BIRD REPRODUCTIVE SUCCESS AND FAUNAL HABITAT SELECTION AS TOOLS FOR UNDERSTANDING THE IMPACTS OF LAND-USE MANAGEMENT ON MOIST HIGHLAND GRASSLAND BIODIVERSITY IN SOUTH AFRICA

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DECLARATION

This thesis reflects original research undertaken towards a PhD degree at the DST/NRF Centre of Excellence, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, which has not been submitted in any form towards a degree at any other university. I submit it as my own work and acknowledge all assistance received.

Signed by candidate

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“We should live here on earth, as though
we are intending to stay here for good,
not just visit for the weekend”
(Damm 2002)

“Biodiversity is both a product of evolution and the essential
raw material for diversification of life on earth”
(Darkoh 2003)

“Humanity stands at a defining moment in history.
We are confronted with a perpetuation of disparities between and
within nations, a worsening of poverty, hunger, ill health and illiteracy
and a continuing deterioration of the ecosystems on which we depend for
our well-being. However, integration of environment and development
concerns and greater attention to them will lead to the fulfillment of basic
needs, improved living standards for all, better protected and managed
ecosystems and a safer, more prosperous future. No nation can achieve
this on its own; but together we can, in a global partnership
for sustainable development.”
(A-1: Preamble Agenda 21 – Rio Earth Summit 1992)

“If the earth were only a few feet in diameter, floating a
few feet above a field somewhere, people would come from everywhere
to marvel at it… the people would marvel at all the creatures walking
around the surface of the ball and at the creatures in the water. The people
would declare it as sacred because it was the only one, and they would protect
it so that it would not be hurt. The ball would be the greatest wonder
known, and people would come to pray to it, to be healed,
to gain knowledge, to know beauty and to wonder
how it could be.”
(Joe Miller “date unknown”)

ABSTRACT

The South African highland grassland system is home to over 3300 plant species, 15 of the country's 34 endemic mammal species, 12 of the 40 endemic bird species (five of these 12 are globally threatened) and five RAMSAR wetland sites. In these grasslands, fire and grazing interplay at the landscape level, directly influencing biodiversity (Engle et al. 2008; Fuhlendorf et al. 2008). As a result, fire and grazing can be managed to influence ecosystem health. Moist highland grassland (MHG) systems in South Africa are naturally maintained by winter and spring fires and by summer grazing by migratory herds of small to medium-sized antelope. It has been suggested that natural fires in these grasslands would have occurred as infrequently as every four or more years. Currently, the majority of the system is managed by livestock farmers who burn their land annually at the onset of the rainy season (early in the austral summer). This coincides with the beginning of the breeding season for grassland-nesting birds. Bird, arthropod and plant assemblages respond to habitat modification in a number of ways and due to a number of drivers. In order to assess these responses I selected eight management treatments for comparison. I collected data describing ten vegetation structural indices; plant species richness and abundance were quantified (for 114 species); > 32 000 arthropods were collected and sorted to order level; 160 km of transects were walked to assess bird species abundance (for 127 species); and 404 grassland bird nests of 12 species were located and monitored to completion. These data were analysed to assess the effects of grassland management on biodiversity and ecological integrity. By focusing on process-oriented data rather than using only inventory-type data, which carry a limited biological signal, this research provides a robust understanding of the effects of agricultural management on biodiversity. Grassland bird nest survival was modelled using Program MARK to assess the effects of management practices on reproductive success. Six of the bird species were modelled individually to assess species-specific responses to management. Both nest success and nest-site selection are driven by vegetation structure, which itself is driven by habitat management. For birds that build cup nests on the ground, nest success rate increased through the season in response to decreasing predation rates as vegetation structural complexity increased after early season fires. This finding supports the majority of Northern Hemisphere studies which conclude that nest success is driven primarily by predation pressure and habitat structure even though the predominant predators are avain rather than reptilian as in this study. Nesting success and abundance of Yellow-breasted Pipits *Anthus chloris* suggest that unconserved areas may house sink populations of this regionally and globally *Vulnerable* species. As an additional means of assessing the ecological integrity of farmed grasslands I used field metabolic rates (FMR) of birds and an adaptation of the Biodiversity Intactness Index (BII), which is a multi-taxon approach using plant, insect and bird diversity data. Current farm management practices have significant negative impacts on avian abundance, species richness, nest density and fledgling output. Overall FMR analysis and BII values both confirm the importance of conserved areas for birds in MHG systems and support the need for further conservation efforts in grassland systems as a whole by both private landowners and reserve managers. Scenarios of potential biodiversity improvement with changes in fire management are also presented. It is recommended that managers in MHGs promote a mosaic of burning regimes with the majority burning biennially or even less frequently and these mosaics can be supplemented with the use of large fire-breaks. I present the 'fodder capacity' method for evaluating stocking densities based on phytomass and metabolic equivalent livestock units. Using this I recommend a minimum sustainable 'forage capacity' of 5000 kg.Large Animal Unit^{-1} for domestic livestock in MHGs as a means of ensuring both economic viability and sustainable ecological integrity.

Key words: grasslands, birds, fire, grazing, arthropods, management.

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TABLE OF CONTENTS

CHAPTER 1

CHAPTER 2

Fire and grazing: grassland management for plant conservation, and introducing the ‘fodder capacity’ index for setting grazing thresholds

CHAPTER 3

Responses of bird and arthropod assemblages to fire frequency and grazing intensity: fire as a driving force

CHAPTER 4

Predation drives nesting success in grassland passerines: management of vegetation structure for avian conservation

CHAPTER 5

Process-oriented techniques for assessing biological integrity in grasslands: a case study in the moist highland grasslands of South Africa

CHAPTER 6

Conclusions and conservation implications

CHAPTER 1

General introduction

The background note for the software package Program MARK begins as follows: “Expanding human populations and extensive habitat destruction and alteration continue to impact the world's fauna and flora. In many cases, these forces are causing population declines, and in some cases extinction, of many species of vertebrates. Examples of population decline and species loss include virtually every taxonomic group. These scenarios are well known to biologists and ecologists throughout most of the world”.

Monitoring biological populations is receiving increasing emphasis in most countries, including the less developed areas of the world (Likens 1989). The estimation of survival probabilities and explaining how these vary according to age, sex, and time, as well as how survival might be correlated with external variables, represent significant challenges (White and Burnham 1999).

Anthropogenic land-use practices cause large-scale modification or transformation of the structure and functioning of natural ecosystems (Furness et al. 1993; Jansen et al. 1999; Damm 2002; Jeanneret et al. 2003a; Darkoh 2003; Driver et al. 2005; Dale et al. 2005; van der Weijden et al. 2010). This degradation disrupts ecosystem functioning and hence has an influence on biodiversity conservation (Bibby 1999; Hilty and Merenlender 2000). Human demands are placing ever-increasing pressure on land resources (Damm 2002; Darkoh 2003) and loss of natural habitat is the most important single cause of biodiversity loss in terrestrial ecosystems (Driver et al. 2005). Therefore, determining the factors leading to current patterns of biodiversity loss in human-degraded landscapes is important in order to assess the likely efficacy of future conservation efforts (Jeanneret et al. 2003a). Sustainable agriculture is defined as the sustainable use of domestic animals and plants for food in conjunction with conserving ecological integrity (Damm 2002). However, it requires foresight and planning, which are often lacking in the face of economic demands. Future demands for agricultural production will grow exponentially with human population growth and it is estimated that by 2025 present agricultural production will have to increase by 50% to sustain the projected human population, most of which will be in developing countries (Damm 2002).

Fuelled by improved farming technology, mechanization and modern irrigation, South African agriculture has intensified in the past 60 years (Downing 1978; Bai and Dent 2007). Along with this, plantation forestry, communal lands (areas grazed by cattle belonging to local communities) and urban development combine to increase the extent of landscape transformation and degradation. These various forms of land use lead to a disjointed mosaic of fragmented, intact and disturbed habitats and place pressure on species to adapt and survive (Morrison 1986; Hockey et al. 1988; Harrison et al. 1994; Allan et al. 1997). The success with which species achieve this will depend on their ability to utilize both intact patches of natural habitat and the surrounding degraded matrix (Wiens 1994; Ricketts 2001). Therefore, changes in habitat structure outside of pristine habitats play a critical role in influencing species composition and can lead to losses of indigenous species and gains of species not representative of the original system (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005).

The land making up the ‘matrix’ among conserved habitats will be crucial in the future conservation of many species and in the context of broader ecosystem functioning (Wiens 1994; Norton 2000; Ricketts 2001; Donald et al. 2002; Hilty and Merenlender 2003). Ecologists have a key role to play in describing and developing indicators that can inform land-use planning (Thomas 1972; Landres et al. 1988; Noss 1989; Lindenmayer et al. 2002; Theobald et al. 2005). Some species’ traits, such as habitat specificity, local rarity, body size, feeding guild, clutch size/reproductive strategy and field metabolic rates, are thought to play a role in determining species’ sensitivities to habitat degradation and fragmentation (Nagy et al. 1999; Suarez-Seoane et al. 2002; Nagy 2005). In this regard, research should focus on mobile and responsive taxonomic groups that are sensitive to changes within and between ecosystems. Birds respond rapidly to habitat change and move in response to anthropogenic habitat alteration (Liversidge 1962; Folse 1982; Knopf et al. 1988; Jansen et al. 1999; Donald et al. 2002; Fox and Hockey 2007) and, along with vascular plants, have been shown to be good surrogates for overall species richness (Sauberer et al. 2004). Indeed, variation in bird assemblages or abundance can be used effectively as indicators of changes in the structure and functioning of the environment (Morrison 1986; Jansen et al. 1999; Donald et al. 2002; Martin and Possingham 2005; Fox and Hockey 2007).

At the landcape level, several processes influence the sustainability of faunal assemblages. These include landscape complementarity (where individuals aquire their required resources by visiting different patches of resources across the landscape); landscape supplementation (where areas supplying similar, limited quantity resources act together to provide sufficient resources for survival and production at the landscape level); source-sink dynamics (where the movement of individuals between patches shows uneven immigration to emigration ratios due to higher reproductive output in the source areas); and neighborhood effects or flows (which encompass all the other movements of individuals and resources in the system - Dunning et al. 1992). The influence of these processes needs to be understood before an accurate understanding of the implications of land-use impacts on biodiversity can be inferred. Other landscape features such as corridors, which affect both connectivity (Beier and Noss 1998; Hannon and Schmiegelow 2002) and edge effects (Yahner 1988; Donovan et al. 1997; Ratcliffe and Crowe 2001), also have recently been shown to be of importance in conservation planning and biodiversity assessment. Further processes that influence ecological integrity as a result of habitat fragmentation include potential ecological traps (Battin 2004), and species-area relationships and island biogeography (Diamond 1975; Lahti 1986; Murphy and Wilcox 1986; Baz and Garcia-Boyero 1996; Debinski and Holt 1999; Lomolino 2001).

1.1. Priority South African habitats in need of research

Grasslands in South Africa cover approximately 16.5% of the country’s land surface, primarily on the high central plateau (Neke and Du Plessis 2004). While only about 6% of South Africa’s land area is formally protected, about 15% of the land surface making up the country’s various ecosystems are under some form of recognized conservation, most being in the mountain fynbos and savanna biomes. The least protected ecosystems are mostly in the succulent Karoo, grassland and lowland fynbos biomes (Driver et al. 2005). According to the National Spatial Biodiversity Assessment (NSBA - Driver et al. 2005), 34% of South Africa’s 440 terrestrial ecosystems are currently regarded as threatened, with 5% (21) being classified as *Critically Endangered*. Most of the *Critically Endangered* ecosystems are within the fynbos (14) and forest (5) biomes, with one in the grasslands. Thirteen percent of ecosystems are *Endangered*, mostly in the grassland and savanna biomes. Sixteen percent (70) are *Vulnerable*, with most of these in the fynbos and grassland biomes. In this same report, it was stated that among the five key strategies for conserving South Africa’s biodiversity it was particularly important to focus action on threatened ecosystems to prevent further loss of ecosystem functioning. The report also highlighted the need for up-to-date information on ecosystems that have been irreversibly transformed or degraded.

1.2. The grassland biome in South Africa

In addition to their biodiversity value, grassland areas provide essential ecosystem services required to support human life and wellbeing. These include food (grain), forage, livestock, water and nutrient cycling, soil stabilization, carbon storage, energy supply, game farming, tourism and recreation (Reyers et al. 2005; Muchai 2002). Despite this, grasslands are poorly protected: internationally, only 1.4% of grasslands are protected, the lowest of any terrestrial vegetation type (Driver et al. 2005). The grassland biome is the second largest biome in South Africa (7750 km^2) yet only 2.2% of its total area is formally conserved (Tarboton 1997; Raimondo et al. 2009): 60% of South Africa's grasslands have been irreversibly degraded (Driver et al. 2005). Grasslands are ancient, complex and slowly evolving systems of diverse plant communities that reproduce largely vegetatively rather than sexually, with bulbous plants and climax grasses featuring prominently (O’Connor and Everson 1998). The global extent of grassland has fluctuated over evolutionary time as a result of fluctuations in the Earth’s orbit, this variously encourages above- or below-ground carbon storage; the earth is currently undergoing a period of global grassland contraction (Mucina and Rutherford 2006).

There are several different types of grasslands within South Africa’s grassland biome, these differences being driven by edaphic and climatic factors (Mucina and Rutherford 2006). Among the Global 200 ecoregions, South Africa’s montane grasslands are listed as *Critically Endangered* (Olsen and Dinerstein 1998). Highland grasslands are among the most threatened biotopes in South Africa, with only 1.5% formally conserved. They are unique within Africa and are rich in plant and animal species, with many of these species being endemic to the biome. One hundred plants, 20 birds, six mammals and two butterflies are endemic to this ecoregion in South Africa and, as a consequence, grasslands have been assigned a high priority for conservation action (Macdonald et al. 1993; van der Weijden et al. 2010). Grasslands generally lack the ability to recover after severe disturbances, including any form of ploughing as well as overly frequent burning and overgrazing(Smit et al. 1997; Little et al. 2005) and are being increasingly degraded through the cumulative influence of over-grazing (Tainton 1981; Hockey et al. 1988; Neke and Du Plessis 2004), extensive burning (Uys et al. 2004), plantation forestry (Allan et al. 1997) and invasion by alien plant species (Le Maitre et al. 1996). Traditionally, these habitats have been used for livestock farming which has allowed the natural ecological processes to continue relatively undisturbed, unlike crop agriculture (O’Connor 2005; O’Connor and Kuyler 2009). However, livestock grazing does not simulate the natural herbivory regimes that would have occurred in the area (McNaughton 1986), and it is uncertain what impact this change in herbivory has had on plant and animal assemblages.

The Moist Clay Highland Grassland, the Moist Sandy Highland Grassland (both almost entirely restricted to Mpumalanga Province in the north-east of South Africa) and the Natal Sour Sandveld Grassland are all examples of poorly conserved grassland types (Mucina and Rutherford 2006; O'Connor and Kuyler 2009). Within these, there are many bird species with restricted ranges, and the conservation of this habitat for the protection of birdlife and biodiversity in general is vital. The International Convention on Biological Diversity (CBD) recommended that 10% of a particular habitat type should be conserved in a near-pristine state and the 2010 Conference of the Parties (COP 10) set a target of 17% land cover under conservation by 2020. The grassland biome falls well short of this standard and is of high conservation priority due to pressure for conversion to agriculture and forestry.

1.3. Grassland management

Although South African grassland systems are naturally maintained by fire, there is concern over the possible detrimental impact of unnaturally frequent fires (coupled with increasing anthropogenic fragmentation) on plant, arthropod and bird diversity (Baker 1992; Swengel 2001; Giliomee 2003; Valentine et al. 2007). Frequent burning practices are maintained by land owners in order to maximize the flush of green grass early in the growing season as well as for the control of ticks. Archaeological evidence indicates that pastoralists began grazing with indigenous livestock about 2000 years ago (Voigt 1983; Hall 1984 in Owen-Smith and Danckwerts 1997). Indigenous ungulates (Blesbok *Damaliscus dorcas*, Black Wildebeest *Connochaetus gnou*, Quagga *Equus quagga*, Springbok *Antidorcas marsupialis* and Eland *Taurotragus oryx*) would have sporadically migrated through the highland grasslands following the summer rains (Owen-Smith and Danckwerts 1997). By the early 20th Century most large game animals were restricted to National Parks due to hunting pressure and, since then, domestic livestock have been the predominant grazers of South Africa's grasslands (Owen-Smith and Danckwerts 1997). It has been suggested that the natural fire frequency in the highland grasslands (determined by lightning strikes) would have been as infrequent as every four years or more (Manry and Knight 1986). Linked to this is the suggestion that controlled burning should be based on the rate of litter accumulation and grazing should not start until sward height reaches

250 mm (Mentis 1981; Tainton 1981). In support of this, the greatest abundance and diversity of gamebirds, small mammals and antelope in the highland grassland of the Drakensberg occur in areas that have not been burnt for three or more years (Mentis and Rowe-Rowe 1979). Small mammal abundance and bird reproductive success are also detrimentally impacted by high stocking rates, with the effects of sheep being more severe than those of cattle (Nyako-Lartey and Baxter 1995; Muchai 2002). The conversion of the majority of remaining grasslands to pastoral land, through the planting of exotic grasses, has resulted in homogenization, an effect that negatively impacts species' abundances (Tichit et al. 2005b). Grazing herbivores modify vegetation structure within a particular successional sere, which can make climax (decreaser dominated) grassland resemble recently burned grassland. Depending on stocking rates, plant species composition can be altered along with the physical structure of the species themselves. Under high grazing pressure, grasses tend not to form vertical swards (Dennis et al. 2001). Under moderate grazing pressure, animals can express their dietary choices allowing for selective defoliation leading to a shift in plant species assemblages. Finally, in wet/moist grasslands, grazing is likely to play a pivotal role in creating and maintaining foraging and nesting habitats for birds (Tichit et al. 2005a).

1.4. Birds in agri-environments

Bird populations associated with agriculture have decreased in many parts of the world (Tucker and Heath 1994; Farina 1997; Pain and Pienkowski 1997; Donald et al. 2002; Laiolo 2005; Batáry et al. 2006; Powell 2008). In many parts of the world, agriculture is the dominant land-use type and there is mounting concern over the status of biodiversity associated with farmland environments (Donald et al. 2002; Jeanneret et al. 2003a; Loialo 2005; Bradbury and Kirby 2006). In Italy, where agricultural landscapes cover almost 60% of the land surface, reduced environmental diversity and increased maize cultivation, combined with changes in land management/farming practices, have resulted in reduced quality of farmland habitat for birds (Laiolo 2005). The degradation of grassland systems in Britain has also been shown to have strong negative impacts on bird diversity (Vickery et al. 2001). As a result of these trends, more than 10 years ago a number of regional agri-environment schemes were developed in Europe in order to introduce measures that reduce the impacts of agriculture on biodiversity (Vickery et al. 2004), such as the sowing of six-metre wide grass margins at the edges of arable fields (Jeanneret et al. 2003a; Marshall et al. 2005). Within the Swiss Law on Agriculture a clause has been introduced stating that only farmers adhering to specific ecological production rules are entitled to subsidies (Jeanneret et al. 2003a). In North America, grassland birds have experienced significant decreases since the 1960s (Knopf 1994) and agricultural practices have been identified as a key contributor to this trend (Best et al. 1995; Batáry et al 2006; Powell 2008).

Because of these wideapread decreases in bird populations in agricultural areas, the impact of agricultural practices is now fairly well understood in many parts of the developed world (Martin 1988; Fuller et al. 1995; Farina 1997; Hagemeijer and Blair 1997; Cueto and Casenave 1999; Zanette et al. 2000; Jobin et al. 2001; Vickery et al. 2001; Benton et al. 2002; Jeanneret et al. 2003a; Vickery et al. 2004; Lepczyk 2005; Marshall et al. 2005; Martin et al. 2005; Reidsma et al. 2006). In Africa, crop agriculture, livestock farming and forestry also have major, large-scale impacts on ecosystem structure and functioning (Downing 1978; Allan et al. 1997; O'Connor 2005). However, these impacts on species diversity and faunal assemblages outside protected areas are yet to be quantified and the implications for ecosystem functioning are not well understood, making effective broad-scale conservation problematic (Macdonald 1989; Tucker 1997).

Several small-scale studies have investigated the effects of land degradation on African avian assemblages in a cross-section of habitat types. These range from open-cast coal mining (Little et al. 2005) to the impact of agriculture in woodlands and grasslands of the KwaZulu-Natal midlands (Ratcliffe and Crowe 2001), the effects of grazing and burning of grasslands in the Drakensburg escarpment of Kwa-Zulu Natal and Mpumalanga (Mentis and Little 1992; Jansen et al. 1999), renosterveld fragmentation (Cameron 1999), strandveld fragmentation (Fox and Hockey 2007) and the implications of deciduous fruit farming on birds in the Western Cape (Little and Crowe 1994).

1.5. Birds as signals of faunal responses to management

Birds are highly mobile, represent multiple functional guilds, are represented by habitat-specific species and do not select nesting sites randomly. Hence, they have the potential to act as good surrogates for ecosystem condition and integrity. Because of a shortage of empirical studies of animals in agricultural lands in the African context, there is little information against which managers can assess which agricultural or management practices are the most compatible with biodiversity conservation. In South Africa, grasslands support 12 of the 40 endemic bird species (five of which are globally threatened: Southern Bald Ibis *Geronticus calvus*, Yellow-breasted Pipit *Anthus chloris*, Rudd's Lark *Heteromirafra ruddi* and Barrow's Korhaan *Eupodotis barrowii* - all *Vulnerable*, and Botha's Lark *Spizocorys fringillaris - Endangered*) (Barnes 2000; BirdLife International 2010). Eighty-five percent of the global population of Rudd's Lark occurs in the grasslands around the town of Wakkerstroom and its overall distribution is highly fragmented (Maphisa 2004; Hockey et al. 2005; Maphisa et al. 2009). Without understanding the influence of land management on grassland fauna the conservation of these taxa is compromised. This study aims to reduce this shortfall by comparing the reproductive performance and abundance of birds (rather than only using inventory-type data, which carry a limited biological signal) across land-use types (O'Connor 2005).

This study focuses on six bird species, namely Yellow-breasted Pipit, African Pipit *Anthus cinnamomeus,* Wing-snapping Cisticola *Cisticola ayresii,* Cape Longclaw *Macronyx capensis,* Long-tailed Widow *Euplectes progne* and African Stonechat *Saxicola torquata*. These species were selected based on sample size availability and habitat specialization.

1.6. Bird reproductive success as a tool for understanding the impacts of land-use

The habitat requirements of bird species are most often inferred by correlating abundance with features of occupied habitats. Such indirect methods might not, however, identify appropriate features for management efforts. Nest-site selection by grassland birds is a non-random process (Fretwell 1972; Muchai 2002), resulting in some areas supporting a high abundance and diversity of birds and yet acting as population sinks due to the habitat being unsuitable for nesting. Effective management of grasslands requires an understanding of (1) the environmental and demographic factors leading to shifts in assemblage structure; (2) the threshold habitat requirements for sufficient reproductive success and survival to ensure population maintenance; (3) how demographic and habitat factors interact to create population sources and sinks; and (4) how grassland management practices may impact on the above. I used reproductive success of grassland-nesting birds as a surrogate for the functional integrity of the system, rather than using bird species richness and abundance alone. While post-fledging survival and adult mortality are also important indicators of habitat quality, they are very difficult to assess without the use of advanced telemetry racking and long-term, mark-recapture studies which are beyond the scope of this study. It is assumed that the long-term effects of post-fledging survival rates would be reflected in the species richness and abundance counts.

It has become increasingly clear that species richness alone is a poor measure of biodiversity because changes in habitat structure influence species assemblages, typically resulting in losses of indigenous species and gains of species not representative of the original system (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005). In other words, species richness can remain constant while proportional species composition changes. Species richness can even be enhanced by land degradation processes, allowing colonization by species normally absent from a particular habitat type or biome, but the ecological consequences of this are not necessarily beneficial due, for example, to changes in patterns of energy flow and failure of ecological processes such as pollination (Fox and Hockey 2007). Furthermore, species richness may be influenced by factors such as territoriality, with the result that high densities of a particular species (assumed to be an indicator of population health) occur in areas of poor-quality habitat (where they form sink populations) because of despotic processes driving settlement patterns (Fretwell and Lucas 1970).

1.7. Plants and arthropods in grasslands; their implications for bird reproduction

There is limited scientific literature which addresses the responses of grassland arthropod communities to fire and grazing in southern hemisphere in general and South Africa in particular. However, many arthropod groups do decrease rapidly in abundance immediately after fire, depending on the intensity and extent of the burn and the mobility of the taxa present:the same response can be effected by heavy grazing because of niche simplification and the loss of protective cover (Swengel 2001). It has also been shown that heavy grazing and annual (as apposed to biennial) burning results in low nesting density and poor nesting success for grassland bird species (Muchai 2002).

Availability of food has frequently been found to be the most important factor influencing the production of offspring and variation in life-history traits among birds (Lack 1968; Ricklefs 1969; Martin 1987, 1995; Roff 1992), with nestling growth and survival being particularly sensitive to fluctuations in food availability (Rondenhouse and Holmes 1992). Food availability can also affect bird densities (Milchunas et al. 1988), limit clutch size (Ruiz et al. 2000) and reduce the number of breeding attempts (Rondenhouse 1986; Martin 1987).

Nest predation has been found to be the primary cause of reproductive failure in many passerine bird species (Ricklefs 1969; Martin and Roper 1988). Management practices, including frequent burning and high stocking rates, reduce vegetation cover and thus reduce nest concealment, increasing the probability of nest predation (Ammon and Stacey 1997). It is thus the performance rather than the abundance of component species that is the key indicator of their conservation status (Fondell and Ball 2004).

1.8. National conservation priorities

South Africa is a signatory State to the Convention on Biological Diversity (CBD) with the objectives of "the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources" (Damm 2002). In South Africa, legislation in the form of a Biodiversity Act has been gazetted (no. 10 of 2004), and a National Biodiversity Strategy Action Plan (NBSAP 2005) has been developed. Similarly, the Millennium Development Goals (MDGs), specifically MDG 7 (on ensuring environmental sustainability) were identified as requiring considerable attention before the end of the first decade of the 21st Century (Driver et al. 2005). The Enkangala Grassland Project and the South African National Biodiversity Institute's Grassland Programme have been established to address part of this conservation concern by developing a co-operative conservation model for an area of approximately one million hectares in the moist highland grasslands (MHG) of Mpumalanga, KwaZulu-Natal and the Free State. An overarching aim of this PhD thesis is to identify what forms of land managment are compatible with long-term biodiversity conservation objectives.

1.9. Study area and study design

The highland grasslands of South Africa occur at elevations between 1400-2400 m, with a mean annual rainfall of 660-1180 mm augmented by frequent mists. The predominant vegetation is short grassland in the high-lying areas with grass swards of increasing height on the lower slopes. Forb diversity is very high within this grassland type (Mucina and Rutherford 2006). The predominant land-use type in moist highland grasslands is cattle farming.

The study area is situated within the Mesic Highveld Grassland Bioregion and is specifically identified as Lydenberg Montane Grassland (Mucina and Rutherford 2006), formerly described as the North-eastern Sandy Highveld by Acocks (1988) and North-eastern Mountain Grassland by Low and Rebelo (1996). It is located between the towns of Belfast and Mashishing (formerly Lydenberg) on the eastern escarpment of Mpumalanga Province.

Fig. 1. Map of study area. The inset shows the locations of the study sites and their associated management regimes.

Lydenberg Montane Grassland is currently classified as *Vulnerable* (Mucina and Rutherford 2006). The conservation target is to have 27% of this biome under formal conservation (Mucina and Rutherford 2006), although currently only 2.4% of this vegetation type is formally protected within reserves. These are made up of the Gustav Klingbiel, Makobulaan, Mt Anderson, Ohrigstad Dam, Sterkspruit and Verloren Valei reserves as well as a number of private conservation areas. The study area falls on the high-altitude plateau in the Dullstroom region (centred at 25º 25"S, 30º 10"E) with Verloren Valei Nature Reserve acting as both a control and management experiment site (Fig. 1). Verloren Valei Nature Reserve was established in 1983 and recognized as South Africa's 17th RAMSAR site in February 2003. The area has been block-burnt biennially since 1985 (Heyns 1985).

The soils are mostly derived from shale and quartzite as well as lavas and dolomites of the Transvaal Supergroup (Mucina and Rutherford 2006). Orographic precipitation and heavy mists throughout most months of the year support a unique flora, including a rich diversity of mesophytic plants such as the Orchidaceae. This region experiences an average of 21 frost days per year (Mucina and Rutherford 2006). Three large rivers originate here - the Sabie, Elands and Crocodile Rivers.

This study uses process-orientated data to identify what economically viable forms of land use are compatible with long-term biodiversity conservation objectives in MHG.

This study aims to use reproductive performances of grassland birds, rather than their abundances, as measures of habitat quality, targeting grassland-restricted taxa across land-use practices. Assessing biodiversity in areas of different land-use practices establishes the degree of congruence in species' responses across treatments. Based on the above, it should be possible to make recommendations about which combinations of burning and grazing regimes are the most 'conservation friendly'.

The final element of the study involves identifying the processes leading to observed differences in reproductive ouput between management types by teasing apart the interacting roles of food supply and predation rate. This aims to capitalize on and expande on previous work, developing it to the point where it is possible to identify thresholds of stocking rates and burning frequencies for biodiversity conservation using bird reproductive success, insect diversity and abundance, and plant species composition as determinants of these thresholds.

Field work was conducted over two years (2007/8 and 2008/9), which raised the possibility that the results could be confounded by inter-annual differences in climate. However, based on data from the local weather station climatic differences between years were minimal and insignificant (Table 1).

Table 1. An analysis of comparative weather conditions between study seasons (Students t-test for dependent samples).

		t	**df**	**p**
DAILY	Average rainfall	0.594	151	0.553
	Average temperature	-1.232	151	0.220
	Wind speed (km/h)	-1.123	151	0.263
WEEKLY	Average rainfall	-0.104	20	0.918
	Average temperature	-0.732	20	0.473
	Wind speed (km/h)	1.097	20	0.286
MONTHLY	Average rainfall	-0.006	4	0.996
	Average temperature	-0.608	4	0.576
	Wind speed (km/h)	-0.797	4	0.470

CHAPTER 2

Fire and grazing: grassland management for plant conservation, and introducing the ‘fodder capacity’ index for setting grazing thresholds

Abstract

In this chapter I propose the use of a ‘fodder capacity index’ for evaluating stocking densities based on phytomass and metabolic equivalent livestock units. I used both univariate and multivariate statistics to assess the effects of grassland management on plant communities and vegetation structure. Fire and grazing interplay at the landscape level, with herbivores altering the accumulation and distribution of litter by eating available biomass before it is consumed by fire. As a result, the effects of fire and grazing can both be used as management tools to influence ecosystem health. However, burning early in the growing season has become common practice among farmers within these grasslands, irrespective of litter accumulation. These burns follow the first rains of the season in order to ensure cool fires and avoid unplanned and uncontrolled fires. This study illustrates the overridingly detrimental effects of this form of management. However, the data presented here also suggest that fenced native herbivores (predominantly Blesbok *Damaliscus dorcas*) in moist highland grasslands (MHGs), even at moderate stocking densities, have a more detrimental impact on both plant diversity and structure than do domestic livestock. To date, there is uncertainty about what livestock densities are agriculturally and ecologically sustainable and how to measure these. From this research I recommend a minimum sustainable ‘fodder capacity’ of 5000 kg.LAU^{-1} (Large Animal Unit equivalent to a 254 kg cow) for domestic livestock in MHGs as a means of promoting both economic and ecological integrity.

Key words: fire, grazing, ‘fodder capacity index’, flora, thresholds.

2.1. Introduction

Grasslands are ancient, complex and slowly evolving systems of diverse plant communities, with an abundant grass component, which reproduce largely vegetatively rather than sexually, with bulbous plants and climax grasses featuring prominently in the species complement of this biome (O’Connor and Everson 1998). Grasslands generally lack the ability to recover after severe disturbance (Smit et al. 1997; Little et al. 2005), but nonetheless are being increasingly degraded through the cumulative influence of over-grazing (Tainton 1981; Hockey et al. 1988; Milchunas et al. 1988; Neke and Du Plessis 2004), extensive burning (Uys et al. 2004), plantation forestry (Allan et al. 1997, Lipsey and Hockey 2010) and invasion by alien plant species (Le Maitre et al. 1996). The conversion of the majority of remaining grasslands to arable land has resulted in landscape homogenization, which in turn compromises plant species' abundances across most of the plant species spectrum (Tichit et al. 2005a). In South Africa, about 60% of the grassland biome has been permanently transformed, 25% is degraded to some degree, and as little as 15% remains as natural grassland. Of particular concern is that the majority of the remaining natural grassland is highly fragmented and most is poorly managed (Mucina and Rutherford 2006). These areas have been traditionally used for livestock farming which has allowed the natural ecological processes to continue relatively undisturbed. However, livestock grazing does not simulate the natural herbivore-grassland interaction that would have occurred in the area historically (McNaughton 1986), and it is uncertain what impact this change in herbivory has had on floral and faunal community structures. A Swiss-based study suggested that conservatively managed pasture land and "conserved" grassland should be maintained together to optimize conservation of montane grasslands (Kampman et al. 2008).

The use of grazing, and more commonly fire, as a management tool in South Africa is primarily to provide a green flush of nutrient-rich grass for livestock production, at the same time as controlling tick abundance (Kruger 1984; Scott 1984; Bond 1997; van Wilgen and Scholes 1997). However, these practices have influenced both vegetation structure and composition. While grasses produce basal tillers which makes them susceptible to overshadowing by old-growth (moribund) vegetation (O'Connor 2005), these grasses now have an obligate dependence on fire or grazing to suppress this old growth. Selective grazing, trampling and nutrient enrichment from urine and dung deposition can influence the competitive advantage of plant species through altered micro-environmental conditions that translate into changes in species composition and vegetation structure (Rook and Tallowin 2003; Veen et al. 2008). Some grass species further respond to grazing pressure by altering growth patterns: this can lead to niche displacement by plants in response to grazing intensity (Milchunas et al. 1988; Mucina and Rutherford 2006). In the absence of grazing, fire plays a significant role in removing above-ground biomass and litter, which influences plant species composition (Kruger 1984; Veen et al. 2008). Previous studies on the effect of fire and grazing on the

Grassland Biome in South Africa have focused on the impact of fire (Uys et al. 2004) or grazing (Owen-Smith and Danckwerts 1997) independently, with limited attention given to their combined effect. However, as mentioned earlier, fire and grazing interplay at the landscape level, with herbivores altering the accumulation and distribution of litter by eating available biomass before it is consumed by fire suggesting that these effects need to be teased apart (van Wilgen and Scholes 1997; Veen et al. 2008). Grazing, through selective preferences of stock animals, alters the structure and species composition of grasslands (Milchunas et al. 1988; Frame 1992; Milchunas and Lauenroth 1993; Owen-Smith 1999). Selective grazing favours those species that are less tolerant of grazing and this in turn causes a change in community species composition (Milchunas et al. 1988; Sternberg et al. 2000). Grazing herbivores modify the structural heterogeneity of vegetation within a particular successional sere. Not only do they alter plant species composition but also the physical structure of individual species, depending on stocking rates (Dennis et al. 2001). Under moderate grazing pressure, animals can express their dietary preferences allowing for selective defoliation which leads to shifts in plant species assemblages.

Fire also modifies the grazing pattern and behavior of herbivores because it reduces above-ground biomass (van Wilgen and Scholes 1997). Although South African grassland systems are naturally maintained by winter and spring fires (Mucina and Rutherford 2006), and fires stimulate flowering in grassland geophytes (Mucina and Rutherford, 2006), there is concern over the possible detrimental impact of unnaturally frequent fires (coupled with increasing anthropogenic fragmentation) on plant diversity (Baker 1992; Swengel 2001; Giliomee 2003; Valentine et al. 2007). It has been suggested that the natural fire frequency in the highland grasslands would have been as infrequent as every four or more years (Manry and Knight 1986). It is further suggested that controlled burning should be based on the rate of litter accumulation and that grazing should not start until sward height reaches 250 mm (Mentis 1981; Tainton 1981). Linked to this, burnt areas should not be grazed immediately after the burn. This is relatively easily managed with domestic livestock, but wild herbivores tend to graze burnt areas selectively and thus their stocking rates in fenced game areas need to be sufficiently low that the total number of animals congregating on burnt areas alone is not detrimental (Van Rooyen et al. 1986).

Despite the ‘natural’ burning interval of four years or more, annual burning after the first rains has become common practice among farmers within these grasslands (Tainton

1981; Everson 1999), irrespective of litter accumulation (van Wilgen and Scholes 1997; Everson 1999). Everson et al. (1989) reported that in order to minimise erosion and optimise vegetation recovery, burning should take place biennially in mid-August. Differences in fire frequency and timing can cause major shifts in grass species composition. If not burnt frequently, some species (e.g. *Themeda triandra* and *Heteropogon contortus*) become moribund and decrease in abundance while other species are more tolerant of self-shading (Owen-Smith and Danckwerts 1997), The abundance of *Themeda triandra* also decreases with increased grazing by livestock (O'Connor 2005). It has been suggested (Tainton 1999) that the carrying capacity for high-altitude climax grassland lies somewhere between 3 and 5 ha.Large Animal Unit (LAU)$^{-1}$. One LAU is defined as being equivalent to one cow or five sheep, and represents the metabolic equivalent of a 454 kg cow (Meissner et al. 1983; Owen-Smith and Danckwerts 1997; Tainton 1999). Despite this, many farmers overstock and burn too frequently, thereby exceeding the ecological carrying capacity of the grasslands to the detriment of the system's ecological integrity. In addition, farmers introduce livestock immediately following a spring burn. This influences the phenological stages of grasses and, eventually, the vegetation structure (because growth is limited to the summer period - Tainton 1999). High stocking densities of indigenous herbivores can also alter plant structure and diversity (Heyns 1985; Tainton 1999). Historically, wild ungulates in highland grasslands moved seasonally along rainfall gradients resulting in the grazing pressure they exerted being temporally and spatially patchy. Indeed, there was probably no grazing by wild ungulates in high-altitude grasslands during the dry, winter months (Mucina and Rutherford 2006).

To assess the ecosystem health of the highland grasslands of Mpumalanga Province, it is necessary to investigate how burning frequency and stocking rates influence vegetation structure and plant species composition. Few data exist for South African grasslands on how plant species richness is influenced by disturbance (Cowling et al. 1989; Everson 1999). The objective of this study is to assess the interactive effect of burning frequency and stocking rates on plant community (vegetation) structure and diversity of highland grasslands. It is hypothesized that with increased stocking rates plant diversity will decrease, accompanied by a shift from predominantly decreaser to predominantly increaser grasses (Tainton 1999). Decreasers are species that are sensitive to degrading veld condition, either as a result of too much or too little disturbance. Increaser I species increase in abundance as a result of too little disturbance (typically when the grassland becomes moribund); increaser II species increase in abundance in response to heavy disturbance (e.g. by fire, grazing or a combination); and increaser III species proliferate in response to selective grazing (i.e. are unpalatable species - Tainton 1999). The study also explores the impacts of indigenous game (predominantly Blesbok *Damaliscus dorcas*) relative to the impacts of (more heavily stocked) domestic cattle.

2.2. Study site and methods

The study area falls within the Mesic Highveld Grassland Bioregion and is specifically identified as Lydenberg Montane Grassland (Mucina and Rutherford 2006). All the study sites were on the plateau around the town of Dullstroom (centred at 25º 25”S, 30º 10”E), and were between 1900 and 2200 m.a.s.l. The soils are mostly derived from shale and quartzite as well as lavas and dolomites of the Transvaal Supergroup (Mucina and Rutherford 2006). The Dullstroom Plateau Grasslands (encompassing this entire study area) have been classified as *Endangered* on the basis of very high irreplaceability of species (National List of Threatened Ecosystems, from the Department of Environmental Affairs, notice 1477 of 2009). This vegetation type includes high-altitude plateaux, undulating plains, mountain peaks and slopes, and hills and deep valleys. The predominant vegetation is short grass in the high-lying areas becoming taller on the lower slopes. While grass species diversity is relatively low, the diversity of non-grass elements of the vegetation (‘forbs’ from here on) is high (Mucina and Rutherford 2006). Orographic and convection-based precipitation (660-1180 mm.year^{-1} – Mucina and Rutherford 2006) and heavy mists throughout most months of the year have promoted a unique flora, including a rich diversity of mesophytic plants such as the Orchidaceae. Indeed, forb diversity is so high, with over 2260 plant taxa and 51 endemic plant species, that this grassland type has been proposed as a ‘centre of plant endemism’ (Mucina and Rutherford 2006).

Eight study sites under differing management regimes, based on their availability, were sampled over two summer seasons. These are the most common types of management in the moist highland grasslands and hence represent the majority of the system. These included an annually burnt farm (AF); communally grazed lands (Com); a biennially burnt farm that was burnt (BF) or was not burnt (BFu) in the study year; a nature reserve site with a high density of indigenous grazing ungulates that was burnt (NRH) or was not burnt (NRHu) in the study year; and a nature reserve site with a low density of indigenous grazing ungulates that was burnt (NRL) or was not burnt (NRLu) in the study year. The biennially burnt farm, and both the heavily grazed and lightly grazed reserve sites had different stocking rates in the burnt vs unburnt years: this was unavoidable and is a result of the flux based on mortality and fecundity. These stocking rates did not change sufficiently to affect the inferences of this work significantly, and the burnt versus unburnt sites should be considered as separate management entities. All nature reserve sites were within Verloren Valei Nature Reserve, a site that acted as both a control and as a management experiment site. The reserve site was selected based on its exisiting good condition and former conservative management: the reserve was proclaimed in 1983 and has been block-burnt biennially since 1985 (Heyns 1985). All of the sites (except communally grazed lands where fire has not used as a management tool for more than 50 years) are burnt in early spring after the first rains. Both the annually burnt and biennially burnt farms have been managed this way for at least three generations (> 100 years).

Within each study site, four 25 hectare replicates were marked out with at least 500 m between replicates. Replicates were nested within replicates which were in turn nested within study sites (each representing a different management type). As far as possible, these replicates were sufficiently far apart to avoid pseudo-replication, based on breeding ranges such that pairs recorded in one replicant are unlikely to be seen in another (Hockey et al. 2005) but were sufficiently close together to standardise as far as possible for extrinsic factors including geology, rainfall, aspect, slope and temperature within and between land-use treatments (Hurlbert 1984). In some instances, such as with the embedded replicates, pseudo-replication was unavoidable and had to be accepted as the only means of providing some form of replication in a system where establishing genuine experimental plots was not possible.

Field work was conducted in the birds' summer breeding season (October to March) for two years. Grazing data were collected by interviewing farmers or managers of chosen sites and were validated with animal counts. Relative grazing intensity was recorded as the number of hectares of grazing land available per large animal unit (ha/LAU).

2.2.1. Vegetation structure

Vegetation structure was sampled monthly throughout the sampling season using two techniques. The first sampling method was modified from Wiens and Rotenberry (1981). Three 500 m transects were established within each of the four replicates per study site. Along each of these, at 50 m intervals, a 10 m tape was laid out perpendicular to the transect line. Vegetation was sampled at 1 m intervals along the tape yielding 100 point samples per transect (in total, 1200 samples per site per month). At each sampling point a 6 mm diameter rod was positioned vertically through the vegetation to the ground. This rod was marked at height intervals 0-50 mm, 50-100 mm, 100-200 mm, 200-300 mm, 300-400 mm, 400-500 mm, 500-600 mm and 600-1000 mm. At each sampling point I recorded a) the number of vegetation contacts with the rod per height interval, and b) whether the contact was a grass or a forb. Open ground (in the case of no contact with vegetation) and overall maximum height of vegetation were also recorded. From these data I calculated three sets of vegetation structural indices.

Cover – Percent grass cover (%grass), percent forb cover (%forb) and percent total plant cover in the form of grass and forb combined (%veg), calculated is the percent of points recording each of these parameters.

Structural measures – Average maximum height of vegetation (AveMaxHt) and horizontal density (AvHorDen), derived from the mean number of contacts with the rod in the 0-100 mm interval, and vertical density (AvVerDen) derived from the mean number of contacts over the entire length of the rod.

Heterogeneity measures – canopy heterogeneity (HorHetHt) given by the coefficient of variation of the maximum height contacts, and overall heterogeneity (HorHetTo) given by the coefficient of variation of the mean total number of contacts over the entire rod and a patchiness index (Patchine) which groups the 10 samples per 50 m and then calculates landscape patchiness according the equation of Wiens and Rotenberry (1981);

$$Patchiness = \sum(Max - Min)/\sum x$$

where Max = maximum number of contacts recorded in each sample group, Min = minimum number of contacts recorded in each sample group, and x = the mean number of contacts recorded in each sample group.

The second technique quantifies vegetation density or biomass. The quantity and quality of herbage available to herbivores is a function of phytomass (O’Reagain and Turner 1992; Smith 2006). Measurement of standing stock is essential for determining herbage production and stocking rates in the management of herbivores (Ganguli et al. 2000).

Phytomass was sampled using a Disc Pasture Meter (DPM - Bransby and Tainton 1977; Danckwerts and Trollope 1980; Trollope and Potgieter 1986). The DPM is made up of a 1.5 kg, 457 mm diameter disc mounted onto a central rod with a measuring scale in 5 mm increments. The disc is dropped vertically from 0.6 m above ground onto the grass sward; the settling height of the disc is then recorded.

Vegetation was sampled every five metres along the three 500 m transects, yielding 100 DPM samples per transect and a total of 1200 samples per site per month.

The DPM is calibrated for a specific vegetation type to convert the DPM reading into biomass estimates (kg.ha^{-1}). Although DPM calibrations were available for a number of vegetation types in South Africa and some outside of South Africa (Bransby and Tainton 1977; Danckwerts and Trollope 1980; Trollope 1983; Trollope and Potgieter 1986), MHG had not been calibrated. Data collected by Colin Everson in the late 1970s were used to calibrate the DPM.

2.2.2. Plant species diversity

Mature plants were sampled at each of the sites. BF, NRL and NRH were only sampled in the year that they were not burnt allowing for plant succession to reach its maximum. Sampling was conducted in late January when the majority of species were in flower, making species identification possible. Those plants that could not be identified in the field were pressed and sent to the South African National Biodiversity Institute (SANBI) herbarium in Pretoria for expert identification. Modified Whittaker nested vegetation sampling plots (O’Connor 2005; Appendix 1) were used to sample floral species diversity based on the methods of Stohlgren et al. (1995). Overall relative floral diversity ssessments were based on one modified Whittaker plot per replicate (four per treatment). All species were recorded and abundance (percentage cover) of each species was estimated from each of the 10m^2 and 1m^2 subplots. Estimated abundances per subplot were summed and the overall estimated abundance per species was calculated as a percentage. Plant species names were based on Germishuizen and Meyer (2003).

2.2.3. Statistical analyses

Data analyses were conducted using the software packages PC-ORD 5.10 (McCune and Mefford 2006) and STATISTICA 9.0 (StatSoft Inc. 2009).

In order to calibrate the Disc Pasture Meter (DPM) for MHG, monthly data collected throughout the season from all of the management types were analysed using a regression analysis where the standing crop of grass harvested from below each disc measurement (converted to kg.ha^{-1}) was the dependent variable and the mean settling height of the disc was the independent variable. The regression analyses were repeated with the standing crop of grass subjected to logarithmic, square, square root and reciprocal transformations in order to obtain the best linear fit of the regression between disc height and the standing crop of herbaceous plant material. The best fit was then compared with former calibrations of the DPM.

To assess the relative impacts of management practices on vegetation structural parameters I conducted Analyses of Variance (ANOVA) with *post-hoc* Tukey Tests. Following this, I ran a Discriminant Function Analysis followed by a Backward Stepwise Discriminant Function Analysis, incorporating only the significant parameters, to extract which of the vegetation structural parameters best revealed the effects of management on vegetation structure.

To assess sampling efficiency, species-area curves were fitted to the plant species-richness data. First- and second-order jackknife estimates of species richness were derived separately for grasses, forbs and all species.

Plant community compositions were contrasted among management types using two statistical approaches; first a one-way pairwise Permutation-based Non-parametric MANOVA (PerManova - Anderson 2001; McCune and Mefford 2006), second a pairwise Multi-Response Permutation Procedure (MRPP - Mielke 1984; McCune and Mefford 2006). In both of these approaches I used the Sørenson (Bray-Curtis) distance measure because this is appropriate for abundance data and gives robust outputs with zero-dominated datasets (McCune and Grace 2002). MRPP is a nonparametric test of differences in species diversity between groups. The A-statistic (chance-corrected, within-group agreement) describes effect size: when A = 0, groups are no more or less different than expected by chance; when A = 1, sample units within groups are identical (McCune and Mefford 2006).

To assess the contribution of each species' abundance to the community and how much their response to disturbance has influenced each of these communities I conducted an Indicator Species Analysis (McCune and Mefford 2006) using a Monte Carlo Test of Significance with 5000 permutations was run (Dufrêne and Legendre. 1997): this method combines species' abundance and occurrence. A 'perfect indicator' should be present in all replicates within a site and not present in any other sites. To test whether grasses and forbs are responding in a similar manner to site management, I conducted a Mantel Test (Douglas and Endler 1982) which tests the null hypothesis of no relationship between matrices. To test whether grass species experienced shifts from high to low palatability (based on Tainton 1999) and from decreaser to increaser grasses with increasing disturbance, I ran Mann-Whitney U Tests and ANOVA by Ranks.

Multi-dimensional Scaling ordinations (MDS) with Bray-Curtis measures were run (in the software PC-ORD) using a Euclidean distance measure with Bray-Curtis original endpoint selection for vegetation structural space and Sørenson distance measure, which is recommended for community analyses, with Bray-Curtis original endpoint selection for plant species space. These ordinations fit matrix data into two dimensional space: in this case the two data matrices analysed were vegetation structural diversity and species diversity (Bray and Curtis 1957; McCune and Grace 2002). DPM data were secondarily overlaid on the ordination, and vegetation structural indices were included as a biplot.

Finally, to assess the shift in plant species assemblages as a result of land-use, a Two-way Cluster Dendrogram (McCune and Mefford 2006) with a Sørenson distance measure (recommended for community analyses; McCune and Mefford 2006) and group-average linking method without relativisation was run. .

2.3. Results

2.3.1. Disc Pasture Meter calibration

In order to utilize a disc pasture meter for sampling phytomass, the instrument requires calibration for the grassland type to be sampled. This had not been previously calculated for MHG. The best calibration for sourveld grassland (which occurs within the moist highland grasslands) was linear (Fig. 1) and had a higher r^2 value and hence a better fit than calibrations derived from the other grassland systems. Nonetheless, existing calibrations exhibit very similar trends to the MHG calibration. The most similar of these is that of the Eastern Cape (EC), which also has a linear fit (Fig. 2). Kruger National Park (KNP), the Caprivi region of Namibia, and Kenya have non-linear fits (Fig. 2).

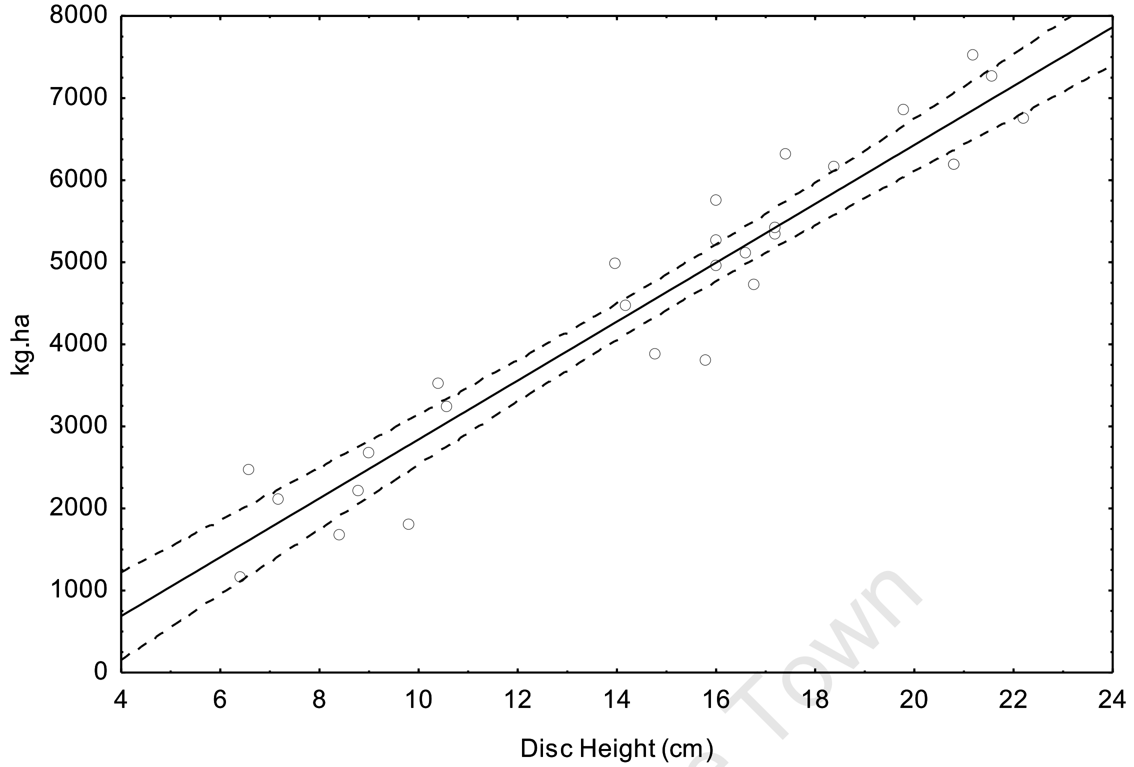


Fig. 1. Linear calibration with 95% confidence limits for the Disc Pasture Meter in moist highland grassland. A linear regression ($y = 358.768x – 746.352$) is the best fit ($r = 0.95$, $r^2 = 0.91$, $p < 0.0001$).

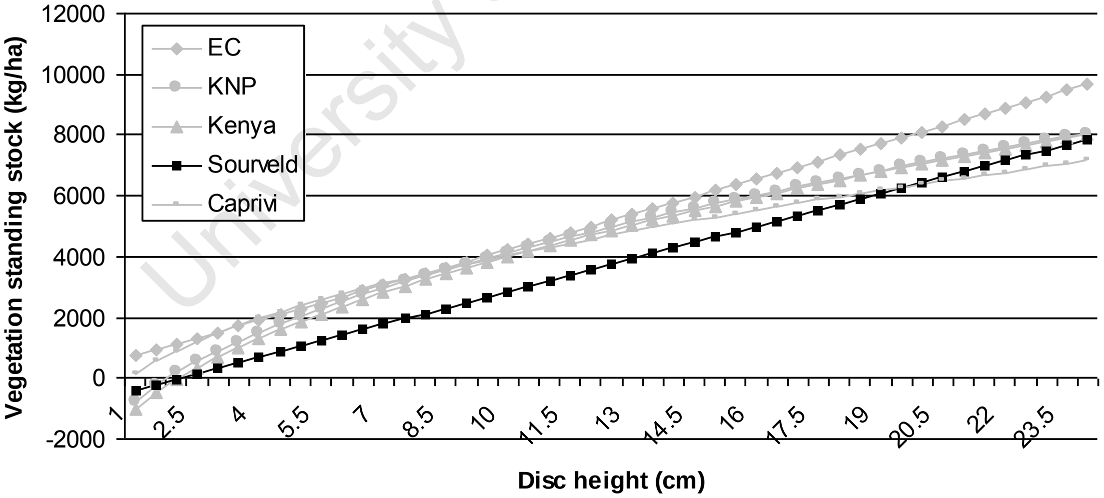


Fig. 2. Existing calibrations for the Disc Pasture Meter in African grasslands (Bransby and Tainton 1977; Danckwerts and Trollope 1980; Trollope and Potgieter 1986). The new calibration for moist highland grassland in South Africa is in black.

2.3.2. Impact of management on vegetation structure

Numbers of grazing animals were constant throughout the summer season at all sites, but stocking rates varied between sites (Table 1). The commercially farmed areas (AF and BF) were rotationally grazed on a four-day cycle by the same herd. In all cases the rotation was between two large camps, each of which contained two replicate study plots. The stocking rate on communal lands, where there is no stock rotation, is thus the number of animals in the area of both camps combined. Offspring of both livestock and indigenous grazers born in early summer were treated as 0.5 LAUs.

Table 1. Grazing intensity in the eight study sites (ha.LAU^{-1}).

	ha/LAU
NRLu	63.671
NRL	46.714
NRHu	13.613
NRH	14.408
BFu	2.092
BF	1.963
AF	1.251
Com	1.071

In order to assess the response of vegetation structure to management it was important to understand which of the measured structural indices were most sensitive to thesedisturbance effects. When all ten of the structural indices are included in the analysis (Table 2), any of the indices could be used to differentiate between management practices but some were more effective than others. For this reason a stepwise analysis is required to identify the most effective vegetation structural indices for sampling grassland structure.

Table 2. Discriminant functions analysis illustrating the differences in vegetation structural indices across management types. Overall Wilks's λ: 0.01102, F = 12.453, p < 0.00001.

	Wilks's - λ	**Partial - λ**	**F**	**p**	**r^2**
%Grass	0.014	0.807	4.351	0.000	0.961
%Forb	0.016	0.697	7.875	0.000	0.464
%Veg	0.013	0.819	4.008	0.001	0.961
AveMaxHt	0.012	0.895	2.133	0.045	0.882
AvHorDen	0.013	0.823	3.898	0.001	0.876
AvVerDen	0.012	0.887	2.321	0.029	0.942
HorHetHt	0.016	0.669	8.984	0.000	0.286
HorHetTo	0.016	0.700	7.777	0.000	0.807
Patchine	0.018	0.610	11.613	0.000	0.845
DPM	0.014	0.767	5.514	0.000	0.687

In order to make these indices functional it is important to identify which of them are most effective at differentiating between management types, in this way it is possible to identifyone of these vegetation structural indices to act as a surrogate for overall vegetation structure. A backwards stepwise discriminant functions analysis (Table 3) identified four of the original ten vegetation structural indices as performing best at discriminating between management types.

Table 3. A backwards stepwise discriminant functions analysis illustrating the four vegetation structural indices which play the most important role in predicting structural differences across management types. Overall Wilks's λ: 0.050, F = 22.29, p < 0.00001.

	Wilks's - λ	**Partial - λ**	**F**	**p**	**r^2**
AvHorDen	0.186	0.268	51.968	0.000	0.234
HorHetHt	0.080	0.626	11.354	0.000	0.080
Patchine	0.083	0.603	12.497	0.000	0.392
DPM	0.091	0.548	15.642	0.000	0.266

High densities of indigenous herbivores depleted grass and vegetation to the point that NRH (13.61 ha.LAU^{-1}) had both less grass cover (ANOVA, *post-hoc* Tukey Test; $p < 0.01$, df = 136) and less vegetation cover (ANOVA, *post-hoc* Tukey Test; $p < 0.0005$, df = 136) than any other site. This site also had the greatest vegetation patchiness (ANOVA, *post-hoc* Tukey Test; $p < 0.01$). Biennial burning, coupled with heavy grazing by domestic stock, resulted in BF (2.09 ha.LAU^{-1}) having less forb cover than any other site

(ANOVA, *post-hoc* Tukey Test; $p < 0.05$). Extremely heavy grazing, regardless of burning such as occurs in AF (1.25 ha.LAU^{-1}) and Com (1.07 ha.LAU^{-1}), resulted in both higher horizontal vegetation density (ANOVA, *post-hoc* Tukey Test; $p < 0.001$ and $p < 0.05$) and lower vegetation biomass (ANOVA, *post-hoc* Tukey Test; $p < 0.05$ and $p < 0.05$) than any other sites.

The conservatively managed reserve site, NRL (63.67 ha.LAU^{-1}), had greater vegetation biomass (ANOVA, *post-hoc* Tukey Test; $p < 0.05$) and lower average horizontal vegetation density than any other site (ANOVA, *post-hoc* Tukey Test; $p < 0.05$).

In order to gain a better understanding of how management type affects vegetation structure and which of the management types have similar or differing effects, an ordination analysis is required (Fig. 4). This allows differentiation between management effects including separating out the relative importance of fire frequency and stocking rate in influencing vegetation structure.

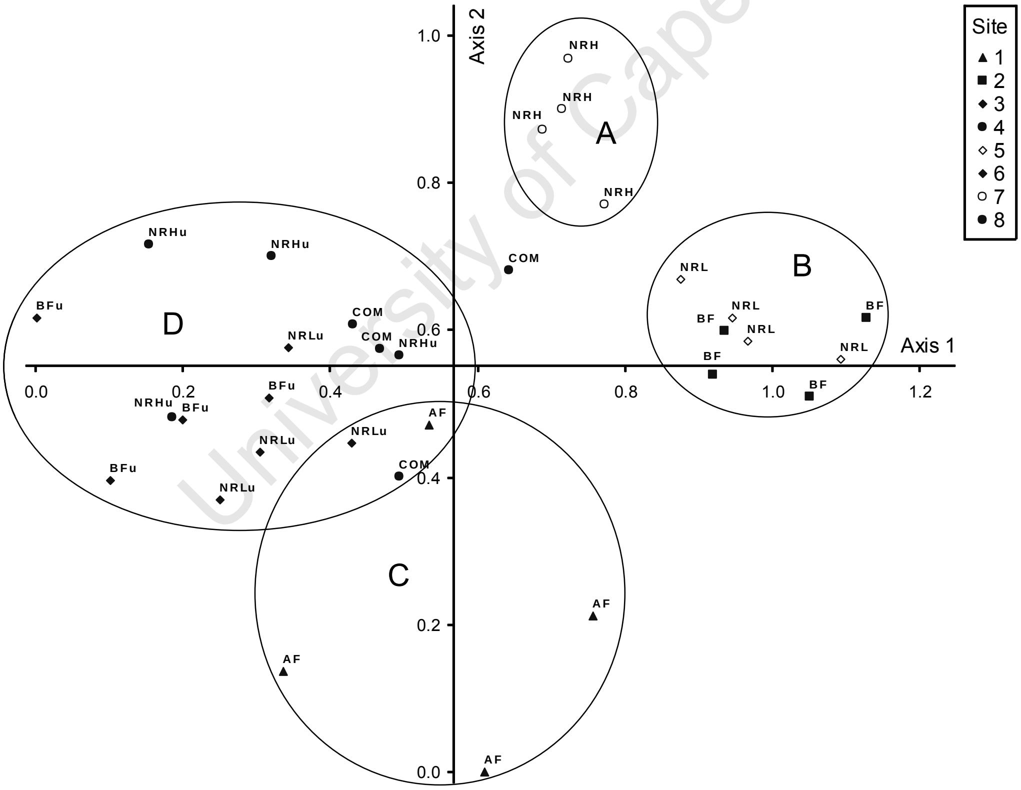


Fig. 4. Multi-dimensional Scaling plot (based on Euclidean distance and Bray-Curtis measures) showing how treatments clustered in terms of vegetation characteristics. The following vegetation parameters were included in the analysis: forb cover (%; log-transformed), vegetation cover (%; log-transformed), average maximum vegetation height, average horizontal density, total horizontal heterogeneity, patchiness, and standing stock of vegetation (kg.ha^{-1}). Axes 1 and 2 accounted for 49.49% and 20.35% of the variance, respectively.

Grazing and burning directly influenced phytomass. Phytomass was highest in the site experiencing the lowest grazing pressure (NRL); this was true towards the end of the season even in the year that this site was burnt (Fig. 5). The biennially burnt farm (BF) had the second-highest standing stocks and again, even in the year it was burnt, recovered to support a higher vegetation biomass than other commercially farmed sites. AF and Com consistently had the lowest standing stocks of vegetation. However, intensive grazing by indigenous ungulates in the conservation area (NRH) resulted in lower phytomass by the end of the year than was present in the communally grazed lands.

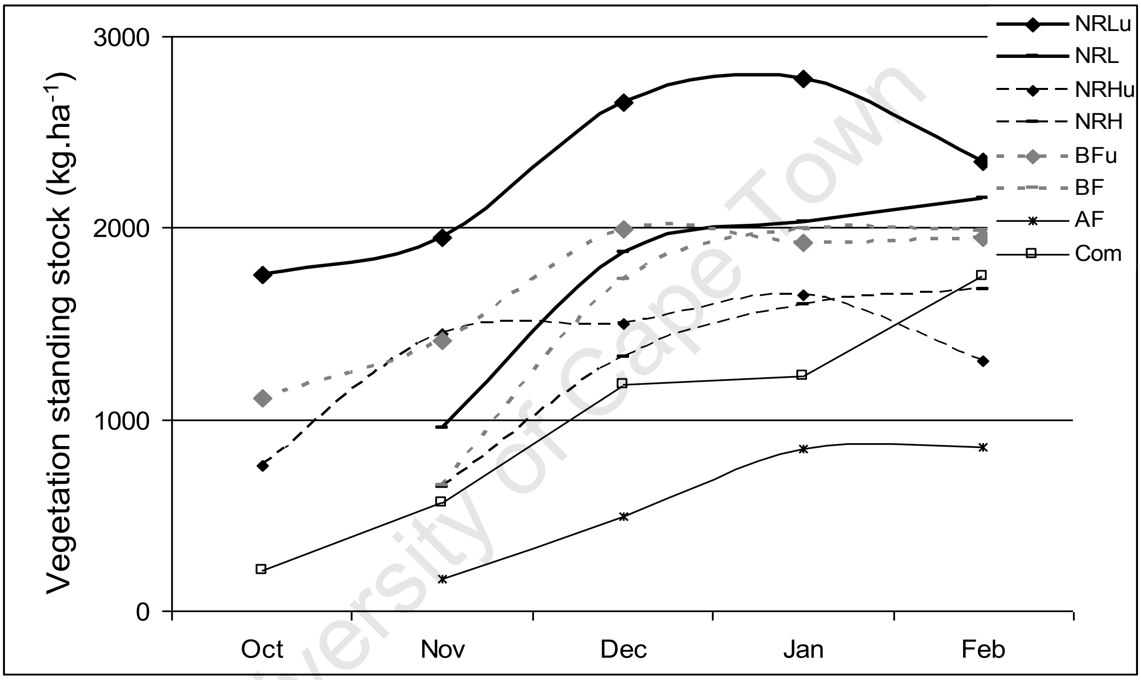


Fig. 5. Standing stock of vegetation (kg.ha^{-1}) in each of the management treatments through the growing season. In all management types except communal grazing lands (com), burning takes place in early September.

With the ability to measure phytomass in a simple and cost-effective manner it is now important to develop a relative measure of forage availability in order to be able to assess how the current stocking density is affecting the sward structure through the season. In order to achieve this, phytomass (kg.ha^{-1}) were combined with grazing intensities (ha.LAU^{-1}) to produce an index of available vegetation per LAU (kg.LAU^{-1}) which gives a clear indication of both the available above-ground biomass for grazing and the seasonal effect of grazing on vegetation biomass (Fig. 6). This allows for the assessment of phytomass and hence forage availability at any stage of the season.

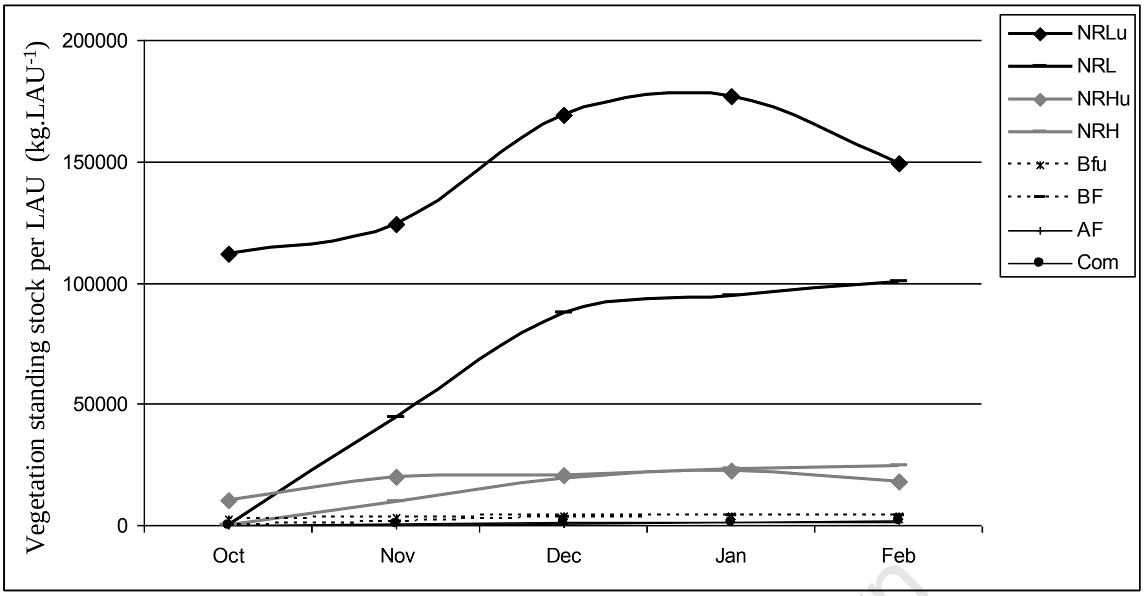


Fig. 6. Phytomass (kg.LAU^{-1}, measured using a Disc Pasture Meter), as a function of grazing pressure (livestock density) across all eight treatements. In all management types except communal grazing lands (com), burning takes place in early September.

2.3.3. Impact of management on plant species diversity

When considering plant species diversity, the five management types were considered only in the years that they were not burnt. Plant species presence does not change according to whether or not the site was burnt in that year, but the plants are easier to detect and identify in the years when burning does not take place. In order to have confidence in the sampling of species data, species-area curves were constructed and Jack-knife estimates derived from these showed small difference between observed and expected species richness (Table 4).

Table 4. Jackknife estimates of species richness derived for grasses, forbs and all plant species combined for all modified Whittaker plots combined.

	Number of species observed	First-order jackknife estimate	Second-order jackknife estimate
Grasses	20	21	18
Forbs	94	117	123
All species	114	138	142

Between-site species diversity was assessed using two methods (PerManova and MRPP) which both yielded similar results, providing support for the between-management-type comparisons (Table 5). A randomization test of significance of pseudo F-values between all sites showed a significant overall difference between sites (F = 2.9022, p < 0.0005, df = 35).

Table 5. Permutation-based analyses used to evaluate differences in botanical composition between sites.

	PerManova		MRPP	
Test	t	p	A	p
NRL *vs* NRH	2.309	0.025*	0.106	0.106
NRL *vs* BF	2.313	0.031*	0.204	0.020
NRL *vs* AF	2.218	0.029*	0.417	0.006
NRL *vs* Com	1.827	0.026*	0.194	0.019
NRH *vs* BF	1.425	0.028*	0.139	0.035
NRH *vs* AF	1.382	0.083	0.379	0.009
NRH *vs* Com	1.361	0.057	0.181	0.037
BF *vs* AF	1.314	0.152	0.398	0.006
BF *vs* Com	1.371	0.056	0.144	0.036
AF *vs* Com	1.453	0.060	0.343	0.006

In support of the findings from the pairwise PerManova and MRPP (Table 5), 37.7% of species occurred in only one management type (NRL). Of these; 3.51% and 7.89% of species were unique to NRH and BF respectively, while 8.77% of the recorded species only occurred in each of NRL, Com and AF. Two species found in the study area are currently threatened (*Eucomis autumnalis* and *Hypoxis hemerocallidea* - Raimondo et al. 2009). One species, *Plantego myosuros* is an exotic weed from South America.

When considering the response of individual plant species to management it is apparent that a large number of increaser and pioneer species are present in the system (Table 6), illustrated by the species that are confined to high-disturbance areas, including the annually burned farm (AF) and the communally grazed area (Com). Only two species were restricted to the conservation area and one of these was most abundant in the area that was heavily grazed by indigenous herbivores (NRH).

Table 6. Indicator plant species for the different management types based on indicator species analysis.

Species	Site	Observed indicator values (IV)	IV from randomized groups		p
			Mean	Std Dev	
Watsonia pulchra	NRL	60.7	24.9	12.4	0.022
Eriospernum flagelliforme	NRH	75.0	20.9	13.9	0.019
Dierama insigne	BF	72.7	24.4	12.1	0.006
Trachypogon spicatus	BF	100.0	23.3	12.8	0.001
Acalypha punctata	AF	57.6	32.0	8.9	0.008
Asclepias albens	AF	97.3	24.5	12.0	0.002
Crassula lanceolata	AF	60.0	26.6	10.6	0.035
Helichrysum pilosellum	AF	56.9	28.2	10.5	0.022
Plantego myosuros	AF	95.0	29.6	14.7	0.002
Schoenoxiphium spartum	AF	75.0	26.5	13.1	0.018
Seteria sphaccelata	AF	100.0	23.5	12.9	0.002
Sporobolus pectinatus	AF	47.2	30.2	8.4	0.043
Vernonia monocephala	AF	72.7	25.3	13.4	0.017
Indigofera hilaris	Com	69.6	25.5	13.6	0.034
Panicum natalensis	Com	7.5	26.4	13.9	0.048
Digitaria monodactyla	Com	60.7	2.7	12.1	0.017
Anthospenum pumilum	Com	83.9	27.5	11.9	0.001
Vernonia natalensis	Com	66.3	28.4	9.8	0.002

Grasses and forbs responded in a similar manner to management according to Mantel's asymptotic approximation (Mantel test, $r = 0.26$, $p < 0.0005$): this statistic uses a t-distribution with infinite degrees of freedom. This suggests that either group on its own whould be sufficient for assessment of plant ecological integrity. Grasses are the best floral group as indicators of habitat management effects because species are more readily identifiable, the group is less spesiose than the forbs, and grasses are the group of interest as forage plants. The grasses can also be divided into four response types (Fig. 7) as well as palatability categories (Fig. 8 - Tainton 1999). Of particular interest is the significantly reduced abundance of decreaser grasses relative to increaser grasses in the heavily grazed conservation area (Mann-Whitney U Test, $Z = -1.59$, $p < 0.05$; Fig. 7), suggesting highly selective grazing by indigenous herbivores. This is supported by the high proportion of increaser III grasses. There was a significantly lower overall abundance of palatable versus unpalatable grasses in the heavily grazed conservation area (Mann-Whitney U Test, $Z = 1.76$, $p < 0.05$; Fig. 8) again suggesting highly selective grazing by indigenous herbivores. The part of the nature reserve experiencing low grazing pressure supported the highest proportion of palatable grass species (Fig. 8).

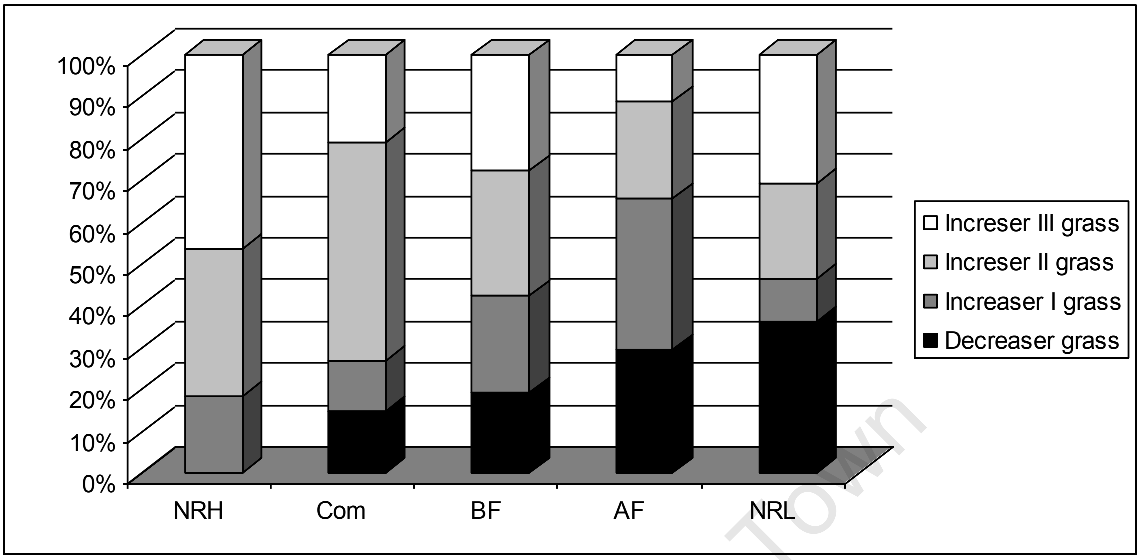


Fig. 7. Proportion of increaser versus decreaser grasses based on species abundances across the five management treatments.

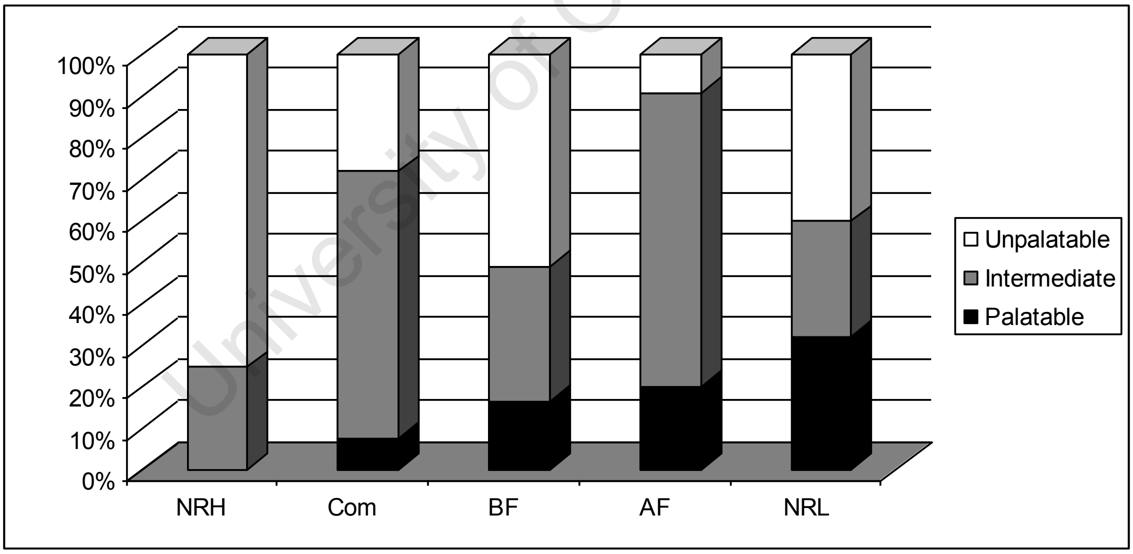


Fig. 8. The relative proportions of palatable and unpalatable grasses based on species abundances across the five management treatments.

Table 7. Differences in palatability scores (palatable *vs* unpalatable – Tainton 1999) and species status (increaser *vs* decreaser) of grasses in different management types (Kruskal-Wallis H). NRH and BF have significantly more unpalatable than palatable plants as well as more increaser than decreaser species.

Test	Site	H	p
Palatability	AF	3.338	0.188
	NRH	12.134	0.002
	NRL	1.057	0.589
	BF	6.610	0.037
	Com	3.389	0.184
Status	AF	2.330	0.507
	NRH	15.706	0.001
	NRL	6.563	0.087
	BF	7.836	0.049
	Com	5.905	0.116

Fire frequency has an overriding effect on plant species diversity, with grazing intensity playing a secondary role in distinguishing the effect of different management practices (Fig. 9). Axis 1 separates sites according to burn frequency, while Axis 2 indicates a response to grazing pressure. Communal lands are defoliated to the point at which it is difficult to distinguish the two responses (close to the origin). DPM data are overlaid illustrating the importance of phytomass in separating out sites. Axis 1 extracted 29.8% and axis 2 extracted 19.9% of the original distance matrix (total 49.7%).

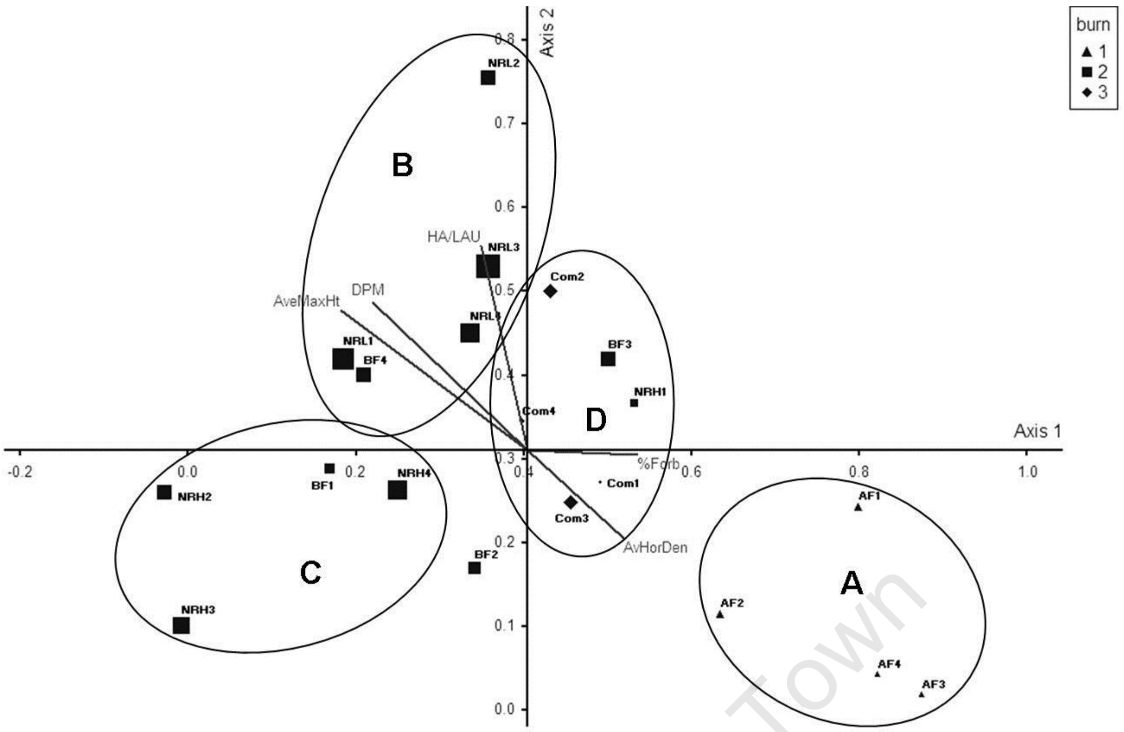


Fig. 9. Multi-dimensional scaling ordination (using Bray-Curtis measures) illustrating the relative influences of fire and grazing in separating out management types based on plant species diversity. Sites are separated out according to species diversity and the sizes of symbols reflect standing stock of vegetation (kg.ha^{-1}).

Assuming that we would expect similar assemblages of plants in each of the sites if there was no difference in management, it is clear that plant species diversity responded strongly to disturbance (Fig. 10). AF separates out first, followed by Com. BF and NRL cluster very closely and these in turn cluster with NRH. Six distinct assemblages separate out according to land use. One of these is specific to the conserved area while the other five show preference for disturbed areas. This suggests that land degradation is characterised more by the gain of pioneer-type species than by the loss of specialist grassland species.

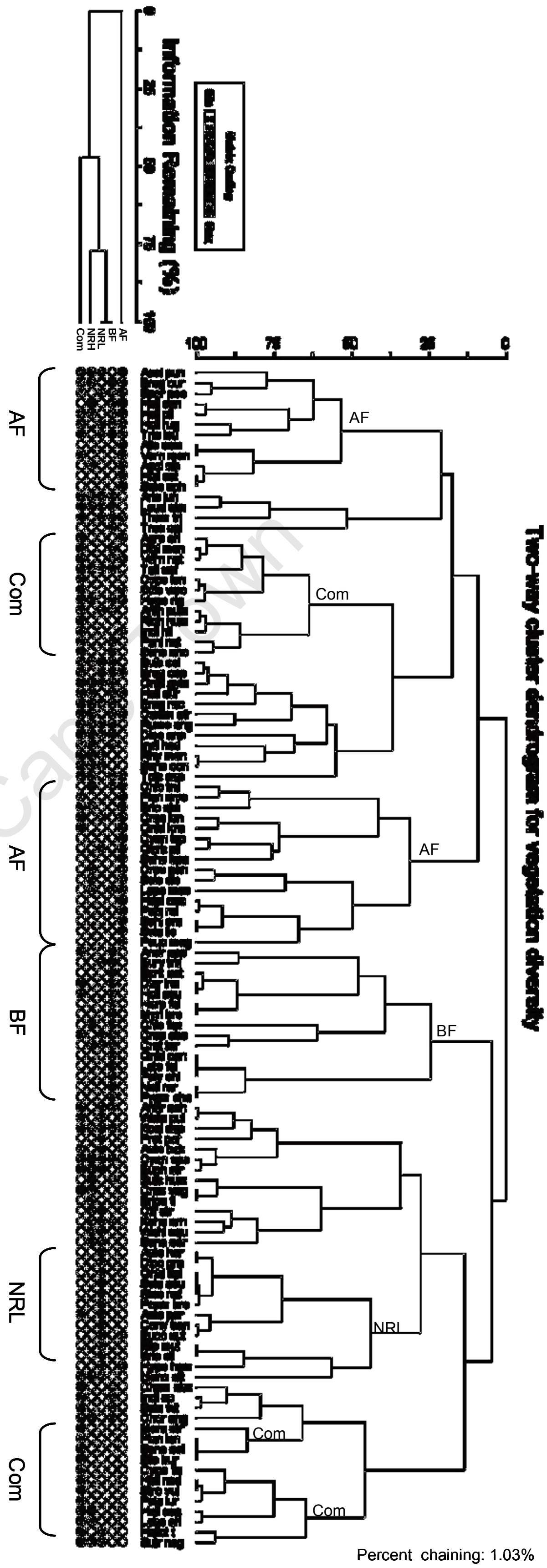


Fig. 10. Two-way cluster dendrogram illustrating the relative diversity of species in each management type and how species and sites group based on these abundances. Darker circles illustrate high abundance of that species at that site. Six clear assemblages are specific to particular management types. For full species names see Appendix 2.

2.4. Discussion

Both fire and grazing together act as the primary disturbance mechanisms in grassland systems, shaping the structure and composition of the vegetation (van Wilgen and Scholes 1997; Veen et al. 2008). With an understanding of how these disturbance effects interplay to drive the system they can potentially be managed to influence ecosystem stability and biological intactness (Savory 1988; Ferwerda et al. 2006). Annual burning within South Africa’s MHGs, irrespective of litter accumulation (van Wilgen and Scholes 1997; Everson 1999), has a detrimental effect on plant diversity and the extent of land surface that is burnt annually is of concern for grassland conservation (Tainton 1981; Everson 1999). It has been suggested that the carrying capacity for moist, high-altitude grassland lies somewhere between 3 and 5 hectares per large animal unit (Tainton 1999) and that historically, lightning-driven fires may only have occurred at intervals of four years or more (Manry and Knight 1986). The dominant management system thus combines high stocking rates with frequent (annual) fires, both suggesting that current pastoral practices may exceed the ecological carrying capacity of these habitats.

In order to understand the effects of burning and grazing on vegetation structure, and to allow farmers to assess pasture condition rapidly, an easy-to-implement and time-conservative technique is required. The DPM has been recommended for these purposes (Bransby and Tainton 1977; Danckwerts and Trollope 1980; Trollope and Potgieter 1986). For this technique to be useful, however, the DPM must be calibrated for the vegetation type in question. This calibration is both strong and linear (Fig. 1) and has a similar trend to previous calibrations in other grassland types (Fig. 2).

Of the ten vegetation indices calculated in this study, four proved useful for illustrating the different effects of different management practices (Tables 2, 3). Of these, three differentiated the impacts of management practices on vegetation structure. Patchiness was highest and vegetation cover (auto-correlated with grass cover because grass accounts for >90% of vegetation cover) was lowest in the NRH. Historically, wild ungulates in highland grasslands would have moved seasonally along rainfall gradients. This in turn would have led to temporally and spatially patchy impacts of grazing, probably with no grazing in the high-altitude grasslands during the dry, winter months (Mucina and Rutherford 2006). Current management on a portion of the conservation area has indigenous ungulates fenced at relatively high density (13.5 – 14.5 ha.LAU^{-1}) throughout the year. Resultant selective grazing, predominantly by Blesbok *Damaliscus dorcas*, leads to a patchwork of bare ground and unpalatable vegetation (Tainton 1999).

Grazing herbivores modify the structural heterogeneity of vegetation within a particular successional sere (Milchunas et al. 1988; Owen-Smith and Danckwerts 1997), but vegetation biomass alone does not reflect this because biomass of the unpalatable component remains relatively high (Figs 5, 8). The data presented here suggest that wild herbivores, stocked at high density, have a greater impact on both plant diversity and structure than do domestic livestock. Even at relatively low stocking rates, highly selective grazing by wild herbivores clears all decreaser species and creates a mosaic of patchy, unpalatable vegetation (Figs 7, 8). By contrast, moderate to heavy grazing by domestic livestock has no significant impacts on vegetation structure or diversity providing the burning interval is at least two years. The only detectable effect in areas grazed by domestic livestock and burned at two-year intervals was the low representation of forbs. This suggests that grazing may play an important role in determining forb diversity: Uys et al. (2004) found that annual versus biennial burning made little difference to forb diversity in this grassland system. This could also be attributed to an intermediate disturbance effect, although this would need to be illustrated more robustly, where species are lost both as a result of intensive management and in response to a lack of fire management when grasses become moribund, stifling forbs. There are few grassland specialist plant species that require low disturbance levels and few pioneer species which require high disturbance levels to thrive (Grime 1973; Horn 1975; Connell 1978; Fox 1979).

Farmers introduce livestock immediately following a spring burn. Because plant growth is limited to the summer period (Tainton et al. 1977), this inevitably influences the phenological stages of grasses and eventually the vegetation structure. Excessive grazing does not necessarily lead to loss of grass species (Fig. 8) because the basal meristem of grass leaves enable re-growth after defoliation. Frequent and excessive defoliation can however, shift species assemblages towards grasslands dominated by increaser II species (Milchunas et al. 1988; Mucina and Rutherford 2006; Fig. 7). As a result, horizontal vegetation density can be used as a surrogate for the presence of a “carpet-like” layer of thick, low vegetation close to the ground. This habitat homogenization is expected when grazing pressure is high and largely unselective (Swengel 2001). Not surprisingly, these conditions result in low vegetation biomass (Fig. 4) and a correspondingly low carrying capacity for grazers (Fig. 5). The similarity of sites with annual burning (AF) and communal grazing (Com - never burned intentionally) suggests that when grazing pressure is intense, the relative importance of fire in controlling vegetation structure diminishes.

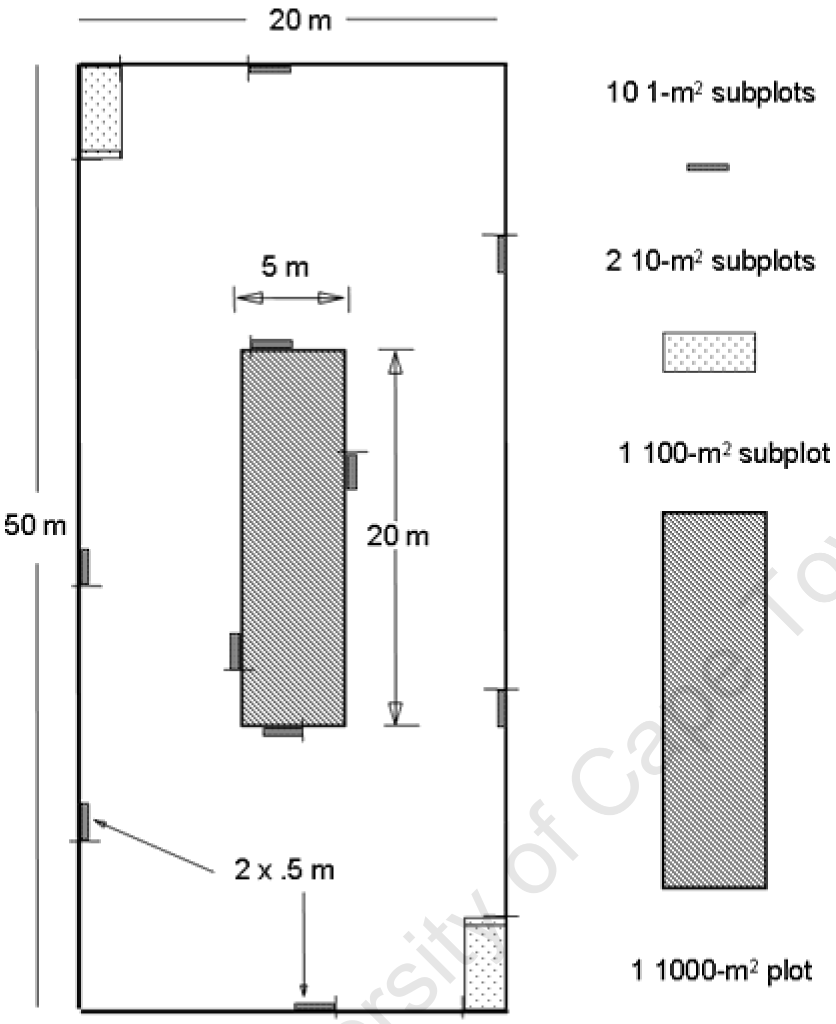
Conservative management (such as burning biennially - BF) resulted in high vegetation biomass along with a greater proportion of increaser grass species and an increase in overall palatability of the vegetation (Figs 6, 7; Table 7). When heavy grazing and frequent burning are combined this results in high horizontal vegetation density: by contrast, low levels of disturbance/defoliation result in MHGs becoming moribund (Mentis and Rowe-Rowe 1979; Trollope and Potgieter 1986; Tainton 1999). This is a state where litter accumulates to the point where plant growth is compromised. NRL had the lowest horizontal vegetation density and thus current management practices in this part of the conserved area (with low densities of indigenous herbivores) appear to be ecologically sound.

Based on the results of this study, I recommend that future assessments of vegetation structural integrity and forage availability use a DPM without the need for any other form of sampling. The DPM, and more specifically vegetation biomass (Fig. 4), has proved an adequate surrogate for all structural indices: its ease and speed of use make for a practical and time-conservative approach. By combining these data with grazing intensity in the form of ha.LAU^{-1}, an estimate of forage availability per LAU can be obtained based on a ‘fodder capacity index’ (Fig. 5). This new estimate encompasses both the current standing stock of vegetation (which has already been impacted by grazing and fire) and the future potential grazing impact based on current stocking rate. Similar research in Britain (Pakeman and Nolan 2009) suggested that sustainable grazing levels should be set using an estimate of the proportion of vegetation utilized rather than stocking density. However, due to rapid vegetative growth rates in grasslands this is not accurate and is unreliable. The approach recommended here is user friendly, accurate and spatio-temporally plastic. In this study, the available stocks of forage on communal lands and the annually burnt farm are, on average, less than 1 100 kg.LAU^{-1} throughout the summer season. This is concerning, considering that for each metabolic equivalent of one kilogram of animal there are just over two kilograms of vegetation per hectare.

According to Tainton’s (1999) recommended minimum of 3 ha.LAU^{-1} and assuming that the stocking rate on BF is sufficient for sustainability of current phytomass (in Fig. 5, BF standing stocks resemble those of NRL), the recommended minimum sustainable threshold of forage per LAU for domestic livestock would be around 5000 kg.LAU^{-1}.

Data on the effects of management on plant species richness in South African grasslands are sparse (Cowling et al. 1989). The use of plant species indicators has been shown to be difficult and time consuming, and has been labelled ineffective as a surrogate for distinguishing plant assemblages (Lindenmayer et al. 2002; Öster et al. 2008). However, assemblages of grassland species do respond to different disturbance pressures, with distinct species groups that are either intolerant or partially tolerant of disturbance, or that thrive in disturbed environments (Milchunas et al. 1988; Bibby et al. 1992; McIntyre and Lavorel 1994). The latter are commonly weeds while the former are decreasers grasses and climax forbs. The presence of *Plantego myosuros* on the annually burnt farm is a strong signal of habitat degradation: this species is a known weed and is often spread in cattle dung. The combination of heavy grazing and annual burning leads to a distinct plant community (group A in Fig. 9), with nine species characterising this group (Table 6). The large number of 'disturbance specialists' illustrates the sensitivity of this system to assemblage shifts favouring increaser or pioneer species. High-intensity, selective grazing by indigenous herbivores promotes a community of unpalatable species (Fig. 7, Table 7) which are largely generalist taxa that are not specific to any particular management type (Fig. 10). In Figure 9, group B (biennially burned nature reserve with low grazing pressure) and group A (annually burned farm) are the most different from one another, illustrating the extremes in the effects in the effects of high-frequency burning (A) and low-intensity grazing (B). These two sites are significantly different to all other sites (Table 5). The (rarely burnt) communal grazing lands (group D) and the biennially burnt lands (which do not separate out in a clear group) are intermediate in vegetation structure between the extremes of high (A) and low (B) disturbance, with the interaction of grazing intensity and fire frequency as complementary disturbance vectors. The separation of sites is driven primarily by high phytomass, associated in this case with low grazing intensity on the low disturbance/defoliation extreme and by high horizontal vegetation density and forb cover on the high disturbance/defoliation extreme. The 114 plant species identified fall into six distinct, management-specific communities and four generalist groupings (Fig. 10), implying that plants show strong responses to both grazing and burning. Two of the 114 species - *Eucomis autumnalis* and *Hypoxis hemerocallidea* - are classified as *Threatened.* Both of these are listed as decreasing (Raimondo et al. 2009). *Eucomis*, a popular plant for traditional medicine, is confined to the conserved area, suggesting that it is sensitive to disturbance. *Hypoxis*, also used in traditional medicine, is confined to unconserved, communal lands that burn infrequently.

Appendix 1. Modified Whittaker Plot design.



Appendix 2. Plant species presence/absence records per management type (names according to Germishuizen and Meyer 2003).

	AF	BF	NRL	NRH	Com
Acalypha punctata	X	X	X	X	X
Agrostis eriantha	X				X
Alloteropsis semialata	X				
Andropogon appendiculatus		X			X
Andropogon schirensis		X	X		X
Anthospenum pumilum		X	X		X
Aristida junciformis	X	X	X	X	X
Asclepias albens	X			X	
Aster bakeranus			X		X
Aster harveyanus			X		
Aster perfoliatus			X		X
Berkheya setifera		X			
Bulbostylis collina		X	X	X	X
B ulbostylis humilis		X		X	
Chamaecrista absus		X			X
Chlorophytum fasciculatum		X		X	
C. transvaalensis	X	X		X	
Chortolirion angolensis		X		X	X
Cliffortia strobilefera			X	X	
Commelina africana	X	X		X	X
Conyza bonariensis			X		
Crassula lanceolata	X		X		X
Crassula obovata		X	X		X
Crassula vaginata				X	X
Craterocapsa tarsodes		X	X	X	
Crocosmia paniculata	X			X	
Cyanotis lapidosa	X				
Cyanotis speciosa		X	X	X	X
Cyperus flavissimus					X
Cyperus longus					X
Dicoma anomala		X	X	X	X
Dierama insigne		X			X
Digitaria monodactyla		X			X
Dipcadi gracillimum			X		
Elionurus muticus			X		
Eragrostis capensis	X	X	X	X	X
Eragrostis curvula	X	X	X	X	X
Eragrostis racemosa		X	X	X	X
Eriosema ellipticofolium			X		
Eriosema simulans	X			X	X
Eriospernum flagelliforme				X	
Eucomis autumnalis	X		X		
Euphorbia striata			X	X	X
Euryops transvalensis		X	X		
Gerbera piloselloides	X		X		
Gnidia canoargentea		X			
Gnidia gymnostachya		X	X	X	X
Gnidia kraussiana	X				X
Gnidia splendens			X		
Hibiscus aethiopicus	X				
Haplocarpha scaposa		X			
Harpochloa falx		X			X
Helichrysum acutatum	X	X	X	X	X
Helichrysum aureonitens	X	X		X	
Helichrysum candolleanum				X	X
Helichrysum cephaloideum					X
Helichrysum nodifolium	X	X	X	X	X
Helichrysum pilosellum	X	X	X	X	X
Helichrysum rugulosum			X		X
Helictotrichon turgidulum	X				
Hypoxis hemerocallidea	X		X		
Hypoxis rigidula	X	X		X	X
Indigofera hedyantha		X		X	X
Indigofera hilaris	X				X
Indigofera sp.		X			X
Koeleria capensis		X	X	X	X
Kohautia amatymbica		X	X	X	
Lapeirousia masukuensis	X	X		X	
Lobelia erinus				X	X
Lotononis foliosa		X			
Loudetia simplex		X	X	X	X
Monsonia attenuata			X	X	X
Moraea stricta					X
Myrica brevifolia		X			
Nolletia rarifolia		X			
Panicum natalensis		X			X
Pelargonium luridum					X
Pelargonium relumonnii	X				
Peucedanum magalismotanum	X				
Plantego lanceolata					X
Plantego myosuros	X				X
Polygala ohlendorfiana		X			
Protea parvula			X		
Psammotropha breviscapa			X		

Continued…	AF	BF	NRL	NRH	Com
Pygmaeothamnus chamaedendrum		X			
Rhynchosia monophylla			X	X	X
Richardia humistrata					X
Rumex acetosella		X	X	X	X
Schistostephium crataegefilium	X				
Schoenoxiphium spartum	X				
Scleria dieterlenii	X			X	
Scleria woodii	X				X
Selago acutibrachea			X		
Selago witbergensis		X			X
Senecio anomalochrous		X			X
Senecio conrathii			X	X	X
Senecio serratuloides					X
Senecio serratus			X	X	
Seteria sphaccelata	X				
Silene burchellii					X
Solanum lichtensteinii	X				
Sporobolus pectinatus	X	X	X	X	X
Stachys natalensis			X		
Strobe vulgaris					X
Sutra neglecta			X	X	X
Talinum caffrum		X	X	X	X
Themeda triandra	X	X	X		X
Tolpis capensis	X	X	X	X	X
Trachypogon spicatus		X			
Tristachya leucothrix	X	X	X	X	X
Vernonia monocephala	X				X
Vernonia natalensis	X	X			X
Wahlenbergia squamifolia			X	X	
Watsonia pulchra			X		X

CHAPTER 3

Responses of bird and arthropod assemblages to fire frequency and grazing intensity: fire as a driving force

Abstract

In this study, I investigated the responses of two faunal groups, birds and insects, to varying degrees of disturbance caused by fire and grazing. Bird assemblages reflect habitat disturbance in a diversity of ways, driven by factors ranging from direct disturbance to changes in habitat structure and functioning, and shifts in food availability. Similarly, arthropod diversity and abundance change seasonally in response to management practices. Fire frequency drives faunal assemblage structure and abundance and, in most cases, overrides the effects of grazing at all taxonomic levels. In particular, fire frequency strongly influences grassland-breeding birds because farms are burnt in the territory-forming stage of the breeding cycle. Insectivores and nectarivores were disproportionately impacted by intensive management. Of particular concern in this system is the Yellow-breasted Pipit *Anthus chloris*, which is regionally and globally *Vulnerable* because of habitat loss. This species is sensitive to any form of habitat disturbance, highlighting the need for conservation attention in these grasslands. Of the ten arthropod orders present in the study area, only Orthoptera respond positively to burning. However, orthopterans made up on average 78% of arthropod biomass in moist highland grasslands (MHGs), resulting in high grasshopper biomass on annually burnt farms: this high biomass in turn supports an abundance of insectivores. This reinforces the importance of process-oriented data where a measure of performance is considered in assessing ecosystem condition.

Key words: Grasslands, arthropods, birds, disturbance, fire, grazing.

3.1. Introduction

Human land-use practices cause large-scale degradation of the structure and functioning of natural ecosystems (Furness et al. 1993; Happold 1995, *in* Jansen *et al*. 1999; Jansen et al. 1999; Darkoh 2003; Jeanneret et al. 2003a; Dale et al. 2005; Driver et al. 2005), with concomitant implications for biodiversity conservation (Bibby 1999; Hilty and Merenlender 2000).

Grasslands are the least protected of any terrestrial vegetation type in the world with only about 1.4% under formal protection (Driver et al. 2005). In South Africa, the grassland biome covers approximately 7750 km^2 yet only 2.2% of its total area is formally conserved (Tarboton 1997) and 60% has been irreversibly degraded (Driver et al. 2005). There are several different grassland types within the greater grassland biome of South Africa, one of which is the highland grassland of which only 1.5% is formally conserved (Mucina and Rutherford 2006). Grasslands are generally very sensitive to disturbance (Smit et al. 1997; Little et al. 2005) and the cumulative impacts of over-grazing (Tainton 1981; Hockey et al. 1988; Neke and Du Plessis 2004), extensive burning (Uys et al. 2004), plantation forestry (Allan et al. 1997, Lipsey & Hockey 2010) and invasion by alien plants (Le Maitre et al. 1996) has led to grasslands being considered a conservation priority. As of 2004, only about 53% of the highland grassland biome remained in a “semi-pristine” state, contained mostly in livestock farms and rangelands (Neke and Du Plessis 2004).

Loss of natural habitat is considered to be the greatest single cause of biodiversity loss in terrestrial ecosystems in South Africa (Driver et al. 2005). Therefore, determining the factors leading to current patterns of biodiversity loss in human-degraded landscapes is a necessary prerequisite to designing future conservation strategies (Jeanneret et al. 2003a). Anthropogenic land use leads to a disjointed mosaic of fragmented, intact and disturbed habitats, testing the adaptability of its component species to persist (Morrison 1986; Hockey et al. 1988; Harrison et al. 1994; Allan et al. 1997). The relative success with which different species do so will depend on their ability to utilize both intact patches of natural habitat and the surrounding degraded matrix (Wiens 1994; Ricketts 2001). The land making up the ‘matrix’ between conserved habitats will be crucial in both the future conservation of many species and in the context of broader ecosystem functioning (Wiens 1994; Norton 2000; Ricketts 2001; Donald et al. 2002; Hilty and Merenlender 2003). Changes in habitat structure outside of pristine habitats thus play a critical role in determining species composition, which is influenced both by losses of indigenous species and gains of species not naturally representative of the original system (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005).

Bird populations associated with agriculture have decreased in many parts of the world (Tucker and Heath 1994; Pain and Pienkowski 1997; Donald et al. 2002; Laiolo 2005). In many parts of the world, agriculture is the dominant land-use type and there is mounting concern over the status of biodiversity associated with farmland environments (Zanette et al. 2000; Jobin et al. 2001; Söderström et al. 2001; Vickery et al. 2001; Benton et al. 2002; Lepczyk 2005; Marshall et al. 2005; Martin et al. 2005; Martin and Possingham 2005; Haslem and Bennett 2008; Herzon et al. 2008).

Worldwide, there have been demonstrations that unnaturally high grazing pressure is detrimental to bird species assemblages (Wiens 1973; Martin and Possingham 2005; Batáry et al. 2006). In the highland grasslands, livestock grazing does not simulate the natural herbivory that would have occurred in the area (McNaughton 1986), but the potential impacts of livestock grazing are confounded by the presence of fire as a disturbance agent in the system. These responses to grazing have not previously been compared in combination with the effects of burning frequency. Although grassland systems are naturally maintained by winter and spring fires, there is concern over the possible detrimental impacts of unnaturally frequent fires (coupled with increasing anthropogenic fragmentation) on floral and faunal community structures (Baker 1992; Swengel 2001; Giliomee 2003; Valentine et al. 2007).

Single-taxon approaches to the assessment of disturbance effects on ecological assemblages have been shown to be inadequate, supporting the use of multi-taxon approaches (Milchunas et al. 1998; Söderström et al. 2001). Few studies have explored the responses of insect communities to fire in grasslands, but it has been shown that many arthropod groups decrease rapidly in abundance directly after fire, depending on both the intensity and extent of the burn and the mobility of the taxa concerned (Dunwiddie 1991). Insects respond similarly in areas which are heavily grazedbecause of structural simplification of the habitat and the loss of protective cover (analogous to the effects of fire - Swengel 2001). Changes in insect community structure are likely to have knock-on effects on insectivorous grassland birds (Benton et al. 2002).

While some studies focus at the species level in order to illustrate biodiversity shifts, others have shown that higher taxon richness acts as an adequate surrogate for insect biodiversity, decreasing the need for exhaustive expert identification (Dunwiddie 1991; Williams and Gaston 1994; Gaston and Blackburn 1995; Prendergast and Eversham 1997; Duelli and Obrist 1998; Biaggini et al. 2007; Öster et al. 2008). Most birds, by contrast, are easy to identify to species level.

When focusing on species-level assessments, it has become increasingly clear that species richness alone is a poor biodiversity measure, because changes in habitat structure influence species assemblages through losses and gains of different species (Liversidge

1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005). In other words, species richness can remain constant while assemblage composition changes. This suggests that the responses of individual species and assemblage shifts are important when assessing the impacts of disturbance (Batáry et al. 2006).

Species whose presence in or absence from a particular system reflects some measure of the character of the habitat have been considered as bio-indicators (McGeoch and Chown 1998). Such indicator species further have the potential to signal the effects of disturbances on other species with similar habitat requirements (Noss 1989) and can thus potentially be utilized as an early warning system for habitat degradation. These species, once identified, can also be useful for future monitoring of the system. These shifts in species presence or absence are reflected in shifts in both assemblages (at the taxonomic level) and functional guilds (at the ecological level - Glennon and Porter 2005). Blair (1996) found that bird diversity and abundance along an urban gradient were highest at intermediate levels of disturbance with some species being disturbance avoiders and others being disturbance exploiters. While the use of indicator species is contentious (McGeoch and Chown 1998; Duelli and Obrist 2003; Sauberer et al. 2004), it is important to take into consideration the importance of single-species responses to disturbance and most importantly the responses of habitat specialists. These responses, along with shifts in functional guilds, allow ecologists to infer disturbance processes (Moretti and Legg 2009).

The functional responses of faunal assemblages or the mere presence/absence of birds and arthropods can be used as indicators of changes in the structure and functioning of the environment (Morrison 1986; Martin and Possingham 2005; Child et al. 2009; Vassiliki et al. 2009). Among birds, functional richness (the diversity of functional guilds within a community) has been shown to be closely correlated with species richness at large spatial scales (Child et al. 2009), but at finer scales species' responses are expected to be more indicative of ecosystem functioning. Birds respond rapidly to habitat change and move in response to anthropogenic habitat alteration (Liversidge 1962; Folse 1982; Knopf et al. 1988). They, along with vascular plants and insects, have also been shown to be good surrogates for overall species richness (Sauberer et al. 2004). However, there has yet to be a broad-scale assessment of both the beneficial and detrimental effects of these habitat changes at a multi-taxon and landscape level in South Africa.

This study focuses on the responses of insect and bird assemblages to fire and grazing pressure in the MHGs of South Africa. The study aims to assess the shifts in assemblage structures through the summer growing season and between management types in order to infer the conservation implications of current land-management practices in both conserved areas and the surrounding matrix.

3.2. Study site and methods

The study area falls within the Mesic Highveld Grassland Bioregion and is specifically identified as Lydenberg Montane Grassland (Mucina and Rutherford 2006). All the study sites were on the plateau around the town of Dullstroom (centred at 25º 25”S, 30º 10”E), and were between 1900 and 2200 m.a.s.l. The study sites all comprised undulating hills ranging from ca 1900 - 2200 m.a.s.l. Within each site, the four replicates were chosen such that one was orientated in each of the four cardinal compass directions. The soils are mostly derived from shale and quartzite as well as lavas and dolomites of the Transvaal Supergroup (Mucina and Rutherford 2006): areas dominated by lava and dolomitic soils were avoided as most of the area falls on shale and quartzite soils. The Dullstroom Plateau Grasslands (encompassing this entire study) have been classified as *Endangered* on the basis of very high irreplaceability of species (National List of threatened Ecosystems, Department of Environmental Affairs, notice 1477 of 2009). This vegetation type includes high-altitude plateaux, undulating plains, mountain peaks and slopes, and hills and deep valleys. The predominant vegetation is short grass in the high-lying areas becoming taller on the lower slopes. Grass species diversity is fairly low, but the diversity of forbs is high (Mucina and Rutherford 2006). Orographic precipitation (660-1180 mm per year – Mucina and Rutherford 2006) and heavy mists throughout most months of the year have promoted a unique flora, including a rich diversity of mesophytic plants such as the Orchidaceae. Indeed, forb diversity is so high, with over 2260 plant taxa and 51 endemic plant species, that this grassland type has been proposed as a ‘centre of plant endemism’ (Mucina and Rutherford 2006).

Eight study sites subject to differing management regimes were sampled over two summer seasons. These included an annually burnt farm (AF); communally grazed lands (Com); a biennially burnt farm that was burnt (BF) or was not burnt (BFu) in the study year; a nature reserve site with a high density of indigenous grazing ungulates that was burnt (NRH) or was not burnt (NRHu) in the study year; and a nature reserve site with a low density of indigenous grazing ungulates that was burnt (NRL) or was not burnt (NRLu) in the study year.

Within each study site, four 25 hectare replicates were marked out with at least 500 m between replicates, the largest territory of any of the grassland passerine species in this study is no more than 100 m in diameter (Hockey et al. 2005). Sampling sites were selected with sufficient distance between sites to avoid pseudo-replication (Hurlbert 1984), but were sufficiently close together to standardise as far as possible for extrinsic factors including soil type, rainfall, aspect, slope and temperature.

Field work was conducted during the birds' breeding season (October to March). Grazing data were collected by interviewing farmers or managers of the study sites and were augmented/validated with animal counts. Relative grazing intensity was recorded as the number of hectares of grazing land available per large animal unit (ha/LAU). One LAU is defined as being equivalent to one cow or five sheep, and represents the metabolic equivalent of a 454 kg cow (Meissner et al. 1983; Tainton 1999).

3.2.1. Vegetation structural sampling

Vegetation structure was sampled monthly throughout the sampling season using two techniques (Chapter 2).

3.2.2. Arthropod sampling

Arthropod abundance was sampled monthly along the same transects where birds were censused (see below), using a circular sweep net with a diameter of 450 mm. These samples consisted of 200 sweeps (a sweep is made with each long stride) per transect (600 sweeps per treatment) per month. Sweep nets are effective in catching most of the prey groups eaten by the Motacillidae (insectivorous wagtails - Brodmann and Reyer 1999). Arthropods samples were immediately placed in a sealed container with ethyl acetate. The arthropods were separated from vegetation matter and preserved in ethanol for later identification to order level, this being sufficient resolution to detect taxonomic responses to land use at local scales (Williams and Gaston 1994; Gaston and Blackburn 1995; Prendergast and Eversham 1997; Duelli and Obrist 1998; Zanette et al. 2000; Vickery et al. 2001; Biaggini et al. 2007; Dennis et al. 2008; Öster et al. 2008; Champlin et al. 2009). Samples were then dried and weighed for biomass assessment (Tsukamoto 1988; Morrison et al. 1990; Cressa 1999; Zanette et al. 2000; Boulton et al. 2008). Pitfall trapping was attempted, but controlling for catch success between sites was not possible because of erratic rainfall patterns and the need for traps to stay out for at least three days, this results in some of the replicate samples being destroyed due to flooding and hence no comparable samples.

3.2.3. Bird sampling

In order to quantify presence/absence and abundance of bird species, censuses were undertaken that encompassed all taxa present.

A 50 m weighted rope was dragged along 500 m long line transects. This is a modification of the fixed-strip or belt transect method (Kendeigh 1944) and is the most appropriate census method in large, open areas (where it is more accurate than point counts - Bibby et al. 1992). Rope drags also obviate problems of having to correct for effective transect width and prevent birds from hiding in taller grass clumps and swards (Krook et al. 2007). Birds not utilizing the habitat directly, i.e. flying over, were not included in the analyses.

For each of the four replicates per management type, three 500 m parallel transects were walked perpendicular to a plot boundary: each 500 m transect covered an area of 7.5 ha. These transects were the same as those used for the vegetation surveys (Chapter 2). Censusing began when breeding territories were established in early October and were conducted monthly throughout the breeding season. These were divided into sampling periods in the morning (06h00-10h00) and in the afternoon (14h00-18h00). Census sessions were spread between the two observation periods in rotation according to a randomly selected schedule (MacNally and Horricks 2002).

3.2.4. Statistical analysis

The Software packages PC-ORD 5.10 (McCune and Mefford 2006) and STATISTICA 9.0 (StatSoft Inc. 2009) were used to analyse these data.

To assess differences in bird assemblages based on management type, as a function of season and in response to burning, I averaged the counts per transect and used these averaged values as the monthly count per replicate. I then used a one-way, pairwise, Permutation-based Non-parametric MANOVA or PerManova with a Sørenson (Bray-Curtis) distance measure and 5000 iterations (Anderson 2001) and a pairwise Multi-Response Permutation Procedure (MRPP) using a Sørenson distance measure and a natural weighting (Mielke 1984). MRPP is a non-parametric test of differences between groups (species assemblages), designed for multivariate analysis of terrestrial communities. The A-statistic (chance–corrected, within-group agreement) describes effect size: when A = 0, groups are no more or less different than expected by chance; when A = 1, sample units within groups are identical (McCune and Mefford 2006). Sørenson distance measures were selected as these are recommended for abundance data and give robust outputs with zero-dominated data sets (McCune and Grace 2002). Both PerManova and MRPP results are reported as MRPP is considered more robust while PerManova has been more extensively published (McCune and Grace 2002).

To assess the relative influences of grazing (domestic *vs* indigenous animals) and burning (burnt *vs* unburnt), based on bird species richness and abundance (calculated as average abundance from the three monthly transects per replicate), I conducted Wilcoxon Matched-Pairs tests. To assess the difference in bird species richness and arthropod biomass between management types as a function of season and in response to burning I conducted Analyses of Variance (ANOVA) with *post hoc* Tukey Tests.

To assess species' as well as functional guild responses to management type and month, I ran an Indicator Species Analysis (McCune and Mefford 2006) using a Monte Carlo Test of significance with 5000 permutations (Dufrêne and Legendre 1997). This method combines species' abundances and occurrence: a 'perfect indicator' should be present in all replicates within a site and not present in any other sites, this would have an indicator value of 100.

To determine which vegetation structural indices play the most important role in predicting bird species richness and arthropod diversity, I used a Backwards Stepwise Multiple Regression with a partial correlation analysis. The *beta* coefficient compares the relative contribution of each independent variable in the prediction of the dependent variable. The tolerance of a variable is defined as 1 minus the squared multiple correlation of this variable with all other independent variables in the regression equation. Therefore, the closer to zero the tolerance of a variable, the more redundant is its contribution to the regression.

Non-metric Multidimensional Scaling Ordinations (Kruskal 1964; Mather 1976) were run using a Sørenson distance measure with 250 runs of the real data and 500 iterations in order to separate out replicate sites in bird species space and monthly samples in arthropod biomass space. DPM data were secondarily overlaid over the ordination with vegetation structural indices as a biplot. Orthopteran abundance data were secondarily overlaid onto the ordination and illustrated as a biplot.

To assess grassland bird assemblage site preference a Two-way Cluster Dendrogram (McCune and Mefford 2006) with a Sørenson distance measure and group-average linking method without relativisation was run.

3.3. Results

3.3.1. Arthropods

Of the 32 159 arthropods collected, Coleoptera accounted for 36.6%, Orthoptera 33.5%, Hemiptera 8.5%, Diptera 7.9%, Hymenoptera (excluding ants) 3.5%, Araneae 3.3%, Caterpillars 2.8% and ants 2.1%. Isoptera, Thysonaptera, Psocoptera, Mantodea, Phasmatodea, Lepidoptera, Blattodea, Ixodida, Trichoptera, Odonata and Dermaptera collectively accounted for the remaining 1.6% (Fig. 1a)

Overall biomass was dominated by Orthoptera (Figs 1b and 1c), which, at any one site, reached highest biomass in the year in which that site had been burnt (Wilcoxon Matched-Pairs Test, $p < 0.001$). When compared between management practices, there were marked differences in orthopteran biomass in between all burnt *vs* all unburnt sites combined (ANOVA, *post hoc* Tukey Test, $p < 0.01$, df = 79), indicating that burning strongly influences orthopteran biomass.

In areas burnt in that year (in the moNth before sampling started), Orthopteran biomass increased towards the end of the summer with significant differences between both October/November and January (ANOVA, *post hoc* Tukey Test, $p < 0.05$), and between October/November and February (ANOVA, *post hoc* Tukey Test, $p < 0.001$ – Fig. 1c). Total arthropod biomass mirrored the patterns of orthopteran biomass, highlighting the overriding contribution of Orthoptera to overall arthropod biomass in this system (Figs 1b, 1c). This is confirmed by the significant relationship between Orthoptera biomass and total arthropod biomass (Mantel Test, $t = 2.92$, $p < 0.005$).

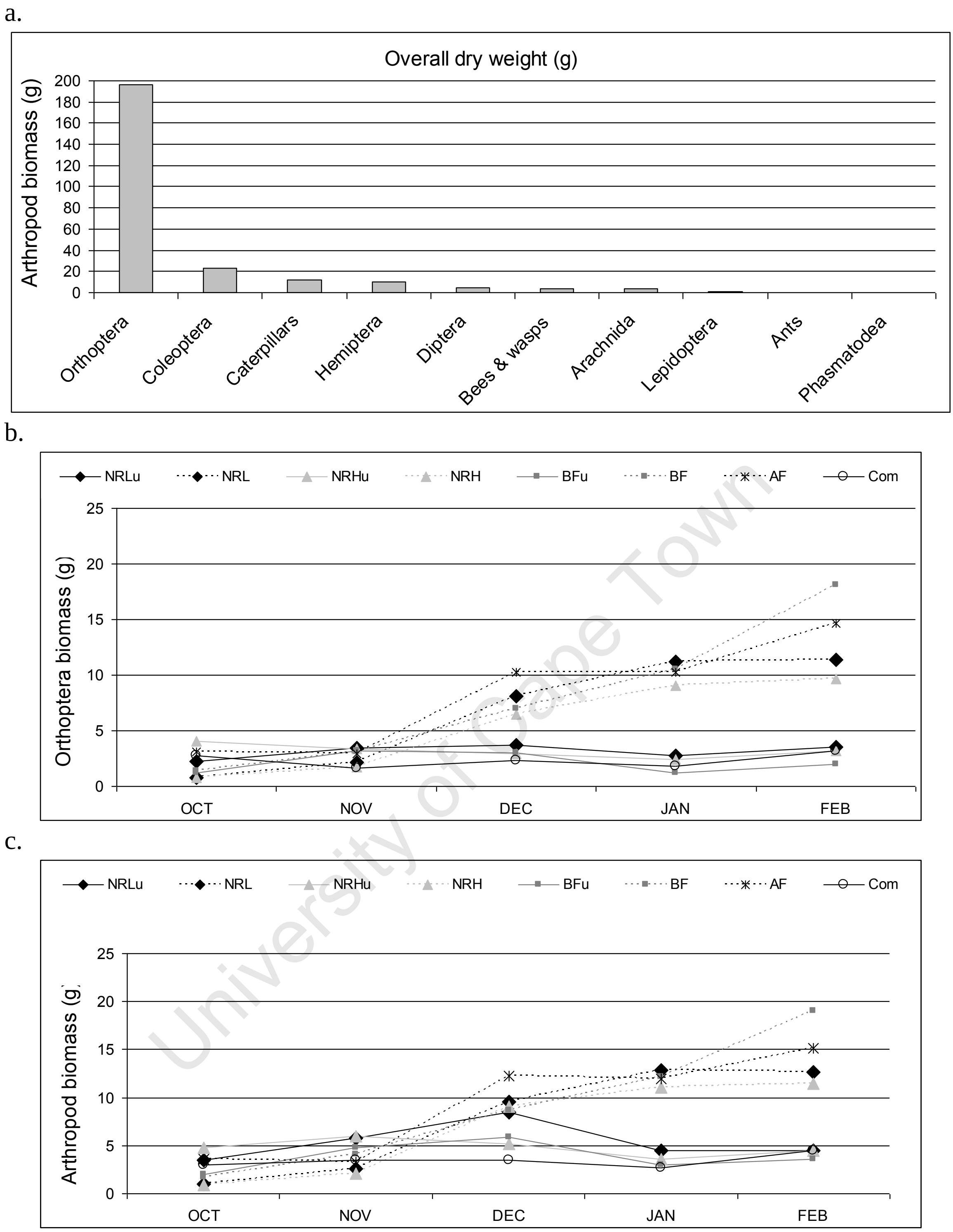


Fig. 1. (a) relative biomass of each arthropod order in MHGs, this pattern was similar in all management types; (b) monthly trends in orthopteran biomass (dry weight in grams per 25 ha) through the summer season; and (c) biomass of all arthropods from all sites and all sampling months.

Vegetation structural indices were explored as possible explanations as to why insect ordinal diversity changes across time and according to management (Fig. 2). Both forb cover and vegetation biomass ($kg.ha^{-1}$) played an roles in structuring insect assemblages at the ordinal level, but this was not convincing given the low r^2 values (Table 1, Appendix 2).

Table 1. Partial correlation analysis illustrating the two vegetation structural indices which play the most important role in predicting arthropod ordinal diversity (measured using the Shannon Index). Overall regression results: $r^2 = 0.52$, $F_{3, 145} = 25.75$, $p < 0.001$ (see Chapter 2 for all ten vegetation structural indices that were included in this analysis).

	Beta	Tolerance	r^2	t(145)	p
%Forb	-0.292	0.978	0.011	-4.065	0.001
DPM	0.453	0.989	0.021	6.315	0.000

Arthropod biomass varied according to time of year and land management. This variation in biomass was similar for all arthropod orders except for orthopterans which showed high biomass in late summer in burnt sites. This variation in arthropod diversity per site per month can be illustrated in 2-dimensional space (Fig. 2), making it possible to identify sites that have similar arthropod biomasses. Group B includes sites that had very recently been burnt and supported the lowest arthropod biomass. Group C were unburnt sites with relatively high biomass of non-orthopteran arthropods (mainly Hemiptera and Coleoptera). Group A comprised sites that were sampled in late summer and were burnt in that year: these had high overall arthropod biomass dominated by Orthoptera.

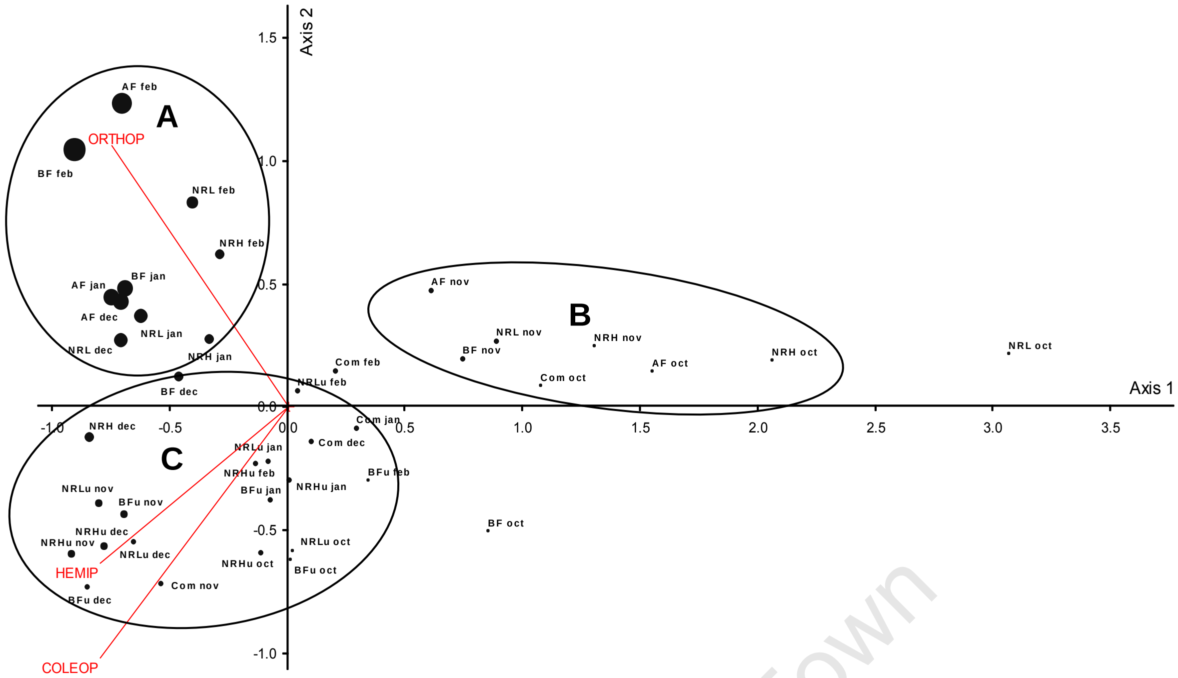


Fig. 2. Non-metric Multidimensional Scaling ordination of arthropod biomass per site per month. Orthopteran biomass per site per month is overlaid and indicated by the size of the black circles. Arthropod ordinal biomass is illustrated as a biplot (lines extending from the centre of the graphic): the length and direction of the lines illustrate the biomass and in which sites these orders were more abundant. Group A was characterized by high Orthoptera (Orthop) biomass while group C was characterized by high Hemiptera (Hemip) and Coleoptera (Coleop) biomass. Axes one and two respectively explained 30.05% and 24.83% of the variance in the original distance matrix.

With the exception of orthopterans, arthropods in general showed a preference for unburnt areas, illustrating a sensitivity to this form of disturbance. However, the dominance of orthopterans in the system resulted in burnt areas having higher overall arthropod biomass in the latter part of the season than unburnt areas.

3.3.2. Birds

Bird species assemblages responded strongly to management (PerManova, $p < 0.001$; MRPP, $A = 0.59$, $p < 0.005$). With an observed decrease in both overall bird abundance and the number of specialist grassland species with increasing frequency of burning and intensity of grazing: this response was significant across all management types (PerManova, $p < 0.05$; MRPP, $A > 0.21$, $p < 0.05$) except NRH *vs* Com, BFu *vs* Com and BF *vs* AF.

Bird species assemblages also changed as the breeding season progressed (PerManova, $p < 0.001$; MRPP, $A = 0.14$, $p < 0.0001$), with abundance decreasing through the season (Fig. 3). Bird abundance in October was significantly greater than in both January (PerManova, $p < 0.05$; MRPP, $A = 0.12$, $p < 0.01$) and February (PerManova, $p < 0.05$; MRPP, $A = 0.11$, $p < 0.05$). Abundance in November was also significantly greater than in both January (PerManova, $p < 0.01$; MRPP, $A = 0.15$, $p < 0.005$) and February (PerManova, $p < 0.005$; MRPP, $A = 0.18$, $p < 0.005$). There was a general shift from assemblages being dominated by specialist grassland insectivores early in the season to dominance by nomadic granivores in the latter part of the season, after most of these insectorous species had completed breeding. Finally, bird species assemblages were affected by whether or not an area was burnt in the year of sampling, regardless of grazing pressure (PerManova, $p < 0.05$; MRPP, $A = 0.24$, $p < 0.05$), with overall abundance and the abundance of grassland specialist species being lower if an area was burnt in that year. Overall, the influence of burning over-rode that of grazing in terms of both species richness (Wilcoxon Matched-Pairs Test, $Z = 2.97$ $p < 0.005$) and abundance (Wilcoxon Matched-Pairs Test, $Z = 3.10$ $p < 0.005$), both of which decreased with annual burning. Grazing intensity plays a role when all four farm sites (high grazing pressure) are compared with all four reserve sites (low grazing pressure). Birds were almost twice as abundant in the nature reserve as they were on farms (Wilcoxon Matched-Pairs Test, $Z = 3.75$, $p < 0.001$).

Burning drives bird assemblage structure early in the breeding season while grazing intensity drives late-season assemblage structure (Fig. 3). Early season (October) assemblages were strongly influenced by whether or not a site was burnt. As the season progressed, however, and burnt areas recovered, recovery of the vegetation structure promoted a within-season shift in bird assemblage structure until, in the late part of the growing season (February), differences in bird species assemblages were driven by disturbance through grazing.

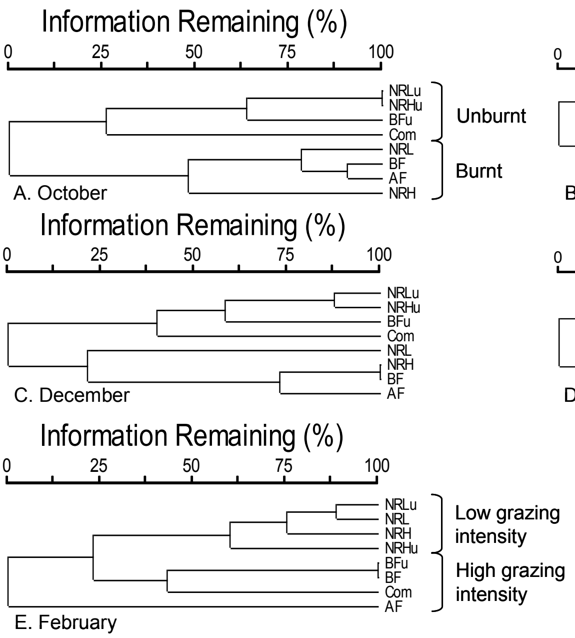


Fig. 3. Cluster analyses showing shifts in the main drivers of bird assemblage structure through the breeding season.

Bird species assemblages and species abundances were significantly different between burnt and unburnt sites for all months of the breeding season (MRPP, A = 0.22, $p < 0.005$). Thus, if a site was burnt at the beginning of a breeding season (prior to the first bird surveys), this had an overriding influence on bird species assemblage structure for the remainder of that season (Fig. 3).

When burnt and unburnt sites were combined, and management strategies were separated into four levels of grazing intensity (NRL, NRH, BF, and AF combined with Com) a seasonal structuring of bird species assemblages was evident. In October, all four levels of grazing were significantly different from one another (MRPP $A > 0.09$, $p < 0.05$). By November and December only NRL was significantly different from all other sites (MRPP, $A > 0.14$, $p < 0.05$). By January, NRH and AF+Com were also significantly different from the other sites (MRPP, $A > 0.08$, $p < 0.05$). By the end of February all treatments had differing species assemblages (MRPP, $A> 0.15$, $p < 0.005$). In this month the reserve treatments grouped together, separate from the livestock farms, suggesting that with increasing time since burning, the grazing regime (pressure and possibly the type of grazers) plays an increasingly important role in determining both bird species diversity and community composition (Fig. 4).

Bird species richness on the other hand showed a marked difference only between the seasonal extremes (October *vs* February - ANOVA, *post-hoc* Tukey Test, $p < 0.05$).

There were marked differences in overall species richness between NRL and all other sites except Com (ANOVA, *post-hoc* Tukey Test, p < 0.01), as well as between AF and all reserve sites (ANOVA, *post-hoc* Tukey Test, p < 0.005).

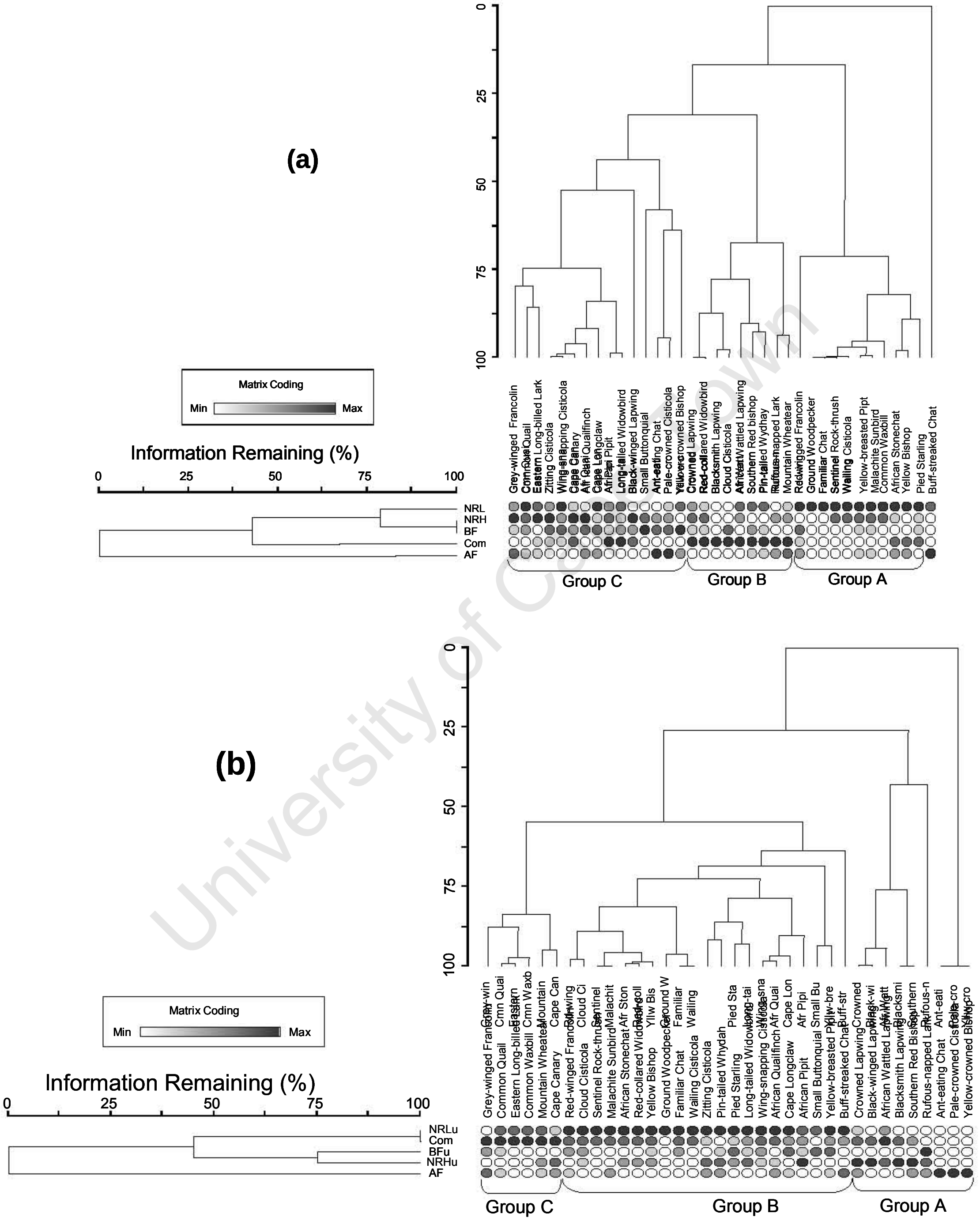


Fig. 4. Bird species assemblages (based on abundance) as a function of whether or not a site was burnt in the focal year: (a) includes only abundance measures from sites that were burnt in that season, while (b) includes only abundance measures from sites that were not burnt in that year. Communal lands and the annually burnt farm were included in both (a) and (b) for comparative purposes (they are both managed in the same way in all years).

When considering species-specific responses to disturbance, abundances did not appear to respond strongly to the presence or absence of fire (Fig. 4). Most species showed a preference for the conserved area with a low density of native ungulates (NRL), while a small proportion of species show a preference for disturbed areas (Table 2). Included within the species assemblage that prefers the conserved area are the grassland specialist species.

Table 2. Grassland associated bird species with site-specific distributions illustrating habitat preference. Scientific names are provided in Appendix 1.

Species	Site	Observed indicator value[ж] (IV)	IV from randomized groups		P
			Mean	Std Dev.	
Jackal Buzzard	NRLu	37.5	21.5	8.4	0.042
Pallid Harrier	NRLu	44.4	18.7	8.4	0.017
Red-winged Francolin	NRLu	34.8	22.5	6.0	0.039
Sentinel Rock-Thrush	NRLu	48.4	20.0	7.4	0.005
Familiar Chat	NRLu	70.8	21.1	9.5	0.001
African Stonechat	NRLu	39.9	20.7	6.1	0.005
Cloud Cisticola	NRLu	35.6	21.2	7.0	0.044
Yellow-breasted Pipit	NRLu	36.7	22.4	6.5	0.033
Cape Longclaw	NRLu	22.9	17.8	1.9	0.014
Malachite Sunbird	NRLu	35.7	19.7	5.5	0.001
Red-collared Widowbird	NRLu	51.1	19.9	8.1	0.006
Common Quail	NRL	32.4	20.7	4.8	0.015
Ground Woodpecker	NRL	40.6	18.7	9.1	0.044
Cinnamon-breasted Bunting	NRL	45.0	19.0	9.3	0.038
Grey-winged Francolin	NRHu	54.0	23.3	10.2	0.019
Eastern Long-billed Lark	NRHu	38.9	22.2	4.9	0.000
Mountain Wheatear	NRHu	34.8	20.6	5.6	0.018
Cape Canary	NRHu	28.4	20.1	2.7	0.006
Banded Martin	BFu	30.6	20.1	2.7	0.002
Amur Falcon	BF	57.4	29.4	11.7	0.024
Southern Bald Ibis	AF	51.1	19.0	9.3	0.008
Ant-eating Chat	AF	50.0	20.1	8.5	0.010
Bokmakierie	AF	50.0	19.6	9.9	0.023
Black-headed Heron	Com	39.5	20.9	8.4	0.036
Blacksmith Lapwing	Com	72.3	18.1	11.4	0.006
Cape Wagtail	Com	44.3	19.9	9.0	0.020
African Pipit	Com	17.6	15.7	1.1	0.040

[ж] Indicator values range from 0-100. A ‘perfect indicator’ scoring 100 is present in all replicates within a site and not present in any replicates in any other sites.

When a similar analysis was run for functional feeding guilds, habitat preferences were also evident with most guilds showing a preference for the conserved area (NRL) and relatively few favouring disturbed areas. Only six of the 15 functional feeding guilds showed significant responses to disturbance (Table 3).

Table 3. Functional guilds (from Hockey et al. 2005) with site-specific distributions illustrating habitat preferences. All the analysed guilds are represented but only those guilds in bold exhibited significant, habitat-related differences in distribution.

Guild	Site	Observed indicator value (IV)	IV from randomized groups		P
			Mean	S.D.	
Water-associated species	**NRLu**	**29.7**	**19.2**	**2.8**	**0.001**
Rocky outcrop insectivores	**NRLu**	**32.0**	**21.6**	**3.6**	**0.010**
Insectivores	**NRLu**	**19.7**	**15.4**	**1.0**	**0.000**
Nectarivores	**NRLu**	**35.4**	**18.1**	**5.6**	**0.010**
Grazers	**Com**	**57.1**	**16.0**	**7.9**	**0.002**
Terrestrial insectivores	**Com**	**37.9**	**20.5**	**3.7**	**0.000**
Generalists	NRLu	19.4	18.9	2.6	0.405
Snake predators	NRLu	40.0	13.0	9.1	0.102
Rodent & insect predators	NRLu	26.1	19.9	3.6	0.066
Bird predators	NRLu	25.0	15.7	7.3	0.191
Frugivores	NRLu	20.0	20.0	0.3	1.000
Terrestrial omnivores	NRHu	22.7	20.1	3.5	0.224
Scavengers	NRHu	24.8	17.4	8.1	0.169
Granivores	NRHu	20.6	18.5	2.8	0.160
Aerial insectivores	BFu	19.4	18.0	2.0	0.225

Grassland birds rely on the structure of the vegetation for foraging, nesting and predator avoidance, but it is uncertain what indices can be derived to provide a rapid assessment of grassland bird species richness and what specific vegetation structural aspects are most important for sustaining a diversity of bird species. Bird species richness increased with increasing vegetation cover and biomass, and decreased with increasing average horizontal vegetation density (Table 4.).

Table 4. Percentage vegetation cover, phytomass (derived from DPM measures) and average horizontal density (out of ten original vegetation structural indices) were extracted by Partial Correlation Analysis as performing best at differentiating between the effects of management types on bird species richness. Overall regression results: $F_{3, 144} = 11.159$, $R^2 = 0.189$, $p < 0.001$ (see Chapter 2 for all ten vegetation structural indices that were included in this analysis).

	Beta	Tolerance	r^2	t(144)	p-level
% Veg.	0.361	0.475	0.525	3.316	0.020
DPM	0.335	0.635	0.365	3.561	0.001
AvHorDen	-0.652	0.407	0.593	-5.535	0.000

To investigate how management treatments separated out according to bird species abundance, bird count data were plotted in 2-dimensional ordination space (Fig. 5). On axis 1, sites separated out according to whether or not they were burnt in that year (groups B and C *vs* groups D and E). On axis 2, the nature reserve areas (A and B) separate out from farmlands (especially C and D, with group E being intermediate between the nature reserve and other farmed sites). Axes 1 and 2 respectively explained 33.42% and 18.90% of the variance in the original distance matrix (total 52.32%).

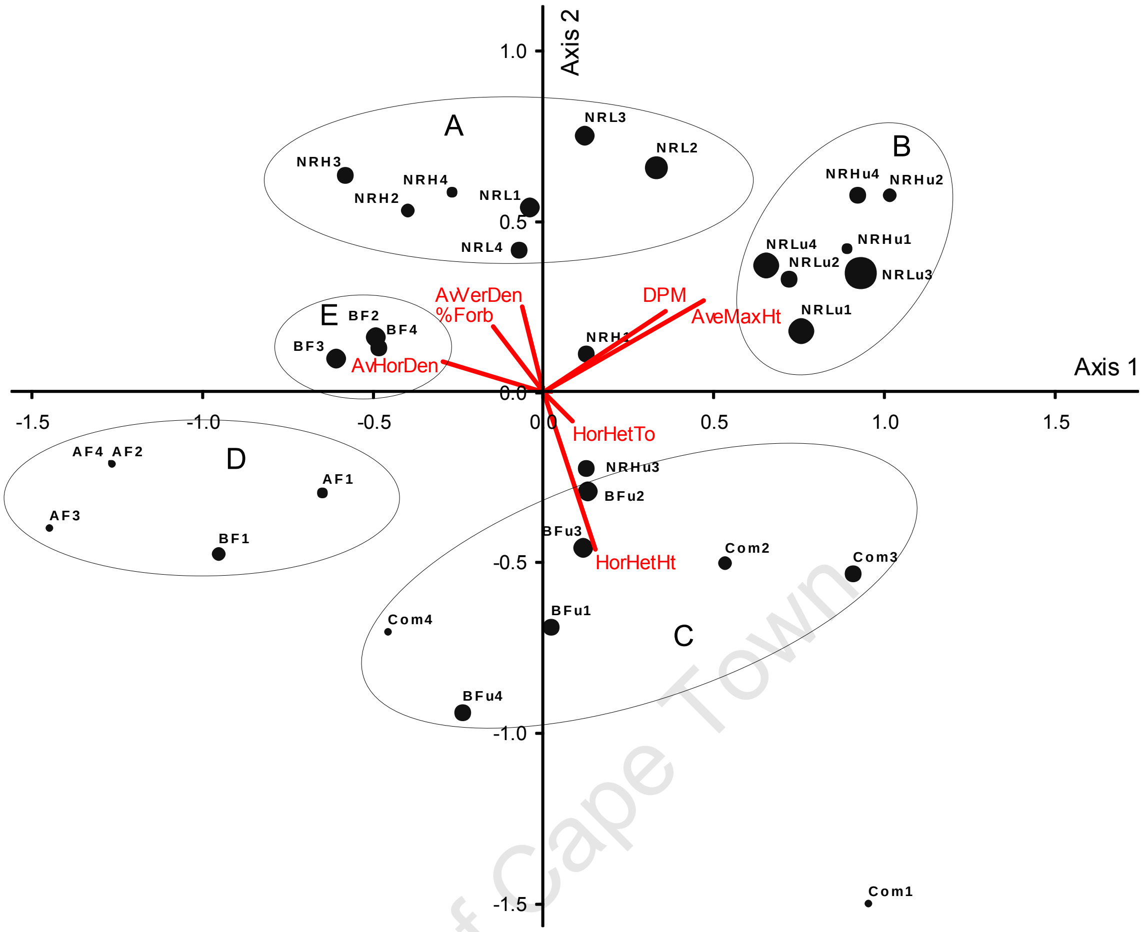


Fig. 5. Non-metric Multi-dimensional Scaling Ordination with ordination space based on bird species counts. Symbol sizes are based on overlaid vegetation biomass values, with larger circles indicating higher vegetation biomass. Axis 1: p = 0.036, Axis 2: p = 0.012. The influence of vegetation structure on bird assemblage is illustrated as a biplot (lines extending from the centre of the graphic), the direction and length of the lines illustrate the strength of the influence of each vegetation structural index on bird assemblages within sites. The groupings A – E were selected subjectively to illustrate the separation of bird assemblages in ordination space.

3.4. Discussion

Multiple factors influence the composition of bird assemblages, including disturbance, changes in habitat structure and variation in food availability (Morrison 1986). These responses can vary from losses or gains of individual species to entire assemblage shifts (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005). Some studies of bird assemblage responses to habitat disturbance have been carried out in South Africa (Mentis and Little 1992; Little and Crowe 1994; Cameron 1999; Jansen et al. 1999; Ratcliffe and Crowe 2001; Little et al. 2005; Fox and Hockey 2007). To date, however, none of these studies has focused on the direct and relative effects of grazing and burning on grassland fauna and flora.

In terms of the arthropod population on which many grassland birds depend, grazing can lead to decreases in some arthropod orders, including spiders, which in turn can lead to concomitant decreases in the species richness and abundance of grassland insectivores (Dennis et al. 2008). Heavy grazing also leads to decreases in forage palatability, suggesting that intensive management can also reduce the carrying capacity for livestock (Milchunas et al. 2005).

The arthropod biomass of MHGs is dominated by Orthoptera: these accounted for 78% of the total arthropod biomass throughout the study period. All arthropod taxa decline markedly immediately following a burn (Swengel 2001). In this study, overall arthropod biomass increased from early spring through to late summer, with the most rapid and substantial increases occurring in sites that were burnt at the start of the current season. This response is a result of grasshopper prevalence in the late summer months in burnt sites, probably explained by their preference for grazing new growth (Swengel 2001). Livestock grazing intensity does not appear to have a marked effect on any arthropod order, even though heavy grazing leads to habitat simplification (Chapter 2, Swengel 2001). Vegetation structure, largely controlled by burning, seems to have some effect on arthropod biomass, with vegetation density and arthropod biomass being positively, but weakly, correlated (Table 1). Similarly, forb cover is high soon after burning because large-leaved forbs re-sprout rapidly after fire (Everson et al. 1989). However, as the growing season progresses, grasses become increasingly dominant. The non-grasshopper arthropod biomass is dominated by Coleoptera, Hemiptera and Lepidoptera larvae. These groups respond negatively to burning in that season and prefer areas that have remained unburnt for more than a year (Fig. 2).

Bird assemblage structure shifts seasonally. Within sites (regardless of burning or grazing regimes), assemblages at the end of the season differ significantly from those at the start of the season (Fig. 3), but much of this shift may reflect the completion of breeding attempts, with species breeding more successfully becoming increasingly numerically dominant and some species forming flocks. A comparison of time since burning, however, shows very clear differences between sites that were burnt in the current season and those that were not, especially at the start of the breeding season. As the summer season progresses, however, the importance of grazing intensity increases and, by late summer, grazing has a strong influence on bird assemblage structure (Fig. 3).

However, if grazing and burning are treated as separate extrinsic forces and compared throughout the season, burning frequency overrides grazing intensity as the main driver of species assemblage structure. Both bird abundance and species richness were higher in all unburnt sites relative to sites that had been burnt in that season. A distinct cluster of bird species showed sensitivity to both grazing intensity and burning frequency (Group A in Fig. 4a and Group B in Fig. 4b). These species have high indicator values (Table 2) specific to the NRLu, suggesting that they are the species most prone to disturbance. Within this assemblage of species, the Yellow-breasted Pipit *Anthus chloris* is regionally and globally *Vulnerable* (Barnes 2000; BirdLife International 2010) and the Pallid Harrier *Circus macrourus* is globally *Near-threatened* (BirdLife International 2010).

Another distinct bird assemblage exploits disturbed areas. These species appear in group A of Fig. 5b and include species that are characteristic of sites AF and Com (Fig. 5). While the majority of the species that benefit from disturbance are common and widespread, the Southern Bald Ibis *Geronticus calvus* (recorded previously as favouring disturbed areas - Jansen et al. 1999) is regionally and globally *Vulnerable* (Barnes 2000; BirdLife International 2010). Overall, however, these farming areas support a lower species richness and abundance of birds than does the conserved area and lack many threatened and specialist species. However, the disproportionate use of farmed areas by even one threatened taxon highlights the need for a large-scale mosaic of habitat management if the focus is to conserve the maximum number of species (Söderström et al. 2001). This mosaic can be sustained and supplemented with the use of large fire-breaks as these have been shown to have little impact on the floral component as well as the soil integrity (O'Connor et al. 2005). These fire-breaks act as annually burnt patches and in conjunction with a paddocks of biennially burnt land create the desired mosaic of habitat management.

Even though not all avian functional guilds were significantly influenced by management practices, it is apparent that the majority (71%) of functional groups are concentrated in the reserve sites and, of these, 75% show preference for the conservatively managed (lower grazing intensity) part of the reserve. In all management types, rocky outcrops provide refuge habitat for a diversity of plants, arthropods and reptiles, because they are a) protected from both fire and grazing (Jansen et al. 1999) and b) provide nesting and feeding habitat for some birds (Milchunas and Noy-Meir 2004). In the MHGs, nectarivores require intact rocky outcrops for feeding purposes because flowering plants (such as *Leonotis* spp.) are confined to these areas. The grassland specialist Red-winged Francolin *Scleroptila levaillantii* is also confined to these rocky outcrop habitats because surrounding grazed grasslands are ecologically unavailable due to the short sward height and depletion of food plants (Jansen et al. 2000, 2001). Further work quantifying the effectiveness of these areas as refuges is recommended. Water-associated species are confined to intact wetlands (for which Verloren Valei has been recognized as a RAMSAR site by the International Convention on Wetlands): these include birds such as flufftails, aquatic cisticolas and warblers. Grassland-nesting insectivorous passerines are sensitive to habitat disturbance (see Chapter 4) resulting in their preference for conserved areas, while terrestrial insectivores (lapwings and thick-knees) and grazers (anatids) prefer open and short-grass areas for foraging, which can lead to disturbed areas being artificially species rich.

Shifts in bird species richness and diversity are driven (at least in part) by vegetation structural change, including phytomass, cover and horizontal density (Erdelen 1984; Martin and Possingham 2005; Wiens 1974; Wiens and Rotenberry 1981). Phytomass is inversely correlated with grazing intensity (Fig. 3), but this is not the only disturbance effect that drives bird species assemblages. In grasslands, where nesting birds require vegetation cover in which to conceal their nests, phytomass is critical for territory selection and effective reproduction (Batáry et al. 2006). Average horizontal density of vegetation is negatively correlated with bird species richness: this is explained by the structure of growing grasses. In areas that are not heavily grazed, tuft-forming grasses produce a canopy in the later seasonal growth stages. This results in low vegetation density close to the ground (but cover above), providing suitable nesting habitat. Intensive grazing results in a more lawn-like structure (Chapter 2) with little opportunity for nest concealment.

In conclusion, it is apparent that fire and grazing interplay as factors influencing both bird and arthropod diversity (Engle et al. 2008; Fuhlendorf et al. 2008). In moist highland grasslands, however, the influence of fire frequency generally overrides that of grazing intensity in influencing both arthropod and bird assemblage structures: this is clearly illustrated by the depauperate faunas that characterize annually burnt areas. Vegetation structural indices are important for predicting both bird and arthropod species richness, as has been shown previously (Wiens 1974; Wiens and Rotenberry 1981; Erdelen 1984; Martin and Possingham 2005). However, focusing on bird diversity and functional guild richness yields more relevant information to guide conservation action. Thus, from the results of this chapter, it is recommended that bird counts can (as well as vegetation and arthropod diversity) be used to assess grassland functional integrity. Of the three taxonomic groups, however, birds are the easiest to count and the most responsive to disturbance.

Appendix 1. A list of the bird species recorded in the study sites during survey transects in different management types (see Chapter 5, Appendix 1).

Reed Cormorant	*Phalacrocorax africanus*
Black-headed Heron	*Ardea melanocephala*
Cattle Egret	*Bubulcus ibis*
Hamerkop	*Scopus umbretta*
African Sacred Ibis	*Threskiornis aethiopicus*
Southern Bald Ibis	*Geronticus calvus*
Hadeda Ibis	*Bostrychia hagedash*
Egyptian Goose	*Alopochen aegyptiaca*
African Black Duck	*Anas sparsa*
Spur-winged Goose	*Plectropterus gambensis*
Secretarybird	*Sagittarius serpentarius*
Cape Vulture	*Gyps coprotheres*
Black Kite	*Milvus migrans*
Black-shouldered Kite	*Elanus caeruleus*
Verreaux's Eagle	*Aquila verreauxii*
Long-crested Eagle	*Lophaetus occipitalis*
Black-chested Snake-Eagle	*Circaets pectoralis*
African Fish-Eagle	*Haliaeetus vocifer*
Steppe Buzzard	*Buteo vulpinus*
Jackal Buzzard	*B. rufofuscus*
Rufous-chested Sparrowhawk	*Accipiter rufivestris*
Ovambo Sparrowhawk	*A. ovampensis*
Black Sparrowhawk	*A. melanoleucus*
Pallid Harrier	*Circus macrourus*
African Harrier-Hawk	*Polyboroides typus*
Amur Falcon	*Falco amurensis*
Rock Kestrel	*F. rupicolis*
Grey-winged Francolin	*Scleroptila africanus*
Red-winged Francolin	*S. levaillantii*
Natal Spurfowl	*Pternistis natalensis*
Common Quail	*Coturnix coturnix*
Helmeted Guineafowl	*Numida meleagris*
Small Buttonquail	*Turnix sylvaticus*
Blue Crane	*Anthropoides paradiseus*
Red-chested Flufftail	*Sarothrura rufa*
Denham's Bustard	*Neotis denhami*
Three-banded Plover	*Charadrius tricollaris*
Crowned Lapwing	*Vanellus coronatus*
Black-winged Lapwing	*V. melanopterus*
Blacksmith Lapwing	*V. armatus*
African Wattled Lapwing	*V. senegallus*
African Snipe	*Gallinago nigripennis*
Spotted Thick-knee	*Burhinus capensis*
Water Thick-knee	*B. vermiculatus*
Whiskered Tern	*Chlidonias hybrida*
Speckled Pigeon	*Columba guinea*
Red-eyed Dove	*Streptopelia semitorquata*
Cape Turtle-Dove	*S. capicola*
Namaqua Dove	*Oena capensis*
Red-chested Cuckoo	*Cuculus solitarius*
African Black Swift	*Apus barbatus*
White-rumped Swift	*A. caffer*
Alpine Swift	*Tachymarptis melba*
Speckled Mousebird	*Colius striatus*
Pied Kingfisher	*Ceryle rudis*
European Roller	*Coracias garrulus*
African Hoopoe	*Upupa africana*
Crested Barbet	*Trachyphonus vaillantii*
Ground Woodpecker	*Geocolaptes olivaceus*
Rufous-naped Lark	*Mirafra africana*
Eastern Long-billed Lark	*Certhilauda semitorquata*
Red-capped Lark	*Calandrella cinerea*
Chestnut-backed Sparrowlark	*Eremopterix leucotis*
Barn Swallow	*Hirundo rustica*
White-throated Swallow	*H. albigularis*
Greater Striped Swallow	*H. cucullata*
Rock Martin	*H. fuligula*
Common House-Martin	*Delichon urbicum*
Brown-throated Martin	*Riparia paludicola*
Banded Martin	*R. cincta*
Black Saw-wing	*Psalidoprocne holomelaena*
Black-headed Oriole	*Oriolus larvatus*
Cape Crow	*Corvus capensis*
Groundscraper Thrush	*Psophocichla litsitsirupa*
Sentinel Rock-Thrush	*Monicola explorator*
Mountain Wheatear	*Oenanthe monticola*
Capped Wheatear	*O. pileata*
Buff-streaked Chat	*Campicoloides bifasciatus*
Familiar Chat	*Cercomela familiaris*
Ant-eating Chat	*Myrmecocichla formicivora*
African Stonechat	*Saxicola torquata*
Cape Robin-Chat	*Cossypha caffra*
Great Reed-Warbler	*Acrocephalus arundinaceus*
Cape Grassbird	*Sphenoeacus afer*
Zitting Cisticola	*Cisticola juncidis*
Cloud Cisticola	*C. textrix*
Wing-snapping Cisticola	*C. ayresii*
Pale-crowned Cisticola	*C. cinnamomeus*
Wailing Cisticola	*C. lais*
Levaillant's Cisticola	*C. tinniens*
Tawny-flanked Prinia	*Prinia subflava*
Drakensberg Prinia	*P. hypoxantha*
Spotted Flycatcher	*Muscicapa striata*
African Pied Wagtail	*Motacilla aguimp*
Cape Wagtail	*M. capensis*
African Pipit	*Anthus cinnamomeus*
Long-billed Pipit	*A. similis*
Plain-backed Pipit	*A. leucophrys*
Yellow-breasted Pipit	*A. chloris*
Cape Longclaw	*Macronyx capensis*
Common Fiscal	*Lanius collaris*
Bokmakierie	*Telophorus zeylonus*
Commom Myna	*Acridotheres tristis*
Pied Starling	*Spreo bicolor*
Red-winged Starling	*Onychognathus morio*
Malachite Sunbird	*Nectarinia famosa*
Amethyst Sunbird	*Chalcomitra amethystina*
Cape White-eye	*Zosterops capensis*
Cape Sparrow	*Passer melanurus*
Cape Weaver	*Ploceus capensis*
Cuckoo Finch	*Anomalospiza imberbis*
Southern Red Bishop	*Euplectes orix*
Yellow-crowned Bishop	*E. afer*
Yellow Bishop	*E. capensis*
Fan-tailed Widowbird	*E. axillaris*
White-winged Widowbird	*E. albonotatus*
Red-collared Widowbird	*E. ardens*
Long-tailed Widowbird	*E. progne*
Common Waxbill	*Estrilda astrild*
African Quailfinch	*Ortygospiza atricollis*
Pin-tailed Whydah	*Viduo macroura*
Yellow-fronted Canary	*Serinus mozambicus*
Black-throated Canary	*S. atrogularis*
Cape Canary	*S. canicollis*
Streaky-headed Seed-eater	*S. gularis*
Cape Bunting	*Emberiza capensis*
Cinnamon-breasted Bunting	*E. tahapisi*

Appendix 2. Summarized invertebrate abundance data (dry mass, grams) per treatment (three sweep-net transects for each of the four replicates). Orders were separated into size classes where possible.

		Orthoptera			Coleoptera		Hemiptera		
Treatment	Month	Small	Med	Large	Small	Med	Small	Med	Large
NRLu	Oct	0.62	0.86	0.74	0.33	0.04	0.14	0.06	0.09
	Nov	3.12	0.29	0	0.93	0.19	0.11	0.16	0.26
	Dec	1.87	1.09	0.74	0.86	1.23	0.07	0.53	0.09
	Jan	1.22	1.15	0.37	0.39	0.54	0.05	0.23	0
	Feb	1.67	1.83	0	0.22	0	0.08	0.05	0
NRL	Oct	0.22	0.23	0.37	0.01	0	0	0	0.09
	Nov	1.09	1.09	0	0.15	0.08	0	0.06	0
	Dec	6.51	1.26	0.37	0.4	0.31	0.11	0.14	0.09
	Jan	5.81	4.29	1.12	0.32	0.08	0.07	0.17	0
	Feb	4.39	5.9	1.12	0.08	0	0.02	0.06	0.09
NRHu	Oct	0.75	1.77	1.49	0.49	0	0.16	0	0
	Nov	2.43	0.92	0	3.09	0.04	0.14	0.06	0
	Dec	2.27	0.69	0	1.14	0.12	0.05	0.19	0
	Jan	1.25	0.8	0.37	0.47	0.08	0.02	0.19	0
	Feb	1.26	1.89	0	0.45	0.04	0.06	0.08	0
NRH	Oct	0.33	0.46	0	0.04	0	0	0.01	0
	Nov	0.64	0.74	0.37	0.1	0	0	0.05	0.09
	Dec	4.41	1.32	0.74	0.86	0.19	0.07	0.4	0.17
	Jan	3.36	4.98	0.74	0.3	0.12	0.02	0.33	0.26
	Feb	3.11	6.18	0.37	0.14	0	0.02	0.15	0
BFu	Oct	0.35	0.86	0	0.39	0	0.12	0.04	0
	Nov	2.31	0.86	0	0.97	0.15	0.06	0.03	0
	Dec	1.73	0.52	0.74	1.2	0.23	0.12	0.11	0.09
	Jan	1	0.23	0	0.46	0.08	0.04	0.43	0.17
	Feb	0.61	1.37	0	0.23	0.08	0.03	0.13	0
BF	Oct	0.25	1.09	0	0.28	0	0.01	0	0
	Nov	0.84	1.89	0.37	0.11	0.19	0.02	0.05	0.43
	Dec	4.12	0.97	1.86	0.4	0.15	0.04	0.28	0
	Jan	7.14	2.98	0.37	0.27	0.19	0.06	0.23	0
	Feb	10.66	6.35	1.12	0.11	0	0.04	0.16	0
AF	Oct	0.26	1.32	1.49	0.07	0.12	0.01	0.05	0.09
	Nov	1.79	1.15	0	0.14	0	0.01	0.07	0
	Dec	7.26	1.49	1.49	0.4	0.08	0.02	0.22	0.09
	Jan	7.8	2.06	0.37	0.4	0.15	0.02	0.24	0.09
	Feb	9.26	3.55	1.86	0.09	0	0.01	0.06	0
Com	Oct	0.7	0.57	1.49	0.08	0.04	0.03	0.01	0
	Nov	1.28	0.34	0	0.87	0.04	0.05	0.08	0
	Dec	1.52	0.46	0.37	0.3	0.04	0.02	0.06	0.09
	Jan	1.49	0.29	0	0.32	0.04	0.03	0.12	0.09
	Feb	1.78	1.43	0	0.21	0.15	0.05	0.2	0
Total		**108.49**	**67.5**	**20.48**	**18.11**	**4.77**	**2.01**	**5.49**	**2.3**

Appendix 2 continued…

		Lepidoptera		Caterpillars			Diptera			Ticks
Treatment	Month	Small	Med	Small	Med	Large	Small	Med	Large	
NRLu	Oct	0.01	0	0.09	0.28	0	0.05	0.03	0.01	0
	Nov	0.03	0.01	0.02	0.09	0.15	0.1	0.2	0	0
	Dec	0.01	0	0.17	1.29	0.25	0.06	0.04	0	0
	Jan	0.04	0	0.04	0.09	0	0.04	0.03	0	0
	Feb	0.02	0.02	0.03	0.3	0	0.03	0.07	0.04	0
NRL	Oct	0	0.01	0	0	0	0	0.01	0	0
	Nov	0	0	0.01	0.04	0	0.01	0.02	0	0
	Dec	0	0	0.01	0.08	0	0.05	0.05	0	0
	Jan	0.01	0.02	0.04	0.4	0.15	0.04	0.03	0.01	0
	Feb	0	0	0.05	0.46	0.05	0.04	0.06	0	0
NRHu	Oct	0	0	0.01	0.02	0	0.02	0.01	0.01	0
	Nov	0	0.04	0.01	0.06	0	0.05	0.05	0.01	0
	Dec	0.01	0	0.03	0.25	0.1	0.02	0.06	0	0
	Jan	0	0	0.03	0.15	0	0.02	0.03	0	0
	Feb	0	0	0.02	0.32	0	0.05	0.13	0.02	0
NRH	Oct	0	0	0.01	0	0	0	0	0	0
	Nov	0	0	0	0	0	0.01	0.05	0	0
	Dec	0	0	0.2	0.38	0	0.02	0.07	0.05	0
	Jan	0	0.04	0.15	0.46	0.1	0.03	0.04	0.02	0
	Feb	0	0.05	0.04	0.64	0	0.05	0.16	0.15	0
BFu	Oct	0	0.01	0.04	0	0	0.05	0.02	0	0.01
	Nov	0	0	0.04	0.09	0	0.08	0.1	0.01	0
	Dec	0	0	0.18	0.3	0	0.19	0.1	0.04	0
	Jan	0	0	0.03	0.15	0	0.05	0.04	0.03	0
	Feb	0	0	0.02	0.23	0.3	0.09	0.05	0.15	0
BF	Oct	0	0.01	0	0.02	0	0.02	0.06	0	0
	Nov	0	0	0.01	0.02	0	0.04	0.11	0.01	0
	Dec	0	0	0.15	0.19	0.05	0.06	0.12	0	0
	Jan	0	0	0.03	0.25	0.1	0.09	0.05	0.01	0
	Feb	0.01	0	0.03	0.13	0.1	0.04	0.12	0	0
AF	Oct	0	0	0	0.02	0	0.01	0.01	0	0
	Nov	0	0	0.01	0	0	0.01	0.02	0.01	0
	Dec	0	0.01	0.07	0.57	0.15	0.02	0.11	0	0
	Jan	0	0.04	0.05	0.28	0.1	0.05	0.08	0	0
	Feb	0	0.01	0.01	0.02	0.05	0.03	0.05	0.04	0
Com	Oct	0	0	0	0.02	0	0.03	0	0	0
	Nov	0	0.01	0.48	0.04	0.05	0.08	0.08	0	0
	Dec	0	0	0.07	0.15	0	0.21	0.04	0	0
	Jan	0	0	0.02	0.13	0	0.02	0.02	0	0
	Feb	0.01	0.01	0.02	0.08	0.4	0.02	0.05	0.02	0
Total		**0.17**	**0.29**	**2.28**	**8**	**2.08**	**1.89**	**2.34**	**0.6**	**0.03**

Appendix 2 continued…

		Hymenoptera			Arachnid		Phasmatodea
Treatment	Month	Small	*Med*	Large	Small	*Med*	All the same
NRLu	Oct	0.04	0.01	0.01	0.07	0.03	0
	Nov	0.02	0.04	0	0.02	0.03	0
	Dec	0.02	0.04	0.01	0.04	0.03	0.04
	Jan	0.01	0.12	0.02	0.03	0.17	0.09
	Feb	0.01	0.06	0.02	0.06	0.04	0
NRL	Oct	0	0	0.02	0	0	0
	Nov	0	0.03	0	0.01	0.01	0
	Dec	0.02	0.02	0.01	0.09	0.02	0
	Jan	0.02	0.07	0.01	0.06	0.13	0
	Feb	0.01	0.11	0.12	0.04	0.02	0
NRHu	Oct	0.03	0.02	0	0.05	0	0
	Nov	0.04	0.06	0.01	0.02	0.01	0
	Dec	0.01	0.12	0.11	0.01	0.04	0
	Jan	0.01	0.09	0.02	0.03	0.07	0.09
	Feb	0.01	0.05	0.02	0.03	0.01	0
NRH	Oct	0	0.02	0.04	0.02	0.01	0
	Nov	0	0.04	0.01	0	0	0
	Dec	0.02	0.11	0.01	0.03	0.06	0
	Jan	0.01	0.04	0.01	0.04	0.06	0
	Feb	0.02	0.21	0.09	0.05	0.03	0
BFu	Oct	0.02	0	0	0.07	0.01	0
	Nov	0.01	0.01	0.01	0.02	0	0
	Dec	0.01	0.24	0.02	0.05	0.03	0
	Jan	0.01	0.06	0.11	0.03	0.04	0
	Feb	0.01	0.08	0.05	0.1	0.06	0
BF	Oct	0	0	0	0.01	0	0
	Nov	0	0.02	0	0	0	0
	Dec	0.01	0.11	0.04	0.04	0.07	0
	Jan	0.02	0.11	0.02	0.06	0.18	0.04
	Feb	0.01	0.07	0.01	0.03	0.07	0
AF	Oct	0	0.01	0.02	0.02	0.04	0
	Nov	0	0.03	0	0	0	0
	Dec	0.01	0.02	0.03	0.04	0.21	0
	Jan	0.01	0.05	0.02	0.06	0.1	0
	Feb	0	0.02	0	0.01	0.03	0
Com	Oct	0.01	0.02	0	0.01	0	0
	Nov	0.02	0.01	0.04	0.03	0.01	0
	Dec	0.02	0.09	0.01	0.01	0.03	0
	Jan	0	0.01	0.08	0.01	0.03	0.04
	Feb	0.01	0	0.01	0.01	0.03	0
Total		**0.48**	**2.28**	**0.98**	**1.32**	**1.72**	**0.3**

CHAPTER 4

Predation drives nesting success in grassland passerines: management of vegetation structure for avian conservation

Abstract

By focusing on process-oriented data rather than using inventory-type data, this study provides a robust understanding of the effects of agricultural management on grassland bird reproductive output in the moist highland grasslands (MHGs) of South Africa. Four hundred and four nests of 12 grassland-breeding bird species were monitored in five different land-use types. Survivorship was modelled using Program MARK to assess the effects of these management practices on reproductive performance. Six of the species were modelled individually to assess species-specific responses. Both nest-site selection and nest success were driven by vegetation structure, which in turn is driven by habitat management. There was an increasing nest success rate through the season for cup (ground) nesting birds as vegetation structural complexity increased after early season fires. Nest success was driven by predation pressure rather than food availability. Analysis of the nesting success of the endemic and *Vulnerable* Yellow-breasted Pipit *Anthus chloris*, which is a habitat specialist, indicated that unconserved areas appeared to house sink populations of this species, although confirmation of this would depend on a measure of adult survival. The generalist African Pipit *Anthus cinnamomeus*, on the other hand, thrives in highly disturbed, communally grazed lands. To conserve the representative grassland bird species, it is recommended that managers of MHGs promote a mosaic of burning regimes (Engle et al. 2008), with the majority burning biennially or less frequently.

Key words: Grassland, birds, land-use, nest success, pipit, predation.

4.1. Introduction

“One of our greatest challenges as researchers is predicting impacts of land use on biota, and predicting the impact of livestock grazing on birds is no exception” (Martin et al. 2005). Several studies have illustrated the effects of grazing at different scales and in different systems (Fondell and Ball 2004; Sutter and Ritchison 2005). Fondell and Ball (2004) and Powell (2008) suggest that grassland birds are the fastest decreasing group of

North American birds. The same studies highlighted the negative effects of grazing on vegetation structure and suggested that this was the cause of a decrease in the availability of preferred nesting habitat.

The habitat requirements of species are most often assessed by correlating bird abundance with features of the habitats they occupy. Such indirect measures may not, however, identify appropriate features for management efforts because abundance and performance are not necessarily correlated (White and Burnham 1999). Effective management of grasslands thus requires an understanding of (1) the environmental and demographic causes of population problems; (2) the habitat requirements necessary for sufficient reproductive success and survival to ensure population maintenance; (3) how demographic and habitat factors interact to create population sources and sinks; and (4) how grassland management practices may impact on the above.

It has become increasingly clear that species richness alone is a poor biodiversity measure because changes in habitat structure influence species assemblages, typically resulting in losses of indigenous species and gains of species not representative of the original system (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005). In other words, species richness can remain constant while community composition changes. Species richness can even be enhanced (at least temporarily) by land degradation processes allowing colonization by species normally absent from a particular habitat type or biome. The ecological consequences of this are not necessarily beneficial due, for example, to changes in patterns of energy flow and failure of ecological processes such as pollination (Fox and Hockey 2007). Because of a shortage of empirical studies of animals, there is little information that managers can use to determine which agricultural or management practices are the most compatible with biodiversity conservation. Without understanding the influence of land management on grassland fauna, the conservation of these taxa is strongly compromised. This chapter focuses on process-oriented data by assessing the effects of management on six grassland bird species, with the aim of comparing their reproductive performance across land-use types. Nest-site selection by grassland birds is a non-random process, with increased nest density signalling improved habitat quality (Fretwell 1972; Martin 1998; Muchai 2002; Davis 2005).

Nesting success and fledgling development can be related to grassland habitat variables and should provide more relevant, quantitative information about habitat quality than do density-habitat regressions (Maurer 1986). Management practices, through frequent burning and high stocking densities, reduce vegetation cover and thus reduce nest concealment, increasing the probability of nest predation (Ricklefs 1969; Ammon and Stacey 1997; Martin and Roper 1988). This study is thus based on the premise that it is the performance, rather than the presence of component species that is the key indicator of their conservation status (Fondell and Ball 2004).

Studying and understanding nest survival is a crucial component of understanding bird breeding biology (Dinsmore et al. 2002). Past studies estimating bird nest survival used simple measures of apparent nest survival or Mayfield constant-nest-survival models (Johnson 1979; Jehle et al. 2004). These methods do not build models with the capability to assess rigorously the importance of a wide range of biological factors that affect nest survival, nor can they model time-dependent or age-specific factors (Dinsmore et al. 2002). Using program Mark (White and Burnham 1999) allows the incorporation of temporal variations and covariates representative of individual nests. This provides a much more powerful statistic and hence a better understanding of the factors influencing nest survival (Dinsmore et al. 2002). This study aims to explain how grassland management affects grassland-nesting passerines, and specifically their nesting success.

4.2. Study site and methods

The study area falls within the Mesic Highveld Grassland Bioregion and is specifically identified as Lydenberg Montane Grassland (Mucina and Rutherford 2006). This vegetation type includes high-altitude plateaux, undulating plains and mountain peaks as well as slopes, hills and deep valleys. The predominant vegetation is short grassland in the high-lying areas, interspersed with wetland troughs and grading to taller grasslands at lower elevations. All the selected study sites were on the plateau around the town of Dullstroom (centred at 25º 25’S, 30º 10’E), falling between 1900 and 2200 m.a.s.l. The soils are mostly derived from shales and quartzites as well as lavas and dolomites of the Transvaal Supergroup (Mucina and Rutherford 2006).

The mean annual precipitation ranges from 660-1180 mm, augmented by frequent mists, and the region experiences an average of 21 frost days per year (Mucina and Rutherford 2006). The Dullstroom Plateau Grassland Ecoregion (encompassing the entire study area) is classified as *Endangered* on the basis of very high irreplaceability of species under criterion F in the National List of Threatened Ecosystems (Department of Environmental Affairs, notice 1477 of 2009).

Eight study sites experiencing differing management regimes were sampled over two summer seasons. These included an annually burnt farm (AF); communally grazed lands (Com); a biennially burnt farm that was burnt (BF) or was not burnt (BFu) in the study year; a nature reserve site with a high density of indigenous grazing ungulates that was burnt (NRH) or was not burnt (NRHu) in the study year; and a nature reserve site with a low density of indigenous grazing ungulates that was burnt (NRL) or was not burnt (NRLu) in the study year. Verloren Valei Nature Reserve (NRH and NRL sites) acted both as a control and an experimental site. Verloren Valei has been burnt biennially, in fixed blocks, since 1985 (Heyns 1985).

Within each study, site four 25 hectare replicates were marked out with at least 500 m between replicates: the largest territory of any of the grassland passerine species in this study is no larger than 100 m in diameter (Hockey et al. 2005). Sampling sites were selected with sufficient distance between sites to avoid pseudo-replication (Hurlbert 1984), but were sufficiently close together to standardise as far as possible for extrinsic factors including soil type, rainfall, aspect, slope and temperature.

Field work was conducted in the birds' breeding (summer) season for two years. Grazing data were collected by interviewing farmers and managers: these data were confirmed/augmented with animal counts. Relative grazing intensity was recorded as the number of hectares of grazing land available per large animal unit (ha/LAU). One LAU is defined as being equivalent to one cow or five sheep, and represents the metabolic equivalent of a 454 kg cow (Meissner et al. 1983; Owen-Smith and Danckwerts 1997; Tainton 1999).

4.2.1. Vegetation structural sampling

In Chapter 3, I illustrated that, of the 10 vegetation structural indices measured, three were informative in explaining bird abundance and diversity. These three were chosen for inclusion in nesting success models. Further details of the vegetation sampling techniques are provided in Chapter 3.

4.2.2. Bird sampling: census data

A 50 m weighted rope was dragged along 500 m long line-transects to quantify bird diversity and abundance. This is the most appropriate census method in large, open areas and is more accurate than point counts: it is a modification of the fixed-strip or belt-transect method (Kendeigh 1944). Rope drags also alleviate problems of having to correct for effective transect width and prevent birds from hiding in taller grass swards (Krook et al. 2007). Distance sampling does, in theory, alleviate the same problem, but is not effectiuve when birds are breeding, because incubating birds do not always flush from the ground and thus remain undetected.All bird species within the transects were identified to species level and counted: birds not utilizing the habitat directly, i.e. flying over, were counted but were not included in all the analyses, with the exception of hunting raptors (which are utilising the grassland habitat).

In each of the 25 ha replicates, three parallel transects were walked perpendicular to the plot boundary, covering a total area of 7.5 ha per replicate. These transects were the same as those used for the vegetation surveys (Chapter 2). Censusing began when breeding bird territories were established in early October and were conducted monthly throughout the breeding season. They were divided into sampling periods in the morning (06h00-10h00), at midday (10h00-14h00) and the evening (14h00-18h00). Census sessions were spread over the three observation periods according to a randomly selected schedule (MacNally and Horricks 2002).

4.2.3. Nest searches and monitoring

The study sites were all searched for nests at least twice per week in an ordered, time-monitored manner within each of the 25 ha replicates per treatment type. Searches were made for nests of all grassland-breeding bird species over the entire breeding season, each search attempt took no longer than two hours. This was done by dragging a 50 m weighted rope (even with weights this rope glides over the grass and does not touch the nests) to flush birds from nests and by behavioural observation based on either flushing while walking zigzags or following adult birds that were carrying food. Nest searching was controlled based on search effort. Each replicate was searched for equal time periods on a set schedule throughout the season. This schedule incorporated both variation in time of day and type of searching method. Once located, nests were marked with coloured sticks or rocks placed nearby. Subsequently, nests were visited at one- to five-day intervals to determine their fate. Human observer visitation has been shown to have limited, if any, affect on nest predation rates in grasslands (Gottfried and Thompson 1978; Lloyd et al. 2000; Muchai 2002). Successful nesting was classified as the fledging (leaving the nest) of at least one chick. Reasons for nest failure were divided into seven possible causes: (1) abandoned, if the nest failed due to abandonment after eggs were laid; (2) starvation, if nestlings were found dead or absent after a period of retarded growth with no visible signs of illness or other causes of mortality; (3) trampling, if eggs were found broken inside the nest; (4) adult mortality, if an adult was found dead in or near the nest; (5) weather, if the nestlings died after an extreme weather event or were flooded; (6) nest parasitism, if a nest was usurped by a nest parasite; or (7) predation, if eggs or nestlings disappeared from the nest (with or without definite evidence of predation). Partial predation was assumed to have occurred when partial losses of a clutch occurred, or if some of the nestlings disappeared with no prior signs of illness or starvation (Muchai 2002). The six species focussed on for nest survival analysis were Yellow-breasted Pipit *Anthus chloris* (a regionally and globally *Vulnerable* grassland endemic), African Pipit *Anthus cinnamomeus*, Wing-snapping Cisticola *Cisticola ayresi*, Cape Longclaw *Macronyx capensis*, Long-tailed Widowbird *Euplectes progne* and African Stonechat *Saxicola torquata*. The latter five species are all widespread in grasslands. Buff-streaked Chat (*Campicoloides bifasciatus*) and Eastern Long-billed Lark (*Certhilauda semitorquata*) nest in rocky outcrops and were excluded from analyses, along with both non-passerine species (Common Quail *Coturnix coturnix* and Red-winged Francolin *Scleroptila. levaillantii*), leaving a total of 376 nests available for analysis. The field method used to find passerine nests rely on observation of feeding parents, this is not possible with precocial non-passerines, making nest finding reliant on chance.

Nest survival rates were modelled using Program MARK, which enables the testing of the influence of covariates (e.g. treatment, nest concealment, nest density) on nest survival, while controlling for temporal variation in nest survival.

4.2.4. Arthropod sampling

Arthropod abundance was sampled monthly, using sweep nets, along the same transects where birds were censused. These samples consisted of 200 sweeps (each sweep being made with each long stride) per transect (600 sweeps per treatment) per month. The net used was a circular sweep net with a diameter of 450 mm. Sweep nets are effective in catching most of the prey groups eaten by grassland-dwelling wagtails (Motacillidae - Brodmann and Reyer 1999). Arthropods were separated from vegetation matter in the field and preserved in ethanol for later identification to ordinal level, order-level analyses being sufficent for distinction of taxonomic responses to land-use at local scales (Williams and Gaston 1994; Gaston and Blackburn 1995; Prendergast and Eversham

1997; Duelli and Obrist 1998; Biaggini et al. 2007; Öster et al. 2008). Samples were then dried and weighed for biomass estimation (Tsukamoto 1988; Cressa 1999).

4.2.5. Statistical methods

Daily and overall nest survival rates were estimated using the nest survival modelling option in Program MARK, with a logit link function (White and Burnham 1999). Daily nest survival is the probability of a nest surviving that particular day within the breeding season, while overall nest survival is the probability of survival of the nest contents from egg laying to fledging. This method is an extension of and advanced version of Mayfield’s method (1961, 1975) method which required the assumption of constant daily nest survival through time and exact knowledge of the dates of hatching or failure (Dinsmore et al. 2002; Jehle et al. 2004). The technique obviates bias based on the observer’s ability to locate nests of varying ages and it is also possible to incorporate covariates into MARK models (White and Burnham 1999). Covariates were used to test the effects of management practices such as grazing and burning, as well as other ecological factors including nest stage, time of breeding, nest type, three measures of vegetation structure (average horizontal density, phytomass and patchiness – Chapter 2), year and food abundance. Akaike’s Information Criterion (AIC_c - Akaike 1973) was used to select the model with the most support (Burnham and Anderson 2002).

Nest initiation dates were assigned to 28-day Julian date categories, because for almost all species under consideration, both incubation and fledging periods were 14 days. It was important to estimate the timing of egg laying because this was not known for all nests. For nests where hatching dates were known to be between two nest visits, the intermediate date minus the incubation period was used to estimate nest initiation date. For nests that were found after clutch initiation and were depredated during either the egg or chick stage, the number of known living days was subtracted from the total incubation or nestling period respectively and this value was then halved to derive an estimate of the initiation date (Johnson 1979). A model with treatments as dummy variables (random factors – White and Burnham 1999) was run to account for the possibility of site-specific conditions influencing nesting success over and above the effects of the ecological covariates within the most robust model. If the lower 95% confidence interval was negative and the upper 95% confidence interval was positive (“including zero”) for the *beta* estimate then the variable was not considered to have any significance in deriving the model (Dinsmore et al. 2002). Following Burnham &

Anderson (2002), *a priori* biological hypotheses were tested using an information-theoretic approach to evaluate the relationship between avian nesting success and environmental covariates. These hypotheses were incorporated and tested in the nest survival model in the order illustrated below:

1) Stocking rate (HaLAU). High stocking densities of herbivores (measured in hectares per large animal unit, ha.LAU^{-1}) have a detrimental affect on nesting success through a) the consumption of vegetation that would otherwise provide nest concealment from predators, and b) the effects of trampling (Fondell and Ball 2004; Sutter and Ritchison 2005; Powell 2008).

2) Timing and frequency of burning (Burn). In the MHGs burning typically takes place just after the first rains, which occur at the beginning of the birds' breeding season. The cumulative effect of annual as opposed to biennial burning leads to sparse vegetation cover and poor seasonal recovery of vegetation for nesting (Powell 2008). All areas, including conservation areas, are burned at least every two years. Birds breeding in sites that were not burnt in the study year were predicted to be more successful than birds breeding in the year when burning took place (Powell 2008).

3) Timing of breeding (Date). Early season nests are hypothesized to be more successful than later nests (Ainley and Schlatter 1972; Klett and Johnson 1982; Fondell and Ball 2004). To evaluate the effects of time of breeding a simple constant nest-survival model was run and then a model with a time trend was fitted.

4). Nest chronology (AgeDay). For altricial bird species, daily nest survival is expected to decrease with increased nest age because of increased visitation rates by feeding parents and the accompanying risk of attracting predators (Dinsmore et al. 2002; Jehle et al. 2004; Nur et al. 2004).

5) Nest type (NestType). Grassland-nesting birds can be separated into two groups based on nest architecture. Cup nesters typically make a small, lined cup nest on the ground below a grass tuft, while ball nesters make a ball or dome of grass, typically with a side entrance, positioned off the ground within the grass sward. It is hypothesized that cup nesters will have lower early season nesting success because nest cover will be limited, while ball nesters will have lower late season nesting success as the number of nest attempts increases with increased vegetation density providing adequate structure to support these nests, resulting in increased predator focus. Previous studies suggest that, overall, cup (ground) nesters will experience higher predation rates than ball nesters (Martin 1987; Martin and Roper 1988; Yanes and Suarez 1995).

6) Food availability (Insect). Arthropod abundance was used as a surrogate for food availability. Areas with high disturbance from fire and grazing, with resultant low vegetation diversity (Chapter 2), are expected to support lower arthropod numbers than less disturbed areas: this may limit food availability for grassland-nesting birds in disturbed sites (Sutter and Ritchison 2005; Dennis et al. 2008).

7) Vegetation structure. It is hypothesized that increased vegetation structural complexity will result in decreased nest predation and concomitantly increased nest success. Vegetation structure was classified based on three vegetation indices – horizontal density, patchiness and biomass (DPM, AvHorDen and Patchiness – Chapter 2).

The main effects model was established using *a priori* hypotheses 1-4; following these, further covariates (5-7) were explored for assessment of their potential improvement to the model (Burnham and Anderson 2002). Once the most robust model had been derived, interactions between the remaining covariates and between the remaining and pre-existing covariates were explored to assess whether their inclusion would improve the fit of the model.

Separate models were evaluated. First, a comprehensive global model was run including all grassland-nesting passerine species and all covariates to assess the overall impact of management on grassland-nesting birds in MHGs. Second, models were run for cup nesters and ball nesters separately. Lastly, a model was run for each of the six most abundant grassland-nesting birds to assess variation in species-specific responses.

The Software package STATISTICA 9.0 (StatSoft Inc. 2009) was used to analyse the data. In addition to MARK models, Wilcoxon Matched-Pairs tests were used to assess the relative difference between estimated nesting success in burnt and unburnt areas as well as between cup- and ball-nesting species. Multiple regression analyses were used to extract the most important factors affecting estimated nest success (derived from MARK models) and nest density (number of nests initiated per replicate per month). Day lengths were captured from the local weather station (www.icon.co.za/~charval) with the shortest day of the breeding season being 1 October (12 h, 20 min) and the longest day 21 December (13 h, 45 min). Model residuals from the AICc best model were visually assessed and the data transformed where appropriate and re-analysed. Stocking rate (Ha.LAU^{-1}) was log-transformed to meet linearity assumptions.

4.3. Results

Twelve species of grassland-nesting birds were found breeding in this study but only six of these yielded sample sizes large enough for robust analysis (Table 1): the majority of these nests were located within the NRLu and NRL sites. The majority of the unsuccessful nests in all sites failed as a result of predation, with most predation events occurring at the egg stage (Table 2). Nests that were included in the analyses were monitored for a total of 3601 exposure days.

Table 1. Numbers of nests of six grassland-nesting bird species monitored and analyzed for nesting success, with breeding information from Hockey et al. (2005).

		nests	Median clutch size	Incubation period	Nestling period	Nest type
African Pipit	*Anthus cinnamomeus*	147	3	13-14	14	Cup
Cape Longclaw	*Macronyx capensis*	66	3	13-14	14	Cup
Long-tailed Widowbird	*Euplectes progne*	57	3	12-14	17	Ball
Wing-snapping Cisticola	*Cisticola ayresii*	35	3	11-14	14-15	Ball
Yellow-breasted Pipit	*Anthus chloris*	27	3	14	14	Cup
African Stonechat	*Saxicola torquata*	20	3	14-15	13-16	Cup
Total		352				

Table 2. Observed fates of all six grassland-nesting bird species across all eight study sites. Neither starvation nor trampling were recorded as causes of nest failures.

	Number	%
Successful	183	51.86
Egg predation	109	31.11
Nestling predation	46	13.03
Adult mortality	7	2.12
Abandoned	3	0.79
Weather	3	0.79
Nest parasite	1	0.26
	352	100

When considering the number of nest attempts per 25 ha (nest density), both cup- and ball-nesting species had lower nest densities in years when sites burnt compared to when they were unburnt. Cup- and ball-nesting species in burnt sites had an average of 31.5% and 27.4% lower nest density respectively through the breeding season relative to sites that had not been burnt in the year of observation (Wilcoxon Matched-Pairs Test between ball nests in burnt *vs* unburnt, n = 136, Z = 10.12, $p < 0.001$; cup nests in burnt *vs* unburnt, n = 136, Z = 10.12, $p < 0.001$). Nest initiation in unburnt areas peaked in mid summer (December) while in burnt areas nest attempts peaked in late summer (January/February - Fig. 1). Similarly, areas not under conservation management (including NRH and NRHu) had an average of 35.3% fewer nest attempts than conserved areas with low stocking densities (NRLu and NRL), illustrating the effect of grazing on the overall number of nest attempts. When comparing management practices across sites, the most nest attempts were made in the conserved area with low densities of indigenous ungulates (NRL), in both the burnt and unburnt season. The next-highest frequency of nesting attempts was in the communal lands (Com), but this was due largely to the high number of attempts by African Pipits at this site. The fewest nesting attempts were made in the nature reserve with high stocking rates (NRH) and on the annually burnt farm (AF): the latter had an average of only 0.04 nest attempts/ha (Fig. 1).

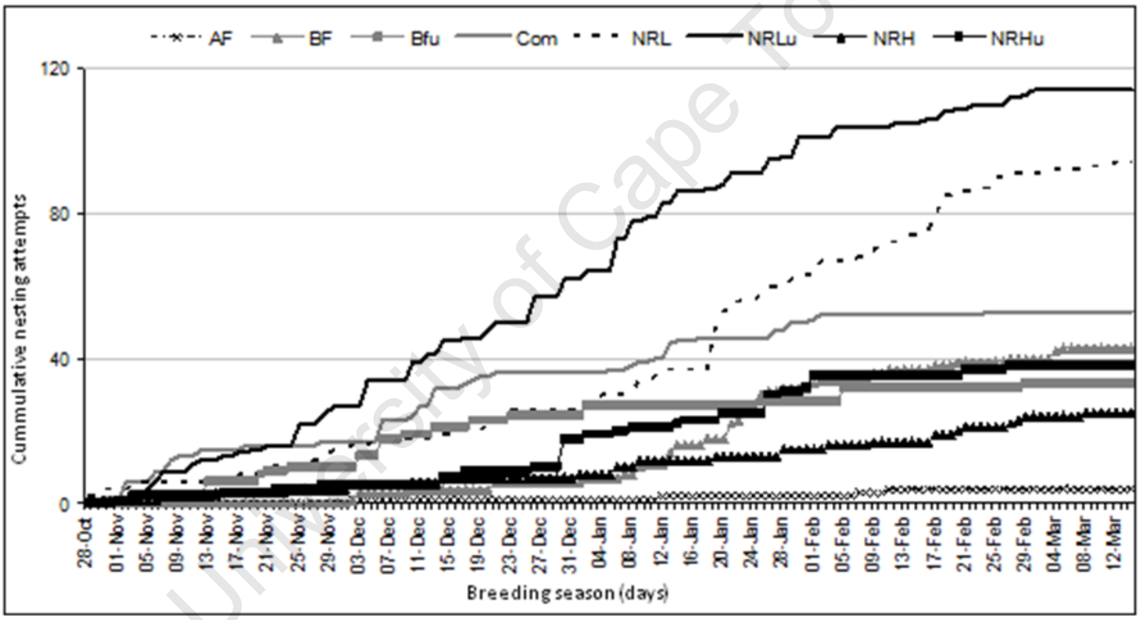


Fig. 1. Cumulative numbers of nesting attempts per treatment by all bird species combined through each season.

In order to understand the functional integrity of faunal diversity, nest-monitoring data were modelled to derive nest success estimates. When all grassland-nesting passerine nests were modelled together (Table 3), the best model was significantly better than any of the other models fitted (AIC weight = 0.54, ΔAIC > 2). According to the AIC weights, the model with the most support was more than three times as well supported as the next-best model. The models with the most support indicated no influence of grazing intensity, food availability, vegetation patchiness or the timing of breeding on nest success. For the three most parsimonious models, the summed AIC weights (*W* AIC) were 0.84 (Table 3), indicating 84% support within the data for the four covariates included in these three models. These four covariates were burnt or unburnt (Burn), nest chronology (AgeDay – which is the age of the nest in days), vegetation biomass (DPM) and nest type. Likelihood-ratio tests with the systematic exclusion of each of these covariates supported their inclusion in the best-fit model (Table 4). Including an interaction term between nest type and average horizontal density of vegetation improved the model significantly. Overall, estimated daily nest success survival of this best-fit model was 0.945, and estimated nest success was 0.204.

In order to account for treatment effects, the best model was run including all the treatments as random factors. This model received little support (AICc = 1111.71) and a likelihood-ratio test between this model and the best model showed no similarity ($p = 0.772$, $\chi^2 = 3.285$, df = 6). The logistic regression equation (β and one standard error - Table 5) for the most parsimonious and robust model was:

$$\text{Logit}(S) = 2.38 - 0.56(\text{Burn}) + 0.02(\text{AgeDay}) + 0.00017(\text{DPM}) + 0.18(\text{NestType X AvHorDen})$$

This model suggests that burning is the most important covariable influencing reproductive performance of all grassland bird species. Following this, nest chronology and phytomass (DPM – a surrogate for nest concealment) play important roles. Finally, an interaction between nest type and average horizontal density of vegetation plays a minor role in bird nest success. Note that these analyses excluded Long-tailed Widowbird because a) this species is not insectivorous, and b) although, like other species in the analysis it has a 14-day incubation period, the nestling period is more than 14 days.

Table 3. Comprehensive global model including 376 nesting attempts by insectivorous grassland passerines. K is the number of parameters per model; Burn = time since last burn (expressed as growing months); AgeDay = nest chronology; DPM = standing stock of vegetation (kg.ha^{-1}); NestType = binary variable distinguishing ball nesters from cup nesters; and AvHorDen = index of average horizontal vegetation density (measured in the 0-100 mm vegetation layer – Chapter 2).

Model	AICc	ΔAICc	*W* AICc	Model likelihood	K	Deviance
$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	1102.65	0.00	0.54	1.00	5	1092.63
$S_{\text{Burn+AgeDay+DPM+NestType}}$	1104.92	2.26	0.17	0.32	5	1094.90
$S_{\text{Burn+AgeDay+DPM+NestType+AvHorDen}}$	1105.56	2.91	0.13	0.23	6	1093.54
$S_{\text{Burn+AgeDay+DPM}}$	1107.76	5.11	0.04	0.08	4	1099.75
$S_{\text{Burn+AgeDay}}$	1107.87	5.22	0.04	0.07	3	1101.86
$S_{\text{Burn+AgeDay+Insect}}$	1109.03	6.38	0.02	0.04	4	1101.02
$S_{\text{Burn+AgeDay+Date}}$	1109.57	6.92	0.02	0.03	4	1101.56
$S_{\text{Burn+AgeDay+Patchiness}}$	1109.71	7.06	0.02	0.03	4	1101.70
$S_{\text{Burn+HaLAU}}$	1109.79	7.14	0.02	0.03	3	1101.78
S_{Burn}	1112.50	9.85	0.00	0.01	2	1108.50
$S_{\text{Burn+Date}}$	1114.49	11.84	0.00	0.00	3	1108.48
$S_{\text{AgeDay+HaLAU}}$	1115.93	13.28	0.00	0.00	3	1109.92
S	1119.13	16.48	0.00	0.00	1	1117.13
S_{HaLAU}	1120.67	18.02	0.00	0.00	2	1116.67
$S_{\text{Date+HaLAU}}$	1121.90	19.25	0.00	0.00	3	1115.89

Table 4. Likelihood-ratio tests comparing the model outputs from Table 3. Tests 1-7 show the process of building the model, following Burnham and Anderson (2002); tests 8-10 show the significance of the impact of removing the selected main parameters one at a time from the best-fit model.

	Reduced model	General Model	χ^2	d.f.	P
1	S	S_{Burn}	8.633	1	0.003
2	S	S_{HaLAU}	0.464	1	0.496
3	S_{Burn}	$S_{\text{Burn+Date}}$	0.015	1	0.903
4	S_{Burn}	$S_{\text{Burn+AgeDay}}$	6.639	1	0.010
5	$S_{\text{Burn+AgeDay}}$	$S_{\text{Burn+AgeDay+DPM+NestType}}$	6.963	2	0.031
6	$S_{\text{Burn+AgeDay+DPM+NestType}}$	$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	4.854	1	0.028
7	$S_{\text{AgeDay+DPM+(NestType,AvHorDen)}}$	$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	12.554	1	0.001
8	$S_{\text{Burn+AgeDay+DPM}}$	$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	7.118	1	0.008
9	$S_{\text{Burn+ DPM+(NestType,AvHorDen)}}$	$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	6.766	1	0.009
10	$S_{\text{Burn+AgeDay+(NestType,AvHorDen)}}$	$S_{\text{Burn+AgeDay+DPM+(NestType,AvHorDen)}}$	3.176	1	0.045

Table 5. *Beta* estimates from logit-link function parameters: parameter codes as in Table 3. *Beta* estimates represent the relative importance of each parameter for predicting nesting success.

			95% Confidence Interval	
	Beta	Std Error	Lower	Upper
Intercept	2.3819152	0.2140651	1.9623476	2.8014827
Burn	-0.5607028	0.1558292	-0.866128	-0.2552776
Interaction	0.1897984	0.0718611	0.0489507	0.3306461
DPM	1.73E-04	9.69E-05	-1.68E-05	3.63E-04
AgeDay	0.0165131	0.0062481	0.0042668	0.0287593

The global model established for all grassland-nesting passerines was used as the basis for a model which considered the effects of burning alone on nest success. Covariates were adjusted according to their contribution to the model. Burning significantly reduced estimated nest success, while both burnt and unburnt sites experienced increasing nest success through the breeding season (Fig. 2). Using the logistic regression equation from the best model, the average overall nest survival rates were 0.126 for areas burnt in the study year and 0.261 for areas not burnt in the study year (Wilcoxon Matched-Pairs Test between burnt and unburnt, n = 141, Z = 10.3, $p < 0.0001$). According to the AIC weights for nests in areas that were burnt in the study year, the most parsimonious model was significantly better supported than the next best model (ΔAIC > 2 - Burnham and Anderson 2002). Along with this, summed AIC weights suggest that, with 93.5% support, nest chronology (AgeDay) is the most important predictor of daily nest survival. According to the AIC weights for nests in areas that were not burnt in the study year, the most parsimonious model had limited confidence over the next best model (ΔAIC = 1.7). Summed AIC weights suggest that nest chronology (AgeDay) was the most important predictor, with 65.2% support.

The best models for cup (n = 260) and ball (n = 116) nesting birds (across all sites) showed higher estimated nest survival rates for cup-nesters (0.23) than for ball-nesters (0.15). According to the AIC weights for cup nests, the most parsimonious model was significantly supported (ΔAIC > 2). Summed AIC weights suggest that nest chronology (AgeDay) is the most important predictor, burning (Burn) is second and vegetation density (DPM) is third, with 68.8%, 65.8% and 57.0% support respectively. According to the AIC weights for ball nests, the most parsimonious model had limited confidence over the next best model (ΔAIC = 1.6). Summed AIC weights suggest that burn frequency is the most important predictor (33.7% support) and time since burning (Date) is the next most important predictor (28.7% support).

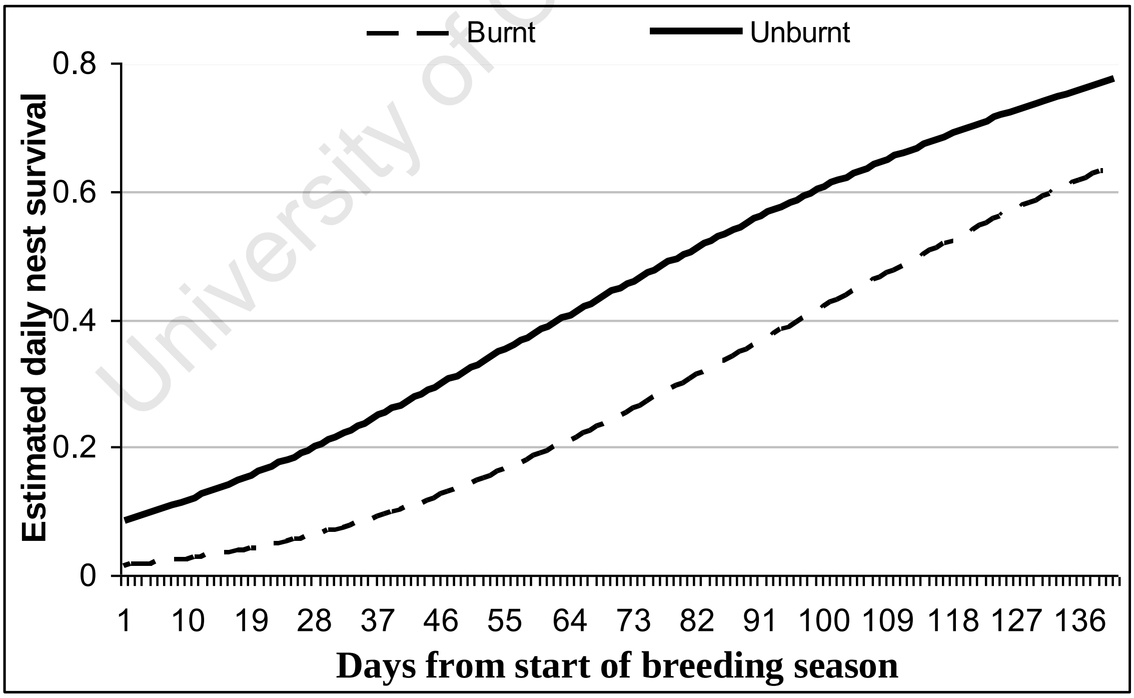


Fig. 2. Estimated daily nest survival for all nests types combined in burnt and unburnt areas across all sites (Julian day 1 on the x-axis is 28 October). Both the positive and negative standard errors have a maximum range from 0.012 to 0.018 for the burnt mean (represented from now on as 0.012<S.E.<0.018) and from 0.007 to 0.016 for the unburnt mean.

Using the logistic regression equation from the most parsimonious model retrieved for each of the four nest groups (cup *vs* ball, burnt *vs* unburnt), the average overall nest survival rates (in all sites) were: ball, burnt 0.13; ball, unburnt 0.24; cup, burnt 0.30; and cup, unburnt 0.47 (Wilcoxon Matched-Pairs test between ball nests in burnt *vs* unburnt sites, n = 28, Z = 4.62, p < 0.001; cup nests in burnt *vs* unburnt sites, n = 28, Z = 4.62, p < 0.001; ball *vs* cup nests in burnt sites, n = 28, Z = 1.41, p = 0.15; and ball *vs* cup nests in unburnt sites, n = 28, Z = 3.80, p < 0.001).

The two nest types of grassland passerines showed opposite patterns of seasonal nest survival Estimated daily nest survival increased with time from day one of the breeding season through to the end of the breeding season for cup-nesting passerines but decreased for ball-nesting passerines (Wilcoxon Matched-Pairs Test between ball vs cup nests in burnt sites, n = 136, Z=5.26, p < 0.0001; and ball vs cup nests in unburnt sites, n = 136, Z = 6.51, p < 0.0001 – Fig. 3).

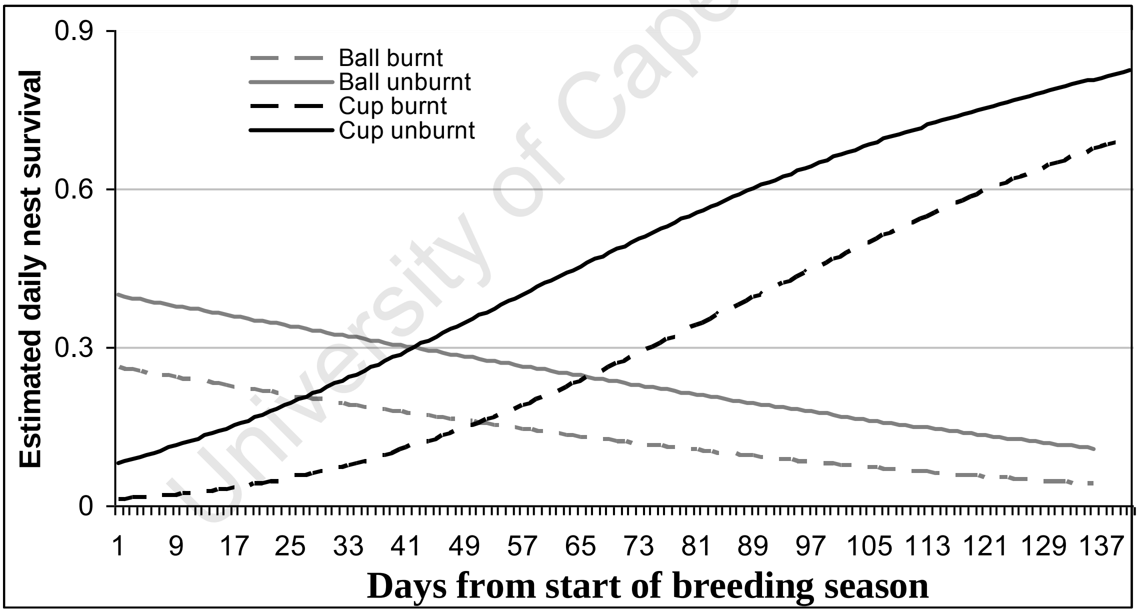


Fig. 3. Estimated daily nest survival through the nesting season for cup- and ball-nesting species respectively (Day 1 on the x-axis is 28 October). For ball nests in burnt sites, 0.014<S.E.<0.020; ball nests in unburnt sites, 0.018<S.E.<0.019; cup nests in burnt sites, 0.011<S.E.<0.014; and cup nests in unburnt sites, 0.016<S.E.<0.019.

When considering differences in nest success from egg laying through to fledging, estimated daily nest survival rates of ball-nesting passerines increased with nest age (from laying to fledging takes 28 days for most passerine species in this system), while cup nesters showed constant estimated nest success, indicating that ball-nesting species experienced heavier predation in the egg phase than in the nestling phase. Again, nests in burnt areas showed consistently lower estimated nest success than those in unburnt areas (all species analysed had an average nesting period of 28 days nesting periods, except Long-tailed Widow which was excluded from this analysis – Fig. 4).

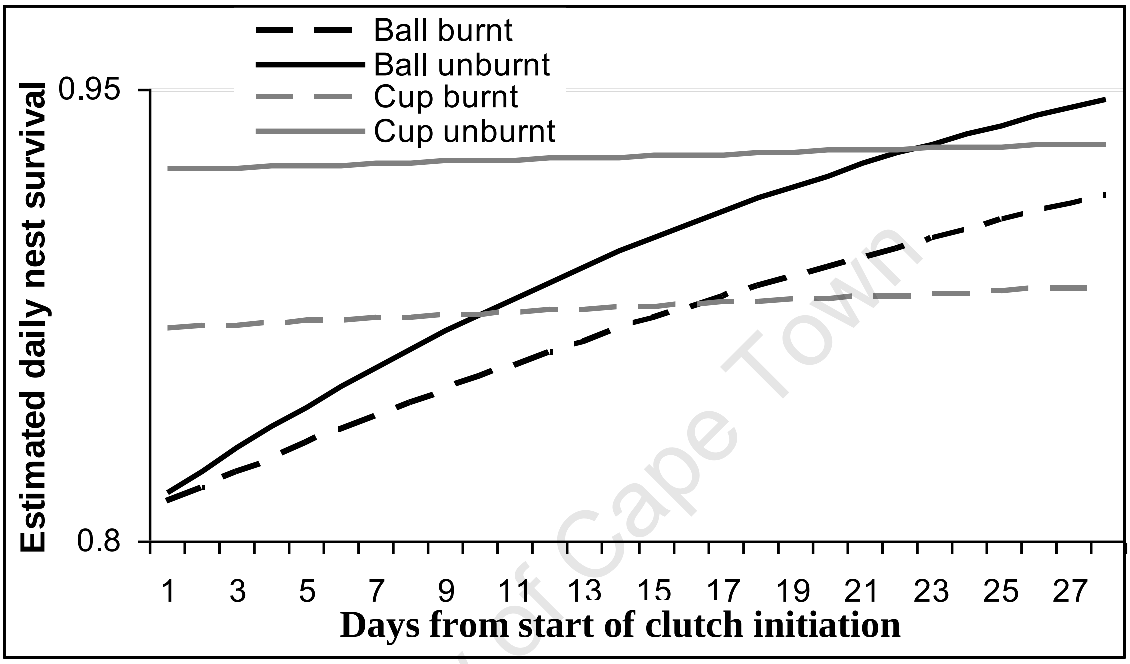


Fig. 4. Estimated daily nest survival, based on nest age, for cup- and ball-nesting passerines respectively (Day 1 on the x-axis is 28 October). For ball nests in burnt sites, 0.000<S.E.<0.014; ball nests in unburnt sites, 0.000<S.E.<0.010; cup nests in burnt sites, 0.031<S.E.<0.034; and cup nests in unburnt sites, 0.014<S.E.<0.016.

In order to investigate vegetation biomass (DPM) as a factor influencing nest success, nests were separated out into three groups according to the vegetation biomass (which the model suggested was a signifactly important vegetation structural factor for overall nest success – Table 3) in which they occurred. When nests are modelled for each of these three vegetation densities, nests in areas of dense vegetation had higher success regardless of whether they are cup- or ball-nesting species (Fig. 5).

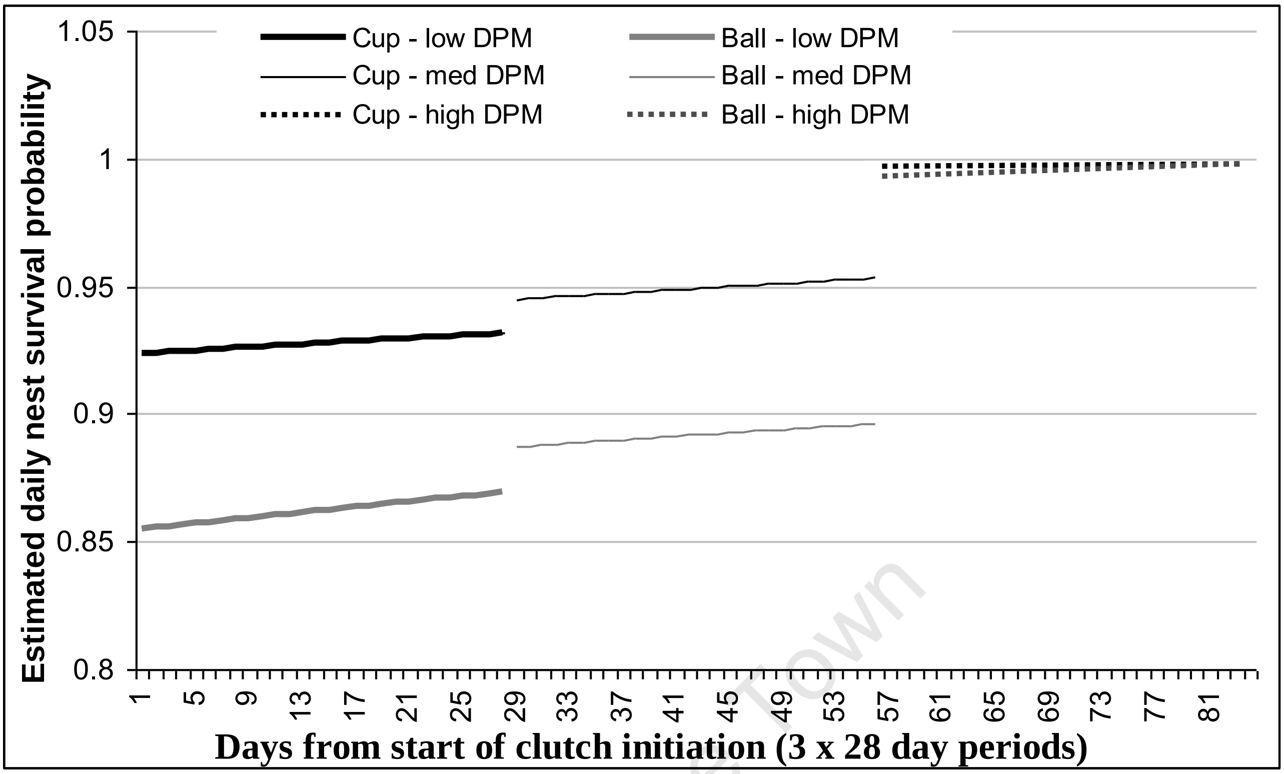


Fig. 5. Estimated daily nest survival (cup- and ball-nesting species separately) per 28-day nesting period for grassland-nesting birds for nests in sites with low (<1200 kg/ha^{-1}), medium (1200-2400 kg/ha^{-1}) and high (2400-3600 kg/ha^{-1}) phytomass. For cup nests, 0.015<S.E.<0.026; for ball nests, 0.017<S.E.<0.027.

In order to gain a better understanding of species-specific responses to disturbance pressures, nest survival rates of the six most abundant grassland-nesting passerines were modelled. These species showed markedly different seasonal trends in estimated daily nest-survival rates (Fig. 6). Five species responded strongly to either burning (3 spp) or grazing intensity (2 spp), and Yellow-breasted Pipits responded to both disturbance types. ΔAIC values > 2 indicate confidence in the results of each of the species' models: results for Yellow-breasted Pipit have low confidence due to small sample sizes (Table 6). When considering seasonal nest density (for all nest attempts throughout the season), rather than nest survival, grazing intensity (Stocking rate, ha.LAU^{-1}) is the most important factor, while day length drives timing of nest initiation with a peak in breeding attempts in all sites in mid-summer (Table 7).

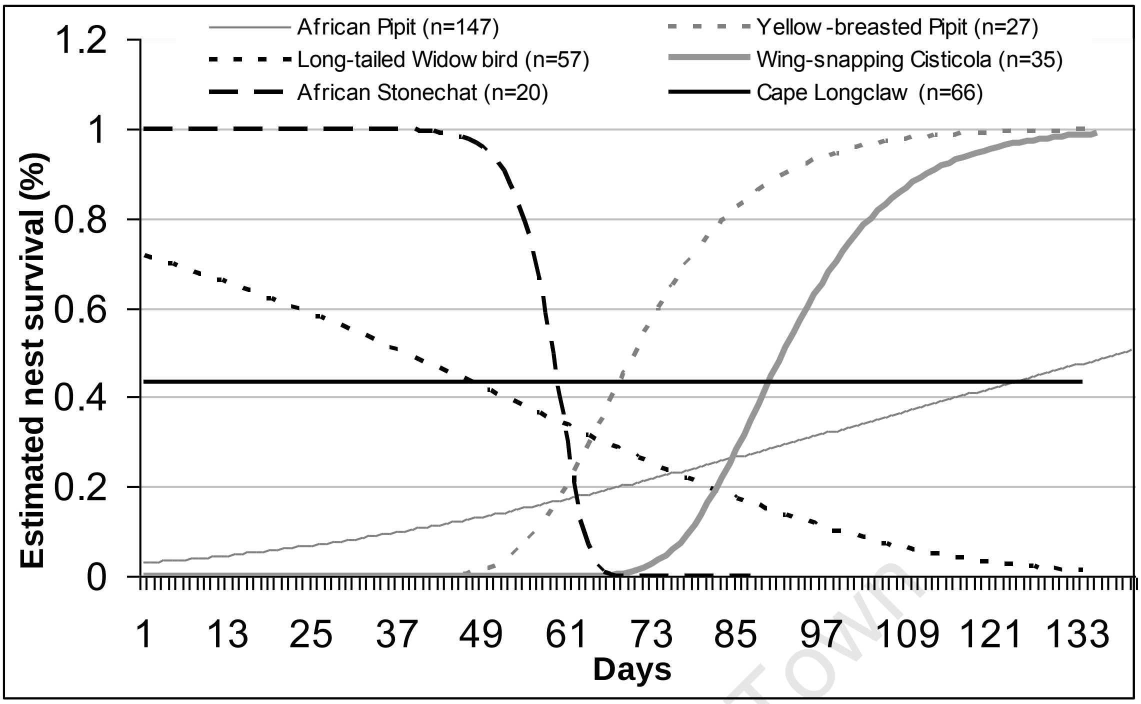


Fig. 6. The seasonal patterns of estimated daily nest survival rates of the six most abundant grassland-nesting passerines: for African Pipit, 0.006<S.E.<0.042; Yellow-breasted Pipit, 0.000<S.E.<0.252; Long-tailed Widowbird, 0.007<S.E.<0.007; Wing-snapping Cisticola, 0.001<S.E.<0.032; African Stonechat, 0.000<S.E.<0.136; Cape Longclaw, 0.009<S.E.<0.070. Julian day 1 on the x-axis is 28 October.

Table 6. Summed AICc weights for Burn and HaLAU indicating the extent of support in the data for inclusion of these covariates within the models. This illustrates the relative influence of each of these factors for each species' nesting success.

		Burn	HaLAU	ΔAIC
Long-tailed Widowbird	*Euplectes progne*	0.936	0.019	2.146
African Stonechat	*Saxicola torquata*	0.898	0.030	3.429
African Pipit	*Anthus cinnamomeus*	0.835	0.074	2.720
Yellow-breasted Pipit	*Anthus chloris*	0.334	0.362	1.200
Wing-snapping Cisticola	*Cisticola ayresii*	0.089	0.714	2.442
Cape Longclaw	*Macronyx capensis*	0.037	0.879	2.460

Table 7. Factors contributing to explaining nest densities of grassland-nesting passerines. Stocking rate (Ha.LAU^{-1}) values are log-transformed.

Nest Density		Significant factors (0.95%)				Model statistics (n = 40)			
Species	**Significant variable**	b	S.E. b	t (33)	p	F	r^2	df	p
Yellow-breasted Pipit	Stocking rate (ha.LAU^{-1})	0.65	0.22	2.82	0.008	7.53	0.50	6.33	0.001
African Stonechat	Stocking rate (ha.LAU^{-1})	0.48	0.14	3.41	0.002	11.64	0.23	1.38	0.002
Long-tailed Widowbird	Day length	0.39	0.16	2.49	0.018	3.36	0.38	6.33	0.010
Cape Longclaw	Stocking rate (ha.LAU^{-1})	0.57	0.26	2.32	0.026	6.86	0.56	6.33	0.001
	Day length	0.40	0.13	3.07	0.004				
Wing-snapping Cisticola	Stocking rate (Ha.LAU^{-1})	0.57	0.26	2.23	0.033	4.98	0.48	6.33	0.001
	Day length	0.29	0.14	2.07	0.047				

To gain further insights into species-specific responses to management, the reproductive performance of African Pipits was modelled across management types. This was the only species for which sufficient nests (n = 147) were located to allow nest survival to be modelled at this level of detail. Estimated nest survival was higher at all sites that were not burnt in that season (Table 8).

Table 8. Estimated nest survival estimates (daily and overall) for African Pipit in each of the study areas. There were insufficient nest attempts (n = 1) on AF to model nest success.

	Number of nests	Daily survival estimate	Overall survival estimate
Com	36	0.964	0.362
NRLu	30	0.934	0.150
NRHu	8	0.918	0.091
BFu	18	0.918	0.090
BF	12	0.915	0.083
NRH	11	0.913	0.079
NRL	31	0.912	0.076

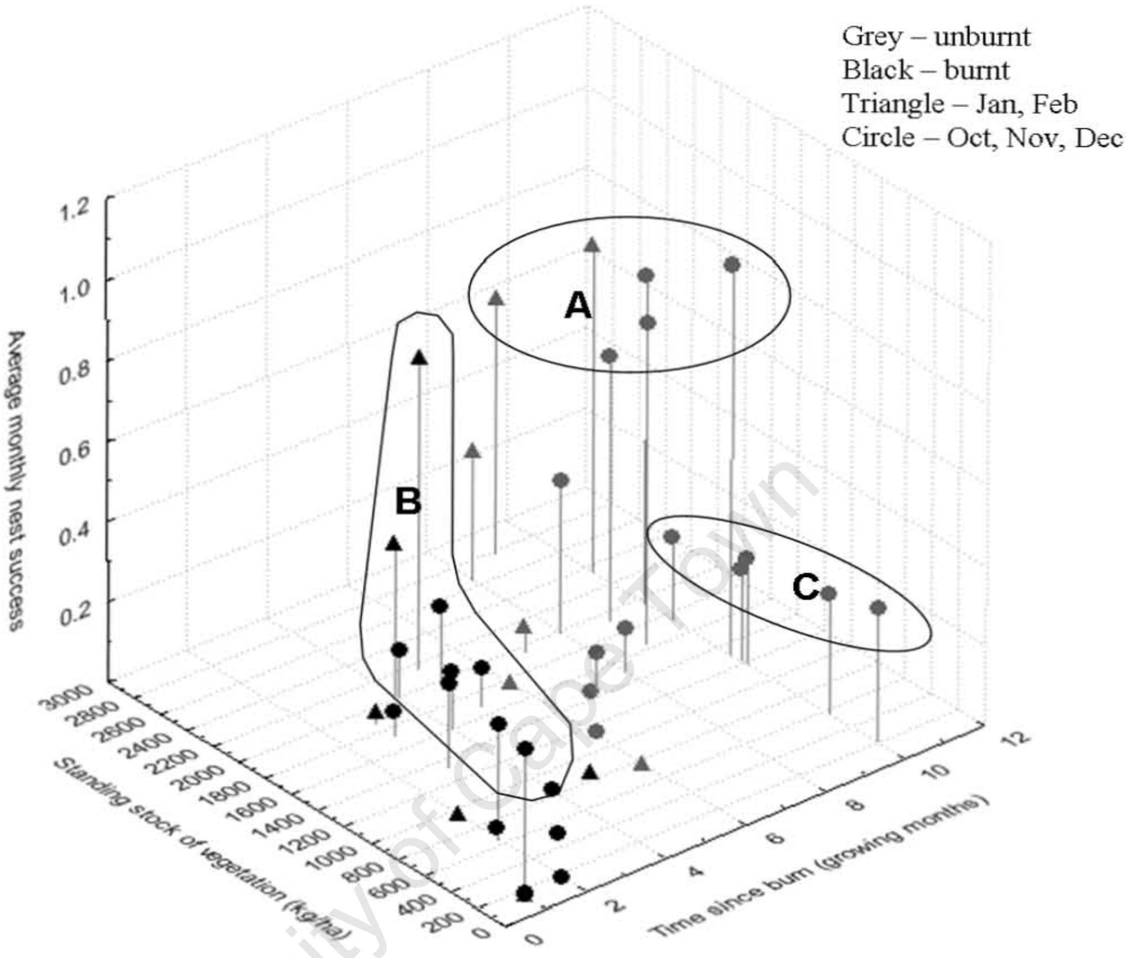
Three-dimensional images assist in untangling the factors influencing nest survival. While phytomass is expected to drive nesting success, through its influence on predation risk, both burning and grazing interact to drive phytomass. Multiple regression analyses consisting of the two main effects showed that neither stocking rate (t = -2.013, p = 0.154) nor time since burn (t = -1.293, p = 0.237) alone explained phytomass ($F_{2,\ 7}$ =

5.074, $r^2 = 0.592$, $n = 10$, $p = 0.043$). However, of the two, time since burn had a stronger influence over nesting success (Table 1).

When looking at the influence of time since burning and phytomass on the average monthly nest success, three different response groups are evident. Those in group A are all unburnt in that year and are in the latter months (Jan/Feb) of the breeding/growing season. Group B consists of sites that were burnt in that year but are grazed by indigenous grazers (NRL & NRH), illustrating the ability of vegetation to recover from fire if grazing pressure is not too high as seen in NRL sites, and group C consists of communally grazed areas that are not actively burnt, resulting in patchy grassland allowing for nesting, even when vegetation cover is low (Fig. 7a,).

When looking at the influence of nest density and phytomass on the average monthly nest success, three different response groups are again evident. Predators are expected to develop an effective search image for nests when nests are at high density (Martin 1988), resulting in decreased individual nest success at high densities regardless of vegetation cover (Group B). A combination of high vegetation cover (nest concealment) and low nest density (poor predator search images) is expected to translate into high nesting success (Group A), while low vegetation cover (poor concealment) and resultant low nest density is expected to result in very low nest success due to the poor concealment of nests (Group C). In Group C (communal grazing lands), nest success is higher than expected (given that the area is heavily grazed and has a low standing stock of vegetation providing poor nest concealment) because the lack of fire leaves isolated large, grass tufts for nesting. Thus, although average vegetation cover is low, within such tufts nest concealment is high.

a)


Grey – unburnt
Black – burnt
Triangle – Jan, Feb
Circle – Oct, Nov, Dec
A
B
C
Average monthly nest success
1.2
1.0
0.8
0.6
0.4
0.2
Standing stock of vegetation (kg/ha)
3000
2800
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
Time since burn (growing months)
0
2
4
6
8
10
12

b)

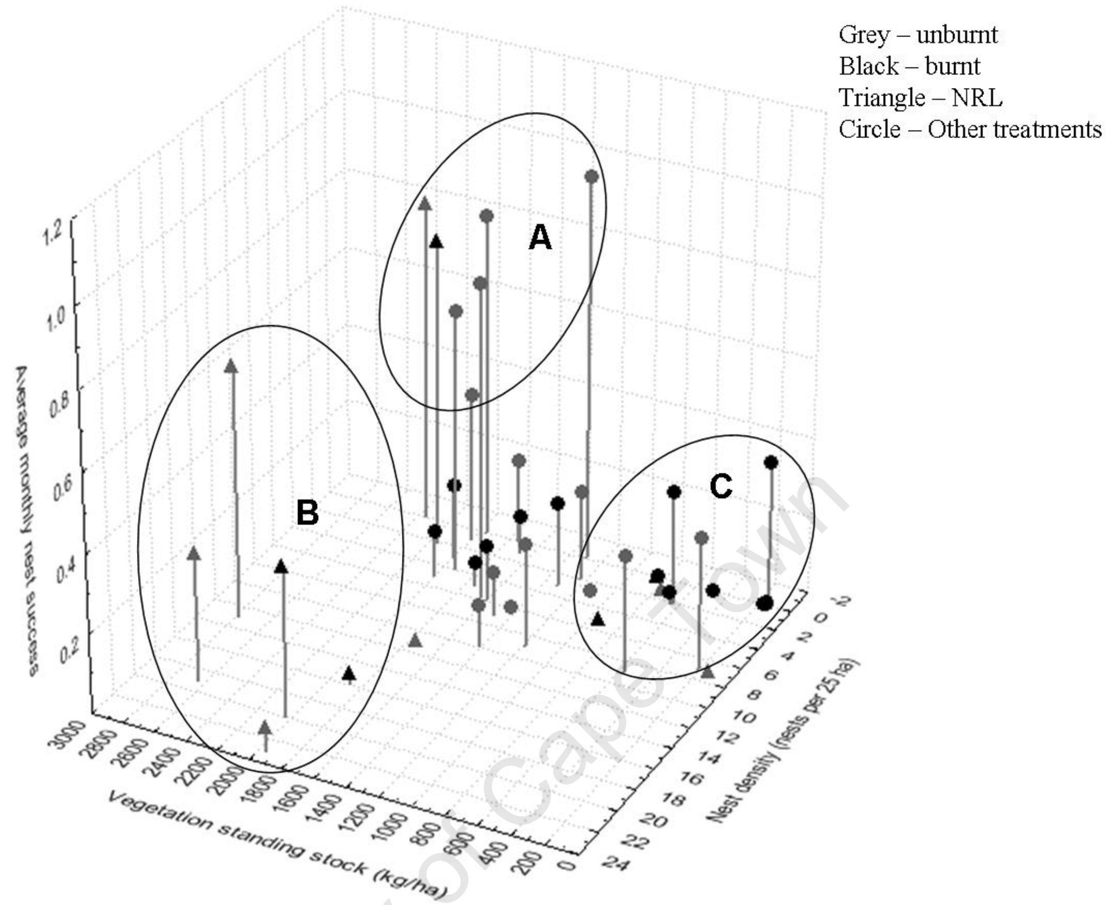


Fig. 7. a) Average monthly nest success as a function of vegetation cover and time since burn; and b) nest success as a function of vegetation cover and nest density. A, B and C represent groups of sites with similar nest success responses to disturbance.

Both standing stock of vegetation and the time since burning are important influences on nesting success in grassland passerines (Fig. 7a, Tables 9, 10). Overall, within-site nest density (nesting effort) increased with increased day length and decreased stocking rate (Tables 9, 10).

Table 9. Assessment of factors influencing nest initiation and nest success of passerine birds in MHGs. Phytomass was log-transformed to meet linearity assumptions.

Nest attempts	**a**. All grassland-nesting passerines				**b**. Cup-nesting birds				**c**. African Pipit			
	beta	S.E. *beta*	t(33)	p	*beta*	SE *beta*	t(33)	p	*beta*	SE *beta*	t(35)	p
Intercept			-1.605	0.118			-0.698	0.490			-0.351	0.728
Phytomass (kg.ha^{-1})	0.010	0.238	0.042	0.967	-0.209	0.252	-0.829	0.413	**-0.416**	**0.203**	**-2.054**	**0.047**
Insect biomass (g/600 sweeps)	0.099	0.163	0.607	0.548	0.068	0.168	0.407	0.686	0.119	0.197	0.605	0.549
Stocking rate log(ha.LAU^{-1})	**0.769**	**0.246**	**3.126**	**0.004**	**0.925**	**0.254**	**3.642**	**0.001**	**0.814**	**0.290**	**2.806**	**0.008**
Time since burn (months)	0.129	0.182	0.707	0.485	0.237	0.187	1.269	0.213	0.349	0.175	1.992	0.054
Treatment effect	0.209	0.269	0.777	0.442	0.200	0.278	0.720	0.476	0.361	0.302	1.196	0.240
Day length	**0.334**	**0.129**	**2.589**	**0.014**	0.093	0.141	0.657	0.516	-0.011	0.166	-0.065	0.949

Nest success	**d**. All grassland-nesting passerines				**e**. Cup-nesting birds				**f**. African Pipit			
	beta	S.E. *beta*	t(33)	p	*beta*	SE *beta*	t(35)	p	*beta*	SE *beta*	t(37)	P
Intercept			1.465	0.152			-1.177	0.247			-1.064	0.294
Phytomass (kg.ha^{-1})	**0.383**	**0.149**	**2.136**	**0.036**	**0.323**	**0.150**	**2.147**	**0.038**	0.245	0.284	0.861	0.395
Insect biomass (g/600 sweeps)	-0.120	0.171	-0.702	0.487	0.065	0.183	0.359	0.722	-0.178	0.141	-1.256	0.217
Stocking rate log(ha.LAU^{-1})	-0.296	0.258	-1.146	0.260	0.275	0.276	0.995	0.327	0.310	0.282	1.100	0.279
Time since burn (months)	**0.433**	**0.191**	**2.271**	**0.030**	**0.367**	**0.150**	**2.439**	**0.020**	**0.316**	**0.142**	**2.225**	**0.033**
Treatment effect	-0.382	0.282	-1.354	0.185	0.170	0.303	0.562	0.578	**0.634**	**0.282**	**2.250**	**0.031**
Day Length	-0.200	0.135	-1.480	0.148	-0.103	0.154	-0.670	0.507	-0.145	0.159	-0.907	0.371

Table 10. Model outputs for the six models (a-f) in Table 9. For each model, n = 40 (8 treatment x 5 months).

	F	**r^2**	**df**	**p**
a	5.762	0.512	6.33	0.001
b	5.095	0.481	6.33	0.001
c	3.388	0.297	4.35	0.019
d	4.745	0.463	6.33	0.001
e	10.052	0.352	2.37	0.001
f	4.087	0.318	4.35	0.008

4.4. Discussion

MHGs are naturally maintained by winter and spring fires and by summer grazing by migratory herds of small to medium-sized antelope (Everson 1999; Mucina and Rutherford 2006). These grasslands are typically dominated by decreaser grasses that only re-seed in the late successional stage (i.e. climax grasses). It has been suggested that the natural fire frequency in the highland grasslands would have been as infrequent as every four years or more (Manry and Knight 1986). Currently the majority of the system is managed by livestock farmers who burn their land annually (a few burn biennially) at the onset of the rainy season in early summer. This coincides with the beginning of the breeding season for grassland-nesting birds. Annual burning and high grazing pressure have both been shown to affect bird diversity negatively, with most specialist grassland species decreasing in numbers in areas that are burnt annually (Mentis and Little 1992; Powell 2008; Chapter 3). Clarke (2008) outlined the need for faunal-based research in order to assess the influence of fire management on biodiversity. In previous chapters I have done this using inventory-type data. Although some recent studies have been conducted on nest success rates and the impacts of nest predation in an African context (Muchai 2002; Schaefer et al. 2005; Hanson et al. 2007; Kotze and Lawes 2007; Lloyd 2007; Boukhriss et al. 2009), with the exception of Muchai (2002), who focused on evolutionary responses rather than relative nest success, and Maphisa (2009) who focused on endangered lark species, these studies have not led to a clearer understanding of ecological and management correlates of nest success because they did not compare the relative effects of different disturbance pressures.

Nesting success increases with increasing vegetation biomass: this is mediated through decreasing predation rates because nests are better concealed in dense vegetation (Muchai 2002). Linked to this, it has been suggested that grassland-nesting passerines select nest sites based on phytomass, which itself is mediated by the interaction between grazing intensity and burning (Fondell and Ball 2004). This study suggests that burning (Tables 3-5, 9-10; Figs 2-4, 7) has a substantial influence on the nesting success of passerines. In the year of burning, the onset of breeding is delayed (because of a lack of vegetation cover), there are fewer nesting attempts and individual nest success is lower (Figs 3-6).

These effects are equally strong for both cup and ball nesters (Fig. 4). In addition to the time since burn, nest age and standing stock of vegetation play important roles in determining nest survival rates (Tables 9, 10; Fig. 7). Phytomass is closely linked to the time since burn and is thus auto-correlated with stage of the breeding season (Fig. 7; Chapter 2). However, neither time since burning nor grazing intensity alone determine the amount of phytomass in any given area: standing stock is determined by an interaction of both of these disturbance factors.

In this grassland system, the success of cup nesters increases as the season progresses: this is contrary to the pattern reported for most Northern Hemisphere passerines, especially migratory species, for which food availability decreases during the breeding season, acting as a limiting factor for many species (Johnson 1979; Klett and Johnson 1982; Hochachka 1990; Wiggins et al. 1994; Fredy et al. 1995; Verhulst et al. 1995; Dinsmore et al. 2002; Fondell and Ball 2004; Grant et al. 2005; Walk et al. 2010). In the MHGs of South Africa, however, nesting success tracks the increasing standing stock of vegetation through the growing season. Increasingly dense vegetation provides increasing nest concealment and leads to reduced nest failure (as reflected in the higher nest success in unburnt areas - Table 8), suggesting that predation is the key factor driving breeding success. Evidence (or lack of it) remaining after nest predation events strongly suggests that the key egg and chick predators in this system are snakes, several species of which are common.

When comparing the most common management strategies practiced in the MHGs, it is clear that annually burnt farms (AF) do not provide suitable habitat for breeding passerines. This is due to the combined effects of intensive grazing and annual burning resulting in reduced phytomass and lack of nesting cover. The effect of high grazing pressure alone is apparent in the biennially burnt farmlands and heavily grazed nature reserve areas (BFu, BF, NRHu, and NRH), where nesting attempts were fewer, and breeding performances poorer, relative to areas with low grazing intensity and biennial burning (NRLu, NRL). The communally grazed area (Com) had high nest densities and nest success (Figs 1, 7b). This is contrary to what was found by Krook et al. (2007) who found almost no successful nesting by passerines in equivalent habitats in KwaZulu-Natal. This is possibly due to the latter area having higher stocking rates of sheep and goats, which are more detrimental to nesting success than cattle (Muchai 2002). While the communally grazed area is not burnt as a management strategy, it is grazed intensively (Table 1, Chapter 2). This results in limited vegetation cover for nest concealment but, because of the lack of fire, clumps of unpalatable grasses and forbs develop which provide nesting cover for the generalist African Pipit (by far the most common bird species in this habitat). It is likely that predation pressure in communal lands is also lower. In these areas, much pedestrian traffic, and the area's close proximity to human settlements, probably reduces the abundance of indigenous mammalian predators. Active persecution of snakes (Thabo Mabuza, pers. comm.), which are assumed to be predominant predators on the managed farms, further reduces predation pressure (Cote and Sutherland 1997; Sperry et al. 2008). The lowered predation pressure is reflected in the high overall survival rate of nests and is clearly apparent in the survival of African Pipit nests (Table 8). Breeding densities of African Pipits in communal lands were not only higher than in any other management type, but birds in the communal lands also achieved more than double the nest success rate of anywhere else.

The six most abundant nesting passerine species responded to different disturbance pressures based on land-management effects and showed different patterns of seasonal nest survival. Although low nest numbers provide limited confidence in the result, it is apparent that Yellow-breasted Pipits responded equally negatively to both frequent burning and intense grazing. This is not surprising: this species is a MHG specialist and is known to be sensitive to any form of disturbance (Jansen 1999; Muchai 2002; Hockey et al. 2005). Of the 27 Yellow-breasted Pipit nests found, 20 (74%) were in the reserve area with low grazing pressure in the year following a burn. Of these, 85% were successful. No Yellow-breasted Pipit nests were found on the annually burnt farm, communal lands or on the biennial burnt farm in the year that it was burnt. Of the Yellow-breasted Pipit nests found outside the NRL, only 43% were successful, suggesting that unconserved areas may act as population sinks for this species. Of the remaining five species, three responded primarily to burning and the other two to grazing intensity (Table 6). When considering nest density as opposed to success rates, all six species responded to grazing intensity, with day length influencing date of initiation (Tables 7, 9-10; Fig. 7) and grazing intensity driving nest density (Table 9). Similar studies found support for day length acting as the cue for nest initiation as opposed to any physical habitat feature (Little and Crowe 1993; Both et al. 2006). As suggested by the model incorporating all species, nest success increases through the season for all species except African Stonechat and Long-tailed Widowbird (Fig. 6). The apparent decreasing nesting success of African Stonechat through the season is a function of this species' early breeding season rather than genuinely decreasing nest success. Most African Stonechats have completed the breeding cycle by midway through the breeding seasons of the other species (Hockey *et al.* 2005). Long-tailed Widowbirds nest in tall, wetland sedges early in the breeding season when predation pressure is lower, but as vegetation cover increases in mid to late summer they also nest in open grassland. This is the time when predation pressure is highest, illustrated by decreased average nest success even though the number of nest attempts is on the increase (Fig. 6).

Some authors suggest that nest predation is higher in the tropics than in north-temperate regions because of a higher nest density and a different suite of predators (Both et al. 2006; Butler et al. 2010). Nest predators in the tropics are a diversity of small mammals and snakes, whereas in Europe and North America corvids and small mammals alone are responsible for the majority of nest predation (Skutch 1949; Ricklefs 1969). Among most precocial, ground-nesting bird species, daily nest success is expected to increase with age of nest because of early predation of nests in high-risk (easily detectable) locations (Klett and Johnson 1982). Altricial species are expected to respond in the opposite manner, with daily nest survival decreasing with age of nest due to a) increased visitation by parent birds causing the nest location to become increasingly detectable by predators, and/or b) food availability failing to keep track with the escalating energy demands of the growing brood (Martin et al. 2000; Dinsmore et al. 2002; Jehle et al. 2004; Nur et al. 2004; Grant et al. 2005). Contrary to this expectation (based on patterns observed in north-temperate grasslands), in the MHGs nest success of altricial ball nesters increased significantly with nest age (Fig. 4). This is a result of the high proportion of nests that failed at the egg stage as compared to the nestling stage. The reason for this is likely the predominance of snake predators, some of which, such as the Rhombic Egg-eater *Dasypeltis scabra*, are egg specialists (Table 2; Appendix 1).

Variation in the nesting success of grassland passerines has mostly been attributed to fluctuations in food availability and predation pressure (Fredy et al. 1995; Both et al. 2006; Dennis et al. 2008; Butler et al. 2010). In this study, all of the models constructed to explain such variation discarded food availability as a significant explanatory variable, suggesting that food availability is not a limiting factor influencing either nest initiation or nest success among these grassland birds.

Predation rate was the primary driver of nest success: the most intense predation occurred at sites where nests were poorly concealed (low vegetation biomass - Fig. 7). However, sites with high densities of well-concealed nests also experienced relatively high predation rates. This is probably explained by predators developing a focussed search image when potential nest-encounter rates are high (Martin 1988).

Optimal management for the conservation of breeding bird populations will be that which combines highest nest success with highest nest density (Table 8, 9, Fig. 7). Based on this it is strongly recommended that land managers in MHGs promote a mosaic of burning regardless of patch size (Engle et al. 2008; Walk et al. 2010), with the majority burning biennially or less frequently and leaving sufficient unburnt grassland for nesting. This mosaic can be supplemented with the use of large fire-breaks which can be used to provide the desired green flush (O’Connor et al. 2005). Furthermore, stocking rates of livestock should be limited to below the thresholds required for successful reproduction by grassland birds, i.e > 2 Ha.LAU^{-1}.

Appendix 1. Potential nest predators present at the study site.

Snakes	
Brown House-Snake	*Lamprophis capensis*
Mole Snake	*Pseudapis cana*
Spotted Skaapsteker	*Psammophylax rhombeatus*
Short-snouted Sand Snake	*Psammophis brevirostris*
Crossed Whip-Snake	*P. crucifer*
Rhombic Egg-eater	*Dasypeltis scabra*
Rinkhals	*Hemachatus haemachatus*
Common Night-Adder	*Causus rhombeatus*
Mammals	
Black-backed Jackal	*Canis mesomelas*
Side-striped Jackal	*C. adustus*
Striped Weasel	*Poecilogale albinucha*
Water Mongoose	*Atilax paludinosus*
Yellow Mongoose	*Cynictis penisillata*
Slender Mongoose	*Galerella sanguinea*
Large Grey Mongoose	*Herpestes ichneumon*
Suricate	*Suricata suricatta*
Civet	*Civettictis civetta*
Brown Hyaena	*Hyaena brunnea*
Aardwolf	*Proteles cristatus*
Cape Fox	*Vulpes chama*
African Wild Cat	*Felis lybica*
Serval	*F. serval*
Caracal	*F. caracal*
Striped Mouse	*Rhabdomys pumilio*
Birds	
Black-headed Heron	*Ardea melanocephala*
Secretarybird	*Sagittarius serpentarius*
African Harrier-Hawk	*Polyboroides typus*
Denham's Bustard	*Neotis denhami*
Cape Crow	*Corvus capensis*
Common Fiscal	*Lanius collaris*

CHAPTER 5

Process-oriented techniques for assessing biodiversity integrity in grasslands: a case study in the moist highland grasslands of South Africa

Abstract

The South African grassland system is home to over 3300 plant species, 15 of the country's 34 endemic mammal species, 12 of the 40 endemic bird species (four of which are globally threatened) and five RAMSAR wetland sites. To assess and address the ecological integrity of farmed grasslands I used process-oriented techniques, including nesting success and field metabolic rates (FMR) of birds, and an adaptation of the multi-taxon Biodiversity Intactness Index (BII) using plant, arthropod and bird diversity data. The appropriateness of the BII for this type of assessment has been criticized (Lindenmayer and Likens 2010), but it is nonetheless a comprehensive tool for assessing ecological integrity using multiple taxonomic groups. Current pastoral management practices have a significant detrimental effect on avian abundance, species richness, nest density and fledgling output. Overall energy turnover and BII values confirm the importance of conserved areas for birds in moist highland grassland (MHG) systems and support the need for further conservation efforts in grassland systems by both private landowners and reserve managers. Findings based on both avian FMRs and the BII in this study are significantly similar, lending support to both of these techniques for the assessment of ecosystem integrity for future studies of this nature. Scenarios of potential biodiversity improvement with changes in fire management regimes are also presented.

Key words: Biodiversity, conservation, fire, grasslands, grazing, processes.

5.1. Introduction

Loss and degradation of natural habitat are the most significant causes of biodiversity loss in terrestrial ecosystems (Driver et al. 2005), with human demands placing increasing pressure on land resources (Damm 2002; Darkoh 2003). This degradation disrupts ecosystem functioning and hence influences biodiversity (Bibby 1999; Hilty and Merenlender 2000). Determining the factors leading to current patterns of biodiversity loss in human-degraded landscapes is thus important in order to assess the likely effectiveness of future conservation efforts (Jeanneret et al. 2003a).

Only some forms of agriculture have the potential to be both productive in terms of human food resources and conservation ‘friendly’: one such form of land use is livestock farming on natural pastures (O’Connor 2005). Future demands on agriculture will grow exponentially with human population growth and it is estimated that by 2025 global agricultural production will have to increase by 50% to sustain the projected human population, the majority of which will be in developing countries (Damm 2002). Rapid population growth in South Africa is a reality: the human population doubled between 1970 and 2010, and some 38% of the populus depends on areas that are degrading, 37% of which are rangelands (Bai and Dent 2007).

In most countries that have grasslands, including South Africa, these constitute the main production landscapes, but in general they are very poorly conserved (Driver et al. 2005; O’Connor and Kuyler 2009). In South Africa, only 2.2% of the grassland biome falls within protected areas (Tarboton 1997; Raimondo et al. 2009) that themselves sit in an extensive matrix of land transformed to varying degrees. The South African grassland system is home to some 42 rivers, many of which originate in grassland catchments, over 3300 plant species, 15 of the country’s 34 endemic mammal species, 12 of the 40 endemic bird species (four of which are globally threatened) and five RAMSAR wetland sites. Of the 340 000 km^2 of grassland, about 60% is thought to have been irreversibly degraded (Mucina and Rutherford 2006).

This matrix currently feeds an estimated 6.4 million cattle and 13 million sheep (Driver et al. 2005). While livestock farming in grasslands is detrimental to biodiversity in general (Donald et al. 2002; Muchai 2002; Dennis et al. 2008), if managed correctly it is likely the most biodiversity-friendly form of land use (Muchai 2002). It is therefore important to assess the relative biodiversity impacts of varying intensities of management in grassland pastoral systems through understanding shifts in species diversity, including both the loss of indigenous species and the gain of species not naturally representative of the original system (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005). The land making up the matrix between conserved habitats will be crucial for the future conservation of many species and for broader ecosystem functioning (Wiens 1994; Norton 2000; Ricketts 2001; Donald et al. 2002; Hilty and Merenlender 2003), making it important to optimise management practices in the matrix.

A diversity of species’ traits, including endemicity, body size, feeding guild, clutch size/reproductive strategy, natural abundance and field metabolic rates are thought to play a role in determining species' sensitivities to habitat degradation and fragmentation (Nagy et al. 1999; Suarez-Seoane et al. 2002; Nagy 2005; Batáry et al. 2006). Ecologists thus have a key role to play in describing and developing indicators that can inform land-use planning (Thomas 1972; Landres et al. 1988; Noss 1989; Dale and Beyeler 2001; Duelli and Obrist 2003; Theobald et al. 2005).

The concept of indicator species as a short cut to assessing impacts of land use has provoked critical debate (Thomas 1972; Landres et al. 1988; Noss 1989; Bibby 1999; Hilty and Merenlender 2000; Dale and Beyeler 2001; Duelli and Obrist 2003; Theobald et al. 2005), but the need still remains for a means of assessing the extent to which ecological integrity is impacted by human activities: if effective indicator species can be identified, these can prove to be very useful (Thomas 1972; Bibby 1999; Prendergast and Eversham 1997). To date, most research has focused on using inventory-type data to determine the effects of human land use: typically, this invloves correlating organismal abundance with features of the occupied habitat (Martin and Possingham 2005; Wretenberg et al. 2010). Some effort has been made to refine this process by defining and partitioning the objectives of identifying indicators, such as those proposed by Duelli and Obrist (2003). They suggested using indicators for monitoring three different ecological assemblages: rare and threatened species, species with high ecological resilience and species that can be used for monitoring the effectiveness of biological control agents. However, such indirect approaches may fail to identify appropriate species assemblage and functional responses to management efforts due, for example, to the replacement of specialist species with generalists. Dale and Beyeler (2001) suggested that a list of criteria need to be fulfilled for a species to satisfy the status of an indicator. Such a species should be sensitive to stresses on the system; respond to stress in a predictable manner; predict changes that can be averted by management actions; be integrative; and have a known response to disturbances, anthropogenic stresses, and changes in species assemblages over time (Dale & Beyeler 2001).

While these and other guidelines (e.g. Opdam et al. 2003; Van Cauwenbergh et al. 2007) are useful (although the likelihood of any one species satisfying all these criteria is low), they still do not address the problem of comparability between sites where species' responses vary geographically. In order to address this shortfall, research needs to focus on processes rather than simply illustrating patterns. As O'Connor and Kuyler (2009) point out, it is important to consider landscape structure, composition and functioning when assessing the ecological integrity of large scale systems. With birds this can be achieved through assessing reproductive performance (Dinsmore et al. 2002; Fondell and Ball 2004) and quantifying the passage of energy flow through organisms in the system (Nagy et al. 1999; Nagy 2005; Fox and Hockey 2007). While single-species studies are important and often allow for easier identification of both ultimate and proximate causes of population-level effects (eg. Sutter and Ritchison 2005), they do not necessarily provide a good indication of the integrity of the system as a whole (which would allow for more informed management decisions). In this regard, both multiple species/taxonomic groups (Milchunas et al. 1998; Söderström et al. 2001), as well as functional group assessment, provide more robust insights into ecosystem functioning (Wiens 1973; Zipkin et al. 2010). Along with this, the use of biodiversity indices can assist with understanding the effects of land use on multiple taxonomic groups (Söderström et al. 2001; Mace 2005; Scholes and Biggs 2005; Rouget et al. 2006; Zipkin et al. 2010). According to the Biodiversity Intactness Index (BII) developed by Scholes and Biggs (2005), South Africa scores at about 84%, which means that populations of 84% of the original fauna and flora (prior to disturbance by modern humans) remains. The ecosystem with the greatest overall biodiversity loss is the grassland system (currently 74% of its original biodiversity remains intact). This study assesses the ecological integrity of MHGs and the impact of land-use management on this integrity, using multiple biodiversity indices.

5.2. Study site and methods

For details of the study site and methods see Chapters 2 (vegetation sampling), 3 (bird and arthropod sampling) and 4 (nest monitoring and survival modelling using Program MARK).

Following Fox and Hockey (2007), field metabolic rates (FMRs) were derived by assigning the most appropriate dietary or taxonomic category to the associated equation for each bird species (from Nagy et al. 1999; Appendix 2). Species' body masses (g), averaged across sexes, were extracted from Hockey et al. (2005) for calculation of FMR and associated confidence limits using these equations.

Biological Intactness Indices (BIIs) were calculated using an adaptation of the calculation developed by Scholes & Biggs (2005). The equation used was:

$$BII = \frac{R_iA_i + R_j A_j + R_kA_k}{R_i + R_j + R_k}$$

where R is species richness, A is abundance, 'i' is arthropods, 'j' is birds and 'k' is plants.

The term ’grassland species’, in reference to birds, means the assemblage of species that utilize grasslands directly and are inidgenous to the grassland system. For this reason, aerial, arboreal and thicket-dwelling insectivores, frugivores, water birds and non-insectivorous birds of prey were excluded from analyses. ‘Focal species’ were grassland-nesting passerines and ground-nesting Common Quail *Coturnix coturnix*.

The Software package STATISTICA 9.0 (StatSoft Inc. 2009) was used for data analysis to assess the relative difference between the results derived from estimated daily nesting success and community Field Metabolic Rates (FMRs) across management types, Wilcoxon Matched-Pairs Tests were used. Mann-Whitney-U Tests were used to compare average monthly avian diversity and reproduction in farmed areas relative to the conserved area. For small to moderate-sized samples, STATISTICA estimates an exact probability associated with the respective U statistic (Dinneen and Blakesley 1973). This leads to only a small underestimation of the statistical significance (Siegel 1956). To assess the similarity of the results derived from the Biological Intactness Index and Field Metabolic Rates (see below), a Pearson Correlation was used.

The Software package PC-ORD 5.10 (McCune and Mefford 2006) was used to assess the relative metabolic energy levels between management types by performing Principle Components Analyses. The results were plotted as ordinations, with functional guilds overlaid to illustrate their relative contribution to the dispersion of points. Indicator Species Analyses (McCune and Mefford 2006) were also run for both species-specific responses and functional feeding guilds using a Monte Carlo Test of significance with 5000 iterations (Dufrêne and Legendre. 1997). This method combines species abundance and occurrence. A ‘perfect indicator’ should be present in all replicates within a site and not present in any other sites (McCune and Mefford 2006).

5.3. Results

As an initial approach to assessing the ecological integrity of areas under different management regimes, nest survival of grassland-nesting birds was modelled. Estimated nest survival rate analyses (the probability of a nest surviving from egg-laying through to fledging) provide a process-oriented approach for assessing the effects of disturbance. Estimated nest survival rate responded strongly to burning regime with communal lands having the highest estimated survival rates (Table 1). The only threatened species, Yellow-breasted Pipit, together with African Stonechat, had the highest overall estimated nest survival rates.

Table 1 Mean nest survival estimates (derived using Program MARK) across management types (all bird species combined), species (all management types combined), grazing type (indigenous grazers *vs* livestock; all bird species combined), nest type (cup or ball; all species combined); time since burn (all bird species combined); and conserved *vs* farmed lands (the latter including the heavily grazed nature reserve; all species combined). For scientific names see Appendix 1 in Chapter 3.

	Daily survival estimate	Std error	Lower confidence interval	Upper confidence interval	Nest survival estimate
All nests (n = 376)	0.945	0.004	0.937	0.952	0.204
Management type					
Com (n = 53)	0.957	0.008	0.938	0.971	0.292
NRLu (n = 111)	0.954	0.006	0.940	0.965	0.270
NRHu (n = 33)	0.950	0.013	0.918	0.969	0.236
NRL (n = 85)	0.946	0.019	0.895	0.973	0.210
BFu (n = 33)	0.945	0.013	0.912	0.966	0.205
NRH (n = 17)	0.932	0.010	0.909	0.949	0.137
BF (n = 41)	0.919	0.015	0.886	0.944	0.095
AF (n = 3)	0.873	0.069	0.669	0.959	0.022
Species					
Yellow-breasted Pipit (n = 27)	0.975	0.010	0.946	0.989	0.495
African Stonechat (n = 20)	0.975	0.012	0.935	0.991	0.490
Cape Longclaw (n = 66)	0.966	0.008	0.947	0.978	0.378
Long-tailed Widowbird (n = 57)	0.941	0.009	0.920	0.956	0.160
African Pipit (n = 147)	0.935	0.007	0.921	0.947	0.155
Red-collared Widowbird (n = 10)	0.933	0.024	0.866	0.968	0.145
Wing-snapping Cisticola (n = 35)	0.933	0.016	0.893	0.958	0.142
Zitting Cisticola (n = 14)	0.917	0.028	0.843	0.958	0.089
Grazing type					
Indigenous grazing (n = 246)	0.946	0.005	0.936	0.955	0.212
Domestic grazing (n = 130)	0.942	0.007	0.928	0.954	0.190
Nest type					
Cup nesters (n = 260)	0.950	0.005	0.940	0.958	0.236
Ball nesters (n = 116)	0.936	0.007	0.920	0.949	0.159
Burning regime					
Unburnt in that season (n = 230)	0.953	0.004	0.944	0.961	0.261
Burnt in that season (n = 146)	0.929	0.008	0.912	0.942	0.126
Management type					
NRL (burnt & unburnt) (n = 196)	0.946	0.005	0.934	0.955	0.211
All farmed treatments (n = 180)	0.943	0.006	0.932	0.954	0.193

When considering areas that had not been burnt, treatments were not significantly different from one another in terms of nest survival, except for BFu which was significantly lower than all other sites. Combined, all unburnt areas had significantly higher estimated nesting success than all burnt areas, suggesting that the presence or absence of burning in a particular season, rather than differences in grazing pressure, is the primary cause of variation in breeding success (Table 2). Of further interest is the lack of a significant difference between burnt and unburnt NRH, suggesting that, in this one instance, high-intensity (and selective) grazing by indigenous Blesbok *Damaliscus dorcas* overshadows the influence of fire. There was also no significant difference between burnt NRL and BF, suggesting that burning biennially confers biodiversity benefits even in the years in which burns occur.

Table 2. A comparison of estimated daily nest survival rates (Program MARK) of grassland passerines through the breeding season between management types.

Comparison	T	Z	p
NRLu > NRL	**0**	**9.546**	**0.000**
NRLu = NRHu	3373	0.821	0.412
NRLu = NRH	3041	1.68	0.093
NRLu > BFu	**0**	**9.546**	**0.000**
NRLu > BF	**478**	**8.309**	**0.000**
NRLu = Com	3326	0.943	0.346
NRL < NRHu	**1438**	**5.826**	**0.000**
NRL < NRH	**2601**	**2.818**	**0.005**
NRL < BFu	**0**	**9.546**	**0.000**
NRL = BF	3016	1.745	0.081
NRL < Com	**2144**	**4**	**0.000**
NRHu = NRH	3272	1.082	0.279
NRHu > BFu	**2757**	**2.415**	**0.016**
NRHu > BF	**2187**	**3.889**	**0.000**
NRHu = Com	3435	0.661	0.509
NRH < BFu	**2725**	**2.497**	**0.013**
NRH > BF	**309**	**8.747**	**0.000**
NRH < Com	**1292**	**6.204**	**0.000**
BFu > BF	**170**	**9.106**	**0.000**
BFu = Com	2964	1.879	0.06
BF < Com	**0**	**9.546**	**0.000**

It is evident from the above that nesting success is influenced by management. In Chapter 4, modelling indicated that individual nest success was not influenced by food availability. However, when the number of fledglings per unit area is considered, it appears that food availability may play a role in determining breeding success. Reproductive output, measured as fledgling density, increased with increasing food availability (arthropod abundance) and bird abundance (Fig. 1). In combination with the results from Chapter 4, this suggests that food availability limits nest density but does not regulate subsequent nesting success.

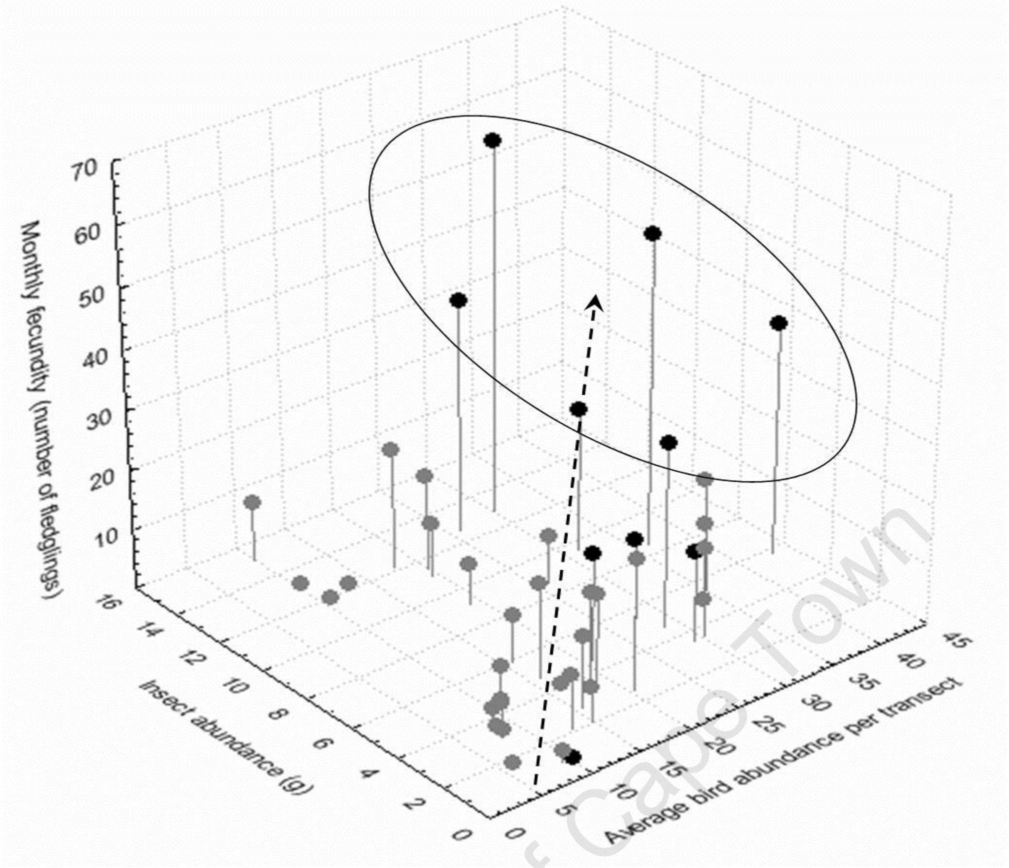


Fig. 1. Monthly fecundity (number of fledglings per 25 ha replicate) as a function of food availability (arthropod abundance in grams per sweep-net transect) and average bird abundance across all sites. Black dots represent the conserved area with low stocking density (all other sites are in grey) and the dots encompassed within the large circle represent the mid to late nesting season. The dotted line illustrates the trend of increasing fledgling density with both increasing insect abundance and increasing bird density.

An understanding of the roles of food availability, vegetation cover, grazing intensity and burning on bird nesting success across management types (Chapters 3, 4) bring us closer to understanding the overall effect of farming on birds in the system as compared to the conservation area. When comparing the well-conserved nature reserve (with a low density of indigenous grazers) to farmed land as a whole (combined with the heavily grazed nature reserve), it is apparent that management for conservation is beneficial to bird species in grasslands. This is evident in both count data (greater bird abundance in conserved areas) as well as process-oriented data (greater reproductive output in the same areas). The magnitude of these differences is exaggerated by the high impact of annual burning on bird abundance and nesting success (Chapters 3, 4).

Table 3. Comparison between bird populations and performance in the conservatively managed (low stocking density) conservation area (NRL) and agricultural management as a whole (which includes the heavily grazed nature reserve, NRH). Nest density and fledgling density are presented as total numbers per month per 100 ha. Nest success values are averaged from estimated daily nest success (Program MARK).

Bird performance perameters	U	p	Average NRL	Average outside NRL
Abundance (birds per transect)	**18**	**0.017**	**0.41**	**0.29**
Species richness	**23**	**0.045**	**40.4**	**30.2**
Shannon diversity	29	0.121	3.16	2.90
Nest density	**8.5**	**0.002**	**20.80**	**6.53**
Fledgling density	**12.5**	**0.005**	**30.10**	**7.90**
Nest success	48	0.910	0.33	0.23

While nest success and reproductive output data are useful and interesting for assessing the functional integrity of the faunal component of grassland systems, nest success data are more time-consuming and less easily collected than are simple count data. For this reason the use of count data converted into an index of system energy flow can provide a form of process-oriented assessment of habitat management and can differentiate which functional guilds are benefitting from, or being detrimentally affected by each management practice. In this way, species as well as functional guilds can be extracted to indicate their responses to land-use management. This is achieved by using the field metabolic rates (FMRs) calculated from the relevant equations in Nagy et al. (1999) by separating species out into their functional feeding guilds (or taxonomic groupings). These data were used in an indicator species analysis to assess the difference in the integrity of the various management types based on avian FMRs (Table 4). Thirteen species had significantly higher cumulative field metabolic rate scoresin the unburnt conservation area with low grazing intensity (NRLu), illustrating the importance of this area and the need for more land under this form of management for the conservation of these species. Only two species showed a preference for the annually burnt farm, these species both feed in open areas and prefer disturbed areas (Hockey *et al.* 2005). Similarly, when the functional feeding guilds themselves are analysed it is apparent that five of the the 15 functional guilds are best represented in the conservation area, with only two guilds (grazers and open-area invertebrate feeders) preferring the communally grazed lands (Table 5). No other management type (other than what NRL and Com) was characterised by an indicator guild. A ‘perfect indicator’ (IV of 100) should be present in all replicates within a site and not present in any other sites.

Table 4. Indicator species analysis based on field metabolic rates (kJ.day^{-1}) showing species with site-specific energy flow rates, illustrating habitat preference.

		Observed indicator values	IV from randomized groups		
	Site	(IV)	Mean	Std Dev	p
Red-winged Francolin	NRLu	34.8	19.3	4.77	0.004
Pin-tailed Whydah	NRLu	42.3	20.3	8.23	0.023
Red-collared Widowbird	NRLu	40.9	18.8	7.52	0.014
Long-tailed Widowbird	NRLu	24.7	18.9	2.58	0.022
African Stonechat	NRLu	39.9	20.0	5.00	0.001
Cloud Cisticola	NRLu	35.6	18.1	5.60	0.010
Yellow-breasted Pipit	NRLu	36.7	19.4	5.52	0.007
Cape Longclaw	NRLu	22.9	16.7	1.44	0.001
Malachite Sunbird	NRLu	35.7	18.3	5.67	0.008
Familiar Chat	NRLu	70.8	18.0	7.70	0.001
Sentinel Rock-thrush	NRLu	48.4	18.1	6.29	0.001
Buff-streaked Chat	NRLu	40.0	18.1	7.23	0.016
Ground Woodpecker	NRLu	36.7	17.2	8.72	0.040
Cinnamon-breasted Bunting	NRL	36.0	16.3	7.78	0.039
Common Quail	NRHu	52.4	21.8	9.72	0.008
Yellow-fronted Canary	NRHu	51.8	15.3	8.88	0.007
Cape Canary	NRHu	28.4	20.7	3.53	0.030
Grey-winged Francolin	NRHu	43.2	17.6	6.81	0.005
Eastern Long-billed Lark	NRHu	38.9	22.3	4.75	0.001
Black-winged Lapwing	NRH	33.8	16.2	6.92	0.039
Yellow-crowned Bishop	BF	39.0	16.4	9.16	0.046
Southern Bald Ibis	AF	40.9	16.0	8.14	0.017
Ant-eating Chat	AF	50.0	16.2	6.96	0.001
Crowned Lapwing	Com	42.4	18.3	6.54	0.004
Blacksmith Lapwing	Com	96.4	15.7	8.05	0.001
African Wattled Lapwing	Com	33.3	17.7	5.91	0.019
Common Fiscal	Com	42.9	17.4	5.98	0.004
Southern Masked Weaver	Com	50.6	19.8	8.88	0.006

Table 5. Indicator species analysis of grassland birds based on field metabolic rates (kJ.day^{-1}) showing functional guilds with site-specific energy flows, indicating habitat preference.

Guild	Site	Observed indicator values (IV)	IV from randomized groups		p
			Mean	Std Dev	
Nectarivores	NRLu	35.4	18.2	5.66	0.010
Birds of prey	NRLu	34.5	23.6	4.78	0.022
Rocky outcrop insectivores	NRLu	32.8	21.8	3.76	0.011
Water-associated species	NRLu	32.2	20.4	3.34	0.001
Grassland insectivores	NRLu	19.1	15.2	0.96	0.001
Grazers	Com	53.9	16.2	7.81	0.002
Open-area invertebrate feeders	Com	34.0	20.6	3.44	0.001

In order to understand the spatial and temporal differences in bird species assemblages, field metabolic rates (Appendix 2) of functional guilds were displayed in 2-dimensional ordination space. This allowed specific guilds to be overlaid onto the ordination, illustrating their influence in separating out sites (symbol sizes based on overlaid data). Field metabolic rates of assemblages of grassland insectivores, rocky outcrop insectivores and nectarivores are higher in conserved areas (with the exception of the heavily stocked area in the year of burn) than elsewhere (Fig. 2). Heavily grazed areas were characterized by high rates of energy flow through the open-area, invertebrate-feeder guild (Charadriformes and Ciconiiformes - Fig. 3). Axes 1 and 2 had Eigen values of 4.313 and 1.952, and p-values of 0.001 and 0.026 respectively, and explained 52.2% and 16.3% of the variance. Figures 2 and 3 are based on the same data and the ordination is the same, but different functional guilds have been overlain in order to highlight the importance of conservation areas (NRL) for grassland insectivores (Fig. 2) and the prevalence of open-area invertebrate feeders in communally grazed areas (Fig. 3).

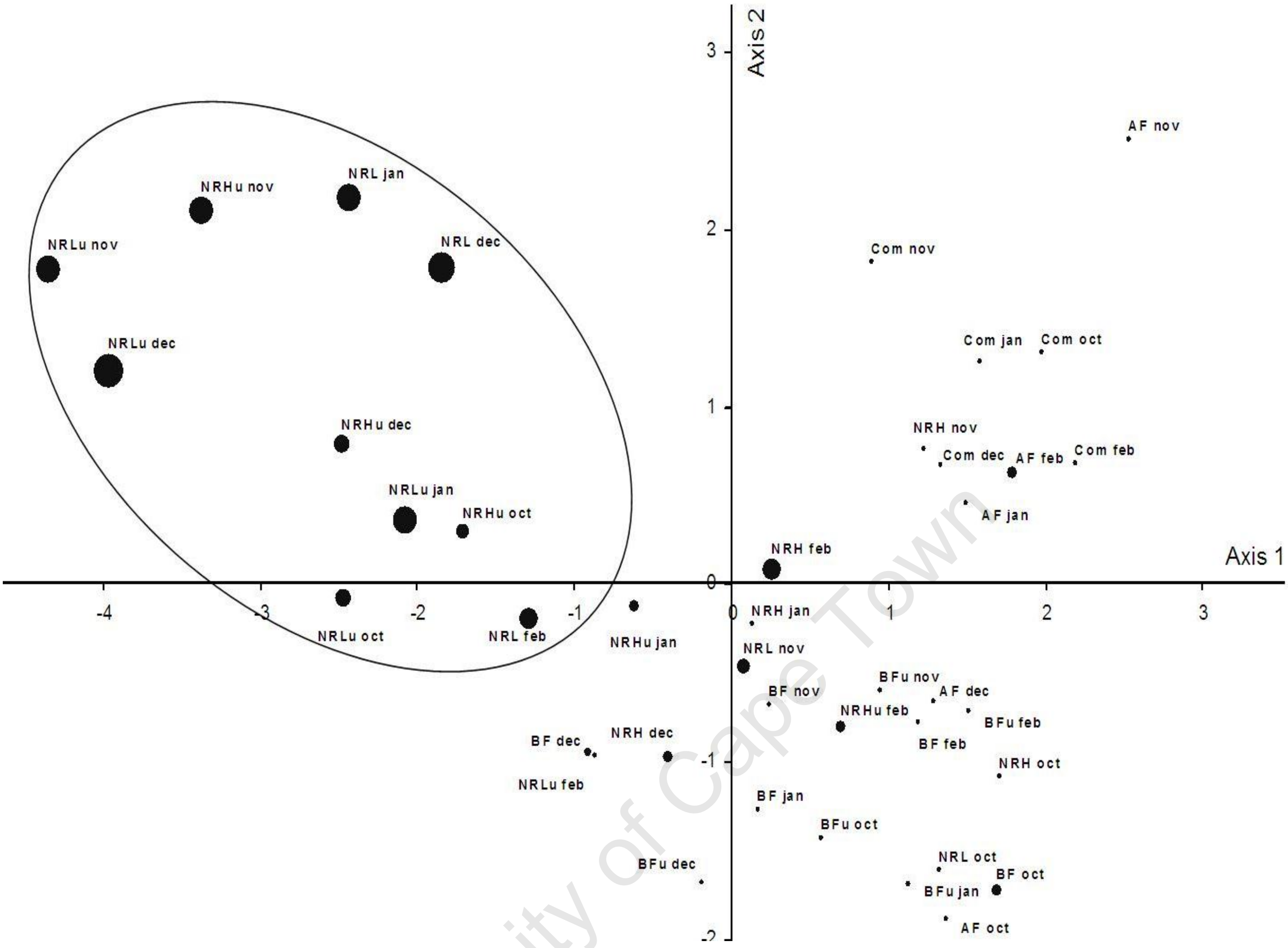


Fig. 2. Ordination diagram illustrating how management sites group, based on field metabolic rates of grassland bird species and season (months). Relative dot proximity represents the cumulative FMR scores of the assemblage of birds at each site. Larger dots show the influence of grassland insectivores in contributing to the separation of sites.

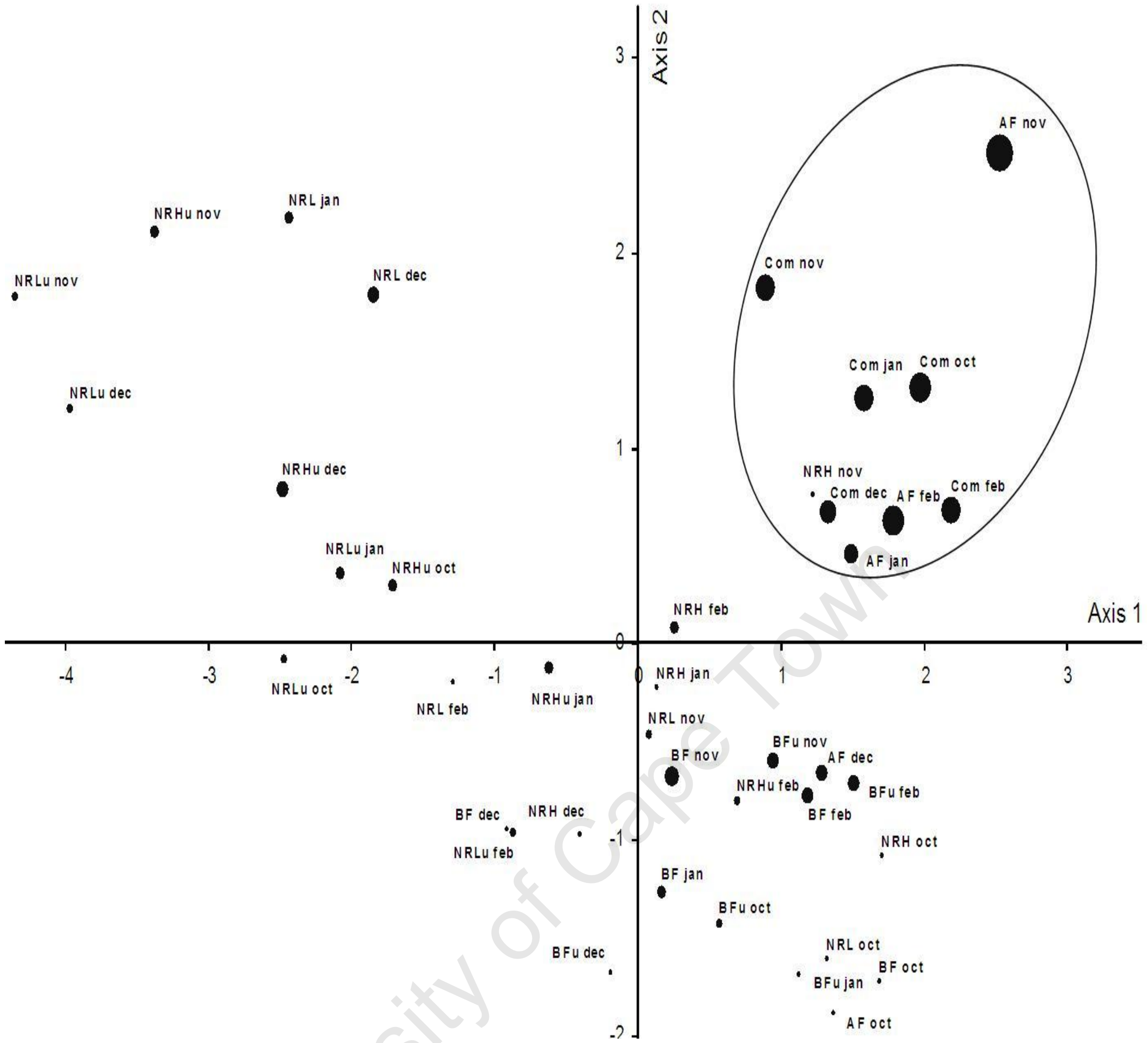


Fig. 3. Ordination diagram illustrating how management sites group based on field metabolic rates of grassland bird species and season (months). Larger dots show the influence of open-area invertebrate feeders in contributing to the separation of sites.

In order to understand the effects of management on each of the functional guilds, their total field metabolic rate scores were compared to equivalent scores from the conservation area with low grazing pressure (NRL). When compared directly between management sites, the conservatively managed conservation area had higher FMR than other sites for all functional guilds except open-area invertebrate feeders (Charadriformes and Ciconiiformes, which regulary forage in overgrazed and bare areas – Hockey et al. 2005). The communally grazed areas had higher field metabolic scores for grazers and open area invertebrate feeders than the conservation area (Table 6). It is apparent that some functional guilds such as the insectivorous grassland passerines and nectarivores had higher energy turnover rates in the conservation area with low grazing (NRL) than in any other management type. This table shows similar results to those presented in Table 5 above: in Table 7, however, each of the management types and all of the functional guilds are represented, with comparative values. This illustrates the significance of differences between all grassland species and focal grassland-nesting species based on management. When considering all grassland species, it is evident that the annually burnt farm is significantly different to both low and high grazing intensity conservation areas (NRL, NRH). When considering the focal grassland-breeding species alone, the low grazing intensity conservation area (NRL) is significantly different to all other management types, again illustrating its importance for the conservation of grassland-nesting birds.

Table 6. Field Metabolic Rates (FMR - kJ.day^{-1}) for functional feeding guilds of grassland birds. Values for each functional feeding guild in each management type are relative to those in the conservation area with low herbivore stocking densities (NRL). Positive values indicate more energy flow through that guild in that site than in the NRL, and negative values indicate less energy flow than the same guild in the NRL.

Guild	NRH	BF	AF	Com	Total
Birds of prey	-661.69	-829.24	-1585.88	-1460.50	-4537.33
Scavengers	**103.72**	-622.34	-1244.69	-1867.04	-3630.36
Gamebirds	-891.74	-116.71	-157.25	-1279.59	-2445.30
Rocky outcrop insectivores	-184.79	-388.83	-319.12	-369.16	-1261.91
Insectivorous grassland passerines	-323.81	-152.07	-334.67	-388.77	-1199.34
Aerial insectivores	**582.71**	**19.46**	-1347.73	-378.08	-1123.64
Granivorous passerines	-10.06	-477.13	-797.81	**533.20**	-751.81
Waterbirds	-139.34	-53.39	-269.23	-79.58	-541.55
Grazers	-480.35	-284.71	-89.0	**420.30**	-433.82
Omnivores/generalists	**6.64**	-270.02	-35.59	-61.27	-360.26
Nectarivores	-28.04	-63.92	-53.8	-74.03	-219.82
Frugivores	-31.51	-31.51	-31.51	-31.51	-126.07
Thicket insectivores	-16.86	**0.20**	**17.64**	**18.27**	**19.25**
Arboreal insectivores	-0	-14.65	**5.48**	**29.69**	**20.52**
Open-area invertebrate feeders	**783.54**	**929.02**	**2381.80**	**2455.73**	**6550.10**

Table 7. Overall field metabolic rates (FMR - kJ.day^{-1}) compared between land-use management types for all grassland species and for the focal species which breed in grasslands as apposed to rocky outcrops, wetlands, embankments and other non-grassland habitats.

	All grassland species				Focal species			
	n	T	Z	p	n	T	Z	p
NRL > NRH	69	977	1.38	0.168	**11**	**8**	**2.22**	**0.026**
NRL > BF	**65**	**737**	**2.19**	**0.028**	**11**	**0**	**2.93**	**0.003**
NRL > AF	**63**	**632**	**2.58**	**0.010**	**11**	**0**	**2.93**	**0.003**
NRL > Com	71	1203	0.43	0.667	**11**	**8**	**2.22**	**0.026**
NRH = BF	65	895	1.16	0.246	11	17	1.42	0.155
NRH > AF	**61**	**656**	**2.08**	**0.037**	11	11	1.96	0.05
NRH = Com	66	1092	0.09	0.931	11	19	1.25	0.213
BF = AF	53	498	1.93	0.054	11	18	1.33	0.182
BF = Com	62	783	1.36	0.175	10	26	0.15	0.878
AF = Com	58	635	1.71	0.087	10	27	0.05	0.959

In order to investigate the rigour of using FMRs for assessing the ecological integrity of a system, the above results were compared to a comprehensive multi-taxon Biodiversity Intactness Index (Scholes and Biggs 2005 - Table 8). The Biodiversity Intactness Index (BII - which includes birds, arthropods and plants) was used for the assessment of ecological integrity. When compared to the results achieved using FMR, the two indices of ecosystem functioning were significantly correlated ($t = 14.011$, $r^2 = 0.985$, $p = 0.001$). This result suggests the potential use of FMR as an index for ecological integrity.

Table 8. Effects of management of moist highland grasslands on the Biodiversity Intactness Index (BII) and relative field metabolic rate (FMR - kJ.day^{-1}, compared to the conserved area with low grazing intensity (NRL). The value of 100 assigned to the NRL is arbitrary and purely for comparative purposes.

	BII	FMR
NRL	100	100
NRH	87.119	89.554
Com	79.746	79.519
BF	77.703	80.947
AF	64.016	68.770

Using BII (or possibly FMR), it is possible to assess the overall integrity of the system by estimating the amount of land under each of the management types and extrapolating the calculated integrity values for the system (Table 9). This is simply a hypothetical sensititvity analysis illustrating the use of this type of index for assessing relative scenarios and establishing conservation targets. When BII scenarios are compared between hypothetical scenarios of differing proportions of land under each of the management types, it is apparent that increasing the proportion of land under biennial burning improves biodiversity intactness. This, however, is unlikely to improve beyond scenario “f” because livestock farmers and communal farmers are unlikely to manage the land in a conservation-friendly manner because they need to trade off ecologically ideal and commercially viable stocking rates. Using FMR reveals slightly higher integrity scores but the relative differences are the same.

Table 9. Overall Biodiversity Intactness Indices for moist highland grasslands in the study area under differing management scenarios (e.g. scenario ‘a’ has a ratio of the different management types of 1:1:2:5:1, which approximates the current scenario; scenario ‘b’ has ratios of 1:1:3:4:1, etc). BII^1 & FMR^1 are the results of each of the scenarios while BII^2 & FMR^2 assume that NRH is managed in the same way as the nature reserve with low grazer densities (NRL).

	Management scenario					
Management type	a	b	c	d	e	f
NRL	1	1	1	1	1	1
NRH	1	1	1	1	1	1
BF	2	3	4	5	6	7
AF	5	4	3	2	1	0
Com	1	1	1	1	1	1
BII^1	74.24	75.60	76.97	78.34	79.71	81.08
BII^2	75.52	76.89	78.26	79.63	81.00	82.37
FMR^1	77.48	78.70	79.91	81.14	82.35	83.57
FMR^2	78.52	79.74	80.96	82.18	83.40	84.62

5.4. Discussion

Land management, and specifically degradation through human land use, is cause for conservation concern. Currently, there is a possibility of continental Africa experiencing its first documented avian extinction since records began. Ethiopia’s Sidamo Lark *Heteromirafra sidamoensis* is threatened with imminent extinction as a result of land degradation (Spottiswoode et al. 2009). While much work in the Northern Hemisphere has targetted the impacts of land degradation, Africa remains poorly studied. Some recent work encompassing both North American and African grasslands suggests that “pyric herbivory” (grazing in conjunction with fire) and the interaction of natural fires and free-roaming herbivores creates a natural and dynamic grassland mosaic which is beneficial to biodiversity (Engle et al. 2008; Fuhlendorf et al. 2008). In grassland systems, grazing intensity can alter the composition and structure of both vegetation and the associated prey base (arthropods) for grassland-nesting birds (Fondell and Ball 2004; Sutter and Ritchison 2005; this study). This study illustrates the very low nesting success of birds in areas intensively grazed by (mainly) domestic livestock, especially when this is combined with annual burning. Such management has detrimental implications for grassland-nesting birds in particular and grassland ecosystem functioning in general. Currently, a large proportion of South Africa's MHGs experience annual burning and are heavily stocked, leading to concern for the future of grassland-nesting birds. Birds breeding in annually burnt areas did so at very low densities and achieved less than half the reproductive output of birds breeding in biennially burnt areas.

While biogeographic and demographic patterns such as ecological traps (where species are attracted to poor condition, artificially altered habitats by their apparent similarity to structurally similar natural habitats -Battin 2004; Schaefer et al. 2005) and source-sink dynamics (Donovan et al. 1995; McCoy et al. 1999; With and King 2001; Perkins et al. 2003) respectively have important conservation implications, they are not necessarily required for a system to show negative population-level effects of habitat management. In this study there was a decrease in overall abundance of birds and an associated decrease in nesting attempts in farmed areas (relative to a conserved control), but this does not necessarily translate into reduced estimated nesting success (Fig. 1). Nest success is significantly reduced in the seasons in which burning takes place (Tables 1, 2), but this pattern is most likely a result of early season nest failure, with burnt areas recovering later in the breeding season to support a vegetation biomass adequate for nest concealment (Chapter 4). The main cue for nest initiation is most likely day length (Little and Crowe 1993; Both et al. 2006; Chapter 4). At face value, this suggests that birds attempting to breed in poor habitats (such as African Pipits, which were abundant in all study sites) could be 'fooled' into initiating breeding attempts in sparse vegetation where the probability of the nest failure due to predation is high. However, this is probably unlikely because territory establishment and nest-site selection take place early in the breeding season: at this time poor-quality habitats have low territory densities and concomitantly low nest densities, conforming with the predictions of an Ideal Free Distribution (Fretwell and Lucas 1970; Fretwell 1972; Martin 1998; Muchai 2002). The magnitude of the differences in bird performance between conserved and intensely managed sites indicates that current management practices in pastoral areas are having significant detrimental effects on avian abundance, species richness, nest density and fledgling output (Table 3, Fig. 1), resulting in a lowered ecological integrity of the system (Tables 6, 7, 8).

When considering field metabolic rates and the differences in their magnitudes between management types, it becomes apparent that conserved areas group separately (Figs 2, 3) and support a greater energy turnover than do livestock farms (Table 7, 8). Conserved areas act as refuges for rocky outcrop insectivores, grassland insectivores and nectarivores (these three guilds include all of the endemic and specialist grassland species, with the exception of gamebirds), in addition to housing water-associated species and birds of prey (Table 5). In support of this, all but three functional feeding guilds have higher energy turnover rates in the conserved area than elsewhere (Table 6). Unsurprisingly, grazers and open-area invertebrate feeders favour communally grazed lands because these species prefer open areas with ‘lawn-like’, or even bare-ground conditions (Chapter 1). The presence of thicket-dwelling and arboreal species outside of the nature reserve illustrates the effects of alien bush encroachment in these farmed areas: such encroached areas are usually retained by farmers because they provide shade for cattle. Half of the species that show significant habitat preference (potential indicator species) prefer the conserved area and these again include all the specialist, endemic and threatened species with the exception of Southern Bald Ibis, which feeds in disturbed areas but requires conserved areas for breeding (Hockey et al. 2005). Interestingly, Red-winged Francolins favour lightly grazed, conserved areas whereas the very closely related Grey-winged Francolins favour reserve areas that are heavily grazed, supporting the findings of Jansen et al. (1999) and Little (1992).

Multi-taxon approaches to the assessment of disturbance effects on ecological assemblages are more robust than single-taxon assessments (Milchunas et al. 1998; Söderström et al. 2001; Jeanneret et al. 2003b; Dennis et al. 2008; Zipkin et al. 2010). Biodiversity Intactness Indices (BIIs) using insects, plants and birds produced very similar results to analyses based on the field metabolic rates of birds alone (Table 8). In order for an area to have a high avian field metabolic rate score, the higher level taxonomic groups such as birds rely upon resources provided by other taxonomic groups in the ecosystem. This suggests that it may be possible to use Field Metabolic Rates as a rapid-assessment technique for ecological integrity providing one has a ‘benchmark site’ on which to base comparisons.

The current overall BII (74%) calculated for South African MHGs using plants, arthropods and birds (Table 9) is the same as that found by Scholes and Biggs (2005) who calculated a BII for South African grasslands using similar taxa, but including mammals. If these findings for the MHGs are projected into scenarios where the entire conservation area is managed well (low grazing intensity) and if farmers were to switch to biennial rather than annual burning, it is possible to achieve close to a 10% improvement in the biological intactness of the system (Table 9). This scenario takes only a shift in burning frequency into account and does not consider additive beneficial effects of reduced stocking densities. A decrease in stocking rate would result in further improvements in ecological integrity (Jansen et al. 1999; Fondell and Ball 2004; Martin and Possingham 2005; Dennis et al. 2008; Powell 2008). However, the extent of such improvement is difficult to model given the profound and confounding effects of fire frequency. A decreased frequency of managed fires and reduced grazing pressure will have a beneficial effect on biodiversity if the pyric herbivory concept of Fuhlendorf et al (2008) is applicable to farmed lands. This would suggest that paddocks should be managed by burning random sections rather than entire paddocks. This will encourage free-roaming antelope (which are attracted to grazing on newly burnt areas) to spread their impact between these various newly burnt areas creating a spatio-temporally dynamic mosaic of conditions in conservation areas. Although this may be the optimal management strategy, most farmers prefer managing land in a more structured and uniform manner (i.e. managing at a minimum spatial scale of the camp). Given that there will be strong resistance to changing this behaviour, biennial burning and less intensive stocking (itself market-dependent) should be promoted in order to maximise the BII and hence ecological integrity of the grasslands (Table 9).

Appendix 1: Average abundance of bird species counted per 7.5 ha for each of the management types. Species are divided into functional feeding guilds. See Appendix 1, Chapter 3 for scientific names. Values represent average number of birds counted across transects.

	NRLu	NRL	NRHu	NRH	BFu	BF	AF	Com
Water associated								
Reed Cormorant	0.125							
Hamerkop				0.125				
African Black Duck	0.167							
Red-chested Flufftail	0.125							
African Snipe			0.125	0.125	0.5			0.313
Water Thick-knee				0.125				
Whiskered Tern						0.25		
Pied Kingfisher	0.375							0.25
Great Reed-Warbler	0.125							
African Fish-Eagle						0.125		
Levaillant's Cisticola	1.575	1.7	0.475	0.469	0.438	0.25	0.542	0.475
African Pied Wagtail		0.125						
Cape Wagtail	0.25	0.125			0.25	0.125		0.542
Grazers								
Egyptian Goose	0.5							0.469
Spur-winged Goose						0.125	0.125	
Scavenger								
Cape Vulture	0.75		0.792		0.5		0.125	
Omnivores/Generalists								
Cape Crow	0.5	0.85	0.525	1.1	0.25	0.375	0.938	0.438
Commom Myna								0.25
Pied Starling	0.969	0.594	0.563	0.625	0.344	0.313		0.625
Red-winged Starling	0.25							0.25
Birds of prey/carnivores								
Black-chested Snake-Eagle	0.125							
Black Kite	0.125							
Black-shouldered Kite	0.15		0.175		0.188			0.167
Long-crested Eagle	0.188							
Steppe Buzzard	0.125		0.125	0.125	0.125			
Jackal Buzzard	0.375	0.125	0.208	0.125	0.188		0.125	
Pallid Harrier	0.25	0.125		0.25	0.125			
African Harrier-Hawk					0.25			
Amur Falcon	0.125	0.188	0.125	0.313	0.375	1.125	0.375	
Rock Kestrel	0.167		0.125	0.125				
Secretarybird	0.5	0.125	0.25	0.188	0.25			
Continued…								
Black-headed Heron	0.125	0.125	0.125		0.125	0.125	0.125	0.313
Rufous-chested Sparrowhawk	0.208		0.125		0.25			0.125
Ovambo Sparrowhawk		0.125		0.125				
Black Sparrowhawk								0.125
Gamebirds/terrestrial omnivores								
Grey-winged Francolin		0.25	0.844	0.375	0.25	0.375	0.313	
Red-winged Francolin	1.35	0.563	1.15		0.625	0.375	0.25	0.25
Natal Spurfowl		0.25						
Common Quail	0.4	2.917	0.85	1.969	0.25	0.906	0.25	
Helmeted Guineafowl	0.25					0.313		
Small Buttonquail	0.25			0.313	0.25	0.375		
Blue Crane		0.375				0.25	0.25	
Denham's Bustard	0.125	0.25				0.5	0.25	
Terrestrial, open-area arthropod-eaters								
Crowned Lapwing	0.125	0.313	1.25	0.688		0.5	0.25	0.975
Black-winged Lapwing			0.313	0.344		0.25		0.333
Blacksmith Lapwing			0.25					1.35
African Wattled Lapwing	0.25	0.667	0.875	0.5				0.675
Spotted Thick-knee			0.813					
Cattle Egret	0.188		0.375		1.375	1.5	1.906	1.175
African Sacred Ibis								0.625
Southern Bald Ibis	0.875			0.5	0.5		1.333	
Hadeda Ibis	0.25	0.125	0.25		0.25	0.875	0.333	0.675
Arboreal insectivores								
Red-chested Cuckoo								0.125
Crested Barbet							0.125	
Black-headed Oriole								0.125
Spotted Flycatcher					0.125			
Frugivore								
Speckled Mousebird	0.375							
Thicket insectivores								
African Hoopoe	0.125				0.125			0.125
Cape Robin-Chat					0.125			
Drakensberg Prinia	0.25							
Groundscraper Thrush								0.125
Bokmakierie	0.125			0.125	0.125		0.25	

Continued… **Aerial insectivores**	NRLu	NRL	NRHu	NRH	BFu	BF	AF	Com
African Black Swift	0.75		0.5	1.875	1			
White-rumped Swift	0.875	1	0.75	1.625	1.125			1
Alpine Swift	1.031	0.375	0.85	1.063	1.313			0.5
Barn Swallow	1.475	3.925	0.975	2.025	1.95	3.5	1.975	2.05
White-throated Swallow	0.25				0.5			0.167
Greater Striped Swallow	0.906	0.458	0.375	0.333	0.875	0.188	0.375	1.156
Rock Martin				0.375				
Common House-Martin				0.5				
Brown-throated Martin	0.125		0.375		0.25			0.25
Banded Martin	1.1	0.792	0.969	0.656	2.35	1.075	0.725	1.083
Black Saw-wing	0.563				0.667			
European Roller	0.125		0.125					
Rocky outcrop insectivores								
Ground Woodpecker	0.344	0.542						
Eastern Long-billed Lark	0.6	0.5	1.4	0.55	0.219	0.125	0.219	0.219
Sentinel Rock-Thrush	1.125	0.425	0.75	0.125				
Mountain Wheatear	0.875	0.188	0.969	0.208	0.292	0.25	0.563	0.344
Buff-streaked Chat	0.563	0.167	0.125				0.325	
Common Fiscal	0.125	0.25	0.125		0.167	0.125	0.125	0.225
Familiar Chat	0.425	0.125	0.125		0.125			
Passerine grassland Insectivores								
Rufous-naped Lark				0.125	0.188		0.125	0.25
Red-capped Lark		0.125		0.25	0.125		0.25	0.125
Capped Wheatear						0.25		0.125
Ant-eating Chat				0.25		1.938	1.6	
African Stonechat	1.725	0.875	0.975	0.25	0.292	0.25	0.438	0.417
Cape Grassbird	0.125							
Zitting Cisticola	1.1	0.906	0.281	1.542	0.25	0.85	0.75	0.594
Cloud Cisticola	0.65		0.575		0.5	0.125		0.188
Wing-snapping Cisticola	2.15	1.975	1.825	1.925	1.45	1.95	1.225	1.4
Pale-crowned Cisticola		0.125		0.188		0.208	0.25	
Cisticola indet.	1.9	0.8	1.625	0.625	1.875	0.781	0.438	1.1
Wailing Cisticola	0.25	0.375	0.25	0.125				

Continued:…	NRLu	NRL	NRHu	NRH	BFu	BF	AF	Com
Long-billed Pipit	0.25	0.188		0.167		0.125	0.125	
Plain-backed Pipit	0.125			0.25		0.625	0.125	
Yellow-breasted Pipit	1.55	1.075	0.458	0.313	1	0.5	0.5	
Cape Longclaw	2.875	1.9	1.425	1.025	1.65	1.575	1.375	0.725
Nectarivores								
Malachite Sunbird	0.875	0.844	0.575	0.563		0.25	0.25	
Amethyst Sunbird		0.125						
Passerine granivores								
Cape Sparrow					0.375			0.688
Cape Weaver	0.25	0.292	0.75	1.875	0.75			1.075
Speckled Pigeon	0.375		0.125					0.25
Red-eyed Dove			0.188	0.125	0.208			0.5
Cape Turtle-Dove	0.375		0.167		0.208			0.344
Namaqua Dove			0.125					
Chestnut-backed Sparrowlark			1.875					
Cuckoo Finch	0.125		0.25	0.125		0.125	0.25	
Southern Red Bishop		1.438	0.25	0.125		1.188	0.25	2.531
Yellow-crowned Bishop		0.5				0.542	0.375	
Yellow Bishop	1.4	1.844	1.125		0.583		0.125	1.25
Bishop indet.	0.708	0.625	0.542	0.313	0.375	0.563	0.25	0.406
Fan-tailed Widowbird							0.125	0.438
White-winged Widowbird		0.375			0.75			
Red-collared Widowbird	1.438	0.125	0.781	0.5		0.125		0.542
Long-tailed Widowbird	3.15	2.05	1.55	1.281	1.313	1.4	0.563	2.1
Common Waxbill	0.55	0.458	2.25	0.625				
African Quailfinch	1	0.417	1.083	1.375	0.563	0.906	0.425	1.25
Pin-tailed Whydah	0.875	0.438			0.125	0.188	0.375	0.344
Yellow-fronted Canary	0.375		0.792					
Black-throated Canary								0.375
Cape Canary	1.333	1.45	3.9	2.25	0.813	1.65	1.225	2.25
Streaky-headed Seed-eater						0.313		0.25
Cape Bunting				0.125				
Cinnamon-breasted Bunting	0.125	0.25		0.125				

Appendix 2: Bird species included in the functional guild analyses, along with their average body masses (from Hockey et al, 2005) and daily Field Metabolic Rates (FMR – from Nagy et al. 1999) with associated upper (C.I. +) and lower (C.I. -) confidence intervals.

Species in functional feeding guilds	Assigned category from Nagy *et al.* 1999	Mass (g)	FMR kJ/day^{-1}	C.I. +	C.I. -
Water-associated birds					
Reed Cormorant	Piscivore	555	610.40	3.12	2.46
Hamerkop	All birds	505	727.99	3.19	2.53
African Black Duck	All birds	1000	1159.28	3.40	2.73
Red-chested Flufftail	Insectivore	37	123.69	2.33	1.85
African Snipe	Charadriiformes	120	324.38	2.79	2.22
Water Thick-knee	Charadriiformes	365	763.93	3.17	2.60
Whiskered Tern	Charadriiformes	100	281.89	2.73	2.17
Pied Kingfisher	Piscivore	85	194.33	2.62	1.96
Great Reed-Warbler	Insectivore	37.5	124.87	2.34	1.86
African Fish-Eagle	Piscivore	2500	1528.76	3.52	2.85
Levaillant's Cisticola	Insectivore	12	55.92	1.98	1.51
African Pied Wagtail	Insectivore	27	99.05	2.23	1.76
Cape Wagtail	Insectivore	20	80.16	2.14	1.67
Grazers					
Egyptian Goose	All birds	2100	1921.41	3.62	2.95
Spur-winged Goose	All birds	4300	3130.26	3.83	3.16
Scavengers					
Cape Vulture	All birds	8500	4978.78	4.04	3.36
Omnivores/Generalists					
Cape Crow	Omnivore	500	463.69	3.06	2.28
Commom Myna	Omnivore	130	198.99	2.68	1.92
Pied Starling	Omnivore	100	168.76	2.61	1.84
Red-winged Starling	Omnivore	135	203.76	2.69	1.93
Birds of prey/carnivores					
Black-chested Snake-Eagle	All birds	1500	1527.94	3.52	2.85
Black Kite	All birds	775	974.54	3.32	2.66
Black-shouldered Kite	All birds	250	451.01	2.98	2.32
Long-crested Eagle	All birds	1050	1198.44	3.41	2.75
Steppe Buzzard	All birds	730	935.64	3.30	2.64
Jackal Buzzard	All birds	1150	1275.04	3.43	2.77
Pallid Harrier	All birds	375	594.43	3.11	2.44
African Harrier-Hawk	All birds	800	995.84	3.33	2.67
Amur Falcon	Insectivore	142.5	320.04	2.78	2.23
Rock Kestrel	All birds	215	406.98	2.94	2.28
Secretarybird	All birds	4000	2979.83	3.81	3.14
Black-headed Heron	All birds	710	918.11	3.29	2.63
Rufous-chested Sparrowhawk	All birds	160	332.80	2.85	2.19
Ovambo Sparrowhawk	All birds	200	387.42	2.92	2.26
Black Sparrowhawk	All birds	720	926.89	3.30	2.64
Gamebirds/terrestrial omnivores					
Grey-winged Francolin	Galliformes	440	291.74	2.71	2.22
Red-winged Francolin	Galliformes	430	285.38	2.70	2.21
Natal Spurfowl	Galliformes	445	294.92	2.71	2.23
Common Quail	Galliformes	95	67.07	2.11	1.55
Helmeted Guineafowl	Galliformes	1450	915.54	3.23	2.69

Small Buttonquail	Charadriiformes	42.5	145.86	2.47	1.86
Blue Crane	Omnivore	4850	1931.62	3.71	2.86
Denham's Bustard	Omnivore	5650	2125.99	3.76	2.90
Terrestrial, open-area arthropod-eaters					
Crowned Lapwing	Charadriiformes	185	452.70	2.94	2.38
Black-winged Lapwing	Charadriiformes	185	452.70	2.94	2.38
Blacksmith Lapwing	Charadriiformes	165	414.52	2.90	2.34
African Wattled Lapwing	Charadriiformes	250	570.82	3.04	2.47
Spotted Thick-knee	Charadriiformes	535	1025.47	3.31	2.71
Cattle Egret	Insectivore	365	621.13	3.12	2.47
African Sacred Ibis	Omnivore	1250	824.39	3.32	2.51
Southern Bald Ibis	Insectivore	1200	1437.45	3.55	2.77
Hadeda Ibis	Insectivore	1250	1479.42	3.56	2.78
Arboreal insectivores					
Red-chested Cuckoo	Insectivore	75	203.55	2.57	2.05
Crested Barbet	Insectivore	70	193.89	2.54	2.03
Black-headed Oriole	Insectivore	65	184.02	2.52	2.01
European Roller	Insectivore	130	299.98	2.75	2.20
Spotted Flycatcher	Insectivore	15	65.450	2.05	1.58
Frugivores					
Speckled Mousebird	Temperate bird	55	168.09	2.59	1.86
Thicket insectivores					
African Hoopoe	Temperate bird	57	171.41	2.60	1.86
Cape Robin-Chat	Insectivore	28	101.62	2.24	1.77
Drakensberg Prinia	Insectivore	10	49.17	1.93	1.46
Groundscraper Thrush	Insectivore	74	201.64	2.56	2.05
Bokmakierie	Insectivore	65	184.02	2.52	2.01
Aerial insectivores					
African Black Swift	Apodiformes	42	513.91	3.02	2.40
White-rumped Swift	Apodiformes	24	260.81	2.66	2.18
Alpine Swift	Apodiformes	75	1037.72	3.41	2.63
Barn Swallow	Hirundines	18	101.33	2.34	1.68
White-throated Swallow	Hirundines	23	115.38	2.39	1.73
Greater-striped Swallow	Hirundines	27	125.62	2.43	1.77
Rock Martin	Hirundines	22	112.70	2.38	1.72
Common House-Martin	Hirundines	13	85.27	2.26	1.60
Brown-throated Martin	Hirundines	12.5	83.52	2.25	1.59
Banded Martin	Hirundines	26	123.13	2.42	1.76
Black Saw-wing	Hirundines	11	78.05	2.22	1.56
Rocky outcrop insectivores					
Ground Woodpecker	Insectivore	120	283.52	2.73	2.18
Eastern Long-billed Lark	Insectivore	39	128.37	2.35	1.87
Sentinel Rock-Thrush	Insectivore	50	152.94	2.4	1.94
Mountain Wheatear	Insectivore	35	118.94	2.31	1.84
Buff-streaked Chat	Insectivore	33	114.11	2.30	1.82
Common Fiscal	Insectivore	40	130.68	2.36	1.88
Familiar Chat	Insectivore	22	85.73	2.17	1.70
Passerine grassland insectivores					
Rufous-naped Lark	Insectivore	42	135.25	2.37	1.89
Red-capped Lark	Insectivore	23.5	89.82	2.19	1.72
Capped Wheatear	Insectivore	25	93.82	2.21	1.74
Ant-eating Chat	Insectivore	47.5	147.51	2.41	1.93
African Stonechat	Insectivore	15	65.45	2.06	1.58
Cape Grassbird	Insectivore	30	106.69	2.26	1.79

Zitting Cisticola	Insectivore	9	45.65	1.90	1.42
Cloud Cisticola	Insectivore	9	45.65	1.90	1.42
Wing-snapping Cisticola	Insectivore	10	49.17	1.93	1.46
Pale-crowned Cisticola	Insectivore	10	49.17	1.93	1.46
Cisticola indet.	Insectivore	9.5	47.43	1.91	1.44
Wailing Cisticola	Insectivore	15	65.45	2.05	1.58
African Pipit	Insectivore	24.5	92.49	2.20	1.73
Long-billed Pipit	Insectivore	30	106.69	2.26	1.79
Plain-backed Pipit	Insectivore	26.5	97.75	2.23	1.76
Yellow-breasted Pipit	Insectivore	25	93.82	2.21	1.74
Cape Longclaw	Insectivore	46	144.21	2.40	1.92
Nectarivores					
Malachite Sunbird	Nectarivore	17.5	80.87	2.24	1.58
Amethyst Sunbird	Nectarivore	15	72.63	2.19	1.53
Granivorous passerines					
Cape Sparrow	Passerines	29	102.67	2.24	1.78
Cape Weaver	Passerines	46	140.51	2.39	1.90
Speckled Pigeon	Temperate bird	350	463.43	3.17	2.17
Red-eyed Dove	Temperate bird	250	385.40	3.05	2.12
Cape Turtle-Dove	Temperate bird	150	291.29	2.90	2.04
Namaqua Dove	Passerines	40	127.77	2.34	1.87
Chestnut-backed Sparrowlark	Passerines	22	85.09	2.16	1.67
Cuckoo Finch	Passerines	20	79.75	2.13	1.67
Southern Red Bishop	Passerines	23	87.70	2.17	1.71
Yellow-crowned Bishop	Passerines	15	65.58	2.05	1.59
Yellow Bishop	Passerines	33.5	113.25	2.29	1.82
Bishop indet.	Passerines	25	92.81	2.20	1.74
Fan-tailed Widowbird	Passerines	25.5	94.07	2.21	1.74
White-winged Widowbird	Passerines	20	79.75	2.13	1.67
Red-collared Widowbird	Passerines	20	79.75	2.13	1.67
Long-tailed Widowbird	Passerines	35	116.68	2.30	1.83
Common Waxbill	Passerines	8	42.76	1.87	1.36
African Quailfinch	Passerines	11	53.11	1.96	1.49
Pin-tailed Whydah	Passerines	15	65.58	2.05	1.59
Yellow-fronted Canary	Passerines	12	56.34	1.98	1.52
Black-throated Canary	Passerines	13	59.49	2.01	1.54
Cape Canary	Passerines	15	65.58	2.05	1.57
Streaky-headed Seed-eater	Passerines	20	79.75	2.13	1.67
Cape Bunting	Passerines	20	79.75	2.13	1.67
Cinnamon-breasted Bunting	Passerines	15	65.58	2.05	1.57

CHAPTER 6

Conclusions and conservation implications

6.1. Introduction

The South African grassland system supports a high species diversity across taxa and a high proportion of the country's endemic bird and mammal species (Driver et al. 2005). The moist highland grasslands (MHGs) are naturally maintained by winter and spring fires (probably at intervals of four years or more – Manry and Knight 1986) and summer grazing by migratory herds of small to medium-sized antelopes (Everson 1999; Mucina and Rutherford 2006). These grasslands are typically dominated by decreaser grasses that only reseed in the late successional stage (climax grasses).

The landscape-level interaction between fire and grazing directly influences grassland fauna and flora (van Wilgen and Scholes 1997; Veen et al. 2008). As a result, their effects can be regulated as management tools to influence ecosystem health (Savory 1988; Ferwerda et al. 2006). This is necessary in modern farming practices where fire is managed and livestock are fenced. Currently, the majority of the grassland system is managed by livestock farmers who burn their land annually (some burn biennially) at the onset of the early summer rainy season. This coincides with the beginning of the breeding season for grassland-nesting birds.

Bird assemblages respond to habitat transformation in a number of ways and in response to a diversity of factors ranging from direct disturbance to changes in habitat structure and functioning, as well as shifts in food availability (Morrison 1986). These responses can vary from losses or gains of individual species to entire assemblage shifts (Liversidge 1962; Wiens 1974; Folse 1982; Erdelen 1984; Knopf et al. 1988; Martin and Possingham 2005).

This research aimed to gain an understanding of the impacts of fire and grazing as well as the interaction between them on vegetation diversity and structure in MHGs (Chapter 2). Following this, insect and bird diversity and abundance were explored in order to assess how these faunal groups respond to the shifts in vegetation structure and diversity as a result of disturbance pressures (Chapter 3). Following these assessments of inventory type data, bird nest success was modelled in order to gain an understanding of process-oriented responses to disturbance (Chapter 4). Finally indices of biological intactness were developed in order to assess the present and potential future integrity of grassland systems under varying management types and intensities (Chapter 5). From the results of this study some management recommendations are suggested for continued ecosystem functioning and species conservation in the MHGs.

6.2. Assessing and monitoring the ecological integrity of grasslands based on current management practices

The ultimate goal of biodiversity conservation is to ensure the wellbeing and conservation of a region's component species and thereby retain ecosystem functioning and provision of ecosystem services. In order to achieve this, ecologists need efficient and effective means of assessing system health based on the biodiversity and ecological integrity of a given system or management type. Using inventory-type data, if interpreted correctly and sampled sufficiently well and in the case of birds converted into Field Metabolic Rates, can illustrate clear trends in ecosystem integrity., Process-oriented research, in this study involving reproductive performance of birds, is also a useful tool for assessing the integrity of systems but requires much more effort. This study adopted both approaches in the MHGs by comparing both the abundance and reproductive performance of grassland-breeding birds, as well as rates of energy turnover through different feeding guilds (Fox and Hockey 2007) and across land-use types. In addition, the study assessed the species richness and abundance of plants and arthropods, along with structural attributes of the vegetation, with the aim of establishing the influences that they may have on one another. A new method for evaluating stocking densities based on phytomass and metabolic equivalent livestock units is introduced. This is termed the 'fodder capacity index' (Chapter 2) that can be used in conjunction with an adaptation of the Biodiversity Intactness Index (BII - Scholes and Biggs 2005, Chapter 5), which is a multi-taxon approach using plant, insect and bird diversity data to assess the stocking rate for ecological integrity of a particular system in order to understand the effects of disturbance on that system.

Both nest success and nest-site selection of birds are driven by vegetation structure, itself a consequence of habitat management (Chapter 4). As vegetation structural complexity increases through the growing (and breeding) season, nest success rates of cup-nesting (ground) birds also increases. This is unusual for the Southern Hemisphere but the same pattern has been observed in the Northern Hemisphere where it has been attributed to a decrease in food availability as the season progresses, leading to progressive decreases in breeding success (Rondenhouse 1986; Martin 1987; Brodmann and Reyer 1999; Boulton et al. 2008). In the MHGs of South Africa, the pattern of increasing breeding performance during the breeding season is a response to decreasing predation rates: nests in dense vegetation are better concealed than are those in the sparse vegetation that characterise the early stages of the breeding season (Chapter 5).

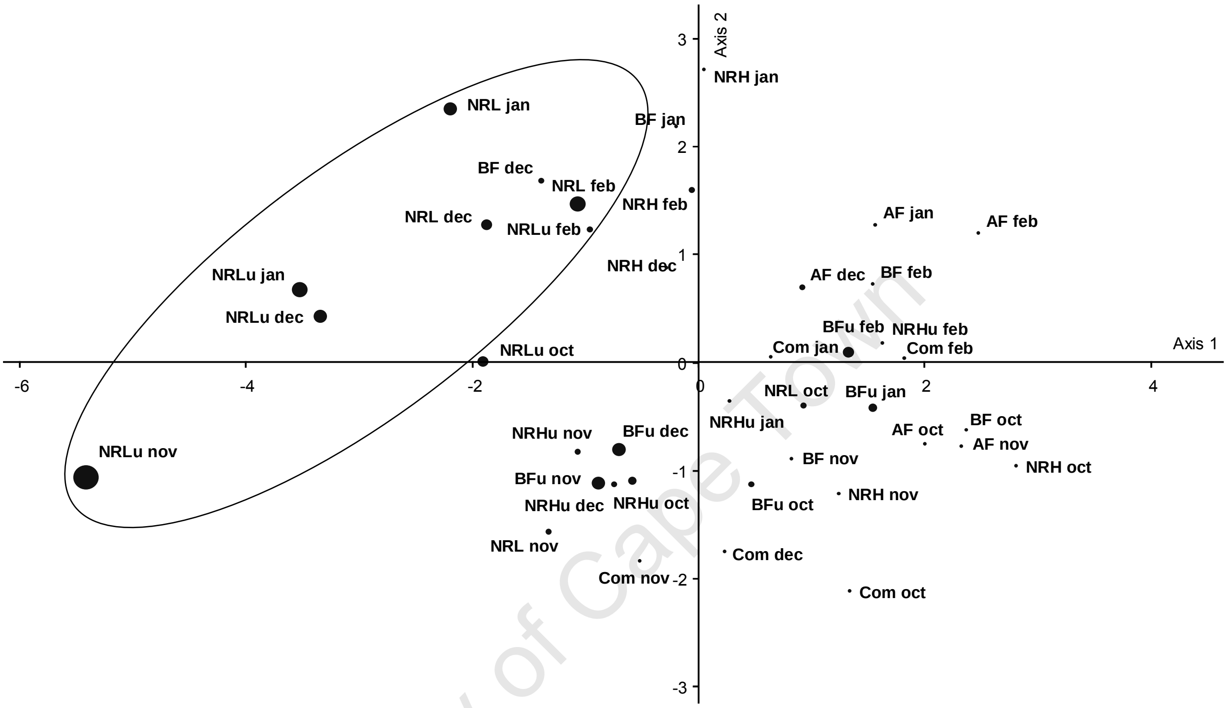


Fig. 1. Principal components analysis performed in PC-ORD (McCune and Mefford 2006) based on field metabolic rates (kJ.day^{-1}) of all of the grassland bird species present per site (Appendix 2, Chapter 5). Sites where thrteatened Yellow-breasted Pipits occur are represented with larger dots. Axes 1 and 2 had Eigen values of 11.45 and 5.94 (both p = 0.001) and explained 29.98% and 19.74% of the variance, respectively.

Current management practices outside of the conserved area have significant negative impacts on general avian abundance, species richness, nest density and fledgling output (Chapters 3-5). Arthropod assemblages showed marked and interesting responses to disturbance, specifically fire. Of the ten arthropod orders, only Orthoptera responded positively to burning. However, Orthoptera contribute 78% to the total arthropod biomass in MHGs (Chapter 3), suggesting that annually burnt areas, which have ample food for reproduction but insufficient nest cover (Chapter 4), could act as sink habitats for grassland-nesting insectivores.

Both the nesting success and abundance of Yellow-breasted Pipits *Anthus chloris* (Fig. 1; Chapters 3, 4), a regionally and globally *Vulnerable* and endemic grassland specialist, suggest that unconserved, bienially burnt areas support only sink populations of this species. No Yellow-breasted Pipits occurred in annually burnt areas or in bienially burnt areas in the year of burn (Fig. 1). By contrast, the generalist African Pipit *Anthus cinnamomeus* thrives in highly disturbed, communal grazing lands (Chapter 4).

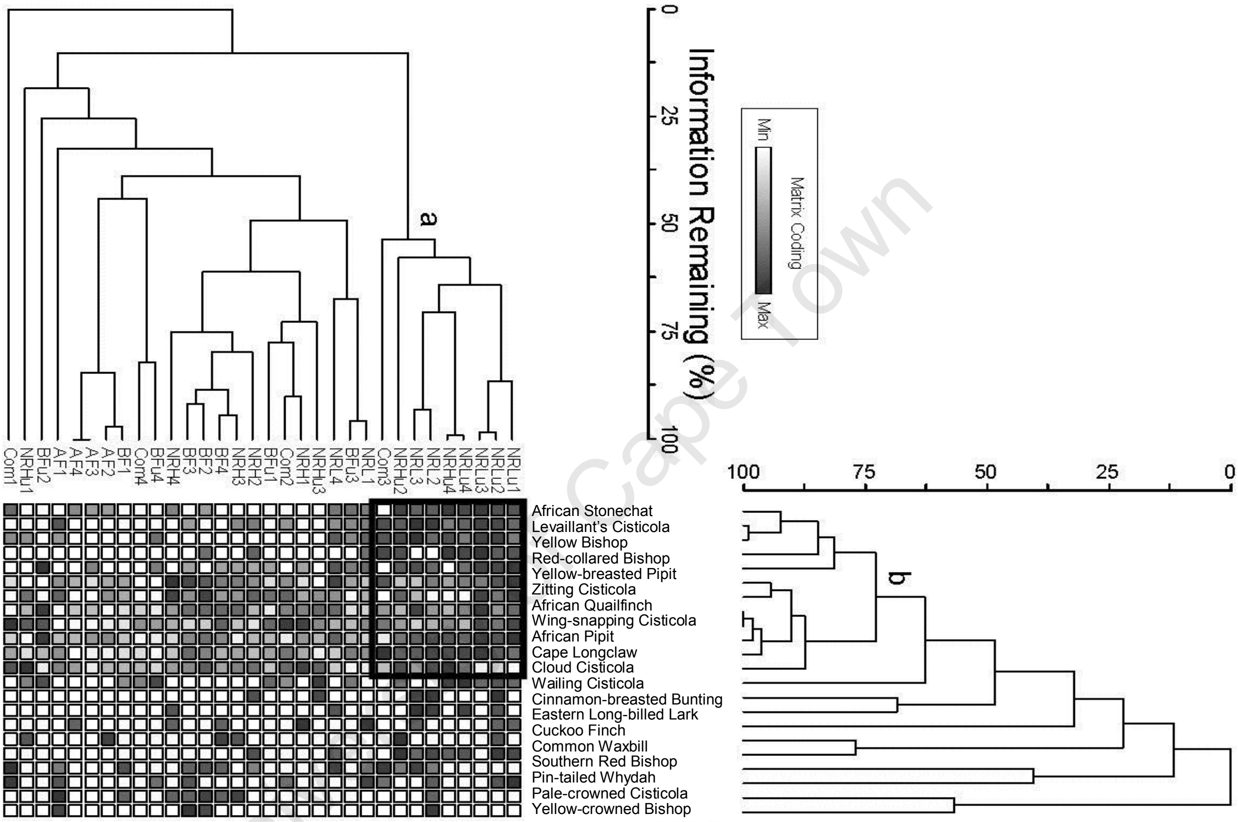


Fig. 2. Two-way cluster analysis performed in PC-ORD (McCune and Mefford 2006) illustrating that specialised grassland passerines favour conserved areas (group "a") over farmed land and that this effect is most pronounced (indicated by dark shading in the matrix squares) for territorial, grassland-nesting species (group "b").

While distinct plant species assemblages characterise the different management types, a few individual species are of particular interest in this system (Chapter 2). The presence of *Plantego myosuros* on the annually burnt farm (and nowhere else) is a sign of habitat degradation. This species is an exotic weed from South America and is a colonist of degraded/disturbed habitats, often spread in cattle dung (Tainton 1999). Two species found in the study area are recognized as globally threatened, *Hypoxis hemerocallidea* and *Eucomis autumnalis*. At present, both of these are classified as ‘declining’ (Raimondo et al. 2009). The former species was confined to communal lands, where it is not conserved. This tuberous grassland perennial, while not palatable to livestock, is utilized extensively in traditional medicine (Tainton 1999), placing increased pressure on the remaining populations. The latter species, also popular in traditional medicine (Tainton 1999), was confined to the conserved area, illustrating its sensitivity to disturbance.

Finally, data presented here indicate that wild herbivores in MHGs (predominantly Blesbok *Damaliscus dorcas*) can have a more detrimental impact on both vegetation structure and species diversity than do domestic livestock, even at relatively moderate grazing intensities (Chapters 2, 3, 5), this suggests that stocking rates of wild herbivores should be more conservative than for domestic livestock. Although historically they were probably only present during the summer growing season (Owen-Smith and Danckwerts 1997), under current management of the nature reserve, these species are fenced and thus exert grazing pressure year round. Relative to cattle, they are highly selective grazers and thus, when stocking densities are high, have the potential to mediate competitive interactions between plant species, leaving patchy, open grassland populated only by unpalatable grasses (Owen-Smith and Danckwerts 1997).

Currently, the MHGs of South Africa are a major conservation concern. Very little intact grassland remains for endemic, specialist and threatened species. This situation has been exacerbated by injudicious management (over-stocking) in existing conservation areas and by excessive burning and livestock grazing in farmed areas.

6.3. Recommendations

It is apparent that fire frequency and grazing intensity together influence both bird and arthropod diversity in South Africa’s MHGs. However, of the two, fire frequency has the greater overall effect. Indeed, this effect is so large that it largely overrides the impacts of grazing in terms of biotic responses at all taxonomic levels. This is not to imply that grazing intensity has no effect on biodiversity, but rather to stress the benefits that would be derived from biennial as opposed to annual burning regimes. These benefits would far outstrip the benefits that could be derived from reduced stocking rates if annual burning persists as the predominant management tool.

It is strongly recommended that land managers in the MHGs promote (in any one year) a mosaic of burnt and unburnt patches regardless of patch size, with the majority burning at intervals of two years or more and limiting stocking rates of livestock (Chapters 2-5). This mosaic can be supplemented with the use of large fire-breaks (O’Connor et al. 2005) where fire-breaks along with biennially burnt farm areas create a mosaic of management types for species diversity maintenance.Linked to this change in management paradigm, the grasslands need to be rested from grazing every three to four years to allow for seed production (Tainton 1999). Based on the relative ecological integrity of the biennially burnt farm in this study, I recommend a minimum sustainable ‘forage capacity’ of 5000 kg.LAU^{-1} (re-assessed as often as is feasible in each season) for domestic livestock in MHGs.

Overall, two different measures of ecological integrity in MHGs (avian energy turnover rates and Biological Integrity Index values) confirm the importance of conserved areas for birds in particular, and biodiversity in general (Chapter 5). However, at present, only about 2.2% of the biotope is conserved and the ecological integrity of the balance of the remaining areas that persist as grassland is threatened, primarily by excessively frequent burning. A shift from annual to at least biennial burning would be the simplest and least economically costly change in management that would result in both immediate and long-term biodiversity benefits.

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