Towards Adaptive Management of High-altitude Grasslands: Ingula as a Case Study

David (*aka* S'shozonke) Hlosi Maphisa

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University of Cape Town

Department of Statistical Sciences

Centre for Statistics in Ecology, Environment and Conservation

Supervisors

Assoc. Prof. Res Altwegg – lead supervisor

Prof. Les Underhill – co - Supervisor

SEEC - Statistics in Ecology, Environment and Conservation

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DECLARATION

> Cited works are any that have been alluded to by author and date in the text of the paper, the implication being that these were especially helpful or anyway inspirational, or maybe just provocative because of their adamantine dumbness to the author citing them.
> David Quammen – *The Song of a Dodo*

I hereby declare that this thesis reflects original research undertaken by myself towards a PhD degree at the University of Cape Town, Department of Statistical Sciences, Centre of Statistics, Ecology and Conservation. I declare that this work has not been submitted in any form towards a degree at any other university and that I have read extensively and duly acknowledge ideas and concepts from other people's work.

David (*aka* S'shozonke) Hlosi Maphisa

Layout of the thesis

Each chapter in this thesis is written in a format readily convertible to appropriate journals with some modifications. As a result, figures and tables are at the end of each chapter. Each chapter is designed to stand alone and there will be repetition of citations in various chapters of the thesis. The thesis adopts the style of the *Journal of Applied Ecology.* I have inserted coloured photographs throughout this thesis with no legend, either to capture the natural beauty of my study area or a conservation problem discussed in the thesis. For example cover picture shows a cisticola clinging unto the only one grass turf that survived burning. Yellow-breasted Pipit end of Chapter 4 is seen with full breeding plumage on recently burned background. Burning grassland late disrupt breeding activity of birds. Beginning of the thesis titled; "Thesis origin and overall goals" have four citations and no references at the end. This is deliberate because these citations are cited accordingly and subsequently referenced in Chapter 1.

Citation

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In memory of my beloved parents and in honour of the late Professor Steven Piper

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Acknowledgements

> Some are born great, some achieve greatness and some have greatness thrust upon them.
> William Shakespeare, *Twelfth Night, Act II, v.*

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Tumelo Motlhaping, who acted as my field assistants during fieldwork. Mpfunzeni Tshindane, a SANBI MSc and GIS-ARCVIEW student, assisted me in making the map of Ingula and thus revived in me the love of working with maps, which I learned from Professor D P Ambrose, and to Mpfunzeni I say, *ndi a livhuwa*. Consequently, I thank Professor Ambrose for proof reading and making comments on Chapter 1 of this thesis. On many occasions I received assistance from Greg Duckworth when R code got badly entangled. I thank Dr Hanneline Smit-Robinson: she was my mother, mentor and friend and, in addition, she made comments on all the chapters. Other than for my parents, many people made me what I am today. From BirdLife South Africa, Ingula, the University of Cape Town and the South African National Biodiversity Institute, I had diverse support from many people, so that mentioning names would do injustice to others not mentioned. To do injustice and in no particular order, I would like to thank the following people: Dr Achim Sanders and Mrs Iris Erbel (my other German parents), Gerhard (BLSA), Paul (RSPB), Pam (my best friend), Margret (librarian), Sue gave me courage when days were dark, Birgit, Theresa, Viwe, Gail, Peter, Francis, Fifi and uBaba Mhlongo. I missed many important family meetings when I moved to Cape Town and this did not go well with my family in Nquthu, to them I say; *sengikhona bafowethu.* Last but not least, I would like to thank my wife (Mamhlongo), my sister (Nomaswazi) and my kids (Sarafina, Nomusa and Mphandle) for unwavering support during an otherwise socially and economically turbulent period when I moved from Ingula to Cape Town.

Thesis origin and overall goals

David Quammen's *The Song of a dodo* likened the current fragmented nature of the earth's wildlife habitats to a Persian carpet, severed with a razor blade hunting knife. Once cut, no man's effort will put it back into the nice Persian carpets it was – in fact we are now left with 'ragged fragments, each one worthless and commencing to come apart'.

A brief history of Ingula

Recognising the importance of climate change and the contribution of coal-fired power stations to rising CO_2 levels, the growing demand for electricity is increasingly met by water-generated power. As part of this development, and to meet peak demand for electricity (Braamhoek Partnership 2004), South Africa's national power supplier, Eskom, decided to build a third pumped storage scheme during the early 1980s, the other ones being the nearby Drakensberg Pumped Storage Scheme and Palmiet Pumped Storage Scheme in the Western Cape Province (Braamhoek Partnership 2004). Contrary to the conventional hydroelectric power station, in a pumped storage scheme, the potential energy of water stored in the upper dam or head pond is released, run through turbines where electricity is produced and then this water is stored in the lower dam or tail pond. Water stored in the lower dam is then pumped back into the upper dam, using excess electricity generated during periods of low demand. In summary, a pumped storage scheme is like a giant battery that stores energy in the form of water with high potential energy that can be transformed into electrical energy on demand (Braamhoek Partnership 2004). Both the Drakensberg and Ingula pumped storage schemes share similar features in that the head ponds of both schemes are located within the Free State Province, while the tail ponds of both schemes are located within KwaZulu-Natal. Both schemes are located within 'Important Bird Areas' (Barnes 1998).

Ingula, initially known as Braamhoek, was chosen from a number of other potential sites as the most suitable site at which to construct a pumped storage scheme. However, the head pond at Ingula would lead to the loss of important wetland and, furthermore, the impounded water would be released directly into the remaining wetland. The presence of the wetland on the upper site at Ingula, and the cool mountain escarpment forest (Fig. 2), made Ingula a priority for conservation in that the area because it was found to host the threatened avifauna of the high-altitude grasslands. Consequently, the choice of the site was criticised by environmental non-governmental organisations (NGOs) as having a negative impact on the environment, especially on rare and threatened bird species of high-altitude grasslands at the proposed site (Barnes 1998). It was eventually agreed that Eskom would buy additional land, to be declared as a protected area, in which conservation of biota would be a primary function. It was understood that the consequent conservation benefits would compensate for the negative impacts that the scheme would have on birds, as well as threatened habitats and associated biota. Following the specialist report on the impact of the scheme on species and habitats (Mentis 2006), above ground construction only began in 2006 and was closely followed by construction of an exploratory tunnel, leading to the proposed machine hall. Because cattle belonging to commercial farmers were seen as having contributed to the degradation of the wetlands and surrounding grasslands (e.g. Mentis 2006), they were removed at the onset of construction activities. The Mentis report (2006) set out the guidelines on how best to manage the wetlands, grasslands and cool mountain escarpment forests at Ingula. However, Mantis's recommendations were not fully implemented regarding burning and grazing, as efforts to remove tenants, who also owned livestock and were left behind by commercial farmers, stalled. During 2010-2012, construction activities were largely confined to the two dams and the underground infrastructure. However, throughout the construction phase, construction companies were closely monitored by both Eskom's own environmental officers and independent environmental officers to ensure that disturbance was kept to a minimum and was confined to construction sites. The remaining area was burned annually (apparently by tenants) and tenants grazed their cattle over the property all year round.

Within this context, my thesis has two goals. The immediate goal is to develop a scientific basis on which to manage Ingula in a way that the conservation targets, set out by the Ingula Partnership, can be met. The wider goal of the thesis is to provide guidance on how to manage other high altitude grassland areas similar to Ingula. Ingula is located within the grassland biome as part of the moist high-altitude grassland of eastern South Africa, the area renowned for high biological diversity and endemism and hence a national priority for conservation (Reyers *et al.* 2001).

Thesis summary

1. Grasslands are among the most endangered ecosystems and represent one of the least protected biomes worldwide. In this regard, the grassland biome of southern Africa has also been identified as critically endangered and requiring conservation attention through implementation of efficient and sustainable conservation planning. In particular, South African moist high-altitude grasslands harbour globally significant biodiversity, supply essential ecosystem services, and support crops, livestock and human settlements. In addition, this biome has been identified as a centre of endemism for faunal and floral diversity, including a significant number of threatened bird species.

2. Several authors associate a high level of endemism and diversity to habitat heterogeneity brought about by wild fires resulting from lightning strikes; a complementary factor may have been roaming wild antelopes long before domestic livestock were brought into grassland biome. Currently, the grasslands are heavily grazed and annually burned to maximise livestock production, with a consequent negative impact on fauna and flora. Other threats come from a network of roads and the introduction and expansion of man-made forests. In order to meet the growing demand for water and electricity, particularly from expanding urban areas, moist high-altitude grasslands have recently been the sites of dams and proposed wind farms. In addition to habitat loss, the power lines associated with these developments also kill birds through collision with power lines infrastructure.

3. Currently there is uncertainty about how to manage wildlife in the face of these increasing threats. This thesis presents Ingula as a case study for grassland conservation and develops key components needed for adaptive management of the study area. Adaptive management is one method for structured decision making in the face of uncertainty. Adaptive management is suitable in situations where the conservation objectives are explicitly stated and recurrent decisions need to be made, such as whether to burn a grassland or not and what stocking density to use. The key concept of adaptive management is that we learn about the system while managing it.

Adaptive management, as I use the concept, consists of the following seven basic steps: 1) understanding the context in which the decision is made, 2) eliciting the fundamental management objectives, 3) developing a set of alternative management actions, 4) evaluating the consequences of the actions relative to the objectives under a set of models that capture uncertainty about the system dynamics, 5) identifying a preferred action that is expected to best achieve the objectives, 6) monitoring to establish whether the action had the predicted consequence, and 7) updating the model weights so that the model that best predicted the outcome becomes more influential in future decisions.

Steps 4 to 7 are repeated every time a management decision has to be made. Unfortunately, during the time of my fieldwork, management had not yet gained control over fire and grazing, and it was not possible to set up experimental plots to fully test the effect of fire and grazing on birds, as I had originally planned. My thesis therefore contributes only to steps 1 to 6. I do not aim to provide a ready-to-use adaptive management tool. Rather, I provide the background information from which such a tool can be developed when Ingula management has control over stocking density and the variety of mammals, and has control over where to burn and when. This is critical under adaptive management to test alternative competing models and the effect on achieving management objectives.

4. In light of the above, this work presents two datasets on birds, the environment and vegetation, collected between 2006 and 2012. The first dataset uses distance samplings design along random transects (2006–11). The second dataset consists of repeated detection/non-detection data of birds on random plots collected from 2011–12. These datasets provide information on how fire and grazing, through grass height and cover, affect the occurrence and density of a number of grassland bird species. Most of my analyses account for species detectability. Separately, I developed a model based on my field understanding of how fire, grazing and rainfall interact to determine habitat suitability for target bird species through vegetation characteristics.

5. The beginning of summer 2006/07 was marked by a change in the grassland management regime from heavy grazing with commercial livestock to much reduced grazing so that the habitat could recover from many years of heavy grazing. Although cattle were removed following Mentis's (2006) recommendations, tenants left behind by commercial farmers continued to burn the whole area annually, as before. Mentis (2006) had suggested cattle be replaced with game, and recommended a minimum fire return period of at least two years. Construction of above-ground infrastructure, including access roads, workers' camps and exploratory tunnels, intensified between the summers of 2006–09. From 2010–12, construction was largely confined to underground engineering work. For the purposes of this study I refer to survey data collected after 2010 as post-baseline data, and before that date as baseline survey data.

6. Chapter 1 provides an overview of the impacts of energy demands on species and habitats in southern African grasslands. Amongst the energy projects, this chapter provides a brief history of pumped storage schemes in South Africa and details the *modus operandi* of a scheme. Within the grassland biome the eastern moist high-altitude grasslands are a priority for conservation while being also a target for future storage projects and wind farm energy projects. After the initial opposition to construction of a pumped storage scheme at Braamhoek, the Ingula Partnership, consisting of environmental NGOs and Eskom, was formulated to suggest measures to negate and mitigate possible environmental damage. The uncertainty surrounding how best to manage this priority area for conservation led me to suggest that adaptive management would be an appropriate way to manage this area, with possible implications for similar habitats within the grassland biome.

7. In Chapter 2, I review the peer-reviewed literature of key management factors responsible for avifaunal diversity within the moist high-altitude grasslands of eastern South Africa. I found only one peer reviewed study within the region where experimental studies were set up to manipulate grassland habitats to maximise avian diversity. The remaining papers relevant to this region were based on observational studies and associated birds, fire and grazing, and were done on mostly privately owned farms where fire was used to maximise domestic livestock production rather

than avian diversity. Overall, the few observational studies that exist for this area point to annual fires and subsequent heavy grazing as detrimental to avian diversity or species richness. The lack of literature on moist high-altitude grasslands made me search for literature outside the South African grassland biome, limiting me to the use of fire and grazing on avian diversity or richness. In grasslands outside South Africa, fire, grazing or both are used as management tools to bring about habitat diversity of birds. Grass height and cover are the most important habitat variables that determine habitat suitability for birds.

8. In Chapter 3, I use the transect data to examine whether there was a change in vegetation, bird species richness and indicator species richness between the baseline and post-construction periods. I use generalised, linear, mixed-effect models with transects as a random effect, and year as a fixed effect, to account for changes in species richness across the specified period. There was an increase in the amount of bare cover between the two periods, despite little grazing. This is the result of annual fires whose intensity is fuelled by grass load and wind, and therefore results in patchiness. Bird species richness was higher in summer compared to the remaining three seasons. Bird species richness and the number of indicator bird species increased slightly between the periods. There was no clear relationship between fire, grazing and species richness because almost the entire study area was burned annually, and the few remaining tenants' cattle grazed everywhere and at any time. After grazing with commercial livestock had stopped bird species richness increased, but not necessarily the individual species' abundance. The weakness of the statistical method used in this chapter is that species richness was used simply as the count of the number of bird species per transect per survey, and it does not take into account heterogeneity in bird species' detectability.

9. In Chapter 4, I use the same data as above but this time I estimated the abundance of the eight grassland birds that were found to be most common during the survey. This analysis was carried out using hierarchical distance-sampling methods, which accounted for species detectability. Based on the literature review, grass height and cover are important variables that work alone or together to determine habitat suitability for different species. I therefore used grass height and cover, first as linear

covariates, and then using regression splines. Overall, grass height and cover had a variable influence on the abundance of the eight species. The use of splines identified the most suitable habitat in terms of grass height and cover for each species. Because grass height and cover are affected by burning and grazing, controlled grazing and burning would result in higher bird species' richness, diversity and abundance by creating a mosaic of grass height and cover.

10. In Chapter 5, I use multi-species dynamic occupancy models to examine occupancy patterns of 12 common, small, grassland birds in relation to grass height and cover during the four summer breeding months. This makes use of the repeated detection/non-detection data collected on bird species from 18 plots. Plot occupancy was variable amongst the twelve species and ranged from species that were recorded on all 18 plots on visits three times a month for four months, to species that declined from high occupancy at the beginning of breeding to low occupancy by February. The majority of species had a high probability of occupancy and persistence with increasing grass height and cover. The probability of unoccupied plots becoming occupied during the course of the season declined with increasing grass height and cover.

11. Chapter 6 integrates my previous knowledge of how birds response to grazing and burning with results from Chapters 2 to 5. I predict the response of bird species richness to management of fire and grazing. This chapter therefore quantitatively represents my best knowledge of how Ingula management could influence bird species richness through varying the stocking density and proportion of grassland patches to burn when management eventually gains control over fire and grazing. Sensitivity analyses showed that rainfall, stocking density and the proportion of burned patches had the greatest effect on species richness. The model can be developed for use in adaptive management. I propose delineating Ingula into polygons of varying management units to account for the spatial variation in habitat characteristics.

12. Chapter 7 is the concluding chapter. I briefly discuss the link between adaptive management and monitoring for conservation of biodiversity. I summarise the findings from Chapters 2 to 5 and how they fit into a broader adaptive management of Ingula grasslands to increase avian diversity. I conclude this chapter by suggesting that, in addition to the grasslands, Ingula's wetland and cool mountain escarpment forests are equally important habitats hosting a variety of nationally, regionally and globally threatened species and equally deserving separate adaptive management to grassland management.

Chapter 1

> Within a few decades, if present trends continue, we'll be losing a *lot* of everything. As we extinguish a large portion of the planet's biological diversity, we will also lose a large portion of our world's beauty, complexity, intellectual interest, spiritual depth and ecological health.
>
> David Quammen – *The Song of a Dodo*

General introduction to the thesis

Introduction

IMPACT OF ENERGY DEMAND ON HABITATS AND SPECIES IN SOUTH AFRICA

More than 90% of South Africa's electricity is generated from coal (Wassung 2010). Coal is the most important energy source in South Africa, acting as the backbone of the metallurgical industry and the main raw material for the petrochemical industry (Prevost 2003). South African coal reserves are limited (Rogers 1999) and it is uncertain whether the country has sufficient reserves to meet future energy demands (Prevost 2003). Given South Africa's heavy dependence on coal for power generation, an anticipated peak production in 2020 will cause problems for future growth (Hartnady 2010). About 40% of coal extraction in South Africa is by open cast mining (Ebernard 2011), and the impacts of this form of habitat destruction are irreversible (Hartmunt 2005). Open-cast mining has a devastating effect on environment and biodiversity in general but, in addition, the combustion of coal is also considered to be a major source of greenhouse gases, which contribute to global warming (Menon *et al.* 2002).

Nuclear power as an alternative to coal also has a number of challenges in the near term (Ramana 2009), the major one of which is the high capital cost and financial uncertainties surrounding the management of nuclear power plants (Gauche, von Backstrom & Brent 2013). The enormous consequences of catastrophic accidents, even if unlikely, make nuclear power unattractive to many. Last, but not least, finding a way of safely disposing nuclear waste is still a problem (Ramana 2009). Although South Africa is blessed with plenty of sunshine, solar power alone seems to not yet to be a financially viable alternative to coal (de Jongh, Ghoorah & Makina 2014).

Because of the uncertainties surrounding coal and nuclear energy, there has been a call for a paradigm shift in energy production from fossil fuels to alternative energy sources (Gauche, von Backstrom & Brent 2013) to mitigate the effects of anthropogenically-induced climate change (Inger *et al.* 2009). In more recent decades there has been a call for wind or marine tidal energy as an alternative source (Inger *et al.* 2009). Wind farms appear to cause fewer environmental problems than fossil fuel technologies and have received strong public support as an alternative energy source (Leddy, Higgins & Naugle 1999; Drewitt & Langston 2006). Newly-emerging evidence, however, suggests that wind farms cause a worrying level of mortality to birds and bats (Drewitt & Langston 2006; Horn, Arnett & Kunz 2008; Farfán *et al* 2009; Fox 2011), especially raptors and migrating songbirds (Kingsley & Whittam 2001; Drewitt & Langston 2006). In addition, the installation of wind farms requires large areas, leading to direct habitat loss or modification.

To be effective, wind farms must be sited in open, exposed areas where there are high average wind speeds (Drewitt & Langston 2006), making grasslands and marine habitat preferred locations (Erickson *et al* 2007; Inger *et al* 2009). In some studies outside South Africa, upland birds have been demonstrated to be the most vulnerable to this form of energy source (Leddy, Higgins & Naugle 1999). In South Africa, the moist, open, high-altitude grasslands of eastern South Africa are a potential candidate area to locate wind farms. However, moist, eastern high-altitude grasslands of South Africa have already been identified as priority areas for conservation due to their high level of animal and plant rarity and endemism (Allan *et al.* 1997; Armstrong & van Hensbergen 1999; Reyers *et al.* 2001; Olson & Dinerstein 2002). Of the moist upland grassland biome in Southern Africa, about 23% is under cultivation (Armstrong & van Hensberggen 1999), and 60% is irreversibly transformed, with about 2% of this area falling within protected areas, while most of the remaining natural land is primarily used to support commercial livestock (Reyers *et al.* 2001; O'Connor & Kuyler 2009). The long-term persistence of wildlife under the current perceived land transformation and estimated global change requires the representation and retention of all elements of biodiversity (Fairbanks & Benn 2000).

Accepting that many wind farms result in only low levels of mortality, even these levels of additional mortality on wildlife may be significant for long-lived species with low reproduction rates that also take a long time to mature; this is especially the case when rarer species of conservation concern are affected by such developments (Drewitt & Langston 2006). In Southern Africa, high-altitude grassland of eastern South Africa are the stronghold of two threatened vulture species: Cape Vulture *Gyps coprotheres* and Bearded Vulture *Gypaetus barbatus*. These two species are already regarded as declining and threatened due to poisoning and energy developments in the 21st century (Maphisa 1997, 2001; Krüger *et al.* 2013).

Whatever the source of electricity, it needs to be transported to the consumer through a network of transmission lines and associated infrastructure with which birds can collide. A high proportion of birds that are killed by transmission lines are threatened species (Jenkins, Smallie, & Diamond 2010) because they forage over large areas. For the majority of already threatened species, collision with man-made structures adds additional levels of anthropogenic mortality (Martin & Shaw 2010; Shaw *et al.* 2010). There seems to be no easy resolution of the conflict between conservation and meeting the growing demand for electricity. Therefore, choosing the sites for future construction of energy projects must be well researched and followed by measureable mitigation effects during and long after construction.

ARE PUMPED STORAGE SCHEMES A LESSER EVIL?

Because most low-carbon electricity plants (wind, solar and nuclear) lack flexibly to adjust their output to match variable power demands, there is increasing need for bulk storage of electricity that would otherwise be wasted (Yang 2010). Pumped storage schemes are perceived as offering one solution to bulk electricity storage (Yang & Jackson 2011). A pumped storage scheme consists of two dams located at two different altitudes and a connecting tunnel, through which water can be pumped from the bottom to the top dam when electricity demand is low and then run down, through turbines, to generate electricity when demand is high. Their impact on species is primarily through habitat loss when dams and associated infrastructure are built. As a result pumped hydroelectric storage (PHS) schemes are thought to be the best-established technology for utility-scale electricity storage and have been commercially used as far back as 1890s, with most schemes now located in Europe and Asia (Yang 2010).

The development of PHS requires suitable terrains with significant elevation differences between the two reservoirs and a constant supply of water to keep the scheme running (Yang 2010). Although the designs of PHS differ (Ibrahim, Ilinca, & Perron 2008), the principle on which the schemes work is the same. Power stations using coal operate continuously, producing a constant amount of electricity; if they meet peak demands during the day and evening, they also produce surplus electricity which goes unutilized and unsold during the night when electricity demand is low. These stations use this "spare" electricity to pump the water from the lower reservoir to the upper reservoir. When demand is high, the water flows out of the upper reservoir or head pond and activates the turbines to generate high-value electricity for peak hours (Ibrahim, Ilinca, & Perron 2008; Yang & Jackson 2011). Water is stored in a lower dam or tail pond until the second cycle, when water is pumped back into the upper dam using electricity from the grid to repeat another cycle. An additional advantage when comparing PHS with coal-generated electricity is that PHS can be activated within minutes to provide electricity on line during peak demands, whereas it takes hours to bring a coal-fired station on line.

The societal benefits of the storage dams range from generation of electricity, the supply of water for agriculture, industry and municipalities, mitigation of flooding and improved river navigation (Rosenberg, McCully, & Pringle 2000). However, the effectiveness of dam technology in delivering these services is debatable (McCully 1996; Davies & Day 1998; Rosenberg, McCully, & Pringle 2000; Nusser 2003; Baghel & Nüsser 2010). Such scepticism is based on evaluating the effect of dams on river ecology, hydrology and modification of habitat downstream. The most important impact is that the construction of storage dams involves the damming of a river to create a reservoir that blocks the natural flow of water and disrupts the aquatic ecosystem. The reservoirs flood previously dry areas with irreversible loss of terrestrial wildlife habitats and significant changes to the landscape (Yang 2010). Controversy surrounding how much water needs to be released to maintain pre-damming natural flow requirements downstream and how to measure and monitor has added to the disapproval of damming the rivers (Berrens, Ganderton, & Silva 1996; Gillilan & Brown, Thomas 1997; Vogel *et al.* 2007).

Although pumped storage schemes seem a lesser evil to augment additional energy to the national power grid, because the scheme conserves water, this solution is temporary as more pumped storage schemes would have to be built at the cumulative cost the environment in order to meet the growing human population demands for electricity. On the same note, the so called renewable energy development projects, such as wind energy, offer a temporary solution because these forms of energy are intermittent and fluctuate (Rahman, Rehman, & Abdul-Majeed 2012). Current research is focused on more efficient energy storage devices to reduce reliance on coal demand, which contributes to increased environmental pollution (Rahman, Rehman, & Abdul-Majeed 2012).

HISTORY OF PUMPED STORAGE SCHEMES IN SOUTH AFRICA

Ingula was the third pumped storage scheme to be built in South Africa. The first pumped scheme is the Drakensberg Pumped Storage Scheme, close to Ingula. The head ponds of both the two schemes are situated in the Free State Province above the escarpment, whereas the tail ponds of both schemes are situated below the escarpment in KwaZulu-Natal. The scheme was commissioned in 1982, with estimated generating capacity of 1 000MW (Braamhoek Partnership 2004). The second scheme, Palmiet, was a dual venture between Eskom and the then Department of Water Affairs and Forestry and is located close to Grabouw in the Western Cape; it was commissioned in 1988, with an estimated generating capacity of 400MW (Braamhoek Partnership 2004). The Ingula Pumped Storage Scheme, which will benefit from newer technology, is estimated to generate up to 1 332MW. The Drakensberg scheme was also designed for water transfer to supplement the Vaal River from of the catchment of the Tugela River.

THREATS TO MOIST HIGH ALTITUDE GRASSLANDS OF EASTERN SOUTH AFRICA

For a pumped storage scheme to work efficiently it must be located in an area where water is readily available all year round and the topography allows the potential energy of the water to be used with minimal costs. Equally, wind farms require vast open areas with wind all year round. In South Africa, the threatened, moist, eastern high-altitude grasslands fulfil both criteria, making then possible targets for future renewable energy development projects, threatening biodiversity.

Grassland habitats are among the most endangered ecosystems in the world (With, King, & Jensen 2008) and represent one of the least protected biomes worldwide (Hoekstra *et al.* 2004). South African grasslands are no exception (e.g. Barnes 2000). The grassland biome of South Africa has been identified as critically endangered, requiring conservation attention through the implementation of efficient, sustainable conservation planning (Matsika 2008).

For example, the grassland biome of South Africa contains 10 grassland bird species that are endemic to the area, of which six are threatened, and, furthermore, 10 of an estimated 14 globally threatened bird species present in South Africa have major strongholds in this region (Neke & du Plessis 2004; Archibald *et al.* 2005; Bond & Parr 2010). South Africa's moist grassland harbours globally significant biodiversity, supplies essential ecosystem services, supports crop and livestock agriculture, forestry and human settlement, and yet is poorly conserved (O'Connor & Kuyler 2009). Despite this, little research has been carried out to investigate how best to manage this threatened ecosystem.

The greatest threats to the grasslands of South Africa are from commercial tree plantations, invasive species, agriculture, changes in grassland management and inappropriate human resettlement plans (Hockey *et al.* 1988; Allan *et al.* 1997; Barnes 2000; Maphisa *et al.* 2009). While some of the Important Bird and Biodiversity Areas (IBAs), including other reserves(e.g. Maloti/Drakensberg Transfrontier Park) located within the grassland biome, are far away from humans, they now face similar threats to other grasslands that are much closer to human populations. Most moist high-altitude grasslands are used for livestock production; this activity is often accompanied by frequent and heavy grazing and annual fires. This has resulted in habitat transformation associated with changes in vegetation height, density and, over long periods, changes in grassland bird species composition (Jansen, Little, & Crowe 1999). When trying to maximise grassland productivity for dairy cattle and beef farming, many grassland habitats are burned annually, without taking into account weather conditions and fuel load. Although in some instances burning of the grasslands is intended as a means of controlling ticks and removing accumulated dead matter (Van Niekerk, Fourie, & Horak 2006), some farms are so heavily grazed that there is hardly anything to burn (Maphisa 2004), and yet they are still burned. In many instances this has led to widespread soil erosion, leading to forb invasion (Brand, Preez, & Brown 2008).

As the human population increases there is also an increasing threat that comes from the damming of the rivers and wetlands to build either storage schemes to generate electricity or to supply water for consumption (Davies & Day 1998). Realising the negative impacts of these developments, it is no longer possible to exploit water resources for human needs without taking into consideration ecological flow needs (Vogel *et al.* 2007). Lack of consensus on how to regulate the release of water from dams to ensure that natural flow is maintained after dam construction, has also been attributed to changes in river flow ecology downstream from the impoundment areas (Gillilan & Brown, Thomas 1997; Vogel *et al.* 2007).

An emerging threat comes from climate change, the consequences of which, on high-altitude grassland and associated biota, are irreversible (Huntley & Barnard 2012). Changing climatic conditions within the grassland biome are anticipated to lead to changes in precipitation and fire regime (Bond, Midgley, & Woodward 2003; Bond, Woodward, & Midgley 2005). Knowing how species respond to fire regimes is particularly important for ecologically sustainable management (Driscoll *et al.* 2010).

Despite the numerous threats facing the grassland ecosystems, there has been little research to investigate methods to manage this dwindling resource in an optimal way and to investigate factors that maintain avifaunal species richness and diversity within the moist high-altitude grasslands. Because of human encroachment into the grassland biome, surviving grasslands today constitute remnants of isolated patches, sometimes with little connectivity between them. The currently remaining large grasslands may not be sufficient to prevent grassland bird declines (With, King, & Jensen 2008). While there is a general lack of funding for research to redress habitat and ecosystem deterioration, rarely do conservation plans suggested by scientists convey a clear strategy for using research data to guide decisions about population status or management decisions (Bakker & Doak 2009).

THE HISTORY AND CONTROVERSY BEHIND THE INGULA PUMPED STORAGE SCHEME

Although the search for a site for the third pumped storage scheme began in the early 1980s (e.g. Braamhoek Partnership 2004), an Environmental Impact Assessment (EIA) was only started in January 1998 and the Record of Decision, detailing steps that had to be adhered to ensure that the environment was not negatively impacted by construction activities, was received from the national Department of Environmental Affairs and Tourism (DEAT) only during December 2002 (Braamhoek Partnership 2004). Because of the ecologically sensitive location, this proposal resulted in resistance from environmental Non-Government Organisations (NGOs) and the public (see also Nusser 2003). This was because the scheme is located within the headwaters of the Wilge River, a major tributary of the Vaal River catchment, an important source of water for Gauteng, the province of South Africa in which the largest proportion (about 23.9%) of the country's population lives (Statistics South Africa

2014). The area also forms an important continental watershed, with part of the water feeding the equally important Tugela River catchment. Moreover, the head pond was likely to destroy a significant portion of an important wetland, with impounded water discharged directly into the remaining wetland.

In later years the study by Barnes (1998), based on available bird distribution records, found that the area coincided with high avifaunal endemism. Based on this study, the area was subsequently designated an Important Bird Area (SA IBA 043 Bedford-Chatsworth) (Barnes 1998). Of major concern was the observation by Barnes (1998) that the wetland and surrounding grasslands, where the head pond would be built, is a home to two 'Critically Endangered' bird species according to South African Red Data Book, namely the White-winged Flufftail *Sarothrura ayresi*, and the Wattled Crane *Bugeranus carunculatus*. Of these, the White-winged Flufftail generated the most interest because the area was considered to be one of the major strongholds for the species in South Africa. The White-winged Flufftail is one of South Africa's rarest birds and, outside South Africa, only occurs in Ethiopia. Following from my own five years' fieldwork records, two additional 'Critically Endangered', species, Rudd's Lark *Heteromirafra ruddi* and the Eurasian Bittern *Botaurus stellaris* were also confirmed occurring in the area, together with several other threatened birds species that occurred as breeding summer visitors or range-restricted breeding residents. These include the Secretarybird *Sagittarius serpentarius*, Denham's Bustard *Neotis denhami*, White-bellied Korhaan *Eupodotis senegalensis* and Southern Bald Ibis *Geronticus calvus*. More recently, the 'Threatened' African Grass Owl *Tyto capensis* has also been confirmed as occurring in the area (Maphisa 2012).

Following lengthy discussions between the affected parties – involving the then Minister of Water and Environmental Affairs, Valli Moosa, the Braamhoek Partnership was established in 2002 and in later years renamed the Ingula Partnership. The main objective of this partnership between Eskom, BirdLife South Africa (BLSA) and Middelpunt Wetland Trust was to propose and suggest measures to mitigate possible negative impacts of the construction and operation of the Ingula PHS on habitats and biota. At a later stage, the Ingula Partnership added to its fold the Ingula Advisory Committee: Conservation (IACC), made up of two relevant provincial environmental bodies and other concerned NGOs. Together, these committees have worked to suggest mitigation measures and monitor adherence to the Record of Decision during the construction and post-construction periods of the scheme. Through the partnership, additional land was bought to compensate for the area lost to the construction of the dams. In total, 8 000 ha was bought and set aside for conservation. It was felt that there were benefits to the project that adequately compensated for the losses (Braamhoek Partnership 2004).

The overall goal of the partnership is to maximise biodiversity beyond the construction phase of the project. This goal sets the stage for my PhD thesis in which I aim to provide information essential for managing Ingula for conservation. Many of the species mentioned above require different habitats, sometimes with conflicting habitat needs. Because of the long history of annual fires and overgrazing, the area has become degraded. Consequently, Mentis (2006) recommended withdrawal of domestic livestock and possible replacement with game. Mentis's (2006) task was to determine where and when grazing should be allowed over a period of 5 to 10 years, determine stocking rate capacity and compare the impact of cattle versus the introduction of game, also taking into account the potential for ecotourism. Hobbs & Huenneke (1992) cautioned that imposing grazing animals on a system, which had not previously experienced that type or level of grazing, would constitute a disturbance, and so would the removal of grazing from a system with a long grazing history. Elsewhere (e.g. Norment, Runge, & Morgan 2010), research concluded that livestock grazing is compatible with the conservation of a number of grassland bird species.

Following the Mentis (2006) recommendations, commercial farmers were compensated for the purchase of their land, leaving behind their tenants with relatively few domestic animals. Although Eskom had good intentions to resettle tenants on land to which they would have title, efforts to relocate them were largely unsuccessful. Unlike the commercial farmers, who moved cattle out of the area in winter to escape harsh winter conditions, the tenants' livestock remains on site all year round. In an effort to encourage grass to grow quickly for their starving animals, the tenants continued to burn the veld annually, but did so much earlier in the year than was the case during occupation by the commercial farmers. In the absence of their former employers, the tenants also plundered the cool mountain forest trees for *muthi* and other natural resources.

Although the tenants' wealth in livestock quickly increased, it did not match the commercial farmers' livestock numbers. The strongly-reduced grazing pressure led to increased fuel load of plant litter during the following winters. The accumulation of dead standing litter within the grassland biome produces highly flammable fuels at a rate surpassing any flammable woody vegetation (Bond, Woodward, & Midgley 2005). Added to that, the area is prone to lightning strikes (Bond, Woodward, & Midgley 2005). Over seven years (2006 to 2012) annual fires have persisted, the origin of which could not always be traced. Even when burning is planned, the accumulation of dead grass causes huge and intense fires and the fires often cross pre-burnt firebreaks.

In addition to Mentis's (2006) recommendations, which so far have not been fully implemented, a more recent report also suggested that the presence of cattle in the area jeopardises the primary aim of optimising fresh water yield (Cauldwell 2012) because cattle degrade the wetland. There is currently a need to balance the ability for the site to perform its primary role of ensuring that there is enough water to run the pumped storage scheme and to promote conservation of biological diversity under which the construction of the pumped storage scheme was granted. The conservation management plan, currently under review, recommends that the area will be run under adaptive management. The primary aim of this thesis is to provide a scientific background for future management of Ingula under adaptive management. A second aim is to provide a case study applicable to the management of similar areas in South Africa. Plans to proclaim Ingula as a nature reserve are at an advanced stage (e.g. Maphisa 2012). The uncertainty of how best to manage the future reserve has given rise to the subject of this thesis.

ADAPTIVE MANAGEMENT: A NEW PARADIGM IN CONSERVATION

Challenges with managing natural wildlife resources and their habitat led to a new paradigm in conservation called adaptive management (Walters & Holling 1990). Adaptive management provides for structured decision making for recurrent decisions made under uncertainty (Runge, Converse, & Lyons 2011). There are a number of sources of uncertainty in the management of wildlife resources and adaptive management is designed to optimise decision making under these uncertainties (Diego *et al.* 2005; Conroy *et al.* 2011; Keith *et al.* 2011; Probert *et al.* 2011; Rumpff *et al.* 2011; Runge, Converse, & Lyons 2011; McFadden, Hiller, & Tyre 2011; Runge 2011; Westgate, Likens, & Lindenmayer 2013). The main causes of such uncertainties are: 1) the current state of the system cannot be determined precisely (observation uncertainty, e.g. we cannot determine the precise densities of the species at Ingula), 2) that management does not know exactly how the system would react to a particular management intervention (structural uncertainty, e.g. does it matter when we burn?), 3) the system is stochastic (environmental uncertainty, e.g. we don't know how much it is going to rain during the coming year), and 4) uncertainty whether the recommended management actions will be implemented (management uncertainty, e.g. we may recommend burning only half of the plots per year but runaway fires anyway burn everything). Some of these uncertainties could be reduced by learning, while other uncertainties will always be present (Grantham *et al.* 2010). The purpose of management is therefore to ensure that decisions are optimal under these uncertainties and to reduce uncertainties where possible (Moore & Conroy 2006; Howell *et al.* 2009; Chee & Wintle 2010; Grantham *et al.* 2010; Probert *et al.* 2011; Runge, Converse, & Lyons 2011). Adaptive management is a tool designed to do this through learning from past management actions.

In a review, Westgate, Likens, & Lindenmayer (2013), summarised adaptive management into six steps as follows: 1) the first step is to clarify and identify management goals, i.e. what do we want to achieve? 2). The second step is to list available management options, one of which could be 'do nothing' 3). The third step is to formulate quantitative conceptual models that sometimes involve rigorous experimental design followed by rigorous statistical analyses to predict how the system responds to different management options in 2 above. 4) The fourth step is to determine the management option that is predicted to have the most desirable effect and then to implement it. 5) The fifth step is to monitor how the system responds after implementation of management actions and compare monitoring results to the model predictions. 6) The last step is to adjust management practice in response to results from monitoring by reweighting the models according to how well they predicted the outcome. The ability to adapt future decisions to new information is a hallmark of adaptive management (Runge 2011). This version of adaptive management is sometimes called the decision-theoretic version of adaptive management (Runge 2011, summarised in Fig. 1). In contrast, the resilience-experimentalist version of adaptive management is applied to the management of large-scale, complex, socio-ecological systems and emphasis is more on governance, resilience and the reduction of uncertainty through experimental manipulations (Runge 2011).

Other versions of adaptive management exist. In South Africa I found two examples of adaptive management in the literature (van Wilgen & Biggs 2011; Scheepers, Swemmer & Vermeulen 2011), both of which were carried out within South African national parks. The first study describes management of rivers, fire regimes, invasive species, a rare antelope and of elephants in the Kruger National Park. The second study is on the management of the sustainable utilisation of three plants. In these examples, the emphasis is on critical thresholds that trigger certain management actions and the thresholds are revised over time. The decisions do not seem to be based on quantitative models and only partly on controlled experiments. They therefore do not neatly fit into the two versions of adaptive management described above.

RELEVANCE OF ADAPTIVE MANAGEMENT TO INGULA

In this thesis, I propose the route of the decision-theoretic version of adaptive management (Runge 2011, Westgate, Likens, & Lindenmayer 2013) to manage Ingula and as a case study on how to conserve grasslands for avifaunal diversity, while learning how to optimise the habitat for bird diversity. Ingula is in the process of being declared as a nature reserve (see Maphisa 2012). The Ingula Conservation Management Plan (under preparation) outlines how to manage the future reserve. The overall goal of management is to conserve wildlife resources under adaptive management to maximise biodiversity at Ingula. In Chapter 2, I use birds as a case study, to review the literature relevant to management of grassland avian diversity. Results from Chapter 2 suggest that, within grasslands, grazing and fire are important tools that management can use to create a mosaic of grass height and cover under which the diversity of avifauna evolved.

Currently we do not fully understand how grassland birds react to the combinations of grazing and fire, including no grazing or no burning. However, there seems to be consensus that fire and grazing are important for South African grassland birds (Hockey *et al.* 1988; Archibald *et al.* 2005). There are also uncertainties about the timing of fire, return period and intensities, and the same could be said of how birds would respond to different grazing intensities (Parr & Chown 2003). Putting grazing aside, there is also uncertainty regarding the importance of rainfall for the vegetation on which grassland birds depend for feeding and nesting. Finally, it is unclear how wind modifies the effects of fires, e.g. by causing particularly hot run-away fires. In Chapter 6, based on my field observations (2006 to 2012) and knowledge gleaned from the literature, I attempt to capture most of these uncertainties into a simple model to predict how individual birds would respond to fire and grazing and make suggestions on the implementation of adaptive management to guide future management decision on the use of fire and grazing, or of no fire.

A key component in adaptive management is an effective monitoring programme (Lindenmayer, Piggott, & Wintle 2013). In Chapter 7, I provide alternative options to monitor Ingula's avifauna as part of future adaptive management, based on the results from Chapters 3 to 5. My efforts to test alternative hypotheses about fire and grazing, and their impacts on birds, were frustrated by a lack of control over fire and grazing between 2005 and 2012. I suggest a simple model where, through experimentation, Ingula management can kick start the adaptive management process to evaluate the impact of implementing different management decisions and through adaptive monitoring (e.g. Lindenmayer & Likens 2009), after which management can evaluate the best option to manage Ingula for avian diversity. Starfield (1997) suggested that starting with a simple model can guide management on what data to collect and how to monitor, and this process should be driven by achieving explicitly stated management objectives (Tester, Starfield, & Frelich 1997; Rumpff *et al.* 2011).

Description of study site

Ingula is located about 23km northeast of the village of Van Reenen at altitudes ranging between 1 400 to 1 700m asl, and has an area of about 8 000ha (Figure 2). This area is located on the boundary between two South African provinces: KwaZulu-Natal and the Free State. It is bisected by the escarpment, which forms an important continental watershed and is covered by cool mountain forest. The area above the escarpment, which I call the 'upper site' throughout this thesis, is located within the headwaters of the Wilge River, a major source of the Vaal River catchment and finally drains water into the Atlantic Ocean at the estuary of the Gareip (formerly Orange) River, the border between South Africa and Namibia. The head of the Wilge River catchment at Ingula is characteristic of the various wetlands, with numerous oxbow lakes, which are the result of an abundance of rainfall, combined with flat terrain. The section below the escarpment, which I call the 'lower site' throughout this thesis, is largely transformed by agriculture but nevertheless considered important by KwaZulu-Natal Ezemvelo Wildlife because remnants of the more threatened moist grasslands of the Free State site crosses the boundary into KwaZulu-Natal at some places (Jewitt 2011). In addition to the already existing construction of the Ingula Pumped Storage Scheme, this area is also earmarked for relief diversion of the N3 national road. However, because of the existence of important wetlands, which would be affected by new development, a report by Mentis (2014), which was based on a desktop study, followed by on-site verification, has objected to some parts of this new development as no-go areas, mainly because of projected negative impact on the wetlands in the area.

GEOLOGY AND GEOMORPHOLOGY

The construction of the Ingula dams and the associated underground tunnels led to a detailed understanding of the geology and geomorphology of the area (Groenewald 2012, Brand et al. 2008). The geology of the Ingula Pumped Storage Scheme comprises a sequence of sedimentary deposits ranging from the lower Volksrust Formation of the Upper Ecca Group to the Verkykerskop Formation of the Middle Beaufort Group or Tarkastad Subgroup (Groenewald 2012). The area is underlain by sedimentary rocks of the Ecca and Beaufort Groups, which have been intruded by dolerites of the Karoo Dolerite suite. The sedimentary rocks comprise mudrocks, claystones, siltstones and sandstones (Groenewald 2012). The long-term weathering of the bedrock has created a gently undulating landscape, with distinct dolorite dykes, in some cases forming prominent ridges in the landscape (Norström *et al.* 2009). The latter are more visible at the upper study site than the lower site, where mudstone is more dominant. The soils of the area are the result of weathering of the underlying bedrock, with sandy to loam soil confined to above the escarpment, while soils below the escarpment are largely clayey, resulting from the underlying grey mud rock. The geology and geomorphology of the area is important for determining the type and distribution of the soil types in the area (Billings 1952; Fenu *et al.* 2014). Ingula is renowned for its high level of plant endemism, which is partly driven by the abrupt changes in geology and geomorphology within a relatively small area.

VEGETATION

The vegetation at Ingula is well studied and described (Acocks 1953; Low & Rebelo 1996; Mucina & Rutherford 2006; Norström *et al*. 2009; Brand *et al*. 2008). According to the latest classification (Mucina & Rutherford 2006), veld cover on the Free State side corresponds to veld type GM 4 - Eastern Free State Sandy Grassland (Fig. 2). The Boundary slope is described as Gs 3 - Low Escarpment Moist Grassland. The lower site is classified as Gs 4 - Northern KwaZulu-Natal Moist Grassland. This latter vegetation, together with the remnants of GM 4 that fractionally crosses into KwaZulu-Natal (although they are largely transformed), are both classified as ‘Near Threatened’ by the relevant provincial conservation body (Jewitt 2011). Many years of heavy grazing and annul fires has largely led to degradation of the habitat within Ingula and surrounding properties (Mentis 2006, Cauldwel, 2012), however, potential and actual vegetation is the same throughout the study area.

Construction of the Pumped Storage Scheme and associated infrastructure did lot lead vegetation conservation other than the area which is taken by construction camps and the storage dams (Fig. 2). Vegetation at the upper site which is the priority area for conservation largely remains intact other than the small portion which is now flooded by the upper storage dam (Fig. 2).

WEATHER AND CLIMATE

The weather in the area is variable with cold winters and occasional snow, mainly on the top of the Ingula escarpment. The winds are strong most of the year but wind speeds peak during late autumn to late spring. Temperatures fluctuate between an average daily maximum of +27°C in the hottest month (January) to an average daily minimum of −2°C in the coldest months (June and July) (Norström *et al.* 2009). Despite the short distance between the upper and lower sites, daily temperatures are markedly different, with the upper sites characterised by lower temperatures at any time of the year compared to the lower site. Summers are cool to hot and sometimes wet, with occasional mist that can last up to midday. Winters are relatively dry with signs of winter some years showing as early as March and lasting to October. Rainfall is orographic in nature with most of the rain falling between November and March. Annually, Ingula receives around 1 400mm, while the nearest official weather station, 100km to the west (Bethlehem, 28° 15’ S, 28° 20’ E), receives c. 680mm annually (Norström *et al.* 2009; Finne *et al.* 2010). However, a more accurate and recent report by Mentis (2014) estimate the mean annual precipitation along the Ingula escarpment at 1 000mm, based on weather records at Wyford Farm, located about 20km from Ingula and situated on Van Reenen’s Pass. Extrapolating from the Mentis (2014) report, the total rainfall during the four summer months of my study averages around 670mm, with most rain falling in December and January. The upper and the lower sites differ in rainfall, based on records from weather stations at the upper Bedford Dam and lower Braamhoek Dam (unpublished records).

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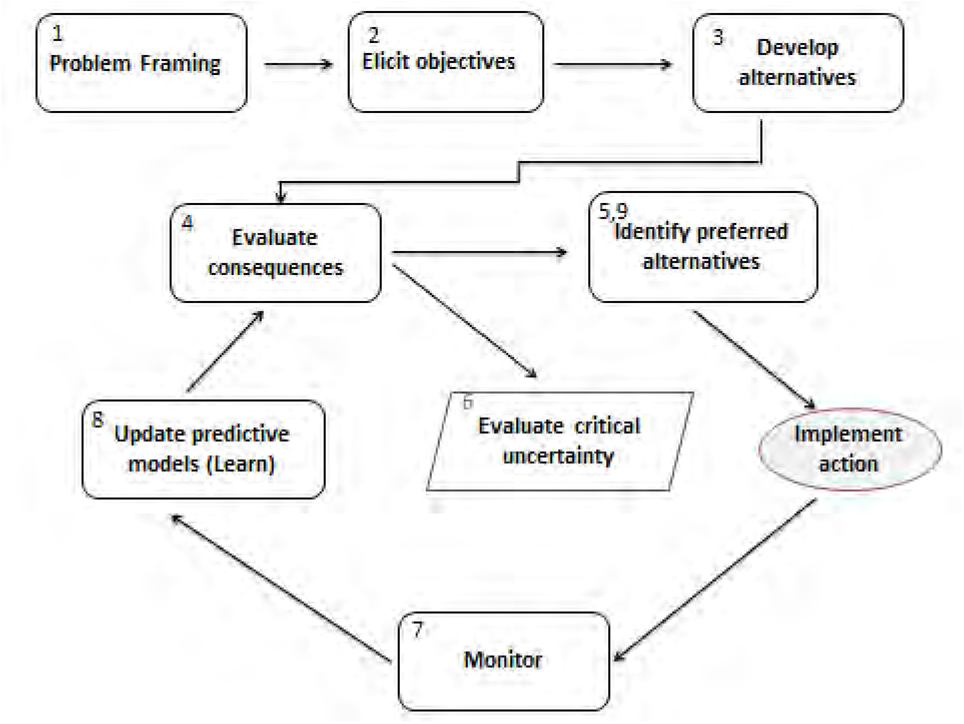

Fig.1. A diagram for adaptive management (from Runge 2011). Under adaptive management there is critical uncertainty that complicates the identification of a preferred alternative. When decisions are recurrent, implementing management actions is followed by monitoring to reduce uncertainty (Runge 2011).

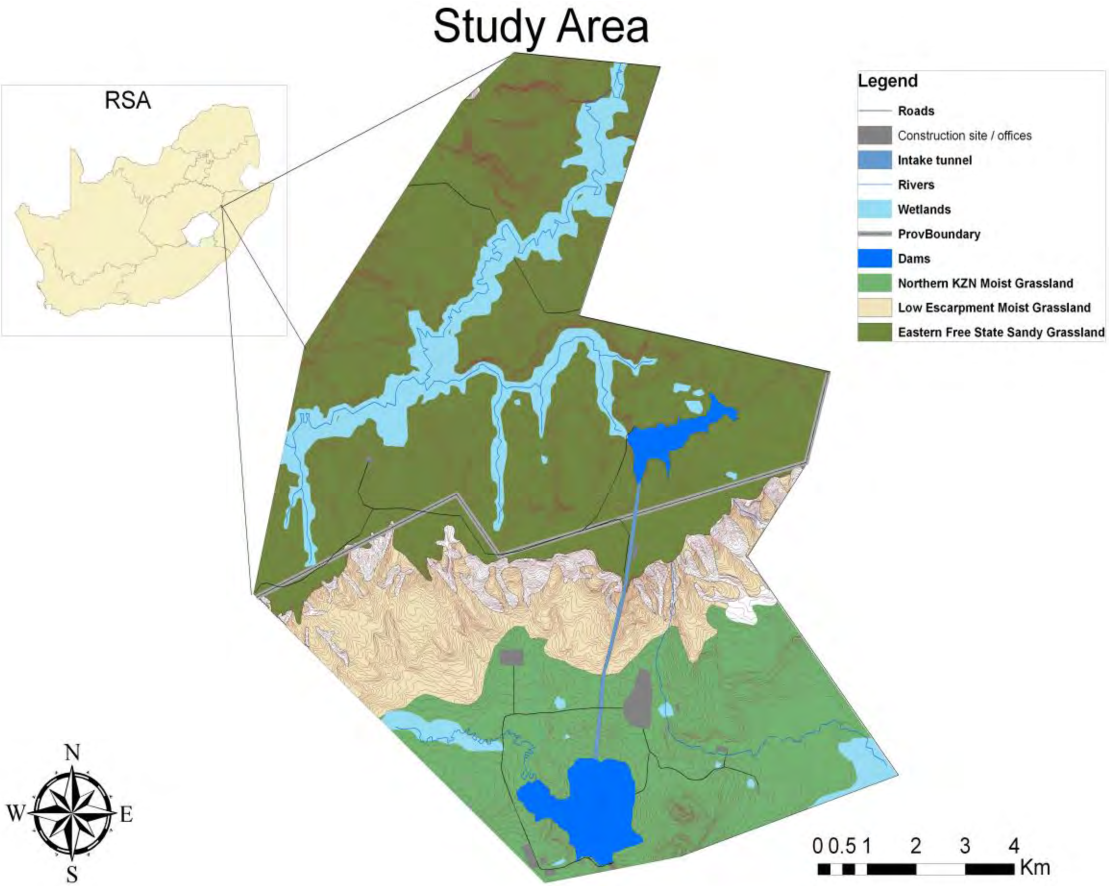

Fig. 2. Location of the study area, showing three vegetation types according to Mucina & Rutherford (2006), and the two dams and connecting tunnel that make up the pumped storage scheme and access roads. The area north of boundary slopes (Low Escarpment Moist Grassland) is referred to as upper site and area below where construction infrastructure is located as lower site throughout the text.

CHAPTER 2

> To do science is to search for repeated patterns, not simply to accumulate facts, and to do science of geographical ecology is to search for patterns of plants and animal life that can be put on the map. David Quammen from *The Song of a Dodo,* citing Robert MacArthur

Road map to managing Eskom's proposed conservation reserve for avian diversity at Ingula: a literature review of the factors affecting birds in moist high-altitude grasslands of eastern South Africa

Summary

1. Grasslands are amongst the most threatened and least conserved biomes in the world. In South Africa the moist eastern high-altitude grasslands have been identified as a priority for conservation. The biggest threats are habitat transformation through afforestation, expansion of human settlement, agricultural intensification and, more recently, expansion of energy projects in the area. The construction of a pumped storage scheme at Ingula and a debate concerning the role of fire and grazing, and the impact on avian species richness, has necessitated investigating factors that affect avian diversity in the area.

2. I conducted a literature search of peer reviewed articles for management factors that are cited as important tools to maximise avian diversity mainly within high-altitude grasslands of Southern Africa. To start with, I targeted 'Ostrich: The Journal of African Ornithology.' I then used various search engines (still confining my search to peer reviewed articles only), using key words such as: high-altitude grasslands, birds' species diversity, richness, management, fire and grazing. Finally, I relaxed the search to include managing grasslands for avian diversity/suitability anywhere in the world but within grasslands if such studies support studies from my core research area.

3. Studies of the factors that influence bird species' richness or habitat suitability within moist high-altitude grasslands of South Africa are scarce and, in most cases, are on individual species. In the studies that have been undertaken, fire and grazing are described as important management tools that influence avian diversity.

4. Amongst the papers that I found on the effects of fire or grazing on birds and came from my core study area there was only one study that was experimental and did not report intensity and duration of fire. Outside South African grasslands, I found reviews and experimental studies reporting fire and grazing as important management tools that bring about habitat heterogeneity. And in the context of this review and habitat heterogeneity/habitat mosaic refers to variable grass heights and cover across the landscape. Different species select patches with different grass height and ground cover, and these parameters, in turn, are dependent on whether the area was burned or not, and how, when and for how long a patch has been grazed throughout the summer. Variation in grass height and cover is the key habitat heterogeneity for grassland birds.

5. Based on the results of this literature review, I argue that neither fire nor grazing alone can bring about the habitat heterogeneity which enables long term persistence of species within the moist high-altitude grasslands. The deterioration of grasslands at Eskom's Ingula Pumped Storage Scheme, as an example, was a result of prolonged prior intensive stocking rates of cattle and annual fires. Nevertheless, proper domestic livestock stocking rates are needed to maintain biological diversity. Replacement of livestock with game must be treated with care, as it is not known what effect this would have on biological diversity. If the current management decide to restore the habitat through withdrawal of livestock, rare species might be lost and, because they are rare, they may not come back, even if suitable habitat is restored.

6. Finally, I argue that adaptive management presents an opportunity for Ingula grassland management to make further research on the type of herbivores and appropriate stocking density to benefit avian diversity.

Introduction

Grasslands are among the most endangered ecosystems in the world (With, King & Jensen 2008) and represent one of the least protected biomes worldwide (Hoekstra *et al.* 2004). In this case South African grasslands are no exception (Barnes 2000). The grassland biome of South Africa has been identified as critically endangered, requiring conservation attention through the implementation of efficient, sustainable conservation planning (Matsika 2008).

Bird species richness, endemism or diversity are important factors that are taken into account when selecting a network of reserves to achieve the targets set by the convention on the protection of the earth's biological diversity (Bonn & Gaston 2005). Until recently, many remote moist, high-altitude grasslands have been characterised by high biological diversity due to limited human modification (Carbutt *et al.* 2011). Although the moist, high-altitude grasslands of eastern South Africa support a large number of threatened species, they are increasingly threatened by agriculture, forestry and urbanisation (Allan *et al.* 1997; O'Connor & Kuyler 2009; Carbutt *et al.* 2011), and more recently roads (e.g. Mentis 2014), wind farms and associated infrastructure. With the increase in the human population, and its use of natural resources, there is an urgent need for conservation managers to emulate natural factors that maintained species' richness and diversity. The managers of such habitats are therefore required to understand factors that contribute to bird habitat suitability.

Many previously remote areas of the eastern South African moist, high-altitude grasslands have been selected as Important Bird Areas due to their high biological diversity, endemism and threat status (Barnes 1998). Some of these areas are threatened by human land use, which is likely to compromise their suitability for birds. To inform management of such areas, we therefore need to know what the key habitats characteristics are that correlates with avian diversity. The goal of this review is to collate published information on factors affecting bird diversity in the high-altitude grasslands of South Africa as an input to future conservation management at Ingula. Apart from synthesising the current state of knowledge, this review also aims to inform the managers of the Eskom Ingula Pumped Storage Scheme as a case study on which habitat factors drive avian species richness. Ingula is located within Important Bird Area SA043 (Bedford/Chatsworth) within the moist, high-altitude grasslands of South Africa (Barnes 1998). When Eskom acquired the land to build the Ingula Pumped Storage Scheme, it was required to buy additional land to compensate for the loss of habitat through construction of the dams (de Bruyn 2009). Altogether, an area of about 8 000ha has been set aside for the management of the existing biological diversity. The overall goal of the management of Ingula is to maintain and maximise the biological diversity. First I start by describing the study area and then I review all literature referring to management of grasslands for avian diversity in the region and draw from similar studies worldwide. Based on these we suggest a roadmap to management of moist high altitude for avian diversity.

Study Site

Because this review is intended at finding appropriate tools to manage Ingula for avian diversity, I first start by giving brief description of Ingula proposed nature reserve. Ingula is situated c. 23km north-east (S 28°14', E 29°35'S) of the hamlet town of Van Reenen at altitudes of 1200 to 1700m asl. Ingula covers *c*. 8 000ha and falls within two provinces in South Africa: KwaZulu-Natal (KZN) and the Free State (FS), with an altitudinal difference of around 400m between the high-altitude grassland biome on the Free State side, dominated by sweet and sour grasslands, and the lower-lying grasslands dominated by *Hyperrhinia hirta* and mainly *Cybompogon* grasses on the KZN side. The vegetation of the study area falls within three vegetation types according to the latest classification (Mucina & Rutherford 2006). The Free State site is classified as type GM 4 Eastern Free State Sandy Grassland, the boundary slopes fall within Gs 3 Low Escarpment Moist Grassland, and the lower site falls within Gs 3 Northern KwaZulu-Natal Moist Grassland (Mucina & Rutherford 2006). Although the Gs 3 Northern KwaZulu-Natal Moist Grassland is of 'least concern' nationally, it is considered 'near-threatened' by the Ezemvelo KZN Wildlife provincial body, because parts of the threatened GM 4 marginally extend into KZN in places (Jewitt 2011).

Until late 2005, the Ingula property was privately owned and was used mainly for cattle farming, with fire used almost annually to optimise cattle feed rather than to enhance biological diversity. The impact assessment studies carried out prior to construction occurred recommended that cattle be removed and replaced with game, because cattle were responsible for degradation of the wetland and surrounding grasslands (Mentis 2006). Mentis (2006) further recommended that the area be block-burned every other year. However, the record of decision (ROD) between the national Department of Environmental Affairs and Tourism and Eskom, under which the construction of the scheme was granted, required that biological diversity of the area be conserved during and after construction of the pumped storage scheme. The Ingula Partnership, made up of BirdLife South Africa, Eskom and Middelpunt Wetland Trust, was formed in 2004 to oversee the latter objective.

Following Mentis's (2006) recommendations, cattle belonging to the commercial farmers were removed during late 2005. However, the tenants who worked for the commercial farmers were left behind to be resettled by Eskom. The combined tenants' livestock was comparatively small compared to the commercial farmers' livestock. With cattle farming no longer the primary use of the habitat, the Ingula Partnership is now tasked with developing new plans to protect biodiversity in this high-altitude grassland. Understanding that bird-habitat interaction is central to management of Ingula, it is home to four of the five nationally Critically Endangered bird species: Wattled Crane *Bugeranus carunculatus*, White-winged Flufftail *Sarothrura ayresi*, Rudd's Lark *Heteromirafra ruddi* (see Barnes 2000), and more recently Eurasian Bittern *Botaurus stellaris,* all of which have been recorded (pers. obs).

Materials and methods

With emphasis on moist, high-altitude grasslands in eastern South Africa/southern Africa, a search was made of the peer-reviewed literature, starting with hard copies of 'Ostrich: The Journal of African Ornithology'. Subsequently, I used Google Scholar and Google engines in searches of factors and management tools used to enhance habitat suitability increase avian species richness or diversity. First, and with no temporal restrictions, I primarily searched using the following key words in various combinations and in no particular order: high-altitude grassland, grassland birds, habitat selection, diversity, species richness, suitability, management, and South/southern Africa and in the first instance, confining myself to high-altitude grasslands the area which will be similar to Ingula. In a second search, I did the same as above except that this time I replaced South Africa/southern Africa with Africa and moist, high-altitude grasslands with just grasslands. Thirdly, because vegetation structure determines habitat suitability for birds, I also searched for peer-reviewed papers world-wide on management of grassland habitat if such papers would support papers from previous search that link habitat management with avian diversity and richness. In Table 1, I put together and summarise studies on factors that are related to management of birds within the high-altitude region of South Africa/southern Africa. I included peer-reviewed papers if they are within remnants of grasslands anywhere within African continent if the subject of such papers links birds and habitat management.

In Table 2, I summarised any other papers that link habitat management and birds if such papers would support summaries of papers in Table 1 and were found using keywords mentioned above on world-wide web search on how grasslands are managed to bring about suitability for birds. Any other papers whose subject are management of grassland habitat or plant diversity and are from eastern southern African grasslands and therefore would support summaries from my core area of research (Table 1) were summarised in Table 2.

The impact assessment by Mentis (2006) that preceded the construction of Ingula Pumped Storage Scheme made suggestions that Ingula grasslands must be managed with fire and grazing to attain mosaic of habitats to benefit biodiversity. A further recommendation was made that domestic livestock must be replaced with game because cattle which were the dominant grazers at Ingula before were blamed for deterioration of grassland habitat and embedded wetland matrix. Mentisis (2006) recommendations were further supported by another study carried out six years later by (Cauldwell 2012) that Cattle must be replaced with game in order to reverse damage caused by many years of heavy grazing by cattle. Since 2005/06, Ingula’s habitats have been annually burned to bring about habitat heterogeneity/mosaic and there has been a little grazing by domestic livestock that belonged to the previous land owners’ tenants. In light of this, and with summaries from Table 1 and 2, I discuss and make arguments as to whether fire alone or grazing alone or in combination could bring about habitat heterogeneity for birds. And Finally, I argue whether cattle should be replaced with game in an area where grazing by cattle is now a dominant disturbance under which birds are now likely to co-exist at least since wild herbivores disappeared from the landscape. I define what habitat heterogeneity/mosaic is and how it can be achieved in the context of Ingula grasslands. I conclude by summarizing the implications of this review to manage Ingula grasslands in the context of adaptive management.

Results and Discussion

COULD FIRE ALONE OR GRAZING ALONE BE USED TO BRING HABITAT SUITABILITY FOR GRASSLAND BIRDS?

Table 1 lists and summarises bird studies that are from moist, high-altitude region and other papers from within remnants of grasslands outside the South African grassland biome but within the African continent. There is a scarcity of study literature on habitat management to bring about suitability for birds within the moist, high-altitude grasslands of South Africa and also outside the South African grassland biome in Africa.

I found one study where fire alone was experimentally and deliberately set out to test different fire regimes on two species of francolin within the high-altitude grasslands of eastern South African (e.g. Mentis & Bigalke 1981). This study tested the hypothesis that developing a fine-scale mosaic of burnt grassland should maintain a higher density of Grey-winged *Scleroptila africanus* and Red-winged *Sleroptila levaillantii* Francolins than when the entire site is burnt all at one time. To do so, they established neighbouring block-burned experimental plots and control plots of similar sizes from November 1973 and May 1977. They alternated fire between neighbouring plots and subsequently estimated densities of these two francolin species in the spring and autumn seasons from 1974 to 1976. The overall finding was that an immediate effect of fire depresses the densities of these two birds and so did long term exclusion of fire. They also found that birds markedly declined in densities when large areas were completely burned, compared to when maintaining a mosaic of habitats of fire and no fire. These results could explain why Red-winged Francolins have not increased at Ingula, despite increased protection (pers. obs). Ingula grasslands have mostly been annually burned from 2005 to 2013 under the new management. It is possible that a lack of habitat heterogeneity, resulting from burning the whole site year after year, depresses the population of this bird species.

The remaining five studies that examined the effects of fire alone on birds were from grasslands within the Savanna Biome (Dean 1987; Pons, Rakotobearison, & Wendenburg 2003; Mills 2004; O'Reilly *et al.* 2006; Bouwman & Hoffman 2007). It appears that all these were observational studies where fire was either set up to maximise cattle or game feed, or were run-away fires (Mills 2004). None of these studies manipulated fire with the goal of enhancing bird diversity or improving habitat suitability. Some of these studies were of short duration (Pons, Rakotobearison, & Wendenburg 2003; Mills 2004), while two other studies were carried out for two years (O'Reilly *et al.* 2006; Bouwman & Hoffman 2007). One study was for four years (Dean 1987).

Mills (2004) classified fires within the Kruger National Park, according to their severity, four to 10 days after fire. He subsequently surveyed and compared the densities of bird communities on burned patches to control patches where there had been no fire. The main results were that these habitats recover rapidly after fire compared to other fire-prone ecosystems and thus even severe fires do not affect bird populations significantly (Mills 2004).

Pons, Rakotobearison, & Wendenburg (2003) studied the response of birds to fire on a range of habitats within the Strict Nature Reserve in north-western Madagascar by comparing abundances on the day before and the day after fire. Their conclusion was that bird abundance in grassland fragments was similar before and after fire, despite the fact that fire resulted in differences when comparing un-wooded and wooded habitats and that unwooded habitats exhibited barer groundcover after fire. Furthermore, they found that there was a big contrast with continental Africa where Dean (1987) recorded 76 species responding positively to the immediate effects of fire. Although the study by Dean (1987) was for a much longer period (1979 to 1982), it was also on the immediate effects of fire during annual burns of fire breaks, blocks burns and runaway fires. Dean (1987) found that mainly insectivorous birds benefited due to an abundance of insects exposed by fire. Non-insectivorous birds declined.

Another study examined responses of the bird community at the Barberspan Nature Reserve in grassland patches that had not been burned for 10 years (Bouwman & Hoffman 2007). It was unclear whether burning was experimental or part of the managed block burn to remove accumulated litter. Species richness and densities increased immediately following fire but, five months after burning, the bird community again reflected the pre-burn period. This study reiterates the conclusions of Mentis & Bigalke (1981) that mosaic burning, with shifting large and small patches, should be considered on a landscape scale to benefit avian diversity. I did not find peer reviewed studies where grazing alone was used to create habitat suitability for birds within high-altitude grassland of eastern South Africa.

Malan (1998) investigated whether a decline in the breeding abundance of Helmeted Guineafowl *Numida meleagris* could be associated with lack of suitable habitat at Spioenkop Nature Reserve. Spioenkop Nature Reserve is at about the same altitude as Ingula and therefore would share some of the vegetation attributes of Ingula. The study measured vegetation and related habitat suitability to early summer breeding. They suggested that heavy summer grazing and winter burning reduces cover that birds needs to breed during early summer. Other factors associated with decline were intensive crop farming, which is often accompanied by the use of pesticides (Ratcliffe & Crowe 2001) and reduction in sheep farming. Helmeted Guineafowl are fairly common at farms bordering Ingula at the lower site but have not increased within the Ingula property, despite increased protection.

The number of studies examining grassland bird habitat selection has substantially increased in recent years (Cody 1981; Zimmerman 1992; Bollinger 1995; Bakker, Naugle, & Higgins 2002; Fisher & Davis 2010; Verón & Paruelo 2010). However, in South Africa the literature on factors that maintain bird habitat suitability or diversity within the moist, high-altitude grasslands is still scarce. The few studies that were conducted in this region focus on one or two species rather than on the community (Mentis & Bigalke 1981; Hockey *et al.* 1988; Jansen, Little, & Crowe 1999). Implementing management recommendations derived from single-species studies may not necessarily favour high bird diversity, however, because species with conflicting management requirements frequently co-exist (Maphisa *et al.* 2009). Nevertheless, all studies within this area (Mentis & Bigalke 1981; Jansen, Little, & Crowe 1999; Maphisa *et al.* 2009) and elsewhere within the grassland biome (Fuhlendorf, Engle, & Moreira 2004; Mills 2004; Fuhlendorf *et al.* 2006; O'Reilly *et al.* 2006; Haarmeyer *et al.* 2010; Nkwabi *et al.* 2011; Perlut & Strong 2011) point to fire and grazing as the key components for shaping grassland ecosystems. Parr & Chown (2003) suggested that at present the information on the effects of fire on fauna in southern Africa is fragmented and management decisions regarding the consequences of burning policies on the conservation of biodiversity both within and outside protected areas are still based on little evidence. It is therefore important to understand how fire and grazing interact to bring about habitat suitability for the targeted species or avian species richness or diversity (e.g. Fuhlendorf *et al.* 2009). A study by Fuhlendorf *et al.* (2009) made a suggestion that fire and grazing complement each other within a landscape to maintain the habitat mosaic.

RECOUPLING OF FIRE AND GRAZING HAVE POSITIVE EFFECTS ON BIRD SPECIES DIVERSITY

Out of four studies looking at the combination of fire and grazing in South African grasslands, three studies* were carried out close to Ingula. Of the three, the first studied the impact of grazing and burning on two species of francolins along the eastern Mpumalanga escarpment between 1 650 and 2 331m asl (Jansen, Little, & Crowe 1999). They surveyed nine sites that were grazed by cattle, sheep or game and found that Red-winged Francolins do not tolerate intense grazing or frequently burned sites. On the other hand, Grey-winged Francolin densities were positively correlated with grazing intensity across the study range.

Apparently, the study was carried out on farms where the primary reason for fire was to maximise livestock feeding and neither grazing pressure nor fire were experimentally manipulated. Their results are consistent with my observations from Ingula, where Red-winged Francolins are confined to near-forest margins, indicating that annual fires do have a negative impact on these birds that have not increased despite increased protection. On the other hand, the authors suggest that Grey-winged Francolins occur throughout the grazing gradient. Of the two species, Grey-winged Francolins do not co-occur at Ingula. I found Grey-winged Francolins occurring at much higher densities at the summit of the Thaba-Putsoa range in Lesotho at an altitude of 3 000m asl, where Red-winged Francolins did not occur (pers. obs). The Lesotho summit is communally owned and heavily grazed and annually burned.

Jansen, Little & Crowe (1999) also reported observations of 19 additional grassland species (five of which are listed as threatened) at their study sites, constituting a similar avifaunal community to the one at Ingula, with few exceptions. Their overall conclusion was that annual fires and heavy grazing are detrimental to birds, resulting in birds getting confined to isolated patches of pristine grasslands.

Maphisa *et al*. (2009) studied the impact of fire and grazing on two species of larks. This study was carried out on farms that are mostly annually burned and sometimes heavily grazed around the town of Wakkerstroom, within the moist, high-altitude grasslands of eastern Mpumalanga. The primary goal of this study was to understand the habitat requirements of the then 'Critically Endangered' Rudd's Lark *Heteromirafra rudii* (BirdLife International 2000). The equally scarce Botha's Lark *Spizocorys fringillaris* (BirdLife International 2000) was also recorded along the transects where Rudd's Lark was surveyed, as was a range of vegetation variables (see Maphisa *et al.* 2009). The authors concluded that mixed stock farming benefits Rudd's Lark and that late burning shorten the breeding this species. On the one hand Botha's Lark bred on either heavily grazed or recently burned grasslands early in the season.

Finally, Little, Hockey & Jansen (2013) studied a high-altitude grassland bird community around the town of Dullstroom. They compared plots on privately owned farms, stocked mainly with cattle, to plots inside Verloren Vallei Nature Reserve and on communally owned lands. They concluded that annual fires had a far more severe impact on birds, compared with grazing, in particular because late fires interrupt the breeding cycle of birds (also see Maphisa *et al.* 2009). Little, Hockey & Jansen (2013) did not record Rudd's Lark, even though their study was carried out in a former stronghold of this species (Allan 2001). Rudd's Lark, therefore, may have gone locally extinct in the area (BirdLife International 2014) and its disappearance is likely to be due to inappropriate grassland management within the Verloren Vallei Nature Reserve, which has been biennially block burned since 1985 (Little, Hockey & Jansen 2013) and possibly grazed with game rather than cattle. Game can have a more detrimental impact on both plant diversity and structure than do domestic livestock even at moderate grazing intensities (Little 2010). These findings have management implications for Ingula where it was suggested that cattle be replaced with game (Mentis 2006; Cauldwell 2012).

The last study out of the four coupling the effect of fire and burning on faunal diversity was carried out within the Savanna biome grasslands of Hluhluwe-iMfolozi Park. The authors identified two types of grasslands: short grass that was mainly grazed by game (particular mention is made of White Rhinoceros *Ceratotherium simum*) and grass in tall bunches that were frequently burned and had other vegetation mixed with the grass. Birds and vegetation were sampled on established transects. They were split into sites that were sampled from August 2003 for one year and additional sites both inside and outside the park that were surveyed only in January 2004. The burned sites, which were within the park, were surveyed from 10 to 20 days before burning and days ranging from three to 300 days after burning. The overall conclusion was that particular groups of birds tended to associate with particular types of grasslands, where birds' distribution tended to be influenced more by vegetation structure than by vegetation floristics. Types of birds that used grassland immediately after fire were replaced by other types of birds adapted to tall, rank grass a distance away from the period of burning.

FURTHER RELEVANT STUDIES ON MANAGING GRASSLANDS FOR PLANT OR ANIMAL DIVERSITY

Three peer-reviewed studies in Table 2 suggest that fire or grazing also bring about plant diversity in the eastern high-altitude grasslands of South Africa (O'Connor 2005; O'Connor *et al.* 2011; Uys, Bond & Everson 2004). Uys, Bond & Everson (2004) experimentally burned plots at five-year intervals to study plant species richness in arid, mesic and montane grasslands. The latter is at about the same altitude as Ingula. On comparing species richness between sites that were burned from autumn to winter and those burned in spring, they suggested that species richness seemed to peak at intermediate fire frequencies, while for sites that were burned in spring, species richness decreased with longer internals, with the latter habitat retaining unique grassland species. With respect to vegetation composition their findings revealed that all grass types showed resilience in the plant communities to fire the only exception being grass types that were not burned for a long time. They concluded that fire frequency in southern Africa has a comparable effect to that of Australia, in that fire frequency has little effect on plant species diversity, which they suggest contradicts the Intermediate Disturbance Hypothesis.

O'Connor (2005) studied the plant diversity of the southern Drakensberg (1 200 to 1 600m asl) across a land-use gradient, including communally owned fields, nature reserves, plantations, and commercial beef and dairy farms. Unexpectedly, communal maize fields and plantations supported more indigenous plant diversity than open grazed pastures, which were mostly invaded by kikuyu *Pennisetum clandestinum* and *Eragrostis carvula.* The explanation for this was that lack of herbicides and hoeing promoted indigenous grasses in cultivated areas, while plantations provided refuge for shade-tolerant indigenous plant species.

O'Connor *et al.* (2011) studied the impact of the cattle to sheep ratio on plant composition and grassland plant richness. This was done within long-term (1989 to 2005) experimental plots, where stocking density was recorded. Overall, increased stocking rates resulted in a high number of forbs and an increasing sheep to cattle ratio resulted in a decrease in the richness of forbs and of total species richness, which was attributed to selective grazing. Maphisa *et al*. (2009) found that farms grazed with cattle and sheep supported a higher density of Rudd's Lark and attributed this to selective grazing of sheep compared to cattle, and consequently created a mosaic of grass height and bare cover: sheep tend to forage on soft grasses and forbs.

The rest of the papers in Table 2 are the reviews and makes a connection between fire and grazing as management tools to bring about habitat heterogeneity for birds. Grazing and fire have been the most common disturbances amongst the grassland ecosystems worldwide for many centuries (Carilla, Aragón & Gurvich 2011). The Parr & Chown (2003) review examined the effects of fire and grazing on biological diversity in southern Africa. This review covers the use of fire in the region on a range of fauna including birds, invertebrates, mammals and reptiles.

The Parr & Chown (2003) review suggested that the relationship between fire and birds was complex and that the use of fire to maintain healthy populations must be carefully studied. The authors highlighted critical gaps in our understanding of how southern African bird species react to fire. Amongst their criticisms was that there have been few studies conducted on this subject in southern Africa. In these studies, focus is on individual species rather than the bird community as a whole. Secondly, study objectives of the use of fire on birds are not well defined. The studies were not well replicated to make generalisations and were mostly of short study duration, done on a small scale, with no distinction between experiments versus observational studies. Last but not least, and with suggestions, they pointed out that management information based on poor research information could have detrimental effects on fauna and biodiversity conservation within nature reserves and other habitats of priority conservation.

Parr & Andersen (2006) reviewed the operational definition and implementation of patch burning mosaics in savannas of southern Africa and Australia. The objective of patch-burning mosaics is to create a suite of habitats with the view that this would attract diversity of biota (also see Wilgen, Biggs & Potgieter 1998). Within the grasslands, habitat heterogeneity or habitat mosaic is also widely suggested as important for bird diversity and biodiversity in general (Tews *et al.* 2004; Uys, Bond & Everson 2004; Archibald *et al.* 2005; Fuhlendorf *et al.* 2006; Krook, Bond & Hockey 2007; Coppedge *et al.* 2008; Driscoll *et al.* 2010). In a global review of the role of fire on biodiversity under global change Bond, Woodward & Midgley (2005) suggest that ecologists must pay attention to the variable roles of fire across the landscape and its impact on biota.

IS HABITAT HETEROGENEITY GOOD FOR BIRDS?

The definition for habitat heterogeneity is variable (Fuhlendorf *et al*. 2001; Tews *et al*. 2004). Relevant to the subject on these reviews it means variability in habitat requirements that are brought about by management to suit variety of grassland birds' species (eg. Fuhlendorf *et al*. 2001). Reynolds *et al*. (2015) traced the origins of the term 'mosaic habitat' and found out that it is often equated to habitat heterogeneity and therefore loosely defined habitat mosaic as range of habitat types. Therefore understanding what habitat heterogeneity is and the context under which it is used is important for grassland habitat managers in the context of the subject of this review. It is also important how it can be created using appropriate management tools and how it can be measured.

Habitat heterogeneity is an important factor promoting bird species richness (Tews *et al.* 2004; Uys, Bond & Everson 2004; Archibald *et al.* 2005; Fuhlendorf *et al.* 2006; Hamer, Flather & Noon 2006). General agreement amongst the authors reviewed here is that fire and grazing (Fuhlendorf *et al.* 2009) are important management tools that could be used to bring about habitat heterogeneity (Jansen, Little & Crowe 1999; Pons, Rakotobearison & Wendenburg 2003; Coppedge *et al.* 2008; Little, Hockey & Jansen 2013). However, the relationship between fire and grazing, and their impact on fauna could be complex and, as a result, how these two factors are used must be well thought through by grassland ecologists (Parr & Chown 2003). As a result, how much heterogeneity is needed should largely be driven by management objectives and can be evaluated through experimentation. Within the moist, high-altitude grasslands, grass wields and dries up in winter, and the amount available during the following spring depends on the intensity of grazing during the preceding summer and autumn. If the grass is burned during spring to early summer, the amount of patchiness that fire causes depends not only on the fuel load present, but also upon the prevailing weather conditions during the time of burning. With a high fuel load, typically after little grazing, fires are hot. Hot fires kill grass tufts, resulting in bare patches during the following summer. To control the amount of patchiness, grassland managers should observe the fuel load and also weather conditions (particularly wind) before burning.

The amount of rainfall during the grass-growing season, which is from September to February at Ingula, affects how high but also how fast the grass grows. The stocking density and type of animals present will also determine patchiness and grass height. It is this mosaic of grass height and openness (habitat heterogeneity) that determines how and which birds make use of this habitat. The third, equally important element of this heterogeneity is the amount of dead and dry grass available.

The amount of dead and dry grass available early in the breeding season is important for nesting in several grassland species (Maphisa *et al.* 2009; Little, Hockey & Jansen 2013). Heterogeneous habitat increases the density of insects on which birds feed (Little, Hockey & Jansen 2013). Heterogeneity in habitat also provides cover for birds themselves, both to evade predators and to conceal their nests (Maphisa *et al.* 2009). In high-altitude grasslands, where many species are seasonal migrants, arrival at the breeding area is staggered (Berruti, Harrison & Navarro 1994). Habitat heterogeneity must therefore be maintained throughout the summer breeding months and into the winter to benefit birds that breed late.

Grassland managers wanting to maximise bird diversity can use fire and grazing to create habitat heterogeneity (Carilla, Aragón & Gurvich 2011). In the absence of natural fires and grazing by wild animals, domestic livestock and prescribed fire are increasingly regarded as important management tools to drive species diversity within the grassland biome. Inappropriate use of these two factors is, however, regarded as responsible for the loss and decline of species diversity within the grasslands (Pillsbury *et al.* 2011).

Grazing and fire are major forces shaping patterns of native and exotic species diversity in many types of grassland, yet both of these disturbances have notoriously variable effects (Harrison et al. 2003), (see Table 2 also). Considering the frequency and nature of fires, and the resultant drastic change in habitat following fire, research on the effects of fire on birds in the moist, high-altitude grasslands of South Africa is surprisingly rare (Bouwman & Hoffman 2007). Fire frequency drives faunal assemblage structure and abundance and, in most cases, overrides the effects of grazing at all taxonomic levels (Little, Hockey & Jansen 2013). The impact of either one or both factors (fire and grazing) is expected to differ with the type of region (Fuhlendorf, Engle & Moreira 2004) and the type of livestock. In shrub-invaded arid grassland, Valone & Kelt (1999) found that some plant communities benefit from fire and grazing while others do not. This is rarely measured because most grassland in South Africa is used for livestock production rather than to protect wildlife (see Van Niekerk et al. 2006).

The joint effects of fire and grazing on avifaunal diversity are better understood in North America than in South Africa (Fuhlendorf & Engle 2001; Fuhlendorf *et al.* 2006, 2009). In tall-grass prairie, disturbance, such as grazing and fire, can generate patchiness across the landscape, contributing to a shifting mosaic that enhances biodiversity (Fuhlendorf *et al.* 2006). Mosaic burning, with shifting large and small patches, should be considered on a landscape scale in South Africa (Bond & Archibald 2003; O'Reilly *et al.* 2006; Bouwman & Hoffman 2007; Krook, Bond & Hockey 2007). There are three important forms of grassland disturbance in South Africa worth reviewing: 1) annual fires, 2) heavy grazing and 3) no grazing. The same can probably be said of high-altitude grasslands in South Africa that are predominantly used for grazing and where both man-made and natural annual fires are a common occurrence. Research is needed to find grassland management practices that would bring about habitat heterogeneity. Fuhlendorf *et al*. (2006) suggested that management-driven reduction in heterogeneity may be partly responsible for declines in the numbers of grassland birds. Disturbance is an important component of many ecosystems, and variations in the disturbance regime can affect ecosystem and community structure and functioning (Hobbs & Huenneke 1992). Active management decisions must now be made on what disturbance regime is required, and this requires decisions on what species are to be encouraged and discouraged (Hobbs & Huenneke 1992). World-wide the need for heterogeneity also extends into habitats that have been modified for crop production (Benton et al. 2003) and therefore is maintained by other management tools other than fire and grazing (Valko *et al*. 2014).

CATTLE CAUSE EROSION: SHOULD CATTLE BE REPLACED WITH GAME?

In South Africa, grassland managers related grassland degradation to overgrazing and consider ungrazed grasslands as 'ideal veld' (Krook, Bond & Hockey 2007). In some areas, cattle and sheep have been replaced with game (*per obs*). Imposition of grazing animals (or different herbivores) on a system not previously grazed by such animals is likely to cause new form of disturbance and so does the removal livestock from the area which has long history of grazing (Hobbs & Huenneke 1992). The same can be said of suppression of fire. Fire suppression has been responsible for a habitat change to new open veld dominated successional shrubs (Cowling, Pierce & Moll 1986). Fire suppression has become a common practice in both government and privately-owned nature reserves where fires and cattle are seen as undesirable elements in South Africa. Mentis (2006) suggested replacing cattle with game at Ingula to halt the widespread erosion that resulted from many years of over grazing and cattle moving along paths to watering points or salt licks. However, there are beneficial effects of cattle grazing on bird diversity (Tichit *et al.* 2007; Metera *et al.* 2010). Moreover, grazing grassland with cattle also benefits plant diversity (Mcintyre, Heard & Martin 2003). Therefore a change from grazing with cattle to grazing with fenced game might bring a new disturbance (e.g. Hobbs & Huenneke 1992), that might not support plant or bird diversity. For Ingula, this information is important because management has objectives to restore habitats for birds and that plant diversity should also be retained. In South Africa, grassland birds have for many years coexisted with grazing by cattle and in some areas sheep after most angulate wildlife was confined to fenced areas. Research is needed to investigate how replacement of cattle with fenced game will affect the avifaunal use of these grasslands. Some studies suggested that grazing with a mixture of sheep and cattle creates a habitat mosaic and improves the breeding abundance of grassland birds (Evans *et al.* 2006; Maphisa *et al.* 2009).

IMPLICATIONS OF THIS REVIEW FOR MAXIMISING BIODIVERSITY AT INGULA

My review of the literature shows that fire and grazing, plays an important role in bringing about habitat suitability for different bird species and that these two factors used in combination compliments each other (e.g. Fuhlendorf *et al.* 2009). Fire is a key ecological process in several biomes worldwide (Parr & Chown 2003), however, the use of fire alone to enhance biological diversity or species richness must be used with caution at Ingula. Because of the high moisture content in the region, grass grows fast after burning and in the absence of controlled grazing; grass height and cover may soon become unsuitable for targeted species. In Particular, this would have negative impact on breeding birds by shortening the breeding duration in an area where summer breeding for majority of birds is fairly short. This review concludes that both fire and grazing have always played a critical role in enhancing biological diversity within the grassland ecosystem. However, the South African grassland biome is now critically threatened by human land-use change (e.g. Allan *et al.* 1997) and the little that remains in its natural state is highly fragmented and continues to be lost. Under the current situation, the use of natural fire or grazing by wildlife is no longer possible to enhance biological diversity. The replacement of cattle with game must be treated with caution in an area where birds are now adapted to breeding under disturbance created by livestock. However, adaptive management (Walters & Holling 1990) offers a room to experimentally test what form of game or even the density would create suitable habitat for birds.

Both fire and grazing are important factors that need to be taken into account when managing grassland habitat for bird diversity. Fire and grazing, if well managed, could complement one another to bring the desired heterogeneity that will attract different species of birds (Fuhlendorf *et al.* 2009). How management makes use of these two factors depends on the specific management goals. Through adaptive management followed by adaptive monitoring (e.g. Walters & Holling 1990; Walters 1997; Lindenmayer & Likens 2009; Keith *et al.* 2011), Ingula grassland management has the opportunity to experimentally study the effect of both fire and grazing to learn which management interventions maximise biodiversity. The new Ingula management has adaptive management as one of its goals (under preparation). Management needs to explicitly state the desired management goals, both over a short and a long period, so that the desired outcomes can be evaluated through adaptive monitoring.

For many birds species moist, high-altitude grasslands serve as summer breeding areas (Berruti, Harrison & Navarro 1994; Little, Hockey & Jansen 2013). As a result, the availability of suitable vegetation is particularly important in summer, when most species are present and breeding. Vegetation features are commonly correlated with grassland bird abundance, density, occurrence, and nest and territory selection (Fisher & Davis 2010). To understand the effects of management on bird diversity at Ingula, I therefore suggest that grass height, grass cover and the amount of dead grass be monitored, along with bird densities during the summer breeding season (e.g. Maphisa *et al.* 2009).

The primary responsibility of the Ingula Partnership, as set out in the Record of Decision, is to mitigate the loss of species in the area due to construction of the Ingula Pumped Storage Scheme. Whether the management will elect to conserve species diversity or focus on maintaining populations of selected species must be clearly stated in the management objectives. However, management is bound by the Record of Decision not to lose threatened species that already occurred in the area. Also, if management decides to focus on a few selected species so that the grassland can recover from the past deleterious management practices, management must be clear which other species are likely to be lost. Understanding the biology of some of the rare and important Ingula grassland bird species is also important. The consequences could be that when rare species are lost, they may not come back even when the grasslands are made suitable at a later stage, simply because they are also rare outside Ingula. The key to not losing any of the rare species would be a proactive management where habitat heterogeneity is encouraged during the grassland restoration phase. It is important that the current Ingula conservation management manage for grassland heterogeneity as described in the context of this review to accommodate species with variety of habitat needs. Mosaic of habitats across the landscape provides birds with areas to nest, search for food and also evade predators (Benton et al. 2003; Maphisa 2009). And more over some of this species could be altricial (e.g. Benton et al. 2003), requiring fairly short grass to breed. In the case of Ingula some of this are threatened and therefore a priority for conservation. Adaptive management (Parr & Chown 2003; Bakker & Doak 2009b), provides Ingula management alternatives on how to monitor the amount of heterogeneity to avoid losing of this key threatened species.

Bush encroachment can be a problem both under heavy grazing or no grazing (Birch, Vuichard & Werkmans 2000). Because of cold temperatures, Ingula habitats are not prone to perennial bush encroachment. However, one grassland invader of concern present at Ingula is Braken fern *Pteridium aquilinum*. It is one of the world's most aggressive grassland invaders, appearing in various plant communities, and an important characteristic is its ability to form dense patches and thereby replace local vegetation (Birch, Vuichard & Werkmans 2000; Cooper-Driver & Maphisa 2006). This species at Ingula is currently confined to within forest margins on steep slopes where animals do not graze well (pers. obs). Under the current exclusion of grazing, this plant is slowly invading into nearby grasslands, including the preferred stronghold of the threatened Yellow-breasted Pipit *Anthus chroris*. This bird is one of the threatened species that can be used as an indicator of grassland health. Birch, Vuichard

& Werkmans (2000) found that encroachment of *P. aquilinum* is linked to changes in grazing management of heaths during the last 200 to 300 years. Planned fire and grazing are needed within the moist, high-altitude grasslands to halt the invasion of grasslands by this cold-tolerant invader.

Based on this literature review, I conclude that grassland management can bring habitat heterogeneity for birds through controlled grazing and managed fire. How much heterogeneity is required depends on the management objectives. Management can influence bird habitat suitability by emulating the interaction between fire and grazing, which shapes the habitat on which birds depend (Fisher & Davis 2010)**.** Adaptive management provides a way to manage this system in an optimally, despite the current uncertainties around the precise effect of different management actions. In conservation biology and natural resource management, adaptive management or 'learning by doing' is an iterative process of improving management by reducing uncertainty via adaptive monitoring (Walters & Holling 1990; Keith *et al.* 2011; Runge 2011).

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Table 1. Studies that examined management tools used to enhance bird species' diversity with more emphasis on the grassland biome within southern Africa

Region	Research target	Tool	Impact	Authors	duration
Kruger NP - savanna	grassland birds	fire	insignificant	Millis 2004	4 weeks, 10 days after fire
Barberspan - savanna	grassland birds	fire	variable	Bouwman & Hoffman 2007	2 years
Northwestern Madagascar	birds & vegetation	fire	positive none	Pons et al 2003	day before and after fire
Mpala Kenya - savanna	birds	fire	significant	O'Reilly et al 2006	2 years after burn in 2003
Highmoor KZN*	2 francolin species	fire	negative	Mentis & Bigalke 1981	1975 - 1976, block burns
Nylsvley NR savanna	birds	fire	positive	Dean 1987	1979 to 1982
Hluhluwe-iMfolozi - savanna	birds assemblages	fire & grazing	mixed	Krook et al 2007	every 2 months for one year
Steenkampsberg*	2 francolin species	fire & grazing	variable	Jansen et al 1999	for 2 years (1995 & 1996)
Wakkerstroom, Mpumalanga*	2 small threatened birds	fire & grazing	conflicting	Maphisa et al 2009	summers 2003-4
Dullstroom, Mpumalanga*	birds & arthropods	fire & grazing	variable	Little et al 2013	2 year, summer study

Notes*:** Studies marked with ** were conducted within grassland of eastern South African of about the same area as Ingula the core of my study review.

Table 2. Other general papers/reviews on the use of fire and grazing as management tools

Focus	Region/type	Tool/type	Authors	comments
Fire regimes on plant diversity	Drakensberg - Cathedral Peak*	fire	Uys *et al*. 2004	forbs with low tolerance require less frequent fire
Plant diversity	Drakensberg*	grazing	O'Connor 2005	Infrequent burning promotes plant diversity
Forb diversity in grassland	Kokstad, KZN, South Africa*	grazing	O'Connor 2011	increase in cattle:sheep ratio increases forb diversity
Critique on use of fire	southern African grassland	review	Parr *et al*. 2003	Most studies were observational
Shortcomings of patch burning	South Africa & Australia	review	Parr & Andersen 2006	lack of operational guidelines on patch mosaic burning
Ecology and evolution of fire	general	review	Bond *et al*. 2005	ecologists must pay attention to variable role of fire
Conservation of grasslands	general	review	Bond *et al*. 2010	loss of bird species may indicate shift to forests
Impact of fire on biodiversity	general	review	Driscoll *et al*. 2010	Fire is as a management tool promotes biodiversity
Animal diversity	general	review	Tews *et al*. 2004	Habitat heterogeneity promotes animal diversity
Management of grassland birds	northern central Oklahoma, US	fire & grazing	Coppedge *et al*. 2008	Recoupling fire and grazing promotes birds diversity

Notes: studies marked with * are from eastern South Africa grasslands of about the same area as Ingula the cores of my study area. They investigate the effect of fire or grazing on plant diversity rather than bird diversity.

Chapter 3

> "Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galapagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats on the mainland."
>
> David Quammen from *The Song of a Dodo*

Drivers of bird species richness within moist high-altitude grasslands in eastern South Africa

Summary

1. Eastern, moist, high-altitude grasslands of South Africa harbour high avian species richness but new developments in the area have resulted in the loss of habitat for birds requiring conservation management.

2. The Ingula Pumped Storage Scheme is one such development that impacts a species-rich grassland area. Because of the predicted negative impact of the scheme on birds and habitat, additional land was bought and set aside to manage the area in a way that will offset the negative effects the scheme is likely to have on biodiversity and habitats.

3. To achieve this objective, management needs to identify, understand and manipulate key vegetation attributes to suit a variety of highly specialised bird species and methods to monitor the success of conservation actions in the face of increasing demand for land for development projects.

4. I collected bird occurrence data along transects, and recorded environment and habitat data between 2006 and 2010 along the same transects where birds were recorded. I used generalised linear mixed models and model selection, firstly to examine changes in vegetation since the new management took over and to estimate bird species

richness over time. Secondly, I examined avian species richness relative to recorded transect attributes to understand in more detail the effect of new management on bird species richness.

5. Grass cover decreased over the years. Transects that were burned showed a higher decrease in vegetation cover compared to transects that were not burned. Grass became higher over the years and was shorter after burning.

6. Seasonality was an important factor influencing bird species richness at Ingula, with summer recording the highest number of species compared to other seasons. There was an increase in bird species richness over time, with 2010 recording the highest number of species. Bird species richness, and the richness of grassland specialists, was much higher when the construction activities were low, compared to years when construction activities were high.

7. Key vegetation features (grass cover, height and dead grass) measured along transects did not correlate with avian species richness. I could not quantify the effects of burning and grazing on species richness because these factors could not be controlled experimentally. In addition effect of fire and grazing have different additive effects likely to affect species differently and that species richness is likely to response to habitat heterogeneity than grass height or cover directly.

8. *Synthesis and applications.* Because the majority of bird species are altitudinal migrants, management should pay particular attention to implementing actions that make the habitat suitable for breeding in summer. Management must use fire and grazing within experimental plots to monitor the impact of management on habitat and the effect on avian species richness. For future monitoring, the methods that take into account heterogeneity in species detection are recommended.

Key-words: Avifaunal species richness generalised linear mixed models, moist high-altitude grasslands, fire, grazing, vegetation cover and height.

Introduction

Worldwide, grasslands have undergone serious habitat loss and are in need of urgent protection (Hoekstra *et al.* 2004). In South Africa, loss of habitat is particularly concerning in the eastern, moist, high-altitude grasslands because the area harbours high avian endemism, including birds that are both nationally and globally threatened (e.g. Barnes 1998). Threats affecting the grassland birds in the area include land transformation due to agricultural activities and human settlement (e.g. Allan *et al.* 1997) but also inappropriate use of fire and grazing (e.g. Jansen, Little & Crowe 1999; Muchai & du Plessis 2005; Maphisa *et al.* 2009; Little, Hockey & Jansen 2013). New, more worrisome developments are the construction of pumped storage schemes and storage dams to store water for consumption. Because high-altitude areas are exposed and are characterised by high wind speeds (e.g. Drewitt & Langston 2006), they are also possible candidates for wind farms. With the current levels of habitat loss, conservation of birds (also other biota) is increasingly focused on identifying and managing key habitat vegetation attributes that sustain bird population (e.g. Fisher & Davis 2010; Johnson *et al.* 2010).

The new Eskom Ingula Pumped Storage Scheme, located within this high-altitude grassland region, is a prime example of the difficult balance between human land use and conservation. While the primary aim of the Ingula Pumped Storage Scheme (IPSC) is to have enough water to generate electricity, the Ingula Partnership has a secondary aim to mitigate the loss of biodiversity during the construction of the scheme and intends to maximise biodiversity after completion. To this end, during 2012, preparations were at an advanced stage to proclaim Ingula as a provincial nature reserve (Maphisa 2012). This requires the conservation management at Ingula to develop a long-term management plan and monitoring programme to offset ecological damage caused by the construction work, while maintaining ecological diversity of the area.

With the current increase in threats facing the moist, high-altitude grasslands (Allan *et al.* 1997; Drewitt & Langston 2006; O'Connor & Kuyler 2009) and in order to prioritise limited conservation resources to conduct effective conservation planning, a better understanding of avian species richness patterns and habitat suitability is needed (Culbert *et al.* 2012). Species richness is a subject of interest in monitoring programmes and is widely used as a biodiversity gauge to measure the effectiveness of management plans (Royle, Nichols & Kery 2005). Definitions and methods to measure species richness differ and are sometimes debated (Dorazio, Nichols & Aaron 2011), therefore it is important for managers to understand the strengths or weaknesses of the method used when monitoring species richness as a measure of how well conservation management objectives have been realised. In this chapter, I use bird occurrence data collected along transects to examine potential drivers of bird species richness at Ingula. I also explore the suitability of this method to inform the new grassland management on the success of grassland management intervention to increase the diversity of the study area.

Ingula is the site of the Eskom IPSC, constructed within a high-priority conservation area of the grasslands of eastern South Africa. In addition to the management offices that are located below the escarpment, the visible infrastructure consists of two water storage dams, with an altitudinal difference of 400m, located at the top and bottom of the escarpment. The main purpose is to generate hydro-electricity for the national grid during periods of peak consumption demand. Water is pumped back to the upper dam during low demand periods. The land surrounding the upper dam falls within an Important Bird Area (SA IBA 043) centred on the Bedford-Chatsworth Wetland (Barnes 1998). This wetland, and its surrounding grasslands, provide habitat for the three nationally threatened birds (i.e. within South Africa) ‘Critically Endangered’ species: Wattled Crane *Bugeranus carunculatus,* White-winged Flufftail *Sarothrura ayresi* and Rudd's Lark *Heteromirafra ruddi*. The global conservation status of the White-winged Flufftail was changed to Critically Endangered in 2013 (IUCN Red List 2013), one of two bird species in South Africa with this global red list status. Although the construction of the pumped storage scheme led to loss of part of this priority area for conservation, additional land was bought with the primary aim of increasing biodiversity in an area that was previously heavily grazed for commercial livestock production.

Here, I use vegetation and bird occurrence data collected along transects (e.g. Olivier & Wotherspoon 2006; Tsoar *et al.* 2007) to understand: (1) how habitat (grass cover and height) changed between the summers of 2006/07, 2007/08 and 2010/11, as the effects of the new management policies were implemented: (2) how bird species richness changed seasonally within years; (3) how bird species richness changed among the years; and (4) how bird species richness changed since the new management took over conservation of the site. I treat the first two summers as baseline data (construction activity high). During this period, the focus of the construction was on building the above-ground infrastructure (roads, quarries, dams and offices), whereas during the last year – referred to as post baseline (construction activity low) – the major construction work was underground, resulting in little direct disturbance from construction.

Materials and methods

STUDY SITE, BIRD AND VEGETATION SURVEYS

This study was conducted from summer of 2005/06 to 2010/11 between 1200 and 1700m asl on both slopes of the Ingula Pumped Storage Scheme (Fig. 2 Chapter 1). The topography at Ingula is rugged, and has an area of *c.* 8 000 ha falling within two of South Africa's provinces (KwaZulu-Natal and Free State), with an altitudinal drop of around 400m between the high-altitude grassland biome in the Free State (henceforth referred to as the upper site) and KwaZulu-Natal (lower site). The escarpment acts as the continental watershed and provincial boundary with the area on the upper site characterised by a series of streams, oxbow lakes and wetlands that eventually drain into the Wilge River, which is one of the headwaters of the Vaal and Orange Rivers. On the lower site, streams originating from the easterly-facing escarpment eventually drain into the Indian Ocean. The area above the escarpment is within the Bedford-Chatworth Important Bird Area (IBA SA 043) (Barnes 1998), the centre of which is the Bedford Wetland. About five per cent of this wetland was lost during the construction of the dam and associated intake tunnel (Braamhoek Partnership 2004). A tarred road linking the lower and the upper dam is largely confined to near the escarpment. To compensate for the lost area, large areas of the grassland and associated wetlands, which include the head waters of the Wilge River, were bought on the Free State site and set aside for conservation.

Following from the recommendations of impact assessment studies (Mentis 2006), cattle belonging to the commercial farmers were removed, leaving behind a few animals belonging to their tenants, with the plan of resettling them later. This was done so that the habitat could recover from a past history of heavy grazing and annual fires. Wide firebreaks were established on the site, so that controlled and planned block burns could be implemented before the next summer to encourage a mosaic of habitats, with a view that this would increase overall biodiversity. However, in spite of the planning, run-away fires occurred apparently due to arson, which burned almost the entire study site every year. Throughout my study, the tenants remained on the site so that the areas around their homes continued to be heavily grazed, while areas far away from the tenants remained largely ungrazed.

STUDY SITE VEGETATION

The vegetation at Ingula falls within three vegetation types (Mucina and Rutherford 2006). The upper site is dominated by both Sweet and Sour Grasslands, and was classified by Mucina & Rutherford as veld type GM 4 Eastern Free State Sandy Grasslands. The boundary slopes, which consist of dense and cool mountain forests, were classified as Gs 3 Low Escarpment Moist Grassland. The lower site was classified into Gs 4 Northern KwaZulu-Natal Moist Grasslands. Although this latter vegetation type is of no conservation value nationally, and has largely has been transformed into fields, it represents the upper limit of moist, high-altitude grasslands on the lower site because the boundary between KwaZulu-Natal and the Free State at places runs above the escarpment where GM 4 is a priority for conservation (Jewitt 2011).

WEATHER AND CLIMATE

The weather at Ingula is variable, with dry and cold winters and occasional snow. Strong directional winds emanating from mountain peaks of the Drakensberg result in the area being cool for most of the year. The highest wind bursts occur during late autumn to late spring. Temperatures fluctuate between an average daily maximum of +27°C in the hottest month (January) to an average daily minimum of −2°C in the coldest months (June and July) (Norström *et al.* 2009). Rainfall is orographic in nature, with most of it falling between November and March. Ingula receives ca. 1 400mm rain, while the nearest weather station, Bethlehem (28°15'S 28°20'E) 100km further west, receives *c.* 680mm annually (Bestelmeyer, Miller & Wiens 2003). A more accurate estimate of the rainfall at Ingula is 1 000mm (e.g. Mentis 2014), based on a weather station at Wyford Farm, which is about 20km from Ingula and lies between Harrismith and Ladysmith. However, despite the short distance between the upper and the lower site, there is sometimes a considerable difference in wind speeds, temperatures and precipitation between the two sites (Ingula Weather station unpublished data).

BIRD SAMPLING

Using 1:50 000 topographic maps, 35 random transects of length 500m were placed perpendicular to farm vehicle tracks (e.g. Maphisa *et al.* 2009) across the 8 000ha of Ingula, avoiding locations that were too rocky or too steep, and not placing more than one transect per kilometre of track. Of the 35 transects, seven were located at the lower site and 28 at the upper site. Birds were surveyed along three 50m bands to both sides of the transect, using the Bibby *et al.* (2000) strip transect method, once per season (winter: May, June and July, spring: August, September and October, summer: November, December and January, and autumn: February, March and April), between the summer of 2006/07 and the summer of 2008/09. Birds seen beyond 150m were not recorded. Seventeen of the 35 transects were surveyed again during 2010/11 after most of the above-ground construction had been finished. One transect was lost through construction at the top site, while five transects out of seven were lost due to construction at the lower site. The fixed-width strip transects method involves counting and identifying all bird species within a pre-determined distance of the line travelled. This is one of the most commonly used methods to estimate bird abundance, species habitat preferences and species richness for monitoring conservation programmes (e.g. Carrascal, Seoane & Palomino 2009). For this chapter, I converted the abundance data into presence/absence data (Carrascal, Seoane & Palomino 2009) but will make use of the abundance data in the next chapter. I carried out all surveys during early morning (07h00 – 11h00) or mid-afternoon (15h00 – 16h00), when birds are most active (Maphisa *et al.* 2009). No surveys were carried out under wet conditions or when visibility was impaired. The weather at Ingula is unpredictable and can change within a relatively short time.

MEASUREMENTS OF VEGETATION AND LAND COVER VARIABLES

Vegetation at each transect was surveyed in summer at the same time as the bird survey was done during the summers 2006/07, 2007/08 and 2010/11, using quadrat sampling (e.g. Maphisa *et al.* 2009). This method makes use of a steel frame of 30cm by 30cm, divided into nine equal squares. The frame was thrown randomly, twice every 100m along each of the 500m transects where a bird survey had been conducted earlier. In each quadrat, I recorded how many out of the nine squares fell on grass, bare soil, forbs or stones. I recorded grass height at each of the four corners of the frame at each sampling point, using a measuring tape. Intensity of grazing along each transect was categorised into light, medium or heavy, based on evidence of grass clipping by animals, rather than by openness or grass height. For each transect, I recorded whether it had been burned or not. The topography around each transect was categorised into four types (plateau top, shallow slope, steep slope or valley bottom).

Data analysis and statistical modelling

Grass height, cover and dead matter are the most frequently cited vegetation variables found to influence bird habitat suitability (Fisher & Davis 2010). These variables act together or independently to bring about habitat suitability for birds (Kneib, Knauer & Küchenhoff 2009). Since the new management took over, Ingula has been mostly annually burned and lightly grazed. First, I compared changes in grass cover and height over the three summers (2006/07, 2007/08 and 2010/11). Secondly, I analysed changes in grass cover between burned and unburned transects. And lastly, I investigated which transect attributes amongst years, burning, grazing and topography best explain changes in grass cover and grass height across the study period.

To examine patterns of bird species richness I compared the number of bird species detected per transect across the four seasons (summer, autumn, winter and spring). Then, using data from the summer surveys only, I also compared species richness during construction (construction activity high) and after construction (construction largely confined to underground). Finally, I examined changes in the number of typical grassland bird species, as grassland indicator species, during construction (activity high) and after construction (low).

All data analyses were carried out in R (R Development Core Team 2013) using generalised linear mixed effects models (GLMMs) through function lmer in package lme4 v 1.1-7 (Bates *et al.* 2014). I treated transect as random effect in all analyses to account for the repeated-measures nature of my data. Each analysis involved model selection using the Akaike Information Criterion (AIC) to rank the models, where the best fit-model has the lowest AIC within model set (e.g. Burnham & Anderson 2002, see also Anderson *et al.* 2001; Johnson & Omland 2004; Thiele 2012) where the best model has the lowest AIC

Firstly, I generated a set of six candidate models representing competing hypothesis about factors that could possibly explain variation in grass cover and height across transects in four years mainly based on my field observation on annual burning with relatively little grazing. The first model assumed that variation in grass height and cover is explained by transect only which I call a constant model. Other models considered fire alone, grazing alone and topography alone. The timing and amount of burning was variable every year and so I considered the model with year and fire.

I assumed a binomial distribution and logit link function for grass cover, which was measured as the number of grids – out of the total of nine – that were covered by grass (see Svensson *et al.* 2013 for a similar method). For grass height, I assumed normally distributed errors and used the identity link function. To reduce heteroscedasticy of the residuals, I log-transformed grass height before analysis. For each model I used transect as a random effect, grass cover or height as a response variable, and year of survey, burning, year, and topography (or in combination) as fixed effects.

Next, I wanted to know how total bird species richness and the number of grassland indicator species changed over the four seasons, across the three summer years, and during two stages of construction activities (construction activity high and construction activity low). Because the preliminary analysis above indicated that there were far more birds in summer compared to other seasons, I wanted to compare bird species richness during two phases of construction (construction activity low and construction activity high). And secondly based on the literature review grass height and cover are the key factors that determines habitat use by birds therefore I wanted to know how these two factors along with other transect attributes affect habitat use by birds. In this case because species richness was a count I assumed a Poisson distribution and log link function to model bird species count data (e.g Svensson *et al.* 2013).

To test the effect of construction activities on species richness, I generated a set of three candidate models to compare species richness during the two phases of construction (construction activities high or construction activity low). I assumed that high construction activities would negatively impact on species richness at the beginning to mid-construction (construction activity high) compared to towards the end of construction when disturbance was largely confined to underground construction (construction low). Together with these models I added a third model with no covariates (constant model) assuming that the only difference will be due to random effects of transects.

Finally, because my primary interest was on how transect attributes, especially grass height and cover affected bird species richness and these two variables could be influenced by grazing (none, light or heavy) or burning (burned or not burned) or both I generated nine candidate models bearing in mind that other transects attributes could also affect species richness. These are the amount of dead matter and topography which have the following levels; plateau top, shallow slope, steep slope or valley bottom. Finally, I added a model with no variables where species richness was determined only by transect random effects as the ninth model. I used my previous field knowledge (e.g. Maphisa *et al* 2009) plus Ingula field observations to determine whether to pair the model or treat them individually. For example, because Ingula was annually burned there was relatively little dead grass along transects resulting in a lot of zeros so that pairing dead grass with other variables could complicate the model output and so I treated the model with dead grass individually. I also avoided combining the model with grazing with other models given that there was relatively little grazing with one or two transects that lie adjacent to tenants being excessively heavily grazed.

Results

Ingula has a rich avifauna including regionally threatened endemics, globally threatened and important international migrants. Some of these species use the Ingula habitat in summer either to breed, feed or both (Appendix 1 provides an annotated species list). Two species, Sickle-winged Chat *Cercomela sinuata* and Sentinel Rock-Thrush *Monticola explorator*, visit Ingula during winter and migrate back to higher altitudes in summer. The Wattled Crane *Bugeranus carunculatus* which is considered 'Critically endangered' (e.g. Barnes 2000) breeds at Ingula between autumn and winter and moves out in summer as soon as its single chick is able to fly on its own.

CHANGES IN GRASS COVER AND HEIGHT DURING THE SURVEY PERIOD

There was a decrease in the amount of grass cover during the three years (2007/07, 2007/08 and 2010/11) (Fig. 1). Transects that had not been burned had denser cover compared to those that were burned (Fig 2). Model selection favoured the model that allowed grass cover to differ among years and between burned and unburned transects (Table 1). On the other hand, average grass height was slightly higher during 2010/11 compared to the other two summer surveys (Fig. 3). A combination of burning and year explained variation in average grass height better than any of the other candidate models (Table 2). Although less well supported by a wide margin, the second and third best models were models with grazing alone and fire alone.

COMPARING BIRD SPECIES RICHNESS ACROSS SEASONS AND YEARS

In total, 76 species were recorded across the 35 transects during three summers, two winters, two autumns and one spring. (Appendix 1). The list includes species that are not necessarily grassland birds but were seen feeding in the vicinity of transects during the survey. Out of 76 species, 10 were classified as nationally threatened (Barnes 1998). The five commonest species were Cape Longclaw *Macronyx capensis*, Wing-snapping Cisticola *Cisticola ayresii*, Banded Martin *Riparia cincta*, African Pipit *Anthus cinnamomeus* and African Quailfinch *Ortygospiza atricollis*, occurring respectively in 35, 33, 31, 29 and 22 of the 35 transects surveyed. The endemic and threatened Yellow-breasted Pipit was the 12th most common and widespread species recorded in all seasons in 16 out of 35 transects surveyed.

When comparing bird species richness across the four seasons, summer had a highest number of species, followed by autumn and then winter while spring had the least species richness at Ingula (Fig. 4). Summer is therefore the season during which Ingula supports most species. Looking at the summer records alone, bird species richness increased from the summer survey 2006/07 through summer 2007/08 and was the highest during the summer survey 2010/11 (Fig. 5). Comparing bird species richness at the height of construction (2006/07, 2007/08) against when construction activity was low (2010/11), the number of species was a little higher when construction activities were low compared to when high (Fig. 6) and the model comparing species richness between these two periods was better supported (Table 3) compared to the model allowing bird species richness to vary across all summer years, or the one that assumed constant species richness. There was a similar increase in the number of indicator species comparing the same period as above (Fig. 7).

RELATING BIRD SPECIES RICHNESS TO TRANSECT HABITAT

When analysing bird species richness in relation to the habitat (grass height, grass cover, intensity of grazing or whether transect was burned or not and the location of transect) the null model was selected as the best model (Table 4). I found no clear relationships between grass height, grass cover and the amount of dead grass (Fig. 8).

Discussion

In this chapter, I examined patterns of bird species richness at Ingula as the area experienced disturbance due to major construction activity and a marked change in management. Over time, grass became less dense and higher, and bird species richness increased. Nevertheless, I found no direct correlation between bird species richness and these habitat variables (see Fig 8). Percentage ground cover and vegetation height determine species richness in other grasslands (Fisher & Davis 2010). My results suggest that average grass height and cover do not directly correlate with species richness at Ingula, i.e. species richness does not clearly peak for any particular value of these habitat variables. One explanation for the lack of such a relationship could be that different species prefer different levels of grass cover and height. The results in table 2 and 4 support other findings that fire and grazing have additive effects that potentially affect species differently (Richardson *et al.* 2014). This results are supported by other studies that fire and grazing should be recoupled (Fuhlendorf 2009). One would then expect that heterogeneity is more important for species richness than average values. Unfortunately, fire and grazing were not under the control of management throughout this study and I could therefore not establish causal relationships between these management tools and habitat features. However, the increase in the amount of bare cover (Fig. 1) in the absence of cattle was likely due to an increase in hot fires under increased fuel loads. The near absence of dead grass in summer (Fig. 8), which is an important habitat feature for grassland birds, can also be attributed to annual burning.

The diversity of species found in this study is high for grasslands and includes a number of threatened species. My data therefore support the decision of designating the study area as an Important Bird Area (Barnes 1998). The observed increase in bird species richness – including a group of grassland specialists that I used as indicator species – between the period during the height of disturbance and the period when disturbance was low at the end of construction is encouraging. The observed increase in bare cover should be a concern for new management because it leads to an increased risk of erosion. In the absence of cattle, increased bare cover may be the result of hot fires.

HABITAT CHANGES UNDER NEW MANAGEMENT

The observed decrease in summer grass cover (Fig. 1) is unexpected because commercial livestock, which was thought to cause soil erosion and grassland degradation at Ingula (e.g. Mentis 2006), have been absent since the summer of 2006/07. In the absence of grazing, the observed increase in patchiness is likely related to hot fires that are fuelled by increased fuel load (e.g. Mentis 2006). In addition, most fires at Ingula occurred during strong winds, which are likely to exacerbate the effects of hot fires on grasslands. Just as hot fires result in patchiness, heavy grazing leads to patchiness, which could lead to forb invasion (Mentis 2006). Increasing bareness, together with protection from grazing, is likely to lead to dominance by fire-tolerant species, which would lead to lower plant species diversity (e.g. Belsky 1992). The few livestock that remained, which were owned by the tenants, did not result in heavy grazing. In particular, the entire upper site at Ingula was burned year after year since the new management took over, with most fires mostly blamed on. Despite these annual fires, I had the opportunity to compare transects that were not burned to those that were burned. In some years, burning happened in the middle of summer on transects that I had surveyed before they were burned. Mentis (2006) recommended a fire period of no less than two years. Because of annual fires it was not possible for me to compare these two types of management strategies (burned and not burned) and the impact on birds.

FACTORS THAT INFLUENCE SPECIES RICHNESS AT INGULA

Ingula is renowned for high avian diversity within the grassland biome (e.g. Barnes 1998). It is home to priority species for conservation (appendix), some of which are endemic within the region, some are charismatic and some are both. Because Ingula is located within mid-altitude it is characterised by cold winters and wet summers. As a result, season alone has a profound effect on species richness, where most species are local altitudinal to regional migrants. In summer, a number of long-distance migrants arrive from the Palearctic too (Berruti, Harrison & Navarro 1994) and add to an already increased species richness (Fig. 3). However, because Ingula lies at mid-altitude, there are also species that move from the Afromontane grasslands at higher altitudes to spend the winters at Ingula. The observed seasonal movement of species in and out of the study area can explain differences in species richness where summer recorded most species.

Since Ingula hosts most species during summer, management should use fire and grazing (e.g. Coppedge *et al.* 2008; Pillsbury *et al.* 2011) to make the habitat suitable for birds to breed in summer. This will also benefit additional species not encountered during the transect surveys because they are rare on site. Among the species not encountered during transect surveys are some that breed outside the summer months at Ingula, indicating that the management of grasslands should extend well beyond the summer months to promote suitable habitat for these species. For example, the critically endangered Wattled Crane, breeds from autumn to winter and produces one chick that fledges during early summer, after which the pair leaves the site with the chick and only returns for another breeding cycle. During its presence at Ingula, the pair feeds partly within the wetland, where it also breeds, but also partly on grassland bordering the wetlands. The study site can potentially harbour additional few more pairs given the extent of habitat available for the species to breed. Southern Bald Ibis and Blue Cranes feed in fairly short grass, which the latter species also uses as a preferred habitat to breed. In the years when fire occurs late and in the absence of grazing, the small colony of Southern Bald Ibis at Ingula delays breeding until the grass is burned.

There has been a slight increase in species richness between the summers 2006/07 and 2010/11, which was also true for indicator species. Ingula management implemented relatively large fire breaks in early winter. Even though ineffective at preventing run-away fires, these wide firebreaks, which were burned early, and other blocks remaining unburned until later in the season, provided alternative refuges for birds so that they did not leave Ingula altogether in the event of fire. However, as the entire property ended up burned, there was an absence of dry grass, of which the majority of grassland birds need to construct nests (Maphisa *et al.* 2009; Little, Hockey & Jansen 2013).

Indicator species include both threatened and charismatic species that the management would not like to lose and are therefore a priority for conservation. These include species requiring different management interventions because their habitat requirements sometimes differ. I also recorded species that are indicative of degraded grasslands. Examples are Red-capped Lark *Calandrella cinerea,* Crowned Lapwing *Vanellus coronatus* and Pied Starling *Spreo bicolor*. These species were largely confined to a few transects that lie in the neighbourhood of homesteads, the areas which were characterised by heavy grazing.

I found no correlation between bird species richness and habitat characteristics (Table 4 and Fig. 8) measured as grass cover and height. Percentage grass cover and vegetation grass height are the most important vegetation features correlated with bird habitat suitability (Fisher & Davis 2010). However, at Ingula, this did not translate into clear relationships between these habitat variables and species richness. If different species have different habitat requirements, one would not necessarily expect species richness to peak at a certain grass height and cover. Rather, habitat heterogeneity would be an important driver of species richness. The small amount of dead grass recorded along transects (Fig. 8) can also be associated with hot fires that burn everything. The presence of dead or dry grass during early summer enables birds to breed early (Maphisa *et al.* 2009; Little, Hockey & Jansen 2013) and improves their chances to replace lost clutches in the event of predation (Maphisa *et al.* 2009).

My results suggest that management can use fire and grazing to create a mosaic of grass heights and cover (e.g. Fuhlendorf, Engle & Moreira 2004) throughout the summer and sometimes beyond the summer, to make Ingula suitable for a variety of birds species. My observational study should be complemented with experimental plots to verify the cause effects of fire and grazing on grass cover and height, and further on bird species richness or habitat suitability (Parr & Chown 2003). Because of lack of control over fire and grazing at Ingula has the impact of vegetation structural features on bird species richness has not been demonstrated fully.

Monitoring the impact of management interventions on bird species richness is important. In order to understand how a system works, monitoring is needed. This improves the biological understanding on which active management of biological resources can be based (Nichols & Williams 2006). For the purposes of monitoring, Ingula management must be aware that there are several ways of measuring species richness, with different limitations (Dorazio, Nichols & Aaron 2011).

The analyses used in this chapter do not take account of the observation process, which can affect the results in important ways (Boulinier *et al.* 1998). In particular, I assumed constant detection probabilities across space and time. Although birds in general are relatively easy to find and identify, this is not the case with some of the grassland species, thus making it harder to ensure that detection probabilities remain constant. I believe that the problem is minimised in my case because I conducted all surveys myself and chose days with favourable conditions to carry them out. However, maintaining homogeneous detection probabilities when implementing these methods for long-term monitoring at Ingula will be challenging. In monitoring programmes and in ecological studies, species richness should be rigorously estimated whenever possible to avoid detection of spurious effects because of changes in species' detectability (Kéry & Schmid 2005). I therefore recommend that management at

Ingula use a method that accounts for the observation process when monitoring species richness in the future. The monitoring design could be improved by visiting each transect at least twice per season (e.g. Kéry *et al.* 2009). Owing to the size and topography of the study area, the unpredictable weather conditions and the fact that the census was done by one person, this was not possible for the present study.

Conclusion

Ingula is species rich and harbours avian species that are a priority for conservation. Even though controlled experiments were not possible, the results of my observational study provided insights into the mechanisms that drive bird species richness at Ingula. In the absence of cattle, the decrease in grass cover indicated the negative impact of intense fires on grassland structure. I suggest that management of Ingula grasslands and similar grasslands use controlled grazing and planned fires (e.g Fuhlendorf *et al*. 2009) to influence grass height and cover to benefit the variety of species (e.g. Richardson, Koper & White. 2009), if management wishes to maintain high avian species richness. I also suggest a suite of avian indicator species and surrogate species on which future monitoring could focus. Surrogate or indicator species are commonly used in conservation planning but they must be chosen cautiously to make sure they represent the desired set of species (Grantham *et al.* 2010b). The indicator species group may need to be adapted as more information becomes available also with a change of management objectives (e.g. Grantham *et al.* 2010a).

As is common practice in the field of community ecology and conservation biology, I used species richness expressed simply as a count of observed species in a given area. The major weakness of this approach is that it assumes equal detectability across space, time and species. This is likely violated for grassland species, where the detection probability could vary with habitat, weather conditions during the surveys and among species. However, the fact that all data were collected by one observer with a lot of experience in the area should have minimised the problem in the current analyses. Because monitoring is not supposed to be a once-off exercise (Lindenmayer, Piggott & Wintle 2013) and because future monitoring will be carried out by different people, and sometimes with more than one person at the time to increase the sample size, I do not recommend this method for monitoring at Ingula. In the next chapter I address the issue of equal detectability using the same data, and this time will account for imperfect detection (e.g. Dorazio *et al.* 2006) to examine patterns of density of selected bird species in relation to habitat, particularly grass height and cover.

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Table 1. Model selection analysis of grass cover in relation to year, burning, grazing and topography. The models were generalised linear mixed models assuming a binomial response and logit link function. Transect was treated as a random effect in all models. K represents number of parameters in each model, Delta AIC represents difference in AIC between the model with the lowest AIC value and the current model.

Models	**K**	**Log likelihood**	**Delta AIC**	**Akaike weight**
Constant	2	-2005.472	274.985	1.94E-60
Year	4	-1924.597	117.236	3.49E-26
Fire	3	-1928.588	123.219	1.75E-27
Year + fire	5	-1864.979	0	1
Grazing	4	-1996.930	261.903	1.34E-57
Topography	5	-2004.307	278.656	3.10E-61

Table 2. Model selection analysis of grass height in relation to year, burning, grazing and topography. The models were linear mixed models assuming a normally distributed response with grass height log-transformed. Transect was treated as a random effect in all models. K is the number of parameters in the model and Delta AIC is the differences in AICs.

Models	**K**	**Log likelihood**	**Delta AIC**	**Akaike weight**
constant	3	-913.67	179.38	1.10E-39
Year	5	-902.17	160.38	1.50E-35
Fire	4	-1928.59	155.69	1.60E-34
year + fire	6	-820.98	0	1
Grazing	5	-857.67	71.377	3.20E-16
Topography	6	-911.59	181.228	4.40E-40

Table 3. Model selection analysis comparing bird species richness during summer across the years 2006/7, 2007/8 and 2010/11, when construction activities were high (2006, 2007 & 2008) with construction activities low (2010/11) and the model where all parameters were held constant. The models were generalised linear mixed models assuming a Poisson response and log link function. Transect was treated as a random effect in all models. K represents the number of parameters in a model, Delta AIC is the differences in AICs.

Models	**K**	**Log likelihood**	**Delta AIC**	**Akaike weight**
All years different	5	-196.86	3.53	0.12
Construction high & low	3	-197.1	0	0.73
Constant	2	-199.69	3.18	0.15

Table 4. Model selection analysis relating bird species richness in summer to grass cover (m.cover), grass height (m.avh), dead matter (m.dead), fire (m.fire), grazing (m.Graz), cover grass cover plus grass height (m.cover_avh), grass cover plus fire (m.cover_Burn) and transect topography (m.Topo). The models were generalised linear mixed models assuming a Poisson response and log link function. Transect was treated as a random effect in all models. K is the number of parameters in a model, Delta AIC is the differences in AICs.

Models	**K**	**Log likelihood**	**Delta AIC**	**Akaike weight**
Constant	2	-151.31	0	0.27
m.cover	3	-151.08	1.53	0.13
m.avh	3	-150.97	1.31	0.14
m.cover.avh	4	-150.95	3.27	0.05
m.Burn	3	-151.22	1.82	0.11
m.cover.Burn	4	-150.88	3.14	0.06
m.Graz	4	-150.67	2.71	0.07
m.dead	3	-151.27	1.91	0.10
m.Topo	5	-149.74	2.85	0.07

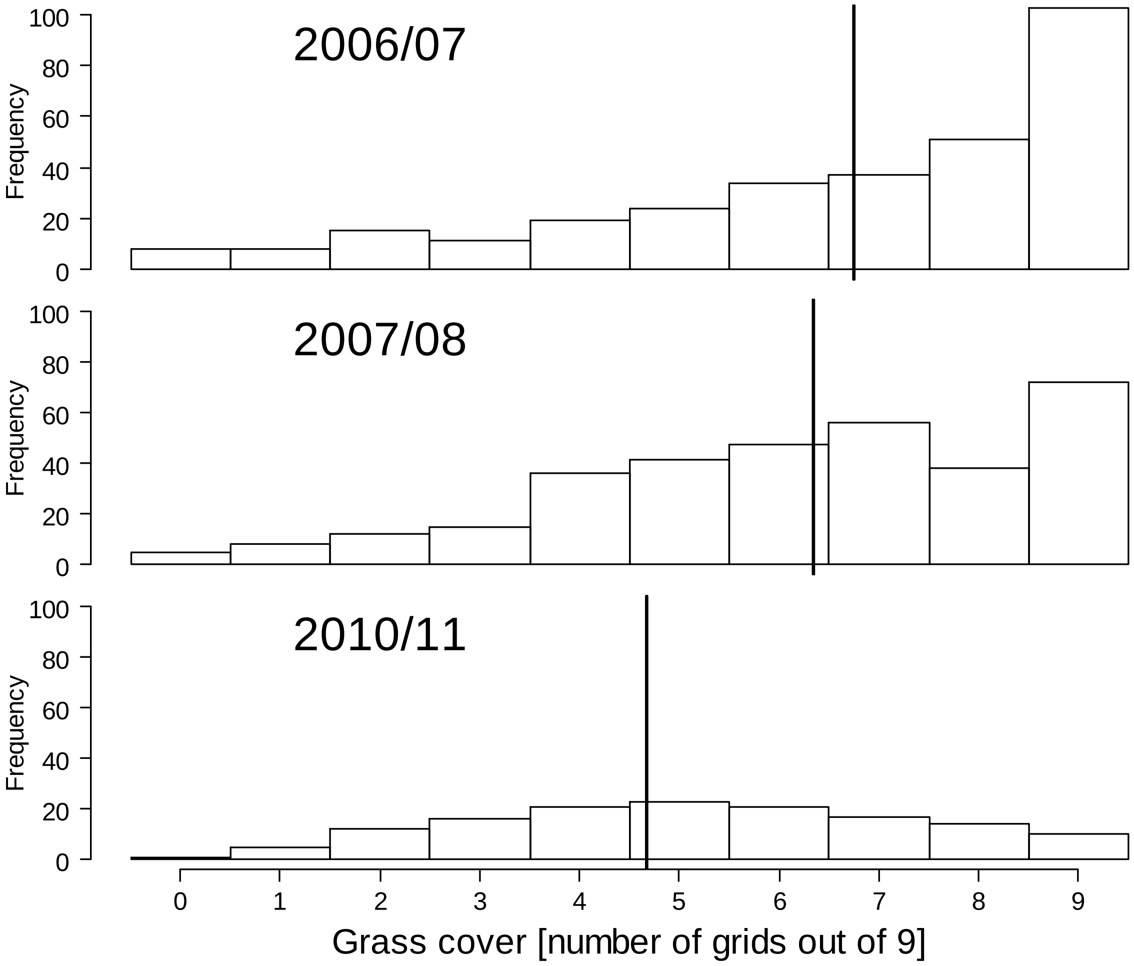

Fig. 1. Comparison of grass cover at Ingula over the three years of surveying. The vertical black solid line represents the mean according to the best model and the histograms show the distribution of the raw data. The data consisted of the count out of nine squares in each sampling grid that fell on grass.

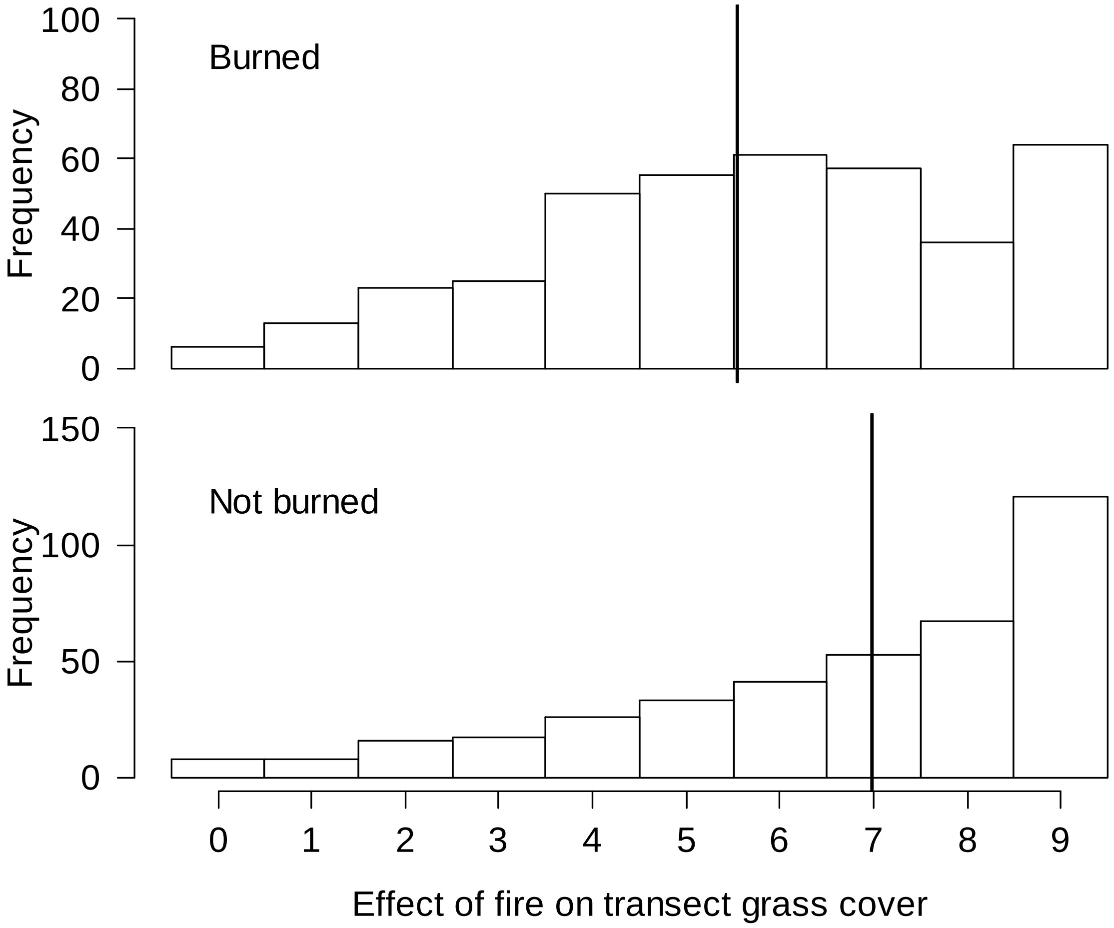

Fig. 2. Comparison of influence of fire on grass cover along transects that were burned and those that were not burned at Ingula using summer data for three years (2006/7, 2007/08 and 2010/11). **Bold** vertical lines show the estimated means.

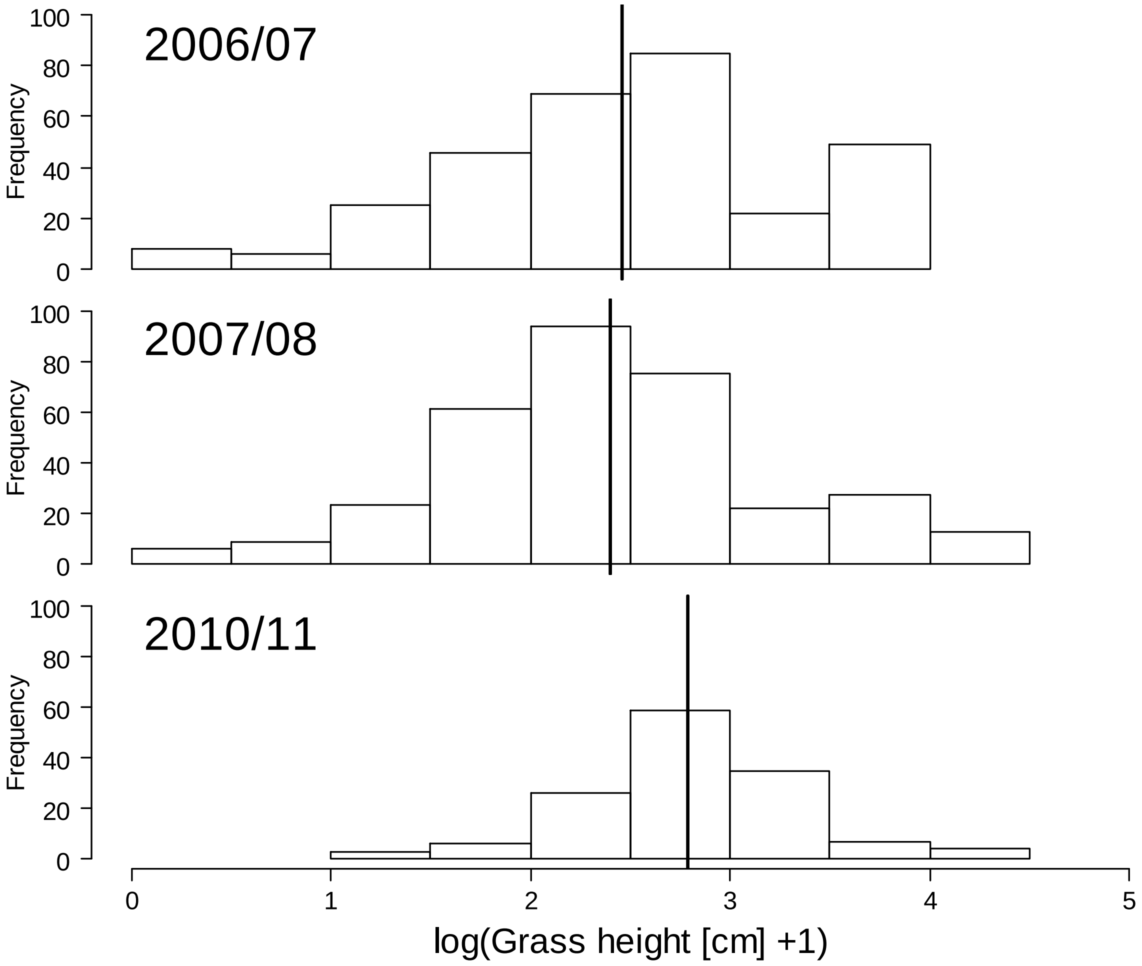

Fig. 3. Comparison of grass height during the three summers of survey at Ingula (2006/07, 2007/08 and 2010/11). **Bold** vertical lines represents the sample means.

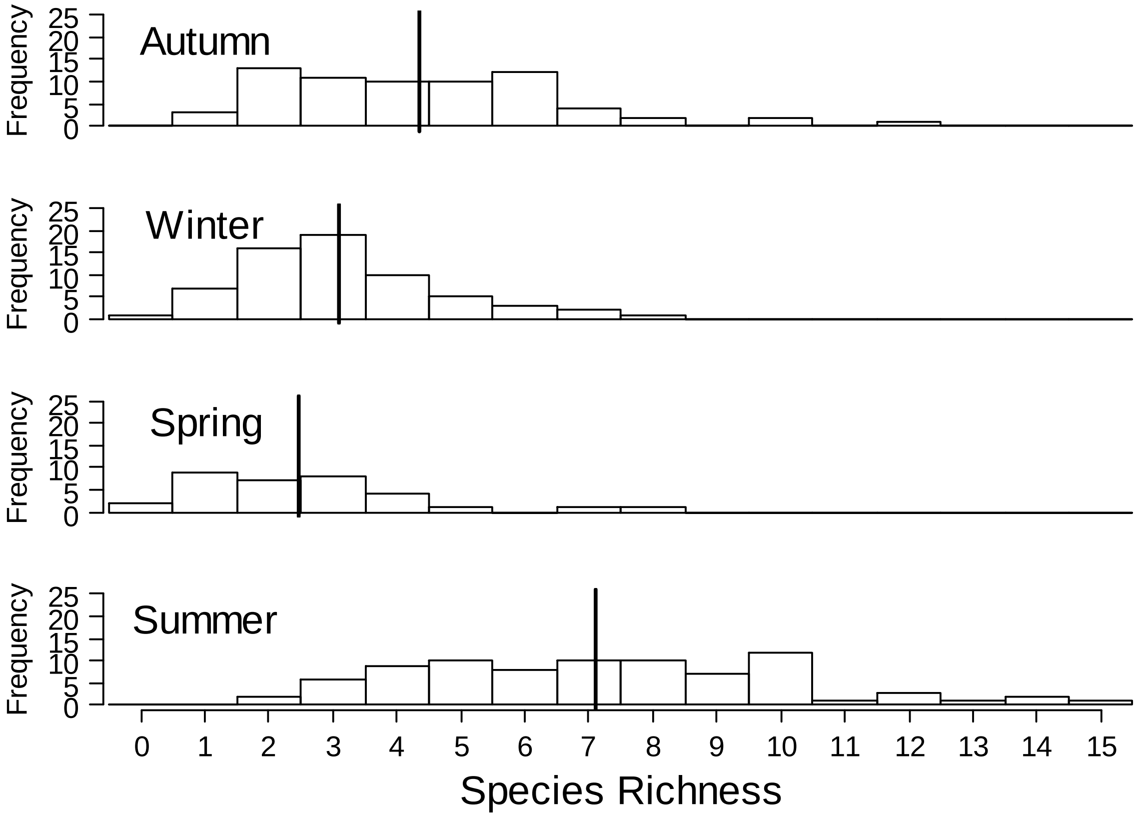

Fig. 4. Comparison of Ingula bird species richness across the four seasons using transect data collected between 2006/07 to 2010/11. The data come from three summers, two autumns, two winters and one spring survey and only half the total number of transects were surveyed during summer 2010/11. Vertical lines show the means.

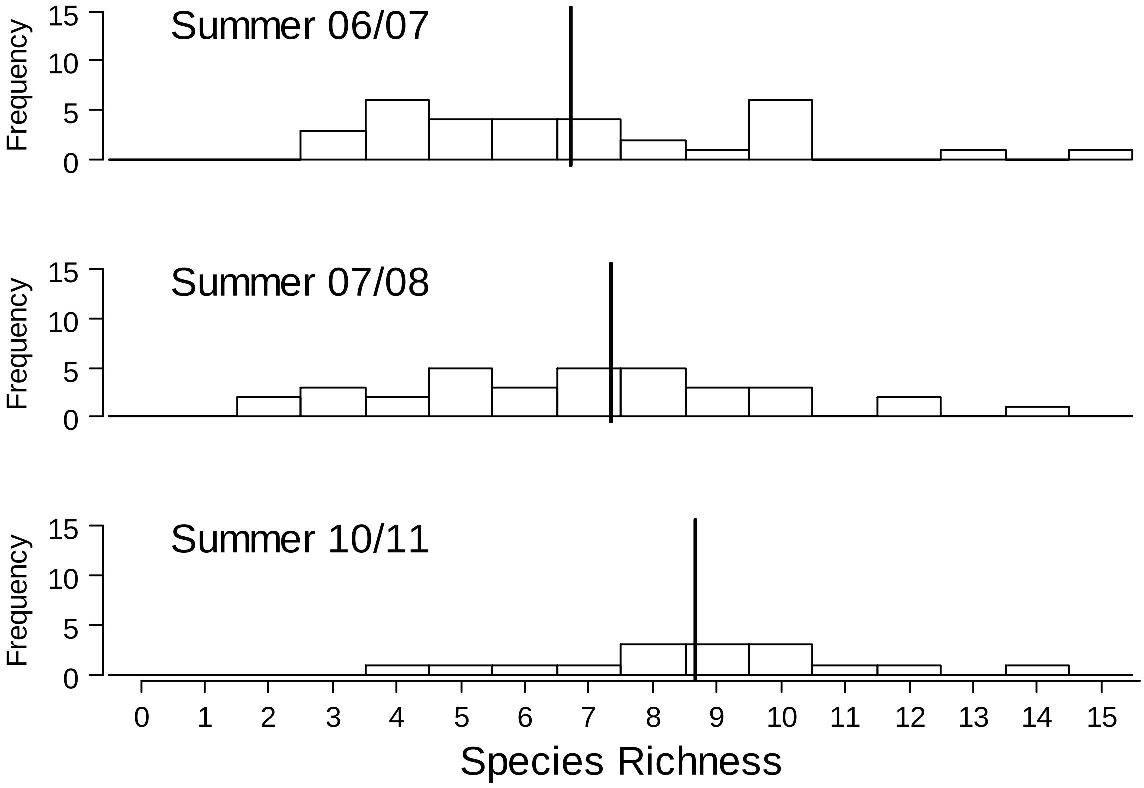

Fig. 5. Comparison of bird species richness at Ingula using data from summer surveys only. **Bold** bars represent the means.

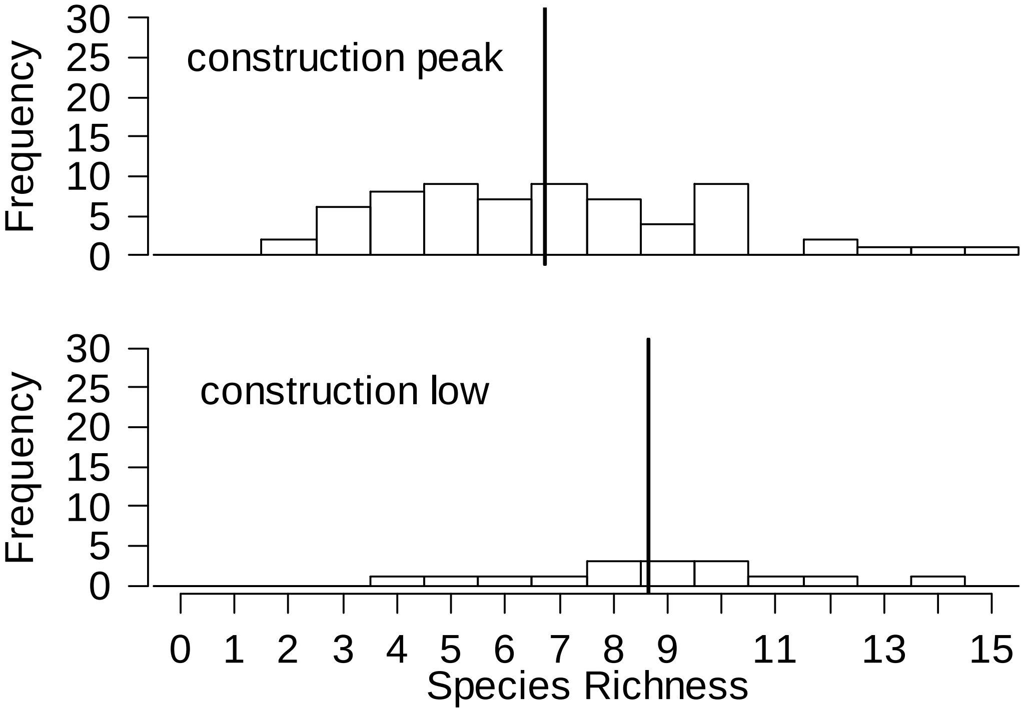

Fig. 6. Comparison of bird species richness when construction activities were high (peak) (summers 2006/07, 2007/08) compared to when construction activities were low (summer 2010/11 only). Vertical **bold** bars represent the means.

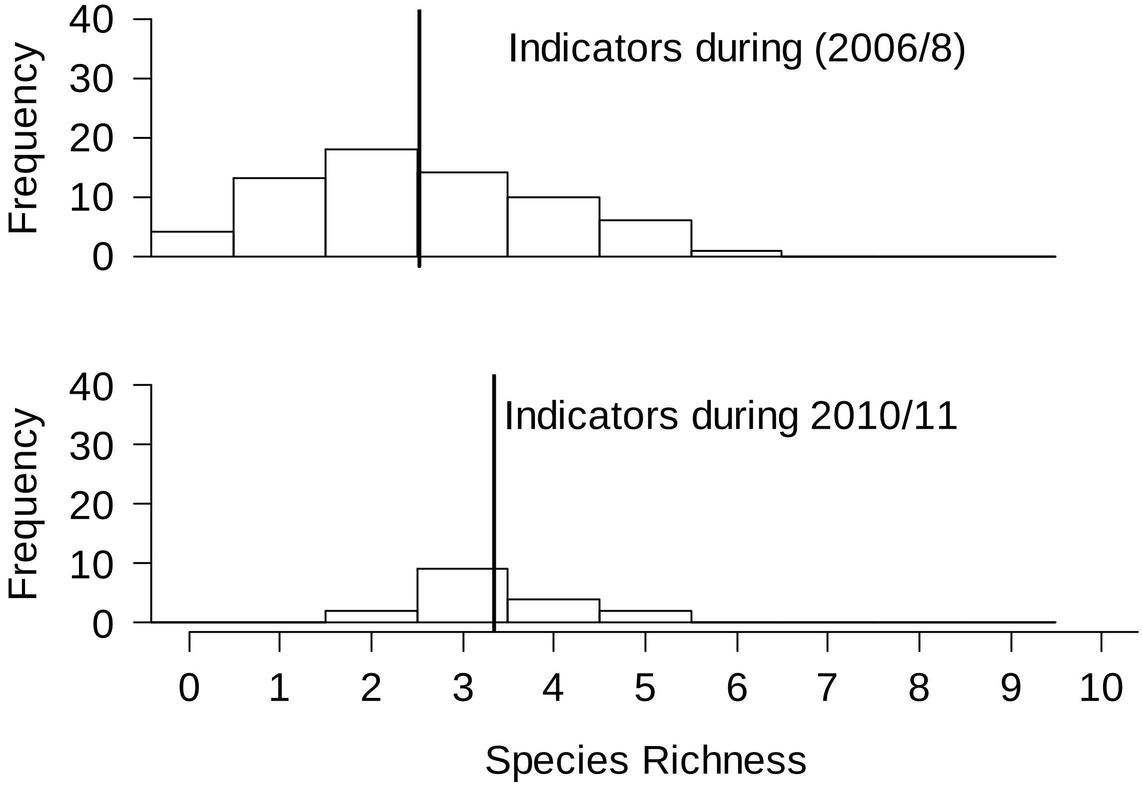

Fig. 7. Comparison of indicator bird species richness at Ingula during the first two summers (2006/07 and 2007/08) compared to the last year (summer 2010/11). **Bold** vertical bars represent the means.

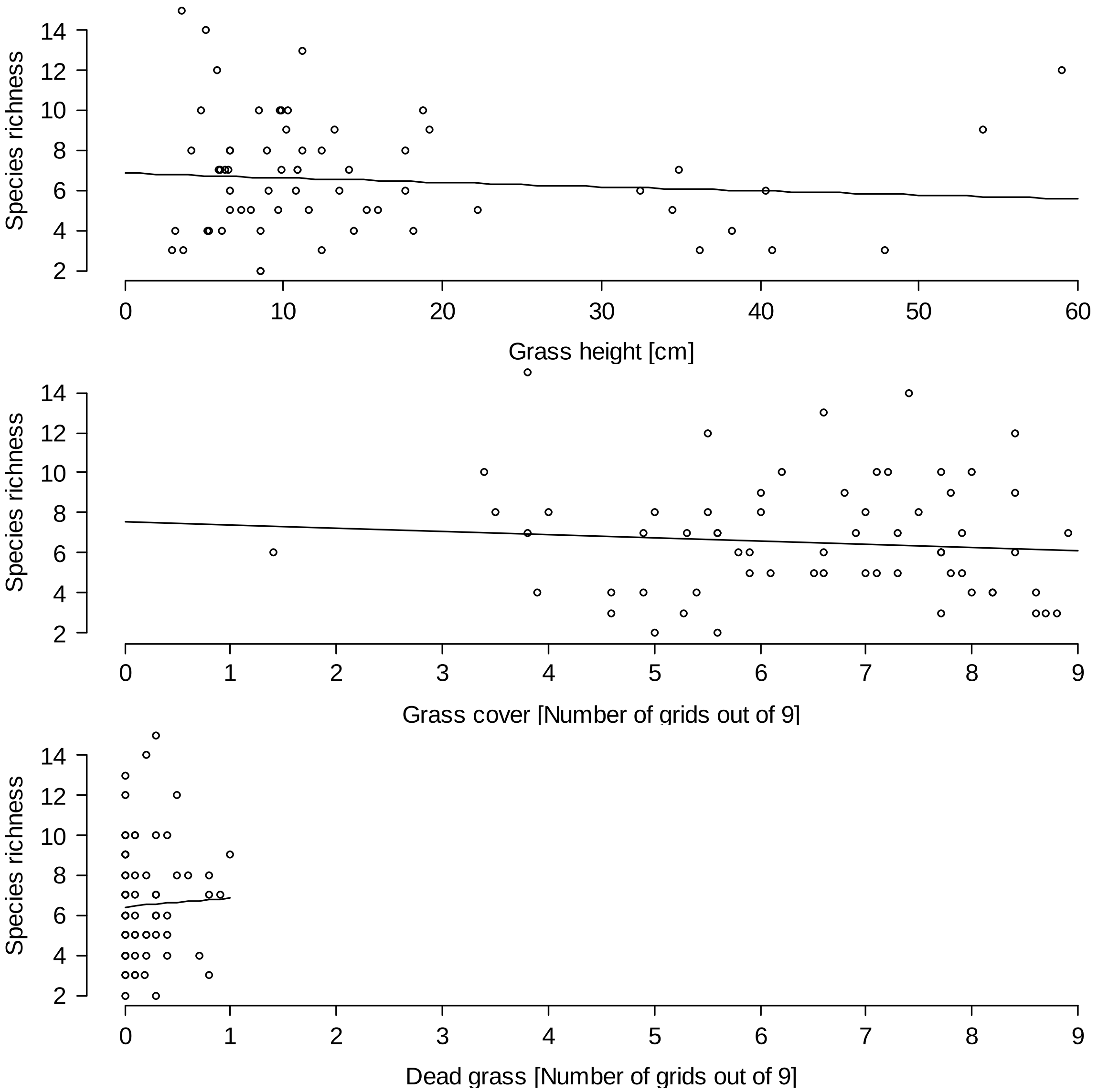

Fig. 8. Response of birds species richness to grass height, cover and presence of dead grass along transect during the three summer surveys (2006/07, 2007/08 & 2010/11) at Ingula.

Appendix 1: Grasslands birds seen during transect surveys between 2006 and 2011. Some bird species in the list do not qualify as typical grassland birds but were using grasslands at the time of survey. Some transects at the lower study site were close to bushes, while others have lone bushes that provided perches for birds that would otherwise not use grasslands. National Red List status is according to Barnes (2000). Type: 'indicator' are species typical for these grasslands. They should be the focus of management. 'Unimportant' are wide-ranging species and 'negative' are species that are indicative of undesirable habitat features in grassland.

Species	Scientific name	National Red List status	Habitat comments	Type
Bishop, Southern Red	*Euplectes orix*	-	Confined to moist rank grass	Unimportant
Bishop, Yellow-crowned	*Euplectes afer*	-	Confined to moist rank grass	Unimportant
Bokmakierie	*Telophorus zeylonus*	-	Transects with bushes	Unimportant
Bulbul, Dark-capped	*Pycnonotus tricolor*	-	Transects with bushes	Unimportant
Bustard, Denham's	***Neotis denhami***	**Vulnerable, non-endemic**	Prefers hilltops	Indicator
Buzzard, Jackal	*Buteo rufofuscus*	-	Feeds on grass rodents	Indicator
Canary, Black-throated	*Crithagra atrogularis*	-	Transects with bushes	Unimportant
Canary, Cape	*Serinus canicollis*	-	Transects with bushes	Unimportant
Chat, Ant-eating	*Myrmecocichla formicivora*	-	Confined to within Aardvark holes	Unimportant
Chat, Sickle-winged	***Cercomela sinuata***	**Endemic**	Rare winter visitor	Unimportant
Cisticola, Cloud	*Cisticola textrix*	-	Confined to plateau tops	Unimportant
Cisticola, Lazy	*Cisticola aberrans*	-	Confined to grass with rocks	Unimportant
Cisticola, Levaillant's	*Cisticola tinniens*	-	Confined to moist rank grass	Unimportant
Cisticola, Pale-crowned	*Cisticola aridulus*	-	Confined to moist rank grass	Unimportant
Cisticola, Wing-snapping	*Cisticola ayrresii*	-	Almost everywhere	Unimportant
Cisticola, Zitting	*Cisticola juncidis*	-	Plateau tops with tall grass	Indicator
Crane, Blue	***Grus paradise***	**Vulnerable, non-endemic**	Early breeder on fairly short grass	Indicator
Crane, Grey Crowned	***Balearica regulorum***	**Vulnerable, non-endemic**	Grasslands near wetlands	Indicator
Crane, Wattled	***Grus carunculatus***	**Critical, non-endemic**	Grasslands near wetlands	Indicator
Crow, Cape	*Corvus capensis*	-	Almost everywhere	Unimportant

Crow, Pied	*Corvus albus*	-	Almost everywhere	Unimportant
Dove, Red-eyed	*Streptopelia semitorquata*	-	Transects with bushes	Unimportant
Eagle, Martial	*Polemaetus bellicosus*	-	Transects near escarpment	Indicator
Egret, Cattle	*Bubulcus ibis*	-	Grasslands with cattle	Unimportant
Falcon, Amur	*Falco amurensis*	-	Grasslands with cattle	Indicator
Fiscal, Common	*Lanius collaris*	-	Transects with bushes	Unimportant
Francolin, Red-winged	*Scleroptila africanus*	-	Unburned grasslands	Indicator
Guineafowl, Helmeted	*Numida meleagris*	-	Grasslands with fields	Unimportant
Harrier, Black	***Circus maurus***	**Endemic**	Grasslands in summer	Indicator
Harrier, Montagu	*Circus macrourus*	-	Grasslands in summer	Unimportant
Heron, Black-headed	*Ardea menalocepha*	-	Wet, rank grasses	Indicator
Heron, Grey	*Ardea cinerea*	-	Wet, rank grasses	Indicator
Ibis, Southern Bald	***Geronticus calvus***	**Vulnerable, endemic**	Breeds early, fairly short grass	Indicator
Kestrel, Rock	*Falco rupicolus*	-	Transects with rocks	Unimportant
Kite, Black-shoudered	*Elanus caeruleus*	-	Transects near fields	Unimportant
Korhaan, White-bellied	***Eupodotus senegalensis***	**Vulnerable**	Breeds late on fairly short grass	Indicator
Lapwing, African Wattled	*Vannelus senegallus*	-	Breeds early on fairly short grass	Unimportant
Lapwing, Blacksmith	*Vanellus armatus*	-	Breeds early, confined to near water	Negative
Lapwing, Black-winged	***Vanellus melanopterus***	**Near-threatened, non-endemic**	Vagrant, breeds early on fairly short grass	Negative
Lapwing, Crowned	*Vanellus coronatus*	-	Breed early on fairly short grass	Negative
Lark, Eastern Long-billed	*Certhilauda semitorquata*	-	Confined to transects with rocks	Unimportant
Lark, Pink-billed	*Spizocorys conirostris*	-	Rare, modified grasses	Unimportant
Lark, Red-capped	*Calandrella cinerea*	-	Breeds early on fairly short grass	Negative
Lark, Rufous-naped	*Mirafra africana*	-	Lower study site with rank grass	Unimportant
Marsh-Harrier, African	***Circus ranivorus***	**Vulnerable, non-endemic**	Grasslands near wetlands	Indicator

Martin, Banded	*Riparia cincta*	-	Prefers lightly grazed grasses	Unimportant
Owl, African Marsh	*Asio capensis*	-	Confined to wet grasslands	Indicator
Pipit, African	*Anthus cinnamomeus*	-	Grasslands with livestock	Indicator
Pipit, Plain-backed	*Anthus leucophruys*	-	Almost everywhere, only after fire	Unimportant
Pipit ,Yellow-breasted	*Anthus chloris*	-	Sedentary, confined to hilltops	Indicator
Prinia, Drakensberg	***Prinia hypoxantha***	**Endemic**	Transects with bushes	Unimportant
Quail, Common	*Coturnix coturnix*	-	Summer visitor, although some birds may stay	Indicator
Quailfinch, African	*Ortygospiza attricollis*	-	Prefers modified or open grasses	Indicator
Quelea, Red-billed	*Quelea quelea*	-	Transects with bushes	Unimportant
Raven, White-necked	*Corvus albicollis*	-	Rarely predates ground birds	Unimportant
Robin-Chat, Cape	*Cossypha caffra*	-	Transects with bushes	Unimportant
Rock-Thrush, Sentinel	*Montocola explorator*	-	Winter visitor	Unimportant
Rush-Warbler, Little	*Bradypterus baboecala*	-	Confined to wet grasslands	Unimportant
Secretarybird	***Sagittarius serpentarius***	**Near-threatened**	Prefers tall, rank grasses	Indicator
Snipe, African	*Gallinago media*	-	Confined to wet grasslands	Indicator
Spurfowl, Swainson's	*Pternistis afer*	-	Confined to modified grasslands	Unimportant
Starling, Pied	*Spreo bicolor*	-	Early breeder on erosion gullies	Negative
Starling, Red-winged	*Onychognathus nabouroup*	-	Transects with bushes	Unimportant
Stonechat, African	*Saxicola torquatus*	-	Grasslands with forbs for perching	Unimportant
Stork, White	*Ciconia ciconia*	-	Summer visitor: few birds show after winter	Unimportant
Sunbird, Malachite	*Nectarinia famosa*	-	Transects with flowering plants	Unimportant
Vulture, Cape	***Gyps coprotheres***	**Vulnerable, near endemic**	Large flocks feed on dead animals	Unimportant
Wagtail, Cape	*Motacilla capensis*	-	Confined to wet grasslands	Unimportant
Waxbill, Common	*Estrilda astrild*	-	Tall, rank grasslands	Unimportant
Wheatear, Mountain	*Oenanthe monticola*	-	Confined to transects with rocks	Unimportant
Widowbird, Fan-tailed	*Euplectes axillaris*	-	Confined to tall, rank grasslands	Unimportant

Widowbird, Long-tailed	*Euplectes progne*	-	Confined to tall, rank grasslands	Unimportant
Buzzard, Steppe	*Buteo vulpinus*		Summer visitor	Unimportant
Widowbird, White-winged	*Euplectes albonotatus*	-	Confined to tall, rank grasslands	Unimportant

Chapter 4

> Small islands are central to the matter of species extinctions, just as species extinction is central to the question of how *Homo sapiens* affects its own world… recognising and understanding that phenomenon is the best route towards understanding our present crisis of extinctions on the mainland.
>
> David Quammen, *The Song of a Dodo*

Factors affecting densities of eight common grassland breeding birds: implications for management

Summary

1. Understanding habitat factors that determine animal densities is important for conservation where the goal is often to maintain stable populations of particular species. Recent methodological developments in distance-sampling techniques make it possible to examine densities of animals in relation to environmental drivers in a statistically rigorous way.
2. Densities of grassland birds are particularly difficult to estimate because these animals are often difficult to detect. There is therefore little information on what drives densities of grassland bird species. In particular, there are no statistically robust density estimates for moist, high-altitude grasslands of eastern South Africa in relation to habitat features that could be influenced by management.
3. Data collected on birds, environment and habitat from the summers of 2006/07, 2007/08 and 2010/11 were used to estimate the density and habitat selection of the eight commonest small grassland bird species at Ingula. I used hierarchical distance sampling methods to estimate densities in relation to season, burning, grazing, grass height and grass cover. The latter two are deemed to be critical habitat variables that determine the niches of grassland bird species and I used regression splines within the distance sampling models to examine their effect on density in detail.

4. Grass height and cover were the most important predictors of density in the species examined, supporting previous studies that grass height and cover are the most important habitat features that managers should manipulate to increase the density of target species. The regression splines showed that the effect of these two habitat variables was well described by linear relationships for most species. The densities of African Pipit, Yellow-breasted Pipit, Red-capped Lark and Common Quail decreased with increasing grass height. African Quailfinch densities decreased with increasing grass cover. Cape Longclaw and Zitting Cisticola densities increased with increasing grass height.
5. This study suggests that grazing and fire are important tools that management can manipulate to create a habitat mosaic of grass height and cover that would support high densities of desired species.
6. *Synthesis and applications*. I found that grass height and cover are two important habitat variables that structure the niches of eight grassland bird species. Since common species are the main drivers of species richness, my results suggest that management should aim to provide heterogeneity in grass cover and height to provide habitat that supports a high diversity of grassland species, including the rare species.

Key-words: conservation priority in grassland, density and detection, grassland birds, grass height and cover, hierarchical distance sampling models

Introduction

Grasslands are one of the most threatened biomes in southern Africa, with 23% under cultivation, 60% irreversibly transformed, 2% formally protected, and most of the remaining natural area used as rangeland for livestock (Fairbanks *et al.* 2000; Reyers 2001; O'Connor & Kuyler 2009). An assessment of conservation priorities in the Grassland Biome in southern Africa identified some 36.7% of the biome as being important for biodiversity conservation (Egoh *et al.* 2011). In particular, South Africa's moist grassland harbours globally significant biodiversity, supplies essential ecosystem services, and supports crop and livestock agriculture, forestry and settlement, yet is poorly conserved (O'Connor & Kuyler 2009). This area also coincides with high avifaunal diversity and endemism and, as a result, a number of Important Bird Areas (IBAs) have been proclaimed in the area (e.g. Barnes 1998). Despite this, only few studies (e.g. Mentis & Bigalke 1981; Jansen, Little & Crowe 1999) have examined bird species' abundance or densities in relation to land management in the area.

For grassland managers it is important to understand factors that determine the density of threatened animals for better conservation planning (Wintle, Elith & Potts 2005). Knowing which habitat characteristics are associated with high or low densities provides management with important information to improve conservation decisions. However, estimating population densities of animals is notoriously difficult because some animals remain undetected during the survey (Diefenbach & Brauning 2003). Many grassland bird species are also difficult to tell apart in the field because they look alike. Furthermore, the detection probability varies across methods and different observers, and changes with habitats and weather conditions. The methods that take into account heterogeneity in detection probability provide robust estimates compared to traditional density-estimate methods. Hierarchical distance-sampling methods account for the detection process and are therefore commonly used to study animal density (Marques *et al.* 2007; Oedekoven *et al.* 2013). Recently developed hierarchical distance sampling models can be used to examine the environmental drivers associated with variation in density across sites and habitat covariates (e.g. Royle, Dawson & Bates 2004). Making inferences based on counts adjusted for detectability results in reliable estimates when compared to traditional methods, which provide insufficient information about true population density because of unrealistic assumptions like constant detectability, and this has conservation implications (Marques & Buckland 2003; Marques *et* *al.* 2007; Thomas *et al.* 2010). Hierarchical distance-sampling methods allow for factors that affect the detection probability, such as habitat, weather covariates and observer identity (Diefenbach & Brauning 2003; Marques & Buckland 2003; Royle, Dawson & Bates 2004; Marques *et al.* 2007; Oedekoven *et al.* 2013). These improvements provide useful tools to assess the impact of some management intervention on the conservation of species of interest (Oedekoven *et al.* 2013).

In grasslands, understanding the habitat factors that are important in determining the densities of grassland-specialist bird species also helps to successfully manage these habitats for other bird species. Ingula, with Important Bird Area (IBA) status, presents a conservation challenge because, while the management would like to reverse the ecological damage caused by past farming practices, it also wants to maintain species that persisted under heavy grazing and annual fires, because some of them are a priority for conservation. Both heavy grazing and mismanaged fires have been implicated for causing environmental damage to the grassland ecosystem around Ingula (Mentis 2006). The key is to understand how fire and grazing work together to bring about habitat suitability or densities of target species without causing environmental degradation. The managers and biologists have to find the most cost-effective methods to survey population of wildlife in order to make reliable conservation estimates (Azhar *et al.* 2008).

In conservation, identifying high-quality habitats is an important part of species conservation and requires information about habitat-specific abundance and demographics (Chandler & King 2011). Also establishing associations between individual species and habitat covariates is important in understanding how individual species make use of habitat (e.g. Marques *et al.* 2007) and is basic knowledge required by conservation managers. Understanding species habitat requirements is one of the most crucial questions in the conservation and management of animals (Kneib, Knauer & Küchenhoff 2009).

In this chapter, I use hierarchical distance sampling models (Fiske & Chandler 2011) to examine the density of eight most commonly recorded grassland bird species at Ingula. Density and abundance are the essential ecological information required for population ecology (Azhar *et al.* 2008). By focusing on these eight species, I also hope to understand how habitat features affect avian diversity more generally and to provide a set of indicators that management can use to monitor the status of avian diversity at Ingula. Finding reliable indicators of species richness within the grasslands will make it easier to manage habitat for other less common species (e.g. Gustafsson 2000; Nally & Fleishman 2004; Lewandowski 2010). Also, given the challenges inherent in detecting some grassland birds, it is much easier to train field ornithologists to survey common species to inform the success of management decisions (Nally & Fleishman 2004). Indicator species have been extensively used to inform grassland management (e.g. Browder, Johnson & Ball 2002). Even when expertise is available, lack of time and funding limits conservation planners from collecting data on the distribution of all species at the scales where most conservation planning occurs. Instead, conservation managers often rely on surrogates to estimate biodiversity of the concerned habitat (Lewandowski 2010). Even when time and funding is available, not enough data can be collected on certain species because they are either rare or hard to find.

A basic goal of ecological research is to understand how habitat features influence species' abundance or occurrence over time and to relate this to management intervention (Fiske & Chandler 2011). However, modelling the effect of abundance covariates without addressing the issue of species detectability can lead to biased estimates of the effect of habitat on species (Royle, Dawson & Bates 2004). Hierarchical distance sampling models consist of two components: the first component models the observation process (detection probability as a function of distance from the transect line) and the second models the biological process (density of the focal bird species). The observation model involves the choice of a distance function whose parameters will be estimated from the data.

In this study I used improvements in distance sampling to associate bird density with habitat variables that I recorded in the field. I used the following eight small grassland birds that were found to be commonest during preliminary transect data analysis: Cape Longclaw *Macronyx capensis*, Wing-snapping Cisticola *Cisticola ayresii*, African Pipit *Anthus cinnamomeus*, African Quail Finch *Ortygospiza atricolis*, Yellow-breasted Pipit *Anthus chloris*, Red-capped Lark *Calandrella cinerea,* Zitting Cisticola *Cisticola juncidis* and Common Quail *Coturnix coturnix*. Of these, only the Yellow-breasted Pipit is threatened (Barnes 2000).

Materials and methods

STUDY SITE, BIRD AND VEGETATION SURVEYS

Ingula is the site of the Eskom Ingula Pumped Storage Scheme (IPSC), the main purpose of which is to augment electricity to the national grid during periods of peak consumption demand. Although the designs of pumped storage schemes differ (Ibrahim, Ilinca & Perron 2008), the principle on which the schemes work is the same. During periods when electricity demand is low, these stations use electricity to pump the water from the lower reservoir to the upper reservoir and when demand is high, the water flows out of the upper reservoir and activates the turbines to generate high-value electricity for peak hours (Ibrahim, Ilinca & Perron 2008; Yang & Jackson 2011). The scheme is situated *c*. 23km north-east (S 28°14', E 29°35'S) of the hamlet town of Van Reenen at an altitude ranging from 1 200 to 1 700m asl.

Ingula has an area of about 8 000ha and falls within the two provinces, KwaZulu-Natal (KZN) and the Free State (FS), with an altitudinal difference of around 400m between the high altitude grassland biome on the Free State site, dominated by sweet and sour grasslands, and the lower-lying grasslands dominated by *Cymbopogon – Hyrpochloa* - *Hyperrhinia sp.* on the KZN site. Thirty-nine percent of the natural vegetation type within which the upper study site is exposed to combined land cover threats of degradation, transformation and roads effects (Reyers *et al.* 2001). The degradation of habitats at Ingula has been linked to past heavy livestock grazing and annual fires (Mentis 2006; Cauldwell & Park 2012). Based on the perceived deterioration of the habitat resulting from heavy grazing and annual fires, an impact assessment report (Mentis 2006), recommended that livestock be replaced with game and recommended a minimum fire return period of two years. The upper part of the scheme is viewed as particularly important because of the presence of an Important Bird Area (SA IBA 043) the centre of which is the Bedford-Chatsworth Wetland (Barnes 1998). This wetland, surrounding grasslands and cool mountain scarp forests are renowned for high avian diversity including the presence of four nationally 'Critically Endangered' birds. Ingula also forms the important continental watershed: hence the location of a pumped storage scheme in the area.

Ingula's climate is characterised by cold winters with occasional snow and strong directional winds coming from a much cooler, nearby Drakensburg range, and wet summers dominated by mist during the morning hours. Most of the rainfall occurs during the summer months (October to February), sometimes with marked rainfall differences between the upper and the lower parts of the study area (unpublished records from the Eskom weather station at Ingula).

Of the two sites, the lower site is of lower conservation value and has been largely transformed into accommodation and offices for site personnel, while most of the remaining part was taken up by the scheme's facilities. Although management has plans to rehabilitate the footprint of most of the temporary facilities, the area may not look the same again (e.g. Azpiroz *et al*. 2012). About 5% (e.g. Braamhoek Partnership 2004) of the wetland at the upper site have been destroyed by the dam and associated intake tunnels. A tarred road running up the escarpment links the lower and the upper dam. To compensate for the area taken by construction, large areas of the grassland and associated wetlands, which include the headwaters of the Wilge River, were set aside for conservation.

One of the major conservation goals of the Ingula management is to maximise biodiversity once construction of the pumped storage scheme is completed. To achieve this, management is tasked with investigating what to measure, how to measure it and how to monitor to achieve these management goals. In 2012 the Ingula conservation management team applied to the Department of Environmental Affairs to declare Ingula as a nature reserve (e.g. Maphisa 2012).

BIRD SAMPLING

Ingula's topography is rugged. Using 1:50 000 topographic maps, I laid 35 random transects of 500m perpendicular to farm roads and tracks separated by 2km. I surveyed birds along three 50m bands on both sides of the observer, using the Bibby *et al*. (2000) strip transect method (Bibby, Jones & Marsden 1998; Azhar *et al.* 2008; Thomas *et al.* 2010), on all the transects at least once per season (winter, spring, summer and autumn) from the summer of 2006/07 until the summer of 2007/08. The surveys range from the beginning of the construction to when the construction activities were high. Half of these transects were surveyed again during the summer of 2010/11 when construction activities were low as most of the aboveground construction was finished at the time. Strip transects (also named fixed-width method) consist of recording individual birds within fixed distance bands and is one of the most commonly used methods to estimate bird abundance, species habitat preferences and species richness for large–scale monitoring programmes (e.g. Carrascal, Seoane & Palomino

2009). All transect surveys were conducted by myself, mostly during early morning (07h00 – 11h00) or mid-afternoon (15h00 – 16h00), when birds are most active (e.g. Maphisa *et al.* 2009). The weather at Ingula is unpredictable and can change within a relatively short time. No surveys were carried out under wet conditions or when visibility was not good.

MEASUREMENTS OF VEGETATION AND LAND COVER VARIABLES

The vegetation at each transect was surveyed in summer, immediately following the bird survey. The vegetation survey makes use of a frame of 30cm by 30cm, divided into nine equal squares (following methods detailed in Maphisa *et al*. 2009). The grid was thrown twice (at random) every 100m along the 500m transects. At each throw I recorded how many out of the nine squares fell on grass, bare soil, dead grass, forbs or stones. Vegetation height was recorded at every corner of the frame, at each throw point, using a measuring tape and then averaged. Intensity of grazing along each transect was categorised independently of grass height and cover as lightly, medium or heavily grazed, based on the signs of grass clipping by animals. Each transect was classified into one of two categories: burned or not. Transects were also categorised into four types, based on the topography: plateau top, shallow slope, steep slope or valley bottom.

Data analysis and fitting the model

Distance sampling is a widely used technique for estimating the size or density of biological populations (Bibby, Burgess & Hill 1992; Bibby, Jones & Marsden 1998; Bibby *et al.* 2000; Buckland *et al.* 2001; Thomas *et al.* 2005, 2010). Within transect-based distance sampling, the observer records individuals at perpendicular distances away from the line of observation. One of the first steps in the analysis of distance sampling data is modelling the probability of detection (e.g. Thomas *et al.* 2010). Distance sampling models assume that individuals at zero distance from the line are observed with certainty (Thomas *et al.* 2010; Weller, Blackwell & Moller 2012) and that the chances of detecting an individual decreases with increasing distance away from the observer (Speed *et al.* 2010; Weller, Blackwell & Moller 2012). Improvements in distance sampling offer the opportunity to model both the observation process and density as a function of covariates (Marques *et al.* 2007; Weller, Blackwell, & Moller 2012). Rigorous statistical techniques have been developed to account for decreasing probability of detection away from the observer and this allows density or abundance to be estimated, based upon the decrease in observed individuals away from the transect line (Thomas *et al.* 2010; Speed *et al.* 2010).

Function ‘distsamp’ in package ‘unmarked’ (Fiske & Chandler 2011) in R version 2.15.1 (R Development Core Team 2013) was used to fit distance sampling models and to estimate the detection and density of eight common grassland bird species. For each species, a half-normal detection function was used (e.g. Fiske & Chandler 2012). This was chosen by visually comparing the distribution of detections against the fitted function. Other commonly used distance functions were tested and gave similar results.

I considered a number of survey variables that could potentially influence how quickly the detection probability declines with increasing distance away from the transect line (e.g. Weller, Blackwell & Moller 2012). These were season, area (lower vs upper study sites), year, burning, grazing, average grass height and grass cover. Despite the close geographic proximity between the lower and upper sites, vegetation and faunal diversity differ markedly between the two sites (pers. obs). This is partly due to differences in temperature and could potentially affect detection and density. Year is also important in its own right; some years are colder or wetter than others and this could also affect bird detection and density because moisture affects vegetation height. Locally, there is some seasonal movement of otherwise resident species between the sites in response to temperature (e.g. Berruti, Harrison & Navarro 1994). In addition, because of differences in habitat moisture content between the years and sites, differences in grazing intensities and of fires, over which Ingula management had no control, grass height and cover differ from one summer to the next, which might affect detection and densities.

MODEL SELECTION

Model selection is an alternative to the traditional null hypothesis, which is commonly used to draw biological inferences. The latter is based on the rejection of null hypothesis when a test statistic generated from observed data falls below an arbitrary probability threshold (e.g. $P < 0.05$) (e.g. Johnson & Omland 2004), the decision upon which a more biologically meaningful alternative hypothesis is assumed (Anderson, Burnham & Thompson 2000; Anderson *et al.* 2001). Model selection has three advantages over the use of null hypothesis (Anderson, Burnham & Thompson 2000): firstly, competing models are compared to one another by evaluating the relative support in the observed data for each model. Secondly, models can be ranked and weighted, thereby providing a quantitative measure of relative support for each competing hypothesis. And thirdly, in cases where models have similar levels of support from the data, model averaging can be used to make robust parameter estimates and predictions based on several models.

Habitat models may be used to make inferences about a species' habitat requirements and likely response to environmental change, or they may be used to predict a species abundance, density, carrying capacity or probability of occupying a location based on its environmental attributes (Wintle, Elith & Potts 2005). The primary use of habitat modelling in conservation planning is in predicting the spatial distribution of suitable habitat for species of interest in a landscape (Wintle, Elith & Potts 2005). Martin *et al.* (2010) made use of this kind of model to simultaneously estimate habitat suitability, abundance and occupancy of elephants in Zimbabwe.

For each species I started by investigating how season, area and year affected detection. To do so, I held density constant while allowing detection to vary. I did the same for, grazing, grass height and cover. I intentionally had one variable in each model to avoid complicating model convergence given that there was overall limited grazing while almost the whole site was burned every year. For the same reason I did expect burning to affect detection, instead I expected grass height plus cover could influence detection and so I included the model with grass height plus grass cover amongst candidate models. I used model selection, based on Akaike's Information Criterion (AIC) (Burnham & Anderson 2002; Mellin *et al.* 2010), to choose the best model out of the list of competing models. The model with the lowest AIC is the best model in the set of candidate models. Finally, I used the best detection model to examine the effects of these covariates on density.

EFFECT OF GRASS HEIGHT AND COVER ON DENSITY OF BIRDS

A key goal of this chapter is to examine the density of grassland bird species in relation to grass height and cover. Based on results from Chapter 2 (Fisher & Davis 2010), grass and cover are important habitat variables associated with bird density. Because vegetation was measured only in summer, I conducted further analyses using just the bird data collected during summer. I followed the same procedure as above, resulting in eight competing models with grazing, burning, average grass height and average grass cover, plus a model without any covariates. Effects of grass height and cover, as influenced by fire and grazing, should be modelled to guide grassland management on how fire and grazing affect the density of grassland birds (Coppedge *et al.* 2008). Both grass height and cover are important variables that act together, or sometimes alone, to bring about habitat suitability or density for birds

(Kneib, Knauer & Küchenhoff 2009). For every species, I started by studying how detection varies with grazing, average grass height and grass cover, while holding density constant. I did not expect burning to affect detectability. Using the best detection model, I then examined how the density of each species varied in relation to habitat.

To examine the effects of grass cover and height on bird density in more detail, I also incorporated regression splines into the hierarchical distance-sampling models, using methods described in Crainiceanu, Ruppert & Wand (2005). For each knot, a basis function is calculated, and the resulting functions are then included in the models as additive terms. I restricted the regression splines to two knots to limit their flexibility. This implementation allows for biologically realistic relationships, such as optima at intermediate covariate values.

Results

EFFECTS OF SEASON, YEAR AND SITE ON DETECTION AND DENSITY

Season was the most important covariate influencing detection of six out of eight species, with the remaining two species best described by area of study site (Table 1). When comparing the densities between the lower and upper sites, Cape Longclaw and African Pipit occurred at about equal densities between the two sites (Fig. 1). Four other species, Wing-snapping Cisticola, African Quailfinch, Zitting Cisticola and Common Quail occurred at higher densities on the lower site compared to the upper site. Of the remaining two species, Red-capped Lark occurred at higher densities on the upper site compared to the lower site, while Yellow-breasted Pipit did not occur at the lower site at all (Fig. 1).

When comparing densities across the seasons, Cape Longclaw, African Pipit, Yellow-breasted Pipit, Zitting Cisticola and Common Quail occurred at higher densities at Ingula in summer compared to other season (Fig. 2). Of these, African Pipit occurred at relatively low densities outside the summer months, while Yellow-breasted Pipit was near-absent in winter, spring and autumn. Zitting Cisticola was absent in winter and spring, while Common Quail was not recorded in spring. Wing-snapping Cisticola occurred at about the same densities in summer and autumn compared to winter and occurred at low densities in spring, with a large margin of error (Fig. 2). African Quailfinch was also more abundant in summer and autumn compared to other seasons. Red-capped Lark is the only species that occurred at the highest densities in spring, with variable low densities outside spring.

Year also had variable effects on the density of the eight species between 2006 and 2010. Cape Longclaw, Zitting Cisticola and African Quailfinch densities were almost stable between 2006 and 2008 and showed a rapid increase in densities in 2010 (Fig 3.). Red-capped Lark was the only species that reached its highest densities in 2008, while Common Quail was near-absent in the same year compared to other years, when its densities were variable. African Pipit was the only species that occurred at near-stable densities for the first three years and was at its lowest in 2010 (Fig. 3).

RELATING DENSITY OF BIRDS TO HABITAT VARIABLES IN SUMMER

Amongst the transect habitat covariates, a model of grass height plus cover best explained the detection of four species, with the remaining species best explained by grass height, grazing and the model without covariates (Table 2).

Using only summer data (2006/07, 2007/08 and 2010/11) to relate detection and density of eight birds to habitat variables, and using the best detection model in Table 2, the model with grass height plus cover best explained the detection four species: African Pipit, African Quailfinch, Yellow-breasted Pipit and Zitting Cisticola. The model with grass height alone best explained the densities of Wing-snapping Cisticola and Common Quail. African Pipit was the only species whose detection was best explained by the model with no habitat covariates, while the detection function of Red-capped Lark differed between transects with different levels of grazing. When the best detection model in Table 3 was used to explain the density of eight species, relative to grazing (none, light or heavy), species varied with their response to grazing (Fig. 4). Cape Longclaw were recorded at the lowest densities on transects that were heavily grazed, compared to none and lightly grazed transects where densities were relatively high. African Pipit, Red-capped Lark and Zitting Cisticola occurred at about equal densities throughout the three types of habitats. Yellow-breasted Pipit occurred at about the same densities on transects that were classified as not grazed and lightly grazed, and were absent from transects classified as heavily grazed. Common Quail densities were lowest on transects classified as none grazed and were highest on transect that were heavily grazed (Fig. 4).

Burning had variable impacts on the densities of eight species. Six of the eight species: Cape Longclaw, Wing-snapping Cisticola, African Pipit, African Quailfinch, Common Quail and Yellow-breasted Pipit, occurred at higher densities on transects that had been burned compared to those that were not (Fig. 5). The remaining two species showed higher densities on transects that were not burned compared to those that were burned (Fig. 5).

When examining the effect of grass height and cover on the densities of the eight species, grass height had a more pronounced effect on the density of some birds than grass cover, which was also confirmed by the regression splines (Figs 6 - 9). African Pipit, Yellow-breasted Pipit, Red-capped Lark and Common Quail densities declined with increasing grass height and the regression splines suggested that these relationships were well described by the linear models (Figs 6 - 9). On the one hand the regression splines suggested an optimum at intermediate values of grass cover for Common Quail, Wing-snapping Cisticolas and the two pipits. Cape Longclaw and Zitting Cisticola were the only species whose densities increased with increasing grass height and the regression splines suggested that this was driven by a preference for very high grass in both species (Figs 6 & 9). The densities of these two species remained constant across the range of grass cover (Figs 6 & 9). Of the eight species, African Quailfinch was the only species whose density was suppressed by increasing grass cover (Fig. 7). Densities of African Quailfinch remain constant across a range of grass heights. Wing-snapping Cisticola and African Pipit preferred short grass, with the regression splines suggesting a non-linear relationship for the former (Figs 6 & 7).

Discussion

For the majority of the eight species I examined, I found that grass height and cover were the best predictors of bird densities at Ingula. These results confirm the findings from Chapter 2 and earlier reviews (Fisher & Davis 2010), that these two factors are important habitat variables that managers should influence and monitor. Because the effects of grass height and cover on density differed among species, the results of this study suggest that Ingula management should use grazing and fire to induce a habitat mosaic of grass height and cover during summer, when the birds are breeding, to make the habitat suitable for a variety of bird species.

Based on my field knowledge, some of these eight species share habitat preferences with rare and threatened species that also occur at Ingula. Maintaining suitable habitat for some of these eight common species should therefore also benefit other species that share habitat preferences (e.g. Nally & Fleishman 2004). However, using some of the eight species examined in this chapter as indicator species needs to be done with caution and be subject to re-evaluation (e.g. Favreau *et al.* 2006; Grantham *et al.* 2010).

EFFECTS OF SITE, SEASON AND YEAR ON DENSITIES OF INGULA BIRDS

All eight species examined showed marked seasonal patterns in density, and most of them used Ingula predominantly during summer. High-altitude grasslands of southern Africa are characterised by seasonal altitudinal migration for some species of birds (Berruti, Harrison & Navarro 1994), which is a response to fluctuating seasonal climatic conditions. This is true for Ingula, which can be classified as medium altitude compared to other studies reviewed in Chapter 2 (e.g. Mentis & Bigalke 1981; Jansen, Little & Crowe 1999; Little, Hockey & Jansen 2013), all of which were carried out in areas that are higher than Ingula. My study reveals that locally altitudinal moves are in response to both area and season. These results agree with my earlier results on patterns of species richness (Chapter 3) showing that more species use Ingula during summer than during the other seasons. Despite a narrow altitudinal difference between the sites, there are species, such as Yellow-breasted Pipit, that are confined to the upper site and species like the African Quailfinch that occur at much higher densities at the lower site (Fig. 1). The lower site is transformed and borders on commercial crop fields. It is dominated by rank tall *Hypperhinia-Cybompogon* grasses that supported high densities of cisticolas (Fig. 1). With the exception of Red-capped Lark, overall densities were lowest in spring (Fig. 2). For birds that appear in loose flocks (e.g. Red-capped Lark and Wing-snapping Cisticola) are virtually absent in some seasons, while in other seasons my density estimates had large confidence intervals (Fig. 2). Flocking can violate the assumption made when using distance-sampling methods that individuals are detected independently of each other.

All species that are known to tolerate tall grass (Cape Longclaw, Zitting Cisticola and African Quailfinch) were recorded at their highest densities during 2010 compared to other years (Fig. 3). When commercial livestock was removed from Ingula, the area was characterised by tall, rank grass throughout the summer, with rapid increase in height after burning, which mostly occurred after the first summer rains. The year 2008 was relatively dry year compared to other years covering the study period. When rains are late, tenants delayed burning, except for the case where burning was caused by run-away fires that occurred mostly in strong winds. In the case of Ingula, the habitat becomes dense and unsuitable for birds to breed, given that it has not been grazed during the previous summer. The year 2008 was a relatively dry year. Five species, African Quailfinch, Yellow-breasted Pipit, Red-capped Lark, Zitting Cisticola and Common Quail showed particularly low densities in that year. The likely explanation is that, due to delayed burning, these species delayed establishing territories at Ingula and did so on the neighbouring farms where the grass was heavily grazed.

Attributing changes in density over time to particular changes in the habitat is difficult in my observational study. In addition to the removal of commercial livestock and associated habitat changes, construction activities were higher during the first two years and resulted in disturbance that is likely to affect avian species differently (e.g. Hobbs & Huenneke 1992). A change of fire regime with increased fuel load is another important new disturbance, locally affecting bird densities from one year to another. In all years of my study, management delayed burning compared to the neighbouring farms until someone burned the area haphazardly. The decline of African Pipit from 2006 through to 2010 could be the result of these changes (Fig. 3).

EFFECTS OF FIRE AND GRAZING ON INGULA BIRD DENSITIES

Fire and grazing in grasslands create a suite of habitats that benefits a variety of birds (Fuhlendorf *et al.* 2006). Fire and grazing are therefore increasingly used by grassland managers to enhance habitat suitability for a diverse bird community (Pillsbury *et al.* 2011). Unfortunately, fire and grazing were not under the control of management during this study, which precluded me from studying their effects experimentally (see Parr & Chown 2003). Instead, I took advantage of haphazard variation in fire and grazing history around the surveyed transects, and my results therefore need to be interpreted carefully. For example, the effects of grazing or burning found here contradicted known habitat preferences of some species. Surprising results were that African Quailfinch and Common Quail had their highest densities in heavily grazed habitats and that Red-capped Lark densities were relatively high on unburned transects compared to those that had been burned. Red-capped Lark is known to respond positively to burned (e.g. Bouwman & Hoffman 2007) and heavily grazed habitats. Due to the lack of control over grazing and burning and the difficulty of determining grazing pressure unambiguously (Maphisa 2004), my results on the effects of burning and grazing on densities need to be interpreted carefully.

GRASS HEIGHT AND COVER PREDICT HABITAT SUITABILITY FOR BIRDS

Since I could not experimentally control fire and grazing, I examined more proximate habitat variables that I could measure along the sampled transects: grass height and cover. Theoretical models show that fire and grazing interact through a series of positive and negative feedbacks to cause a mosaic of vegetation patterns across the habitat (e.g. Fuhlendorf, Engle & Moreira 2004). A mosaic of grass height and cover is created under different fire intensities (Fuhlendorf & Engle 2004) and also by selective grazing of animals. Both grass height and cover are important variables that act either together or alone to determine habitat suitability for birds (Kneib, Knauer & Küchenhoff 2009).

Supporting the above arguments, grass height and cover were the best predictors of density for most species (see tables 2 & 3). However, there were clear differences among the species in their habitat preferences. African Pipit, Yellow-breasted Pipit, Red-capped Lark and Common Quail preferred short and intermediate grass cover, while Zitting Cisticola preferred tall grass. Zitting Cisticolas construct their nests by binding the top of grass tufts together and enter the nest from the top. While most species preferred relatively dense grass, African Quailfinch strongly preferred open patches. African Quailfinch typically occur on fallow fields where they feed on seeding weeds (Fig. 7); its preference can explain why this species occurs at higher densities at the lower site than the upper site (Fig. 1). During my surveys, I found nests of Wing-snapping Cisticola in specialised habitats, including along path verges and islands of unburned grasslands and correspond to the narrow response to both grass height and cover (Fig. 6).

The use of regression splines with two knots in the hierarchical distance sampling models gave these results realistic relationships such as optima at intermediate values for grass height and cover and for most species these results agreed with my known habitat preferences for most species. Alternative to this approach would be to use non-linear parametric models with quadratic terms during model fitting (e.g. Chandler & King 2011; Sillet *et al.*2012). However, in my case, I choose model with linear relationships and one based on regression splines for their flexibility to track species preferences over a range of grass heights and covers.

Management implications of this study

The results of this chapter and the preceding chapter complement each other. Management must make habitat suitable to accommodate species with differering habitat requirements in summer when most birds are likely to be breeding. Important vegetation attributes that contribute to habitat suitability for grassland birds are grass height, cover and dead grass (Fisher & Davis 2010). These results suggest that a mosaic of grass height and cover is needed to support a diversity of birds. Management can use fire and grazing to create such a mosaic and thereby bring about habitat suitability for birds (Fisher & Davis 2010). For Ingula and similar habitats, mixed livestock grazing (e.g. Lipsey & Hockey 2010) could benefit grassland birds, given that that different livestock have different grass preferences, leading to selective grazing.

Decision making within an adaptive management framework is designed to reduce uncertainty over time (Nie & Schultz 2012). Even though I recommend the decision theoretic approach to adaptive management, where uncertainty is reduced through management and monitoring of the outcomes (McFadden, Hiller, & Tyre 2011), there is a need to verify my results experimentally. In particular, patch burning (e.g. Parr & Andersen 2006) could be used to examine the effects of fires of different intensities and the effects of different stocking densities. Moreover, within this controlled patch burn, Ingula management has the opportunity to test the effects of livestock grazing with game grazing on avian diversity.

Maintaining preferred habitat for the eight common species examined in this chapter should also benefit large, threatened birds that occur at Ingula in densities that were too low to use distance sampling methods (see appendix of Chapter 3 for a species list). For example, maintaining habitat for Red-capped Lark early in the breeding season will also benefit Southern Bald Ibis and Blue Crane *Anthropoides paradiseus*. Southern Bald Ibis *Geronticus calvus,* which has a small roosting and breeding colony at Ingula, delays breeding in years when there are no early fires (personal observation). The only pair of Blue Cranes present bred three times at Ingula during the beginning of this study but then stopped nesting within the Ingula property. This could be for a delayed effect of disturbance or a lack of short grass early in the breeding season. White-bellied Korhaan *Eupodotis cafra* – another threatened species present at Ingula – is largely confined to the lower site and only comes above the escarpment in late December to breed. Lack of heavy grazing within Ingula at this time of year forced some pairs to look for alternative breeding on neighbouring farms. At the lower site, outside Ingula, the korhaan occurs at much higher densities, where evidence of breeding is known from a number of neighbouring farms. Ensuring that some patches become heavily grazed beyond early summer will also provide breeding habitat for this species within the Ingula property.

Maintaining habitat requirements for Yellow-breasted Pipit and African Quailfinch will benefit ground-nesting Denham's Bustard *Neotis denhami,* except that it additionally prefers tall, open grassland in which to nest. Maintaining habitat for Cape Longclaw and Wing-snapping Cisticola will also benefit Grey Crowned Crane *Balearica regulorum* and Secretarybird *Sagittarius serpentarius,* both of which are threatened and breed on site. The population of Grey Crowned Cranes has increased to close to 10 pairs (Maphisa unpublished data) since the withdrawal of livestock. The 'critically endangered' Wattled Crane *Grus carunculatus* occurs at Ingula. It breeds from autumn to winter within the wetland but also uses grasslands bordering the wetlands. Managing grasslands outside the summer months to accommodate target species that breed beyond summer months is therefore also necessary.

Another critically threatened species, Rudd's Lark *Heteromirafra ruddi,* (Barnes 2000) was not encountered during the line-transect surveys but was recorded twice early in the summer of 2006, just before cattle were removed. Ingula is well within this species' restricted range (e.g. Maphisa *et al.* 2009) and attracting this species back to the area should therefore be a management priority. The species does well under heavy to light grazing, maintained by mixed livestock of sheep and cattle (Maphisa *et al.* 2009).

Conclusion

One of the major goals of the new Ingula grassland management is to maintain high diversity of grassland bird species. Because of the various sources of uncertainty, adaptive management is recommended for Ingula. A key piece of the adaptive management cycle is to monitor the outcome of the management actions (Bakker & Doak 2009; Westgate, Likens & Lindenmayer 2013). Monitoring is needed to evaluate how well the management action has worked in terms of reaching the objectives and to determine which of the models predicted the outcome the best. In this chapter I used recent improvements in distance sampling (e.g. Fiske & Chandler 2011) as one of the alternatives to monitor the impact of grazing and fire on avian diversity at Ingula. In the next chapter, I examine plot-based occupancy surveys as an alternative to transect line sampling.

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Table 1. Summary of model selection analysis of factors affecting the detection process in eight grassland bird species at Ingula. The models were hierarchical distance sampling models and the table displays the AIC values. The best model for each species is highlighted in bold. Density (dens) was held constant while considering the effects of season, area and year on detection p(.)

Environmental models	**CLC**	**WSC**	**AP**	**AQF**	**YBP**	**RCL**	**ZC**	**CQ**
dens(.)p(.)	1326.12	909.12	908.71	600.36	604.29	699.34	547.91	502.69
dens(.)p(Season)	1323.82	**833.75**	**863.06**	582.02	**550.86**	**644.96**	**460.77**	**461.30**
dens(.)p(Area)	**1321.91**	909.40	909.03	**581.06**	556.98	700.20	516.69	503.03
Dens(.)p(Year)	1326.61	889.97	889.97	592.28	590.74	694.03	543.32	494.82

Notes. Species are sorted from the most common (left) to least common (right); Cape Longclaw (CLC), Wing-snapping Cisticola (WSC), African Pipit (AP), African Quailfinch(AQF), Yellow-breasted Pipit (YBP), Red-capped Lark (RCL), Zitting Cisticola (ZC) and Common Quail (CQ).

Table 2. Summary of model selection analysis of factors affecting the detection process in summer on eight grassland bird species at Ingula. The models were hierarchical distance sampling models and the table displays the AIC values. The best model for each species is highlighted in bold. Density dens(.) was held constant while considering the effects of transect habitat on detection p(.). I examined the effects of grazing, average grass height (avh) and grass cover on the detection function.

Habitat models	**CLC**	**WSC**	**AP**	**AQF**	**YBP**	**RCL**	**ZC**	**CQ**
dens(.)p(.)	**444.72**	331.46	394.24	180.40	334.23	221.81	265.44	270.86
dens(.)p(grazing)	447.05	333.24	397.48	292.30	334.73	**208.46**	259.98	273.63
dens(.)p(avh)	446.72	**324.12**	389.93	182.18	329.64	221.89	259.41	**269.50**
dens(.)p(cover)	444.79	332.75	395.82	175.93	334.52	215.74	267.43	271.83
dens(.)p(avh + cover)	446.01	325.7	**388.88**	**165.99**	**324.51**	214.85	**255.18**	271.79

Notes. Species are sorted from the most common (left) to least common (right); Cape Longclaw (CLC), Wing-snapping Cisticola (WSC), African Pipit (AP), African Quailfinch(AQF), Yellow-breasted Pipit (YBP), Red-capped Lark (RCL), Zitting Cisticola (ZC) and Common Quail (CQ). Avh and cover represents average grass height and average grass cover respectively.

Table 3. Summaries of AIC values according to the best models (**bold**) describing the effect of habitat on the density dens() of eight Ingula small grassland birds. For each species, I used the best-supported detection model (shown in Table 2). I examined the effects of grazing, burning, average grass height (avh) and grass cover on density.

Habitat models	**CLC**	**WSC**	**AP**	**AQF**	**YBP**	**RCL**	**ZC**	**CQ**
dens(.)	444.72	331.46	394.23	180.40	334.23	221.81	265.44	270.86
dens(burning)	**438.96**	**309.16**	395.63	175.33	**311.17**	216.24	266.54	268.81
dens(grazing)	444.72	333.24	397.51	175.14	334.53	208.40	253.93	269.50
dens(avh)	443.66	325.79	373.67	182.35	320.51	215.67	234.42	**266.56**
dens(cover)	444.13	330.56	395.24	155.45	335.86	220.43	267.43	268.87
dens(avh + cover)	445.01	327.61	**361.74**	**147.33**	314.44	**204.15**	**219.68**	267.80

Notes. Species are sorted from the most common (left) to least common (right); Cape Longclaw (CLC), Wing-snapping Cisticola (WSC), African Pipit (AP), African Quailfinch(AQF), Yellow-breasted Pipit (YBP), Red-capped Lark (RCL), Zitting Cisticola (ZC) and Common Quail (CQ). Avh and cover represents average grass height and average grass cover respectively.

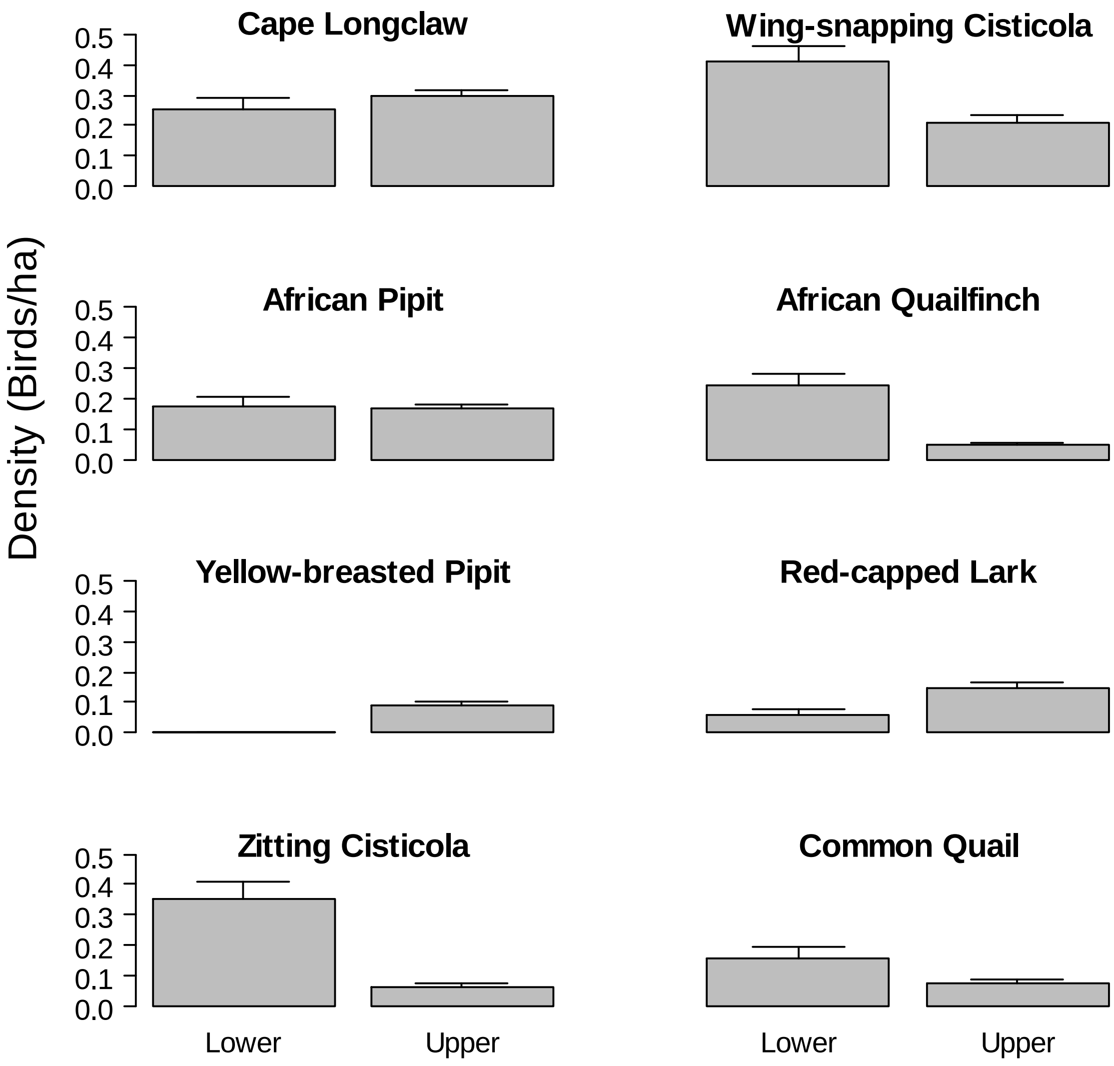

Fig. 1. Density of eight common grassland birds, comparing the upper and lower sites at Ingula. The survey was carried out for the four seasons of the year, running from 2006 to 2008 and about half of the transects were surveyed again during the summer of 2010/11. The error bars are standard errors.

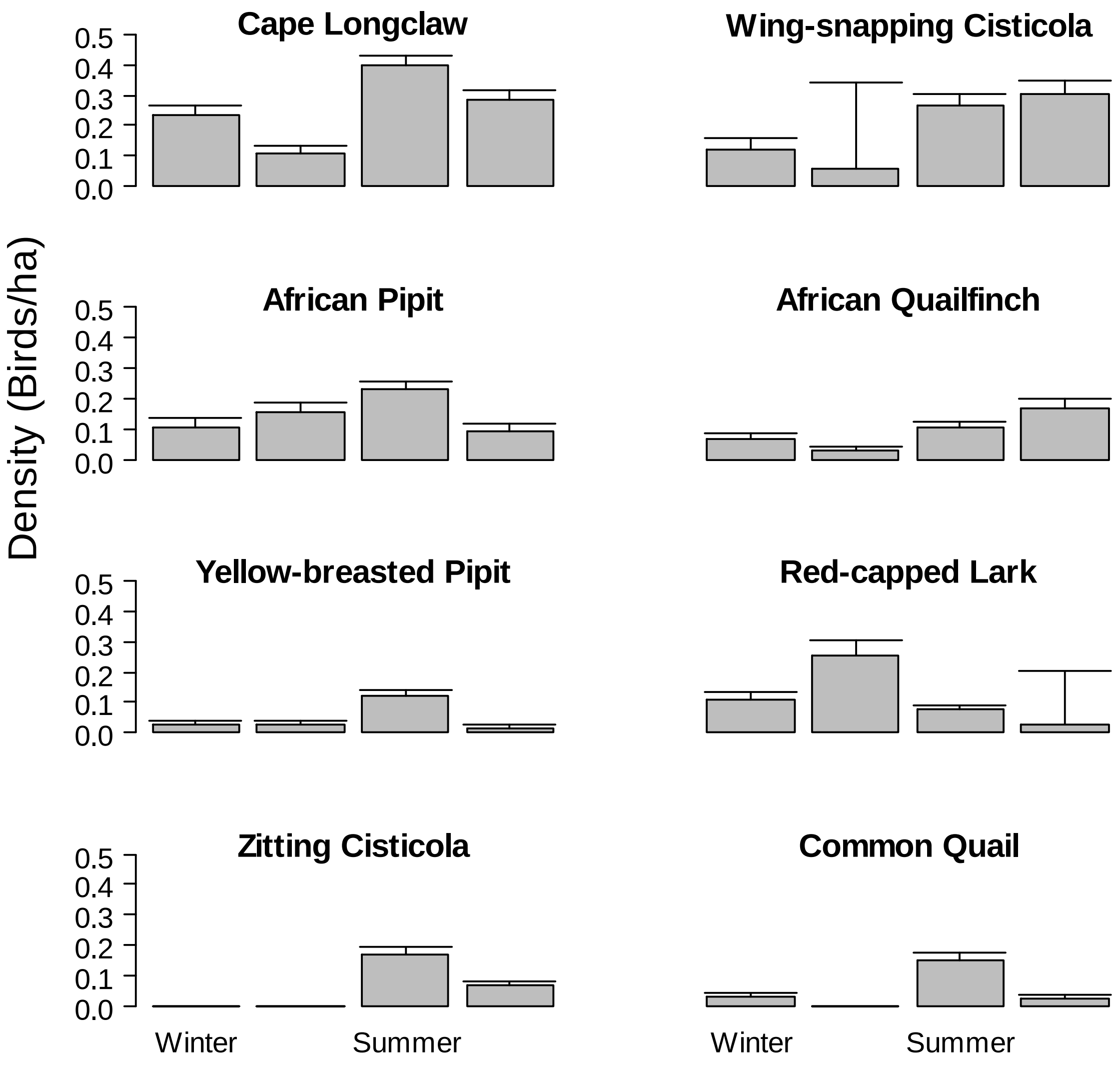

Fig. 2. Density of eight common grasslands birds compared according to the seasons – winter (May, June and July), spring (August, September and October) and summer (November, December and January). The survey ran from 2006 to 2008 and half of transects were surveyed during the summer of 2010/11. The error bars are standard errors.

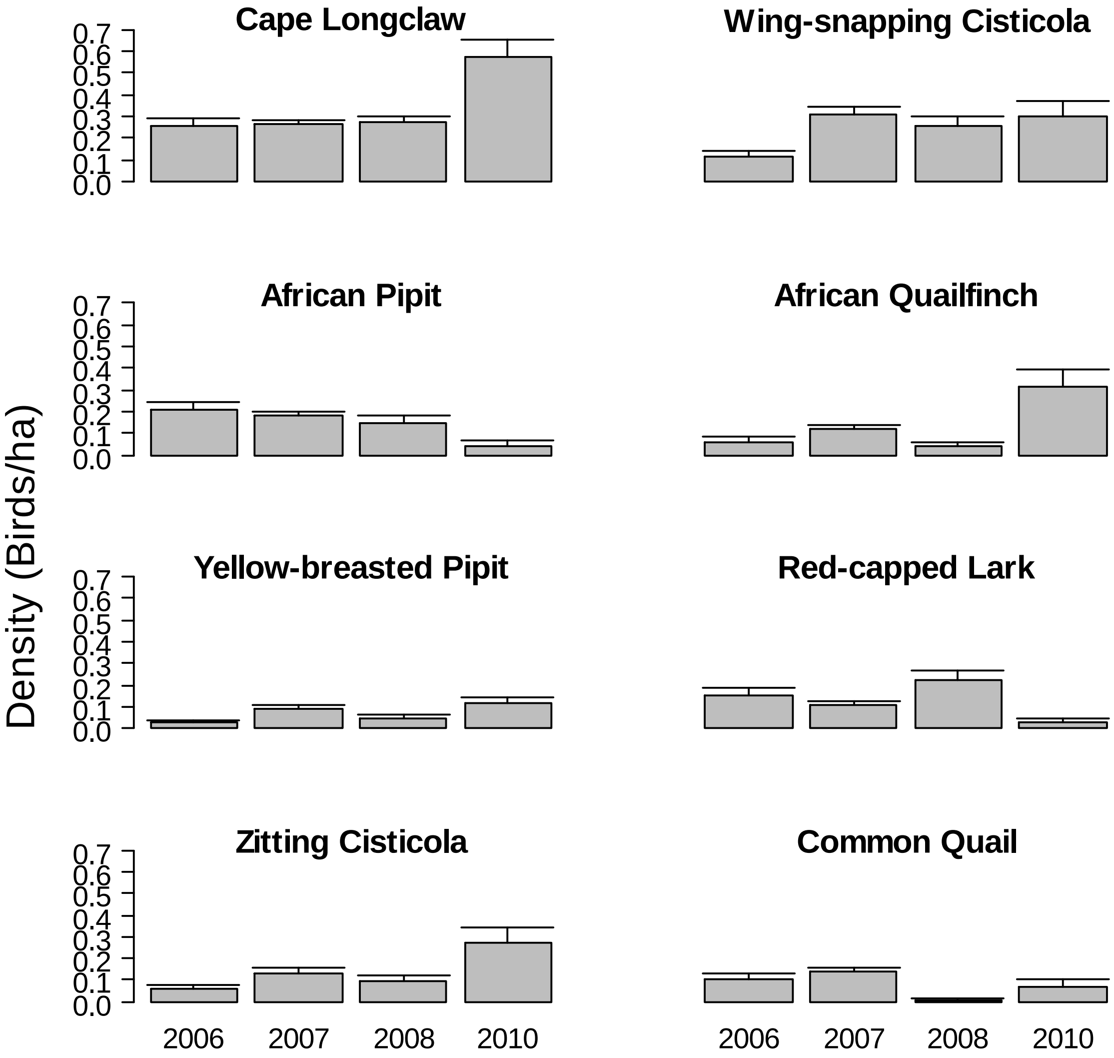

Fig. 3. Density of eight common Ingula grassland birds compared across summers, with only about half the number of transects surveyed during the summer of 2010. The error bars are standard errors.

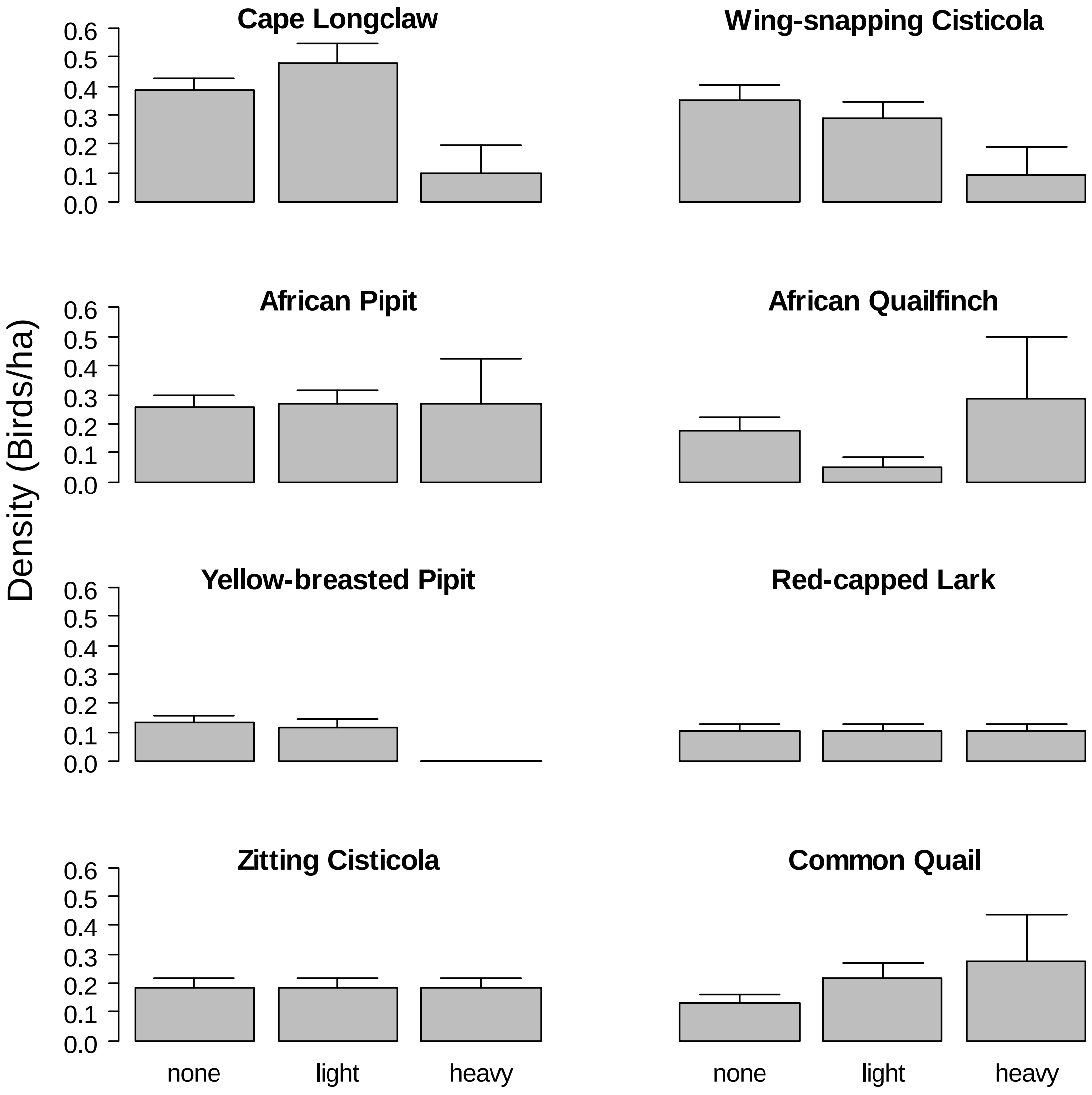

Fig. 4. Density of eight common grassland birds at Ingula along transects that were classified as not grazed ('none'), lightly grazed ('light') and heavily grazed ('heavy') based on the three summer surveyes carried out from 2006/08 to 2010/11. The estimated densities are from Model 3, Table 3. The error bars are standard errors.

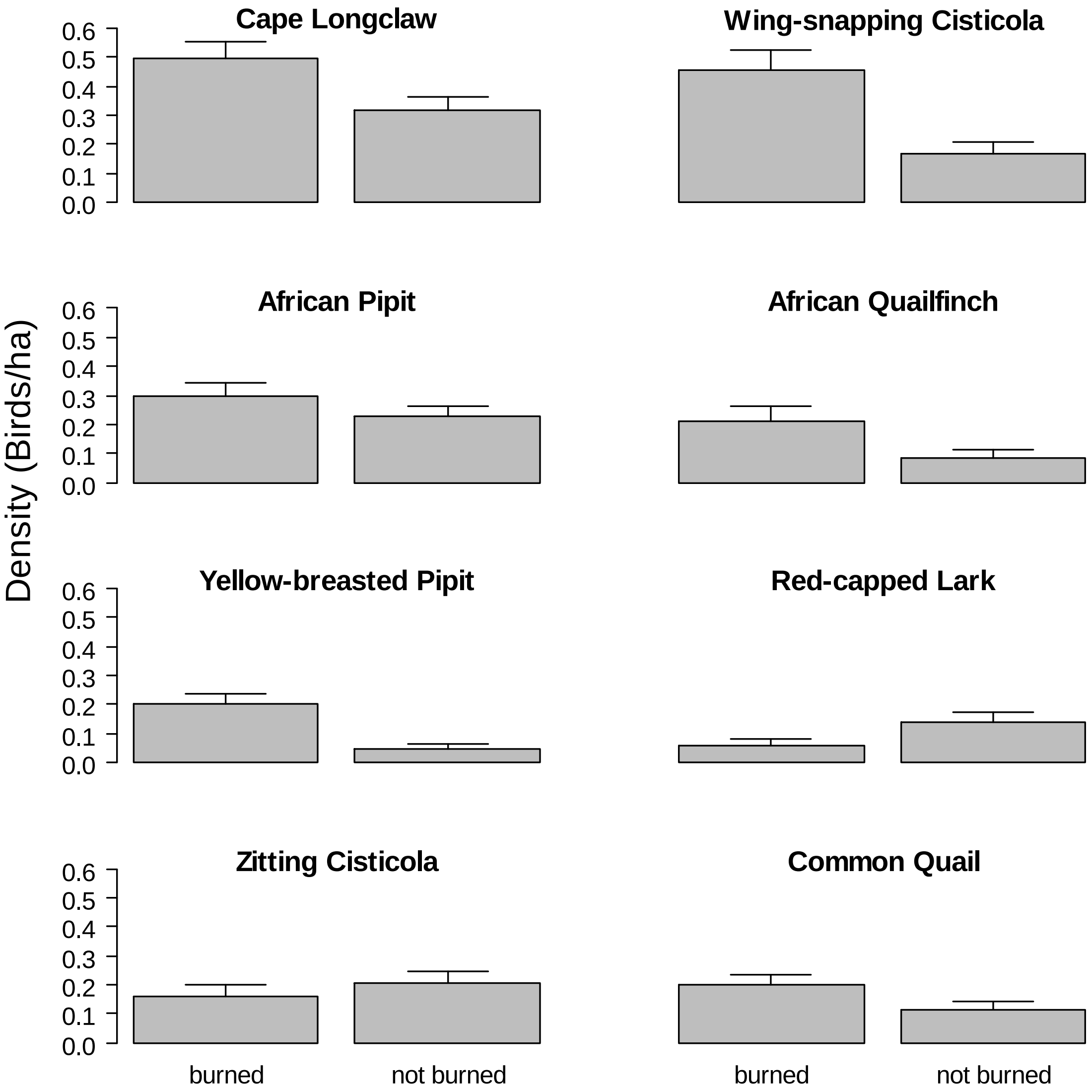

Fig. 5. Density of eight of the commonest Ingula grassland birds on transects classified as burned or not burned, from a survey carried out during the summer months from 2006 to 2008. Only about half of these transects were surveyed during the summer of 2010/11. The estimated densities are from Model 2, Table 3. The error bars are standard errors.

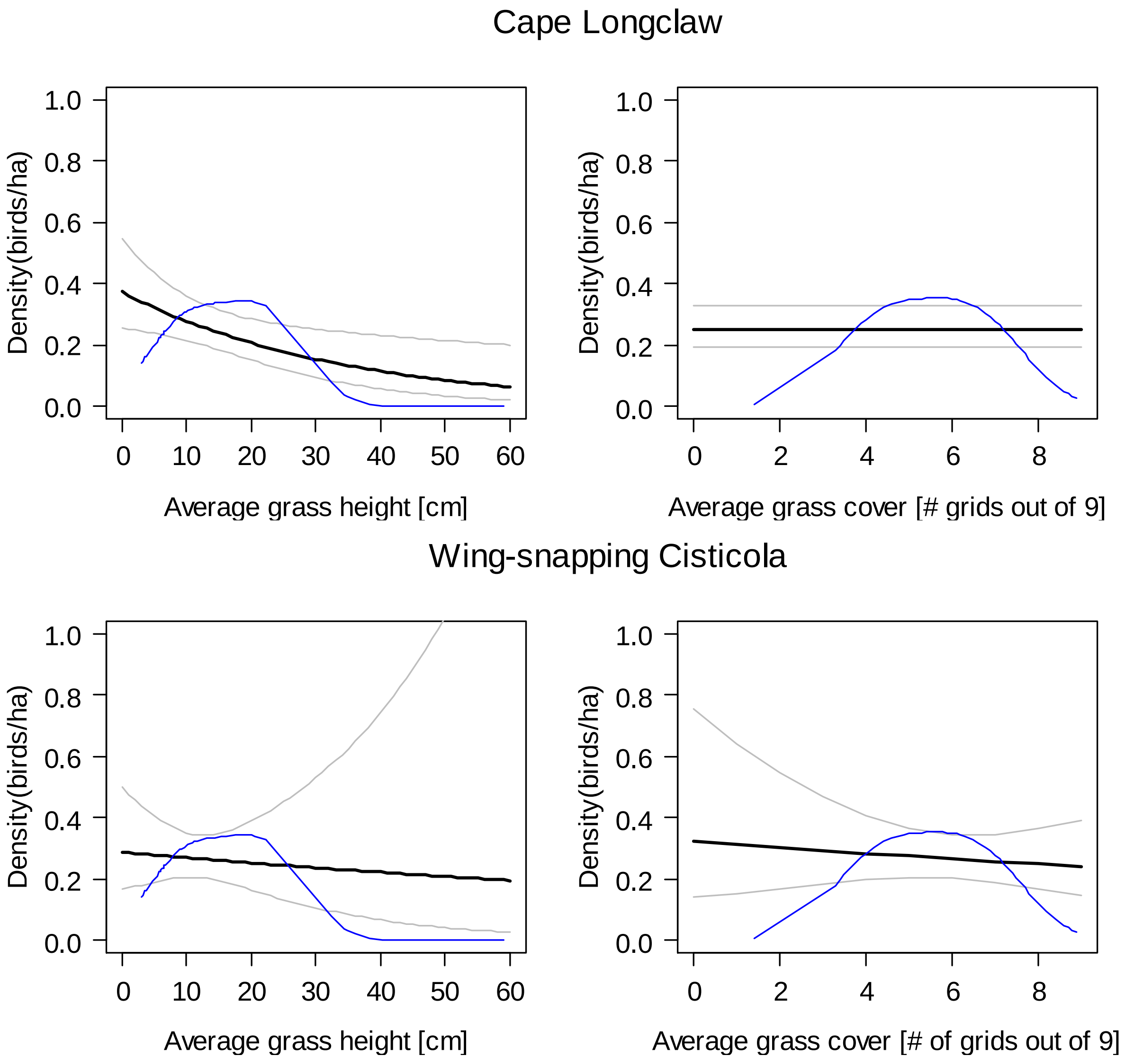

Fig. 6. The influence of average grass height and cover on the habitat suitability of Cape Longclaw and Wing-snapping Cisticola at high-altitude grasslands of eastern South Africa. Light-grey lines are 95% confidence intervals around the fitted response shape, while the blue lines are the regression splines predicting the most suitable habitat for the two species. These results represent summer surveys carried out from 2006 to 2008 and only about half of the transects were surveyed during the summer of 2010/11.

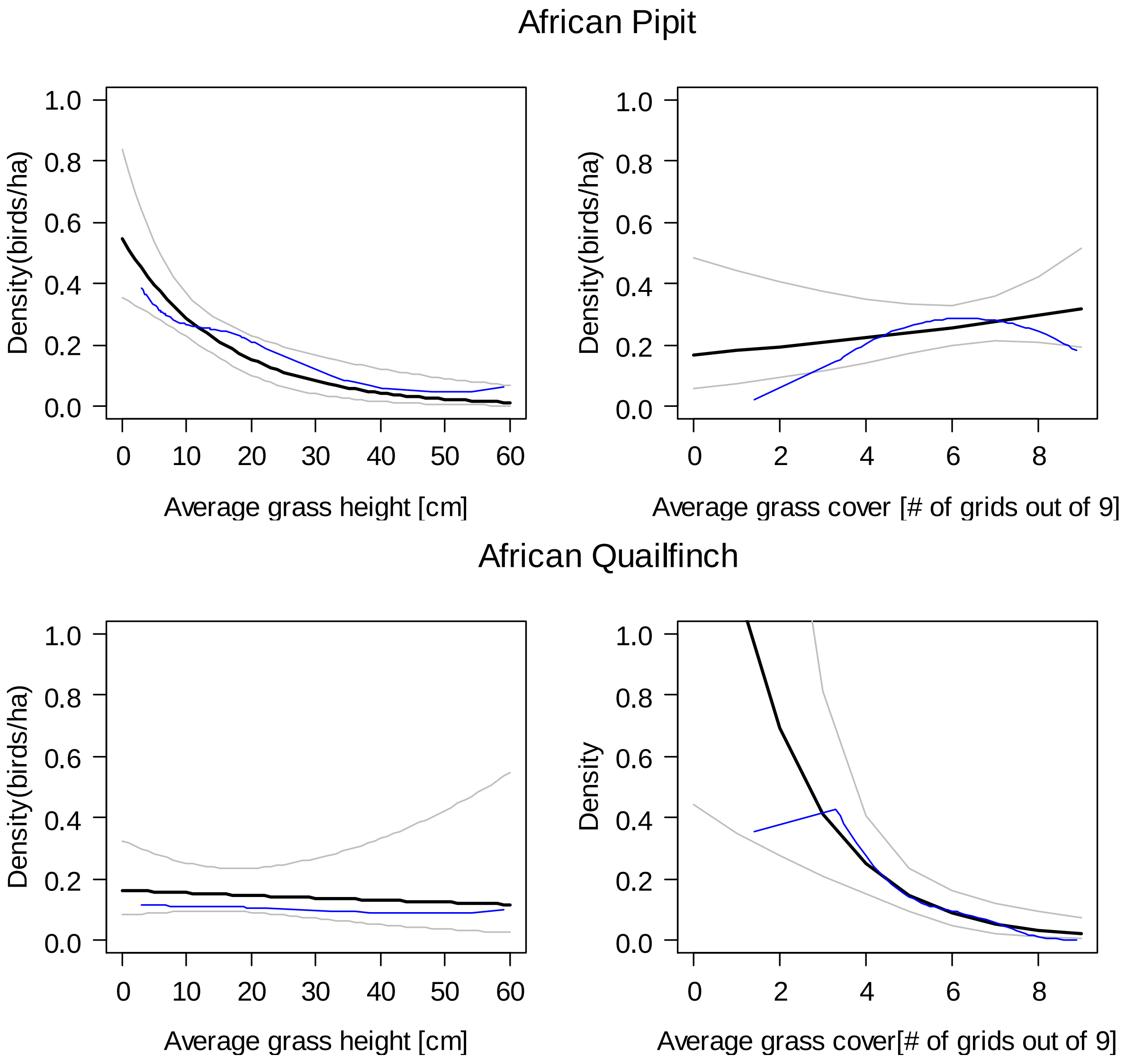

Fig. 7. Influence of average grass height and cover on the habitat suitability of African Pipit and African Quailfinch at high-altitude grasslands of eastern South Africa. Light-grey lines are 95% confidence intervals around the fitted response shape, while the blue lines are the regression splines predicting the most suitable habitat for the two species. This survey was carried out during the summers of 2006 to 2008 and only about half of the transects were surveyed during 2010/11.

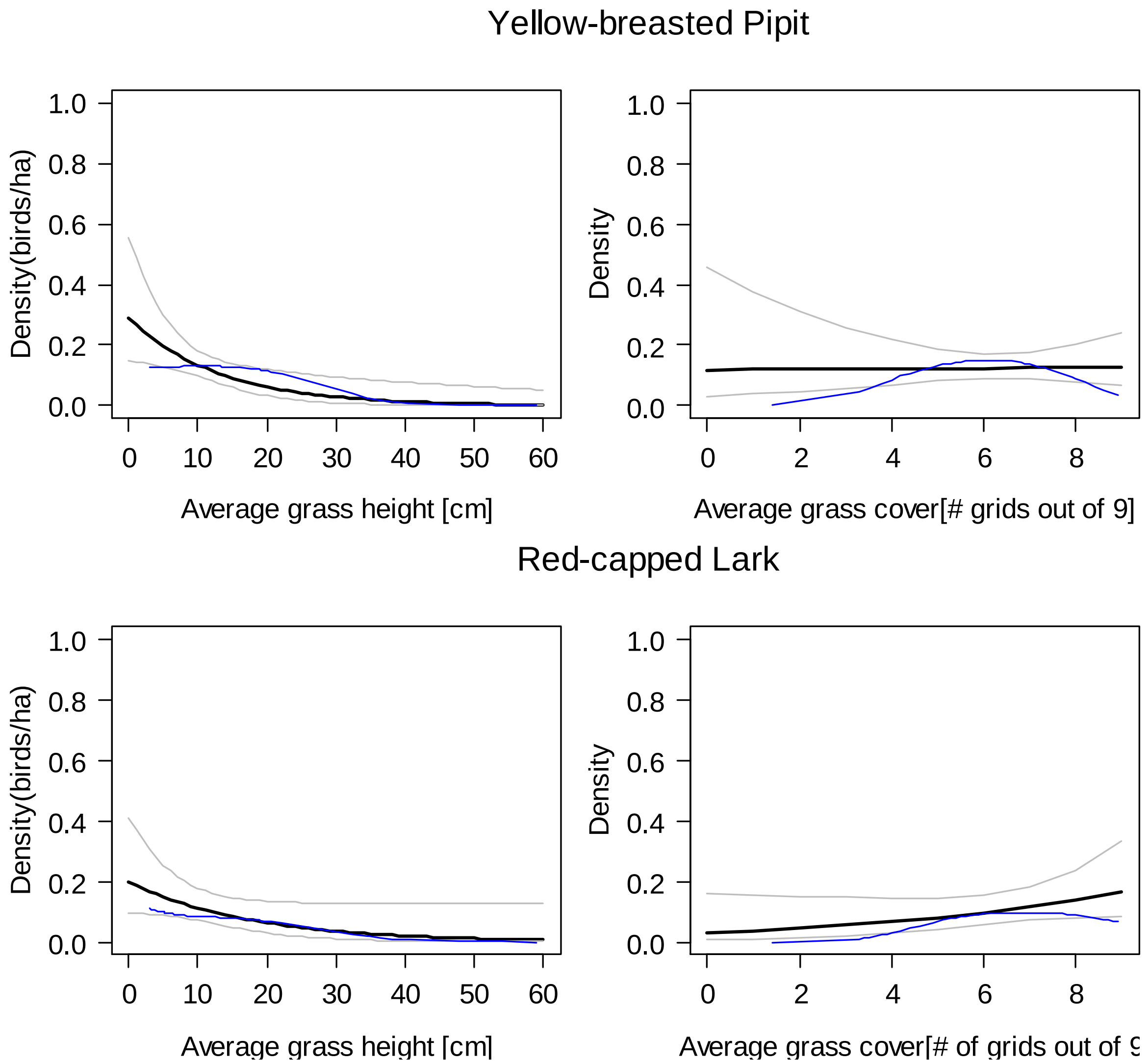

Fig. 8. Influence of average grass height and cover on the habitat suitability of Yellow-breasted Pipit and Red-capped Lark at high-altitude grasslands of eastern South Africa. Light-grey lines are 95% confidence intervals around the fitted response shape, while the blue lines are the regression splines predicting the most suitable habitat for the two species. This survey was carried out during the summers of 2006 to 2008 and only about half of the transects were surveyed during summer of 2010/11.

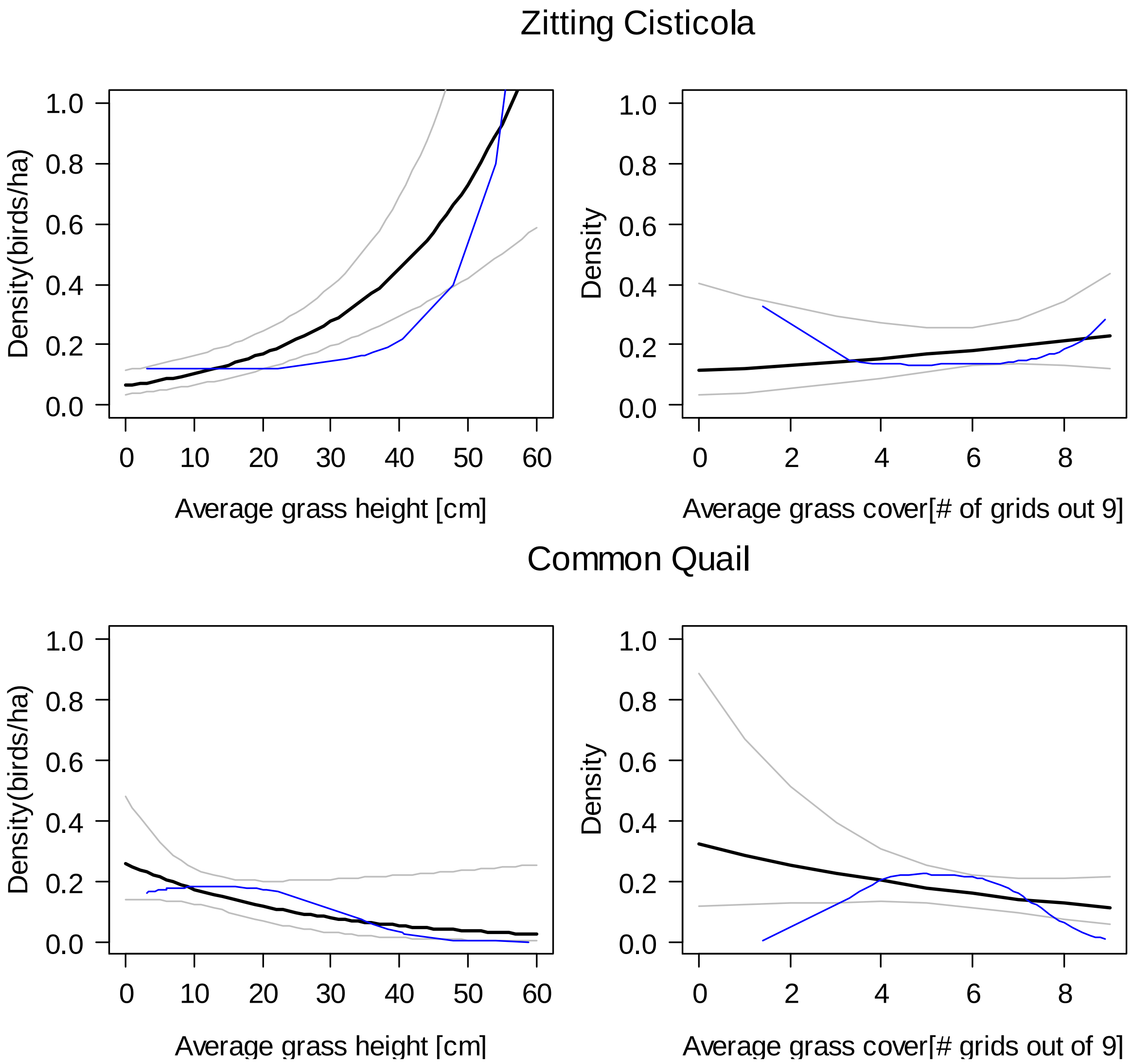

Fig. 9. Influence of average grass height and cover on the habitat suitability of Zitting Cisticola and Common Quail at high-altitude grasslands of eastern South Africa. Light-grey lines are 95% confidence intervals around the fitted response shape, while the blue lines are the regression splines predicting the most suitable habitat for the two species. The result represents summer surveys from 2006 to 2008 and only about half of the transects were surveyed during the summer of 2010/11.

Chapter 5

Species occurrence and its dynamic components, extinction and colonisation probabilities, are focal quantities in biogeography and metapopulation biology, and for species conservation assessments.

Royle and Kery 2007 Ecology 88: 1813-23

Hierarchical occupancy models for avian detection-nondetection data to inform adaptive management of moist, high-altitude grasslands in South Africa.

Summary

1. Moist, high altitude grasslands of eastern South African coincide with high species diversity and endemism in plants and animals. This area has recently become a priority for conservation because of threats related to an increase in agricultural activities and more recently the area has been selected for new energy projects.

2. For the majority of bird species occurring in this biome, the area is an important altitudinal summer breeding area. Because the natural dynamics of fire and grazing are largely disrupted by human land use, their habitat requires management to maintain suitable breeding niches for a variety of species during summer months. The effectiveness of management should be monitored but grassland birds are notoriously difficult to identify in the field. This makes traditional monitoring methods unreliable and makes inference about the effect of habitat management difficult.

3. Ingula is an Important Bird Area located within the least conserved moist, eastern, high-altitude grasslands of South Africa. It is also the site of Eskom’s Ingula Pumped Storage Scheme. The area was previously privately owned, and subjected to heavy grazing and annual burning to maximise livestock feeding, to the detriment of biodiversity. The new management seeks solutions to maximise biodiversity through manipulation of habitat variables to provide habitat for the full spectrum of threatened fauna and flora.

4. I apply a multi-species occupancy model to replicated detection-non-detection data of the 12 commonest small grassland bird species and use it to examine habitat suitability for these birds with implications to other large and sometimes rare threatened avifauna that share habitat with this 12 birds. Specifically, this model estimates plot-specific monthly occupancy, colonisation and persistence in relation to grass height and cover throughout the summer breeding season of 2011/12. I incorporate a combination of cloud cover and prevailing wind at the time of the survey to account for variation in detectability.

5. For the majority of species, initial plot occupancy was high; it increased with increasing grass height and decreased with increasing grass cover. Persistence and colonisation decreased with increasing grass height and cover. However, the 12 species varied considerably in their response to grass height and cover. The 12 selected species occur in about the same number within Eskom's property and on privately owned neighbouring farms that were more heavily grazed.

6. *Synthesis and application*. These results demonstrate the importance of grass height and cover as key variables that need to be managed to suit ecological needs of various avian grassland species with variable habitat preferences. This study develops methods that can be used for monitoring management effects on grassland birds of high-altitude grasslands in eastern South Africa.

Key-words*:* high-altitude grassland birds, biodiversity conservation, multi-species hierarchical models, grass height and cover, monitoring, occupancy.

Introduction

In South Africa the grassland biome and its associated biota are increasingly becoming threatened due to expansion of agricultural activities, human settlements and associated road infrastructure (Allan *et al.* 1997; Reyers *et al.* 2001; Egoh *et al.* 2011). The increase in human population is accompanied by increasing demands for water and electricity. These threats are likely to impact on bird species richness in remote eastern, moist, high-altitudes grasslands. These were previously used mainly for summer pastoral farming. However, at the start of the 21st century, this area has been subjected to large water schemes and is also targeted for wind farms.

Because of socio-political pressure and despite objection from environmental organisations, development in the area cannot be completely prevented. Because of the current threats facing mountain grassland habitats, there is an urgent need for biodiversity information so that the areas that are most important for conservation can be identified and conservation considerations can be implemented in land use planning. The abilities (1) to predict which areas of conservation importance are most vulnerable to transformation and (2) to rank the relative damage that transforming land uses could cause to biodiversity are important components of an effective and realistic conservation planning process (Neke & du Plessis 2004).

Grazing and fire are key ecological factors maintaining habitat suitability for different bird species within the grassland biome. In particular, grazing by mixed livestock and fires of different intensities create a habitat mosaic in grass height and cover that benefits a variety of species across the landscape at different times of the year (Hobbs & Huenneke 1992; Parr & Chown 2003; Tews *et al.* 2004; Vandvik *et al.* 2005; Evans *et al.* 2006; Fuhlendorf *et al.* 2006; Fahrig *et al.* 2011; Little, Hockey & Jansen 2013). Understanding how species of management concern respond to these disturbances is essential for sustainable ecological management of the species (Driscoll *et al.* 2010). In the absence of herds of roaming wild antelopes that are thought to have been responsible for creating a habitat mosaic in pristine times, planned man-made fires and grazing by domestic livestock are now important tools that grassland managers can use to manage grasslands for biodiversity.

Site occupancy models were initially developed as an approach to investigate the dynamics of species occurrence and to understand how factors of interest affect the vital rates that determine occurrence (rates of local extinction and colonisation) (MacKenzie *et al.* 2003, 2006). Site occupancy models offer opportunities to frame and solve decision problems for conservation that can be viewed in terms of site occupancy (Royle & Kéry 2007; Martin *et al.* 2009). These models have several characteristics (e.g. they account for detectability) that make them particularly well suited for addressing management and conservation problems (Martin *et al.* 2009). Non-detection of a species at a site does not imply that the species is absent unless the detection probability is one (MacKenzie *et al.* 2003). Occupancy models account for imperfect detection, which is the inability of investigators to detect a species at a site with certainty (Zipkin, DeWan, & Royle 2009). Incorporating detection probabilities into estimates of species richness is important for obtaining unbiased estimates of species numbers, particularly in communities with large numbers of rare or elusive species (Govindan, Kéry & Swihart 2012). Accounting for detectability is important for grassland birds, where many species are hard to identify or highly elusive.

Russell et al. (2009) used a Bayesian hierarchical, multi-species occupancy analysis, to identify the effects of prescribed fires on wildlife communities. These same models can be used for other management-induced habitat changes such as effects of grazing intensity or burning on avian occurrence within the moist, high-altitude grasslands. Understanding the drivers of occupancy dynamics in grassland bird species is necessary for the Ingula management to decide on actions that favour certain target species (e.g. MacKenzie *et al.* 2003), and limit undesirable species, depending on the set management objectives.

Occupancy estimation and modelling based on repeated detection-non-detection data provides an effective way of exploring change in the distribution of a species across time and space in cases where the species is not always detected with certainty (Nichols & Bailey 2008). Occupancy models can incorporate covariates that might affect site occupancy dynamics (MacKenzie, Nichols & Lachman 2002; MacKenzie *et al.* 2003; Tyre *et al.* 2003; Popescu *et al.* 2012). These models have been extended to include community-level (Dorazio & Royle 2005; Kéry & Royle 2008) and multi-state approaches (Royle &, Kéry 2007; Martin *et al.* 2010). It has been increasingly appreciated that species colonisation and extinctions need to be estimated separately from detection probability to avoid the biases induced by non-detection error (Royle & Kéry 2007).

In this chapter, I use repeated detection-non-detection data and state-space dynamic occupancy models to evaluate how grass height and cover influence the habitat use by birds. Multi-species, dynamic occupancy models provide a convenient framework for making structured decisions when the management objective is focused on a collection of species (Sauer *et al.* 2013). At Ingula, several species sometimes occur with conflicting habitat requirements. Habitat manipulations by the reserve managers that enhance habitat for some species may limit habitat for other species. Through use of dynamic, multi-species occupancy models (Doré, Grillet & Thirion 2011), management will be able to evaluate and guide conservation decisions needed for long-term avian monitoring at Ingula as a case study to manage similar grasslands in South Africa. Additional plots from the neighbouring farms, which are often heavily grazed but also annually burned, were also sampled to increase the number of plots studied. Hierarchical, multispecies site-occupancy models combine information across the sites without losing site and species-specific information (Nichols & Boulinier 1998; MacKenzie, Nichols & Lachman 2002; Kéry & Royle 2008; Nichols & Bailey 2008; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009; Ruiz-Gutiérrez, Zipkin & Dhondt 2010; Zipkin *et al.* 2010; Jones *et al.* 2012; Giovanini *et al.* 2013; Sauer *et al.* 2013).

Materials and Methods

BACKGROUND

A dynamic, multi-species occupancy model is implemented that estimates species-specific occupancy, colonisation and extinction probabilities in relation to grass height and cover as the main habitat structuring factors (e.g. Dorazio & Royle 2005; Dorazio *et al.* 2006; Altwegg, Wheeler & Erni 2008). The model examines changes in occupancy from one month to the next over the course of a breeding season and accounts for imperfect detection. The basic idea is that (1) non-detection can be distinguished from absence through repeated sampling and (2) species-specific estimates of occurrence can be improved using collective data on all species observed during sampling (Zipkin *et al.* 2010). The dynamic model describes occupancy as a state process based on: (1) persistence: the probability of an occupied site continuing to be occupied from one month to the next, and (2) colonisation: the probability of an unoccupied site becoming colonised (Popescu *et al.* 2012).

STUDY SITE AND BIRD SURVEYS

The study area covers an area of about 8 000ha that falls within two provinces, KwaZulu-Natal (KZN) and the Free State (FS), with an altitudinal difference of 400m between the high altitude grassland biome on the Free State site, which is dominated by sweet and sour grasslands, and the lower lying grasslands dominated by *Hyperrhinia hirta* on the KZN site (see Chapter 1). The weather at Ingula is characterised by cold winters with occasional snow and strong directional winds and wet summers dominated by morning mist. Most of the rainfall occurs during summer (October to February), sometimes with marked rainfall differences between the upper and the lower parts of the study area.

A total of 19 randomly selected plots of 500 × 500 m were surveyed for birds and vegetation between November 2011 and February 2012. Twelve plots were located within the Ingula property and seven plots on neighbouring privately owned farms. Occupancy models need repeated visits to a site recording the detection (1) or non-detection (0) of species (Royle, & Kéry 2007; Altwegg, Wheeler & Erni 2008; Kéry, Gardner & Monnerat 2010) and covariates that influence occupancy or detection of species (e.g. Martin *et al.* 2010). The repeated surveys must be carried out within a relatively short period to ensure that extinctions and colonisations do not happen between surveys within a month. This is known as the closure assumption (MacKenzie, Nichols & Lachman 2002; MacKenzie *et al.* 2003; Royle & Nichols 2003; Russell *et al.* 2009; Kéry, Guillera-Arroita & Lahoz-Monfort 2013). From one month to the next, the dynamic model allowed for colonisation and extinction. Each plot was visited three times each month and the detected species were recorded. Out of the three visits, two were spent recording birds only and lasted up to thirty minutes. The third visit was for recording vegetation but I also made a list all of birds seen and mostly took longer than 30 minutes. Bird surveys were undertaken in the mornings, from 07h00–11h00, and sometimes in the afternoons from 15h00–16h00.

The vegetation was surveyed in a similar way to Maphisa *et al.* (2009), and consisted of recording grass height and cover. In occupancy studies, recording additional environmental covariates increases precision in model prediction of detection and occupancy (MacKenzie, Nichols & Lachman 2002; Royle & Kéry 2007; Mattsson, Brady & Matthew 2009; Kéry, Guillera-Arroita & Lahoz-Monfort 2013). Cloud cover (clear, partly cloudy or cloudy) and temperature (cold, cool, warm or hot), together with wind conditions (calm, moderate or strong), were scored. Because of my small data set, I reduced these weather covariates into a single variable representing observability by subjectively scoring their effects on my ability to detect birds (Appendix S1). The purpose of the observability covariate was simply to capture some of the variability in the detection probabilities. No survey was carried out when poor visibility would impact the identification of birds. Other plot attributes that were recorded during the vegetation survey were grazing and burning. However, because management had no control over grazing and burning during the time of my surveys, these disturbances happened in a haphazard way and I decided not to include this information in the model but rather focus on grass height and cover as proximate habitat variables.

I used multi-species dynamic occupancy models using the 12 bird species that I found most common during the survey. Some of these birds could serve as indicator species to evaluate future management decisions through adaptive monitoring. I relate occupancy dynamics of these 12 species to grass height and cover during the summer months, which coincides with breeding for a majority of grassland bird species. The justification for choosing these species is that they are all typical grassland species with a diversity of habitat requirements that should also support rarer grassland species. Low plot occupancy, persistence or colonisation would therefore mean that habitat plots are not suitable for breeding. My second justification is that because these birds are widespread and relatively common they should be relatively easy to spot even to the less experienced fieldworker during the monitoring phase. With a view to the monitoring of bird diversity in the future, all these species breed at Ingula during the summer, when they can be detected fairly easily, which results in more precise occupancy estimates (e.g. Ruiz-Gutiérrez, Zipkin & Dhondt 2010). These species were African Pipit *Anthus cinnamomeus*, Cape Longclaw *Macronyx capensis*, Wing-snapping Cisticola *Cisticola ayresii*, Red-capped Lark *Calandrella cinerea,* Zitting Cisticola *Cisticola juncidis*, Yellow-breasted Pipit *Hemimacronyx chloris*, Common Quail *Coturnix coturnix,* Long-tailed Widowbird *Euplectes progne,* African Quailfinch *Ortygospiza atricolis,* Banded Martin *Riparia cincta*, Ant-eating Chat *Myrmecocichla formicivora* and Eastern Long-billed Lark *Certhilauda semitorquata.* Of this species Yellow-breasted-Pipit is considered threatened (Barnes 200).

Model description

I developed a multi-species hierarchical model (Appendix S2) to estimate occupancy dynamics of grassland bird species through the southern hemisphere summer, from

November to February. Occupancy models need repeated visits to a site and the information whether or not the species was recorded (Altwegg, Wheeler & Erni 2008; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009; Zipkin *et al.* 2010). I used a state-space formulation where the site-specific occupancy state for species i = 1, 2, …, N at site j = 1,2.., J, is denoted z(i,j), where z(i,j) = 1 if species i occurs at site j and otherwise z(i,j) = 0. The occupancy state z(i,j), is assumed to be constant for the duration of the study, and is the stochastic binary outcome governed by the occupancy probability (Ψ) of species j at site assumed to be the outcome of Bernoulli random variables denoted by:

$z_{i,j} \sim \text{Bern}\ (\Psi_{i,j})$

I assumed that a species can only be detected at a site if it actually occurs there, i.e. there are no false positives. A detection of species j at site i on visit k depends on the detection probability θ(i,j,k) and the occupancy state:

$x_{i,j,k} \sim \text{Bern}(\theta_{i,j,k} \times z_{i,j})$.

(Dorazio *et al.* 2006; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009; Zipkin *et al.* 2010; Sauer *et al.* 2013)

I was interested in the seasonal changes in the bird communities and therefore used a dynamic extension of the model above, allowing the occupancy status to change from one month to the next. I modelled occupancy during the first month (November, t=1) as above,

$z_{i,j,t} \sim \text{Bern}\ (\Psi_{i,j})$

for t=1. Occupancy during the subsequent months depended on occupancy during the preceding month:

$z_{i,j,t}\ |z_{i,j,t\text{-}1},\ \varphi_{i,j,t}\ ,\ \gamma_{i,j,t} \sim \text{Bernoulli}\ (\varphi_{i,j,t} \times Z_{i,j,t\text{-}1} + \gamma_{i,j,t} \times (1 - Z_{i,j,t\text{-}1}))$

for t>1, where the colonisation probability (γ) is the probability of an unoccupied site to become occupied and the persistence probability (φ) is the probability of an occupied site to remain occupied. The occupancy probabilities during December, January and February (t=2, 3, and 4) were calculated as derived parameters.

Initial occupancy, colonisation and persistence were constrained to be linear functions of the covariates grass height (avh) and grass cover (cover) on the logit scale:

$$\text{Logit}(\Psi_{i,j}) = \beta^0_j + \beta^1_j \times \text{avh}_{i,j,t} + \beta^2_j \times \text{cover}_{i,j,t} \qquad \text{for } t=1$$

$$\text{Logit}(\gamma_{i,j,t}) = \nu^0_j + \nu^1_j \times \text{avh}_{i,j,t} + \nu^2_j \times \text{cover}_{i,j,t} \qquad \text{for } t>1$$

$$\text{Logit}(\varphi_{i,j,t}) = \mu^0_j + \mu^1_j \times \text{avh}_{i,j,t} + \mu^2_j \times \text{cover}_{i,j,t} \qquad \text{for } t>1,$$

where the β, ν and μ are species-specific coefficients. Each of these nine coefficients was modelled as a random effect, i.e. $\eta_j \sim N(\eta_{\_bar}, \sigma_\eta)$ where $\eta_{\_bar}$ is the mean and σ_η the standard deviation of the species-specific coefficients and $\eta = \{\beta, \nu, \mu\}$.

I modelled the detection probability (p) as a function of field conditions measured by the continuous covariate obs, and a random effect ε. α^0 and α^1 are coefficients:

$$\text{Logit}(p_{i,k,t}) = \alpha^0 + \alpha^1 * \text{obs}_{i,k,t} + \varepsilon_{i,k,t}$$

I calculated the number of species, out of the 12, that are present at a site in a given month (local species richness, $r_{i,t} = \sum_j z_{i,j,t}$) and the number of plots each species occupied in a given month ($o_{j,t} = \sum_i z_{i,j,t}$) as derived parameters. Each covariate was centred and scaled before analysis.

Model fitting and analysis

I estimated the parameters using a Bayesian analysis of the model with vague priors (e.g. Royle, Kéry & Ke 2007; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009) for all parameters. Vague priors, also known as non-informative priors, are meant to introduce little or no information about the model parameters that are under investigation (Chen *et al.* 2013). I used the Uniform distribution U(–10,10) for the coefficients and Inverse Gamma (0.01,0.01) for the variances of the random effects. I tested the sensitivity to the choice of priors for the latter by also using U(0,15) as priors for the standard deviations (Zipkin, DeWan & Royle

2009) (appendix S2). I carried out the analysis in JAGS (Plummer 2003) called via package rjags (Plummer 2014) from R (R development Core Team 2013). JAGS (Karreth 2011) is a general purpose software for Bayesian analysis that uses Markov Chain Monte Carlo (MCMC). The MCMC procedure requires an initial burn-in period for the chains to converge to a stationary process, after which the subsequent estimates can be used to calculate medians and credible intervals associated with the parameters of interest (Sauer *et al.* 2013). A critical issue in using MCMC methods is how to determine when random draws have converged to the posterior distribution (Jiao, Hayes & Cortés 2009). I assessed convergence using the Gelman-Rubin statistic (Gelman & Shirley 2011) and visual inspection of the chains. The Gelman-Rubin statistic compares the variance within and among chains in a fashion similar to ANOVA, and is close to 1 at convergence (Kéry & Royle 2008). I ran three chains of length 60 000 each, with a burn-in of 30 000 and thinned the remaining results by taking each 20th value from the chains. With these settings, the model converged for all parameters.

Results

Plot occupancy was variable among the 12 species across the four months, with overall high initial plot occupancy followed by a gradual decline in the number of occupied plots for a majority of the 12 species as the season progressed (Fig. 1). The Wing-snapping Cisticola was recorded in almost every plot throughout the four months and occupancy for this species was estimated to be 1. Four other species, Cape Longclaw, African Pipit, Zitting Cisticola and Banded Martin, exhibited high plot occupancy throughout the four months. Two other species, Red-capped Lark and Common Quail, were common early during the season but showed a rapid decline to a low number of occupied plots by the fourth month. Long-tailed Widowbird and Eastern Long-billed Lark occupied the fewest number of plots throughout the season, with Eastern Long-billed Lark showing a rapid decline between the third and fourth months (Fig. 1).

HABITAT EFFECTS ON OCCUPANCY, PERSISTENCE AND COLONISATION

Species varied in their responses to grass height and cover with initial plot occupancy tending to be higher in plots with high grass and low grass cover (Fig. 2). Across the 12 species, persistence and colonisation decreased with increasing grass height and cover suggesting that plots with low, open grass were more likely to be occupied. However, the relationship between the occupancy parameters and habitat variables differed among species, suggesting that the species prefer different levels of grass height and cover (Fig. 2). Overall, colonisation declined with increasing grass height and cover for a majority of the 12 species, with African Quail, Banded Martin and African Pipit being the exceptions as they were little affected by increasing grass cover (Fig. 2).

Four species, Common Quail, Cape Longclaw, Banded Martin and Zitting Cisticola were found on almost all plots and were only marginally affected by increasing grass height and increasing grass cover (Figs 1 & 2), suggesting that variation in grass height and cover affected these two species little. The Common Quail was recorded almost everywhere during the first two months with subsequent decline (Fig. 1). This species was little affected by increasing grass height, but experienced a steep decline with increasing grass cover (Fig. 2). The Yellow-breasted Pipit, the only threatened and endemic species of the 12, was more common at the beginning of the summer but was scarce by the end of the summer (Fig. 1) and its persistence was affected more negatively by increasing grass height than by increasing grass cover, while its plot colonisation was negatively affected by both increase in grass height and increase in grass cover (Fig. 2). The Red-capped Lark was common everywhere during the first month and thereafter showed a rapid decline (Fig. 1), with decline in plot occupancy and persistence with both increasing grass height and cover (Fig. 2). The Long-tailed Widowbird showed an increase in the number of occupied plots over the first two months and then remained steady thereafter (Fig. 1), persisting across increasing grass heights and covers, indicating positive impact by lack of grazing (Fig 2). Of the remaining three species, the African Pipit was found in most plots in all months of the survey (Fig. 1), where its persistence within plots was affected negatively by both increasing grass height and cover. The Ant-eating Chat and Eastern Long-billed Lark occupied the fewest number of plots throughout the summer (Fig. 1). Persistence of Ant-eating Chats was affected more by increasing grass cover than increase in grass height, while persistence of Eastern Long-billed Lark was affected by increase in grass height and cover (Fig. 2).

SPECIES RICHNESS: COMPARING INGULA WITH NEARBY PRIVATE FARMS.

Of the 12 species examined here, eight to10 were estimated to occur per plot (Fig. 3). Species richness did not vary much over the months and was similar on Eskom's property compared to private farms (Fig. 3).

Discussion

The increasing demand for land for development necessitates more effective management of the remaining ecosystems and biodiversity (e.g. Zipkin, DeWan & Royle 2009). Detection /non-detection data and multi-species occupancy models provide a cost effective way of monitoring the response of a collection of species for management of the habitat (Sauer *et al.* 2013). Using occupancy models that incorporate environmental and habitat covariates (e.g. Kéry & Royle 2008), I examined the response of common grassland species to grass height and cover which has been affected by a change in land use from heavy grazing to little grazing. Habitat structure is a major determinant of how species use a landscape, both in space and time, and affects species diversity (Martin & Possingham 2005). For grassland ground-nesting bird species that use the grassland for both feeding and breeding, vegetation structure is critical for their use of habitat.

My study focused on common species because they are easy to monitor and could serve as indicator species to evaluate the effects of management actions on Ingula's bird community. I found that these species varied in their habitat requirements, measured by grass height and cover, and managing for healthy populations of these species should therefore also benefit the less common species, whose populations are harder to monitor. However, a disadvantage of using common species is that they may be less sensitive to changes in the habitat, especially those species that occur on all plots. Ingula's avian community is characterised by summer altitudinal migration. Provided that grassland had been burned or grazed at the beginning of the summer season, I expect high occupancy probabilities and that, in the absence of grazing, thereafter birds would vacate plots as the season progressed (Fig. 1) in response to tall thick grass. Avifaunal shift in response to vegetation height induced by cattle is documented in some studies (Martin & Possingham 2005; García *et al.* 2007; Tichit *et al.* 2007). When birds arrive at the beginning of the season, grass height and cover are important factors in determining whether they stay to breed or move elsewhere. These two habitat features affected species differently according to their ecological needs and their effect on initial occupancy differed slightly from their effects on later occupancy, determined through persistence and colonisation (Fig. 2). Burning of grassland which was mostly carried out by tenants, occurred before birds arrive and led to short grass, and depending on the fuel load, fire intensity led to increased bare cover. Given enough rain and depending on the grazing regime (of which there was little at Ingula), early burning then leads to faster grass growth and high grass later in the season.

Habitat structure is a key determinant of habitat use by birds (Martin & Possingham 2005). Using foraging woodland and riparian vegetation height data to model response of birds to vegetation height that is influenced by grazing, Martin & Possingham (2005) found that decreasing vegetation height had a negative impact on the habitat use by birds. In my study, increasing grass cover had more negative impact than increasing grass height on plot occupancy for most species, with Banded Martin being the only exception. Being an aerial feeder, the Banded Martin was able to use plots across the range of grass height and cover observed at Ingula. African Quailfinch and Long-tailed Widow occupied the fewest number of plots because they are birds of tall, rank grass.

Species richness, out of the 12 species considered here, was about the same on Eskom property and private farms, even though the two areas were managed differently (Fig. 3). On Eskom property, annual burning was combined with almost no grazing, which led to high and dense grass (see Chapter 3), while annual burning was followed by heavy grazing on private land. These results suggest that species richness alone, especially if based on the common species, is not a sensitive indicator of habitat condition.

I modelled occupancy, persistence and colonisation as logit-linear functions of grass height and cover from one month to the next for four months (multi-seasons). This was a simple approach. The alternative approach under managed grazing or burning would consider logit models with quadratic terms (e.g. Ruiz-Guiterrez, Zipkin & Dhondt 2010; Zipkin et al. 2010; Zipkin, DeWan & Royle 2009) to provide species specific-optima in grass height and cover to differ between the two habitats (burned or not burned or grazing or no grazing). However, I did not do this due the small sample size (12 plots within Eskom compared to 7 on private land). The small sample size was a result of the study site rugged topography and the fact that I had to survey all plots by myself.

SUGGESTED IMPROVEMENTS TO MODELLING HABITAT FOR ALL GRASSLAND BIRDS

Rare species, which are often of conservation priority, are frequently more sensitive to changes in habitat compared to common species (Zipkin *et al.* 2010). By virtue of being rare, these species are also harder to monitor routinely to inform management (MacKenzie *et al.* 2005; Zipkin *et al.* 2010). My study design and statistical model could be expanded to include rarer species by monitoring more plots with a larger replication of surveys. This would allow estimation of occupancy dynamics for species that are less often encountered. A further suggestion is to relax the assumption closure to allow for temporary emigration (e.g. Kéry *et al.* 2009) and to allow estimation of total species richness (Dorazio *et al.* 2006). On the other hand, the Ingula avifauna may not need to be monitored every month during the breeding season. My approach could be used to monitor colonisation and extinction dynamics from one year to the next with little modification: for example, if the plots were surveyed a number of times at the beginning of the breeding season each year. Species of high conservation concern (Barnes 2000) that I did not include in my study are Amur Falcon *Falco amurensis*, White-bellied Korhaan *Eupodotis senegalensis*, Denham's Bustard *Neotis denhamani*, Blue Crane *Anthropoides paradeseus,* Secretarybird *Sagittatarius serpentarius*, Southern Bald Ibis *Geronticus calvus* and the 'Critically Endangered' (Barnes 2000) Wattled Crane *Bugeranus carunculatus*. Data on these species were too sparse (Kéry *et al.* 2009) to be included here. For example, Amur Falcons only arrive at Ingula in late December. White-bellied Korhaan mostly occurs below the escarpment where I had few plots. Blue Crane and Southern Bald Ibis breed early and extend their range of feeding well outside the boundaries of the study area during chick provisioning. The local Secretarybird population is estimated at about only five pairs, with only one pair confirmed breeding on the site; these birds also have a large foraging range.

Often land managers are tasked to make habitats suitable for a variety of species, sometimes with conflicting habitat needs (Sauer *et al.* 2013). Accounting for both species-level effects, as well as the aggregated effects of landscape covariates on the community as a whole, is a strength of multi-species, hierarchical models (Zipkin, DeWan & Royle 2009). Monitoring programmes are increasingly being used to assess spatial and temporal trends of biological diversity, with an emphasis on evaluating the efficiency of management policies (Yoccoz, Nichols & Boulinier 2001). Species richness is often used as a tool for prioritising conservation action (Zipkin, DeWan & Royle 2009). Because not all species (including threatened species) are present at Ingula at the beginning of the summer breeding season, the method that relaxes the closure assumption is recommended in future monitoring that will include rare and late-coming species (e.g. Kéry *et al.* 2009).

Implications for management

For the 12 species I studied, occupancy tended to increase with increasing grass height and decreasing grass cover, even though there was considerable variation among species in their response. In the absence of grazing, as is currently the case at Ingula, grass is becoming thick and tall as the season progresses, and my results suggest that many small grassland species leave such patches during the breeding season. This could be a problem for species that have several breeding attempts per season or need to replace lost clutches. Management of Ingula grassland should encourage a mosaic of grass heights and cover through fires of different intensities and variable grazing stocking rates. In particular, there is a need to design experiments to test the effects of fire (Parr & Chown 2003) but also grazing with clearly defined questions (Parr & Chown 2003) and such experiments should be carried out long term (Parr & Chown 2003) in order to better understand how fire and grazing, as management tools, affect species richness.

Many monitoring programmes are most successful at monitoring common species, while rare species that are a priority for conservation are little known resulting in lack of conservation implementations (Sanderlin, Block, & Ganey 2014). An advantage of my approach is that it accounts for variable detection probabilities and could be extended to include more species or to estimate total species richness (Zipkin, DeWan & Royle 2009; Zipkin *et al.* 2010; Sauer *et al.* 2013; Sanderlin, Block & Ganey 2014). This would, require more plots to be surveyed to increase the current sample size.

Unfortunately, grazing and burning were not under the control of management during my study and I therefore my results does not fully, explain causal relationships between these management tools and habitat suitability for birds. Little, Hockey & Jansen (2013) studied a grassland bird community at an altitude slightly higher than Ingula and found that cattle stocking density affected grass height and cover, which in turn influenced species richness. Because these two sites share in common nearly similar bird communities, their results provide a guideline for stocking densities at Ingula. Additional plots need to be surveyed on privately owned farms to include a broader range of management regimes. This monitoring design should help management to evaluate the effectiveness of their conservation actions (e.g. Zipkin *et al.* 2010) under adaptive monitoring. In a wildlife monitoring context, site occupancy may be used as a coarse surrogate for actual abundance because of the simplicity of relying on presence-absence data, which is less costly to collect compared to time and effort spent on collecting abundance data, especially when multiple species are to be monitored (MacKenzie, Nichols & Lachman 2002; MacKenzie & Bailey 2004).

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Supporting Information

Appendix S1. Scores allocated to three categories based on personnel field observation, each weighted according to how I perceived a variable to influence observability. Conditions were optimal with a clear sky (score 1 = 100), cool temperatures (score 2 = 100) and calm wind conditions (score 3 = 100). For other weather conditions, observability was reduced and I chose the scores according to my subjective judgement of how much it affected my ability to detect birds. For example, observability was similarly reduced in strong winds as in hot weather, etc. I then averaged the three scores to get a single value for observability.

score 1	score 2	score 3	Sky	Temperature	Wind	observability
100	100	100	clear	cool	Calm	100
100	100	80	clear	cool	Moderate	93.33
100	100	60	clear	cold	Strong	86.67
100	50	80	clear	cold	Moderate	76.67
100	50	60	clear	cold	Strong	70
100	60	100	clear	hot	Calm	86.67
100	60	80	clear	hot	Moderate	80
100	60	60	clear	hot	Strong	73.33
70	100	100	cloudy	cool	Calm	90
70	50	80	cloudy	cold	Moderate	66.67
70	50	60	cloudy	cold	Strong	60
70	100	80	cloudy	cool	Moderate	83.33
70	100	60	cloudy	cool	Strong	76.67
70	70	100	cloudy	warm	Calm	80
50	100	100	misty	cool	Calm	83.33
50	100	80	misty	cool	Moderate	76.67
50	100	60	misty	cool	Strong	70
80	50	80	partly cloudy	cold	Moderate	70
80	50	60	partly cloudy	cold	Strong	63.33
80	100	100	partly cloudy	cool	Calm	93.33
80	100	80	partly cloudy	cool	Moderate	86.67
80	100	60	partly cloudy	cool	Strong	80

80	60	100	partly cloudy	hot	Calm	80
80	60	80	partly cloudy	hot	Moderate	73.33
80	60	60	partly cloudy	hot	Strong	66.67
80	70	100	partly cloudy	warm	Calm	83.33

Appendix S2. Multi-Species, dynamic hierarchical model: R and BUGS code used to fit the model. R script with the JAGS model specification for multi-species hierarchical occupancy model with effect of grass height and grass cover on occupancy (Ψ), persistence (φ) and colonisation (γ) probabilities with additional effect of environment (cloud cover and wind) on detection probability (p).

```
################################################################################
# Define model and write text file into R working directory
#################################################################################
sink ('MultiSpeciesDynoccRandCovs3.txt')
# this code writes the model text file for a multi-species model with random effects
# observability as a covariate on p; and avh and cover as covariates on psi, phi, and gamma
# psi, p, phi, and gamma are all time dependent
cat("
model {
# Specify priors and constraints
for (s in 1:nspecies){
  for (i in 1:nsite) {
    for (k in 1:(nyear)){
      for (j in 1:nrep){
        logit(p[i,j,k,s]) <- mu.p + betaobs * obs[i,j,k] + eps.s[s]
        } # j
      } # k
  logit(psi1[i,s]) <- max(-100, min(100, psi.temp[i,s]))
  psi.temp[i,s] <- mu.psi[s] + betapsiavh[s] * avh[i,1] + betapsicov[s] * cover[i,1]
  for (k in 1:(nyear-1)){
```

```
    logit(phi[i,k,s]) <- max(-100, min(100, phi.temp[i,k,s]))

#  persistence depends on grass at t=k+1

    phi.temp[i,k,s] <- mu.phi[s] + betaphiavh[s] * avh[i,k+1] + betaphicov[s] * cover[i,k+1]

    logit(gamma[i,k,s]) <- max(-100, min(100, gamma.temp[i,k,s]))

    gamma.temp[i,k,s] <- mu.gam[s] + betagamavh[s] * avh[i,k+1] + betagamcov[s] * cover[i,k+1]
# colonisation depends on grass at t=k+1

    } # k

  } # i

} # s


for (s in 1:nspecies){

eps.s[s] ~ dnorm(0, tau.p)

mu.psi[s] ~ dnorm(mpsi, tau.psi)

mu.phi[s] ~ dnorm(mphi, tau.phi)

mu.gam[s] ~ dnorm(mgam, tau.gam)

betapsiavh[s] ~ dnorm(bpsiavh, tau.bpsiavh)

betaphiavh[s] ~ dnorm(bphiavh, tau.bphiavh)

betagamavh[s] ~ dnorm(bgamavh, tau.bgamavh)

betaphicov[s] ~ dnorm(bphicov, tau.bphicov)

betapsicov[s] ~ dnorm(bpsicov, tau.bpsicov)

betagamcov[s] ~ dnorm(bgamcov, tau.bgamcov)

}

# hyperpriors

mpsi ~ dnorm(0,0.01)
```

```
tau.psi ~ dgamma(0.01,0.01)  #<- pow(sd.psi, -2)
sig.psi <- pow(tau.psi, -1)   #~ dunif(0,15)

mphi ~ dnorm(0,0.01)
tau.phi ~ dgamma(0.01,0.01)  # <- pow(sd.phi, -2)
sig.phi <- pow(tau.phi, -1)   # ~ dunif(0,15)

mgam ~ dnorm(0,0.01)
tau.gam ~ dgamma(0.01,0.01)  # <- pow(sd.gam, -2)
sig.gam <- pow(tau.gam, -1)   # ~ dunif(0,15)

bpsiavh ~ dnorm(0,0.01)
tau.bpsiavh ~ dgamma(0.01,0.01)  # <- pow(sd.bpsiavh, -2)
sig.bpsiavh <- pow(tau.bpsiavh, -1)  #  ~ dunif(0,15)

bphiavh ~ dnorm(0,0.01)
tau.bphiavh ~ dgamma(0.01,0.01)  # <- pow(sd.bphiavh, -2)
sig.bphiavh <- pow(tau.bphiavh, -1) #   ~ dunif(0,15)

bgamavh ~ dnorm(0,0.01)
tau.bgamavh ~ dgamma(0.01,0.01)  # <- pow(sd.bgamavh, -2)
sig.bgamavh <- pow(tau.bgamavh, -1)  #  ~ dunif(0,15)

bpsicov ~ dnorm(0,0.01)
```

```
tau.bpsicov ~ dgamma(0.01,0.01)  # <- pow(sd.bpsicov, -2)
sig.bpsicov <- pow(tau.bpsicov, -1)  #  ~ dunif(0,15)

bphicov ~ dnorm(0,0.01)
tau.bphicov ~ dgamma(0.01,0.01)  # <- pow(sd.bphicov, -2)
sig.bphicov <- pow(tau.bphicov, -1)  #  ~ dunif(0,15)

bgamcov ~ dnorm(0,0.01)
tau.bgamcov ~ dgamma(0.01,0.01)  # <- pow(sd.bgamcov, -2)
sig.bgamcov <- pow(tau.bgamcov, -1)  #  ~ dunif(0,15)

# let detection probability vary among species
mean.p ~ dunif(0, 1) # Prior for mean detection probability
mu.p <- log(mean.p / (1-mean.p)) # Logit transformation
sig.p <- pow(tau.p, -1)   # ~ dunif(0, 10) # Prior for standard deviation
tau.p ~ dgamma(0.01,0.01)  # <- pow(sigma.p, -2)
betaobs ~ dunif(-10,10)

# Ecological submodel: Define state conditional on parameters
for (s in 1:nspecies){
 for (i in 1:nsite){
   z[i,1,s] ~ dbern(psi1[i,s])
     for (k in 2:nyear){
     muZ[i,k,s]<- z[i,k-1,s]*phi[i,k-1,s] + (1-z[i,k-1,s])*gamma[i,k-1,s]
```

```
      z[i,k,s] ~ dbern(muZ[i,k,s])
    } # k
  } # i
} #s
# Observation model
for (s in 1:nspecies){
  for (i in 1:nsite){
   for (j in 1:nrep){
     for (k in 1:nyear){
       muy[i,j,k,s] <- z[i,k,s]*p[i,j,k,s]
       y[i,j,k,s] ~ dbern(muy[i,j,k,s])
     } # k
   } # j
  } # i
} #s


# Derived parameters: Sample and population occupancy, growth rate and turnover
for (s in 1:nspecies){
#  psi[1,s] <- psi1[s]
  n.occ[1,s]<-sum(z[1:nsite,1,s])
  for (k in 2:nyear){
#    psi[k,s] <- psi[k-1,s]*phi[k-1,s] + (1-psi[k-1,s])*gamma[k-1,s]
    n.occ[k,s] <- sum(z[1:nsite,k,s])
#    growthr[k,s] <- psi[k,s]/psi[k-1,s]
```

```
#    turnover[k-1,s] <- (1 - psi[k-1,s]) * gamma[k-1,s]/psi[k,s]
  } # k
} # s
for (i in 1:nsite) {
  for (k in 1:nyear) {
    srichness[k,i] <- sum(z[i,k,1:nspecies])      # species richness per site and season
  } # k
  for (s in 1:nspecies) {
    sppres[i,s] <- min(sum(z[i,1:nyear,s]),1)
  } # s
  siterichness[i] <- sum(sppres[i, 1:nspecies])    # species richness per site
} # i

} # end of model
",fill = TRUE)
sink()
```

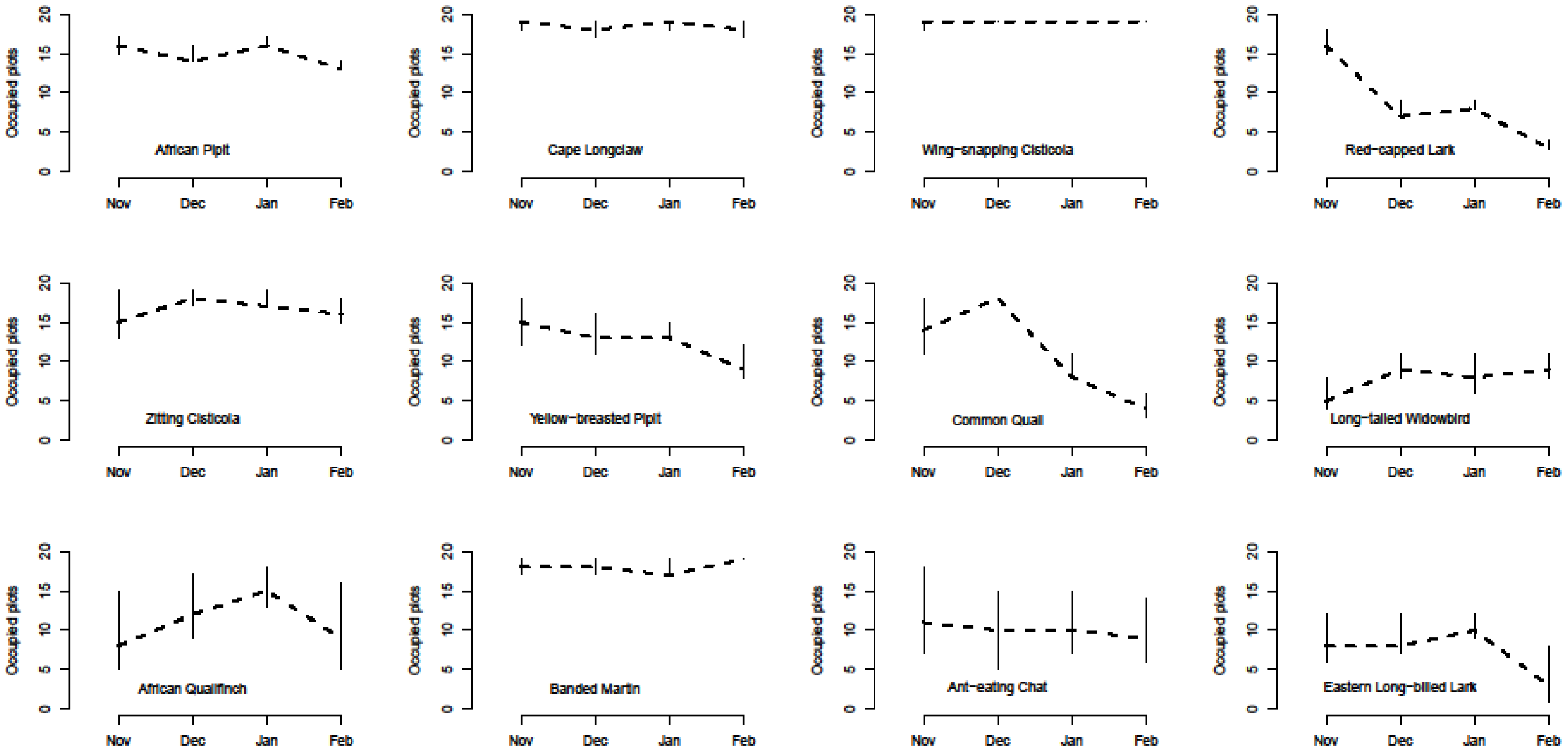

Fig. 1. Estimated number of plots occupied by each species through time at a moist, high-altitude grassland in eastern South Africa. The total number of plots was 19. Solid vertical lines show the 95% credible intervals.

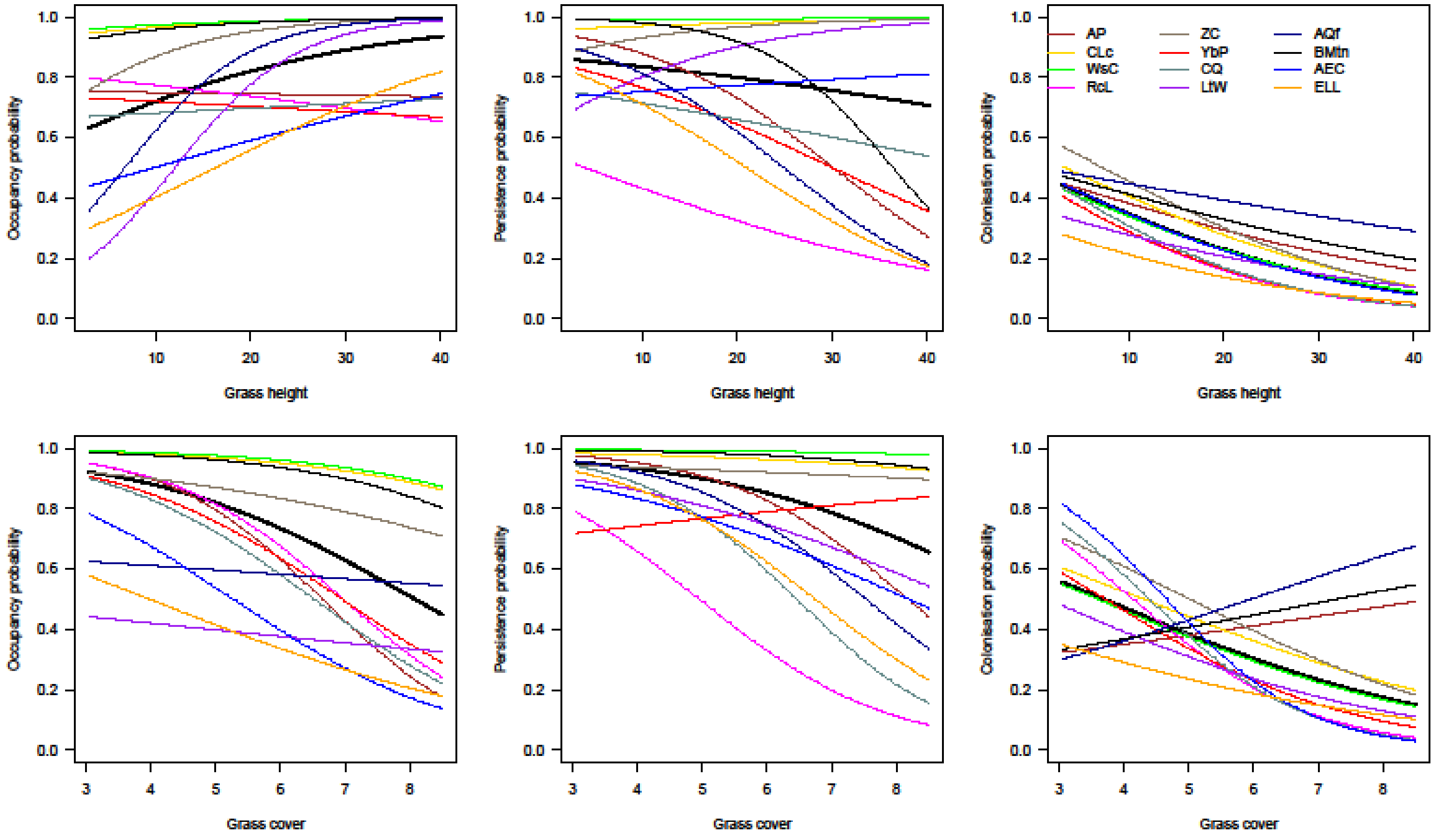

Fig. 2. Mean (bold) marginal probabilities of occupancy, persistence and colonisation for 12 small, grassland bird species in a moist, high-altitude grassland in relation to grass height (cm) and grass cover (number of squares out of nine that were covered by grass). The thick, black line shows the average response across the 12 species and the thin, coloured lines show the responses of individual species. The legend applies to all graphs

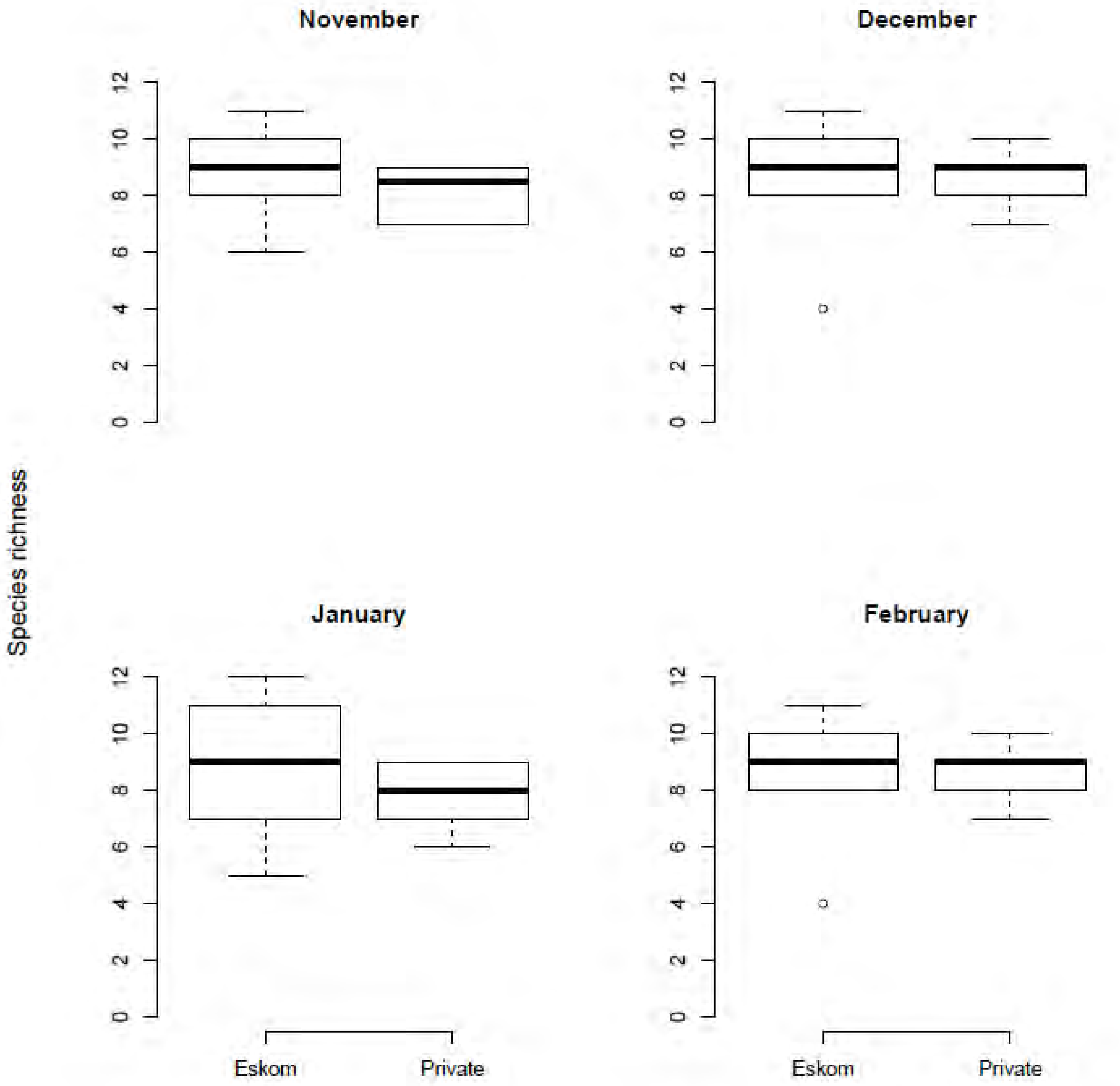

Fig. 3. Estimated plot-specific bird species richness of the 12 species included in this study inside Eskom's property (Eskom) compared to neighbouring farms (Private) each month. From a total of 19 plots, 12 plots were on Eskom's property and seven on neighbouring private farms.

Chapter 6

> The promise of adaptive management is that learning in the short term will improve management in the long term; that promise is best kept if the focus of learning is on those uncertainties that most impede achievement of management objectives.
>
> Runge 2011 *Biological Conservation* 144: 1214-1223

Towards adaptive management of high-altitude grasslands: a system model of management effects on bird community dynamics at Ingula.

Summary

1. Eskom bought land within an Important Bird Area (IBA), located within the high-altitude grasslands of eastern South Africa, to offset the negative impact of construction and operation of a pumped storage scheme in the same area. The goal is to manage the area to maximise biodiversity but it is unclear how to best do that.

2. Impact assessments before construction suggested that heavy grazing and annual fires during previous commercial livestock farming had degraded the grassland and wetlands. Cattle were therefore moved out and an attempt was made to lengthen the fire cycle. Due to lack of control however, annual fires persisted and a few cattle that belonged to the previous owners' tenants also remained and grazed on the property with no restrictions.

3. I developed a system model that integrates what I learned from the literature on grassland management (Chapter 2), the data I collected at Ingula (Chapters 3 to 5) and less easily quantifiable knowledge gained during my five years working in the area. I divided Ingula into 63 polygons intended as management units with relatively homogeneous habitat. Assuming that grass height depends on rainfall and grazing, and that grass cover depends on fire and grazing, I use the dynamics of these habitat characteristics to determine habitat suitability for selected core grassland birds in each polygon. With this model, I simulated the effects of different management scenarios on the bird community over 50 years. Habitat heterogeneity in grass height and cover brought about by managed fire and grazing was important for maintaining species diversity.

4. I examined the sensitivity of species richness after 50 years to changes in each parameter one-at-time to identify the model parameters that were most influential. These were: the effect of rainfall on grass height, followed by the proportion of polygons that were burned, and the effect of grazing on grass height and cover.

5. *Synthesis and applications*. I present a basic system dynamics model to explore possible effects of management actions on bird species richness in high-altitude grasslands. The model considers burning and grazing as management options and assumes that grass height and cover are the main determinants of habitat suitability. The model suggests that habitat heterogeneity is key to maintaining high diversity. For many of the parameters, I did not have a strong quantitative basis to support particular values. However, I used sensitivity analysis to identify the parameters that have the greatest effect on species richness and for which reducing uncertainty is likely the most important. I suggest further improvements to this model and propose it as a starting point for developing alternative models that could be used as a core component for adaptive management of Ingula.

Key-words*:* expert knowledge, grassland bird diversity, management uncertainty, adaptive management, sensitivity analyses, habitat suitability

Introduction

Grassland biomes have been identified as a priority for conservation worldwide (Olson & Dinerstein 2002) and efforts are now being made to reverse the loss of grassland biodiversity (Egoh *et al.* 2011). In South Africa, the grassland biome is the most threatened biome with *c*. 60% transformed into field, urbanisation and afforestation (Allan *et al.* 1997). The remaining area is heavily grazed and annually burned (Muchai & du Plessis 2005). Only about 1.4 % of the grassland biome is protected in South Africa (O'Connor 2005). In particular, the moist, eastern high-altitude region, which coincides with high species diversity and endemism, is the most threatened biome in southern Africa (Jansen, Little & Crowe 1999), and has been identified as a conservation priority in South Africa (Armstrong & van Hensbergen 1999).

Ingula is a pumped storage scheme located in the moist, high-altitude grassland in eastern South Africa. The scheme's primary purpose is to generate electricity using the potential energy of water between two dams with an altitudinal difference of about 400m. The upper dam is constructed above the escarpment within the Free State Province and occupies about 5% of a renowned wetland (Braamhoek Partnership 2004). The lower dam is constructed below the escarpment within KwaZulu-Natal Province, within the headwaters of one of the important tributaries of the Klip River, the major historical source of water for Ladysmith, located about 40km away. Because the area above the escarpment is located within an Important Bird Area (SA043), the centre of which is a unique, moist, high-altitude grassland wetland, the national electricity supplier, Eskom, was asked to set aside additional land to offset the negative impact of the construction and operation of the scheme. In total, an area of about 8 000ha was set aside for which the primary objective was to maximise biodiversity. This area is renowned for high avifaunal endemicity (Barnes 1998), including three bird species that are 'Critically endangered'. Before Eskom bought the area to build the pumped storage scheme, it was used mainly as summer pasture subjected to heavy livestock grazing and winter annual fires to optimise livestock feeding. Over the years, overgrazing has led to deterioration of the grasslands and wetlands (Mentis 2006). The new management is seeking ways to manage the remaining area under conservation principles.

The impact assessment that was conducted at the inception of the project, before construction commenced (e.g. Mentis 2006), found that the wetland and surrounding grasslands were deteriorating badly due to heavy grazing and annual burning, and made suggestions on how to redress the effects. The impact study suggested that cattle be removed and be replaced with game and that fire in a form of block burning be implemented at minimum intervals of two years. While commercial livestock was removed during the summer of 2005/06, the previous land owners' tenants refused to leave and continued to graze the area with a small number of cattle. Commercial farmers used to move their herds to lower altitude in winter and moved them back to above the escarpment in summer. In contrast, the tenants' animals remain at Ingula throughout the year. Their animals grazed everywhere inside the property and the tenants were largely responsible for annual burning intended to rejuvenate growth of green grass for their cattle. During my study, management therefore had no control over grazing and fire, which prevented me from conducting rigorous experiments to establish causal relationships between these potential management tools and bird species richness.

Grassland birds have evolved under grazing and burning (Hockey *et al.* 1988), and grass height and cover are the important vegetation features that determine habitat use by birds (e.g Fisher & Davis 2010). Livestock grazing is a major driver of ecosystem dynamics and overgrazing has been associated with significant declines in various bird species in Britain and worldwide (Evans *et al.* 2006). However, livestock grazing alters habitat structure and can improve habitat suitability for birds to breed so that grazed habitats support a higher diversity of bird species (Martin & Kuhnert 2005; Evans *et al.* 2006). Carefully managed livestock grazing and planed fire is therefore an important management tool to increase grassland birds' species richness (Pillsbury *et al.* 2011). Some authors (e.g. Titshall, O'Connor & Morris 2000) have linked exclusion of herbivores and fire to soil degradation and change in vegetation structure in systems that have evolved under grazing. A study carried out in the mountains of central Argentina found that complete exclusion of livestock leads to a decrease in bird density and species richness (García *et al.* 2007). The study by Garcia et al. (2007) suggested that combining fire and grazing with domestic livestock creates a habitat mosaic similar to past historical patterns under which these birds evolved. Within humid grasslands with a long history of grazing, selective grazing results in a mosaic of grass heights and. when herbivory is excluded, tall grasses dominate the landscape (Milchunas, Sala & Lauenroth 1998). The type of grazing animal also matters. For example, in South African moist, high-altitude grasslands, fenced wild herbivores have a more negative impact on plant diversity than domestic livestock, even at moderate densities (Little 2010). There is no experimental study examining the effects of fire and grazing on bird diversity in South Africa's high-altitude grasslands (Parr & Chown 2003). There is therefore uncertainty about the causal link between fire and grazing management and avifaunal diversity. Here, I develop a model that is based on our current understanding of the system and use it to examine possible effects of different management actions.

In South Africa, few studies have examined the effects of fire and grazing on species diversity or species richness within high-altitude grassland. The literature review in Chapter 2 suggested that mimicking historical patterns of fire and grazing through management supports birds species richness (e.g. Fuhlendorf, Engle & Moreira 2004; Fuhlendorf *et al.* 2006; Coppedge *et al.* 2008; Pillsbury *et al.* 2011). Grazing too heavily and/or burning too frequently will lead to soil erosion. Removing livestock altogether also negatively impacts birds (e.g. Milchunas, Sala & Lauenroth 1998; Krooks *et al.* 2007; García *et al.* 2007). Conservation management at Ingula needs to use controlled grazing and fire as management tools to avoid both extremes. The bird species found at Ingula have different habitat needs that range from a preference for heavily grazed short grass to tall, rank grass (Fig. 1). I follow a modelling philosophy that starts with a simple prototype and then adds more features as necessary (Starfield & Bleloch 1991). I first develop a simple conceptual model (e.g. Starfield & Bleloch 1991; Kéry, Gardner & Monnerat 2010) to predict the response of bird species richness to grazing and burning through their effects on grass height and cover. Rainfall is important for grass growth and I explicitly include this driver in the model. I then adapt the model more closely to the situation at Ingula by incorporating more information on the actual landscape. To do so, I delineate Ingula into management polygons with homogeneous habitat.

Study area and methods

The study area is described in detail in Chapter 1. The study area straddles the escarpment near the town of Van Reenen (S 28°14', E 29°35'). The escarpment marks the provincial boundary between the Free State and KwaZulu-Natal. The upper site is in the Free State and has average altitude of 1 700m asl, while the lower site is in KwaZulu-Natal and has average altitude of 1 200m asl. Ingula has three main habitat types: grassland, wetlands and escarpment forest. However, grassland covers the majority of the 8 000ha area and the model developed in this chapter focuses solely on this habitat. Due to its altitude, the area receives orographic rainfall mostly in the austral summer between October and March, with annual precipitation estimated at 1 400mm (Norström *et al.* 2009; Finne *et al.* 2010). The model I develop in this chapter determines habitat suitability for birds as a function of grass height and cover. Grass height and cover of the study area depends on burning, grazing and rainfall. Average rainfall during the four months when birds breed is 670mm (e.g. Mentis 2014). Of this amount, January receives the most, followed by December, February and November in decreasing order. Rainfall early in the season is particularly important for grass growth and, in the event of grazing, rainfall is important to rejuvenate the grass. Commercial livestock was removed from Ingula during 2005/06. However, only a fraction of the mean annual precipitation is needed to rejuvenate the grass, and the amount of rain needed per month will depend on current stocking density. In the absence of livestock, and with no control over fire by management, I use observational data (see Chapters 4 to 5) and, in addition, more qualitative observations to determine the habitat niche in terms of grass cover and height for each species. As a simple approach, I assume habitat suitability for each species is determined by minimum and maximum values of grass height and cover and that habitat outside these values is unsuitable.

Models description and simulation

Conceptual model

The goal of my models is to predict apparent habitat suitability rather than abundance or demographic rates (Johnson *et al.* 2010). The avian community responds to habitat changes induced by grassland management through the use of fire and grazing (Coppedge *et al.* 2008). I first develop the model for an arbitrary grid of 10 x 10 identical cells. Within each cell, habitat suitability for each species is determined by grass height and cover, both of which are determined by whether or not the cell is burned, the intensity of grazing and the amount of rainfall. Through a randomisation process all cells have equal probability of being chosen.

My modelling approach rests on a few simple premises that are based on empirical data on grazing and burning (Mcintyre, Heard & Martin 2003; Martin & Possingham 2005; Bond & Keeley 2005; García *et al.* 2007; Fuhlendorf *et al.* 2009; Metera *et al.* 2010; O'Connor *et al.* 2011), and literature review (chapter 2) that grass height and grass cover are key determinants of habitat suitability (e.g. Fisher & Davis 2010). (1) Grazing and fire are the most important tools for grassland management. (2) Habitat suitability is determined by grass height and cover, and each species has an upper and lower limit for both variables that determine its habitat niche. The conceptual model was conceived and implemented in the middle of fieldwork and therefore maximum values of grass height and cover are purely based on my field knowledge of habitat under which each species is likely to be confined. (3) The area is divided into management units of homogeneous habitat and these units can be managed independently. (4) Grazing reduces height and cover, i.e. grass height and cover depend on the stocking density. (5) The grass dies back in winter whether it was grazed or not and the amount of dying grass determines the intensity of fire when burned (Birch 2000). (6) Plots are burned during winter, through to spring, reducing grass cover as some grass tufts get killed. (7) Grass height during the previous season determines fuel load and therefore the degree to which burning reduces grass cover. (8) Rainfall drives grass growth: with more rain, grass can grow higher and thicker. (9) Grass never grows higher than a certain maximum height per species.

I modelled the effects of rainfall (rain_t in millimetres) and grazing ($\text{grazing}_{i,t}$) on grass height ($\text{height}_{i,t}$) in unit i in year t as additive linear changes between minimum (minheight, set at 1 cm) and maximum (maxheight, set at 50 cm) grass height for each management unit at time t as follows:

$$\text{height}_{i,t} = \max(\min(r \times \text{rain}_t - \text{grazing}_{i,t} \text{ x stdens}, \text{maxheight} - \text{grazing}_{i,t} \text{ x stdens}), \text{minheight}) \qquad \text{(eqtn 1)}$$

where max and min are the maximum and minimum functions, respectively, r is the constant determining the relationship between rainfall and height, and stdens is the stocking density. Since standing grass dies back during the winter, grass height does not depend on the previous year's grass height or fire. I allowed the grazing effect to vary among units to account for the possibility that not all units will be grazed equally at a certain stocking density. The grazing effect was thus randomly drawn from normal distribution with parameters gmju and gsig. Setting gsig = 0 causes the grazing effect to be homogenous across units.

Grass cover ($\text{cover}_{i,t}$) depends on grass cover during the previous year ($\text{cover}_{i,(t-1)}$) as surviving turfs continue to grow between a minimum (mincover, %) and maximum (maxcover, 100%) according to the following equation:

$$\text{cover}_{i,t} = \max(\min(\text{cover}_{i,t-1} - f \times \text{fire}_{i,t} \text{ x } \text{height}_t - \text{grc} \times \text{grazing}_{i,t} \text{ x } \text{stdens} + \text{cr} \times \text{rain}_t, \text{maxcover}), \text{mincover}). \qquad \text{(eqtn 2)}$$

where fire is a binary variable capturing whether the unit was burnt or not, f determines the relationship between fuel load (previous year's grass height) and the amount by which a fire reduces cover, grc is the effect of grazing on cover, and cr is the effect of rain on cover. In this basic version of the model, I let units burn randomly with a probability determined by the proportion of units to be burned. I make an assumption that the study area is a matrix of 10 x 10 grid (consisting of grass only) where within each grid habitat suitability for each species is determined by maximums and minimum values of grass height and cover determined at random. To start with, and to test model performance, I first predicted habitat suitability for the following six small common grassland birds: African Pipit *Anthus cinnamomeus*, Cape Longclaw *Macronyx capensis*, Wing-snapping Cisticola *Cisticola ayresii*, Yellow-breasted Pipit *Anthus chloris*, Common Quail *Cortunix coturnix* and Long-tailed Widowbird *Eupletes progne*. Each year, I randomly determined the number of patches that are suitable for these six species found at Ingula, assuming that they have lower and upper tolerance limits for grass height and cover (Table 1, Fig. 1). If the grass in the unit was within these limits, I assumed the species could occur there and would otherwise be absent. The model could easily be expanded to allow for more sophisticated habitat suitability functions but I opted to model a simple form of presence/absence as a starting point. The model makes a further assumption that species-specific habitat optima differ amongst the species and are determined more by grass height than grass cover or vice-versa or both values are important (Table 1).

I chose model parameter values that were most consistent with my knowledge of the system (Fig. 2, Table 2.) and explored the behaviour of this model on a hypothetical landscape of 10 x 10 identical management units. I initiated the model by randomly generating values for grass height and cover from a uniform distribution between the minimum and maximum grass height and cover, respectively. I then let the model run for 50 years and determined how many species would find suitable habitat at the end of each simulation. I implemented and analysed the model in R (R Development Core Team 2013).

Adapting the model to the landscape at Ingula

Next, I adapted the model to the actual Ingula landscape to reflect that because of variable topography and grassland habitats some birds can only be confined to certain areas of the study and not others. To do so, I divided study site (grassland habitat only) into management polygons using 1: 50 000 topographic maps and ArcView GIS 10.1 (Fig. 3). Integration of GIS, together with expert knowledge, is increasingly used to delineate suitable habitat to assist conservation of fauna and flora (e.g. Lauver, Busby & Whistler 2002; Provencher *et al.* 2007; Johnson *et al.* 2010; Pillsbury *et al.* 2011; McFarland & Mathewson 2012; Yackulic *et al.* 2012; Reza *et al.* 2013). Also, spatial modelling might be more meaningful to managers if the model is applied to the digital version of a habitat with which they are familiar, where they can test alternative scenarios and view simulation results on maps of habitat with which they are familiar (e.g. Hardesty & Adams 2000; Hemstrom, Korol, & Hann 2001; Keane, Parsons & Hessburg 2002; Provencher *et al.* 2007). In this improved version, the maximum upper limits of grass height and cover and minimums for each species were adjusted following the data analysis and results of chapter 4 and 5 of this thesis plus my previous field knowledge of how each species is likely to respond from these variables.

I considered only grassland that Eskom is planning to manage for bird conservation and that excluded wetlands, mountain forests, areas that are too heavily degraded through construction and a few areas that are otherwise not expected to be actively managed for conservation. I used a close-up version of a free, online 1Map GIS mapping software tool to delineate the boundaries of each polygon with homogeneous habitat and topography. These polygons were digitised in ArcView GIS 10.1 using an on-screen digitising approach and subsequently captured into ArcView as shapefiles. Each polygon was numbered and its area subsequently calculated within ArcView. Through the use of a high-resolution, close-up contour map of online 1Map, the boundaries of each polygon were accurately estimated. This resulted in 63 grassland polygons of varying topographic aspects and altitude (Fig. 3), which replaced the arbitrary management units of the more basic model described above.

In addition to grass height and cover, there are other habitat features that might limit bird species. For example, Denham's Bustard *Neotis denhami* does not occur on steep slopes, regardless of whether grass height and cover are suitable or not. I therefore created a mask to exclude species from polygons where they are not actually found based on my field knowledge of where species were actually recorded during fieldwork represented by 1 otherwise 0 if I have no field evidence to suggest that a species were ever recorded within a polygon. And in most cases the chosen species were known to breed within such polygons. I increased the number of bird species to 20 by including several large species that are threatened and rare (Barnes 2000) which are a priority for conservation (Table 1). I ran the model with these modifications (and improvements of my conceptual model) and examined the conditions that led to persistence of the most species after 50 years.

EFFECT OF FIRE AND GRAZING ON HABITAT SUITABILITY FOR BIRDS

To test the effect of fire on habitat suitability for these 20 species, I set up 10 replicate simulations with increments of 10% between 0 and 100% of proportion of polygons burnt. Similarly, to test the effect of grazing on habitat suitability, I increased the stocking density in increments of five animals per mean polygon area (60ha) between 0 and 50 animals. For both effects I then plotted the number of species for which suitable habitat persisted under each scenario.

SENSITIVITY ANALYSIS

Sensitivity analysis is a procedure carried out to identify the model parameters that exert most influence on model outputs (Hamby 1994) or to investigate which model parameters are responsible for variation in model prediction (Quillet *et al.* 2013). Hamby et al. (1994) reviewed techniques for parameter sensitivity analysis of environmental models and their merits and demerits. Among several techniques, the simplest is to vary one parameter at a time, while keeping other parameters in the model fixed (Starfield & Bleloch 1991; Hamby 1994; Cariboni *et al.* 2007; Smith *et al.* 2007; Frolking *et al.* 2010; Thogmartin 2010; Quillet *et al.* 2013), which I used here. I carried out sensitivity analysis on the improved version of my original model.

The key output variable of my model is the number of species for which suitable habitat (expressed in terms of maximum grass heights and cover and their minimums suitable for each species) persisted after 50 years, and I examined sensitivity of this variable to variation in the parameters. I increased the value of each parameter by 10%, one at the time, and recorded the difference in number of species to model runs with the original parameter values.

Results

At the chosen parameter values, suitable habitat for all six species in the conceptual model persisted over 50 years (Fig. 4). In the second model, the number of species for which suitable habitat persisted over 50 years varied around 15 species. Figures 5-8 show the result of one simulation run for 12 small grassland and six large species, separately. Separating into groups of five was done for better visual graphical presentation. Amongst the 12 small grasslands birds, Wing-snapping Cisticola, Cape Longclaw, African Pipit and Zitting Cisticola occupied the highest number of suitable polygons during repeated runs, standing out from the rest of small grassland species (Figs.5 & 6). The Yellow breasted Pipit, the only threatened species amongst the small birds occupied few polygons characterized by extinctions and colonisation in 50 years (Fig. 5). The large species were generally rare and tended to go extinct during the 50-year-run period. Of the large birds Southern Bald Ibis and Secretarybird occupied the highest number of habitats (Figs. 7 & 8).

No suitable habitat persisted for any of the species in the absence of fire (0% burned) or when all polygons were burned every year (100%). The highest habitat suitability was attained at 20 to 30% of proportion of burnt polygons (Fig. 9). This corresponds to an average fire return interval of three to five years. Similarly, intermediate levels of grazing led to suitable habitat for the highest number of species, while either no grazing (0 animals) or 50 animals per polygon led to the lowest number of species finding the habitat suitable after 50 years (Fig. 10).

The sensitivity analysis showed that habitat suitability was most sensitive to variation in the rain constant (cr), followed by the proportion of polygons that were burned (f), the grazing effect cover (grc) and the grazing effect on height (gsig). The model thus suggests that grazing and burning are indeed important drivers of habitat suitability, but that rainfall is also important.

Discussion

Models offer a tool for integrating different types of knowledge about a system and can tell us which factors are likely to be important. Models are also are increasingly used to guide conservation decisions (Li *et al.* 2002, 2009; Rasmy *et al.* 2002; Store & Jokimäki 2003; Johnson & Gillingham 2004; Chee & Wintle 2010). In this chapter, I combined my knowledge about the drivers of avian diversity, acquired through a literature search, my own data collection and more qualitative field knowledge, to develop a simple system model for Ingula. The model showed that grazing and burning are indeed likely to be powerful management tools. The effect of rainfall on grass growth was also a critically important parameter. The next step should be to conduct controlled experiments to measure the effects of grazing, fire and rainfall on avian diversity. Results from such experiments could be used to update the model so that we can have more confidence in the predictions. The model could be used as a basis for developing a set of alternative models that form the core of an adaptive management process.

The explicit representation of management polygons on which birds are actually known to occur is strength of this model. Yet, many features could be improved to make the model more useful for management. The model is currently initialised by randomised grass heights and cover within polygons, and I ran the simulations for 50 years to minimise the effects of particular initial conditions. For adaptive management, one-year forecasts under different management interventions are needed. However, it would be straightforward to start the model from known grass height and cover once that information is collected for each polygon. In the current model set-up, polygons are burned at random. However, it would again be straightforward to simulate the effect of burning specific polygons once management has gained control over fire. Because of the random burning, my simulations likely underestimate the possibilities for management to create suitable habitat for rare species by targeting specific interventions at the polygons that are most important for these species. Another straightforward extension of the model would be to replace the simple habitat selection functions by more realistic ones. The model could then be easily used to predict densities, rather than just occupancy.

In the absence/little grazing one would expect Long-tailed Widowbird (Fig. 6) to occupy the highest number of plots like the first four commonest species. But this is not the case because it occupies only few polygons that lie adjacent to the wetlands. Red capped Lark and Crowned Lapwing (Figs. 5 & 6) should be everywhere only if the habitat is heavily grazed. Overall all large bird species occupied only a few polygons in all simulations with the exception of Southern Bald Ibis and Secretarybird which have large home range. Denham's Bustard too has a large home range except that at Ingula it occurs only on few polygons upon hilltops where it has been proven breeding. For most large birds it is not a management concern that they occupy few polygons because they are naturally rare at Ingula, i.e. they have only a few polygons that they can occupy, because of factors that are not under the control of management. However, this group is a priority for conservation, both nationally and globally, according to respective BirdLife International species factsheets and South African Red Data lists. Of the species at Ingula, Southern Bald Ibis, Blue Crane, Secretarybird and Wattled Crane are now classified as Vulnerable. Blue Crane and Wattled Crane both had one breeding pair at Ingula at the beginning of my study. As of 2010 to 2013 Blue Crane did not breed at Ingula but occasionally still used habitat for feeding during breeding and out of breeding seasons. This can be attributed to human distance but also lack of heavily grazed habitat early in the breeding season. Only one pair of Wattled Crane breeds at Ingula (2005/06-2013/13). Lack of grazing after burning makes adjacent wetlands where it breed too thick resulting in the pair moving between three alternative habitats to nests in response to unsuitable habitat (pers com). I estimated that Ingula could potentially host four more pairs if the breeding habitat within the wetland is made suitable during autumn to winter the times which coincides with its breeding at Ingula.

A recent analysis of Coordinated Avifaunal Road counts data (CAR) revealed that Secretarybird have declined nationally since 1983 and are threatened due to habitat loss (Hofmeyr, Symes & Underhill 2014). Denham's Bustard is currently listed as 'Near-threatened', while Red-winged Francolins and White-bellied Korhaans are of 'Least Concern'. White-bellied Korhaans breed on heavily grazed grasslands and were common at the beginning of the project throughout Ingula grasslands but have since declined to about two pairs at Ingula. It was, however, still widespread outside Ingula in neighbouring farms in 2013, indicating that the removal of cattle had a negative impact on this species inside Ingula. The Grey Crowned Crane has been recently up-listed to 'Endangered' (BirdLife International, 2014), however, at Ingula this species has increased from one pair to about 10 pairs (pers. obs) between 2005-13, indicating a positive influence through the lack of grazing within Ingula wetlands.

The majority of grassland bird species require open grasslands to search for food and sometimes dense and tall grass to hide from predators or to hide their nests. Both grass height and cover are important attributes that provide these requirements (Jansen *et al.* 2001; Fuhlendorf *et al.* 2006; Maphisa *et al.* 2009). The result of this study are consistent with the notion that grassland birds evolved with fire and grazing (Fuhlendorf & Engle 2001; Fuhlendorf, Engle & Moreira 2004; García *et al.* 2007; Pillsbury *et al.* 2011). My model suggests that a low proportion of burned polygons, and light grazing, promotes suitable habitat for the largest number of species. However, the model parameters and assumed relationships need to be backed up by experiments before more precise recommendations can be made.

The sensitivity analysis revealed model parameters that need future attention because they had a large effect on the results. Amongst the reasons that ecological modellers carry out sensitivity analysis is to identify the parameters that require additional research to further strengthen model predictions (Hamby 1994). In particular, the strong effect of rainfall-related parameters suggested that the relationship between rainfall and grass growth should be examined in more detail. This includes a need for better empirical support for the parameter values, and also a need to examine alternative ways of modelling the rainfall effects.

Conclusion and management implications for conservation

Based on my current knowledge of how birds react to fire and grazing, the current model has performed its function of linking habitat suitability and management actions at Ingula. It forms a starting point for further studies and a basis for more refined models. The species included in this study (Fig. 1) can be broadly split into three main groups that could be used as indicators: (1) Bird species that indicate heavy grazing or recently burned grass (e.g. Red-capped Lark, Crowned Lapwing, Southern Bald Ibis and White-bellied

Korhaan). (2) Bird species that prefer intermediate grass height and cover (e.g. African Quailfinch, Common Quail, Zitting Cisticola and Wattled Crane). (3) Bird species that occupy tall rank grass (e.g. Long-tailed Widowbird and Grey-crowned Crane).

Conserving avian diversity, with an emphasis on species of high conservation priority, presents a management challenge because different species have conflicting habitat needs. The first group, species that prefer heavily grazed grasslands, is probably the most difficult group if threatened birds are involved. Heavy grazing leads to habitat degradation, such as the problem with erosion – in the long run. However, because most of these species breed early (August to November), burning shortly before they start breeding will provide short grass and ensure that their habitat requirements are met. In the case of Southern Bald Ibis, Ingula Management has built an artificial nesting colony, with ledges to compensate for the loss of their former breeding cliffs, which are now inundated by the dam. If the foraging habitat is not made suitable for these birds, they may not find artificial ledges attractive. The White-bellied Korhaan is a conservation challenge because it breeds outside the burning season and yet requires fairly short grass. This requires targeted, heavy grazing during the breeding season of the few polygons where the species breeds. Modifying the model to include the month of grazing or burning, or even the timing of rainfall, could increase the predictive power of this model. Species in the third group, with a preference for tall grass, are associated with wet grasslands and are benefiting under the current management of no grazing. For example, Grey-crowned Crane has increased from one pair at the start of the project to about 10 pairs, as of 2013, based on my monitoring records (pers. obs).

Heavy grazing will have to be regulated, and fire be applied proactively. With no grazing and no fire, these grasslands become too thick and will only be suitable for a few species. The delineation of the study area into management units will help guide management to ensure that habitat is made suitable in different polygons that coincide with the period during which priority species will be breeding.

There is more to conservation of Ingula than just grassland birds

Moist, high-altitude grasslands are important, not only for birds, but for a variety of other organisms and ecosystem processes. At Ingula, the grasslands surround a wetland and border cool mountain escarpment forest, all of which are unique and contain threatened flora and fauna. These two latter habitats are also a priority for current Ingula management and therefore require a separate approach of adaptive management. In particular, the wetlands have attracted most management attention (e.g. Norström *et al.* 2009; Finne *et al.* 2010). At the onset of the Ingula construction project, cattle were taken out of Ingula because they were seen as responsible for the deterioration of the wetland and surrounding grasslands (e.g. Mentis 2006). Other than for the much publicised White-winged Flufftail, Ingula wetlands are important for a variety of other threatened birds such as African Grass-Owl *Tyto capensis* (Maphisa 2012) and two species of cranes. African Marsh-Harriers *Circus aeruginosus* and Black Harriers *Circus maurus* were regular visitors during the early years of the project, and a variety of crakes, rails and waders were regularly heard calling but have now become rare.

Since cattle were removed, the wetland is fast becoming thick, with fine sedges overtaken by *Typha capensis*. Tichit *et al.* (2007) developed a dynamic model to predict how livestock grazing may be used to improve a wetland for nesting wader birds. Their overall findings were that grazed wetlands had a more diverse wader community compared to wetlands without grazing. In this regard, the Ingula approach will be the same except that the objective of Ingula management would be to balance biodiversity targets with wetland degradation that can only happen if the wetland is heavily grazed.

Based on the oral questionnaire surveys that I carried at the beginning of the project, hunting and debarking trees for muthi (pers. obs) was rampant within the Ingula escarpment. Based on this survey and my own observations, Ingula's escarpment forests are a home to a variety of charismatic and threatened fauna and flora. These include at least one pair of Martial Eagles *Polemaetus bellicosus*, Blackcap *Lioptilus nigricapilus*, Bushpig *Potamochoerus larvatus*, Bushbuck *Tragelaphus scriptus*, Serval *Leptilurus serval* and Caracal *Caracal caracal*. At least two species of *Podocarpus* trees occur within Ingula's forest, with two species of *Protea* confined to mountain forest margins while a third species is confined to rocky habitats on the lower site. Other threatened tree species include *Ocotea bullata*, *Warburgia salutaris*, *Rapanea melanophloes* and *llex mitis*. There is uncertainty about how to manage these forests (Mentis 2006). Following wet years, the forest is susceptible to fire because of increased grass fuel load, which bridges the interface between grassland and forest. Such fires, as happened for example in 2003 and 2011, have long-lasting effects because forests take decades to recover. Targeted grazing along to along the forest margins would reduce the risk of fire entering the forest. My spatially explicit modelling approach offers a starting point for a more integrated model that would allow management to predict the effects of specific management actions (especially burning and grazing) in specific management units, including the wetland and forest with the transition zones between these habitats.

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Table 1. Core Ingula grassland bird species used in the model of management effects on avian diversity at Ingula

Species (abbreviation)	**Gheight [cm]**	**Gcover [%]**	**Regional threat status**	**Known habitat preferences**	**Breeding**
African Pipit (AP)	5-40	10-50	unclassified, abundant	heavy to lightly grazed areas	Nov - Feb
Cape Longclaw (CLclaw)	5-40	10-70	unclassified, abundant	heavy to lightly grazed areas	Nov - Feb
Wing-snapping Cisticola (WsC)	5-40	5-50	unclassified, abundant	heavy to lightly grazed areas	Nov - Feb
Red-capped Lark (RcL)	5-20	5-50	unclassified, abundant	heavy grazing or recently burned	Sept - Nov
Yellow-breasted Pipit (YbP)	15-35	30-60	VU & declining Barnes 2000	medium grass height with grazing	Dec - Jan*
African Quailfinch (AQf)	30-50	30-80	unclassified, abundant	rank, tall grass height open & modified	Jan - Mar
Common Quail (CQ)	20-50	30-60	unclassified, abundant	medium grass height with grazing	Dec - Jan
Long-tailed widowbird (LtWbd)	20-50	40-90	unclassified, abundant	Tall, rank, moist grass	Nov - Jan
Crowned Lapwing (CLwg)	5-15	10-50	unclassified, abundant	short-heavily grazed/burned	Aug - Oct
Zitting Cisticola (ZC)	10-50	10-80	unclassified, abundant	construct nest in medium grass heights	Dec - Jan
Eastern Long-billed Lark (ELbL)	10-45	30-40	unclassified, localised	short-medium grass height	Sept - Nov
Ant-eating Chat (AEC)	10-40	10-50	unclassified, abundant	short-medium grass height	Oct - Nov
Southern Bald Ibis (SBI)	5-20	10-60	VU & declining Barnes 2000	heavily grazed/recently burned lands	July - Nov*
Denham's Bustard (DB)	10-45	10-60	VU & declining Barnes 2000	hilltops, short-medium grass heights	Jan - Feb*
White-bellied Korhaan (WbK)	5-40	10-50	VU & declining Barnes 2000	fairly short-medium grass height	Jan-Feb*
Grey-crowned Crane (GcC)	20-50	50-90	VU & declining Barnes 2000	moist grasses and sedges bordering wetlands	Dec - Jan*

Blue Crane (BC)	5-25	15-80	VU & declining Barnes 2000	short - medium grass height	Oct - Nov*
Wattled Crane (WC)	20-50	30-80	CR & declining Barnes 2000	autumn-winter, moist grasses and sedges	Apr - Jun*
Red-winged Francolin (RwF)	30-50	30-80	unclassified, localised	medium grass height with grazing	Jan - Feb
Secretarybird (SB)	20-50	30-70	declining Barnes 2000	medium to tall grass	Mar - Oct*

Notes: The second column shows the minimum and maximum grass height (cm), followed by minimum and maximum cover (%) that define a species habitat niche. In the model, I assume that a species can exist in a patch with suitable grass height and cover. The last column gives the main breeding seasons based on evidence of monitored nests data 2005/06 – 2012/13 (pers obs), or estimated on individuals seen with young. Species that are Vulnerable and Critically Endangered (e.g Barnes 2000)are represented by VU and CR respectively.*

Table 2. List of parameters and constants that were subjected to sensitivity analysis to determine parameters exerting most influence on model outputs. The range indicate the amount to which the model was tweaked to yield the maximum number of birds surviving over 50 years. Positive sensitivity values mean that increasing the parameter value increases species richness, whereas negative values mean that increases in the value of this parameter causes species richness to decrease.

Parameter name	Parameter abbreviation	Range examined	Best setting	Change in species richness (number of species)
Effect of rain on height	R	0 - 1	0.1	1.7
Grazing effect on height (mean)	gmju	0 - 1	0.5	1.6
Grazing effect on height (sd)	Gsig	0 - 10	6	-0.2
Scaling of grazing effect on height for cover	Grc	0 - 1	0.05	-0.4
Amount by which fire reduces cover	f (fire constant)	10-50	40	0.7
Rain constant for cover	Cr	0 - 1	0.05	-2.3
Amount of rainfall	rain (mm)	200 - 600	250	0.9
Stocking density	stdens (animal unit)	5 - 50	10	0.9
Proportion of burning	Fire	0 - 1	0.3	-0.7

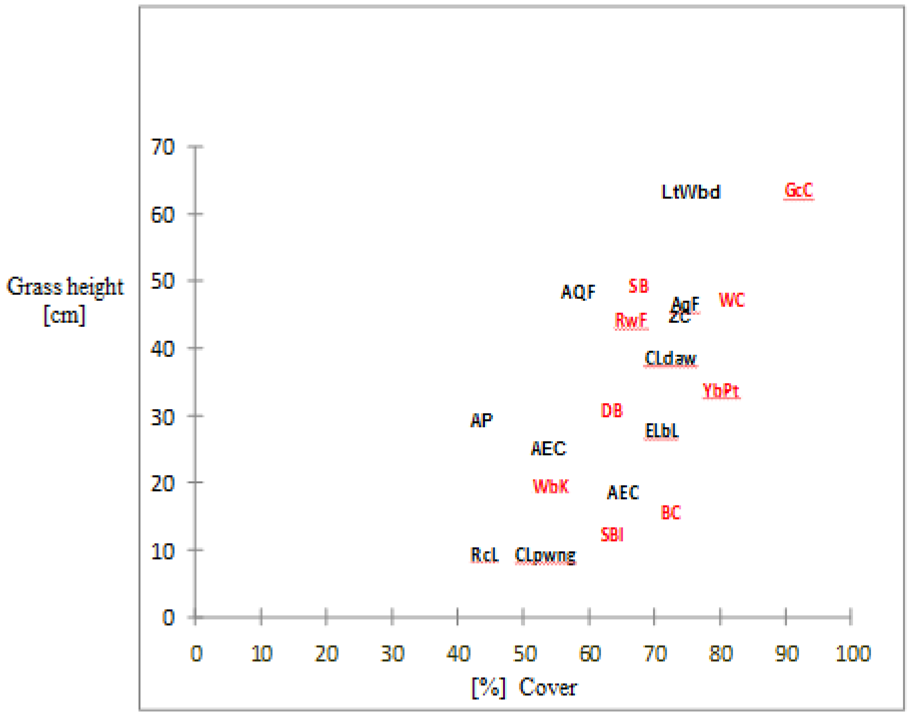

Fig. 1. Schematic representation showing habitat preferences of 20 grassland bird species relative to grass height and cover. See Table 1 for abbreviated species names. Species in red are priority for Ingula management. This qualitative figure is based on the data presented in Chapters 4 and 5 and additional my additional observations on how each species is likely to respond to increasing grass height and cover.

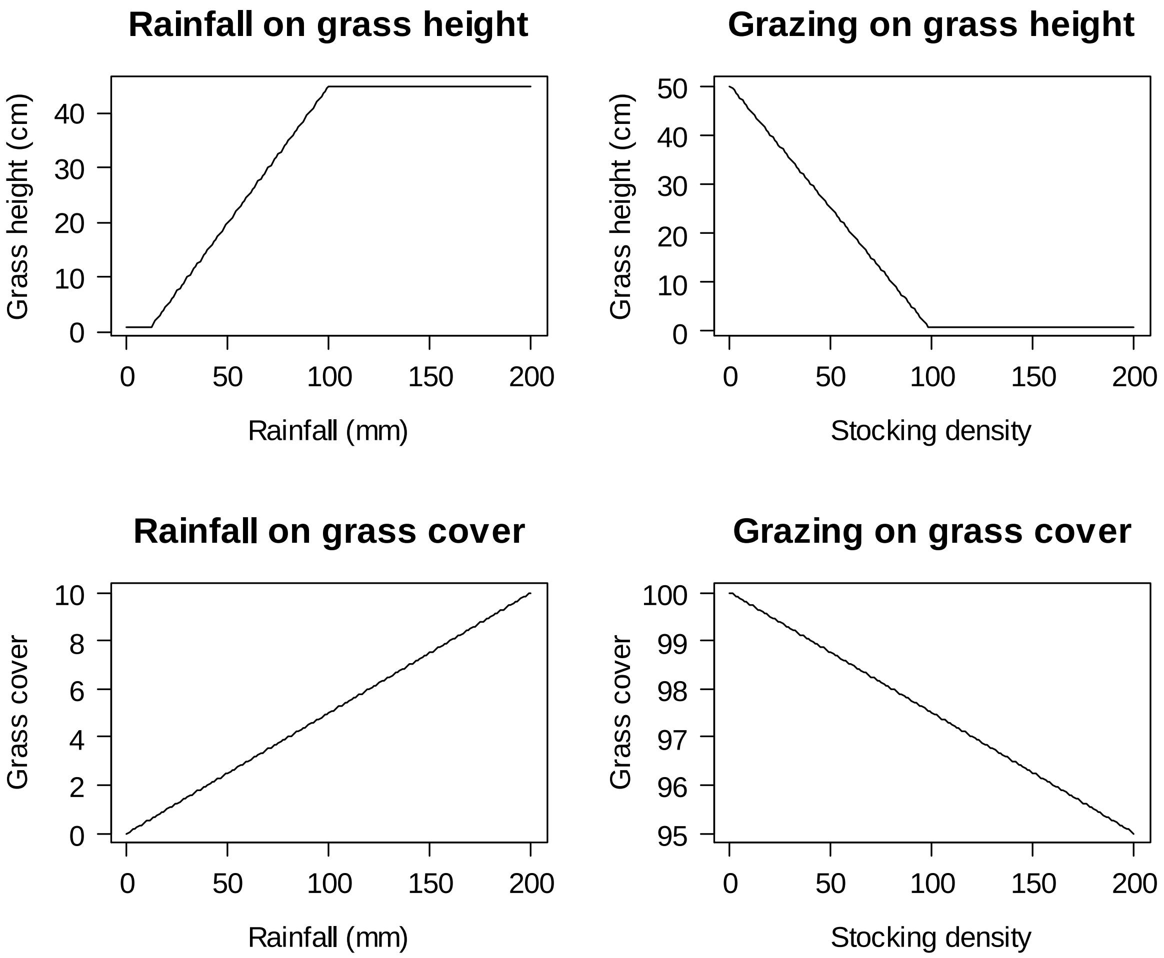

Fig. 2. Assumed relationships between rainfall and stocking density on the one hand and grass height and cover on the other hand for the standard parameter settings.

Fig. 3. Map of Ingula overlaid with three vegetation types and additional features important for managing biodiversity. Sixty-three polygons represent homonegneous grassland habitats and were used as management units in the model.

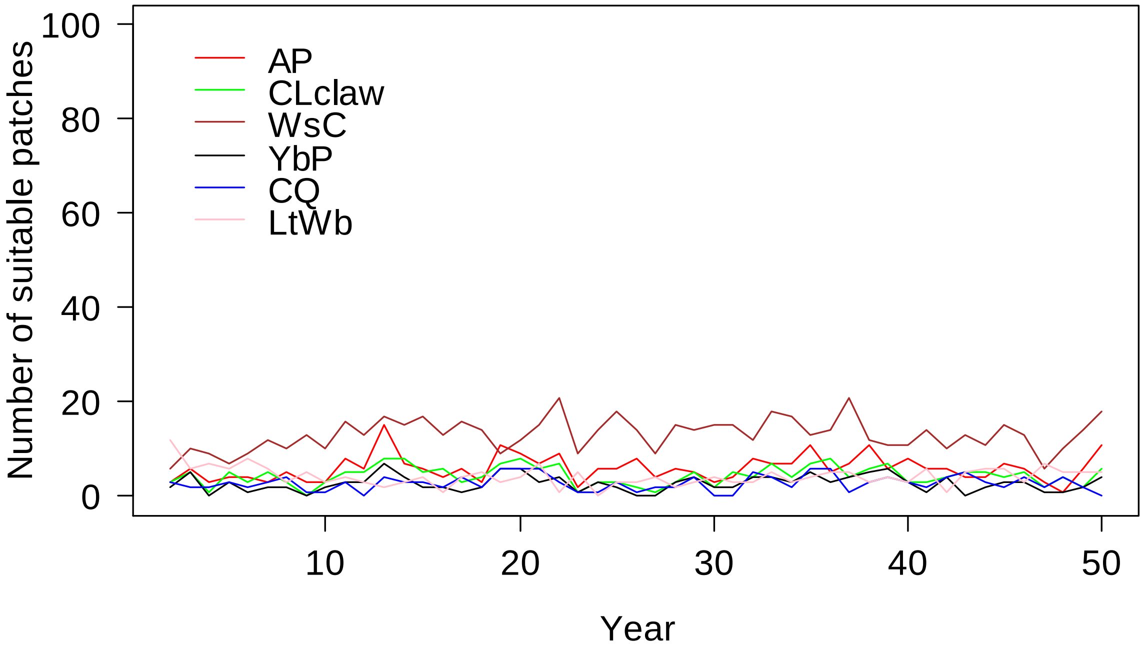

Fig. 4. Example of a simulation using the conceptual model. The figure shows the number of suitable patches persisting over 50 years under the parameter settings given in Table 2. Specifically, 30% of the plots were burned each year and the stocking density was 10 animal units per plot.

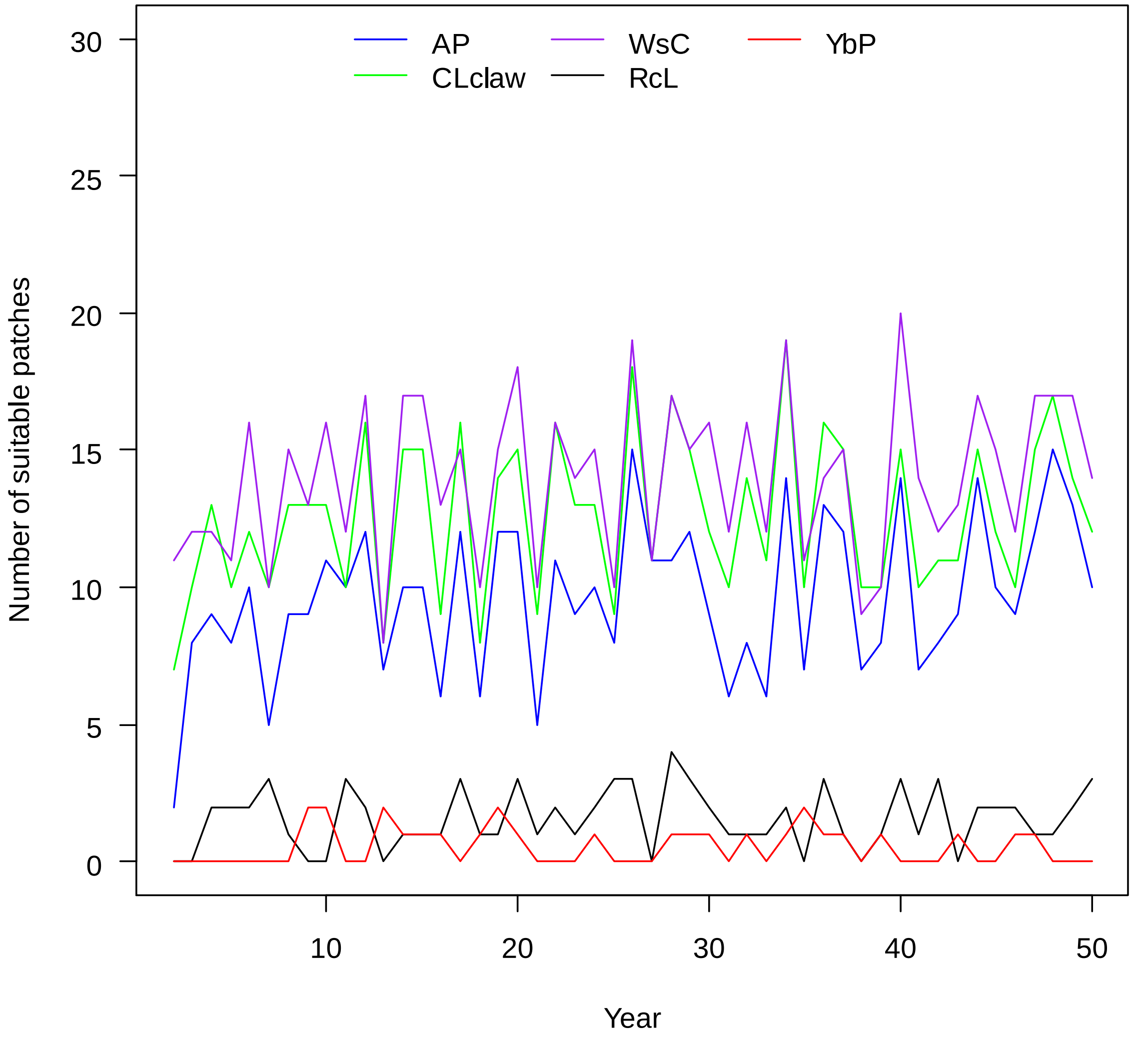

Fig. 5. Persistence of first group of small grassland birds at Ingula with simulation set at 50 years, with 30% of habitat polygons burned and the area stocked with 10 animal units per polygon. Number of plots occupied is determined by random number of polygons where a species is proven to occur and minimums and maximums of grass height and cover.

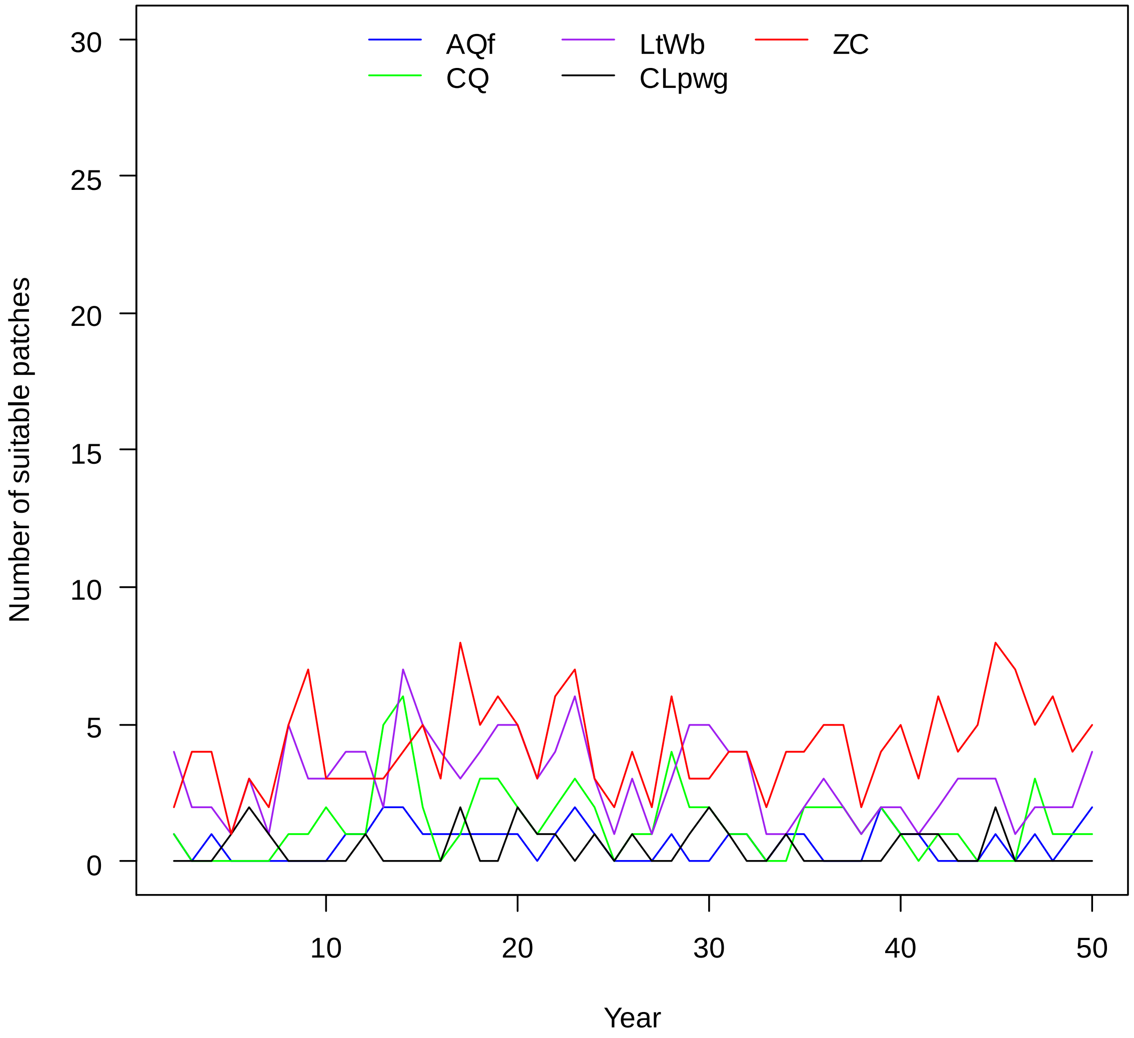

Fig. 6. Persistence of second group of small grassland birds at Ingula with simulation set at 50 years, with 30% of habitat polygons burned and the area stocked with 10 animal units per polygon. Number of plots occupied is determined by random number of polygons where a species is proven to occur and minimums and maximums of grass height and cover.

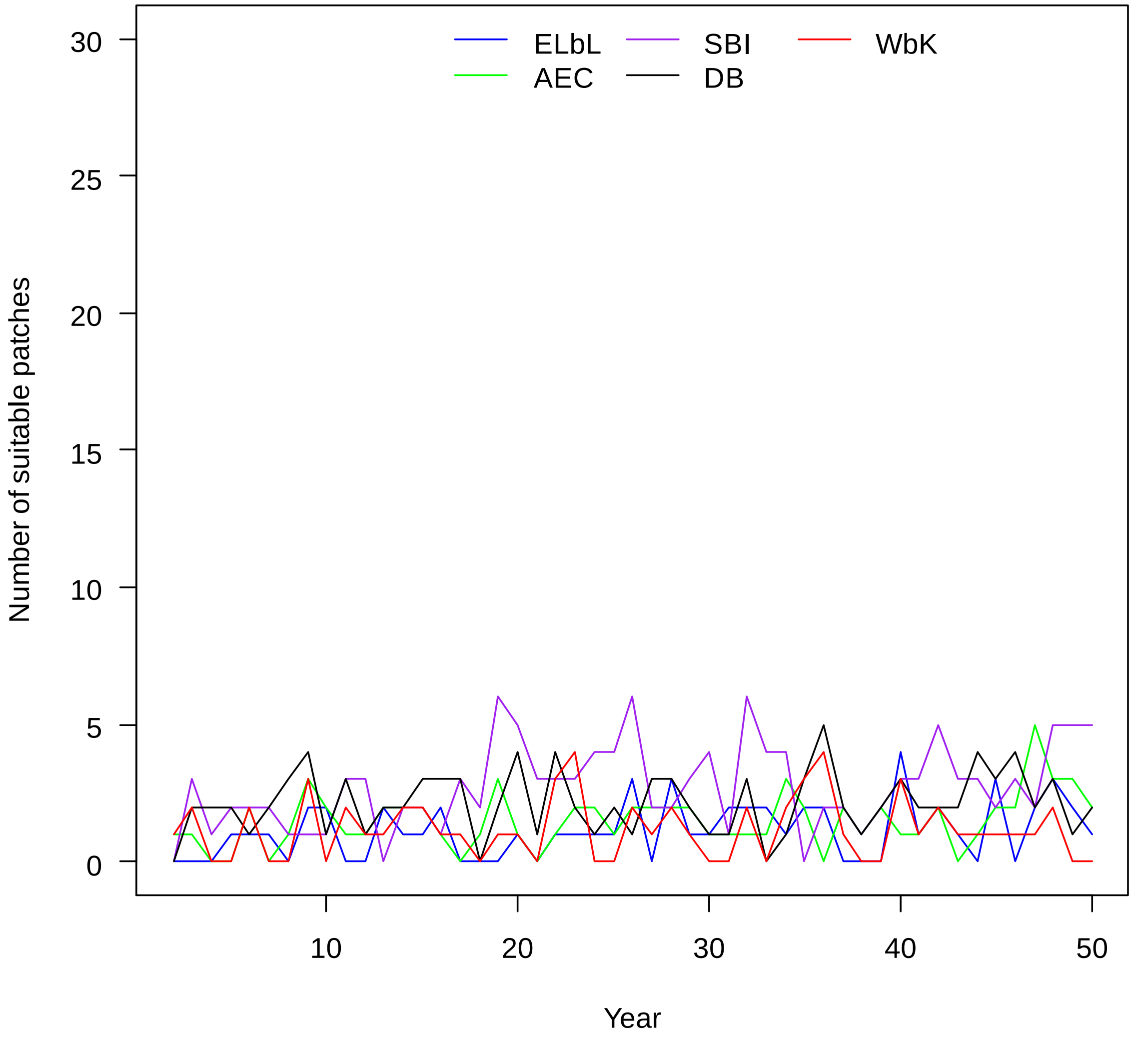

Fig. 7. Persistence of third of two small common grassland plus three large threatened birds at Ingula with simulation set at 50 years, with 30% of habitat polygons burned and the area stocked with 10 animal units per polygon. Number of plots occupied is determined by random number of polygons where a species is proven to occur and minimums and maximums of grass height and cover.

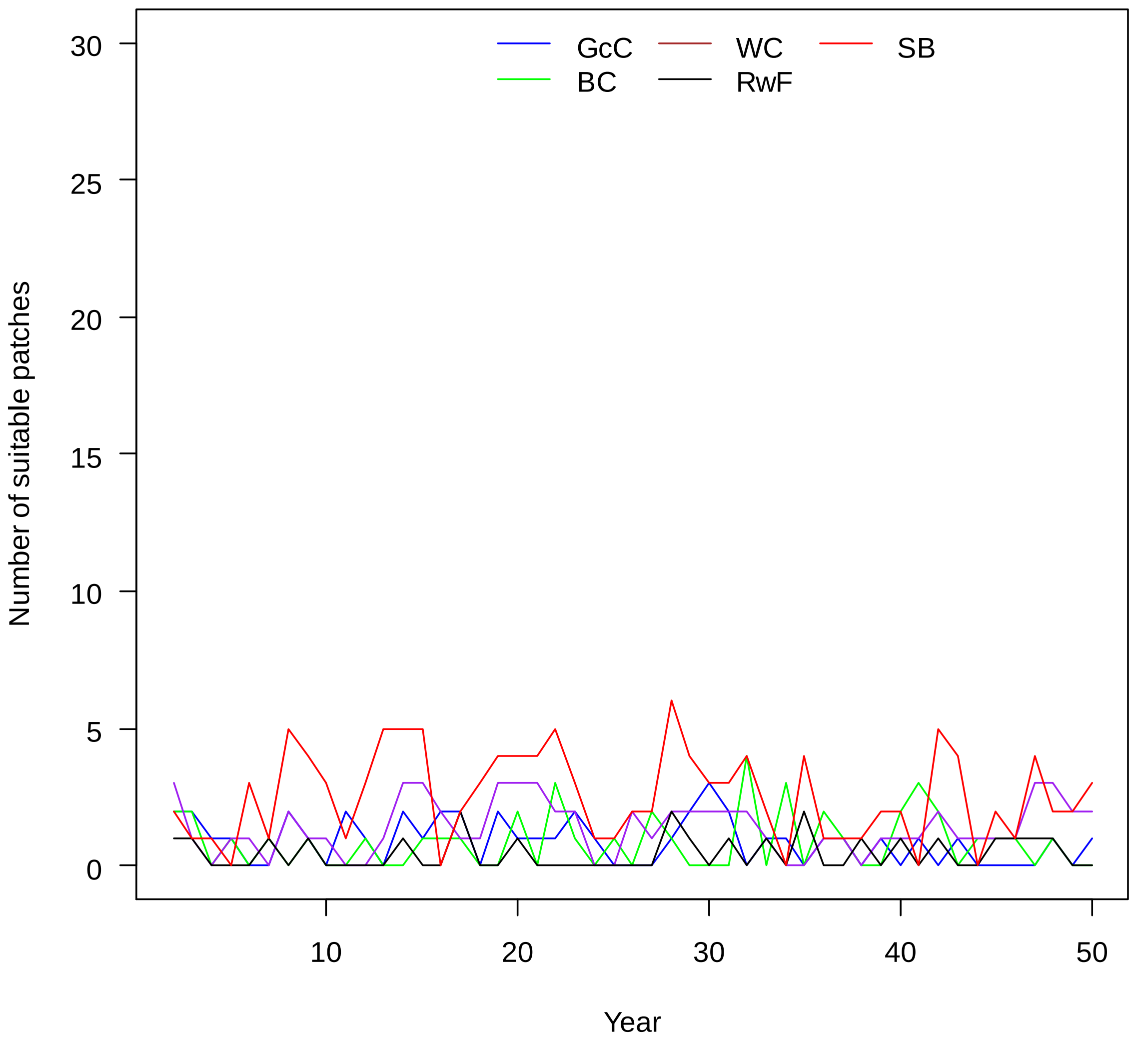

Fig. 8. Persistence of fourth group of large five threatened grassland birds plus one uncommon grassland game bird at Ingula with simulation set at 50 years, with 30% of habitat polygons burned and the area stocked with 10 animal units per polygon. Number of plots occupied is determined by random number of polygons where a species is proven to occur and minimums and maximums of grass height and cover.

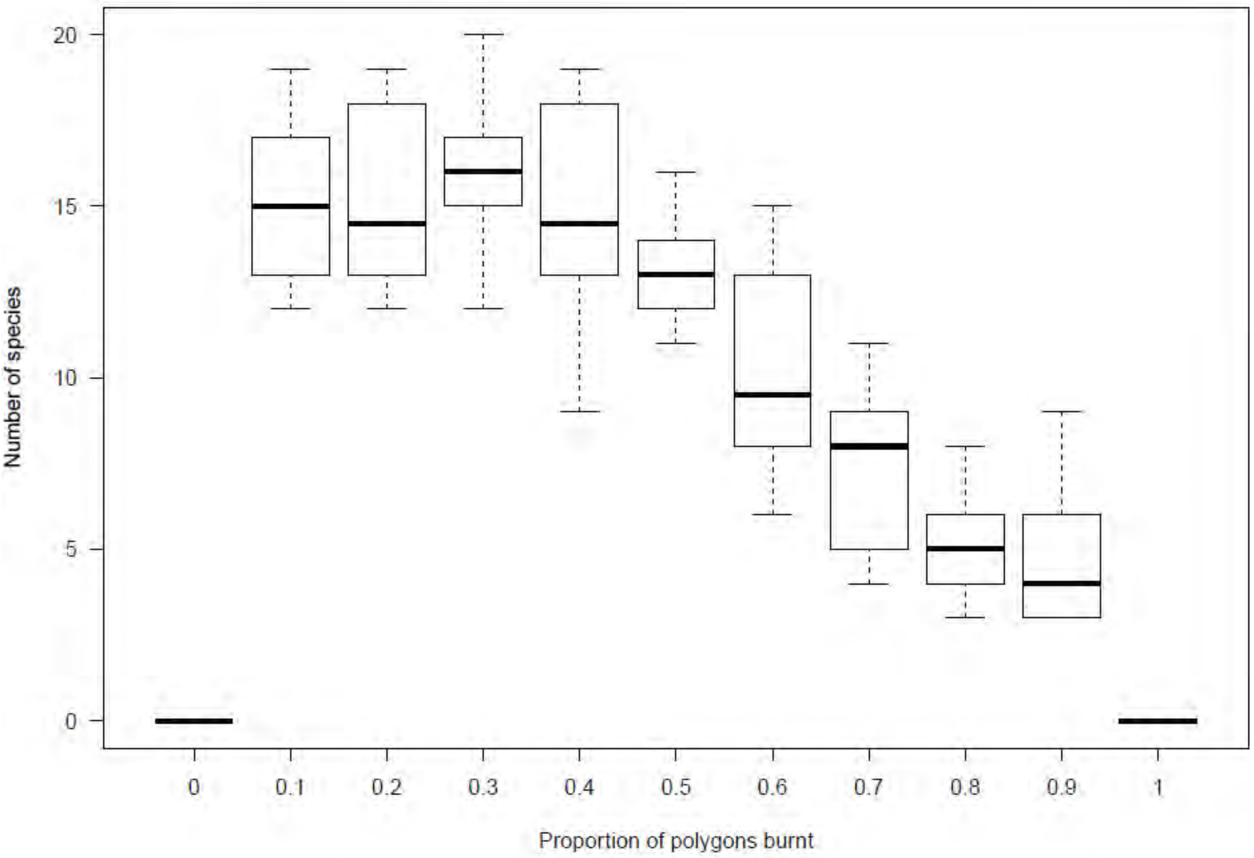

Fig. 9. Habitat suitability for 20, core grassland birds relative to the proportion of polygons burned, with 10 replicates of 50 years simulations per run.

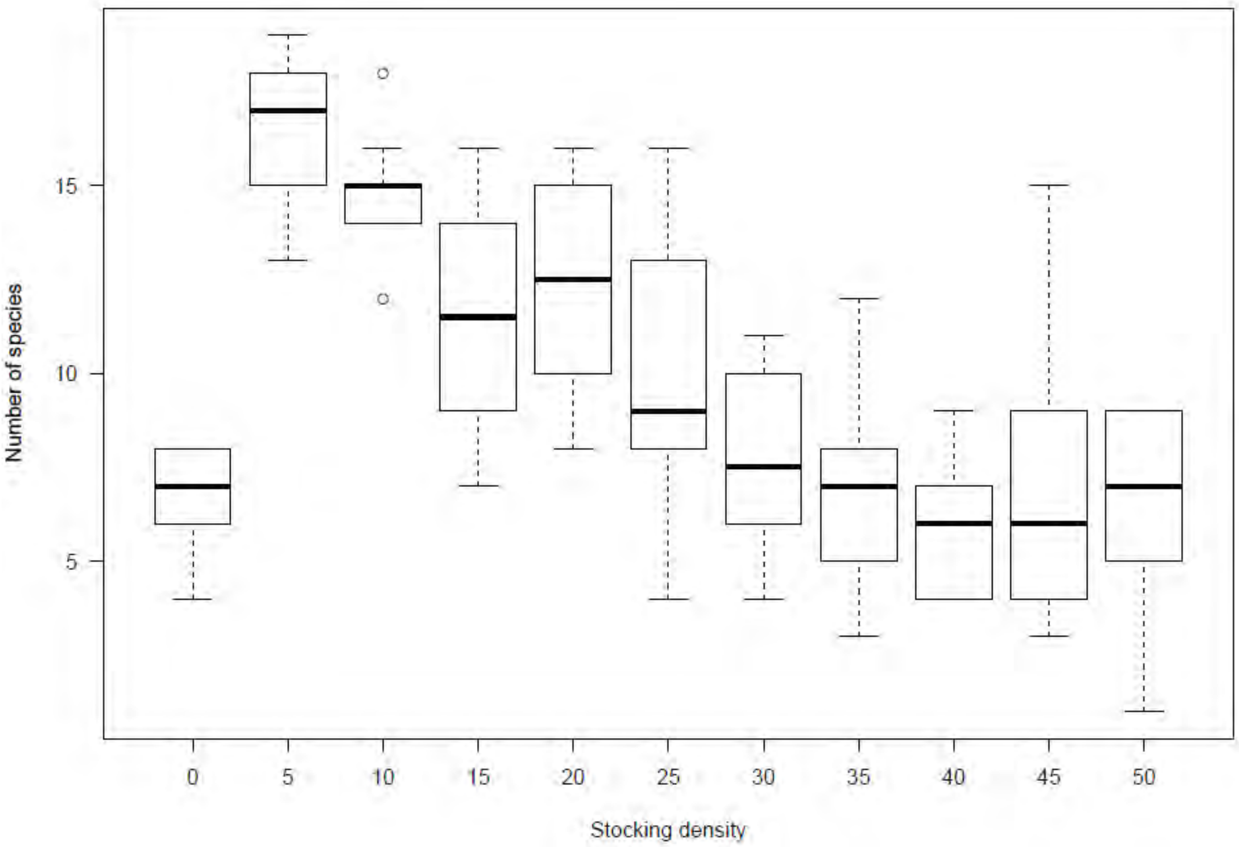

Fig. 10. Habitat suitability for 20, core grassland birds relative to stocking density per animals/unit set between 0 and 50 animals per random polygon, with 10 replicates of 50 years simulations per run.

Chapter 7

> Monitoring is the process of gathering information about some system state variables(s) at different points in time for the purpose of assessing system state and drawing inferences about changes in state over time.
>
> Yaccoz et al. 2008 *Trends in Ecology*

General conclusions and implications for conserving Ingula for avian diversity.

Introduction

The moist, high-altitude grasslands of eastern South Africa is a national priority for conservation (e.g. Allan, Harrison, Navarro & Wilgen, 1997; Hockey, Allan, Rebelo, Dean & Rabelo, 1988; Jenkins, Smallie & Diamond, 2010; Krüger, Allan, Jenkins & Amar, 2013; Maphisa *et al.* 2009; O'Connor & Kuyler, 2009) but little research has been carried out on how to manage this area for biological diversity. Harsh environmental conditions limit species richness. However, the area is renowned for both faunal and floral endemism, marked by relatively high species diversity, including threatened species requiring conservation planning and management intervention (Neke & du Plessis 2004; Archibald *et al.* 2005; Bond & Parr 2010). In the case of birds, the area is also an important breeding and wintering ground for several local altitudinal migrants and Palearctic migrants. As a result of growing threats resulting from modification of wildlife habitats and natural ecosystem in the area, there is an urgent need to prioritise conservation planning.

The value of this study

My thesis aimed to evaluate key drivers of avian diversity within moist, high-altitude grasslands of eastern South Africa to suggest a management strategy that would benefit conservation of the bird species at Ingula. Experiments that would allow me to establish causal links between particular management actions and avian diversity were not possible because management had no control over fire and grazing during my study period. Instead, I used a correlative approach with observational data, augmented by a literature review and a system model. The most important finding of my thesis is that grass height and cover were important predictors of presence and abundance for most species, although the relationships varied among species. High diversity therefore requires a mosaic of patches that vary in grass height and cover. Grass height and cover can be managed though planned grazing and fire.

Grassland bird species evolved under grazing and burning. Historically, grazing was by wildlife (Hockey *et al.* 1988) and burning was ignited by lightning (Jansen, Little & Crowe 1999; Bond & Parr 2010). Currently, fire is used as a tool to optimise grazing condition for livestock, mostly cattle and sheep, with little consideration for biodiversity. As a result, South Africa's eastern grasslands are currently heavily grazed (Jansen *et al.* 2001; Maphisa *et al.* 2009) and annually burned, which has led to habitat degradation in many places. Ingula has been set aside for biodiversity conservation and the question now is how to best manage the land for this goal. Taken together, my results suggest that some grazing is needed but high stocking densities are detrimental for avian diversity (Chapter 6). Likewise, my results suggest that intermediate levels of burning optimise the habitat for birds (Chapter 6). My results are consistent with previous observational studies suggesting that grazing and burning result in a habitat mosaic of grass height and cover that benefits the grassland bird community (e.g. Little & Crowe 1993; Jansen *et al.* 2001; Maphisa *et al.* 2009;Parr & Chown 2003; Parr & Andersen 2006; Fisher & Davis 2010). At Ingula, maintaining a mosaic of grass heights and cover is critical in summer, when birds breed, but species that breed outside summer also need management attention.

Managing grasslands with indicator species

My thesis focuses on groups of typical grassland bird species, using them as indicators for grassland diversity more generally. My justification for using indicator species is that time and resources do not allow to investigate habitat needs for all priority species (e.g. Nally & Fleishman 2004; Favreau *et al.* 2006; Mace *et al.* 2008). Some of the highest priority species are also rare or elusive, making them difficult to study or monitor. As a result, conservation managers use indicator species to infer habitat condition.

In Chapters 4 and 5, I used the most common bird species to understand how current management at Ingula is impacting birds. However, not all of these species are suitable indicator species that I would recommend to be monitored by management in the future, because common species may not be sensitive to changes in grassland management (e.g. Favreau *et al.* 2006). However, my work does suggest species that may be good indicators because they show a clear response to grass height and cover (e.g. Chapter 4 & 6). One such species is the African Pipit *Anthus cinnamomeus,* which has shown a decline within Ingula in response to increasing grass height and this observation is supported by results in Chapter 4.

Amongst others, good indicators in Chapter 4 are African Quailfinch *Ortygospiza atricolis,* a bird of fallow fields that rapidly decreased with increasing cross cover (Chapter 4). Zitting Cisticola *Cisticola juncidis* constructs a cup-shaped nest by binding tall grass tufts and enters the nest from the top; in Chapter 4 this species shows rapid increase with increasing grass height, which is its preferred habitat for nesting. In Chapter 5, persistence of Red-capped Lark *Calandrella cinerea* declined with increasing grass height and grass cover in line with its known habitat preferences (Chapter 6, Fig. 1). Since these species are common and easy to detect, they can be monitored easily.

Preparations are at an advanced stage to declare Ingula as a nature reserve (Maphisa 2012). The current Ingula conservation management plan under preparation would like to conserve Ingula's fauna and flora under adaptive management. My study has provided some key elements needed for the process of adaptive management. One key component of adaptive management is a monitoring programme that monitors the effects of management actions on the system.

Monitoring is the process of gathering information about some system state variable(s) at different points in time for the purpose of assessing the system state and drawing inferences about changes in state over time (Yoccoz, Nichols & Boulinier 2001). Biodiversity monitoring is therefore an important tool for conservation managers to evaluate whether conservation actions lead to the desired outcomes. However, biodiversity monitoring is sometimes criticised for being ineffective at integrating information into decision making and insufficiently relevant to the needs of land and resource managers (Sheil 2001; Danielsen *et al.* 2005). It is therefore important that monitoring programmes are designed carefully to ensure that they provide the necessary information to evaluate how well the management objectives have been achieved. Because monitoring has financial implications, the need and the implications of monitoring must be explicitly conveyed to the funders to ensure funding for long-term projects.

Conservation monitoring programmes are critical for detecting changes in key system variables, e.g. population size of a species that is the target of management. However, without unambiguously stating how monitoring information will trigger relevant conservation actions, some monitoring programmes have monitored species until they became extinct (e.g. Lindenmayer, Piggott & Wintle 2013). Management intervention actions may include specific experimental interventions to determine the reasons behind the observed population declines (Runge, Converse & Lyons 2011; Lindenmayer, Piggott & Wintle 2013). However, often poorly designed or implemented biodiversity monitoring programmes (Yoccoz, Nichols & Boulinier 2001; Nichols & Williams 2006; Lindenmayer & Likens 2009) that lacked a sound decision framework have failed to trigger conservation actions to halt observed declines (Nichols & Williams 2006; Mackenzie & Keith 2009; Probert *et al.* 2011; Nie & Schultz 2012; Westgate, Likens & Lindenmayer 2013; Lindenmayer, Piggott & Wintle 2013).

The importance of adaptive management and its links with adaptive monitoring

Adaptive management and adaptive monitoring are intertwined. Adaptive monitoring because it relies on long-term research to provide ecological insights into some managed system whereby conservation programmes evolve iteratively as we understand better how the system works (Fig. 1) (Lindenmayer & Likens 2009). Integrating monitoring and management intervention is clearly within the realm of strategic adaptive management, where adaptive management is ‘learning by doing’, with the aim of combining the need for immediate action with a plan for learning (van Wilgen & Biggs 2011; Lindenmayer, Piggott & Wintle 2013).

Many conservation agencies present adaptive management as diluted theory that resembles and misrepresent the actual meaning of ‘learning while doing’” (Ruhl & Fischman 2010; Biber 2011; Willians & Brown 2012). Such approaches may not be based on experimentation framework or research design that allows for understanding how the system works, may not be designed to proactively track achievement of management decisions, and may not include clear feedback loops that indicate how information will be used to evaluate or change management actions (Ruhl & Fischman 2010; Nie & Schultz 2012). The failure of decision makers to understand the need to carry out experiments is one of the greatest difficulties facing the implementation of adaptive management, and the proposal of such experimental measures is often met with negative reactions (Walters 1997; Probert *et al.* 2011). In essence, adaptive management is seen as an experiment and can therefore be implemented in the face of uncertainty as a means to reduce uncertainty.

Monitoring, therefore, is a necessary component of management and, just as management is adaptive, so is monitoring. Lindenmayer & Likens (2009) refer to adaptive monitoring as a new paradigm (Fig. 1) in conservation of wildlife resources. Adaptive monitoring provides a means to intergrate new questions into a monitoring approach for long-term research while the focus of management is not lost (Lindenmayer & Likens 2009). The key attributes here are that monitoring should be long term and that it should be geared at answering stated questions that may change or evolve over time. These questions determine how to monitor, the type of data to collect, data analysis and interpretation of the results. An adaptive monitoring framework enables monitoring programmes to evolve iteratively as new knowledge becomes available which may sometimes leads to a changed of management questions (Lindenmayer & Likens 2009).

Ingula and adaptive management

The literature review (Chapter 2), my data (Chapters 3 to 5) and the model (Chapter 6) suggest that maintaining a mosaic of grass heights and cover are key habitat attributes important for high avian species richness in within grassland biome. Fire and grazing are important management tools that can be used to maintain a habitat mosaic (Fuhlendorf *et al.* 2009; Pillsbury *et al.* 2011; Allred *et al.* 2011). The optimal stocking density and fire frequency is unclear because active experimentation has so far not been possible. Under adaptive management, the anticipated best action is implemented and its outcome monitored. This requires a set of system models that predict the effects of alternative management actions. The model developed in Chapter 6 could be used as a basis for a set of more refined models that encompass the uncertainty in our knowledge of the processes. Until these models are developed, stocking densities recommended by Little, Hockey & Jansen (2013) could be used as a base to test the impact of livestock on birds in the region. Mentis (2006) suggested a minimum fire return period of two years, which agrees with the results of Chapter 6.

This thesis has provided three possible means to monitor effects of management on avifauna (Chapters 3, 4 & 5) with varying complexities. In Chapter 3, I used the list of all species seen along transects as a measure of species richness. This method does not account for species detectability and is therefore sensitive to variation in observer effort and skills, which may make it less useful as a monitoring tool. In any case, this chapter showed that summer is the most species rich season on which monitoring should focus.

The distance-sampling methods used in Chapter 4 accounts for detectability and estimate density for each species. The down side is that only relatively common species can be monitored easily with this method. However, for the species with sufficient data, the use of regression splines (see also Rovero *et al.* 2014) gives detailed estimates of the relationship between density on the one hand, and grass height and grass cover on the other. These relationships suggest habitat preferences and how grass height and cover can be managed through grazing and burning to bring about habitat suitability for such target species. Distance sampling (e.g. Thomas *et al.* 2010) did not prove to be a good monitoring tool for large, rare species because they were not encountered often enough to yield reliable estimates. Even though distance sampling could have been used for more species than I did, if more transects were sampled, some species are rare and therefore the quality of data will affect the model prediction. Transect sampling is labour intensive and requires field personnel with skill to tell apart many similar looking grassland birds and, in addition, estimate accurately distances from the transect line to each detected bird. This may limit the usefulness of this method as a monitoring tool at Ingula.

Chapter 5 presents my most preferred method to monitor Ingula avifaunal diversity to inform adaptive management. This method requires detection/non-detection data only at the species level and may be a bit less demanding on field skills. The twelve species I included in this analysis are present throughout the summer season and, because these species are common, they should be relatively easy to monitor in the future. Occupancy models can also account for variation in detection probability among observers and years (Royle & Nichols 2003; Dorazio *et al.* 2006; Taylor & Pollard 2008). Key assumptions are that birds are identified correctly (no false positives) and that species do not colonise or vacate plots between the repeat surveys (closure assumption) (e.g. MacKenzie *et al.* 2003; Royle & Nichols 2003; Dorazio *et al.* 2006; Kéry *et al.* 2009; Ruiz-Gutiérrez & Zipkin 2011). The hierarchical nature of the analysis yields species-specific estimates of detection, occupancy, colonisation and extinction probabilities that can be related to management actions (Dorazio *et al.* 2006; Dorazio & Royle, 2005; Kéry, Royle, Plattner & Dorazio, 2009; Royle & Dorazio, 2008; Ruiz-Gutiérrez, Zipkin & Dhondt, 2010), making this my most preferred method to use for future adaptive monitoring.

Should management wish to monitor total species richness, the hierarchical occupancy model can be modified to estimate total species richness (Zipkin, DeWan & Royle 2009; Zipkin *et al.* 2010; Sauer *et al.* 2013). With a few modifications to the sampling design, I anticipate that occupancy surveys could be used for relatively rare species (e.g. Kéry *et al.* 2009; Russell *et al.* 2009; Zipkin, DeWan & Royle 2009; Zipkin *et al.* 2010; Ruiz-Gutiérrez, Zipkin & Dhondt 2010; Burton *et al.* 2012; Sauer *et al.* 2013). I recommend carrying out one survey per year during the height of the breeding season, when most species are present, but increase the number of repeat surveys and the number of plots. For monitoring purposes I suggest that future surveys be carried out from mid-December to mid-January and that such surveys be carried out by more than one person. Increasing the number of plots, both within Ingula and outside, would give analysis statistical power to infer the response of bird species to fire and grazing. Surveying Ingula can be challenging, given a rugged terrain and inclement weather. However, the occupancy is fairly forgiving with unequal replication and can give useful estimates, even if some sites have not been surveyed in some years because of inclement weather (e.g. Royle & Dorazio 2008). Through an added hierarchical level it is also possible to estimates species richness across the entire moist, high-altitude grasslands of the region (e.g. Royle & Dorazio 2008), making Ingula a case study from which similar habitat can be monitored under adaptive management.

With Ingula about to attain the status of nature reserve (Maphisa, 2012), the area is expected to serve as a source (e.g. Donovan *et al*. 1995; McCoy & Ryan 1999; Foppen, Chardon & Liefveld 2000) for some species given heavy grazing and annual burning in the surrounding farms where the aim is to maximize livestock feeding rather than to maximise biodiversity. Due to the relatively high altitude of the upper site at Ingula, most species have a short breeding season before which the habitat must be made suitable through controlled burning and grazing. In Chapter 6, I suggest management units that are homogeneous in habitat. Burning and grazing could be used in a targeted way to improve the habitat for the species that are typically found in a particular polygon. This will benefit much rarer and more sedentary species such as the 'Critically Endangered' Wattled Crane *Bugeranus carunculatus*. This latter species occurs as the lone breeding local migrant producing a chick every other year. It breeds in late winter, which coincides with the fire season and burning has, on a number of occasions, resulted in breeding failure. In the polygons where the Wattled Crane breeds, management must also ensure that the habitat is suitable outside the summer months.

Conservation importance of the upper site compared to the lower site

The upper site is of more conservation value compared to the lower site and, because of its bird species composition, is declared an Important Bird Area (e.g. Barnes 1998). The vegetation at the lower site is dominated by tall *Hyparrhenia – Cymbopogon* grasses and the area has seen an increase in the number of wild mammals, which include the threatened Oribi *Ourebia ourebi* and Common Reedbuck *Reduna arundinum*. Because the area is much closer to the Ingula management offices, the lower site has not been burned annually. The combination of lack of frequent fires and tall grass is providing a refuge for wildlife that is hunted outside the Ingula property. Ingula management must maintain tall bunch grasses at the lower site to benefit large mammals. As for the upper site, a minimum fire return period of two years should be adhered to, except that this must depend on achieving particular management objectives rather than a general rule.

While some form of grazing by herbivores needs to be incorporated in the management of Ingula, the type of animals (cattle versus game) must be largely driven by management objectives and the effects need to be determined through a strong monitoring programme. In South Africa, the suppression of fire has been implicated in the conversion of open grassy veld now dominated by undesirable non-native shrubs (Cowling *et al.* 1986). Fire suppression has become a common practice in both government and privately owned nature reserves where fires and cattle are seen as undesirable elements and are being replaced with game. In the absence of grazing, some grassland at Ingula is invaded by bracken fern *Pteriddium aquilinum,* which was previously confined to the escarpment forests margins where cattle did not graze heavily. Bracken fern can be controlled by grazing with cattle, provided that such grazing does not lead to overgrazing or trampling (Birch 2000).

There is more to the conservation of Ingula than just birds

In addition to grassland, which was the focus of my thesis, Ingula also has two other important ecological habitats: the wetlands and moist, cool, mountain scarp forests, which equally harbour threatened priority species. The Ingula wetland habitat and the mountain scarp forest would require a different management approach to the one discussed in Chapter 6.

Other than for birds, removal of commercial livestock has some noticeable, negative impacts on other forms of biota at Ingula. For example, some species of orchid appear to be outcompeted by tall rank grass (pers. obs). Although heavy grazing equally has negative impact on orchids (e.g. Alexander *et al.* 2010), lack of grazing, in addition to hot fires could, over long periods, lead to the exhaustion or dying of orchids' underground reserves, which could lead to some orchid going locally extinct. The Montane Grass-snake *Psammophis crucifer* was fairly common at the beginning of the project, mostly confined to hilltops. No records exist from 2010/13, despite a thorough search at its preferred localities (Maphisa unpublished data). Another South African rare endemic snake, Breyer's long-tailed seps *Tetradactylus breyeri,* is only known from three records (Bates *et al.* 2014) and is listed as threatened (World Conservation Monitoring Centre 1996). Both Ingula records came from individuals hibernating beneath old, intact cow dung (pers. obs.). I had more encounters with this snake swimming through grass at the beginning of the project compared to later years. The list is long; this is just an attempt to show that there is a lot more to conserve Ingula grassland than just birds but, because birds are mobile, they may be quick and reliable indicators of conservation-relevant changes at Ingula.

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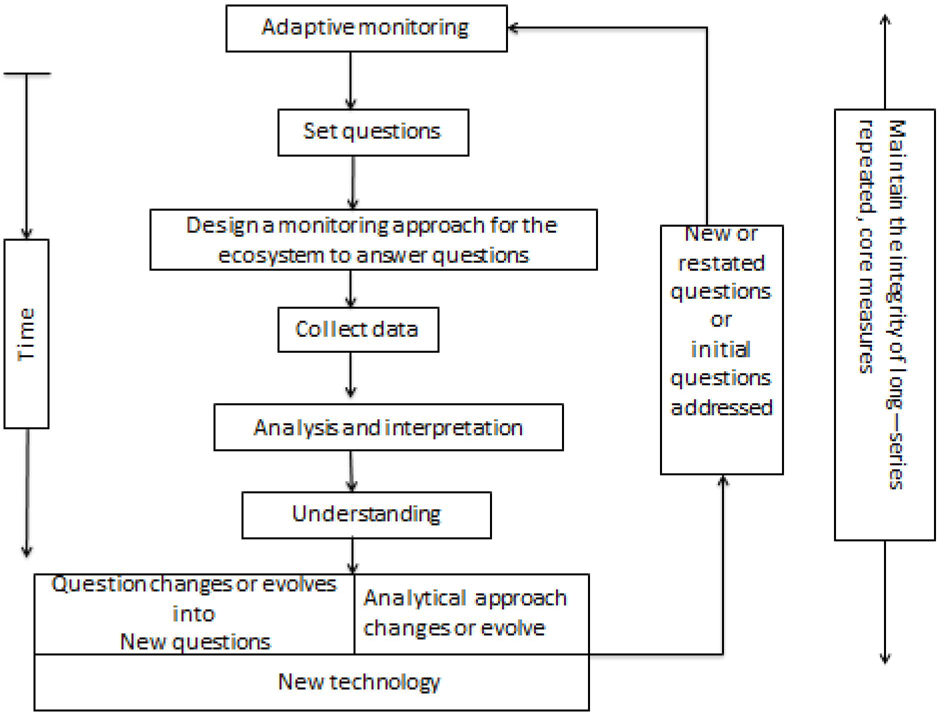

Fig. 1. A diagram for adaptive monitoring as defined by Lindenmayer & Likens (2009). Adaptive monitoring provides a framework for incorporating new questions into a monitoring approach for long-term research, while maintaining the integrity of the core measures. Initial key steps are the development of critical questions and a robust statistical design.