills of various sizes. These hills account for a substantial proportion of the land area, and are variously grazed by domestic livestock, as are the flatlands. This begs the question: are these hills scattered all over the Karoo landscape the same as the flatlands in their biodiversity or do they create spatial heterogeneity resulting in unique assemblages of fauna and flora. Spatial heterogeneity of landscape elements such as hills and flatlands will have important consequences for population dynamics depending on the dispersal rates of individuals and the spatial scales at which the process is considered (Turchin, 1991; With and Crist, 1996).

While some workers have reported that topographic elements are important in grasshopper distribution pattern (Stabaev, 1972; Claridge and Singhrao, 1978; Samways, 1990; Wachter, 1998), others have reported that topography as well as aspect were not significant (Narisu et al., 2000). However, these studies were conducted on small areas, and hence the results may not be conclusive and applicable at a regional scale. Here we report results of a study undertaken in the Karoo at a regional scale covering a total area of several square kilometers.

3.2. Study area and methods

3.2.1. Study area

The study area was in the Karoo located in the central plateau of South Africa. A dominant feature of the Karoo landscape is the occurrence of mesas and inselbergs of various sizes. The Karoo is also characterized by semi-arid conditions with erratic and patchy rainfall pattern, ranging from 125-375mm per annum. The major land use system is sheep grazing and to some extent cattle grazing. Temperatures are low during winter months (June-August) with a mean monthly minimum of 3°C and high during summer months (December-February) with a mean monthly maximum of 36°C

The study was undertaken in Middelberg, Eastern Cape Province on four separate farms with a total area of about 360 km ^{2}, which were under grazing. Each of the four farms had hills ranging from gentle undulation to large ones, located randomly in the flatlands. Three categories of hills were selected arbitrarily from each farm. They consisted of small hills, medium hills, and large hills, which were replicated (see below) on the four farms. The flatlands, surrounding these hills, with an average elevation of 1200 m a.s.l., was also part of the sampling area.

Elevation relative to the flatlands was the major criterion in choosing and assigning size to a hill, and hills were selected that had minimum difference in shape. Hills with an elevation of 1300-1350 m a.s.l. were considered small (SH), those with an elevation of 1351-1450 m a.s.l. were considered medium (MH), and those with an elevation of 1451-1550 m a.s.l. were considered large (LH). On each hill, sampling was made from the flatlands surrounding it, the slope, and the summit. Hence each hill had three sampling sites. A transect of 50 m long and 15 m wide was considered as a single replicate. Six of these replicates constituted one site. The distance between transects was 10 m to avoid counting the same grasshopper individual more than once. Data from the transects across the sides on the slope of a hill were pooled together to yield a single value for the slope. Each transect on the slope ran along the contour to maintain uniform elevation.

Sampling was undertaken from January to May 2000, a year of good rains and good vegetation growth in the Karoo, and comparatively high grasshopper abundance (Chapter 2). Sampling was continued until the first frosts killed most of the adult grasshoppers. Sampling was undertaken only on sunny days with < 15 % cloud cover and when wind movement was minimal (< 30 km hr^{-1}).

3.2.2. Sampling methods

3.2.2.1. Grasshoppers

The voucher collection resulting from the study in Chapter 2 served as the main reference in recognizing grasshoppers in the field, and unfamiliar ones were returned to the laboratory for identification and /or confirmation. Sampling of grasshoppers was by visual counting as they flushed during the transect walks. This was supplemented with sweep netting to determine individuals that were still unfamiliar. This method of visual recording was found in previous studies to be the most accurate and efficient means of documenting grasshopper species and abundances in the rugged African terrain (Samways, 1990; Chambers and Samways, 1998; Armstrong and van Hensbergen, 1999; Gebeyehu and Samways, 2001). Visual sampling has also been shown to be effective elsewhere (Kemp and Dennis, 1993; Kemp et al., 1989). Close-focus binoculars (Sigma-armada series 10 × 23 wp compact) were an essential recognition aid. Only adult individuals were counted. Grasshopper species were assigned to one of three size categories: Adult size of up to 20 mm were considered small, 21 to 35 mm were considered medium, and > 35 mm were considered large. This method of size category was used with a slight modification of the method used by With and Crist (1996) for modelling interaction between grasshopper size and landscape heterogeneity.

3.2.2.2. Vegetation

The vegetation parameters at each site were recorded by estimating percent basal cover of the two most commonly occurring vegetation groups, i.e., grasses and shrubs in 15 randomly placed 4 m^2 quadrtas along the lines of the transects where grasshoppers were sampled. Each quadrat was subdivided in to twenty units of 20 cm^2, and the relative proportion of grasses, shrubs, rock and bare ground were estimated. Percent greenness of the grasses was estimated by using a 0-100 % scale , where 0 %= not green; 25 %= slightly green; 50 %= moderately green; 75 %= green, and 100 % = very green. Cragginess of the sites was estimated using a 0-4 scale, where 0= smooth; 1= slightly craggy; 2= moderately craggy; 3= craggy, and 4= very craggy. Vegetation density was estimated using a 0-5 scale where 0= bare; 1= very sparse vegetation; 2= sparse; 3= moderate; 4= dense, and 5= very dense. Average height of grasses was estimated by measuring grass heights at 40 random points in a transect and the tallest inflorescence was taken to give the maximum grass height. Surface soil temperature at a depth of 15 cm was measured in each quadrat using a soil thermometer. A pointed iron peg marked at 15 cm was inserted in four random points in each quadrat to open up a hole in the soil. Then the thermometer was inserted into the hole for 5 minutes before recording the temperature. The average of the four point readings in each quadrat was taken to represent the soil temperature of the quadrat. The depth of 15 cm was selected on the basis that arid and semi-arid grasshopper species generally tend to lay their eggs deeper, averaging between 11-15 cm, although this could vary depending on the soil condition and the female size (Popov, 1958; Braker, 1989).

3.2.3. Data analyses

Both univariate and multivariate statistics were used in data analyses. Detrended Correspondence Analyses (DCA) was used in preference over Correspondence Analysis to avoid the arch effect, as recommended by ter Braak (1986). The arch effect is a mathematical artifact corresponding to no real structure in the data, but a situation where the second axis shows a systematic, often quadratic relation with the first axis. This problem was remedied by detrending at the level of second order polynomials, the order indicating the number of axes to be used in the ordination plane (Hill and Gauch, 1980). DCA, as an ordination technique, operates on a site-by-species data matrix and represents it in 2-D space (ter Braak and Smilauer, 1998), such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. Conversely, from a species-by-site matrix DCA ordinates the data such that the closer two species are to one another on the ordination plane, the greater the likelihood that they will occur at the same or similar sites, and vice-versa.

CCA was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the biplot, and is therefore a measure of how much species distributions differ along that environmental variable. Important environmental variables therefore tend to be represented by longer arrows than less important environmental variables (ter Braak, 1986; ter Braak and Looman, 1995). All grasshopper abundance data were square-root transformed and all vegetation proportion data were log-transformed to maintain normality and to satisfy the requirements of ANOVA and the multivariate analyses. The computer program CANOCO version 4 (ter Braak and Smilauer, 1998) was used for multivariate analyses, and PRIMER (Ludwig and Reynolds, 1988) was used to calculate Hill's diversity indices and the Bray-Curtis similarity index.

Recognizing the difficulties of interpretation arising from diversity indices because parameters such as species richness, evenness and number of individuals and the area sampled are compounded when a single diversity index is used (Ludwig and Reynolds, 1988; Curry, 1994), an alternative approach that avoids these difficulties with indices of diversity is the use of rank-abundance curves in which both species richness and evenness are graphically displayed. The curves are drawn such that the percentage abundance (dominance) is plotted against ranked species sequence (Ludwig and Reynolds, 1986; Curry, 1994).

3.3. Results

3.3.1. Hill size and grasshoppers

There were significant differences among hill sizes with respect to both the number of grasshopper species and individuals. Small hills had the highest number of species ($F= 6.40$; $P< 0.01$), followed by medium and large hills which were not significantly different. Similarly, small hills had the highest number of grasshopper individuals ($F=3.63$; $P<0.05$), followed by medium and large hills which were not significantly different (Fig. 3.1 a, b).

There was a significant difference between organism sizes with respect to the number of grasshopper species and individuals across all hill sizes. There were significantly higher numbers of small-sized grasshopper species ($F=2.82$; $P<0.05$) and individuals ($F=3.52$; $P<0.05$) than medium and large-sized grasshopper species, which were not significantly different, although there were higher number of large-sized species than medium- sized ones (Fig. 3.1 a, b). There was a significant difference between the flatlands surrounding the three hill sizes in the number of grasshopper species. The flatlands surrounding small hills contained a significantly higher number of grasshopper species (F=4.55; P<0.05) compared

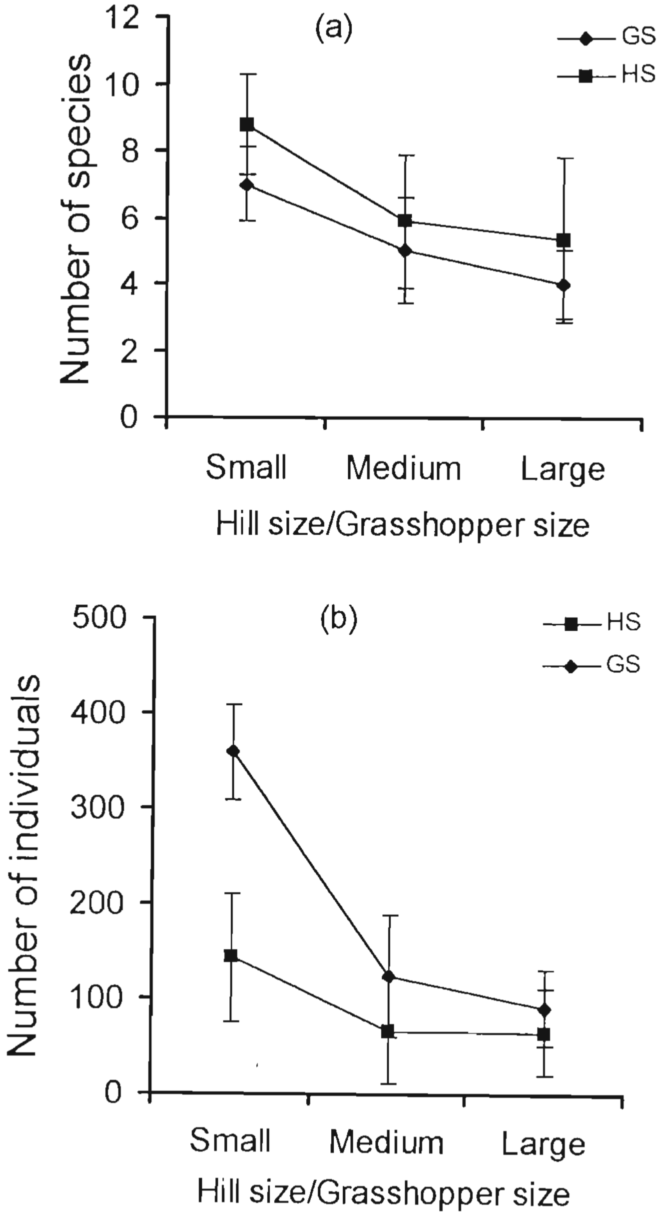


Fig. 3.1. Mean number of grasshopper species (a) and individuals (b) on three hill and grasshopper sizes.

to those around medium and large-sized hills, which were not significantly different. There were also significantly higher number of grasshopper individuals on flatlands around small hills (*F*=3.82; *P*<0.05) than those surrounding medium and large hills which did not differ significantly, although flatlands surrounding large hills had higher grasshopper abundance (Fig. 3.2 a, b).The slopes of the three hill sizes did not show significant variation either in the number of grasshopper species or abundance (Fig. 3.2 a, b). The summits of the three hill sizes did not show significant variation in the number of grasshopper species, but there was a significant variation in the number of grasshopper individuals (*F*=4.19; *P*<0.05) with the summits of small hills having the highest abundance followed by large hills. Medium hills showed the lowest grasshopper abundance (Fig. 3.2 a, b).

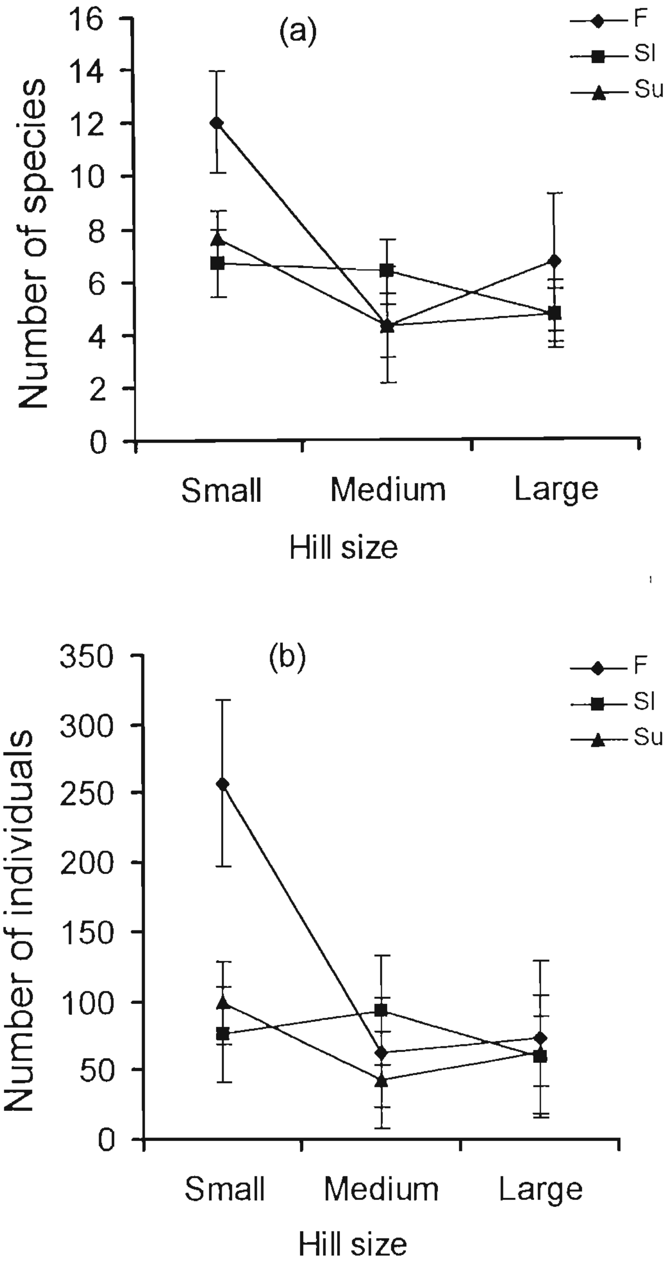


Fig. 3.2. Mean number of grasshopper species (a) and individuals (b) on the flatlands (F), slopes (Sl) and summits (Su) of three hill sizes.

3.3.2. Hill size and environmental variables

Some of the measured environmental variables were significantly different on the three hill sizes, whereas others were not (Table 3.1). Grass cover was significantly lower on small hills than on medium and large hills. Percent greenness was highest on medium hills, and lowest on small hills. Vegetation density was significantly higher on medium and large hills but low on small hills.

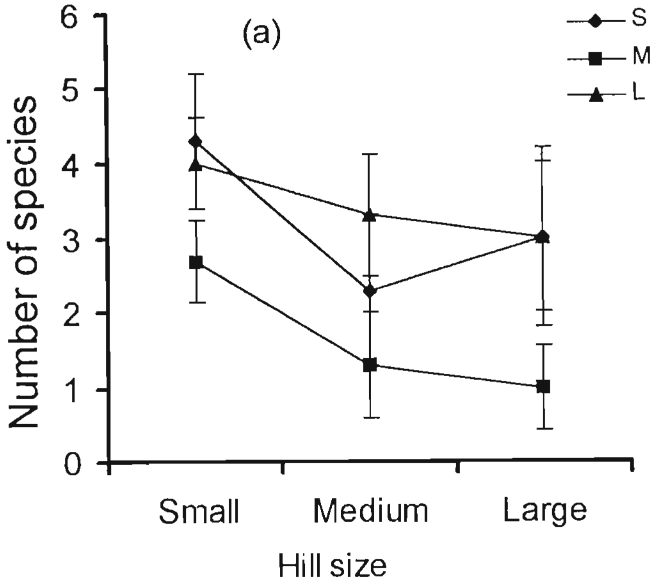
3.3.3. Grasshopper size versus hill size

The distributional pattern of the size of grasshoppers on the three hill sizes is presented in Fig. 3.3 a, b. On small hills slightly higher number of small-sized grasshopper species occurred followed by large- and medium--sized grasshoppers, but this difference was not statistically significant. In contrast, small hills contained a significantly higher number of small-sized grasshopper individuals (F=5.36; P<0.05) than medium and large hills. On medium hills, there were higher number of large-sized grasshopper species and individuals followed by small medium-sized grasshoppers, but this difference was not statistically significant. On large hills, there were equal numbers of small and large-sized grasshopper species followed by medium sized ones, and there were higher but statistically non-significant numbers of large-sized grasshopper individuals than small and medium-sized ones, which have equal numbers of individuals.

Table 3.1. ANOVA results of measured environmental variables (± SE) across the three hill sizes. SH=small hills; MH=medium hills; LH=large hills.

Variable	SH	MH	LH	*F*	*P*
Grass (%)	19.2 (11.6)b	42.5 (10.8)a	40.0 (5.8)a	1.7	0.02*
Shrub (%)	18.3 (10.9)	9.2 (2.2)	14.2 (3.0)	0.5	0.60
Rock (%)	41.7 (23.2)	40.0 (20.8)	25.8 (12.9)	0.2	0.82
Bare (%)	5.8 (3.8)	8.3 (4.2)	20.0 (11.5)	0.7	0.50
Avgrht	40.0 (7.6)	48.0 (13.4)	43.0 (11.7)	0.2	0.80
Maxgrht	69.2 (7.4)	70.8 (19.2)	58.3 (12.0)	0.5	0.71
Greenness of grass (%)	25.0 (0.9)	50.0 (7.2)	33.3 (8.3)	4.0	0.07
Cragginess (scale)	1.8 (0.6)	2.3 (1.2)	2.7 (1.3)	0.2	0.80
Veg. density (scale)	2.2 (0.4)b	3.3 (0.2)a	3.5 (0.3)a	5.2	0.04*
Soil temp. (°C)	33.3 (2.6)	33.2 (2.5)	31.3 (4.8)	0.1	0.90

*Significant at 5 % level of probability.



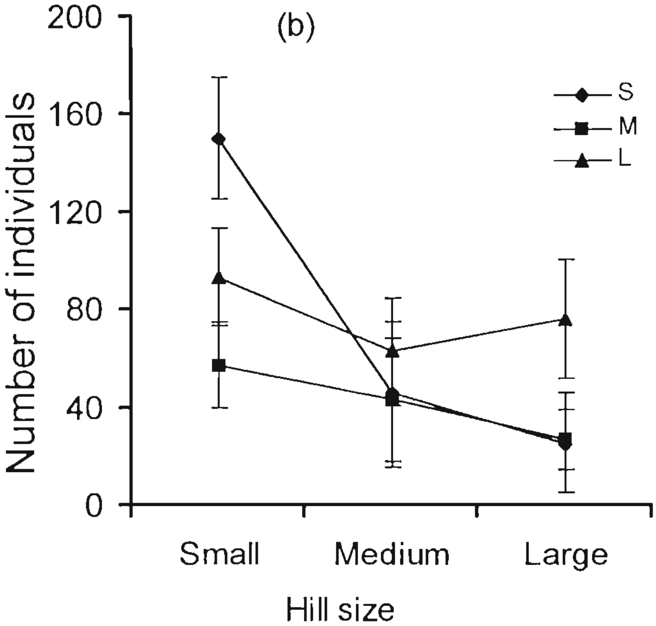


Fig. 3.3. Mean number of small (S), medium (M) and large (L) -sized grasshopper species (a) and individuals (b) on three hill sizes.

3.3.4. Elevation, hill sizes and grasshoppers

There was no significant difference between the flatlands, slopes and summits in number of grasshopper species and individuals across the hills. Hill's diversity and evenness indices showed variation between the sampling sites (Table 3.2). Flatlands of small hills had the highest N1 and N2. In contrast, slopes of large hills had the lowest N1, followed by flatlands of medium hill, which also showed the lowest N2 followed by slopes of large hills. Slopes of medium hills had the highest E followed by flatlands of small hills and large hills. This trend was also shown by the pattern revealed on Fig. 3.7, in which sites with lower dominance pattern showed higher evenness and vice versa.

Table 3.2. Hill's diversity indices and measures of evenness for all sites sampled on the three hill sizes. Site abbreviations as in Fig.3.5.

Site	N1	N2	E
SHF	11.50	10.50	0.88
SHSl	7.30	6.81	0.86
SHSu	6.47	5.42	0.77
MHF	2.61	2.13	0.69
MHSl	7.18	6.23	0.85
MHSu	5.77	5.72	0.90
LHF	4.17	4.03	0.88
LHSl	2.29	2.17	0.75
LHSu	4.12	3.61	0.79

Clustering of sampling sites using the Bray-Curtis similarity index (Fig. 3.4) showed that the slopes and summits of small hills had the highest similarity (70 %), followed by slopes and summits of medium hills with a similarity of 65 %. There was a similarity of 50 % between flatlands of medium and large hills. Slopes of large hills showed the least similarity to the rest of the sites.

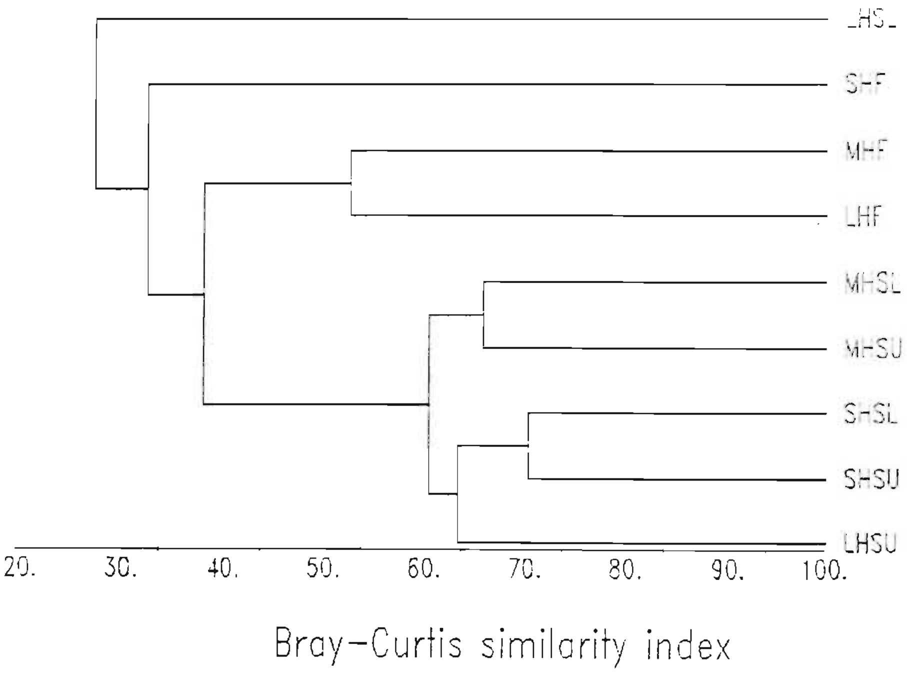


Fig. 3.4. Dendrogram for hierarchical clustering of the sampling sites using group average linking of Bray-Curtis similarities calculated on square root-transformed abundance data of grasshoppers. Site abbreviations:SHF=small hill flatlands; MHF=medium hill flatlands; LHF=large hill flatlands; SHSL= small hill slopes; MHSL=medium hill slopes;LHSL=large hill slopes; SHSU=small hill summit; MHSU=medium hill summit; LHSU=large hill summit.

3.3.5. Multivariate analyses

The list of grasshopper species sampled in this study, and their codes used in the ordination are given in Table 3.3. DCA of sites and grasshopper species showed that the flatlands of the three hill sizes had a different position on the 2-D ordination space in contrast to the slopes and summits (Fig. 3.5).

Table 3.3. Grasshopper species recorded during this study. Species codes are those used in the multivariate analyses.

Family	Subfamily	Species	Code
Pamphagidae	Porthetinae	*Hoplolopha horrida* (Burmiester, 1838)	Hoho
Lentulidae	Lentulinae	*Lentula callani* Dirsh, 1956	Leca
Acrididae	Calliptaminae	*Sphodromerus gilli* (Uvarov, 1929)	Spgi
		Acorypha pallidicornis (Stål , 1876)	Acpa
	Euryphyminae	*Rhachitopis crassus* (Walker, 1870)	Rhcr
		Calliptamulus hyalinus Uvarov, 1922	Cahy
		Calliptamicus sp.	Casp
	Eyprepocnemidinae	*Heterachris* sp.	Hesp
	Cyrtacanthacridinae	*Cyrtacanthacris tatarica* (Linnaeus, 1758)	Cyta
	Acridinae	*Acrida turrita* (Linnaeus, 1758)	Actu
	Oedipodinae	*Locustana pardalina* (Walker, 1870)	Lopa
		Oedaleus nigrofasciatus (De Geer, 1773)	Oeni
		Acrotylus insubricus (Scopoli, 1786)	Acin
		Sphingonotus scabriculcus (Stål, 1876)	Spsc
		Picnodictya flavipes (Miller, 1932)	Pifl
	Gomphocerinae	*Pseudogmothela* sp.	Psgm
		Dnopherula crassipes (Uvarov, 1921)	Dncr
		Pnorisa squalus Stål, 1861	Pnsq

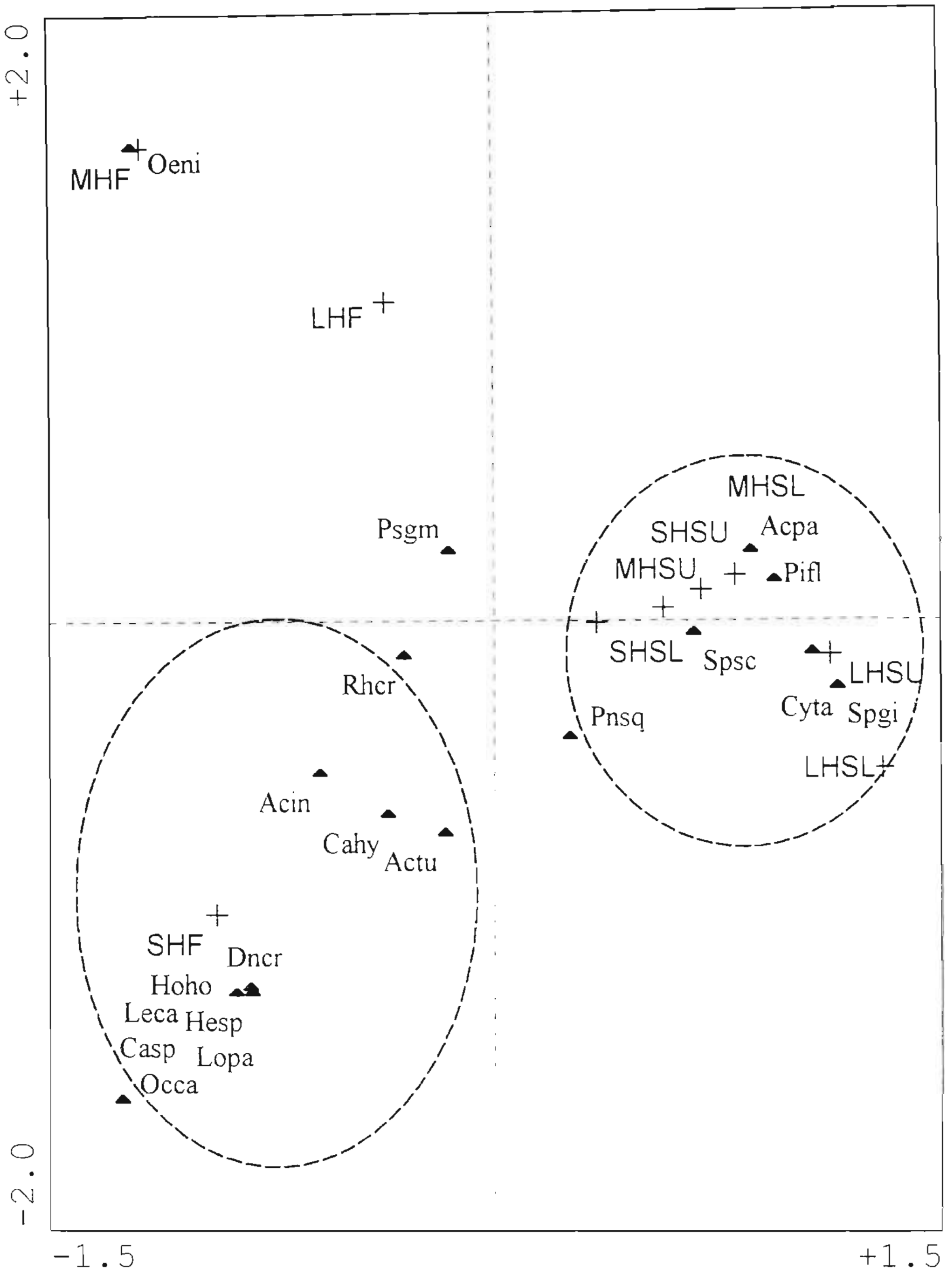


Fig. 3.5. DCA of grasshopper species (▲) and sampling sites (+). Species codes are as in Table 3.3. Site abbreviations: SHF=small hill flatlands; MHF=medium hill flatlands; LHF=large hill flatlands; SHSL= small hill slopes; MHSL=medium hill slopes; LHSL=large hill slopes; SHSU=small hill summit; MHSU=medium hill summit; LHSU=large hill summit.

While the flatland of small hills formed a separate assemblage of several grasshopper species, their slopes and summits appeared to form another assemblage of a few grasshopper species. The flatlands of medium hills appeared to be associated with only one grasshopper species, *Oedaleus nigrofasciatus*. The flatlands of large hills seemed to have no detectable association with any one of the other sites, and no grasshopper species seemed to have affinity to these sites, although *Pseudogmothela* sp. was the closest to these sites on the ordination. The eigenvalues of the first two axes of DCA and CCA, and the intraset correlations between the CCA axes and the environmental variables are given in Table 3.4.

Table 3.4. Eigenvalues of the first two axes of DCA and CCA, and the intraset correlations between CCA axes and the measured environmental variables. Avgrht=average grass height; Maxgrht=maximum grass height

	DCA		CCA	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.55	0.36	0.56	0.38
Grass			-0.59	0.31
Shrub			-0.71	-0.57
Rock			0.84	-0.26
Bare			-0.59	0.34
Avgrht			0.92	-0.38
Maxgrht			0.52	-0.66
Greenness of grass			-0.10	0.66
Cragginess			0.90	-0.19
Vegetation density			-0.32	0.33
Soil temperature			0.58	-0.18

CCA revealed the pattern of relationships between the measured environmental variables, sampling sites and grasshopper species (Fig. 3.6). The flatlands of small hills appeared to be dominated by shrubs as opposed to the flatlands of medium and large hills, which appeared to occur along increasing gradients of grass, bare ground, vegetation density and greenness of grasses. The slopes and summits of all the hills occurred along increasing gradients of rock cover, cragginess, grass heights and soil temperature.

3.3.6. Grasshopper dominance patterns

Patterns of grasshopper dominance varied markedly among hill sizes and elevations within a hill. Small hills contained more number of grasshopper species. However, dominance patterns were generally lower than medium and large hills (Fig. 3.7a). Of all species that occurred on the summits of small hills (Fig. 3.7a), *Acorypha pallidicornis* was relatively dominant (35%), followed by *Picnodictya flavipes* (20 %). Several species were rare. The next level of dominance was on the slope, by *A. pallidicornis* (25 %). Although the flatlands had a greater number of grasshopper species, they did not have a dominant species. Most species were rare, except *Acrotylus insubricus* (17 %) which was relatively abundant, followed by *Locustana pardalina* (13 %).

On medium hills (Fig. 3.7b), there were fewer grasshopper species on the flatlands than on the slopes and summits. Also, there was greater dominance on the flatlands than on the slopes and summits. The dominant species on the flatlands was *O. nigrofasciatus* (>65 %), followed by *Pseudogmothela* sp.(>20 %). *A. insubricus* and *Rhachitopis crassus* each

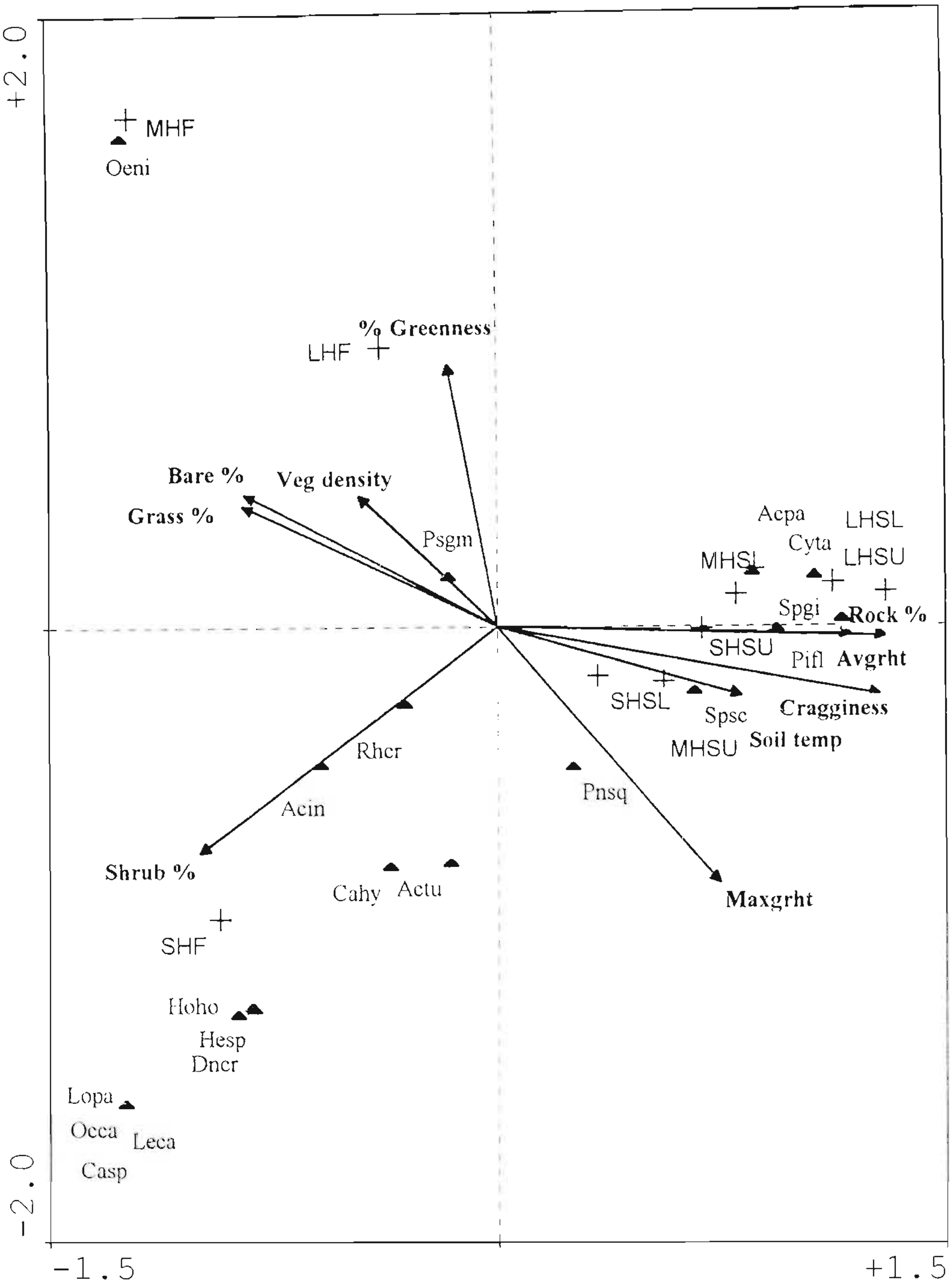


Fig. 3.6. CCA triplot of grasshopper species (▲), sampling sites (+) and environmental variables (arrows) of three hill sizes. Species codes are as in Table 3.3. Site abbreviations: SHF=small hill flatlands; MHF=medium hill flatlands; LHF=large hill flatlands; SHSL=small hill slopes; MHSL=medium hill slopes; LHSL=large hill slopes; SHSU=small hill summit; MHSU=Medium hill summit; LHSU=large hill summit. Environmental variables abbreviations: Maxgrht=maximum grass height; Avgrht=average grass height; Soil temp=soil temperature; Veg density=vegetation density.

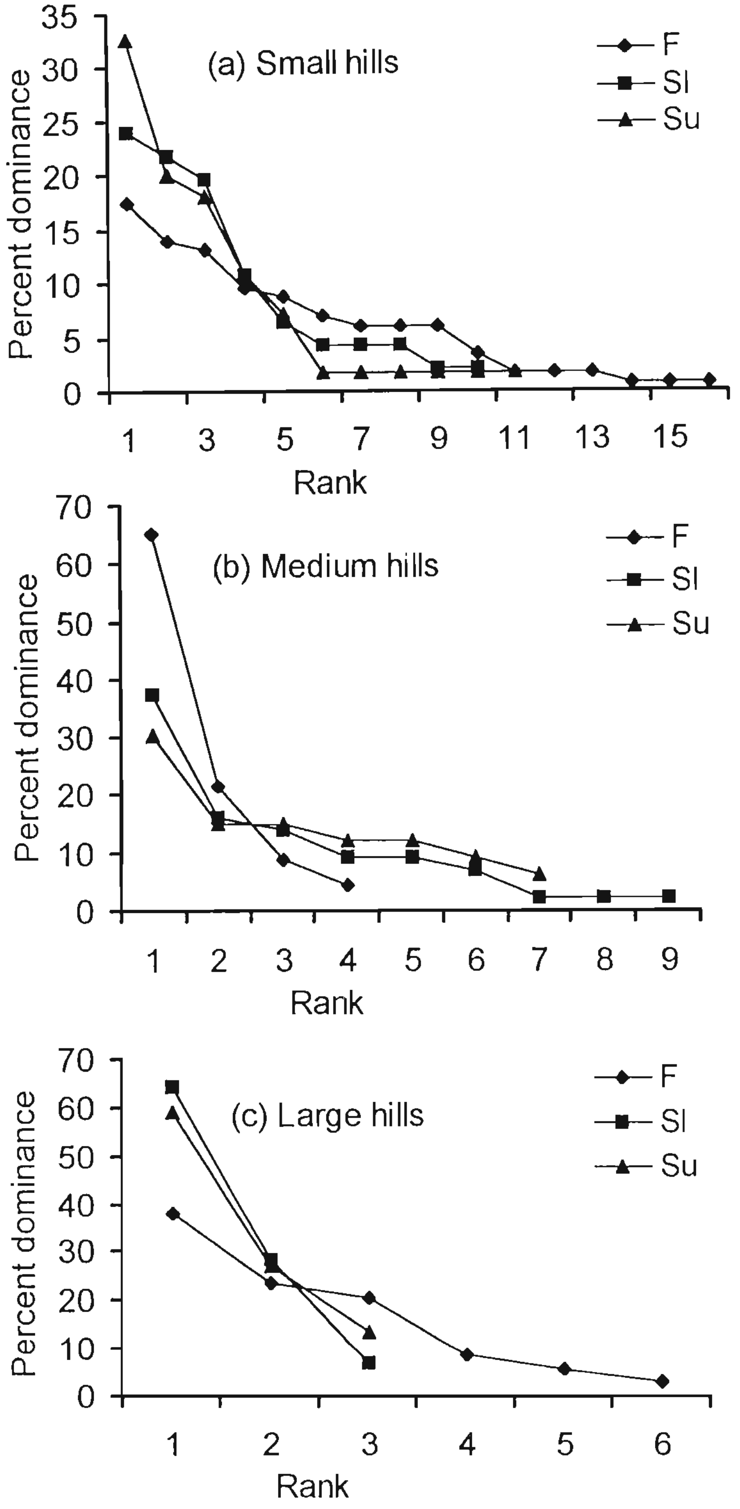


Fig. 3.7. Rank-abundance curves of grasshopper species from the surrounding flatlands (F), slopes (Sl) and summits (Su) of hills of different sizes.

contributed about 10 % and 5 % respectively to the total abundance on the flatlands surrounding medium hills. The slopes and summits were both dominated by *A. pallidicornis* (about 40 % and 30% respectively), and the pattern of the other species on the slopes and summits were similar, except that the slopes had slightly higher number of grasshopper species than did the summits.

The slopes and summits of large hills (Fig. 3.7c) had only three species, dominated by *Cyrtacanthacris tatarica* (about 60 %) and *A. pallidicornis* (about 65 %) respectively. The flatlands showed lower dominance than the slopes and summits, with *O. nigrofasciatus* contributing 40 % to the abundance.

3.3.7. Higher grasshopper groups and hill sizes

In general, there were variations among the three hill sizes with respect to the occurrence and distribution of higher taxonomic levels of grasshoppers (Table 3.5). Small hills had representatives from four families and nine sub-families, but medium and large hills had only members of Acrididae belonging to five sub-families. Acrididae / Eyprepocnemidinae and Acrididae / Cyrtacanthacridinae were not represented on medium and large hills. Nearly 50 % of the total number of grasshopper individuals were associated with small hills, followed by medium hills (27 %) and large hills (23 %). Aside from their association with only small hills, Lentulidae / Lentulinae and Acrididae / Acridinae were the most rare overall. In contrast, Acrididae / Oedipodinae accounted for nearly a third of the total grasshopper abundance, followed by Acrididae / Calliptaminae, which contributed nearly a quarter. Thus these two subfamilies of Acrididae alone contributed about 50 % to the total grasshopper abundance.

Table 3.5. Relative proportion of higher taxonomic classes of grasshoppers (Percentage of total number of individuals) across the three hill sizes. SH=small hills; MH=medium hills; LH=large hills.

Family	Sub-family	SH	MH	LH
Pamphagidae	Porthetinae	37 (2.1)	-	-
Pyrgomorphidae		32 (1.8)	-	-
Lentulidae	Lentulinae	8 (0.5)	-	-
Acrididae	Calliptaminae	139 (8.0)	-	-
	Euryphyminae	156 (9.0)	109 (6.30)	143 (8.3)
	Eyprepocnemidinae	20 (1.6)	28 (1.6)	69 (4)
	Cyrtacanthacridinae	44 (2.5)	29 (1.7)	102 (5.9)
	Acridinae	8 (0.5)	-	-
	Oedipodinae	251 (14.5)	224 (13)	83 (4.8)
	Gomphocerinae	163 (9.4)	77 (4.45)	4 (0.2)

3.4. Discussion

3.4.1. Hill sizes and grasshoppers

There was a clear difference between small hills on the one hand, and medium and large hills on the other with most grasshopper species and greatest abundance being affiliated with small hills. Above the spatial scale of isolated small hills, it appears that both medium and large hills are viewed similarly by most of the grasshopper species, indicating that the transition from small to medium hills is a critical threshold for most of the grasshoppers in the Karoo.

There also appeared to be a clear dichotomy in the size of grasshoppers into small or large, with most species falling in to the small category. Although differences were not statistically significant, small grasshoppers were most often associated with small hills, while large grasshoppers were encountered more often on large hills.

Despite the significantly higher species richness and abundance on small hills than medium and large hills, the slopes and summits of all hill sizes having similar species richness implies that the number of species that occur on the slopes and summits is generally few, irrespective of the hill size, and that the few that occurred were geophilous species (Uvarov, 1977), adapted to rocky and craggy patches.

Furthermore, DCA revealed that the flatlands had a different assemblage compared to the slopes and summits. Interestingly, not only were most of the grasshopper species associated with the flatlands, but they were associated only with the flatlands surrounding small hills, indicating that slopes and summits could act as critical thresholds as the size of the hill gets larger. This was emphasized by the fact that the flatlands of medium and large hills were avoided by most grasshopper species.

Increasing gradients of percent shrubbiness across flatlands is the result of of sheep and cattle grazing these sites more often than around medium and large hills, removing palatable grasses and leaving behind unpalatable shrubs. On the other hand, as elevation increases, slopes and summits are less frequently grazed, particularly by cattle, although sheep occasionally climb up to the summits of the larger hills. Thus the occurrence and cover of tall grasses was highest on slopes and summits of medium and large hills.

3.4.2. Grasshopper dominance patterns

The pattern of dominance on small hill slopes by *A. pallidicornis* and on the summits by *A. pallidicornis* and *P. flavipes* appears to be due to the association of these species with rockiness and cragginess, both environmental attributes being dominant features of slopes and summits of small hills. Both *A. pallidicornis* and *P. flavipes* did not occur on the flatlands. The pattern of dominance by *A. pallidicornis* on the summits and slopes of medium hills was similar to that on small and large hills, except that the slopes of large hills were dominated by *C. tatarica.*

Unlike the fltalands surrounding small hills, *O. nigrofasciatus* was dominant on flatlands surrounding medium and large hills. This pattern by *O. nigrofasciatus* in these sites was also seen in the study in Chapter 2, where it was largely associated with grassiness coupled with bare ground that appears to be a suitable habitat for its green and brown morphs (Chapter 2). The relative dominance of *A. insubricus* on the flatands of small hills with less cover concordes with its preference for more open patches, a pattern also observed in Chapters 2, 4 and 5. It is evident from these patterns that the flatlands have a generally different assemblage of grasshopper species from the slopes and summits of the hills, although the flatlands are generally more species rich than the slopes and summits. However, it is important to note that the slopes and summits provide the only suitable habitat for a few species, particularly *A. pallidicornis*, *Picnodictya flavipes* and mostly *C. tatarica*.

3.4.3. *Significance of variable hill sizes for Orthoptera conservation*

It is to be noted that both small hills (as in the case seen in this chapter) and large hills (as in the case of Chapter 2) are important for Orthoptera conservation. However, the trend observed in this study indicates that, regionally, most grasshopper species are rare, including the brown locust, *Locustana pardalina*, which is considered as a pest species when it occurs in swarms. This implies that if the grazing pressure on small hills continues, as with overstocking for example, many grasshopper species could undergo local extirpation. This trend has also been seen on the highly grazed and trampled sites on the farm outside the Mountain Zebra National Park (MZNP) (Chapter 4). Under such circumstances, physical elements of the landscape such as the largest mesa (Chapter 2) and / or the MZNP (Chapter 4) might serve as habitat refugia, where populations of species that are extremely sensitive to anthropogenic disturbances may find suitable habitat and maintain viable populations.

Any region may be scaled along at least two axes, distance and organisms. Distance scaling is simply measured as the aerial extent of the region in question (Collins and Glenn, 1997). Given that heterogeneity increases as distance between two habitat patches increases, the extent of the area sampled also increases. This means that patterns of species' regional distribution will shift in such a way that the number of regionally rare species increases and the number of regionally abundant species decreases (Brown, 1984; Hanski and Gyllenberg, 1993). These patterns were observed in this study. There was less dominance on the flaltlands, where most species occurred as rare and the number of regionally abundant species decreased.

3.4.4. Patterns of distribution of higher grasshopper groups

The rarity of Lentulinae species in this system may be due to their brachypterous nature, which makes them vulnerable to trampling by domestic herbivores, and also exposes them to predators such as birds and spiders (Belovsky and Slade, 1993). The general rarity of Acridinae species, including *O. dasycnemis*, appears to be due to their high responsiveness to grazing disturbances and the associated modified vegetation structure. Acridinae species are predominantly green in colour with an elongated body shape, and are associated with tall densely-packed grasses with high greenness. Most of the sites in this study were accessible to domestic livestock, which precludes such habitats. Indeed, the study in Chapter 2 revealed a similar pattern where *Or. dasycnemis* occurred only on the summit where domestic livestock were excluded. Most families and species were associated with small hills, and as half of all grasshopper individuals occurred on them, it indicates that, as the size of hills increases, the relative proportion of preferred habitats is reduced.

3.4.5. Patch preference and critical thresholds

The relative abundance of preferred habitat in the landscape may be the primary determinant of distributional pattern for habitat specialists and may even override the importance of the species' dispersal capabilities (Kemp et al., 1990; Kemp, 1992; With and Crist, 1995; Samways and Sergeev, 1997; Gebeyehu and Samways, 2001). In turn, a species may prefer a given habitat on the basis of its suitability as a source of food (Mulkern, 1967; Beckerman, 2000; Narisu et al., 2001), as an escape space (Isely, 1938), or a thermoregulatory requirement (Anderson et al.,1979; Chappell, 1983; Chappell and Whitman, 1990; Lactin and Johnson, 1997, 1998) or a combination of two or more of these habitat factors.

Since the occurrence of the critical threshold is a function of whether or not a particular species perceives the landscape as connected, it is unlikely that a single threshold value can adequately describe the response of all species in a community to changes in landscape pattern (With and Crist, 1995), particularly because each organism observes the environment on its own unique suite of scales of time and space (Levin, 1989). Also, the critical threshold is not an inherent property of a landscape, but emerges from the interplay of species interactions with landscape structure (Levin, 1992; Plotnick and Gardner, 1993; With and Crist, 1996). Indeed, the patterns of occurrence and distribution shown by the grasshopper species in this study concur with this notion. For example, what *C. tatarica* views as a connected landscape is viewed by *A. insubricus* or *O. nigrofasciatus* as patchy as the structure of the landscape changes from a flatland to a hill. Similarly, while *O. nigrofasciatus* views a patch made up of bare ground and grasses as connected, *Or. dasycnemis* considers the mere occurrence of bare ground as a critical threshold because its preferred landscape is one made of homogenous stand of tall green grasses. At a regional scale, flatlands and small hills are generally considered as connected by most grasshopper species, but transitions from small to larger hills are considered critical thresholds, resulting in clumped rather than random distributions.

3.4.6. The significance of size in grasshoppers

Most of the grasshopper species in this study were small in size, and were mostly associated with small hills, whereas greater incidence of large species was observed on large hills. The most common of the large species was *C. tatarica,* which showed a sustained flight covering long distances compared to most small species whose displacement was less than 100 m. Since rate of movement is an allometric consequence of hind-leg length in grasshoppers (Gabriel, 1985; Bennett-Clark, 1990), this species is highly mobile and, therefore, interacts with landscape at a coarser scale than do small species. After studying how small and large grasshoppers perceive the landscape, With (1994) found that the larger species moved six times faster than the smaller species. This indicates that larger species interact with landscape structure in a functionally different manner than do smaller species.

3.4.7. Conclusion

It has been suggested that since animal movement is likely constrained by processes operating at different scales, extrapolation of information on fine-scale movement across broad scales may provide poor quantitative prediction of the spatial dynamics of populations. Even the most detailed spatially explicit population models cannot predict the exact location of individuals across a landscape, or reproduce precise statistical properties of population distributions (Dunning et al., 1995). The best application of this type of modelling approach is in making comparative and qualitative statements about likely population responses to a set of potential or real landscape scenarios (Dunnig et al., 1995). Indeed, such is the case with the interaction between grasshopper assemblage patterns in the Karoo, as shown in this study. While small scale studies such as at the level of just one hill (Chapter 2) or at the level of an experimental plot (Chapter 5) serve to show a fine-scale picture of patch preference by individual grasshoppers, region-level studies serve to make qualitative as well as quantitative comparisons between major physical elements of the landscape and their influence on assemblage patterns of small herbivores such as grasshoppers.

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CHAPTER FOUR

Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa)

This chapter has been submitted for publication to *Biodiversity and Conservation*, and is in press.

4.1. Introduction

Grasshoppers are among the most important native herbivores of rangelands (Kemp and Dennis, 1993). A striking feature is their role in ecological processes (Samways, 1997). They are major primary consumers and significant generators and transporters of nutrients (Gandar, 1980), major players in energy flow (Samways, 1997), and account for a high percentage of the above-ground phytophagous insect biomass (Gandar, 1982). Also, they are good indicators of certain threatened habitats (Anderson et al., 2001) and, as such, Orthoptera have played important roles in the conservation of natural areas and preservation of habitats (Rentz and Weissman, 1981; Devoka and Schmidt, 2000). Their local-level abundance can represent landscape or regional abundance (Kemp et al., 1990; Sergeev, 1997), and their relative abundance can be a sensitive indicator of land use (Bei-Bienko, 1970; Lockwood, 1997; Samways and Sergeev, 1997). This does not, of course, assume that they are the perfect umbrella taxon for all aspects of biodiversity (Kotze and Samways, 1999; Lawton et al., 1998).

Managed grasslands are frequently subjected to large perturbations that alter the habitats of herbivorous insects (Quinn and Walgenbach, 1990). Vertebrate grazers in particular, can change plant community architecture by altering the coverage of grasses, shrubs, forbs, and bare ground (Belsky, 1986; Taboda and Lavado, 1993; Dahlberg, 2000). Grazing-and livestock-induced disturbance is a complex and composite factor, with both direct and indirect impacts on plant and invertebrate communities (O' Connor and Roux, 1995; Ledergerber et al., 1997). The impacts consist principally of defoliation, trampling, defaecation and urination, and the associated modification to soil structure, nutrient status, food supply, shelter and microclimate (Abensperg-Traun et al., 1996; Taboda and Lavado, 1993; Maliha et al., 2000).

Most vegetation throughout South Africa has been subjected to some disturbance (Acocks, 1988), and the proportionately few areas that have been under protection for a comparatively long time can serve as reference for the natural diversity of the land mosaic. Landscapes inside reserves can serve as baselines for comparison with the outside where the landscapes are continually disturbed (Abensperg-Traun et al., 1996; Rivers-Moore and Samways, 1996; Norman et al., 2000). The Mountain Zebra National Park (MZNP), South Africa, and the surrounding landscapes, are cases in point. Inside the park, the major, large faunal component is indigenous mammals and the vegetation is the result of 62 years of restoration from earlier domestic livestock activities. Outside the park, the adjacent farms are grazed regularly by sheep, goats and cattle, with effects on the vegetation composition and cover. This study investigates how the grasshoppers assemblage has responded to this inside restoration relative to outside the park where livestock continue to graze.

4.2 Study area

The MZNP (32E 15'S, 25E 41'E, 24 km west of the town of Cradock) is situated in a north-south orientated transitional zone (Tidmarsh, 1948) between the arid Karoo bushveld of the western and central Karoo and the drier “sweet” grassveld in the east (Fig. 4.1). The first part of the park (1712 ha) was purchased from farmland in 1937,

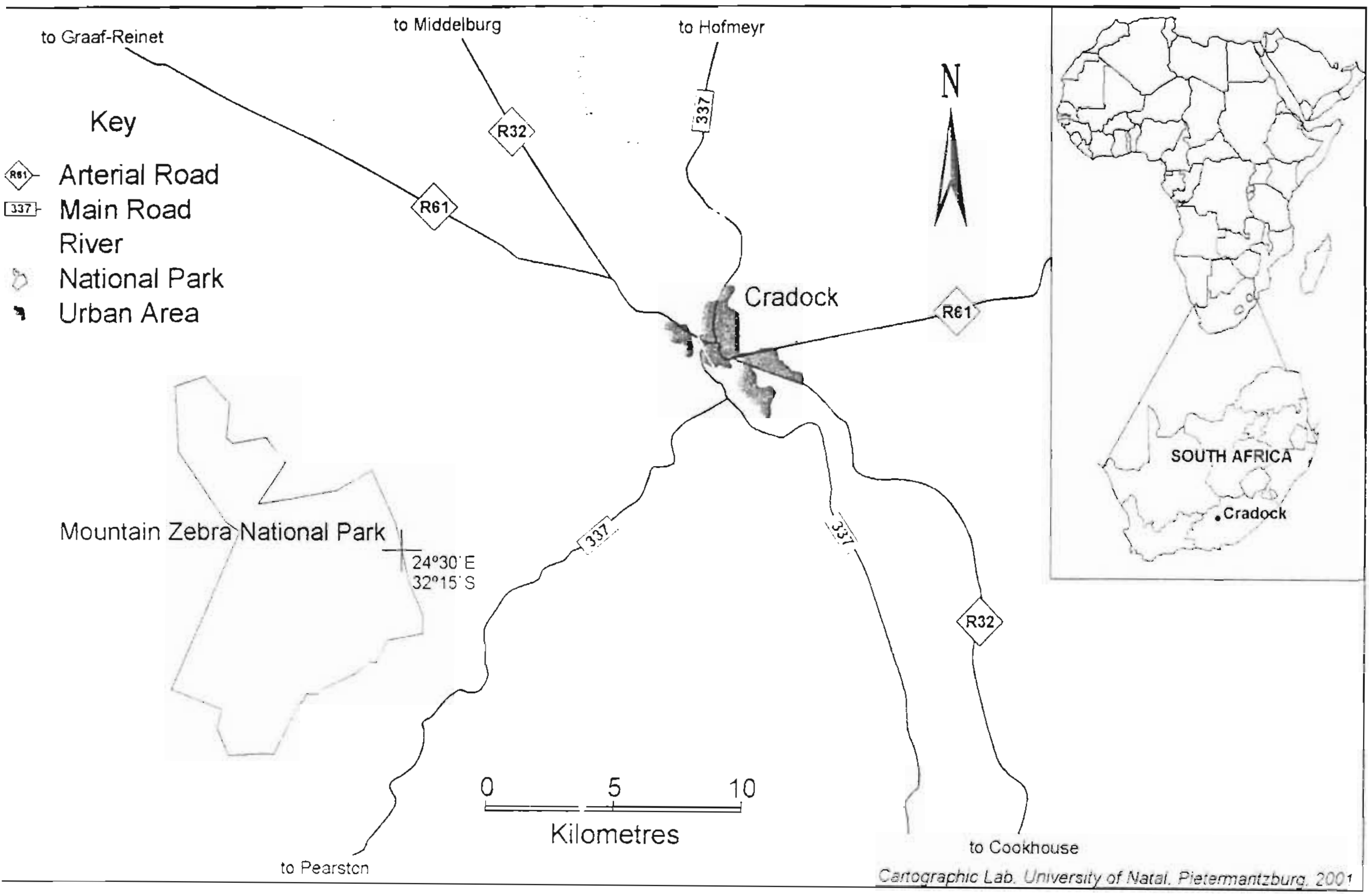

Fig. 4.1. Location of the study site, MZNP, South Africa.

Figure 4.1. Location of the study site, MZNP, South Africa

and since then, adjacent farms have been added, so that today it encompasses about 6500 ha. The study here was undertaken in the original core area, making the restoration term 62 years. The mountainous terrain of the MZNP is part of the southern quarter of the Karoo Mountain Veld Complex ,which forms part of the most outstanding feature of South Africa's physiography, the Great Escarpment (King, 1942; Fair and King, 1954). The landscape of the MZNP has evolved on sedimentary rock types of the Beaufort series of the Karoo system (Dohse, 1976). The veld type is the eastern mixed Karoo veld, where there is an overall co-dominance of grasses and Karoo bushes/dwarf shrubs (Acocks, 1988). Elevation ranges from 1200 m -1957 m a.s.l. Mean annual rainfall is about 398 mm, 70% of which falls between October and March and 30% between April and September. Mean annual temperature reaches 18 °C, while mean monthly temperature varies between 29.1 °C in January (range of 18-37 °C) and 15°C in June (range of 7-23 °C).

MZNP management maintains a genetically-viable, uncontaminated, representative population of the Cape Mountain Zebra (*Equus zebra zebra* Linn., 1758). Secondary objectives are (i) to conserve a representative spectrum of the typical faunal elements of the MZNP under natural conditions, and (ii) to conserve a representative spectrum of vegetation types that are unique to this region (van Der Walt, 1980). Outside the MZNP, stocking rates of megaherbivores have, over the years, varied substantially. This made it difficult to put a figure on these rates, as well as the fact that the animals move a great deal. Nevertheless, the pressure on the land from domestic animals outside the park was substantially greater than that from game animals inside the park, and these effects are illustrated here in terms of vegetation structure and composition.

4.3. Sampling methods

4.3.1. Grasshoppers

A total of 12 sites were selected, six inside (Sites 1-6) the park and six outside (Sites 7-12). The sites were selected to represent major topographical and land-use features. The sites were at different distances from the park boundary (Table 4.1). A transect of 100 m long and 5 m wide was used as a sampling unit (SU), which was replicated six times at each site to avoid the area effect (MacArthur, 1972). The distance between transects was 10 m to minimize risks of sampling of grasshoppers twice (Kisbenedek, 1995). Extensive preliminary sampling of grasshoppers was done using a sweep net over one year prior to the quantitative sampling. Identification of the resident grasshopper species was done from a voucher collection. In addition, intensive familiarization was undertaken on the jizz of each species in the field so that they were recognizable in the field with no or minimal error. Sampling of grasshoppers was then done visually, by making transect walks and counting them as they flushed. This was supplemented with sweep netting to determine individuals that were still unfamiliar This method of visual recording was found in previous studies to be the most accurate and efficient means of documenting grasshopper species and abundances in the rugged African terrain (Samways, 1990; Armstrong and van Hensbergen, 1999; Chambers and Samways, 1998). Visual sampling has also been shown to be effective elsewhere (Kemp and Dennis, 1993; Kemp et al., 1989). Close-focus binoculars (Sigma-armada series 10 x 23 wp compact) were an essential recognition aid. Only adult individuals were counted. Sampling was done daily from 15 January-15 April 1999 on relatively still and sunny days between 11h00 and 15h00. The voucher collection is retained at the Invertebrate Conservation Research Centre.

4.3.2. Vegetation

The relative proportions of ground cover were recorded i.e. number of grass species, percentage cover of dominant grasses, shrubs, bush, rock and bare ground. These were estimated for each transect by laying five 1 m² iron rods which were divided in to ten units of 10 cm². Maximum and mean heights of grasses were also estimated. Mean heights of grasses were obtained by taking average heights of 30 random points in a transect, and maximum height was obtained by measuring the tallest inflorescence. Both univariate and multivariate statistical packages were used for data analyses. PRIMER (Clarke and Warwick, 1994; Ludwig and

Table 4.1. Sites sampled inside and outside the Mountain Zebra National Park.

Sites			
Inside	Outside	Distance from fence (m)	Description
1	7	50	Adjacent to fence
2	8	500	Medium hills closer to fence
3	9	1000	Medium hills far from fence
4	10	2000	Water points far from fence
5	11	3000	Medium hills near water points
6	12	3500	Flat lands far from fence

Reynolds, 1988) was used for hierarchical clustering of sampling sites. Both richness and abundance data were 4th-root transformed for site clustering, and richness data were log-transformed to satisfy the requirements of ANOVA (Johnson and Wichen, 1992). Ordination techniques such as Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were performed using CANOCO (Ter Braak 1986, 1988). The ordination plots were drawn using CANODRAW version 3. Non-parametric statistics and ANOVA were run using MINITAB and SPSS.

4.4. Results

4.4.1. Vegetation between sites

The dominant plant species sampled in this study are listed in Table 4.2. Mean grass cover was significantly higher at sites inside the park than at sites outside ($T = 3.18$, df = 62, $P<0.01$). In contrast, the mean shrub cover was significantly higher at sites outside the park than those inside ($T = -3.47$, df = 63, $P<0.01$). The maximum grass height was significantly higher outside the park than inside ($T = -2.11$, df = 64, $P<0.05$). The average grass height was also significantly higher outside the park than inside ($T = -3.44$, df = 65, $P<0.01$). The other measured environmental variables were not significant at the 5 % level (Table 4.3).

Table 4.2. Dominant plant species sampled in this study.

No.	Species name	Higher taxa	Occurence	
			Inside the park	Outside the park
1.	*Digitaria erianthra* Steud.	Paniceae	+	+
2.	*Setaria sphacelata* (Schumach.) Moss		+	-
3.	*Setaria pallide-fusca* (Schumach.) Stapf & C.E. Hubb	.	+	-
4.	*Panicum colourtum* L.		+	-
5.	*Melinis repens* (Willd.) C.E. Hubb		+	-
6.	*Eragrostis curvula* (Schrad.) Nees	Eragrosteae	+	-
7.	*Eragrostis obtusa* Munro ex Fical & Hiern		+	-
8.	*Sporobolus fimbriatus* (Trin.) Nees	Sporoboleae	+	+
9.	*Aristida congesta* Roem. & Schult	Aristideae	+	+
10.	*Aristada diffusa* Trin.		+	+
11.	*Cynodon incompletus* Nees	Chlorideae	+	+
12	*Traghus koelerioides* Aschers		+	-
13.	*Chloris virgata* Swartz		+	-
14.	*Themeda triandra* Forssk.	Andropogoneae	+	+
15.	*Heteropogon contortus* Roem. & Schult.		+	+
16.	*Hyperanea hirta* (L.) Stapf.		+	+
17.	*Cymbopogon plurinoides* (Stapf.) Stapf. ex Burtt Davy		+	-
18.	*Eneapogon scoparius* Stapf.	Pappophoreae	+	+
19.	*Merximulera disticha* (Nees) Conert	Arundineae	+	-
20.	*Melica decambens* Thunb.	Meliceae	+	-

Table 4.3. Mean (± 1SE) values of vegetation variables recorded for the six sites inside and six sites outside the MZNP. Also shown are significant (S) and non-significant (NS) differences of the means with the respective probability values resulting from the different two-sample t-tests.

Variable	Inside	Outside	Significance	P-value
Grass %	45.8(3.9)	30.1(3.1)	S	0.002**
Rock %	18.4(2.3)	24.7(3.0)	NS	0.100
Shrub %	12.3(2.3)	25.4(3.0)	S	0.001**
Bare %	11.5(2.2)	15.3(4.1)	NS	0.420
Bush %	2.9(0.6)	3.0(0.8)	NS	0.940
Nogrsp	1.6(0.10)	1.8(0.2)	NS	0.320
Grmaxht (cm)	65.0(3.5)	74.6(3.0)	S	0.030*
Gravht (cm)	42.2(2.1)	53.5(2.6)	S	0.001**

Significant correlations: $*P<0.05$; $**P<0.01$. Nogrsp = number of grass species; Grmaxht = grass maximum height; Gravht = grass average height.

4.4.2. Grasshopper species richness and abundance inside and outside the park

In general, there was no significant difference between mean number of grasshopper species at sites inside the park and those outside (Fig. 4.2). However, mean number of individuals were significantly different at sites inside the park compared to sites outside (Fig. 4.3). In general, the sites inside the park supported a significantly higher grasshopper abundance than the sites outside ($T = 1.45$, df = 10, $P<0.05$). When the sites inside the park and those outside were considered separately, there was a significant difference among the six sites inside the park in the mean number of grasshopper species ($F = 5.15$, $P<0.01$), but the sites did not differ significantly in the mean number of grasshopper individuals. Site 1 had the highest number of species, and Site 4 the least.

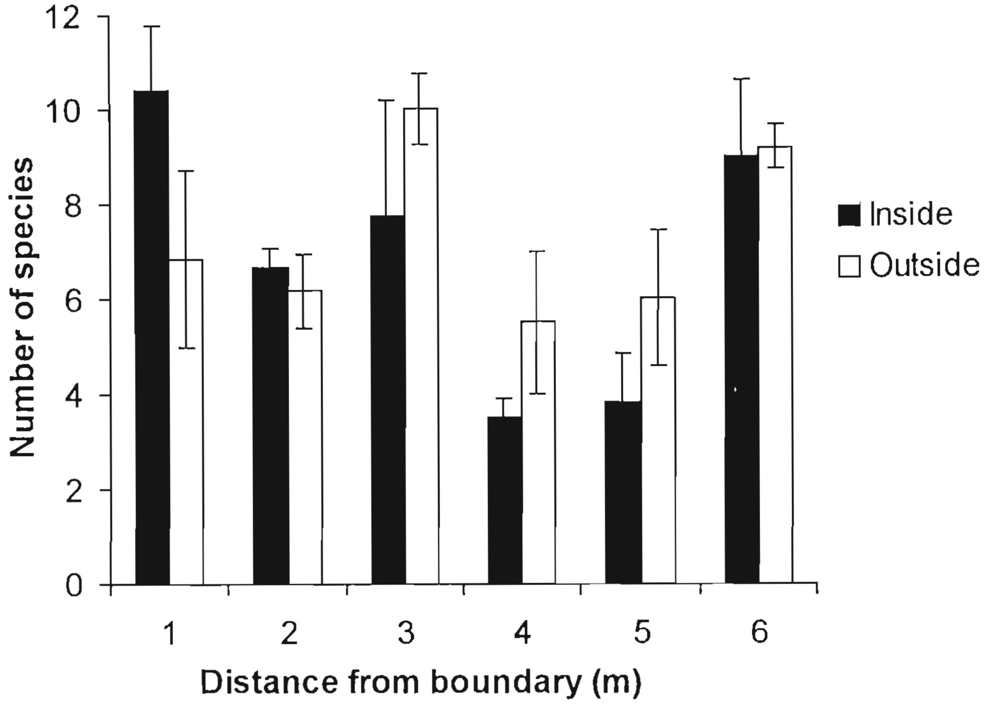

Fig. 4.2. Mean (±SE) number of grasshopper species inside vs. outside the MZNP. Distances are as in Table 4.1. Sites 1/7 (Inside/Outside) are the closest, and sites 6/12 are the farthest from the boundary fence.

In contrast, the six sites outside the park differed significantly in the mean number of grasshopper individuals (F = 3.38, $P<0.05$), but there was no significant difference in the number of grasshopper species (Table 4.4). Site 6 had the highest number of grasshopper individuals and Sites 4 and 5 the least.

Table 4.4. Mean (± 1SE) number of grasshopper species and individuals at the six variable distances inside versus six outside the park boundary fence. Data for number of grasshopper individuals are log-transformed. Also shown are the F-values resulting from the different ANOVAs (3, 30 degrees of freedom). Mean separation according to Tukey's family error test.

	Inside		Outside	
Distance (m)	No. species	No. individuals	No. species	No. individuals
50	10.3 (1.39)a	6.7 (0.54)a	6.8 (1.87)a	4.4 (0.79)ab
500	6.6 (0.23)b	6.9 (0.93)a	6.1 (0.79)a	5.2 (0.67)ab
1000	7.8 (1.09)a	7.1 (1.24)a	10.0 (0.77)a	5.6 (0.29)ab
2000	3.5 (0.23)b	4.7 (0.39)a	5.5 (1.48)a	3.6 (0.52)b
3000	3.8 (0.55)b	5.9 (0.87)a	6.0 (1.41)a	3.6 (0.67)b
3500	9.0 (0.86)a	7.9 (0.77)a	9.1 (0.47)a	6.1 (0.20)a
F-value	6.0**	2.0	2.2	3.8*

Numbers followed by the same letters in the column are not significantly different at the 5% level of probability.***P*<0.01; **P*<0.05.

4.4.3. Overall grasshopper abundance

A total of 2950 individuals in 28 species, belonging to four families, and nine sub-families, was counted (Table 4.5). When all the sites were combined, 48 % of the species had fewer than 50 individuals, 81% had fewer than 100 individuals, 88.8% had fewer than 250 individuals, and three species (11.1%) had more than 300 individuals.

Table 4.5. Grasshopper species sampled in this study, and their codes used in the multivariate analyses.

					Occurrence		
No.	Family	Sub-family	Scientific name	Code	Common to both inside and outside	Only inside	Only outside
1	Pamphagidae	Porthetinae	*Hoplolopha horrida* (Burmiester, 1938)	Hoho	*		
2			*Lamarkiana* sp.	Lasp		*	
3	Pyrgomorphidae		*Zonocerus elegans* (Thunberg, 1815)	Zoel	*		
4			*Phymateus leprosus* (Fabricius, 1793)	Phle	*		
5	Lentulidae	Lentulinae	*Lentula callani* Dirsh, 1956	Leca	*		
6	Acrididae	Callipataminae	*Sphodromerus gilli* (Uvarov, 1929)	Spgi	*		
7			*Acorypha pallidicornis* Stal., 1876	Acpa		*	
8		Euryphyminae	*Rhachitopis crassus* (Walker, 1870)	Rhcr	*		
9			*Euryphymus tuberculatus* (Martinez, 1898)	Eutu	*		
10			*Calliptamulus hyalinus* Uvarov, 1922	Cahy	*		
11			*Calliptamucus* sp.	Casp	*		
12		Eyprepocnemidinae	*Heteracris* sp.	Hesp	*		
13		Cyrtacanthacridinae	*Cyrtacanthacris tatarica* (Linnaeus. 1758)	Cyta	*		
14		Acridinae	*Acrida turrita* (Linnaeus, 1758)	Actu	*		
15			*Truxalis burtti* Dirsh, 1951	Trbu	*		
16			*Orthochtha dasycnemis* (Gerstaecker, 1869)	Orda	*		
17			*Paracinema tricolor* (Thunberg, 1815)	Patr	*		
18			*Tmetonota* sp.	Tmsp	*		
19			*Gastrimargus crassicolis* Sauss., 1888	Gacr	*		
20		Oedipodinae	*Oedaleus nigrofasciatus* (De Geer 1773)	Oeni	*		
21			*Acrotylus insubricus* (Scopoli, 1786)	Acin	*		
22			*Sphingonotus scabriculus* (Stal., 1876)	Spsc			*
23			*Scintharista saucia* (Stal., 1873)	Scsa	*		
24		Gomphocerinae	*Pseudogmothela* sp.	Psgm			*
25			*Dnopherula crassipes* (Uvarov, 1921)	Dncr	*		
26			*Aulacobothrus dorsatus* (I.Bolivar, 1912)	Audo	*		
27			*Pnorisa squalus* Stal., 1861	Pnsq	*		
28			*Pseudoarcyptera* sp.	Psar	*		

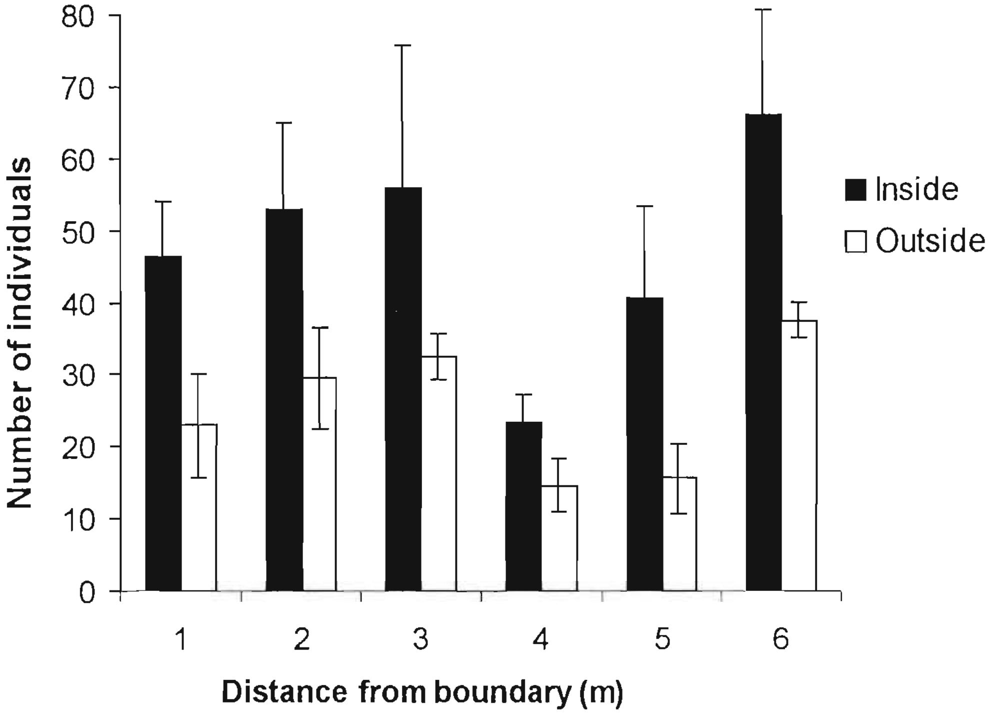

Fig. 4.3. Mean (±SE) number of grasshopper individuals inside vs. outside the MZNP. Distances1-6 are as in Table 4.1. Sites 1/7 (Inside/Outside) are the closest, and sites 6/12 are the farthest from the boundary fence.

The five most abundant species were *Oedaleus nigrofaciatus, Acrotylus insubricus, Dnopherula crassipes, Orthochtha dasycnemis* and *Heteracris* sp., with *O. nigrofasciatus* being represented by more than 700 individuals. These five species accounted for 64.5% of the total number of individuals. The occurrence of the individual species varied across the 12 sites. The three most habitat-tolerant species were *O. nigrofaciatus* (in 12 of the sites), *A. insubricus* (in 12 of the sites), *Acrida turrita* (in 11 sites), followed by *Rhachitopis crassus, Heterachris* sp., *D. crassipes, Truxalis burtti* and *Acorypha pallidicornis* which occurred in ten sites each. In contrast, the most habitat-restricted, and one of the rarest species was *Sphingonotus scabriculus*, which occurred in only one site outside the park (Site 7) and only two individuals were counted.

Spearman's rank-correlation of site variables to grasshopper species richness and abundance indicated that inside the park, percent rock cover and number of grass species was positively correlated with species richness, while percent bare ground cover was negatively correlated with richness. Outside the park, percent shrub cover was positively correlated with species richness and abundance (Table 4.6).

Table 4.6. Spearman's Rank Correlation of site variables to grasshopper species richness and abundance inside and outside the MZNP.

	Inside		Outside	
	Richness	Abundance	Richness	Abundance
Grass (%)	0.32	0 .27	0 .07	0 .25
Rock (%)	0.54**	0 .25	-0.08	0 .25
Shrub (%)	-0.51**	-0.31	-0.07	-0.21
Bare (%)	-0.51**	-0.31	-0.07	-0.21
Bush (%)	0.21	0.12	-0.16	-0.15
Nogrsp	0.37*	0.17	0.12	0.19
Grmaxht (cm)	0.22	-0.05	0.20	0.15
Gravht (cm)	0.34	-0.12	-0.16	-0.25

Significant correlations: $**P<0.01$; $*P<0.05$. Nogrsp = number of grass species; Grmaxht = grass maximum height; Gravht = grass average height.

The hierarchical cluster analysis revealed four main grasshopper assemblages. Although the identification of assemblages from this dendrogram is somewhat subjective (Ludwig and Reynolds 1988) I follow the general guideline suggested by those authors, not to divide so finely and end up with a large number of fragmentary and uninterpretable groups. Accordingly, there were at least four distinct clusters of sites by arbitrarily considering the Bray-Curtis similarity index of 50% (Fig. 4.4). The most similar sites were Sites 3 and 6 (inside the park), with 13 species in common, and Sites 11 and 12 (outside the park), with 14 species in common. Site 2 inside was similar to Site 7 outside, having 13 species in common. Sites 9 and 10, both outside, had 11 species in common.

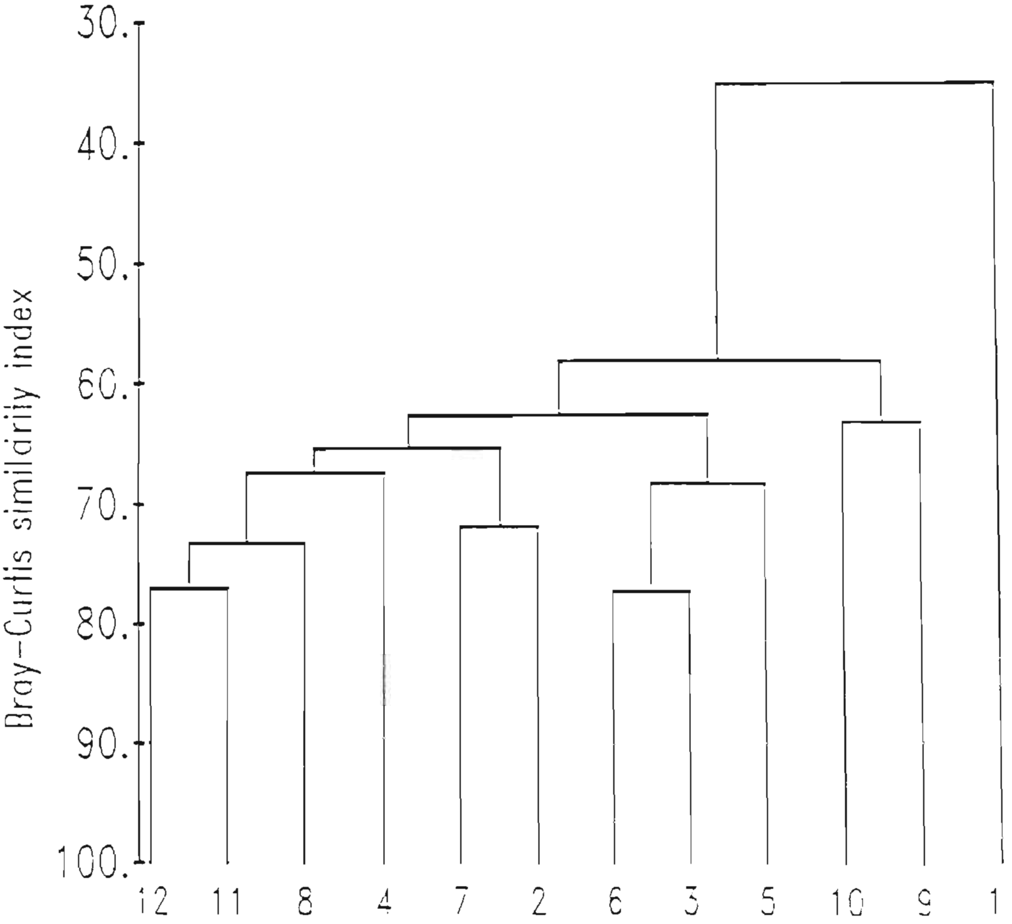

Fig. 4.4. Dendrogram for hierarchical clustering of the 12 sites (1-12), using group average linking of Bray-Curtis similarities calculated on the 4th root-transformed abundance data of grasshoppers.

There were similarities in the shapes of the dominance curves of the species according to the species-rank inside and outside the park, and when the species from all sites inside and outside the park were combined together (Fig. 4.5). However, there were small differences in the pattern of dominance inside versus outside the park. Inside the park, the dominance values were higher, with one species particularly dominant, and another species occurring as a sub-dominant with most species being rare. In contrast, outside the park, the dominance values were lower, with one species slightly dominant, and there were two equally sub-dominant species, with most other species being rare.

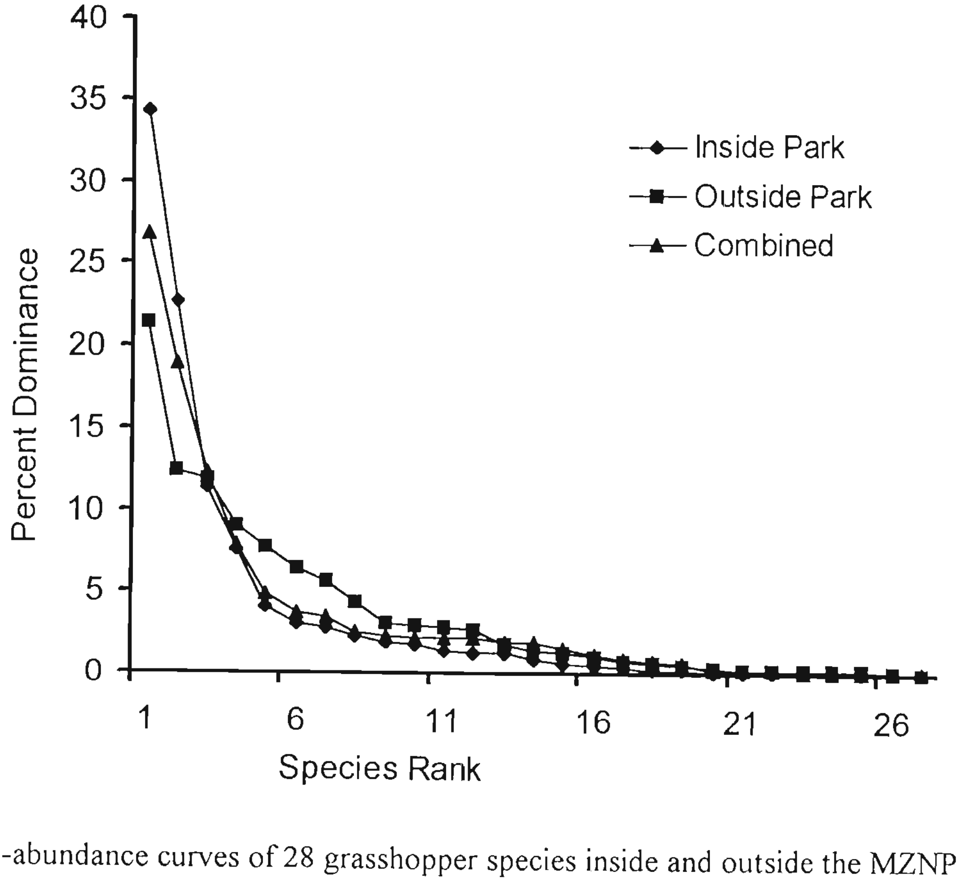

Fig. 4.5. Rank-abundance curves of 28 grasshopper species inside and outside the MZNP.

The dominant and sub-dominant species inside the park were *O. nigrofasciatus* and *A. insubricus* respectively. Outside the park, the dominant species was *D. crassipes* while the two sub-dominant species were *O. nigrofasciatus* and *A. insubricus*.

4.4.4. Detrended Correspondence Analysis (DCA)

The ordination biplot of grasshopper species and sites (Fig. 4.6) showed that certain grasshopper species were closely correlated with certain sites on the ordination plot. The group *Lamarkiana* sp., *A. insubricus, O. nigrofasciatus, Gastrimargus crassicolis, Phymateus leprosus, Paracinema tricolor* and *Calliptamicus* sp. were closely correlated with Sites 1 and 3 (inside) and 11 (outside). In turn, *S. scabriculus, Aco. pallidicornis, Rhachitopis crassus* and *Ac. turrita* were correlated with Site 7 (outside). The other close groupings are those of *Cyrtacanthacris tatarica* and *Lentula callani* with Site 9 (outside), and *Or. dasycnemis, Calliptamulus hyalinus*, and *Scintharista saucia* with Site 5 (inside).

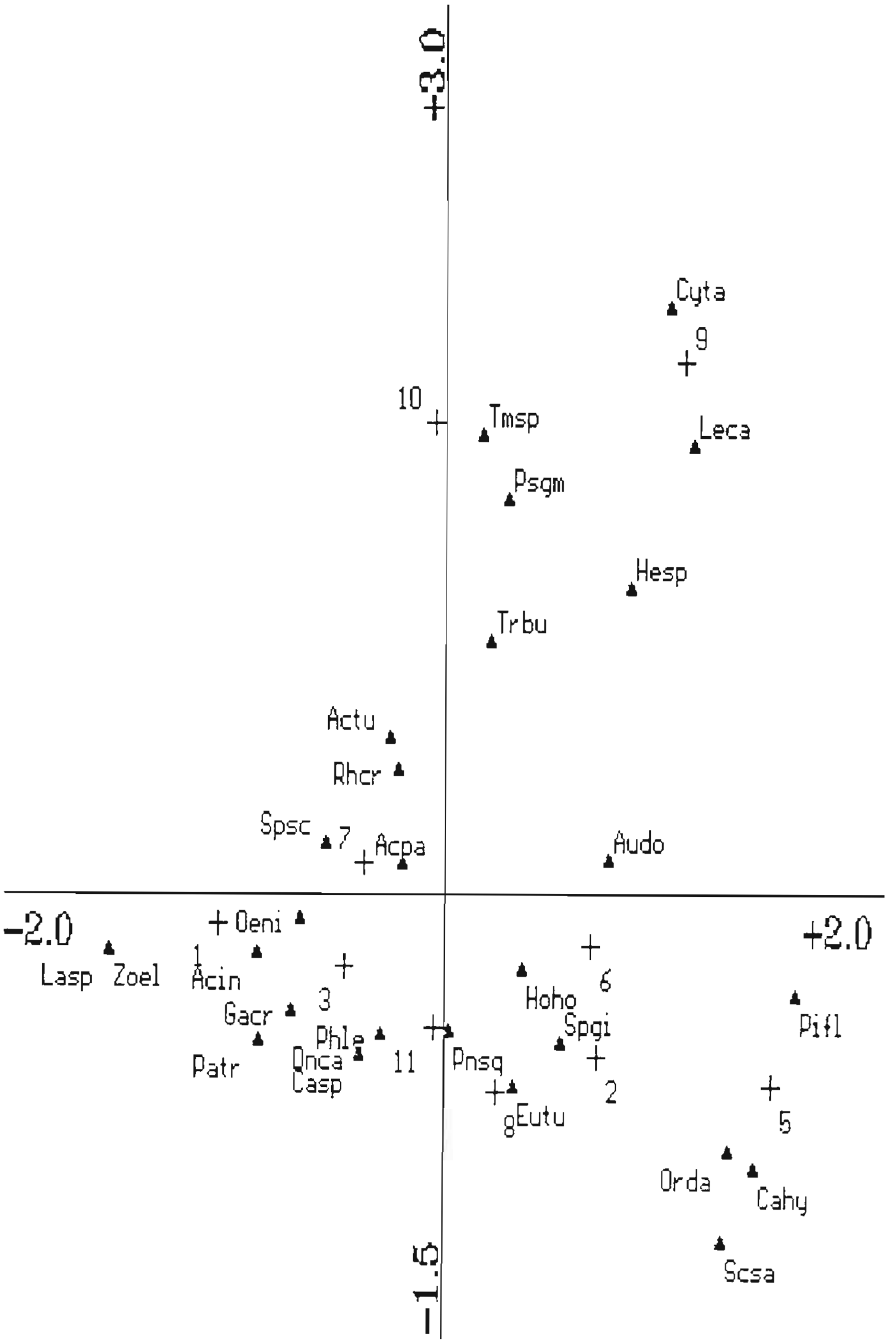

Fig. 4.6. DCA biplot of grasshopper species (▲) and sites (+). Species codes are given in Table 4.5. The first Axis is horizontal and the second axis is vertical.

4.4.5. Canonical Correspondence Analysis (CCA)

A species-sites-environmental variable triplot (Fig. 4.7) showed grasshopper assemblages were related to certain environmental variables, and indicated how species responded to gradients of environmental variables. Important environmental variables tend to be represented by longer oblique lines than less important environmental variables (Ter Braak, 1986). Accordingly, percent 'shrubbiness' and 'rockiness' appear to be the most important, 'maximum' and 'average' grass heights the next most important, followed by percent 'grassiness' with percent 'bare ground' being the least important environmental variable. The other recorded environmental variables were not significant in determining patterns of grasshopper species assemblages, and hence did not appear on the ordination plot.

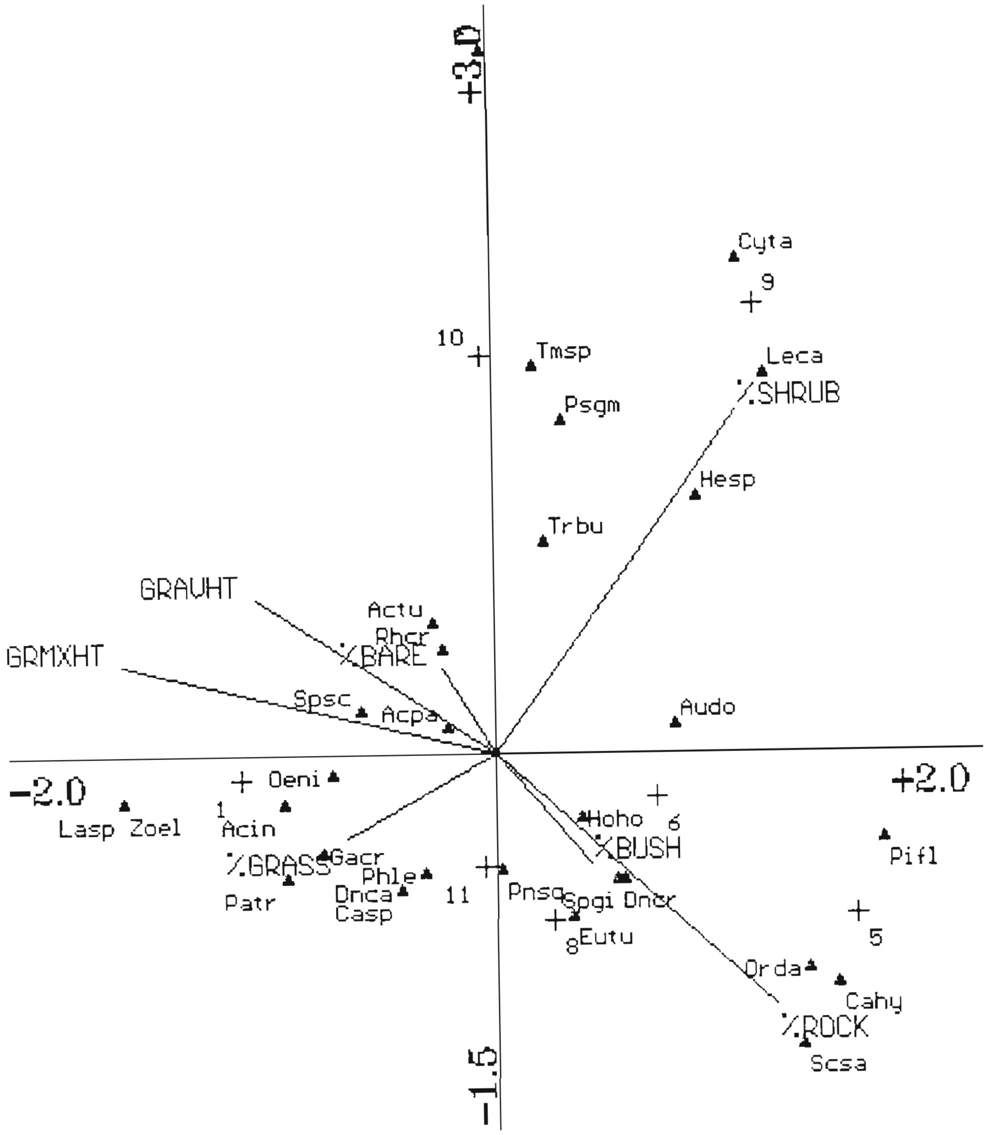

Fig. 4.7. CCA triplot of grasshopper species (▲), sites (+) and environmental variables (oblique lines). Species codes are given in Table 4.5. The first Axis is horizontal and the second axis is vertical.

Clear grasshopper assemblages were at 'grassy' Sites 1 and 3 where *Lamarkiana* sp., *O. nigrofasciatus, A. insubricus, G. crassicolis, Pa. tricolor and P. leprosus* occurred. Another clear grasshopper assemblage was on rock-dominated Sites 2 and 5, characterized by *Pnorisa squalus, Sphodromerus gilli, D. crassipes, Euryphymus tuberculatus, Or. dasycnemis, C. hyalinus* and *Sc. saucia*. *Herterachris* sp., and *Le. callani* were highly correlated to 'shrub'-dominated Site 9 , as was, to some extent, *Cy. tatarica*. In turn, *Ac. turrita, R. crassus* and *S. scabriculus* were highly correlated to 'bare ground', mainly at Site 7.

Some grasshopper species, such as *Pseudogmothela* sp., *Tmetonota* sp., *Pseudoarcyptera* sp. and *T. burtti*, showed no significant correlation to any of the environmental variables, although *A. pallidicornis* showed some association to 'maximum' and 'average' grass heights. Site 9 outside the park is characterized by high shrub dominance, while Sites 2, 5 and 6 inside, and Site 8 outside were rock dominated. Whereas Sites 1, 3, 4 and 7 were grass dominated, Sites 10, 11 and 12 appeared to show no particular association to any one of the environmental variables, indicating that the measured environmental variables occurred in more or less comparable proportions. The respective eigenvalues and cumulative percentage variances according to the Monte Carlo tests of DCA and CCA are given in Table 4.7.

Table 4.7. Weightings of the first two axes of Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA).

	DCA		CCA	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigen value	0.47	0.41	0.46	0.32
Percentage varaince	47	41	46	32
Cumulative percentage variance	47	88	46	78
P-value	0.3		0.8	

4.5. Discussion

4.5.1. Importance of vegetation cover, structure and architecture

The impacts on the vegetation, and the pattern of grazing by the indigenous mammals inside the park is very different from the livestock outside, principally because the herbivorous mammals inside the park were highly diverse, with over 15 species (Grobler, 1979). These have differential food selection and grazing behaviours compared to the sheep, goats and cattle outside the park. These domestic animals have a comparatively narrow food range, and hence are compelled to exploit a few palatable grass species, leaving the unpalatable grasses and shrubs behind (Botha et al., 1983; Norman et al., 2000; Dahlberg, 2000). Furthermore, the mostly non-aggregating behaviour while grazing by the mammals inside the park in comparison with the high aggregating tendency of livestock outside, leads to differential trampling and defoliation intensities.

Outside the park, the grazing pattern is mainly patch grazing (Lütge et al., 1996). This meant that the shrub cover showed high dominance outside the park compared with inside, and any patch having grass was dominated by *Aristida diffusa* and *A. congesta*, indicators of overgrazing (Rusell et al., 1990). Thus there was a significant change in the vegetation composition and structure inside versus outside the park. Patch grazing results in a change in species composition, and patches may be the foci from which rangeland degradation proceeds (Tainton 1972; Dahlberg, 2000).

The contrasting high shrub cover outside the park suggests a distinct shift in vegetation dominance from herbaceous to woody plant species. This process, termed bush encroachment (Dougill and Trodd, 1999), has been experienced similarly in open savanna worldwide, especially elsewhere in southern Africa (Ringrose et al., 1995; Dahlberg, 2000), Sahelian Africa (Warren and Agnew, 1988), North America and Mexico (Archer, 1990; Norman et al., 2000). Indeed, land degradation studies highlight that for many savannas, the most widespread problem affecting sustainable ecosystem functioning remains invasion by the thorn scrub (Warren and Agnew, 1988; Dougill and Trodd, 1999) resulting in a clearly marked effect on the abundance and species composition of grasshoppers. The number of grasshopper species richness was significantly positively correlated ($r = 0.37$, $P<0.05$) with gradients of grass species richness inside the park (Table 4.6). Similarly, Otte (1976) found significant correlation between the numbers of plant and grasshopper species in several North and South American grasslands.

The grass maximum and average heights were significantly higher outside the park, mainly due to tall *Aristida* species which dominated the patches, and hence were recorded many times compared to the inside sites, which were a mixed stand of short grasses such as *Cynodon dactylon*.

Increased intensity of grazing progressively reduces the amount of vegetation available for consumption by grasshoppers due to heavy defoliation (Holmes et al., 1979; Maliha et al., 2000), while trampling brings about associated modifications in nutrient status, soil structure, shelter and microclimate (Abensperg-Traun et al., 1996). Although no significant differences were found in terms of grasshopper species richness inside versus outside the park, there were significant differences in total abundance. This suggests that grasshoppers respond to changes in their habitats first by showing a decrease in abundance and then by extirpation of species (Rivers-Moore and Samways, 1996). However, there is a complex interplay of factors, with topography being one (Samways, 1990; Smith et al., 2000; Wachter et al., 1998), which means that there is great variation in grasshopper species richness and abundance within the park and among sites outside. Such variation would initially mask inside/outside comparisons unless there were dramatic differences.

4.5.2. Significance of the park boundary fence

Comparison of the six sites inside the park showed a significant variation among the sites in terms of species richness but not of abundance. This suggests that a more heterogenous habitat supports a more diverse array of species with varied food and microclimate preferences (Mulkern, 1967; Skinner, 2000; Beckerman, 2000). Site 1, being only 50 m from the park boundary, had higher grasshopper species richness compared to Site 4, which was 2 km from the boundary and near a megaherbivore watering point (Table 4.4). Most grasshopper species avoid sites that are heavily grazed and trampled, and where there is less food (Holmes et al., 1979; Dukas and Bernays, 2000), minimal shelter from natural enemies, and high physical disturbance from hooves (Roux and Opperman, 1986).

The six sites outside the park did not show significant differences in species richness, suggesting greater homogeneity of environmental factors. However, the variation in grasshopper abundance among the sites was suggestive of the differential trampling and grazing impacts of the herbivores among the sites. Site 7, being adjacent to the boundary fence, was heavily grazed and trampled by the livestock, which follow the fence trying to find access to the increased grass cover inside the park. Site 10, outside the park, being a watering point, was very heavily grazed and intensively trampled. As a result, it had the lowest grasshopper species richness and abundance, although species richness was not significantly different from the other sites. This impact around the watering point outside the park was higher than that around the watering point inside. This was because the livestock outside the park tend to regularly aggregate around watering points, rarely moving far away from water. Also, the small shade trees around the water provide shade from the intense Karoo sunshine (Butler, 2000).

Livestock impacts are particularly severe during summer when the animals seek shelter from the heat (Abensperg-Traun et al., 1996; Butler 2000). The hot and sunny conditions that are suitable for maximum grasshopper dispersal and other activities coincide with a high livestock aggregation and associated overgrazing and heavy trampling. Grasshoppers appear to be compelled to abandon these sites, as part of their ecological strategy (Kemp et al., 1990) and move to more suitable habitats with better conditions for survival (Lockwood, 1993). In contrast, the sites near the watering point inside the park were not heavily grazed and trampled because the indigenous game animals visit these points very briefly then go away. Also, game animals do not congregate near watering points as there are no shade trees and also as there is increased disturbance from tourists.

4.5.3. Dominance and biotope preferences of certain species

The higher dominance values for the sites inside the park are directly related to the increased abundance of grasshoppers, which, in turn, are related to the increased habitat heterogeneity inside the park compared to most of the heavily defoliated and trampled sites outside the park.

The occurrence of *O. nigrofasciatus* and *A. insubricus* in large numbers inside the park, and dominance of *D. crassipes* outside, reflected the microclimatic conditions of the sites, and the differential food preferences of the different species. *O. nigrofasciatus* and *A. insubricus*, being in the Oedipodinae, are more generalized foragers (Jepson-Innes and Bock, 1989) hence exploiting the more diverse vegetation inside the park. Although they were not as abundant as *D. crassipes*, they were still the next abundant species outside the park, indicating their wider habitat preference, whether for grasses inside the park or a shrubland outside. These oedipodines occurred in very high numbers on *C. dactylon*-dominated patches, where they benefitted from short grass with low canopy cover (which these species seemed to prefer (Gandar, 1982)). In contrast, *D. crassipes* occurred in abundance on rocky and tall-grass (*Aristida* spp.) sites with a relatively high canopy cover. Such sites were mostly outside the park.

The two species that occurred only outside the park, *Sphingonotus scabriculus* and *Pseudogmothela* sp. (Table 4.5) were both rare. Only two individuals of *S. scabriculus* were sampled, and only at Site 7. This site, being adjacent to the boundary fence, was heavily grazed and trampled because the fence directs the livestock outside the park along the edge (Rivers-Moore and Samways, 1996). This species could, then, have been attracted to this site characterized by low vegetation cover and high proportion of bare ground. It was closely associated with the assemblage of those species that preferred bare ground, as clearly shown in the ordination plot (Fig. 4.7). *Pseudogmothela* sp. showed no strong correlation to any one of the measured environmental variables. However, it was comparatively closer to 'shrub' on the ordination plot than the rest of the environmental variables. Shrub cover was significantly higher outside the park than inside (Table 4.3), and this comparatively homogenous shrub stand outside the park appears to have offered *Pseudogmothela* sp. an optimal escape space owing to the background resembling its cryptic colouration (Quinn and Walgenbach, 1990; Kisbenedek, 1995; Capinera et al., 1997; Dukas and Bernays, 2000).

Grasshoppers could be attracted to a habitat patch by factors such as greater cover, rather than food availability (Gandar, 1983; Bock et al., 1992). For example, the abundance and high incidence of *G. crassicolis* and *O. dasycnemis* on tall and green grasses inside the park and the abundance and incidence of *L. callani* and *Heterachris* sp. on shrub-dominated patches appears to be due mainly to adaptive resemblance to their background than use of these habitats as food (Fogden and Fogden, 1974). Gandar (1982) reported a similar situation, particularly for *O. dasycnemis*. Preferences among grasshopper species may also be linked to enemy-free space (Isely, 1938a, b; Otte and Joern, 1977), optimal thermoregulatory sites (Coxwell and Bock, 1995; Chappel and Whitman, 1990) and oviposition sites (Isely, 1938a).

4.5.4. Significance of elevated grasshopper abundance

Grasshoppers, being predominant herbivores in grassland ecosystems, play crucial roles in ecosystem processes. Notably, they convert plants to nutrient-rich frass, as do sheep. But the insect frass being more finely divided, presumably becomes available to plants faster than sheep dung which takes years to break down in the arid Karoo (Milton and Dean, 1996). Indeed, grasshopper frass is a vehicle for rapidly recycling nutrients (Belovsky, 2000). Elevated grasshopper abundance can accelerate and escalate nutrient turnover, and this may be an essential function for the long-term stability and optimal productivity of the Karoo (Boshoff, 1988), particularly in view of the fact that the Karoo is an arid ecosystem with poor soil organics and nitrogen (Milton et al., 1992; Milton, 1995).

As shown in this study, while grasshopper distribution and abundance pattern is principally governed, among other factors, by patch heterogeneity, grasshoppers, in turn, play important roles as regulators of ecosystem processes and as engineers creating landscape pattern. Grassshoppers control the flow of critical resources and modify ecosystem structure (Belovsky, 2000), and as such are 'webmasters' in arid ecosystems (Whitford, 2000).

4.6. Conclusion

The indigenous mammals inside the park, in some respects, had similar effects on the grasshopper assemblage as the domestic livestock outside, in terms of intensity of defoliation and trampling. This means that the park boundary does not determine grasshopper assemblages on a simple inside-versus-outside basis.

From restoration point of view, the MZNP plays a crucial role because its diverse mix of plant species provides a range of heterogenous patches. These then potentially provide varied microhabitats for a range of grasshopper species. With increasing bush encroachment, and reduction in cover and/or disappearance of several grass species with intensive livestock grazing on open savannas such as the Karoo, it can be seen that invertebrates respond first by occurring in markedly lower populations, followed by species extirpation. This in future may lead to local extinction of some of the species that are currently rare. Hence it can be seen that parks and reserves which are primarily designed to conserve vertebrates and the local flora do also have conservation role for invertebrates such as grasshoppers. Grasshoppers, in turn, play significant role in bird conservation because they constitute significantly as food for birds. This is particularly important in view of the fact that the Karoo is an important endemic bird area (Bibby et al., 1992).

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CHAPTER FIVE

Grasshopper assemblage response to a long-term grazing management experiment in an arid African savanna

This chapter has been submitted for publication. A Few editorial changes have been made to ensure continuity of the thesis.

5.1. Introduction

Grazing has both direct and indirect impacts on plant and animal communities. Direct impacts include selective damage to individual plants through herbivory and trampling. This has consequences for competition between the damaged plant and its neighbors, and changes establishment opportunities for new plant recruits (O'Connor and Pickett, 1992; Abensperg-Traun et al., 1996). Longer-term and less direct impacts follow, through changes in community composition and perturbations of soil and water processes. These, in turn, have consequences for the availability of resources for the sustainability of habitats for other biota (Landsberg et al., 1999; Cury, 1994). Changes in plant composition caused by livestock are likely to have the greatest competitive impact on host-specific herbivores, which are most commonly invertebrates (Crawley, 1983).

Large mammalian herbivores consume about half of plant production. Insects, particularly orthopterans, account for a large part of the rest (Philipson, 1973; Sinclair, 1975; Gandar, 1982). Many studies have shown marked differences in insect communities found in sites that are similar in all respects except their grazing history (Quinn and Walgenbach, 1990; Rivers-Moore and Samways, 1996; Gebeyehu and Samways, 2001).

In an attempt to predict key habitat changes resulting from grazing and responses by different faunal groups, Morton et al. (1996) constructed conceptual models. They summarized the key habitat changes as loss of surface horizon, reduced or more concentrated litter, lower diversity of perennial grasses, higher density of shrubs and greater heterogeneity of productions. Their predictions suggested marked shifts in grasshopper assemblages, with population explosions in a few favored species. It has often been assumed that the invertebrate communities are determined primarily by the vegetation species composition and structure (Otte, 1976; Evans, 1988), and that management practices designed to maintain productivity of vegetation are therefore of equal benefit to invertebrate communities. Very little work has been done to quantify the importance of spatial variation in factors such as vegetation species composition and successional stages of arid African savannas on the invertebrate communities.

Most investigations into the effect of grazing in rangelands have centered on the vegetation (Seymour and Dean, 1999; Moretto and Distel, 1999; O'Connor and Roux, 1995; Fynn and O'Connor, 2000; Humphrey and Patterson, 2000; Kuehl et al., 2001). The extent to which changes in vegetation composition brought about by various grazing management affects resident insect herbivores remains largely unknown. Changes in vegetation are commonly used as indicators of disturbance. However, Rivers-Moore and Samways (1996) and Chambers and Samways (1998) found that arthropod assemblages yielded a much finer classification of sites than grasses. Thus through their rapid response to habitat changes, coupled with their mobility which allows them to choose suitable microhabitat, insects may be more sensitive and/or more rapid indicators of environmental degradation than vegetation (Samways, 1994).

Livestock grazing is one of the major threats to biodiversity in the Karoo, South Africa (Davis and Heywood, 1994). The major decrease in potential stocking rates for domestic livestock (generally > 50% over the last 100 years) (Dean and Macdonald, 1994) is thought to reflect this degradation, and it has been suggested that the threat to biodiversity from overgrazing is most severe on continuously grazed lands (Cowling and Hilton-Taylor, 1994). Management of the grazing enterprise traditionally involves sequential movement of livestock through designated portions of land or camps to optimize harvest of digestible nutrients. Although it has long been suggested that rotational grazing and seasonal grazing are likely to produce the most satisfactory results in maintaining characteristic grassland and enhancing its diversity (Morris, 1967), the effects of these on the fauna compared with intensive grazing are not known.

Over the last 45 years, the Grootfontein College of Agriculture has been running field experiments to monitor long-term changes in vegetation on land which has been subjected to various grazing treatments including seasonal, rotational and continuous grazing, and continuous resting. Although the result of this experiment with respect to vegetation shifts and land degradation has been published (Milton and Dean, 1999), the response of invertebrate herbivores has never been assessed. This study, therefore, investigates the response of grasshopper assemblage patterns resulting from this long-term grazing management field experiment.

5.2. Sites and methods

5.2.1 Site

A set of grazing trials was established in December 1943 on an experimental field site by the Grootfontein Agricultural Development Institute (31° 22'S, 24° 45' E), Middelberg, Karoo to investigate the long term influence of seasonal, rotational and continuous grazing, as well as continuous resting, on vegetation composition and cover. The area is classified as the veld type Sweet Mixed Karoo according to Acocks (1988). The annual median rainfall is 359 mm, distributed as 15% of the rain falling Spring, 30 % in Summer, 50 % in Autumn and 5 % in Winter. The frost free period lasts for about 180 days from Mid-October to mid-April. The mean January temperature is 20.9°C and the mean July temperature is 7.9°C.

The field was divided in to six separate camps. In camp 1, grazing was in Spring (September-October) on 0.9 ha. It had a moderate mixture of grasses, *Aristida disticha*, *Digitaria erianthra* and *Themeda triandra,* as well as Karoobushes, *Chrisocoma ciliata* and *Dimorphotheca cuneata.* Over a period of 10 years of monitoring, the grazing capacity stayed close to the norm applicable to the area. In camp 2, grazing was in Summer (November-February) on 1.8 ha. Dominant vegetation was Karoobushes *Dimorphotheca cuneata* and *Chrisocoma ciliata.* In camp 3, grazing took place in Autumn (March-April) on 0.9 ha. It was a mixture of grasses, *A. disticha*, *D. erianthra* and *Sporobolus fimbriatus*, and Karoobushes, *P. incana* and *C. ciliata.* Over a period of 10 years of monitoring, the grazing capacity stayed close to the norm applicable to the area. In camp 4, grazing was in Winter (May-August) on 1.8 ha. The dominant vegetation in this camp were late developmental stage grasses including *Themeda triandra*, *Sporobolus fimbriatus*, *Digitaria erianthra* and *Cymbopogon plurinodis,* although the mid-developmental stage grass *Aristida diffusa* and some palatable Karoobushes, mainly *C. ciliata,* also occurred. The grazing capacity stayed close to the norm applicable to the geographical area, over 10 years of monitoring. Camp 5 was a continuously-rested camp with an area of 0.9 ha. It was mainly dominated by the palatable and late developmental grass, *D. erianthra* and palatable Karoobushes, mainly *Pentzia incana.* Camp 6 was a continuously-grazed camp of 10 ha, and dominated by the early developmental stage grass, *A. congesta* dense stand of tall shrubs, particularly *Diospyros austro-africana*, *Diospyros lycioides*, *Rhus undulata*, *R. erosa* and *Tarchonanthus camphoratus*. The grazing capacity of this camp was much lower than the surrounding geographical area as a result of dominance of tall shrubs and absence of grasses. Except on the rested camp, four adult Merino sheep were allowed to graze on the other camps for the duration of the season in each camp.

The rotationally grazed experimental site was 3 km from the seasonal grazing sites, and began in 1989 on a total area of 200 ha, divided in to 11 camps. The size of the camps was variable, with four having 13 ha each, four 14 ha each and the remaining three 31 ha each. Thirty-six Merino sheep and six cattle grazed in each camp for 14 days on rotation except on camps with 31 ha each, where the animals were allowed to graze for 31 days to ensure uniform grazing intensity in each camp. In both the seasonal and rotational experiments, animals were replaced every year to ensure uniformity in the ages of the grazers.

5.2.2. Sampling methods

5.2.2.1. Grasshoppers

Extensive preliminary sampling of grasshoppers was done using a sweep net over one year prior to the quantitative sampling. Identification of the resident grasshopper species was done from a voucher collection. In addition, intensive familiarization was undertaken on the jizz of each species in the field so that they were recognizable in the field with no or minimal error. Sampling of grasshoppers was then done visually, by making transect walks and counting them as they flushed. This was supplemented with sweep netting to determine individuals that were still unfamiliar. A transect consisted of 100m long and 5 m wide replicated 6 times to make up a sampling unit. This method of visual recording was found in previous studies to be the most accurate and efficient means of documenting grasshopper species and abundances in the rugged African terrain (Samways, 1990; Armstrong and van Hensbergen, 1999; Chambers and Samways, 1998; Gebeyehu and Samways, 2001). Visual sampling has also been shown to be effective elsewhere (Kemp and Dennis, 1993; Kemp et al., 1989). Close-focus binoculars (Sigma-armada series 10 × 23 wp compact) were an essential recognition aid. Only adult individuals were counted. Sampling was done from February-April 2000 on still and sunny days between 11h00 and 15h00.

5.2.2.2. Vegetation

The vegetation at each site was characterized by estimating percent basal cover for each plant species with 20 randomly placed 2 m^2 quadrats (Daubenmire, 1965) along the lines of the transects where grasshoppers were sampled. Each quadrat was subdivided in to twenty units of 10 cm^2, and the relative proportion of grass, shrubs, rock and bare ground were estimated. Percent greenness of the grasses was estimated by using a 0-100 % scale , where 0 %= not green; 25 %= slightly green; 50 %= moderately green; 75 %= green, and 100 % = very green. Cragginess of the sites was estimated using a 0-4 scale, where 0= smooth; 1= slightly craggy; 2= moderately craggy; 3= craggy, and 4= very craggy. Vegetation density was estimated using a 0-5 scale where 0= bare; 1= very sparse vegetation; 2= sparse; 3= moderate; 4= dense, and 5= very dense vegetation. Soil temperature at a depth of 10 cm was measured in each quadrat using a soil thermometer. Average height of grasses was estimated by taking 40 random points in a transect and the tallest inflorescence was taken to give the maximum grass height.

Both univariate and multivariate statistics were used in data analyses. Application of

Canonical Correspondence Analysis (CCA) revealed that there was a situation of multi-collinearity between maximum and average grass height. Multi-collinearity is a problem that often arises when explanatory variables are highly correlated in the sample (ter Braak, 1986; ter Braak and Looman, 1995). As recommended by ter Braak (1986) one of the variables (maximum grass height) was removed from the analyses, and was not included in the multivariate ordination as the species-environment correlations decreased only slightly when CCA was run after its removal.

Detrended Correspondence Analyses (DCA) was used in preference over Correspondence Analysis (CA) to avoid the arch effect, as recommended by ter Braak (1986). The arch effect is a mathematical artifact corresponding to no real structure in the data, but a situation where the second axis shows a systematic, often quadratic relation with the first axis. This problem was remedied by detrending at the level of second order polynomials, the order indicating the number of axes to be used in the ordination plane (Hill and Gauch, 1980). DCA, as an ordination technique, operates on a site and species data matrix and represents it on two-dimensional plane (ter Braak and Smilauer, 1998). It uses a site-by-species scores data matrix, and summarizes it such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. Conversely, from a species-by-site matrix DCA ordinates the data such that the closer two species are to one another on the ordination plane, the greater the likelihood that they will occur at the same or similar sites, and vise-versa. CCA was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the biplot, and is therefore a measure of how much the species distribution differ along that environmental variable. Important environmental variables therefore tend to be represented by longer arrows than less important environmental variables (ter Braak, 1986; ter Braak and Looman, 1995). The computer programs CANOCO version 4 and CANODRAW version 3.1. (ter Braak and Smilauer, 1998) were used.

5. 3. Results

5.3.1. Seasonal grazing, grasshoppers and environmental variables

The grasshopper species sampled are listed in Table 5.1. There was no significant difference in grasshopper species richness among sites with seasonal grazing treatments, although spring grazing had the highest species richness, and autumn grazing the lowest (Table 5.2). Similarly, there was no significant difference in grasshopper abundance between sites under seasonal grazing although summer-grazed sites had the highest abundance and autumn-grazed the lowest (Table 5.2). While some of the measured environmental variables were significantly different between seasonally grazed sites, others were not (Table 5.3).

Table 5.1. Grasshopper species recorded during this study. Species codes are those used in the multivariate analyses.

Family	Subfamily	Species	Code
Pamphagidae	Porthetinae	*Hoplolopha horrida* (Burmiester, 1838)	Hoho
		Lamarkiana sp.	Lasp
Pyrgomorphidae		*Zonocerus elegans* (Thunberg, 1815)	Zoel
Acrididae	Calliptaminae	*Sphodromerus gilli* (Uvarov, 1929)	Spgi
		Acorypha pallidicornis (Stål, 1876)	Acpa
	Euryphyminae	*Rhachitopis crassus* (Walker, 1870)	Rhcr
		Calliptamulus hyalinus Uvarov, 1922	Cahy
		Calliptamicus sp.	Casp
	Cyrtacanthacridinae	*Cyrtacanthacris tatarica* (Linnaeus, 1758)	Cyta
	Acridinae	*Acrida turrita* (Linnaeus, 1758)	Actu
		Truxalis burtti Dirsh, 1951	Trbu
		Tmetonota sp.	Tmsp
		Gastrimargus crassicolis Saussure, 1888	Gacr
		Orthochtha dasycnemis (Gerstaecker, 1869)	Orda
	Oedipodinae	*Locustana pardalina* (Walker, 1870)	Lopa
		Oedaleus nigrofasciatus (De Geer, 1773)	Oeni
		Acrotylus insubricus (Scopoli, 1786)	Acin
		Sphingonotus scabriculcus (Stål, 1876)	Spsc
		Picnodictya flavipes (Miller, 1932)	Pifl
	Gomphocerinae	*Pseudogmothela* sp.	Psgm
		Dnopherula crassipes (Uvarov, 1921)	Dncr
		Pnorisa squalus Stål, 1861	Pnsq
		Pseudoarcyptera sp.	Psar

Table 5.2. ANOVA of mean grasshopper species richness, abundance and measured environmental variables at sites grazed at different times of the year. Means followed by the same letter in a row are not significantly different at the 5 % level of significance. Mean separation according to Tukey's family error test.

Variable	Summer-grazed	Winter-grazed	Spring-grazed	Autumn-grazed	*F*	*P*
No. grasshopper species	4.34	5.00	6.00	3.34	0.53	>0.05
No. grasshopper individuals	34.34	25.67	29.00	9.67	0.58	>0.05
No. grass species	0.33b	3.00a	2.00a	2.67a	16.25	<0.01
Grass (%)	0.90b	71.67a	41.67a	65.00a	15.90	<0.001
Shrub (%)	43.34a	1.66b	15.00b	3.34b	13.97	<0.05
Rock (%)	55.00a	26.67b	33.33b	31.67b	2.59	<0.05
Bare (%)	1.67	1.67	23.33	1.67	3.25	>0.05
Avg. grass height (cm)	0.05b	86.65a	85.00a	85.66a	295.70	<0.001
Max. grass height (cm)	0.04b	116.67a	103.33a	111.66a	296.24	<0.001
Greenness of grass (%)	16.67b	91.65a	66.62a	66.67a	8.14	<0.01
Cragginess (scale)	3.67	2.33	1.67	2.34	2.53	>0.05
Veg. density (scale)	2.00b	4.67a	3.66ab	4.68a	4.75	<0.05
Soil temperature (°C)	41.16a	33.34b	31.33b	31.83b	75.50	<0.001

Table 5.3. ANOVA of mean grasshopper species richness and abundance and measured environmental variables relative to grazing management regimes. Means followed by the same letter in a row are not significantly different at the 5 % level of significance. Mean separation according to Tukey's family error test.

Variable	Continuously-grazed	Seasonally-grazed	Rotationally-grazed	Continuously-rested	*F*	*P*
No. grasshopper species	4.0b	5.50b	14.00a	6.00b	64.73	<0.001
No. grasshopper individuals	1.38c	1.36c	2.21a	1.62b	358.26	<0.0001
No. grass species	0.03c	1..91b	1.5b	3.00a	4.37	<0.05
Grass (%)	0.05b	44.58a	42.33a	50.00a	2.57	<0.05
Shrub (%)	52.50a	15.83b	20.10b	7.50b	5.09	<0.05
Rock (%)	47.50	36.67	12.83	42.50	3.67	>0.05
Bare (%)	2.50	7.08	24.75	0.02	2.44	>0.05
Avg. grass height (cm)	0.12b	64.33ab	51.50ab	95.00a	4.43	<0.05
Max. grass height (cm)	0.23b	82.92ab	74.88ab	135.00a	5.12	<0.05
Greenness of grass (%)	0.05b	60.42a	52.50a	75.00a	5.85	<0.05
Cragginess (scale)	4.00a	2.49a	0.77b	1.01b	6.43	<0.01
Veg. density (scale)	4.50	3.74	2.95	5.00	2.86	>0.05
Soil temperature (°C)	41.25a	34.41a	27.51b	22.75b	16.13	<0.001

5.3.2. Comparison between seasonal grazing, continuous grazing, rotational grazing and continuous resting

5.3.2.1. Grasshoppers and environmental variables

The number of grasshopper species varied significantly between grazing categories, with rotationally-grazed sites having the highest and continuously-grazed sites the lowest species richness. There was also a significant difference between grazing categories in grasshopper abundance with rotationally-grazed sites having the highest and seasonally-grazed sites the lowest (Table 5.3). While some of the measured environmental variables were significantly different between the gazing categories, others did not show significant differences (Table 5.3).

5.3.2.2. Higher grasshopper taxonomic groups and grazing treatments

There was a taxonomic cleavage in the pattern of affinity of grasshoppers in sites under various grazing management regimes, with variation in relative abundances (Table 5.4). While rotationally-grazed sites contained the highest number of taxonomic groups, autumn-grazed sites had the lowest. Pamphagidae and Pyrgomorphidae occurred only in the rotationally-grazed sites. In contrast, Acrididae was represented in all grazing regimes. Calliptaminae, Cyrtacanthacridinae and Gomphocerinae were represented in all the grazing management categories. Oedipodinae occurred in all except autumn-grazed sites. In contrast, Euryphyminae occurred only in spring-grazed, rotationally-grazed and continuously-rested sites. Acridinae were not encountered in summer-grazed, autumn-grazed and continuously-gazed sites. More than a third (37%) of the total number of grasshopper individuals occurred in the rotationally-grazed sites while autumn-grazed sites had the least (less than 5 %) of the total grasshopper abundance.

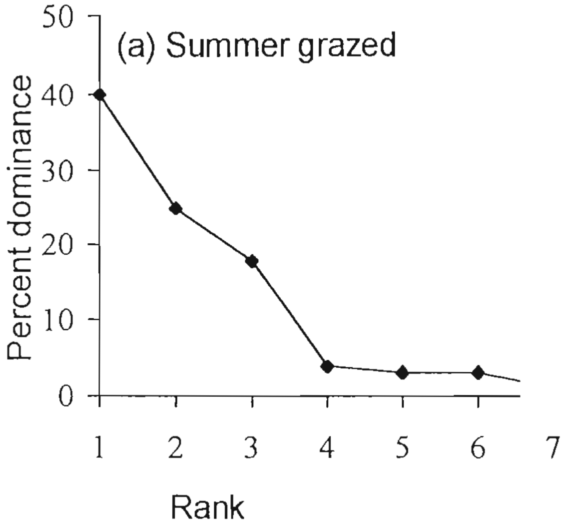
Table 5.4. Relative abundance of higher taxonomic groups of grasshoppers recorded in this study.

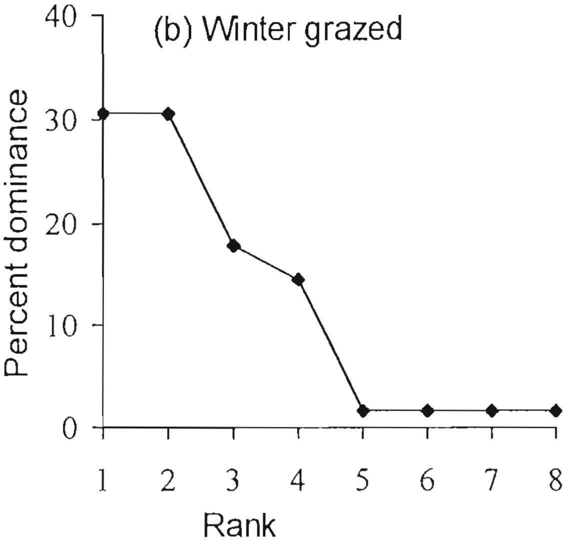
Family	Sub-family	Summer-grazed	Winter-grazed	Autumn-grazed	Spring-grazed	Rotationally-grazed	Contiuously-grazed	Coninuously-rested
Pamphagidae	Porthetinae	-	-	-	-	6	-	-
Pyrgomorphidae		-	-	-	-	6	-	-
Acrididae	Calliptaminae	48	48	20	24	33	104	30
	Euryphyminae	-	-	-	4	96	4	-
	Cyrtacanthatcridiane	12	80	16	28	39	16	4
	Acridinae	-	4	-	24	22	12	-
	Oedipodinae	156	4	-	36	214	8	92
	Gomphoceriane	12	124	52	124	322	136	28
Total		228 (11.4%)	260 (13 %)	88 (4.41 %)	240 (12.0 %)	738 (37 %)	280 (14 %)	160 (8.0%)
Grand Total	1994							

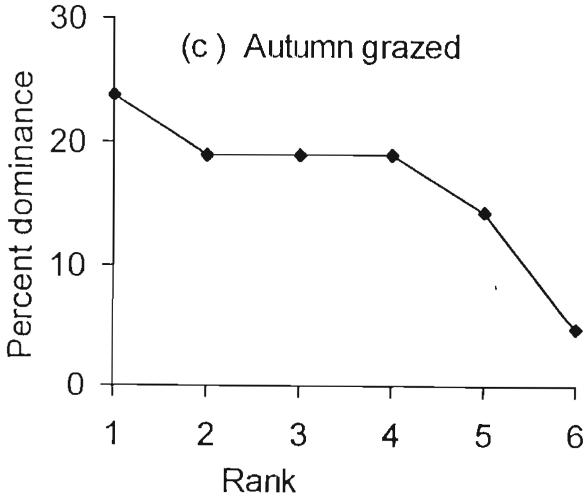
5.3.2.3. Grasshopper dominance patterns and grazing treatments

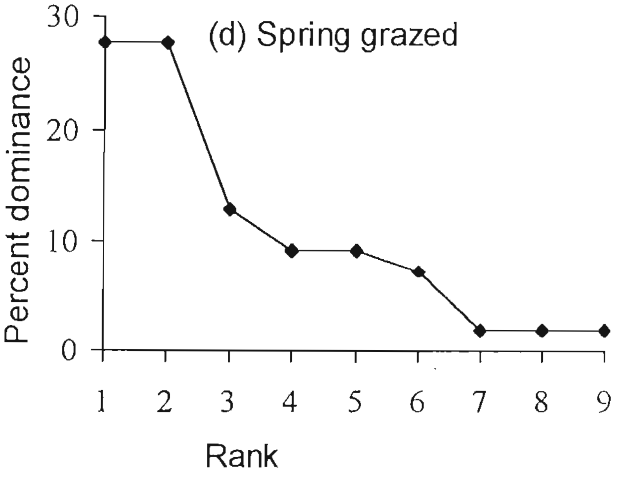
The pattern of dominance varied among different grasshopper species in the various grazing categories. The number of grasshopper species that occurred in each one of the grazing treatments, and the pattern of dominance is shown in Fig. 5.1. Recognizing the difficulties of interpretation arising from diversity indices because parameters such as species richness, evenness and number of individuals and the area sampled are compounded when a single diversity index is used (Ludwig and Reynolds, 1986; Curry, 1994), an alternative approach that avoids these difficulties with indices of diversity is the use of rank-abundance curves in which both species richness and evenness are graphically displayed. The curves are drawn such that the percentage abundance (dominance) is plotted against ranked species sequence (Ludwig and Reynolds, 1986; Curry, 1994). Accordingly, in the summer-grazed sites (Fig. 5.1a), there were seven species with *Picnodictya flavipes* making up 40 %, followed by *Acrotylus insubricus* contributing about 25 %. *Acorypha pallidicornis* contributed 20 %. The rest (*Zonocerus elegans, Cyrtacanthacris tatarica, Dnopherula crassipes* and *Pseudoarcyptera* sp.) had abundances less than 5 % each .

In winter-grazed sites (Fig. 5.1b), out of eight species, two, *C. tatarica* and *Pseudoarcyptera* sp., were co-dominant, each making up 30 % of the total abundance in these sites. They were followed by *Pseudogmothela* sp. and *A. pallidicornis* which contributed between 10-17 % each. The remaining, including *Sphodromerus gilli, Orthochtha dasycnemis, Oedaleus nigrofasciatus* and *Pnorisa squalus*, each contributed under 5 %. There were six species in autumn-grazed sites (Fig. 5.1c), of which, *Pseudoarcyptera* sp. made up over a quarter (28.5 %), while *P. squalus, C. tatarica* and *Aco. pallidicornis* each contributed about 18 % each, followed by *Pseudogmothela* sp.


(a) Summer grazed
Percent dominance
50
40
30
20
10
0
1
2
3
4
5
6
7
Rank


(b) Winter grazed
Percent dominance
40
30
20
10
0
1
2
3
4
5
6
7
8
Rank


(c) Autumn grazed
Percent dominance
30
20
10
0
1
2
3
4
5
6
Rank


(d) Spring grazed
Percent dominance
30
20
10
0
1
2
3
4
5
6
7
8
9
Rank

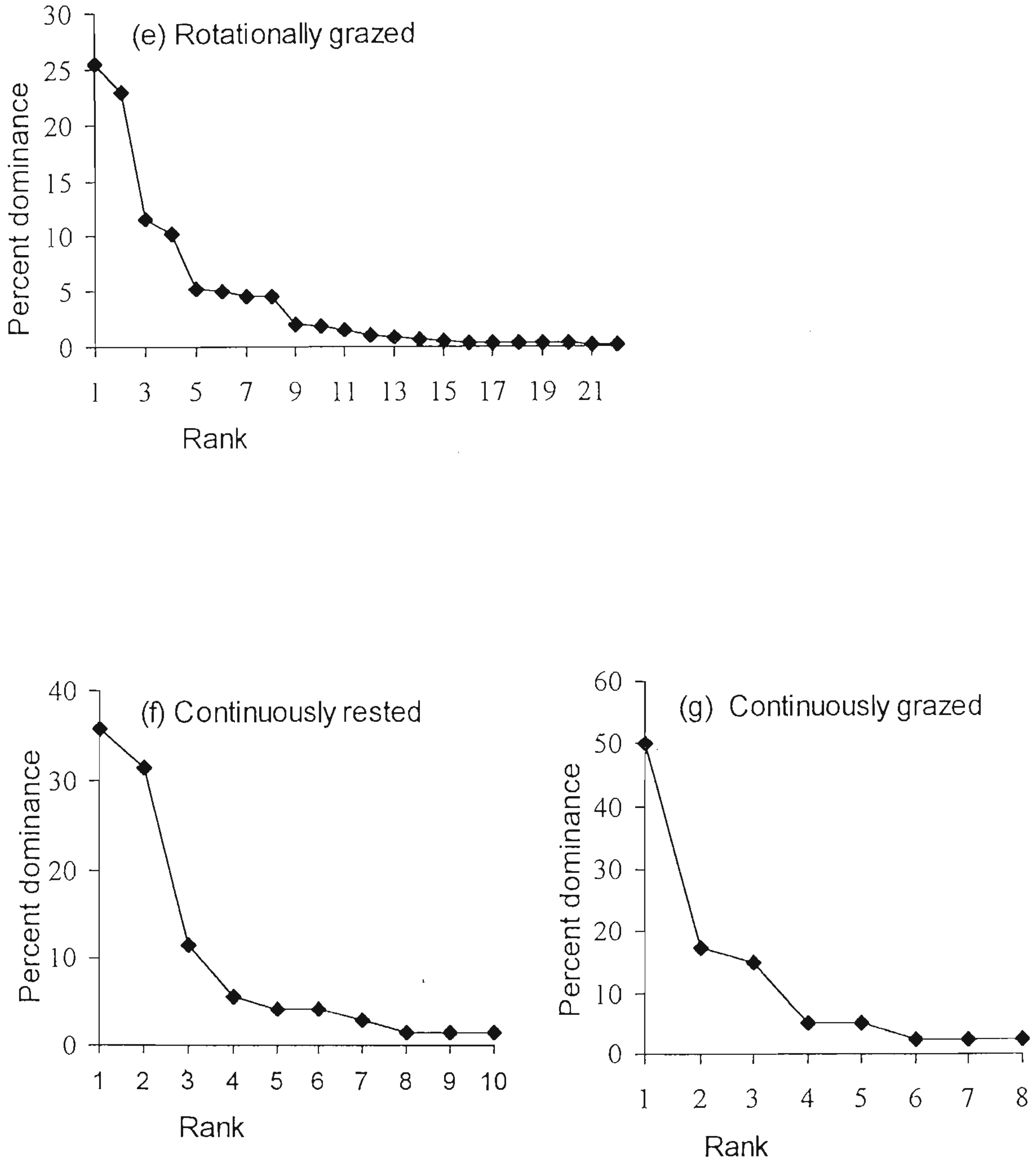


Fig. 5.1 (a-g). Rank-abundance curves of grasshoppers at sites with different grazing regimes.

which constituted 12 %. *S. gilli* was less than 5 %. Spring-grazed sites (Fig. 5.1d) contained nine species, two of which, *Pseudoarcyptera* sp. and *Pseudogmothela* sp. occurred as co-dominants each making up about 28 % to the total abundances in these sites, followed by *C. tatarica* which contributed about 12 %. While *O. nigrofasciatus, Aco. pallidicornis* and *A. insubricus* each shared just over 5 %, and the remaining (*Calliptamulus hyalinus, S. gilli* and *D. crassipes*) contributed only 2 % each. In the rotationally-grazed sites (Fig 5.1e) twenty-two species occurred with only two species making up nearly 50 % of the total abundances, with *O. nigrofasciatus* contributing 25 % and *A. insubricus* 23 % to the abundances in these sites. *Rhachitopis crassus* and *Pseudoarcyptera* sp. made up 10 % and 12 % respectively, with most of the species accounting for less than 2 % each. The least abundant ones were *Truxalis burttii*, *Locusta pardalina*, *Gastrimarghus crassicolis* and *Tmetonota* sp. which were represented by only 1 or 2 individuals.

Continuously-rested sites (Fig. 5.1f) contained ten grasshopper species, with *Pseudogmothela* sp. and *A. pallidicornis* accounting for 36.5 % and 32 % respectively. *Pseudoarcyptera* sp. contributed about 12 %, with the remaining including *C. tatarica, Or. dasycnemis, S. gilli, C. hyalinus, D. crassipes, O. nigrofasciatus* and *A. insubricus* contributing less than 5 % each to the total grasshopper abundance in these sites. Of the eight grasshopper species that occurred in the continuously-grazed sites (Fig. 5.1g) *P. flavipes* was dominant by contributing about 50%, while *Aco. pallidicornis* and *Pseudogmothela* sp. had 18% and 16% of the total abundance respectively. The rest, including *S. gilli, A. insubricus, C. tatarica, O. nigrofasciatus* and *Pseudoarcyptera* sp. contributed between 2-4 % each.

5.3.3. Multivariate analyses

DCA biplot showed three clear groupings of the sampling sites and grasshopper species (Fig. 5.2). While rotationally-grazed sites had a separate assemblage, winter-grazed, spring-grazed, autumn-grazed and continuously rested sites formed close grouping on the ordination. Continuously-grazed sites had a separate assemblage of species. In contrast, summer-grazed sites did not show strong association with any of the other grazing sites. CCA triplot (Fig. 5.3) showed association between environmental variables, sampling sites and grasshopper species. The eigenvalues of the first two axes and the intra-set correlations between the axes and the environmental variables are given in Table 5.5.

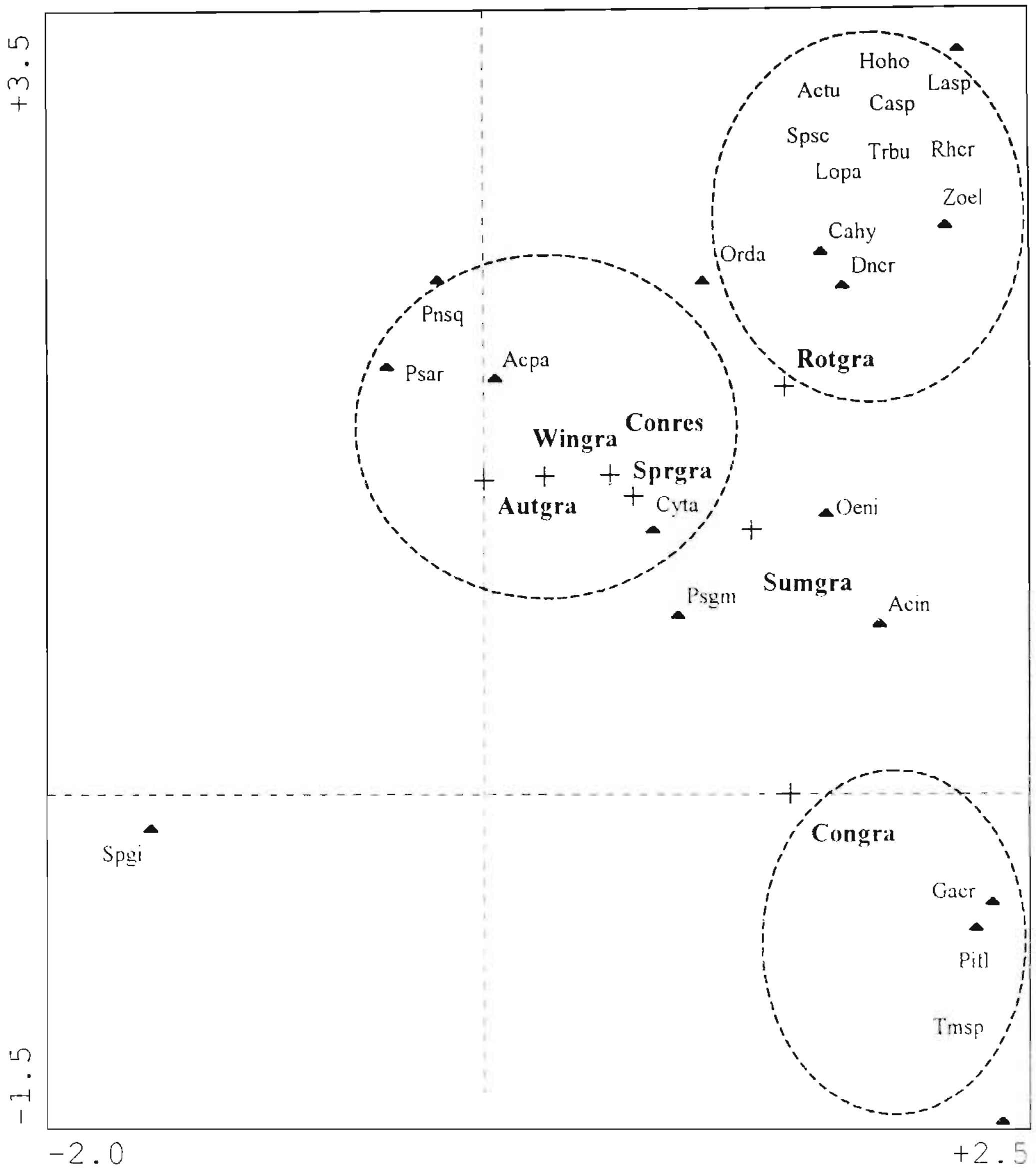


Fig. 5.2. DCA biplot of grasshopper species (▲) and sampling sites (+). Axis 1 is horizontal and Axis 2 is vertical. Species codes as in Table 5.1. Site abbreviations: Sumgra=summer grazed; Wingra= winter grazed; Autgra= autumn grazed; Sprgra= spring grazed; Congra= continuously grazed; Conrest= continuously rested; Rotgra= rotationally grazed. Note that not as many species symbols are visible on the ordination as the species codes because of overlapping of symbols.

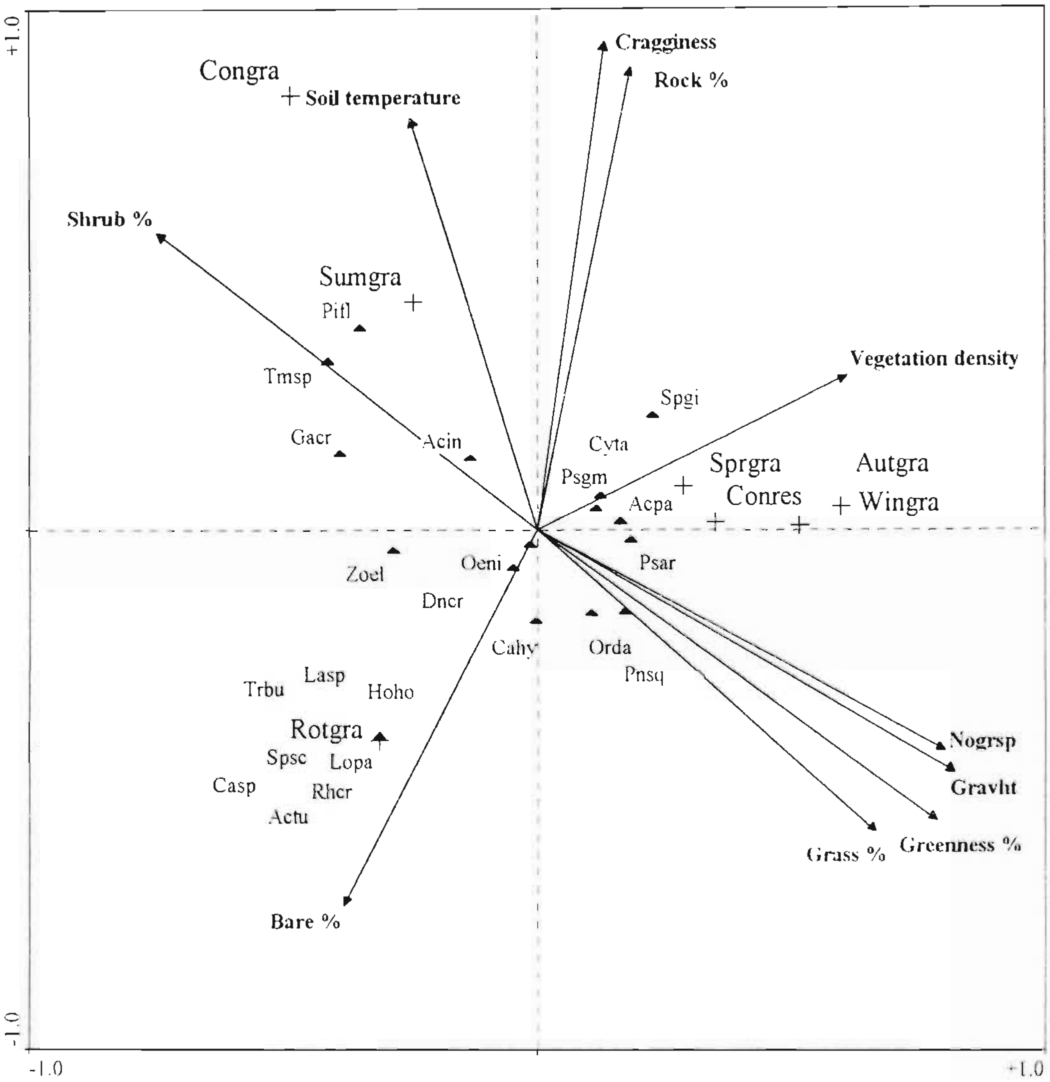


Fig. 5.3. CCA triplot of grasshopper species (▲), sampling sites (+) and environmental variables (arrows). Axis 1 is horizontal and Axis 2 is vertical. Species codes as in Table 5.1. Site abbreviations: Sumgra=summer grazed; Wingra= winter grazed; Autgra= autumn grazed; Sprgra= spring grazed; Congra= continuously grazed; Conrest= continuously rested; Rotgra= rotationally grazed. Gravht=grass average height; Nogrsp=number of grass species. Note that not as many species symbols are visible on the ordination as the species codes because of overlapping of symbols.

Summer-grazed and continuously-grazed sites occurred on the ordination along increasing gradients of shrub percentage, soil temperature, cragginess and rock percentage. Grasshopper species that showed close association with theses sites were *A. insubricus, G. crassicolis, Tmetonota* sp. and *P. flavipes*. In contrast, spring-grazed, autumn-grazed, winter-gazed and continuously-rested sites occurred on the ordination along increasing gradients of vegetation density.These sites were dominated by *Pseudogmothela* sp., *C. tatarica, S. gilli* and *Aco. pallidicornis*. *Pseudoarcyptera* sp. *Or. dasycnemis* and *Pn. squalus* occurred along increasing gradients of grass percentage, percent greenness, grass average height and number of grass species.

Rotationally-grazed sites occurred along increasing gradient of percent bare ground. Species that occurred in these sites were *O. nigrofasciatus, Z. elegans, D. crassipes, T. burtti, Lamarkiana* sp., *H. horrida, S. scabriculus, L. pardalina, Calliptamulus* sp., *R. crassus* and *Acr. turrita*. Although rotationally-grazed sites had bare ground as an explanatory variable for the grasshopper species assemblages, species such as *O. nigrofasciatus, Z. elegans* and *D. crassipes* occurred toward the base of the arrow, indicating that they most likely occurred in patches having bare ground, yet with a significant vegetation cover. Those grasshopper species that were at the tip of the arrow were more likely to occur on bare ground with some vegetation cover. Summer-grazed and continuously-grazed sites were characterized by high percentages of shrub and rock cover, high values of soil temperature and cragginess. *A. insubricus* occurred at the base of the arrows, indicating that it preferred patches characterized by lower to moderate values of these environmental variables, while *P. flavipes* occurred at sites with higher levels of these environmental variables, as is also clearly shown on the rank-abundance curves (Fig.5.1a, g).

Table 5.5. Summary of CCA and DCA in terms of variance accounted for by the first two axes, and intra-set correlation between each of the environmental variables and CCA axes.

	CCA		DCA	
Variable	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.32	0.21	0.53	0.21
Cumulative percentage variance of species data	41.9	70.1	56.4	74.5
Cumulative percentage variance of species-environment relation	42	70.4		
Species-environment correlations	0.81	0.76		
Grass	-0.86	0.76		
Shrub	0.88	-0.37		
Rock	0.68	0.65		
Bare	-0.42	-0.73		
Number of grass species	-0.77	0.5		
Grass average height	-0.82	0.48		
Greenness of grass	-0.86	0.43		
Cragginess	0.71	0.63		
Vegetation density	-0.09	0.66		
Soil temperature	0.83	0.22		

The cluster analysis of sites resulting from the Bray-Curtis similarity index revealed a more refined grouping of the sampling sites (Fig.5.4). Spring-grazed and winter-grazed sites had the highest similarity index of about 65 %, followed by a 50 % similarity index of continuously-rested sites to spring and winter-grazed sites. Summer-grazed and continuously-grazed sites showed a similarity index of about 47 %. Rotationally-grazed sites had the least similarity to the rest of the sites under various grazing treatments.

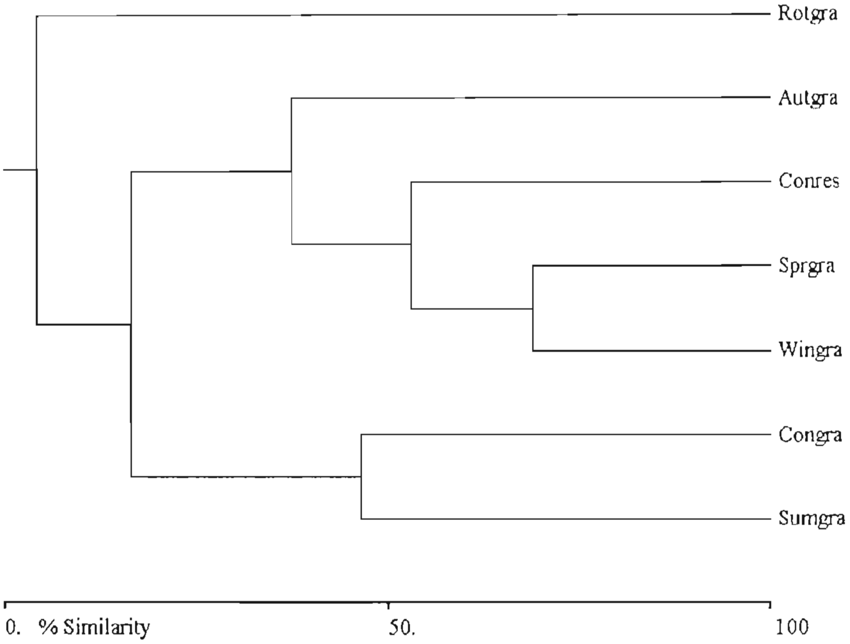


Fig.5.4. Dendrogram resulting from clustering of the sampling sites using Bray-Curtis similarity index on a square-root transformed species data. Site abbreviations as in Fig. 5.2.

Hill's indices of diversity and evenness (Table 5.6) showed that rotationally-grazed sites had the highest index of N1, and the second highest index of N2, but the lowest index of E. In contrast, autumn-grazed sites showed the highest index of N2 and E. The pattern shown by these diversity and evenness indices is very similar to the dominance patterns shown by the rank-abundance curves, indicating that the higher the evenness index, the lower the dominance pattern, and vice-versa.

Table 5.6. Hill's diveristy and evenness indices at sites with different grazing management regimes.

Site	N0	N1	N2	E
Summer-grazed	7	4.43	3.79	0.63
Winter-grazed	8	4.85	4.37	0.6
Spring-grazed	9	6.24	5.57	0.69
Autumn-grazed	6	5.54	6.77	0.92
Continuously-grazed	8	4.54	3.42	0.56
Rotationally-grazed	22	9.31	6.61	0.42
Continuously-rested	10	5.46	4.42	0.54

5. 4. Discussion

5.4.1. Seasonal grazing, vegetation and grasshoppers

Grazing by cattle removed some palatable grasses and forbs, while trampling affected soil structure and vegetation composition (Taboda and Lavado, 1993; Cole, 1995). Trampling of soil and changes in vegetation composition and biomass have dramatic effects on resident fauna (Maliha et al., 2000). Within the seasonal grazing treatments alone, the sites were different in vegetation composition and cover, which influenced the grasshopper assemblage patterns. Aside from the frequency and severity of defoliation, which have direct impact on vegetation cover and composition, timing of grazing was also crucial. The summer-grazed sites had the lowest number and percentage cover of grasses, and the highest percentage cover of shrubs. Rockiness and cragginess was significantly higher in these sites.

Summer is the time of the year when perennial grasses have active growth after cold-induced dormancy during the winter, and the soil receives significant moisture from the rain. Defoliation and trampling by domestic grazers has the most impact on grasses, particularly perennials, at this time of the year, as it reduces their competitive abilities relative to less palatable grasses and shrubs. In a study to assess the long-term (1949-71) influence of various grazing management systems on botanical composition in the Karoo, O'Connor and Roux (1995) found that perennial grasses were almost eliminated by grazing during the summer. This led to shifts from dominance by grassy plants to that by woody plants, and development of woodland (Archer, 1995, 1996; Good et al., 1993). The recruitment success of one plant species relative to another is very frequently associated with differential selective grazing. Although studies of competition often focus on adult plants, the ability of species to colonize and competitively exclude others from gaps may be of even greater importance in grazed systems (O'Connor, 1996; Crawley, 1983; Bullock, 1996).

Perennial grasses are key players in stabilizing soils (O'Connor, 1996). Their absence or minimal cover on the summer-grazed sites in our study led to erosion of shallow top soil, exposing the underlying rocks, with the percentage rock cover in the summer-grazed sites being markedly higher than in the rest of the seasonal grazing treatments. Consequently, these sites were more craggy, had higher soil temperature and high shrub percentage

(Table 5.2; Fig. 5.3). Such impacts on soil lead to changed water and/or nutrient availability favoring deeper-rooted shrubs in the long term (O'Connor, 1996; Dougill and Trodd, 1999; Manzano and Navar, 2000). In contrast, the winter-grazed sites were characterized by higher grass cover relative to shrubs, higher number of grass species (Table 5.2) and dominance by perennial grasses. The soil was less craggy and soil temperature was significantly lower due to insulation by the higher vegetation cover. This contrast with summer-grazed sites was mainly due to most perennial grasses going into dormancy during the cold winter, which enabled them to avoid or reduce impacts of defoliation by the grazers on their growing points. In spring, these grasses break their dormancy as temperatures rise and rains commence. Their growth continues as temperature and rainfall increase. Consequently, these sites had more perennial, stabilizing grasses, more litter and are less prone to erosion.

While the differences in vegetation between summer-grazed sites and the rest of the seasonal grazing treatments was much higher than the differences between winter, spring and autumn-grazed sites, there were slight differences in some of the measured environmental variables, which, though not statistically significant could still influence grasshopper assemblage patterns in these sites. Although the one-way ANOVA revealed no statistically significant differences in grasshopper species richness and abundances between the seasonally-grazed sites (Table 5.2), there were marked differences in the composition and pattern of dominance in each of these sites. On summer-grazed sites, *P. flavipes* was dominant, but it did not occur in the other seasonal grazing sites. Its body colour is cryptic against the exposed brown-rocks dominating summer-grazed sites. *A. insubricus* was also abundant at these sites, but rare at the spring-grazed sites. It prefers exposed and sunlit patches (Gandar, 1982; Gebeyehu and Samways, 2001).

As the summer-grazed sites had minimal grass cover, yet a high percentage of unpalatable tall shrubs, they provided these grasshoppers with a habitat suitable for satisfying thermoregulatory requirements of shade to avoid excessive heat loads from the summer sun and the high temperatures of exposed rocks (Chappell, 1983; Chappell and Whitman, 1990). In contrast, the dominant grasshopper species in winter-grazed sites were *C. tatarica* and *Pseudoarcyptera* sp. which have a strong preference for patches dominated by tall grasses (Belovsky and Slade, 1993; Manzano and Navar, 2000). The association of these grasshoppers with sites of high vegetation density and high grass height, and the fact that they were not common on the adjacent summer grazed sites indicated that, aside from their taxonomic preference for grasses as food (Joern, 1979; Gandar, 1982) these habitats offered them oviposition sites, shelter, and perhaps more importantly, escape space from their natural enemies, mainly birds and lizards (Belovsky and Slade, 1993; Vitt et al., 2000).

This study is consistent with patterns found by other workers (Isely, 1938; Fogden and Fogden, 1974) where numbers of phytophagous insect species were highly correlated with a priori estimates of numbers of colours and substrates available as hiding places. *Or. dasycnemis*, a species highly sensitive to disturbance by grazing was recorded only in the winter-grazed sites. This species was reported by Gandar (1979) to have high association with long grasses, while Gebeyehu and Samways (2001) observed that owing to its great sensitivity to disturbance, this species occurred only on the summit of a large mesa, a cattle-ungrazed elevational island amidst intensively grazed flatlands.

Grasshopper composition and dominance patterns at autumn- and spring-grazed sites were different. Firstly, more species were on spring-grazed sites than on autumn-grazed sites (Fig.5.1c,d), although the difference was not statistically significant (Table 5.2). *Pseudoarcyptera* sp. occurred in comparatively equal proportions both in spring- and autumn-grazed sites, but *Pseudogmothela* sp. was dominant only in the autumn-grazed sites. Although both these species are known to be associated with long grasses (Gandar, 1979), *Pseudoarcyptera* sp. prefers closed canopy grasses, while *Pseudogmothela* sp. occurs in more open habitats. Spring-grazed sites have more open patches than autumn-grazed sites, as shown by the preference of *A. insubricus* and *O. nigrofasciatus,* which require both good vegetation cover coupled with sunlit patches. Spring-grazed sites were dominated by annuals, particularly *Ar. congesta,* compared to autumn-grazed sites, which were dominated by perennials.

During spring perennial grasses break their dormancy and shoot. This new growth is selectively grazed by sheep, giving the unpalatable annuals a competitive advantage. As the season progresses annuals benefit the most, leaving open patches where perennials have been grazed short. This resulted in a structurally heterogenous sward, with greater grasshopper species richness in spring- than in autumn- grazed sites (Curry, 1994). In contrast, autumn-grazed sites had a greater proportion of tall perennial grasses, since they were rested over spring and summer. Moreover, 50 % of the annual rain in this area falls in autumn and so contributes to quick regeneration of grazed patches. This concurs with McNaughton's (1985) finding that when grazing is coupled with high rainfall on well established sward, it triggers rapid compensatory growth which leads to higher vegetation density. This mechanism appears to explain why grasshopper species richness was lower on autumn-grazed sites, since the thick and uniformly tall sward excludes grasshopper species such as *A. insubricus* and *O. nigrofasciatus* which require open microhabitats.

5.4.2. Rotational grazing, vegetation and grasshoppers

The other grazing treatments including rotational grazing, continuous grazing and continuous resting were markedly different from the seasonal grazing treatments with respect to their vegetation cover and composition, and their grasshopper assemblage patterns. Rotationally-grazed sites had significantly higher grass species richness and abundance compared to seasonally-grazed sites (Table 5.3). These sites also had the greatest grass species richness, ranging from short palatable species such as *Cynodon dactylon* to long palatable grasses such as *D. erianthra*. Interspersed with these grasses were different forb species along with dwarf shrubs. These vegetation variables, along with patches of bare ground, attracted more grasshopper species than did seasonally-grazed sites. Rotationally-grazed sites maintained more variation in vegetation structure than did either season-long, continually-grazed or continually-rested sites.

In the rotational grazing area, herbivore grazers were present for only 14 days before they were transferred to another camp, giving this area a chance to regenerate. This created a mosaic of vegetation structures. A rotationally grazed site in the long-term enhances seedling recruitment in gaps (Bullock et al., 1994). The cycle of grazing also distributes defoliation over a higher proportion of plants. During the interval between two grazing periods, new tillers proliferate and fill the bare spots created by patch grazing or excessive trampling. Thus a patch that was made bare (Onsager, 2000) during the first cycle of grazing was occupied by new tillers, while patches with vegetation cover were opened by grazing and trampling. Such a successional defoliation of sites means that different areas are defoliated at different times which results in heterogenous structural formations with a characteristic spectrum of plants with varied growth forms, structural attributes and chemical composition (Joern, 1979).

5.4.3. Habitat heterogeneity and grasshoppers

Within a grasshopper assemblage, individual species have different environmental and management requirements. For example, in South Dakota there were marked differences in the patterns of grasshopper assemblages in long-ungrazed grasslands compared with adjacent grasslands managed for grazing by sheep and cattle. Sites within long-ungrazed grasslands supported a high diversity of obligate grass feeders, obligate forb-feeders, and mixed grass- and forb-feeders, in contrast to grazed sites, which were dominated by obligate grass-feeders (Quinn and Walgenbach, 1990). The problem of catering for these different requirements simultaneously, to conserve maximum species richness and diversity can be solved by a system of rotational management (Chambers and Samways, 1998), thus allowing a wider spectrum of grasshoppers species with respect to food and habitat requirements. There can sometimes be a conflict between management of grasslands for plant diversity and management for diversity in other groups such as invertebrates (Van Wieren, 1989; Grant et al., 1996), as it is rarely the case that all management objectives can be realized within the same area at the same time (Van Wieren, 1989; Bakker, 1998).

Invertebrates benefit from greater structural variety resulting from a fine-scale mosaic of different sward heights (Fry and Lonsdale, 1991; Kirby, 1992) as well as increased plant species diversity. The findings here that there is substantially higher grasshopper species richness on rotationally grazed sites accords to this notion. Indeed, rotational management has previously been recommended for grassland butterflies (Morris and Thomas, 1991), Coleoptera (Morris and Rispin, 1988; Rushton et al., 1990), and Hemiptera (Morris and Lakhani, 1979). Rotational management has proved effective in reserves for conserving a broader community of invertebrates compared to seasonal or continuous grazing (Morris, 1989). In this way, grasshoppers of short and tall grasses, early and late successional species, and eurytopic and stenotopic species can find suitable microhabitats. Moreover, the successive stages in a grasshopper's life-cycle that require different niches (Dempster, 1963) are provided with such a management-induced mosaic (Chambers and Samways, 1998).

Where bare ground favours grasshopper pest outbreaks, rotational grazing has been recommended by Onsager (2000) as a means of mitigating the outbreaks by deliberate variation in timing and intensity of grazing events. This comes about by having increased canopy cover rather than bare soil that often results from season-long or continuous grazing. Fielding and Brusven (1993) also found that maintenance and rehabilitation of annual grasslands with perennial grasses and shrubs can contribute to more diverse grasshopper assemblages with lower proportion of pest species. Here, although only two species, *O. nigrofasciatus* and *A. insubricus,* accounted for half the total grasshopper abundance, several rare species such as *Tmetonota* sp., *Z. elegans* and *G. crassicolis* occurred only in rotationally-grazed sites, indicating that even stenotopic species found suitable microhabitats in rotational grazing systems.

5.4.4. Continuous grazing, vegetation and grasshoppers

Continuously grazed sites were dominated by shrubs, which is a consequence of excessive defoliation and trampling. At such sites, the perennial grasses were almost none, although sparsely distributed unpalatable annual grasses were present. These sites were craggy, eroded and bush covered, with little grass. Such vegetation changes destabilize the soil system, leading to soil degradation and an irreversible decline in primary production. Such habitat changes have a major impact on indigenous biota (Landsberg et al., 1999). Here, this was manifested by dominance by only one species, *P. flavipes*, with all other species being rare.

5.4.5. Continuous resting, vegetation and grasshoppers

The continuously-rested sites supported grasshopper species with an affinity for long grasses and high vegetation density e.g. *Or. dasycnemis*. These sites are preferred mostly by grasshopper species that are highly sensitive to disturbance by grazing and/or the associated habitat modification. Generally, continuously rested sites were species poor compared to seasonally grazed and rotationally grazed sites. The dominant grass species in these sites was *D. erianthra* and a few tall shrubs, with associated grass species richness being low. Exclusion from grazing causes a decline in vegetation species richness, with exclusion of the invertebrate herbivores that depend on a wide spectrum of vegetation growth forms, structure and species composition.

5.4.6. Grazing and biodiversity

Grazing by ungulates creates or recreates species-rich grasslands by increasing chances of establishment of seeds from surrounding sources (Gibson et al., 1987). Grant et al. (1996) found that when grazing is systematically controlled, it improves availability of nutrients to plants because of urine and dung, particularly under nutrient-stressed soil conditions, leading to increased floristic diversity on grazed compared with ungrazed areas. Similarly, Bockdam and Gleichman (2000) hypothesized that replacement of the traditional land uses by free-ranging cattle would lead to nutrient redistribution rather than nutrient removal, which in turn, might lead to the emergence of shifting mosaics.

After comparing communally-grazed sites with those protected from grazing in South Africa, Shakelton (2000) found that vegetal species richness was higher on communally-grazed than on protected sites. A similar result was found by Verdú et al. (2000) in Spain where they studied the effects of protection from grazing on the biodiversity in a nature park. These results agree with my finding that grass species richness, heterogeneity and structure increase grasshopper species richness in grazed sites. The Karoo soils being poor in nitrogen and organcis (Milton and Dean, 1996) benefit from grazing due to the dung and urine from domestic livestock when a judicious system of grazing is adopted. Furthermore, frass from grasshoppers enhances nutrient-redistribution, owing to its fast rate of decomposition, thereby releasing the nutrients back to the soil quicker than cattle and sheep dung which takes several years to break down (Milton and Dean, 1996; Belovsky, 2000).

5. 5. Conclusion

This long-term trial provided an opportunity to study the dynamic interaction between grazing systems, vegetation and the grasshopper fauna. The shift from palatable grasses and shrubs to dominance by unpalatable ones in grasslands has important implications in the dynamic function of vegetation. Once unpalatable grasses and shrubs attain a high level of dominance as is the case with the continuously-grazed and summer-grazed sites in this study, it is extremely difficult to reverse the change even if grazing is relaxed or removed, since the soil has become highly degraded. This, in turn, affects resident invertebrate herbivores such as grasshoppers (Sanderson et al., 1995).

In an effort to curb the trend of bush encroachment and to maintain biodiversity, grazing by domestic livestock is considered to be the best and safest way (Shakelton, 2000; Verdù et al., 2000), especially as the alternative of fire releases undesirable gases into the atmosphere (Fishman et al., 1991; Cicerone, 1994; Mano and Meinrat, 1994; Savory and Butterfield, 1999). This is particularly so for most African savannas where free grazing by cattle and sheep is common. Mowing is not feasible as only a small proportion of African savannas is mowable (Scott, 1970), mainly owing to the rugged terrain. Rotational grazing produces the most satisfactory results in maintaining floral and faunal diversity, as shown in this study. Seasonal grazing is a second alternative, but different sites need to be grazed in different seasons, as repeated summer grazing on the same site exterminates palatable perennial grasses.

Rotational grazing is being recommended in African savannas (P. Du Toit unpublished data) and is also recommended to North American land managers (Onsager, 2000; Boyd et al., 2001) due to recent realization that weight gains and general performance of livestock was found to be much better on rotationally-grazed sites than on season long and continuous grazing. Moreover, the mixing of cattle and sheep has been shown to produce efficient utilization of grazing resources than grazing by sheep only or by cattle alone (P. Du Toit unpublished data). Such management practices appear to be a way forward to maintain biodiversity while ensuring livestock productivity.

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CHAPTER SIX

Final comment and conclusions

Although the four chapters are complete studies in their own right, there is some merit in exploring some common threads to highlight significant findings of the study as a whole.

6.1. Topography, grazing pressure and grasshopper conservation

The vertical dimension in the Karoo landscape (Chapters 2 and 3) is significant in terms of grasshopper ecology. The mesas and inselbergs, which are scattered across the Karoo, are more than just physical features of the landscape. They are also islands of floral and faunal biodiversity. Indeed, for some invertebrate species, as indicated by the grasshoppers studied here, the hills are the sole habitats for particular geophilous species. Other functionally-different species also inhabit these hills in addition to the surrounding, low-lying flatlands. One prominent role played by mesas in the Karoo, particularly the larger ones, is that they act as island refugia for grasshoppers that have been virtually extirpated from the flatlands as a result of anthropogenic disturbances (Chapter 2). Thus, the vertical dimension, as well as being critically important habitats for certain species, also plays, in recent times, a second crucial role by moderating the extent of species loss through maintenance of residual populations.

The predominant mechanism by which species are extirpated and ultimately lost from an ecosystem is through habitat loss. Grasshoppers are major indigenous, savanna herbivores that inhabit a range of habitats with varying floral composition and structure. Any major anthropogenic disturbance factor which degrades such an ecosystem, results in significant shifts in vegetal cover and composition which, in turn, is followed by significant changes in the dependent faunal assemblages. Furthermore, the stochasticity in rainfall pattern in the

Karoo magnifies the fragile properties of this arid ecosystem. It was evident from the results in Chapter 2 that grasshopper populations closely track availability of food, which is mainly regulated by rainfall levels in such systems. The fact that the number of grasshopper species remained unchanged despite marked variation in rainfall between the three years, suggests that the grasshopper species in this region are localized residents. High increases in grasshopper individuals during years of good rains, and crashes during dry years, are due to variation in relative survival that is closely linked to food availability, and not due to dispersal or immigration. This is a crucial factor from the point of view of biodiversity conservation. The majority of these resident species are rare with only three or four species making up 80 % of the total abundance.

The brown locust, *Locusta pardalina*, which is known to form swarms and hence considered a pest species, was among the rare species over the entire sampling period in all the sites sampled and reported on in the four Chapters. In fact, personal historical accounts by the landowners in the Karoo, particularly around the Mountain Zebra National Park (MZNP), indicates that the brown locust was last seen in its swarm-forming phase over 30 years ago. Samways (2000) looked critically at the pest status of this species and contended that control efforts should be at the microscale of a farm or group of farms based on site thresholds, and not at the level of the Karoo region as a whole. Indeed, Brown (1988) showed that any single area in the Karoo should not be sprayed more than once in about five years, with about 90 % of spray targets being smaller than 0.25 ha because the spatial nature of the outbreaks is such that potentially habitable vast area is highly varied and inevitably would have variable population levels of the locust. Since insecticide treatment for the brown locust affects non-target species (Stewart, 1998), such treatment of small areas allows rapid recovery of the more vagile grasshopper species from the surrounding untreated areas. However, bushhoppers, many of which are endemic to the Karoo, and thus of important conservation value, take longer to recover because of their low vagility. Indeed in view of the historical account by landowners mentioned above, the suggestion outlined by Samways (2000) should be taken seriously. The sudden and unexplained extinction of the Rocky Mountain grasshopper, *Melanoplus spretus* (Walsh), which had literally blackened the skies of the western United States for decades had migrated in swarms for at least 750 years (Lockwood and DeBrey, 1990). Its demise represents one of the most compelling ecological and entomological events of our time. It has been suggested that small scale intensive anthropogenic alteration of habitats is probably the most frequent cause of extinction in recent history (Lockwood and DeBrey, 1990). A similar situation is not unlikely in the Karoo, with pressure being most pronounced on the already rare non-target species, most of which are endemic to the region.

6.2. Patch heterogeneity and grasshopper conservation

The presence of hills of varying sizes adds to patch-scale heterogeneity, and as such acts as a prominent feature of spatial heterogeneity at the landscape or regional level (Chapter 3). Individual grasshopper species interact with these elements of the landscape on their own measure of scales, with each fine scale interaction producing a pattern that adds up to an aggregate response of the grasshopper fauna to regional heterogeneity. This variability in hill sizes is a desirable attribute of the landscape, particularly in such an arid system, as it creates spatial heterogeneity. Spatial heterogeneity also implies heterogeneity in resource availability, which buffers herbivores against climatic variation (Scoones, 1994). Indeed, spatial heterogeneity caused by large hills such as the Tafelberg mesa (Chapter 2) can even buffer invertebrate herbivores against severe anthropogenic disturbances.

Currently, there is debate between proponents of the 'new' rangeland science that predicates on the non-equilibrium conception of rangeland dynamics, in which pastoralists should adopt an opportunistic strategy allowing animal numbers to fluctuate widely in response to climatic variation (Ellis and Swift, 1988; Behnke and Scoones, 1993; Scoones, 1994). The alternative view advocates a pastoralism which is based on conservative stocking rates (Cowling, 2000). Illius and O'Connor (1999) challenge the non-equilibrium conception of African semi-arid rangeland systems and falsify many of its precepts. They argue that animal numbers are regulated in a density-dependent manner by the limited forage available for use in the dry season. The strength of the forces tending to equilibrium vary spatially and temporally. They diminish during the wet season or years (when water is widely available), and with increasing distance from dry-season range and water points. The presence of dry-season ranges, chiefly in areas along perennial rivers or at artificial water points, enables heavier use of wet-season ranges than if these key resources were absent. A consequence of this is that domestic animal numbers and range production tend to become uncoupled, especially during droughts. This carries the risk of ecological change and reduced productivity. This intensifies further when invertebrate herbivores are extirpated, as seen in the sampling site near the water point outside the MZNP (Chapter 4). Intensive defoliation and trampling, coupled with absence of nutrient turnover, make these sites more prone to ecological damage. There seems to be more empirical, positive evidence presented by the proponents of equilibrium theory than by those proposing a shift of paradigm to a non-equilibrium system in arid rangelands (Cowling, 2000).

Aside from serving as good baseline references for comparing the degree of land degradation and speed of restoration process, protected areas such as the MZNP (Chapter 4), play a crucial role in maintaining typical floral and faunal components of the region. Although the primary aim of the reserve was to maintain a genetically uncontaminated population of the Cape Mountain Zebra, *Equus zebra zebra*, it is clearly also a suitable umbrella habitat for a range invertebrate herbivores, as shown by the elevated grasshopper abundance within the park. However, the fact that there was no variation in the number of grasshopper species between inside and outside the park suggests that the park is not exploited by other grasshoppers other than those generally resident in the area. Furthermore, there appears to be a similarity in the MZNP (Chapter 4) and the summit of Tafelbereg mesa in that they are both a preferred habitat by the highly responsive (to land degradation) species *Orthochtha dasycnemis*. These restored and topographic habitat refugia hold promise as sites that conserve both eurytopic as well as stenotopic species. However, unless the current anthropogenic disturbances outside these refugia are relaxed, grasshopper populations outside the refugia will remain very low, and their role as generators and diffuse distributors of soil nutrients will be very restricted. Additionally, the refugia populations will forever be at risk from severe stochastic events and from genetic bottlenecks.

One practical means of mitigating the undesirable consequences resulting from intense anthropogenic disturbance, especially overgrazing, is the adoption of rotational grazing (Chapter 5). The shift in vegetation cover and composition, as well as the associated response by the grasshopper fauna, clearly demonstrates that overgrazing is a major disturbance factor that leads to land degradation and ecosystem deterioration. The indication given by several studies (Du Toit, 1998 ; Onsager, 2000), as well as here (Chapter 5), is that rotational grazing better ensures viable livestock productivity compared to season-long and continuous grazing, and at the same time maintains ecosystem health. This is encouraging, as this means that there is no conflict between profitable livestock production and conservation of floral and faunal biodiversity. The long-term trial by Grootfoentein College of Agriculture (GCA) clearly shows that injudicious land management systems with short-term goals of maximizing profit will result in catastrophic ecosystem changes (Chapter 5). These undesirable changes are difficult to reverse, given the highly stochastic rainfall patterns and the fragile, shallow, slow-forming, nutrient-poor soils of the Karoo.

6.3. Future research

The establishment of the MZNP (Chapter 4), and the long-term trial under the auspices of the GCA (Chapter 5) are very valuable research sites for conducting similar research on other invertebrate fauna besides grasshoppers, and even on vertebrates such as birds which depend on invertebrates for food. Assemblage response of other functional groups such as pollinators to 'inside-versus-outside the park' variation in vegetation cover and composition, and their response to hills of variable sizes, are all subjects that need exploring. The data on various groups of organisms would be useful for formulating predictive models on strategies for conserving a wider cross-section of biodiversity. But as the grasshopper fauna varies so much between years, it means that any meaningful changes in overall biodiversity patterns could only be determined through longer-term studies.

6.4. Overall conclusions

- The refugia concept, as applied in this thesis (Chapter 2), is the result of topographical inaccessibility to domestic livestock rather than an island effect per se.

- The extent to which such an island is exploited as a refugium largely depends on the degree of sensitivity of a grasshopper species to anthropogenic disturbance, especially grazing intensity from domestic livestock. Furthermore, vagile species which have greater mobility are more likely to escape to the summit of the mesa compared to less mobile and brachypterous species.

- Besides the refugium effect of the summit, a mesa such as Tafelberg allows variability in the level of insolation on different faces of the slope. This creates thermally heterogenous shady and sunlit patches, and allows grasshoppers to move between shady and sunlit patches to survive excessive heat loads by means of behavioral thermoregulation.

- The variability in hill sizes in the Karoo (Chapter 3) generates topographic heterogeneity that results in habitat heterogeneity. Habitat heterogeneity, in turn, serves to maintain grasshopper biodiversity, as species have differential responses to patch as well as to landscape features.

- Most grasshopper species in the Karoo are small in size, and most of the hills fall in the small category. The affiliation of small grasshoppers with small hills and the few large species with larger hills indicates that body size, particularly length of hind legs dictates the scale at which individual species interact with the landscape.

- Variability in grasshopper assemblage patterns is not absolute, and only has meaning relative to the particular scale of observation. Hence it is important to recognize that resource availability, in its various forms, changes on many scales, and that there are interactions among phenomena at different scales. Accordingly, grasshopper assemblage patterns are reflections of landscape configuration and dynamics.

- The Mountain Zebra National Park (MZNP) is one of few areas that has been restored and under protection for long time. It retains the natural vegetal and faunal diversity, compared to the surrounding landscapes which are used for grazing by domestic livestock (Chapter 4).

- The marked difference in the land use inside versus outside the reserve shows a remarkable difference in vegetation cover, composition and structure, Such variability in vegetation characteristics is accompanied by strong responses in grasshopper population dynamics. The elevated grasshopper abundance inside the reserve indicates that the reserve provides optimal habitat patches for most grasshopper species and that is lacking outside the reserve where livestock change vegetation characteristics. Heterogeneity inside the reserve is encouraged by the diverse mix of mammals which show differential food selection, leading to patch grazing. Patch grazing leads to variable vegetation structure allowing a range of highly suitable grasshopper habitats. This is accompanied high fecundity and increased nymphal survival leading to higher abundances.

- The park boundary does not determine grasshopper assemblages on a simple inside-versus-outside basis. It is the intensity of defoliation and trampling that is important, and not the type of mammals.

- Aside from maintaining viable uncontaminated population of the Cape Zebra, *Equus zebra zebra* and indigenous vegetation. The MZNP also plays a crucial role in invertebrate biodiversity conservation, as indicated by high grasshopper abundances. Such elevated grasshopper abundances, in turn, accelerate and escalate nutrient turnover, an essential function for the long-term stability of the Karoo, particularly in view of the fact that this arid ecosystem is poor in soil organics and nitrogen.

- Livestock grazing is considered as one of the major threats to biodiversity in the Karoo. However, the extent of deterioration of biodiversity depends on the particular grazing system. If grazing is managed judiciously, it enhances biodiversty. The long term grazing experiment (Chapter 5), which was designed to show dynamics of vegetation succession under seasonal grazing, continuous grazing, continuous resting and rotational grazing, illustrated that rotational grazing is recommended as the best grazing system in terms of vegetation biodiversity, soil stability and also profitable livestock production. Similarly, rotational grazing supports the highest level of grasshopper diversity in the Karoo.

- In contrast, summer grazing and continuous grazing leads to land degradation by aggravating the process of bush encroachment where palatable perennial grasses (that also play crucial role in stabilizing soils) are exterminated and replaced by unpalatable grasses and undesirable shrubs. The successional vegetation changes are associated with significant undesirable shifts in grasshopper assemblages.

- It should be noted that, grazing, if managed judiciously and responsibly, is a desirable land disturbance factor which is crucial in creating a landscape mosaic ensuring balance between palatable and unpalatable vegetation elements. This, in turn, ensures survival of a range of invertebrate fauna that depend on a wide spectrum of vegetation structure.

- Total protection from grazing has been shown from several studies including Chapter 5, to lead to dominance by only perennial grasses, which become densely packed, leaving less chance for the survival of annual grasses and short forbs that contribute greatly to the variability in vegetation structure. Loss of heterogeneity in vegetation characteristics leads also to loss of faunal groups that depend on annuals, forbs , and even bare ground for their survival.

- Grazing land managers, therefore, should take cognizance of the merits of rotational grazing which is supported by empirical data based on long-term studies, to ensure profitable livestock production as well as maintain floral and faunal biodiversity.

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