# Effects of Protected Areas and Climate Change on the Occupancy Dynamics of Common Bird Species in South Africa

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# ABSTRACT

Protected areas are tracts of land set aside primarily for the conservation of biodiversity and natural habitats. They are intended to mitigate biodiversity loss caused by land-use change worldwide. Climate change has been shown to disrupt species' natural distributions and patterns, and poses a significant threat to global biodiversity. The goals of this thesis are to address these important issues, and understand how protected areas and climate change affect the range dynamics of common, resident bird species in South Africa. Common species were used because they have been shown to drive important ecosystem patterns, and a decline in abundance and diversity of common species can indicate drastic declines in ecosystem integrity. This thesis comprises four data chapters; in the first three I model the occupancy dynamics of 200 common, resident bird species in South Africa to gain an understanding of how the proportion of protected areas within a landscape affects common species. For the last data chapter, I examined the effects of protected areas and a changing climate on the range dynamics of Cape Rock-jumper (*Chaetops frenatus*), a species endemic to the southwestern part of South Africa and whose population is declining rapidly in response to climate change. I modelled its occupancy dynamics in relation to climate, vegetation, and protected area. Overall, my key findings show bird abundances vary widely as a function of protected areas, but on average, bird abundances are higher in regions with a higher proportion of protected areas, compared to regions with a lower proportion. I found that the conservation ability of protected areas was influenced by the type of land-use found in the surrounding landscape. For example, the extent of agricultural land in proximity to a protected area significantly increased the mean abundance of birds in that protected area, whilst the average abundance of most species was not affected by the extent of urban area near protected area. On average, species preferentially colonized and persisted within landscapes with a higher proportion of protected area, compared to landscapes with a lower proportion of protected area. However, protected areas were not able to slow the extinction rate for all species, and the average extinction rate for some groups of species actually increased as the extend of protected areas within a landscape increased. Furthermore, Cape Rock-jumper also preferentially occupied regions with higher proportions of protected area. Despite this, Cape Rock-jumper's range is predicted to shrink considerably in response to a hotter and mildly drier climate forecast for the region. As a result, Cape Rock-jumper will likely be of conservation concern as the climate over its range continues to change. I conclude that, in general, protected areas are effective at conserving common bird species over a heterogeneous landscape in South Africa, and should be prioritised as key conservation strategies in the future. I further conclude that climate change will be a concern to an endemic species, and to biodiversity in general. This will likely place extra stress on the importance of protected areas to mitigate responses of species to climate change.

# ACKNOWLEDGEMENTS

This thesis has occupied five and a half years of my life. Little did I realise, when I first began this thesis, the enormity of the task on which I would embark. I have gained experience and skills in ways I had not even imagined when I originally took up the project, but am all the more grateful for these learning opportunities. Many people have influenced, guided, and helped me along this long path, each of whom have in one way or another shaped this thesis into its final product. It would be remiss to forget anyone's contribution. If I have overlooked anyone and your name doesn't appear below, then I'll firstly accuse the University's uploading system. If that doesn't work, then I'll have to reprint this with your names added.

It should go without saying, but I'm going to say it anyway; this thesis would not exist if it were not for my supervisor Res Altwegg. I am deeply indebted him for his professional guidance, support, and encouragement throughout the duration of this study. His continued professional excellence inspired and pushed me throughout my thesis, and encouraged me to make the most of each chapter, particularly towards the last stages. I must mention especially his patience during many discussions in his office about interpretations of the complex analyses and datasets, and for returning chapter drafts so timeously when I was under pressure. I must also express my gratitude to him for giving me the opportunity to present this research at international conferences, and for allowing me to share this research during international research visits. Res' enthusiasm for statistics, ecology, and science in general is inspiring, and ultimately motivated me to be a better scientist, something which I hope is evident throughout this thesis. Further thanks must go to Res for his patience, understanding, and support during the last two and a half years of my thesis when I was working on my PhD alongside a full-time job.

This thesis exclusively analysed bird atlas data taken from the South African Bird Atlas Project (SABAP). Grateful thanks therefore go to Professor Les Underhill for running and maintaining this project and for allowing me access to the great volumes of collected data. Thank you to René Navarro and Michael Brooks for maintaining and updating the databases. I am grateful to Michael for helping me with SQL code to obtain the data, and for other such IT-related queries throughout most of the thesis. Furthermore, I am deeply indebted to the atlassers for spending long hours in the field collecting valuable bird distribution data over such large areas. I hope this thesis serves as justification for your continued effort in monitoring biodiversity. Thanks to Richard Flack for permitting me to use his photo of the Cape Rock-jumper in Chapter 5.

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Finally, I would like to thank everyone who has supported me all the way along this journey. Particularly my parents, who encouraged me to take on this PhD whilst I was in two minds right at the beginning. Thanks for always providing a welcoming home, support, lending a sympathetic ear, and for seeing the light at the end of the tunnel when things seemed dire to me. Thanks to my sisters Toni and Lisa; although together we occupy two different continents throughout the world, your encouragement and senses of humour helped ease me along the journey. And lastly, I must extend my utmost thanks to my wife Joanna, who celebrated every

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## THESIS LAYOUT AND OUTLINE

*Layout*

This thesis is comprised of six chapters, four of which (Chapters 2 – 5) were written up as self-contained papers ready for submission to an academic journal. As a result, some repetition was unavoidable, especially in the methods and introduction sections. Where relevant, I referenced an already described method or figure in subsequent chapters. Figures and tables are imbedded in text where appropriate, but appendices follow the chapter text. In order to avoid significant repetition of references, a single reference list is located at the end of the thesis (page 178).

All data used in this thesis were collected by citizen scientists who partook in a national bird atlas project over South Africa. I was responsible only for accessing these data, which were stored at the Avian Demography Unit at the University of Cape Town. I was responsible for analysis and writing up of each chapter. Raquel Garcia helped with the formatting, and preparation of the climatic data used in Chapter 5. Res Altwegg commented on each chapter, and provided statistical and theoretical assistance where necessary.

*Outline*

This thesis focussed on the range dynamics of common bird species, and how these varied with protected areas and climate change. A short description of each chapter, and its primary objectives is given below.

Chapter 1 (page 1) gives a short general introduction, and outlines the study context and rationale. Thereafter, it introduces the importance of studying species' range dynamics through space and time. Then, it provides background information on protected areas, how large scale biodiversity data are collected via atlas (citizen science) projects, and how these data are analysed using site-occupancy models and their extensions. Finally, a brief account of the study area and the study species is given.

Protected areas are generally considered to provide a net conservation benefit to species (Gaston et al., 2008). This assumption is tested in Chapter 2 (page 27). Analysing bird detection / non-detection data collected over regular grids in the study area, I modelled the abundances of 200 common, resident bird species as a function of the proportion of protected areas in each regular grid, and I used this as a measure of protected areas' ecological effectiveness. The work from this chapter has been published this year (2018) in an international peer reviewed journal (see section below thesis outline).

Protected areas are tracts of land that are set aside specifically to conserve biodiversity. It is generally hoped that these areas are effective regardless of the land-use types which surround, or are situated nearby to protected areas (Hansen & Defries, 2007; Hansen et al., 2011; Leroux & Kerr, 2013). Chapter 3 (page 54) studied how the landscapes in which protected areas are imbedded can affect the ecological effectiveness of protected areas. Natural, agricultural, and urban areas form the majority of land-use types within this study area, and this chapter studied the effect of these land-use types on the abundance of 200 common birds in regions with higher proportions of protected areas, compared to those with lower proportions of protected areas.

The reliance on protected areas for conservation is predicted to increase in future, as natural land is often converted to urban or agricultural land in order to meet the demands of an ever increasing human population. How species use protected areas over time is therefore a crucial consideration. To assess this further, Chapter 4 (page 97) examined the dynamic components of 200 common species' ranges, colonization and extinction, and studied the changes in species' ranges as a result of protected areas. It specifically looked at whether species preferentially colonized areas with a higher proportion of protected areas, and if protected areas slowed the extinction rate of species over time.

Global climate change has decreased general biodiversity, and is predicted to continue to do so in future. Chapter 5 (page 132) focussed on the occupancy dynamics of Cape Rock-jumper (*Chaetops frenatus*) a species that has recently declined in response to climate change (Frazer, 1997; Simmons et al., 2004; Huntley et al., 2012; Lee & Barnard, 2016) and has been recently regarded as near threatened (Taylor et al., 2014). I developed an occupancy model to examine the range dynamics of Cape Rock-jumper over the periods 1987-1992 and 2007-2015, and relate contractions in its range to climate.

Chapter 6 (page 166) provides overall conclusions for this thesis by consolidating the results of each chapter. It interprets the key results of each chapter in context of the broader knowledge of species' range dynamics, protected areas, climate change, and conservation. The work in this thesis has identified further knowledge gaps which further research should aim to address, and these are presented here. Finally, it outlines the main contributions and findings of this thesis.

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"I confirm that I have been granted permission by the University of Cape Town's Doctoral Degrees Board to include the following publication(s) in my PhD thesis, and where co-authorships are involved, my co-authors have agreed that I may include the publication(s), based on the second Chapter of this thesis:"

Duckworth, G.D. & Altwegg, R. (2018) Effectiveness of Protected Areas for Bird Conservation Depends on Guild. *Diversity and Distributions*, DOI: 10.1111/ddi.12756. 1–9.

Chapter 1

# General introduction and background information

Egyptian Goose *(Alopochen aegyptiaca)* in the Kruger National Park, South Africa. Photograph by Allan Duckworth.

## 1.1 GENERAL INTRODUCTION

*Study context and rationale: Why examine species' ranges in relation to protected areas?*

Human-mediated climate and land-use change have substantially altered a considerable amount of earth's natural environment over the last 100 years (Vitousek et al., 1997; Chapin et al., 2000; Foley et al., 2005). This has led to great losses in biodiversity, and natural habitat (Parrish et al., 2003). The current rate of biodiversity loss is higher than in recent recorded history, and is projected to increase in future, putting many species at risk of population decline or extinction (Parmesan & Yohe, 2003; Buckley et al., 2013). While climate change has been identified as a cause for large-scale local biodiversity loss, it is thought to have directly contributed to the extinction of at least two species (Pounds et al., 1999, Waller et al. 2017). Monitoring and prioritising biodiversity to prevent similar extinctions in future is therefore an urgent conservation goal (Gaston et al., 2008; Cottee-Jones et al., 2015).

One land-use type that prioritises biodiversity conservation is protected areas. These are tracts of land specifically set aside for biodiversity conservation, and are considered as a primary tool for conservation worldwide (Gaston et al., 2008; UNEP, 2011). Protected areas currently cover 12% of the earth's land area, and a global aim is to increase coverage to at least 17% by 2020 as one of the Aichi targets (target 11; UNEP, 2011), testament to the important role protected areas play as a conservation tool. Each protected area is generally managed to achieve individual, specific goals, which can be diverse and vary from region to region. Nonetheless, goals common to most protected areas are to conserve and increase biodiversity (especially threatened species), maintain natural habitats, provide ecosystem services, sustain ecological function, and be of recreational value (Naughton-Treves et al., 2005; Gaston et al., 2008; UNEP, 2011). Often, however, measuring how well protected areas achieve these goals is arduous owing to lack of data, logistical difficulties with monitoring programs, time, and finances (Parrish et al., 2003). As a result, the degree to which protected areas fulfil their functions is generally unknown (Chape et al., 2005; Gaston et al., 2008). Reliance on protected areas and continued investment in them is based on the assumption that they provide a net conservation benefit. Indeed, protected areas have been shown to greatly benefit biodiversity in various areas throughout the world (Walpole & Leader-Williams, 2002; Rodrigues et al., 2004; Owen-Smith et al., 2006; Dalerum et al., 2008; Watson et al., 2011; Geldmann et al., 2013). Despite this, a growing body of work indicates that in some protected areas, biodiversity in general has decreased (Hoekstra et al., 2002; Craigie et al., 2010; Watson et al., 2014), and even flagship species have decreased in abundance (Western & Henry, 1979; Newmark, 1996; Brashares et al., 2001; Hilton-taylor et al., 2004; Rands et al., 2010; Ogutu et al., 2011). This has resulted in a resurgence of interest in protected areas, and attempts to quantify their ecological effectiveness.

The uncertainty in the level of protection that is offered by protected areas to biodiversity and habitats has led to the question 'Are we conserving what we say we are?' (Parrish et al., 2003). Consequently, the assumption that protected areas generally provide net positive conservation benefits may not be the case in reality. Already the dependence on protected areas for biodiversity conservation is high (Naughton-Treves et al., 2005; Gaston et al., 2008; Cabeza, 2013), and this is predicted to increase in future as an increasing human population places even more pressure on the environment (UNEP, 2011). Therefore, an urgent conservation goal is to understand how effective protected areas are at conserving, maintaining, and increasing biodiversity (Gaston et al., 2008). Additionally, it is also crucial to determine whether species persist in protected areas over time, because protected areas are often static and species' ranges are dynamic (e.g., Yackulic et al., 2015). Furthermore, climate change causes species to shift their ranges which may result in mismatches between a species' range and protected areas (Araújo et al., 2004; Hole et al., 2009; Gillingham et al., 2015b; Thomas & Gillingham, 2015). Therefore, the value protected areas provide to biodiversity varies through time, and it is necessary to look at the range dynamics of species to understand how the benefit of protected areas changes through time.

Common species are generally the most abundant, and therefore constitute the majority of species within protected areas. Often overlooked at the expense of rarer and more charismatic species, the impact of protected areas on common species has not received widespread attention. Nonetheless, common species play an important ecological role in the landscape, including shaping the structure of food-webs, as well as influencing ecosystem structure and function (Gaston, 2010; Maas et al., 2015). Species richness patterns tend to be driven by common species (Lennon et al., 2011; Winfree et al., 2015), and common species may have a greater per capita influence on terrestrial ecosystems than do rare species (Gaston & Fuller, 2008; Gaston, 2011). Additionally, a decline in abundances and diversity of common species can indicate drastic declines in ecosystem integrity (Gaston, 2011). Therefore, a general goal of conservation managers is to include a healthy representation of common species within protected areas. It follows, then, that monitoring common birds within protected areas can provide an important basis from which conservation (or ecological) action may be initiated. Collectively assessing the response of common species to protected areas requires distribution data on each species, something that is difficult and time consuming to obtain. Fortunately, the recent popularity of atlas projects has provided an abundance of distribution data on common species to analyse. Meaningful insights, from which ecological action may arise, depend on suitable methods by which to analyse these data.

Species distribution models (SDMs) are usually used to model species' distributions, and correlate species' presences to environmental characteristics. Whilst SDMs provide useful information across a variety of disciplines (Araújo et al., 2004; Elith et al., 2009; Jones, 2011), they don't account for two key aspects inherent to species ranges: (i) detection probability in species' presence / absence data; and (ii) the inherent dynamic nature of species' distributions (i.e. species' ranges are dynamic and not static). Not accounting for these two aspects in modelling may lead to considerable biases in model parameter estimates (Boulinier et al., 1998; Nichols et al., 1998; Yackulic et al., 2015). Site-occupancy models provide a good modelling tool which accounts for these two aspects; they hierarchically separate the detection component from the biological components (for example, occupancy and abundance), which enables the modelling of a species' true distribution (Mackenzie, 2006; Kéry, 2011). Furthermore, site-occupancy models estimate directly species' dynamic components colonization and extinction (which have also been referred to as vital rates, e.g. Bailey et al., 2014), making it possible to model the change in species' distributions through time. Together, these features make site-occupancy models an ideal tool with which to analyses atlas data (or species' detection / non-detection data in general).

*Rationale of this study*

In this thesis, I use site-occupancy models and their extensions to analyse bird atlas data and examine species' occupancy dynamics throughout South Africa in relation to protected areas and climate change. In Chapters 2 and 3, I examine how effective protected areas are in increasing the abundance of common bird species. Abundance is a good measure of ecological effectiveness (Skerratt, 2013), and areas of higher ecological quality for a particular species are generally expected to correspond to relatively higher abundances of that species (Martinez-

Meyer et al., 2012). In Chapter 2 I examine how effective protected areas are at increasing the abundance of common birds, relative to regions outside protected areas. In Chapter 3, I examine how the land-uses surrounding protected areas influence the abundances of common birds within protected areas, and hence the ecological effectiveness of protected areas. Thereafter, I switch my focus to species' occupancy dynamics in Chapters 4 and 5. In Chapter 4, I examine how effective protected areas are at reducing local extinctions or increasing colonization probabilities. In Chapter 5, I model the range dynamics of a species under threat of climate change. I model the change in this species' distribution directly, and link this to climate.

An overall objective of this thesis is to use novel statistical methods to understand better the effects of climate change and protected areas on common species. It specifically aims to contribute to the long-standing debate regarding the effectiveness of protected areas; in this case, the ability of protected areas to increase abundances of common birds, as well as to retain them, reduce extinctions, and increase colonizations through time. It further aims to understand the impact and severity of climate change on a susceptible species. A further objective, and a common thread running throughout this thesis, is to highlight the use and effectiveness of site-occupancy models and their extensions as methods with which to analyse species' ranges.

The following sections provide some background information on the importance of assessing species' occurrences through time and space, protected areas, atlas data, and site-occupancy models. Thereafter, the study sites are explained briefly as are the focal species of this study.

## 1.2 BACKGROUND INFORMATION

### *1.2.1 Importance of assessing species' occurrences through space and time*

The dynamics of species' ranges are among the most fundamental variables in ecology (Elton, 1930; Brown, 1984; Gaston, 2003). The study of species' occurrences through space and time attempts to explain why some species are observed in particular areas, and not in others (Gaston, 2003). These observations have played an important part in the formulation of basic theories, most notably evolution and natural selection (Darwin, 1859; Wallace, 1876).

Species' distributions are the physical realisations of a species' potential occurrences in patches through space and time. Typically, a species' range is determined by the interaction among biotic and abiotic factors (Andrewartha & Birch, 1954; Parmesan et al., 2000; Gaston, 2003). Examples of abiotic factors include physical factors, such as rainfall, temperature, soil nutrients, or water availability. Gradients in abiotic factors can cause a range boundary (Parmesan & Yohe, 2003; Marini et al., 2009; Gillings et al., 2015). Examples of biotic factors include inter- or intra-species interactions; for example, predation, competition, or parasitism (Péron & Altwegg, 2015; Péron et al., 2016). The complex interaction among the many biotic and abiotic factors gives rise to the observed and detectable niche a species occupies (Soberón, 2007). The dynamics of species' ranges are multifaceted, and change over time (Crisci et al., 2003; Morrone, 2008). The abundance of literature focussing on understanding and modelling the distributions of species confirms the necessity and importance of species' distribution modelling (Austin, 2002; Araújo & Guisan, 2006; Rodríguez et al., 2007; Elith et al., 2009; Maggini et al., 2011).

Understanding why some patches within a landscape are more suitable for species occurrence than others is an increasingly important tool in understanding species' range dynamics, and formulating conservation plans that mitigate the negative effects of climate or land-use change (MacKenzie et al., 2006; Gaston et al., 2008). Already, there is compelling evidence that shows a substantial number of species are shifting their ranges in response to a warming climate (Walther et al., 2002; Parmesan & Yohe, 2003; Randin et al., 2009; Normand et al., 2011; Gillings et al., 2015), whilst others have been negatively impacted (i.e. experience a decrease in abundance or shrinking in range) by land-use conversion (i.e. habitat loss) and related intensification (Gaston, 2003; Butchart et al., 2010; Mora & Sale, 2011). Given that land-use and global climate changes are projected to intensify in the future (Parmesan & Yohe, 2003; Buckley et al., 2013), there is an urgent need to understand species' range dynamics in order to develop effective conservation strategies.

### *1.2.2 Protected areas*

The current rate of biodiversity loss is higher than it has ever been in recent recorded history (Buckley et al., 2013). Pressures on the natural environment due to human land-use and anthropogenic climate change have resulted in an indisputable loss of biodiversity worldwide (Parmesan & Yohe, 2003; Smith et al., 2003). Together, these processes increase the extinction risks to many species throughout the world and drastically reduce or shift the ranges of many species (Bender et al., 1998; Walther et al., 2002; Parmesan & Yohe, 2003; Struhsaker et al., 2005). In response to these pressing issues, protected areas are considered a means to protect, conserve, and maintain the remainder of earth's biodiversity and natural habitat. Protected areas are defined as geographic areas set aside and managed for the conservation of nature or of pristine habitats, promotion of ecosystem services, and cultural values whilst minimising the impact of human-related activities (IUCN, 1994; James et al., 1999; Parrish et al., 2003). The goals for protected areas, as set by conservationist or protected areas' managers, have expanded over the last few decades and now include social aspects such as national development and poverty reduction as key functions (Naughton-Treves et al., 2005).

Protected areas are generally accepted as one of the key ways to conserve biodiversity, and are implemented globally (Gaston, 2003; Gaston et al., 2008). Almost every national and international conservation plan involves protected areas to some degree (IUCN, 1994). Since the 1980s the number of protected areas world-wide increased rapidly, and in 2011 approximately 12% (17.1 million $km^2$) of the earth's land surface was protected (Hilton-taylor et al., 2004). This is projected to increase to about 17% as part of the Millennium Development Goals (United Nations, 2013a). Every year, millions of dollars (US) are spent on maintaining, upgrading, or developing protected areas world-wide (Balmford et al., 2003), showing how important they are considered as a conservation tool.

A general assumption is that protected areas provide a net conservation benefit to biodiversity contained within them. This assumption is true in some cases; for example, some threatened or endangered species only exist in protected areas (Simberloff, 1998; Sergio et al., 2006). Other species are found within protected areas at a higher abundance than they are outside them (Walpole & Leader-Williams, 2002; Hilton-taylor et al., 2004; Owen-Smith et al., 2006; Dalerum et al., 2008; Bennett & Watson, 2011). Habitats within some protected areas are more pristine than those immediately outside them (Geldmann et al., 2013). This generally serves as justification for the continued reliance of conservationists and scientists on protected areas to conserve biodiversity effectively (Gaston et al., 2006; Hansen et al., 2011; Thomas et al., 2012). However, an increasing body of work shows that even within large, national protected areas, despite keystone species or habitats benefiting, the remaining biodiversity in general is declining (Hoekstra et al., 2002; Craigie et al., 2010; Watson et al., 2014). Flagship species of conservation concern such as lions and rhinos are decreasing in abundance in some protected areas (Western & Henry, 1979; Newmark, 1996; Brashares et al., 2001; Rodrigues et al., 2004; Craigie et al., 2010; Rands et al., 2010; Ogutu et al., 2011; Cantú-Salazar et al., 2013). It is therefore apparent that although protected areas may be ecologically effective in some cases, they are not always effective at halting the loss of biodiversity in general. Thus, it is important to examine how ecologically effective protected areas really are, and if biodiversity (both common and endangered) really does receive the ecological benefits protected areas are assumed to convey.

Protected areas may fail, or be less successful than envisaged, for a variety of reasons, the most prominent of which include lack of funding, political interferences, geographical divides, or judicial reasons (Adams & Hutton, 2007). However, ecological failure can be largely attributed to the functioning and health status of the greater ecosystem of which protected areas form part (DeFries et al., 2007; Hansen et al., 2011; Leroux & Kerr, 2013). Indeed the types, intensity, and quality of land-uses that surround protected areas can have a substantial effect on their ecological effectiveness. This has been examined in detail for urban and agricultural land-uses, mostly because they are the land-uses that often surround protected areas, and are indeed the most common land-uses within landscapes. For example, rural populations tend to settle immediately outside, or near protected areas where they benefit from ecosystem services protected areas provide, such as clean water, firewood, food, and materials with which to build shelter (Chown et al., 2003). The presence of human settlements near protected areas correlates strongly with biodiversity declines, species extinction, fire frequency, and poaching (Herremans & Herremans-Tonnoeyr, 2000; Brashares et al., 2001; Parks & Harcourt, 2002; Cardillo et al., 2004; Knapp et al., 2008). Agricultural areas have also been shown to affect negatively the ecological effectiveness of protected areas; activities associated with farming practices such as planting, fertilizing, tilling, and draining of soil are generally associated with declines in biodiversity and general habitat quality (Burel et al., 1998; Stoate et al., 2001; McLaughlin et al., 2002; Dauber et al., 2003; Feehan et al., 2005). Thus, protected areas are not isolated islands of conservation, and the effectiveness of protected areas can depend on what type of land-use surrounds them.

The earth's population is predicted to increase considerably in the near future (United Nations, 2013b). Agricultural and urban land-uses are expected to intensify and dramatically increase in area to feed and house such a large human population. As a result, the reliance on protected areas for conservation will intensify, and the opportunities for creating new protected areas are likely to reduce. Thus, there is an urgent need to understand how protected areas ecologically affect species and habitats contained within them, as well as to examine how the landscape as a whole affects the ecological effectiveness of protected areas. This understanding will not only aid in making current protected areas more ecologically effective, but also in conservation planning for future protected areas - an important consideration given the projected intense competition for land in future (United Nations, 2013b)

### *1.2.3 Atlas data*

Detecting changes in species' ranges requires repeat survey data over large spatial extents (Walther et al., 2002; Robertson et al., 2010). Unfortunately, up until recently, such datasets were difficult to obtain, primarily due to the amount of effort in terms of time, as well as the total costs required to collect them (Wright et al., 2015). Consequently, data on the occurrences of species over large geographic extents were sparse. However, the recent interest and participation in citizen science projects (particularly 'atlas projects') has partially alleviated this problem. Most large citizen science projects involve registered members of the public who collect data, in a standardized manner, over large geographic extents (Irwin, 2001), although there are deviations from this protocol (Cohn, 2008). The volume of data collected by volunteers during these projects is almost impossible for single researchers or research teams to collect (Cohn, 2008; Harrison et al., 2008; Bonney et al., 2009; Silvertown, 2009; Devictor et al., 2010; Dickinson et al., 2012), substantially increasing the value of atlas or survey projects.

Despite the popularity of these projects, concerns over citizen science data have been expressed, and in particular the quality of the data, sampling bias (over space and time), sampling efficiency, and protocol (Dickinson et al., 2010). In response, many projects have implemented some quality control procedure that flags irregular or inconsistent records for further checking (Bonney et al., 2009). Furthermore, protocols are constantly updated to ensure processes and data are as reliable as possible (Dickinson et al., 2010; Conrad & Hilchey, 2011).

The Southern African Bird Atlas Project (SABAP)

This thesis makes use of atlas data collected over South Africa during two citizen science projects, SABAP 1 and 2 (Harrison et al., 1997; Harebottle et al., 2007). The first phase of this project (SABAP 1) ran from 1987 – 1992, and the second phase (SABAP 2) began in 2007 and is still ongoing in 2018. During both projects, registered volunteers surveyed a regular grid and submitted checklists of all species seen over a fixed time period which differed for each SABAP. Only the detected presence of each species was recorded, not the total number of birds. SABAP 1 utilized a quarter-degree grid (15’ x 15’ in arcminute resolution, total area of approximately 550 $km^2$; henceforth termed QDGC). SABAP 2 utilized a pentad grid (5’ x 5’ in arcminute resolution, approximately 61 $km^2$; nine pentads make up a QDGC).

Inherent with citizen science projects are imperfections within the data (Cohn, 2008), and this exists too in the SABAPs. For example, it was possible not to detect a species where it did occur. Such cases are termed 'false negatives'. Other problems include uneven sampling and variable effort per survey. I accounted for these issues in my analyses by using specialist statistical models. However, there still existed the possibility of incorrectly identifying a species. To account for this potential problem, a committee vetted out of range records as well as likely misidentifications to ensure occurrence data were as reliable as possible (Harrison et al., 2008).

*1.2.4 Species distribution modelling with site-occupancy models*

Atlas data present a good opportunity to model the occurrences of species spatially and temporally as a function of environmental conditions, such as rainfall, temperature, or habitat. Here, the aim is to estimate the probability with which a species occupies a site under given environmental conditions, and potentially, over regular time intervals (for example, years). However, one cannot simply relate species' occurrences across space to some form of environmental measurement; the type and nature of the data collection process and the assumptions thereof necessitates the use of a specific model. Firstly, it must be acknowledged that species are generally not observed everywhere they occur; that is, the detection probability (the probability of seeing a species during a survey of a grid cell given that it occurs there) is rarely equal to one (Dormann, 2007; Kéry, 2011). Furthermore, detection probability may not be constant in all habitats in which the species does occur (Altwegg et al., 2008; Lennon et al., 2011). If one were to estimate occupancy across space without accounting for imperfect detection, occupancy estimates are biased low, and consequentially the occupancy - environment relationship may also be biased (Kéry, 2011). This discrepancy between model assumptions and real-world characteristics leads to biased model predictions of species' ranges (Nichols et al., 1998; MacKenzie et al., 2006; Yackulic et al., 2015).

Site-occupancy models explicitly account for the observation process, and allow it to be modelled independently from the ecological process (MacKenzie et al., 2002). Furthermore, the detection or ecological process can depend on a number of independent covariates. A key point is that by accounting for the detection process, site-occupancy models allow for the modelling of a species' true ecological distribution (Kéry, 2011). Modelling the detection process separately is an important consideration, because the detection probability of a species is likely to vary spatially, and it accounts for false negatives (i.e., occasions where a species was not recorded at a site in which it occurred).

#### 1.2.4.1 Single-season occupancy model

Site occupancy models estimate the occupancy probability of a species at site $i$ over a single season (which can be any reasonable period of time in relation to the study species), whilst accounting for the detection process (MacKenzie & Kendall, 2002; MacKenzie et al., 2006). These models assume closure; i.e. a site is either occupied or not for the whole duration of the season. The single-season occupancy model consists of two sub-models that are hierarchically linked; one models the ecological process and the other models detection. The state-space formulation (Royle & Kéry, 2007; Skerratt, 2013) of this model has the form:

*Ecological process*

$$Z_i \sim Bernoulli(\psi_i) \quad (1)$$

where $Z_i$ refers to the true occupancy status (1 for occupied and 0 for not occupied) at site $i$, and is modelled using a Bernoulli distribution with occupancy probability $\psi$. This models the true ecological process, occupancy at site $i$.

*Observation process*

$$y_{ij} \sim Bernoulli(Z_i \times p_{ij}) \quad (2)$$

where the detections $y_{ij}$ at site $i$ during survey $j$ follow a Bernoulli distribution. The probabilities ($p_{ij}$) of being seen at site $i$ during survey $j$ are dependent on whether or not the species really occurs there. This method assumes no false-positives. $p_{ij}$ and $\psi_{ij}$ can each be modelled as a function of covariates.

#### 1.2.4.2 Multi-season occupancy model

Models that do not account for the change in species' ranges over time essentially assume that a species is in dynamic equilibrium with its environment; i.e., these models consider the environment where the species currently occurs to be suitable, and environments where the species does not currently occur to be unsuitable. However, many species are unlikely to be at equilibrium with the environment, primarily because of continual colonization and extinction processes, as well as ongoing changes to the natural environment (Yackulic et al., 2015). Thus, explicitly accounting for the species' dynamics enables a more accurate, truthful measure of a species' range dynamics.

In 'multi-season occupancy models', the change in occupancy through time is modelled as a function of the dynamic components colonization and persistence (i.e., the complement of extinction). Colonization is defined as the probability with which a previously unoccupied site becomes occupied, and persistence the probability with which a previously occupied site stays occupied (MacKenzie et al., 2003, 2006). Species' occurrences across time are modeled as a function of the previous time step's occupancy state and the dynamics colonization and extinction. Thus, although the occupancy during the first period or season is directly estimated, the remaining occupancy probabilities are derived estimates. These models assume closure during seasons but allow for colonization and extinction between seasons (MacKenzie et al., 2006).

*Ecological process*

Occupancy during the first season is modelled as a Bernoulli process:

$$Z_{i1} \sim Bernoulli(\psi_{i1}) \quad (3)$$

where $Z_{i1}$ is the estimated occupancy at site $i$ in the first season.

Occupancy in subsequent seasons is derived as a function of the dynamic processes colonization and persistence, which follow a Bernoulli process.

$$\psi_{it} = (Z_{it-1} \times (1 - \varphi_{it-1}) + (1 - Z_{it-1}) \times \gamma_{it-1}), \qquad \text{for t > 1} \quad (4)$$

where $\varphi_{it-1}$ and $\gamma_{it-1}$ are persistence and colonization probabilities respectively at site $i$ between season $t-1$ and season $t$, and can depend on independent covariates.

*Observation process*

The probability of detecting a species at site $i$, during survey $j$, over season $t$ ($p_{ijt}$) is modelled as a Bernoulli trial, and is conditional on occurrence:

$$y_{ijt} \sim Bernoulli(Z_{it} \times p_{ijt}) \quad (5)$$

where the $y_{ijt}$ is the detection history made up of detections and non-detections from site $i$, during survey $j$, over season $t$.

#### 1.2.4.3 Royle-Nichols model of abundance

A variant of the single-season occupancy model is the Royle-Nichols abundance model, which estimates abundance of species while accounting for the detection process (Royle & Nichols, 2003).

*Ecological process*

The latent abundance is estimated by exploiting the relationship between species detection probability, individual detection probability, and latent abundance:

$$p_{ij} = 1 - \left(1 - r_{ij}\right)^{N_i} \tag{6}$$

where, $p_{ij}$ is the species detection probability at site $i$ and survey $j$, $r_{ij}$ is the individual detection probability for an individual at site $i$ and survey $j$, and $N_i$ is the latent abundance at site $i$. Variation in $N_i$ is assumed to follow a Poisson distribution.

*Observation process*

The detections during at site $i$ and survey $j$ are modelled with a Bernoulli distribution:

$$y_{ij} \sim Bernoulli\left(p_{ij}\right) \tag{7}$$

Thus $p_{ij}$ hierarchically links the detection and ecological process, which enables the true modelling of latent abundance per site whilst accounting for the detection probability. For Chapters 2 and 3, I utilize the Royle-Nichols abundance model to estimate the abundances of resident, common bird species (see section 1.2.6 below). For these analyses, I was most interested in the relative abundances among the species considered, and not in the absolute measures of abundance for each species. Model inferences are most reliable for the Royle-

Nichols model of abundance (and models like it) when comparing relative abundances, and not absolute abundances (Barker et al., 2018).

*Notation*

Throughout this thesis, I denote model coefficients in italics when presenting model structures (e.g. $\beta_1$). Estimates for model estimates, as returned by models, are denoted with a cap on the coefficient (e.g. $\hat{\beta}_1$).

### *1.2.5 Study area*

I conducted my study within South Africa, and focussed on two different study sites throughout the thesis. Chapters 2 – 4 analysed detection data from the SABAPs for a list of 200 common, resident bird species in the greater Gauteng region, *sensu* Hockey et al. (2005; see section 1.2.6.1 below for details on the species list). Chapter 5 analysed the distribution of the Cape Rock-jumper *(Chaetops frenatus)* as a function of temperature and rainfall throughout the south-western Cape of South Africa (Fig. 1.1).

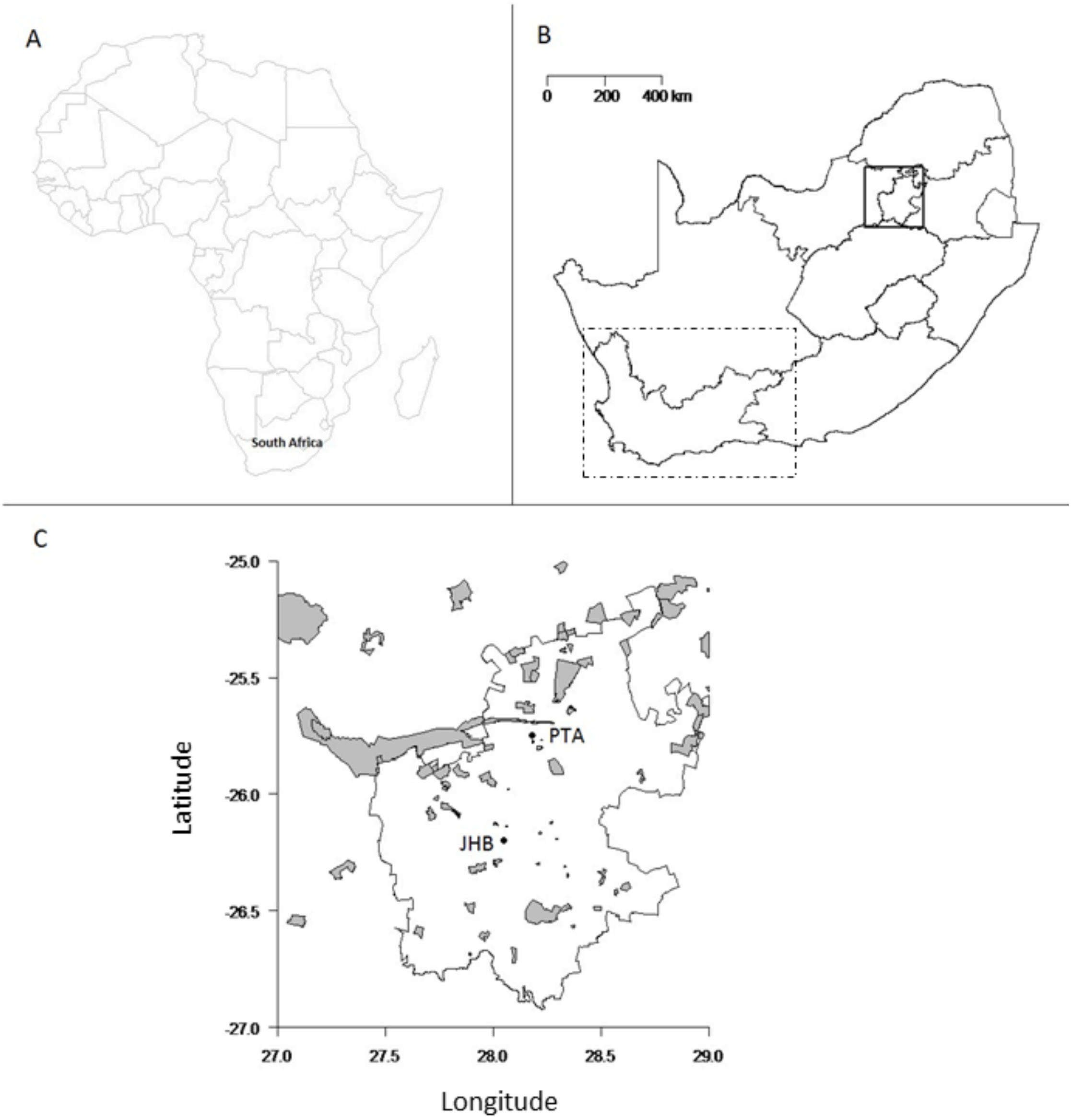


**Figure 1.1.** Study locations for Chapters 2-5. Chapters 2-4 were conducted in the greater Gauteng region (panel C, and the relative location of this study area within South Africa shown in by the solid-lined square in panel B), whilst the greater Western Cape region was the study area for the 5th Chapter (relative location within South Africa indicated by dash-lined rectangle in panel B). The large polygon in panel C is the Gauteng province, which contains the cities Johannesburg (JHB) and Pretoria (PTA), two of the most populous cities in South Africa. The areas shaded in dark grey are national and private protected areas. The area in panel C is approximately 35 000 $km^2$, whilst the study area in panel B is approximately 195 000 $km^2$.

The study area over the greater Gauteng region occupied approximately 35 000 $km^2$ (panel C, Fig. 1.1). This area contained a rich mix of land-uses (Fig. 1.2) and was made up of eight main land-use types (South African National Biodiversity Institute (SANBI), 2009). These were mines (0.80% of the study area), plantations (0.32%), waterbodies (2.80%), degraded (2.54%), protected areas (6.40%), urban (8.13%), agriculture (28.71%), and natural land (50.30%). Protected areas, urban, agriculture and natural land collectively made up approximately 94% of the study area, and were examined in detail in Chapters 2-4 of this thesis.

Protected areas, agriculture, and natural land contribute economic and societal value to the area and are predicted to do so in future. Agriculture, for example, primarily provides significant employment for many individuals that permanently reside in rural areas, despite only contributing 2.3% to South Africa's Gross Domestic Product in 2015 (DAFF, 2015). Nonetheless, the sector is prioritised by the South African government, which has strategic plans in place to enable economic and employment opportunity growth by 50% in the next 3 years (DAFF, 2016). Consequently, in the near future, agricultural land-use is predicted to increase considerably in area. Urban areas are also predicted to increase in area in future; at the time of the last national census (2011), almost two-thirds of the South African population lived in major cities, and this is projected to increase to around 72% by 2020 (Turok, 2012). Urban areas will have to continue to expand to accommodate increasing levels of urbanisation. This study area includes 81 protected areas, ranging in size from 0.08 $km^2$ to 816.70 $km^2$, at an average of 27.65 $km^2$. The initiation date of each public protected area across the study area is generally unrecorded or unknown. Protected areas in South Africa fall under the Protected Areas Act which was initiated in 2003 and aims to manage, conserve, and control protected areas in a manner that aligns with prior agreed management goals (Paterson, 2009). Currently 8% of the country is protected (DEA, 2014), which is a goal set out in the original Protected Areas Act of 2003 (DAFF, 2003).

The country is committed to protecting 17% of the area by 2020 under the Aichi targets (DEA, 2014). To meet these conservation goals, the area occupied by protected areas will also need to increase in the near future, alongside urban and agricultural lands.

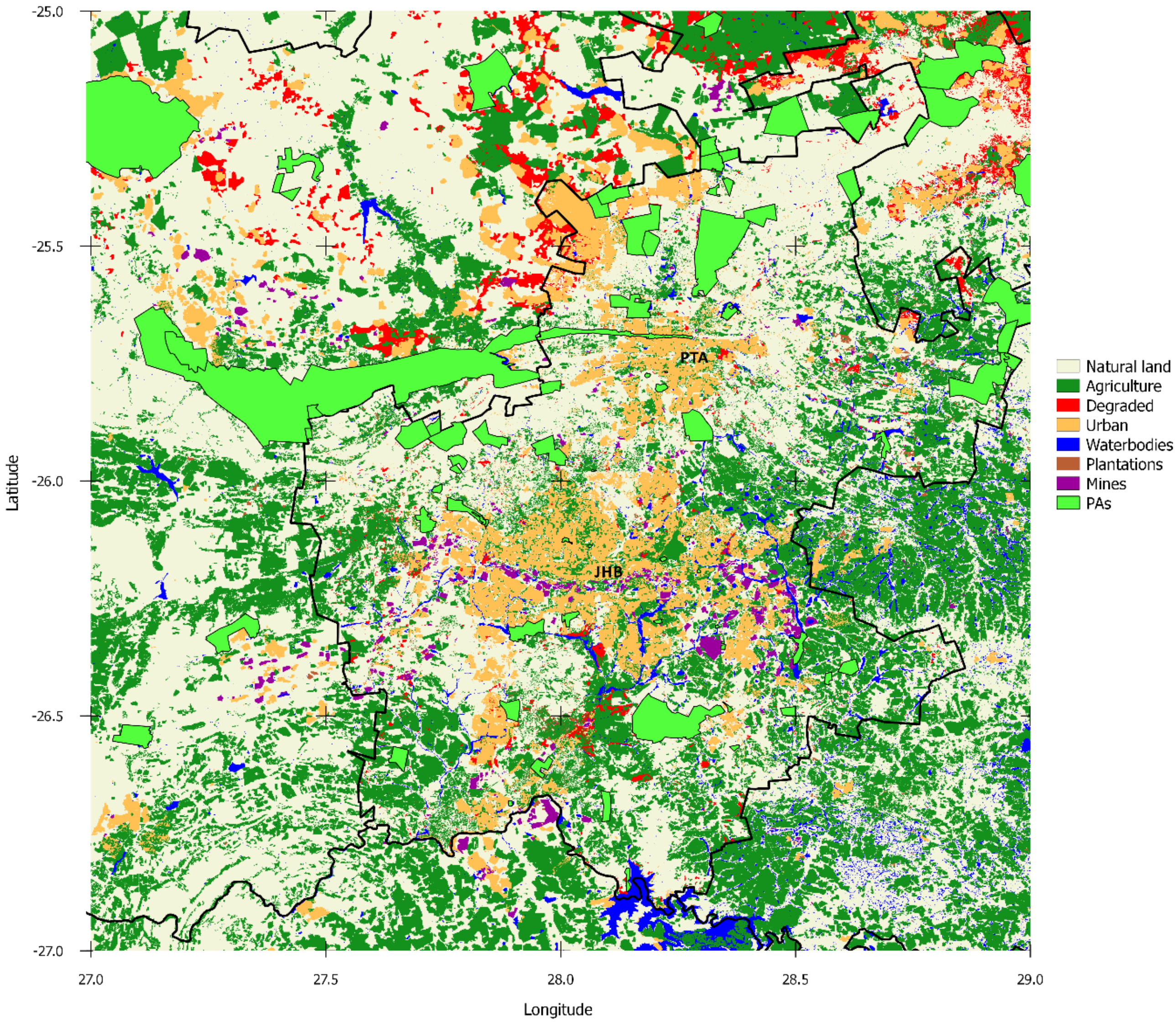


**Figure 1.2.** Land-use types over the greater Gauteng area, South Africa, which constituted the study area for Chapters 2 – 4, and included the cities Johannesburg (JHB) and Pretoria (PTA), two of the most populous cities in South Africa. The thick black line (relative to others) indicates the provincial boundaries, and Gauteng province is the polygon in which JHB and PTA are situated. The relative location of this area in South Africa is shown in panel B, Fig. 1.1.

I also selected this area because it was very well surveyed during SABAP 2. The study area included the cities of Johannesburg and Pretoria, two of the most populated cities in South Africa (Statistics South Africa, 2012), as well as small- to medium- sized private and public protected areas to which people frequently travelled and for which they submitted atlas data. It was important to select a data-rich study area, because the complexity of the analytic models I ran required large volumes of repeat survey data. The area itself covered 576 pentads, and from Jan 2008 up until December 2015, an average of 51 checklists per pentad was submitted, with a maximum of 1 253 and a minimum of 8 (total of 29 626).

The study area for the 5$^{th}$ Chapter encompassed the entire range of the Cape Rock-jumper. This included the Western Cape and its immediate surroundings, incorporating 354 QDGCs. Of these QGDCs, 350 were sampled during one or both projects. The methods I used didn't require all QDGCs to be sampled; occupancy and dynamic probabilities (colonization and extinction) for each QDGC within the study area can be generated using model coefficients and the climatic covariates of each QDGC. The area was well-atlased; during SABAP 1 (1987 – 1992) 14 565 checklists were submitted for 306 QDGCs in the study area (maximum of 615 checklists for a single QDGC, minimum of 1, average of approximately 48 checklists per QDGC), while for SABAP 2 (2007 – 2015), 27 179 checklists were submitted over 348 QDGCs in the area (maximum 1007 checklists for a single pentad, minimum 1, average approximately 78 per pentad ).

I was interested in how temperature and rainfall affect the distribution of the Cape Rock-jumper. This area experiences a Mediterranean climate with cool, wet winters whilst summers are hot and dry. Mean annual rainfall ranges from 150 mm over the driest parts (the Klein Karoo – a large desert which occupies a small portion in the north-east region of the study) to around 1900 mm in the wettest areas (Kogelberg region in the South West; Maitre et al., 1996).

Summer temperatures can reach over 40 °C in some places, whilst in the winter temperatures can drop below freezing. However, temperatures are generally warm to mild (Conradie, 2012). The Western Cape is classed as fynbos biome, which is typified by small to medium sclerophyllous shrubs and an obvious lack of tall woody trees (Manning, 2008).

### *1.2.6 Study species*

#### 1.2.6.1 Chapters 2, 3, and 4: Common and resident species

For Chapters 2 – 4, I selected common resident bird species within the region. The two main biomes in the region were grassland, which occupied the south, and savanna, which occupied the north. The boundary between these two biomes was approximately around latitude 26 degrees south. I included only common species within those biomes, according to Hockey et. al. (2005), and omitted any nomadic, alien, and migratory species. This produced a list of 200 species.

I considered common, resident bird species over the study area because such species tend to be abundant and widespread. In general, common species can drive patterns in terrestrial biodiversity and ecosystem functionality such as community assemblages, species richness, primary productivity, and nutrient cycling (Gaston & Fuller, 2008; Lennon et al., 2011; Winfree et al., 2015). Even slight changes in the population dynamics of common species (for example, quantities such as abundance, or occupancy, colonization, and extinction probabilities) can have disproportionate effects on ecosystem functioning, and indicate significant losses of ecosystem integrity (Gaston, 2010; Winfree et al., 2015). Therefore, monitoring how common species fare across the landscape is crucial to gain insight into the ecological integrity of specific regions. Understanding how protected areas affect common species is especially important, as this can infer the ecological integrity of protected areas, and therefore, the general ecological effectiveness of protected areas.

I further grouped the species into guilds based on the type of food the species preferentially consumed, and its primary mode of foraging. I used seven guilds based on the definitions in Hockey et. al., (2005). These were: frugivores (species that primarily consume fleshy fruit, totalling 9 species); gleaners (species that primarily consume insects and other invertebrates caught off plants, totalling 31 species); granivores (species that primarily consume seeds and grains, totalling 48 species); ground-feeders (species that primarily consume insects and invertebrates caught off the ground, totalling 63 species); hawkers (species that primarily consume insects and other invertebrates caught in the air, totalling 11 species); predators (birds of prey, species that primarily consume the flesh of vertebrates, totalling 19 species), and vegivores (vegetative herbivores; species that primarily consume vegetative parts of plants, totalling 19 species).

For Chapters 2 - 4, I considered all 200 species during the data analyses. However, during each chapter's data analysis, models for some species did not converge due to either sparse detection data, complex models (with statistical interactions), or a combination of both. Consequently, models for species that did not converge were discarded, and, the species in question was omitted from the analysis and results. As a consequence, the final number of species on which the results of Chapters 2 – 4 discuss are less than the initial list of 200 species. In Chapter 2, I discarded 4 models and thus discuss results for 196 species. In Chapter 3, I discarded 2 models and discuss results for 198 species. Finally, in Chapter 4 I discarded 14 models and discuss results for 186 species. Because different models are run in each chapter, it is possible that some species omitted from one chapter appear in the remaining chapters. A list of species for each chapter is contained in that chapter's appendix. It is unfortunate that some species were omitted from the species list. However, these are few relative to the total, and because my analyses focus on guild level responses, omissions of a few species do not diminish the overall results and subsequent conclusions.

#### 1.2.6.2 Chapter 5: Cape Rock-jumper (*Chaetops frenatus*)

For the 5$^{th}$ Chapter, I examined the range distribution and patch occupancy of the Cape Rock-jumper over the greater Western Cape region between the periods 1987-1992 and 2007-2015 (Fig. 1.3). The Cape Rock-jumper is endemic to the Western Cape of South Africa. It is a conspicuous bird with an obvious, far-reaching call which makes it easy to identify both visually and by ear (Hockey et al., 2005). The Cape Rock-jumper's threshold for evaporative water loss is much lower than for similar birds in the region, and it has experienced population declines in parts of its range that have undergone considerable warming (Milne et al., 2015). In future, It is expected to decrease further in abundance and range extent in response to climate change (Huntley et al., 2012). Thus, it is a good species to study in order to understand the effects of climate change on endemic biodiversity within the Western Cape.

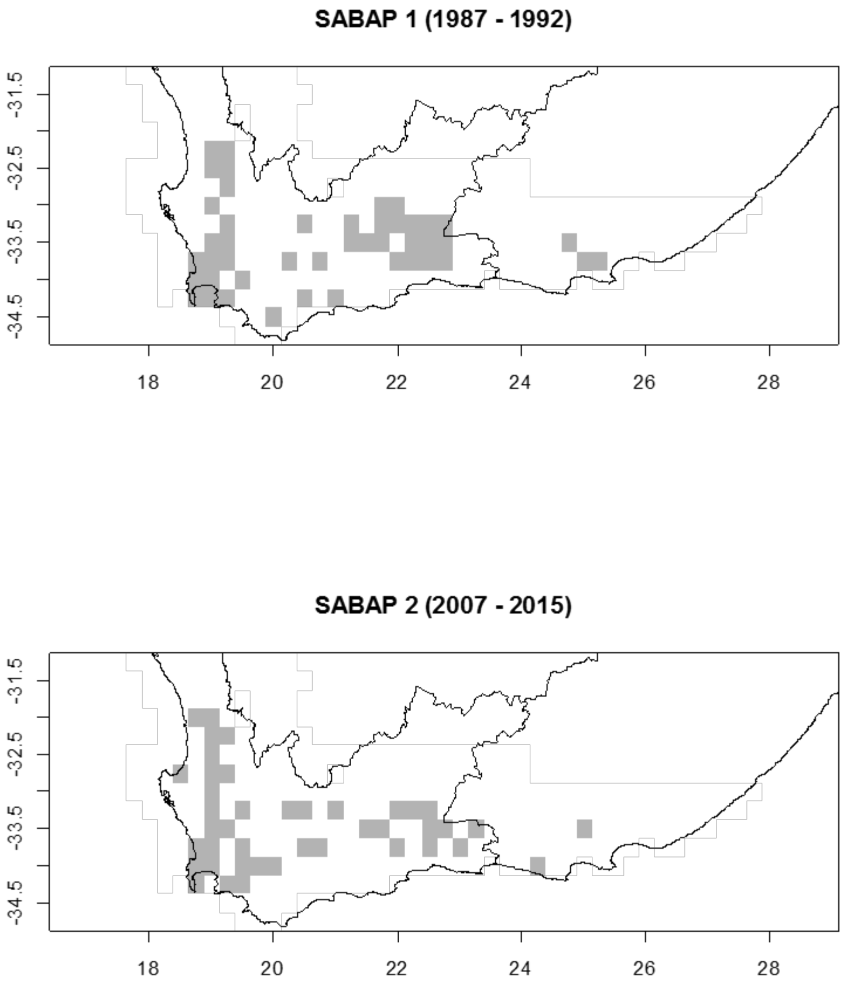


**Figure 1.3.** The endemic Cape Rock-jumper (*Chaetops frenatus*) distribution records from 1987 – 1992 (top panel) and 2007-2015 (bottom panel) over the greater Western Cape region of South Africa. The Cape Rock-jumper is a Western Cape endemic, and population sizes have decreased over regions of its range that have experienced significant warming. Grey squares indicate quarter degree grid cells (QDGCs, 15’ × 15’ in dimension, unit is arcminutes) in which the species has been recorded during the two time windows. These are raw data and thus provide a biased indication of the real distribution. Data are taken from the two phases of the Southern African Bird Atlas Project. The study area is made up of 354 QDGCs, which cover approximately 195 000 km$^2$.

Chapter 2

# Effectiveness of protected areas for bird conservation depends on guild

Martial eagle (*Polemaetus bellicosus*) in the Kruger National Park. Photograph by Greg Duckworth.

## 2. 1 ABSTRACT

**AIM:** Protected areas are key conservation tools intended to increase biodiversity and reduce extinction risks of species and populations. However, the degree to which protected areas achieve their conservation goals is generally unknown for many protected areas world-wide. I assess the effect of protected areas on the abundance of 196 common, resident bird species. If protected areas were beneficial to avian biodiversity, I expect landscapes with a higher proportion of protected areas will have higher densities of species compared to landscapes with no protection.

**LOCATION:** Greater Gauteng region, South Africa.

**METHODS:** I analysed bird survey data collected over regular grid cells across the study area. I estimated bird abundance in relation to the proportion of a grid cell that was protected with the Royle-Nichols model, and fitted the model once for each of the species. I examined variation in estimated abundance as a function of avian guild (defined by the type of food a species preferentially ate and its foraging mode) with a regression tree analysis.

**RESULTS:** Abundance was significantly positively related to the proportion of protected areas in grid cells for 26% of the species, significantly negatively related in 15%, and not significantly related in 59% species. I found three distinct guild groups which differed in their average abundance, after accounting for associated variance. Group 1 consisted of guilds frugivores, ground-feeders, hawkers, vegivores, and predators, and average abundance was strongly positively related to the proportion of protected areas. Group 2 included granivores, and average abundance was strongly negatively related to proportion of protected areas. Group 3 included gleaners only, and average abundance was not related to proportion of protected areas.

**MAIN CONCLUSION:** I conclude that the network of protected areas within the greater Gauteng region sustained relatively higher abundances of common birds, and thus perform an important conservation role.



**KEY WORDS:** Protected areas, hierarchical models, species abundance, citizen science, avian conservation.

## 2.2 INTRODUCTION

Protected areas are geographic areas set aside and managed for conservation of nature, ecosystem services, and cultural values (IUCN, 1994). They are a key tool used to conserve biodiversity, and are central to virtually all national and international conservation efforts (Gaston et al., 2006). The successful contribution of protected areas to biodiversity conservation is globally recognised, and every year billions of U.S. dollars are spent to maintain, improve, and develop protected areas (Balmford et al., 2003). In 2011 there were approximately 160 000 protected areas worldwide, covering an estimated 12% of the earth's land surface (IUCN, 2011). In addition, one of the Aichi targets specifically aims to increase this to 17% by 2020 (United Nations, 2013a), testament to their perceived importance for conservation of the world's biodiversity.

Most protected areas are developed and maintained to conserve particular species or habitats. For example, the Addo Elephant National Park in South Africa was designed to conserve elephants (Swemmer & Taljaard, 2011), or the Great Barrier Reef Marine Park in Australia was designed to protect corals and associated marine communities (Great Barrier Reef Marine Park Authority, 2009). A substantial body of work examining the effect of protected areas on biodiversity confirms that these parks are effective at conserving the target species or habitat (Owen-Smith et al., 2006; Watson et al., 2011; Geldmann et al., 2013). However, it is not clear whether protected areas are generally also effective at protecting non-target species. Despite some keystone species or focal habitats benefiting within large, national protected areas, some of the remaining biodiversity may decline (Hoekstra et al., 2002; Craigie et al., 2010; Watson et al., 2014). For example, the Maasai Mara National Reserve is a wildlife sanctuary situated in the south of Kenya and was inaugurated in 1961. Its primary conservation goals include conserving mammalian wildlife, specifically, endangered carnivores. This goal has largely been achieved as lion densities have remained high since the onset of conservation programs (Ogutu & Dublin, 2002), although other non-target species have declined in density, such as wildebeest (Ottichilo et al., 2001; Newmark, 2008), vultures (Virani et al., 2011) and ungulates (Ogutu et al., 2011). Thus, managing an area for protection of one group or species does not necessarily protect all wildlife species, nor does it ensure the presence of specific species or taxa (Jaarsveld et al., 1998). This suggests that there are still critical gaps in knowledge of how effective protected areas are at protecting biodiversity in general.

In this chapter, I use bird abundances to explore the broad-scale ecological effectiveness of protected areas on avian biodiversity. Birds are a good group to study because they are easily monitored, wide spread, well-studied, and occupy many niches (Furness & Greenwood, 1993). Furthermore, they are mobile and easily travel between areas with different land uses, which should allow them to react more quickly to changes in habitat quality. I consider common, resident bird species over the study area. Common species tend to be abundant, widespread, and in general, drive patterns in biodiversity and ecosystem functionality such as community assemblages, species richness, primary productivity, and nutrient cycling (Gaston & Fuller, 2008; Lennon et al., 2011; Winfree et al., 2015). Even slight declines in common species can have disproportionately negative effects on ecosystem functioning, and indicate significant losses of ecosystem health (Gaston, 2010; Winfree et al., 2015). Therefore, monitoring how well common species fare in protected areas can give insight into the ecological health of protected areas. Here, I examine how the abundance of common species is affected by protected areas. If protected areas are beneficial for avian biodiversity in general, I expect higher bird abundances within protected areas relative to non-protected areas.

## 2.3 METHODS

### *2.3.1 Species detection / non-detection data*

I used data from the second Southern African Bird Atlas Project (SABAP 2). This project was initiated in June 2007 (Harebottle et al., 2007) and was still on-going in 2018. Because the statistical models I used assume abundances of common birds remain similar for the duration of the study, I restricted the analysis to data from years 2014 and 2015. These were the most data rich years of SABAP 2. Registered volunteers collected checklists of all bird species observed within a regular, pre-defined area called a pentad, which is a 5' x 5' grid cell (unit is in arcminutes, approximately 61 $km^2$). My study area covers 576 pentads (a 24 pentad by 24 pentad grid), for which 10 400 checklists were submitted at an average of 18 checklists per pentad; the maximum number of checklists submitted for a single pentad was 468, and the minimum was 1 (all pentads were visited). Similar to Broms *et al.* (2014), I used at most 100 checklists per pentad. Where pentads had more checklists than this, 100 were randomly selected. This was done because some pentads were extremely well sampled relative to the others.

Submitted checklists must have involved at least 2 hours of dedicated birding, and can be collected over a period of up to five consecutive days. Volunteers were asked to record each species only once, regardless of how many individuals were seen. Not all areas inside the pentad were surveyed, but observers were asked to try to sample all habitats. Submitted checklists were examined thoroughly to identify possible misidentifications. When a species was reported from a pentad in which it had not previously been recorded, a vetting committee requested more information from the volunteer, and then accepted or rejected the record

(Harebottle et al., 2007).

Species selection

Within the study area, I chose 200 common, resident bird species as defined by Hockey *et al.* (2005), and omitted any nomadic, alien, and migratory species. I included detection / non-detection data that were collected between 1 January 2014 and 31 December 2015 and had been submitted to the project by February 2016.

### *2.3.2 Study area*

I selected the greater Gauteng Province, South Africa as the study area (comprising of a square with coordinates NW: 25S 27E, SE:27S 29E) because of its good mix of protected areas and heavily modified landscapes proximally situated to each other (Fig. 2.1). Gauteng is the most densely populated province in South Africa with average human density of 675.1 people $km^{-2}$ (Statistics South Africa, 2012). This ensured the study area was well atlassed, and that my data were of sufficient volume for the analyses (see below), and accurately represented the bird community. The study area covered approximately 35 000 $km^2$, of which 6.4% (approximately 2 240 $km^2$) is protected (South African National Biodiversity Institute (SANBI), 2009) either privately or publicly. The proportion of protected areas per pentad ranges from 0 to 1. The study area incorporates 81 protected areas, ranging in size from 0.08 $km^2$ to 816.70 $km^2$, at an average of 27.65 $km^2$. Vegetation is a major driver of bird diversity in the study area, which contained savanna and grassland biomes.

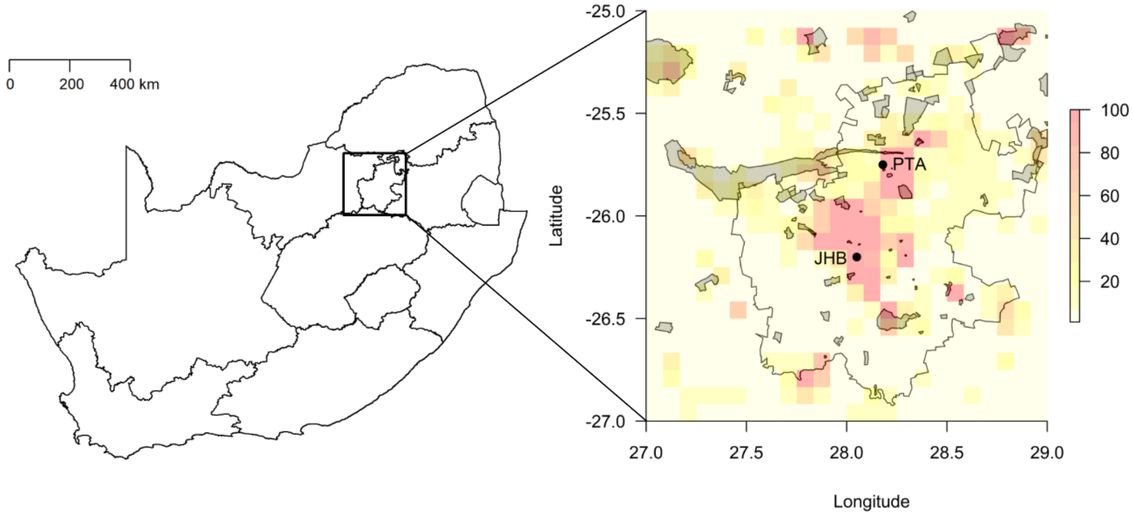


**Figure 2.1.** The study Area was the greater Gauteng region of South Africa and covers approximately 35 000 km$^2$. The left panel shows South Africa, and the relative location of the study area. The right panel is the enlarged study area. Coloured squares show the pentads (5' X 5' grid, unit is arcminutes) and the colour scale indicates sampling effort (the minimum was 1 checklist and I capped the maximum at 100). The shape outlined by a dark line is Gauteng Province in South Africa. The areas shaded in dark grey are protected areas (public and private).

### *2.3.3 Analyses*

#### 2.3.3.1 Abundance Models

I used abundance models to estimate bird abundances across the study area. Abundance models fall under the broader category of occupancy models (Royle & Nichols, 2003; MacKenzie et al., 2006), which are often used to analyse ecological atlas data. They recognise that species can go undetected during surveys of sites where they occur. Occupancy models account for this by including a component which models the detection process separately from the biological process (abundance in this case). Failure to account for the detection process will lead to biased results (Altwegg et al., 2008; Kéry, 2011; Bailey et al., 2014).

*Model Structure*

I used the Royle-Nichols abundance model (Royle & Nichols, 2003) to estimate the average latent abundance of individuals in pentad $i$ ($N_i$). The model exploits the relationship between species detection probability, individual detection probability, and latent abundance, with the following equation:

$$p_{ij} = 1 - \left(1 - r_{ij}\right)^{N_i} \tag{1}$$

where $p_{ij}$ indicates the probability of detecting the species in pentad $i$ during survey $j$, $r_{ij}$ the probability of detecting an individual in pentad $i$ during survey $j$, and $N_i$ the latent abundance in pentad $i$.

The detection probability for a single individual in pentad $i$ during survey $j$ ($r_{ij}$) is modelled as a Bernoulli process:

$$\omega_{ij} \sim Bernoulli\left(r_{ij}\right) \tag{2}$$

and variation in $r_{ij}$ was modelled with survey specific covariates using a logit link function:

$$logit\left(r_{ij}\right) = \alpha_0 + \alpha_1 \times \text{ħ}_{ij} \tag{3}$$

where $\text{ħ}_{ij}$ indicates the log of the number of hours spent birding during in pentad $i$ during survey $j$, and the $\alpha$ are coefficients to be estimated by the model.

Latent abundance in pentad $i$ ($N_i$) was modelled using a Poisson process with rate parameter $\lambda$ in the following form:

$$N_i \sim Poisson(\lambda_i) \tag{4}$$

$\lambda$ was modelled with pentad specific covariates using the log link function:

$$log(\lambda_i) = \beta_0 + \beta_1 \times PA_i + \beta_2 \times S_i \tag{5}$$

where for pentad $i$, $PA_i$ is the proportion of protected areas, and $S_i$ the proportion of savanna vegetation. Grassland and savanna are the major vegetation types in the study region, and together make up 99% of the vegetation in the study area (therefore, only savanna or grassland vegetation need be included in the model; including both will confound the model). The $\beta$ are coefficients to be estimated by the model, and I fitted a single model for each of the 200 species considered.

$\beta_1$ estimates the relationship between abundance and the proportion of the grid cell covered by protected areas. I interpret positive $\beta_1$ estimates as an indication that the species benefits from protected areas and is more abundant inside protected areas than outside. I interpret negative $\beta_1$ estimates as an indication that the species is relatively more abundant outside protected areas than inside them. As a cautionary note, estimates produced by the Royle-Nichols abundance model are best interpreted as relative measures of abundance (across pentads in my case), and not as absolute ones (Barker et al. 2018). Therefore, my estimates of abundance for each species should not be considered an absolute measure of abundance per species, but rather, comparative estimates of species abundance across the study site.

I included the vegetation parameter ($\beta_2$ in eqn. 5) to account for the effects of vegetation on bird abundance, and to estimate the effects of protected areas on abundance more accurately. Therefore, I do not focus on parameter $\beta_2$ in extensive detail here.

Since the $N_i$ are unknown, it is necessary to sum over reasonable values for species abundance (*K*) when maximising the model likelihood. I used an estimate *K* = 100 for all species in the models and checked that the estimated abundances were always well below this value.

A key assumption of the Royle-Nichols abundance model is that the population remains demographically closed over the study period (i.e., no gains and losses of individuals). I restricted the analysis to common, resident species whose densities were unlikely to change significantly over the duration of the study. Furthermore, my methods are robust enough to withstand slight violations in model assumptions (e.g. Mackenzie et al., 2003). I used package "unmarked" (Fiske & Chandler, 2011) in program R version 3.0.1 (R Development Core Team, 2016) to run the abundance models.

#### 2.3.3.2 Regression tree and guilds

I further examined variation among species in $\beta_1$ using a regression tree implemented in R package "rpart" (Therneau et al., 2018). Regression trees group observations as a function of multiple predictor variables (Breiman et al., 1984). They recursively split the response up into nodes, dependent on the predictor variables, in a way that minimises the remaining variance. The node after which there are no more splits is termed a "terminal" node. Each terminal node can be viewed as a group or cluster, since they are similar in terms of their response.

To account for the variable precision with which the $\beta_1$ were estimated, I weighted them by the inverse of their standard error to obtain a weighted $\beta_1$ $(w\beta_1)$. This gives a higher weight to the more precisely estimated coefficients (i.e., those with a smaller standard error) in the overall average calculation.

I further grouped the species into guilds based on the type of food the species preferentially consumed, and its primary mode of foraging. I used seven guilds based on the definitions in Hockey et. al., (2005). These were: frugivores (species that primarily consume fleshy fruit, totalling 9 species); gleaners (species that primarily consume insects and other invertebrates caught off plants, totalling 31 species); granivores (species that primarily consume seeds and grains, totalling 48 species); ground-feeders (species that primarily consume insects and invertebrates caught off the ground, totalling 63 species); hawkers (species that primarily consume insects and other invertebrates caught in the air, totalling 11 species); predators (birds of prey, species that primarily consume the flesh of vertebrates, totalling 19 species), and vegivores (vegetative herbivores; species that primarily consume vegetative parts of plants, totalling 19 species). In the regression tree model, I modelled the weighted $\beta_1$ estimates of each species as a function of the guild to which each species belongs.

## 2.4 RESULTS

*Estimated abundance in relation to proportion of area protected*

A single Royle-Nichols abundance model was fitted for each of the 200 species. Models for 4 species failed to converge, likely due to data sparsity. This left 196 species to which the remainder of the results refer. The parameter $\beta_1$ measures the slope of the linear (on the log scale) relationship between mean local abundance of each species and the proportion of protected areas per pentad, while accounting for the observation process. Species with a positive estimate for $\beta_1$ were relatively more abundant in pentads with a high proportion of protected areas and this was interpreted as the species having higher abundance inside protected areas, whereas a negative estimate for $\beta_1$ indicates the opposite. On average across all species, estimated abundance was higher inside protected areas than outside because mean $\hat{\beta}_1$ was slightly positive (0.12, range from -4.53 to 4.23 across species). Of the 196 species, 50 (26%) had a positive $\hat{\beta}_1$ and confidence intervals, 30 (15%) species had negative $\hat{\beta}_1$ and confidence intervals, 116 (59%) species had their confidence intervals overlap zero (Fig. 2.2).

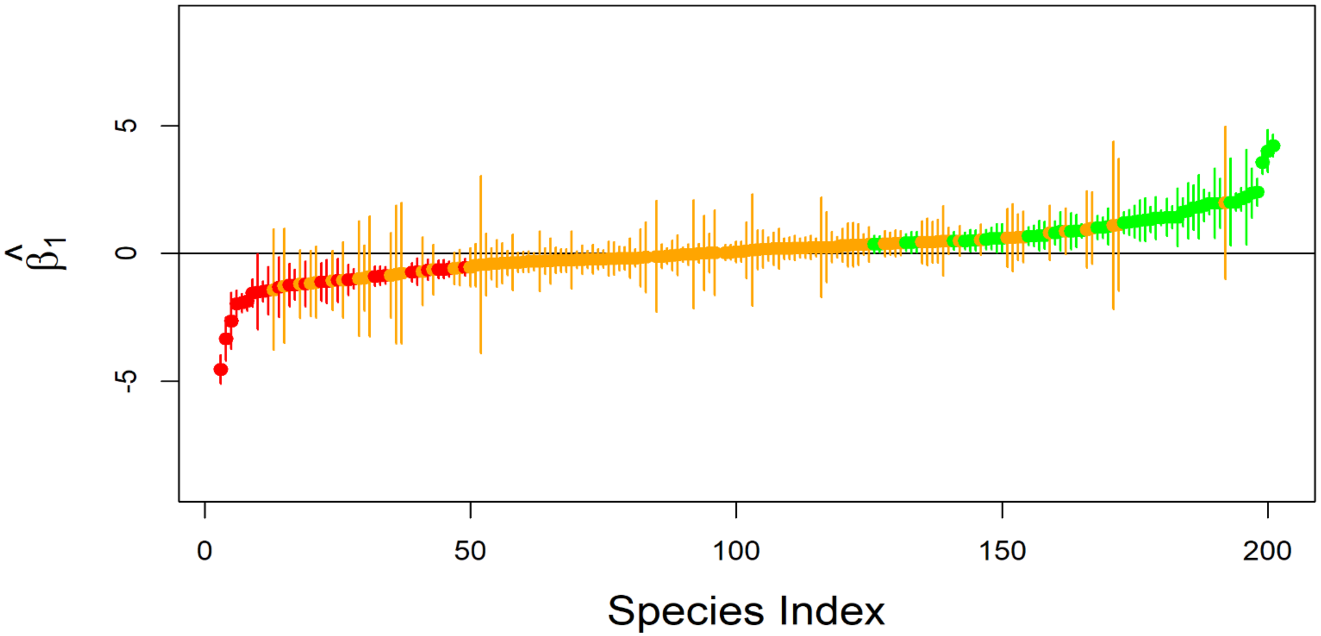


**Figure 2.2** Estimated slope of the linear (on the log scale) relationship between abundance and proportion of protected area per pentad for 196 common bird species in the greater Gauteng area in South Africa over the period Jan 2014 – Dec 2015. The species are sorted by magnitude of this slope, and the vertical lines are 95% confidence intervals. Red dots and lines indicate species with estimated mean and confidence intervals less than 0 (assumed to be less abundant inside protected areas). Green dots and lines represent those species with estimated mean and confidence intervals greater than 0 (more abundant inside protected areas). Orange dots and lines represent species with confidence intervals that overlapped zero, and average abundance was not significantly influenced by the proportion of protected areas.

*Regression trees and guilds*

The regression tree identified three distinct groups that differed markedly in their average $\hat{\beta}_1$ estimate. Group 1 consisted of guilds frugivores, ground-feeders, hawkers, predators, and vegivores. On average, and accounting for error associated with each $\hat{\beta}_1$ estimate, group 1 were strongly more abundant inside pentads with a higher proportion of protected areas, ($w\hat{\beta}_1$ = 0.34, *n* = 121; Table 2.1), which I infer as being more abundant within protected areas than outside them. Group 2 comprised of gleaners, which neither increased nor decreased in average estimated abundance with an increase in protected areas ($w\hat{\beta}_1$ = 0.0, *n* = 30; Table 2.1). From this, I infer that on average, gleaners were as abundant within protected areas as they were outside them. Group 3 included granivores, which were, on average, much less abundant within pentads with a higher proportion of protected areas ($w\hat{\beta}_1$ = -0.35, *n* = 45; Table 2.1). Model results for each species, and the guild group to which it belongs are situated in Appendix 2 (Table A2.1).

**Table 2.1**. Summary statistics of groups identified by a regression tree analyses modelling the relationship between estimated abundance and the proportion of protected area in a pentad ($\hat{\beta}_1$ estimates taken from the Royle-Nichols abundance model) as a function of guild, for 196 species. $w\hat{\beta}_1$ indicates the weighted mean of $\hat{\beta}_1$ (see methods text for details on this calculation). I considered only common and resident bird species in the greater Gauteng area of South Africa over the period Jan 2014 – Dec 2015. A positive estimate for $w\hat{\beta}_1$ indicates that group is more abundant within pentads with a higher proportion of protected areas, and the opposite is true for negative $w\hat{\beta}_1$ estimates.

| Group Classification | Guild | *n* | $w\hat{\beta}_1$ of Guild | $w\hat{\beta}_1$ of Group |
|---|---|---|---|---|
| Group 1 | Frugivores | 9 | 0.35 | 0.34 |
| | Ground-feeders | 63 | 0.34 | |
| | Hawkers | 11 | 0.24 | |
| | Predators | 19 | 0.50 | |
| | Vegivores | 19 | 0.29 | |
| Group 2 | Gleaners | 30 | 0.00 | 0.00 |
| Group 3 | Granivores | 45 | -0.35 | -0.35 |
| | | Σ 196 | | |

*__Relative estimated abundances per group across the study area__*

To examine spatial patterns in estimated abundance in more detail I predicted the average estimated abundance in each pentad for each species, using the coefficients as estimated by the Royle-Nichols model, and the pentad-specific covariate values. I then calculated the average estimated abundance for each of the three groups (Fig. 2.3). This figure clearly shows a higher average estimated abundance of group 1 species inside protected areas, on average similar estimated abundances for group 2 species inside and outside protected areas, and lower average estimated abundance of group 3 species inside protected areas. Confirming the importance of vegetation for avian diversity, estimated abundances for gleaners were higher in the northern part of the study area, occupied by the Savanna biome.

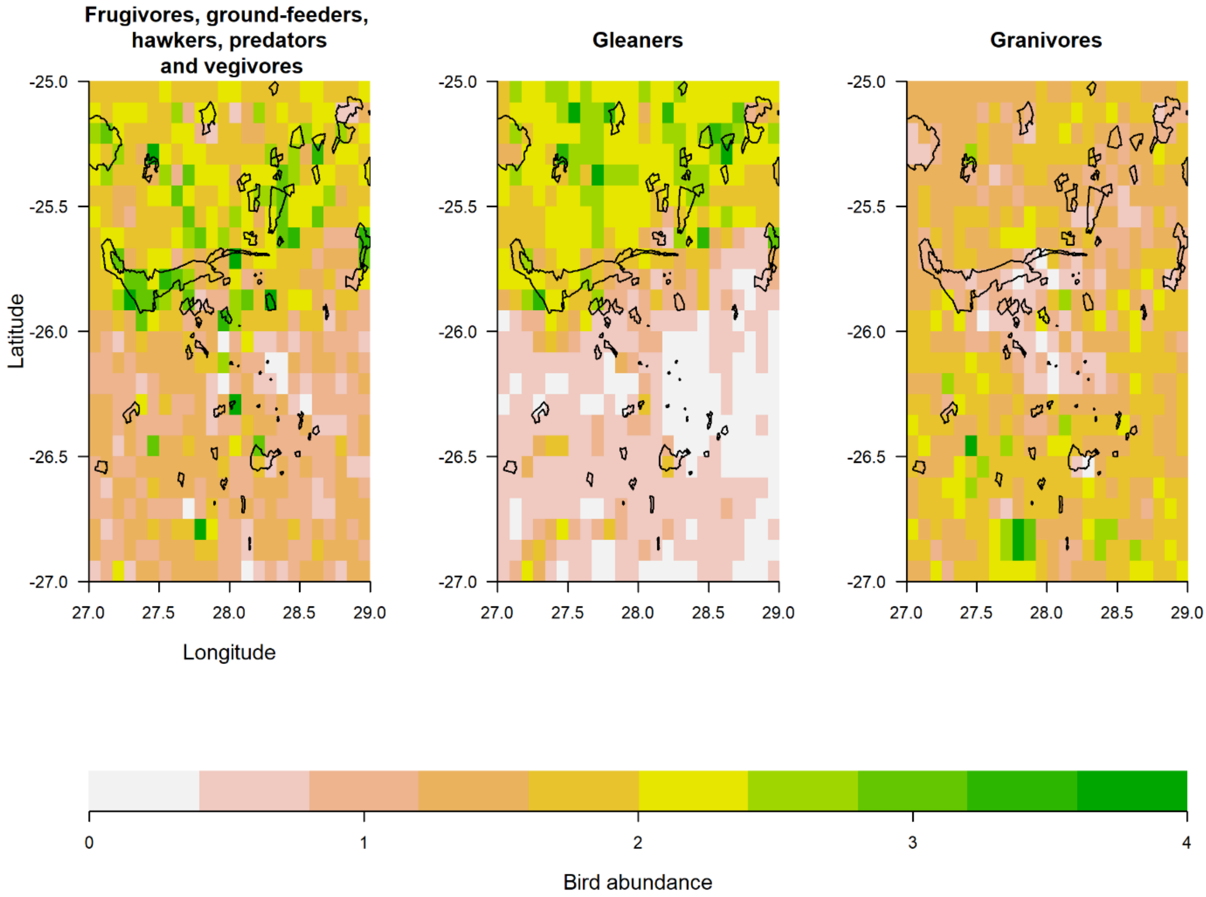


**Figure 2.3**. Estimated bird abundances per pentad averaged across all species within each of the three distinct groups identified by the regression tree analysis. Abundance predictions from Royle-Nichols abundance model run independently for each of the 196 common species examined within the greater Gauteng area over Jan 2014 – Dec 2015. The plots from left to right correspond to groups 1 – 3 in Table 2.1. The colour of the pentad refers to the abundance estimate: white pentads correspond to a lower estimated abundance and green ones to a higher abundance. The outlined shapes are protected areas, both public and private. Guilds frugivores, ground-feeders, hawkers, predators, and vegivores (group 1) were, on average, more abundant in pentads with a higher proportion of protected areas. On average, gleaners (group 2) were neither more abundant nor less abundant in pentads with a higher proportion of protected areas. Conversely, average abundance for granivores (group 3) was lower pentads with a higher proportion of protected areas.

## 2.5 DISCUSSION

Protected areas are one of the most important tools for biodiversity conservation. It is therefore critical to know how well they perform this function. In this study, I examined how protected areas affected the abundance of common, resident bird species in South Africa. Since birds are well monitored, easy to observe (this particularly applies to common birds) and are good indicators of ecosystem health (Furness & Greenwood, 1993; Gaston, 2010; Winfree et al., 2015), decreases in their abundance, especially within protected areas, can indicate a decline of ecosystem functionality. I found that for most species, estimated abundance increased with the proportion of protected area within a pentad. However, this relationship varied strongly among species and was in part explained by differences in guild.

My results suggest that, on average, ground-feeding and hawking insect eaters, frugivores, vegivores and predatory birds were more abundant in pentads with a higher proportion of protected areas, whereas granivores were relatively less abundant in such pentads. The average estimated abundance of gleaners was not affected by the proportion of protected areas (Table 2.1). My results are consistent with other studies conducted in South Africa which find that in general, common species are more abundant within protected areas compared to outside them (Child et al., 2009; Greve et al., 2011), as well as elsewhere throughout the world (Laurance et al., 2012; Coetzee et al., 2014; Gray et al., 2016). Thus, my results show that protected areas are supporting a rich diversity of common bird species. Because common birds are good indicators of ecosystem health and functioning (Furness & Greenwood, 1993; Gaston, 2010; Winfree et al., 2015), my results suggest that in general, protected areas over the study area successfully maintain relatively healthy and functioning habitats.

The conservation benefit provided by protected areas to biodiversity can dependent on the type of land surrounding them (DeFries et al., 2007; Hansen & Defries, 2007; Laurance et al., 2012). This is especially true for birds because they are a very mobile species, and can travel easily between multiple land uses within a landscape. My study primarily comprised of protected areas, urban, and agricultural land-use types. The level of protection provided by protected areas to a species may depend on the degree to which the species is able to adapt to neighbouring land-use types (or, to habitats disturbed due to human-related activity). Group 1 includes many species recorded to adapt poorly to disturbed habitats (including human-modified landscapes), or, are habitat specialists (Chace & Walsh, 2006; Santos et al., 2008; Greve et al., 2011; Thomas et al., 2012; Rayner et al., 2014). Thus, for these species, protected areas play an important conservation role, as they provide natural and undisturbed habitat in which they may persist. For example, in this case, these include ground-feeding species such as Cape Rock-thrush (*Monticola rupestris,* $\hat{\beta}_1$ = 4.23), Sentinel Rock-thrush (*Monticola explorator,* $\hat{\beta}_1$ = 3.56), Plain-backed Pipit (*Anthus leucophrys,* $\hat{\beta}_1$ = 2.13); vegivorous species including the Cape Bunting (*Emberiza capensis,* $\hat{\beta}_1$ = 2.40) and Red-winged Francolin (*Scleroptila levaillantii,* $\hat{\beta}_1$ = 2.21); predatory species including African Grass-owl (*Tyto capensis,* $\hat{\beta}_1$ = 2.02), Jackal Buzzard (*Buteo rufofuscus,* $\hat{\beta}_1$ = 1.96), Rock Kestrel (*Falco rupicolus,* $\hat{\beta}_1$ = 1.82); hawking species including Rock Martin (*Ptyonoprogne fuligula,* $\hat{\beta}_1$ = 0.87), Fiery-necked Nightjar (*Caprimulgus pectoralis,* $\hat{\beta}_1$ = 0.81); and finally, frugivorous species including Yellow-fronted Tinkerbird (*Pogoniulus chrysoconus*, $\hat{\beta}_1$ = 1.11), and Dark-capped Bulbul (*Pycnonotus tricolor,* $\hat{\beta}_1$ = 0.61). Generally, my results indicate that protected areas play an important role to the persistence of many species within group 1.

Conversely, on average, granivores were more abundant in pentads with lower proportions of protected areas (group 3, Table 2.1). Granivores can be opportunistic, adapt quickly to new environments (Beissinger & Osborne, 1982; Chace & Walsh, 2006), and benefit from additional food sources and variety of nesting and roosting spots available in urban and agricultural land-use types (Gaston & Evans, 2004; Chace & Walsh, 2006). Thus, my study suggests granivores, on average, favoured the conditions offered in urban and agricultural land-use types over those provided by protected areas. Indeed, granivores with the most negative $\hat{\beta}_1$ included the Village Indigobird (*Vidua chalybeatae,* $\hat{\beta}_1$ = -2.63), Scaly-feathered Finch (*Sporopipes squamifrons*, $\hat{\beta}_1$ = -1.93), Red-headed Finch (*Amadina erythrocephala*, $\hat{\beta}_1$ = -1.86), and Red-capped Lark (*Calandrella cinerea*, $\hat{\beta}_1$ = -1.55), all of which have been shown to adapt well to agricultural land-use types (Barnard, 1997; Dean, 1997; Herremans, 1997a, 1997b). A landscape matrix including agricultural land-use type is therefore important for these species. Gleaners, on the other hand, were on average as abundant within pentads with a high proportion of protected areas as they were in those with low proportions (group 2, Table 2.1). This is probably because gleaners eat insects that are attracted into urban gardens (Chace & Walsh, 2006). For example, species in this group such as the Black-chested Prinia (*Prinia flavicans*, $\hat{\beta}_1$ -1.27), Grey-headed Bush-shrike (*Malaconotus blanchoti,* $\hat{\beta}_1$ = 0.55), Tawny-flanked Prinia (*Prinia subflava,* $\hat{\beta}_1$ = 0.49), and Southern Boubou (*Laniarius ferrugineus,* $\hat{\beta}_1$ = 0.89) are commonly observed in gardens of suburban areas (Berruti, 1997a, 1997b, Parker, 1997a, 1997b). Furthermore, in some cases, agricultural practices may increase the abundance and species richness of insects (Benton et al., 2002; Newton, 2004), which may support relatively dense populations of gleaning species in agricultural lands. Thus, the ecological benefit provided by protected areas to gleaning species appears to depend strongly on the land-use types surrounding protected areas.

Like all observational studies, I cannot infer causal relationships. An alternative explanation for my findings could be that protected areas were in areas that can naturally sustain high abundances of birds, for example, if they were located in areas with higher productivity.

However, productivity is less likely to have a direct influence on my findings since protected areas are generally placed in areas of low economic value and in unwanted space, and productivity is not a major factor in the establishment of protected areas (Joppa & Pfaff, 2009). Furthermore, my study consisted of 81 protected areas of varying sizes, scattered over the landscape matrix (as opposed to just one, large protected area) and I accounted for biome as one of the most important drivers of avian diversity in the study area.

In conclusion, even though I cannot clearly attribute my findings to protection status in general, results indicate that the current network of protected areas within the greater Gauteng region does sustain a relatively higher abundance for many of the species I investigated, and thus perform an important conservation role. The next step in further understanding the role played by protected areas is to gain insight into the mechanisms by which they are able to sustain higher abundances of common species. This can be done by examining local colonization and extinction dynamics using dynamic occupancy models. As I suggest here, land-use types neighbouring protected areas may affect significantly the conservation performance of protected areas. A further consideration, then, is to understand carefully the ways in which neighbouring land-use types affect the ability of protected areas to house large abundances of common species, which is what I explore in my next chapter. Additionally, the conservation performance of protected areas can be significantly affected by management practices. Future studies should quantify how differences in management influence performance. Tackling these concepts will considerably increase the general understanding of the of the conservation role played by protected areas, and the value they provide to biodiversity.

## 2.6 APPENDIX: Supplementary material for Chapter 2

**Table A2.1.** Mean and standard error estimates produced by the Royle-Nichols model of abundance for each species (*n* = 196). Abundance estimates presented on the log scale, and detection presented on the logit scale. Model coefficients $\hat{\beta}$ relate to estimated abundance, $\hat{\alpha}$ to estimated detection, and correspond to those in equations 3 and 5 in the Methods section. 'Group' refers to which of the three groups a species was assigned based on the results from the regression tree analyses. Species are sorted alphabetically, firstly by guild, and secondly by species (common name).

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Frugivore | Acacia Pied Barbet *(Tricholaema leucomelas)* | 0.05 ± 0.10 | -0.22 ± 0.29 | 0.01 ± 0.00 | -2.23 ± 0.07 | 0.03 ± 0.01 | 1 |
| Frugivore | African Olive-Pigeon *(Columba arquatrix)* | -0.20 ± 0.12 | 1.13 ± 0.50 | -0.02 ± 0.00 | -2.07 ± 0.07 | 0.02 ± 0.01 | 1 |
| Frugivore | Black-collared Barbet *(Lybius torquatus)* | 0.64 ± 0.08 | 0.39 ± 0.18 | 0.01 ± 0.00 | -1.76 ± 0.06 | 0.12 ± 0.02 | 1 |
| Frugivore | Cape Glossy Starling *(Lamprotornis nitens)* | 1.05 ± 0.08 | -0.45 ± 0.18 | 0.01 ± 0.00 | -1.43 ± 0.08 | 0.11 ± 0.01 | 1 |
| Frugivore | Crested Barbet *(Trachyphonus vaillantii)* | 0.90 ± 0.07 | 0.07 ± 0.18 | 0.00 ± 0.00 | -1.32 ± 0.07 | 0.11 ± 0.01 | 1 |
| Frugivore | Dark-capped Bulbul *(Pycnonotus tricolor)* | 0.86 ± 0.06 | 0.61 ± 0.15 | 0.01 ± 0.00 | -1.19 ± 0.06 | 0.11 ± 0.02 | 1 |
| Frugivore | Red-faced Mousebird *(Urocolius indicus)* | 0.89 ± 0.09 | -0.34 ± 0.21 | 0.00 ± 0.00 | -1.62 ± 0.09 | 0.09 ± 0.01 | 1 |
| Frugivore | Red-winged Starling *(Onychognathus morio)* | -0.52 ± 0.13 | 1.22 ± 0.21 | 0.01 ± 0.00 | -2.21 ± 0.07 | 0.05 ± 0.01 | 1 |
| Frugivore | Yellow-fronted Tinkerbird *(Pogoniulus chrysoconus)* | -2.54 ± 0.26 | 1.11 ± 0.21 | 0.03 ± 0.00 | -2.05 ± 0.08 | 0.03 ± 0.01 | 1 |
| Gleaner | Ashy Tit *(Parus cinerascens)* | -2.39 ± 0.31 | -1.19 ± 0.74 | 0.02 ± 0.00 | -2.68 ± 0.14 | 0.06 ± 0.02 | 2 |
| Gleaner | Barred Wren-Warbler *(Calamonastes fasciolatus)* | -6.87 ± 01.71 | -1.03 ± 0.70 | 0.06 ± 0.02 | -2.27 ± 0.18 | 0.00 ± 0.04 | 2 |
| Gleaner | Bar-throated Apalis *(Apalis thoracica)* | -0.33 ± 0.13 | 1.34 ± 0.24 | 0.01 ± 0.00 | -2.40 ± 0.08 | 0.03 ± 0.01 | 2 |
| Gleaner | Black-backed Puffback *(Dryoscopus cubla)* | -1.41 ± 0.18 | 0.43 ± 0.20 | 0.03 ± 0.00 | -2.31 ± 0.08 | 0.05 ± 0.01 | 2 |
| Gleaner | Black-chested Prinia *(Prinia flavicans)* | 1.54 ± 0.07 | -1.27 ± 0.26 | 0.00 ± 0.00 | -1.88 ± 0.08 | 0.02 ± 0.01 | 2 |
| Gleaner | Black-headed Oriole *(Oriolus larvatus)* | -1.07 ± 0.16 | 0.80 ± 0.21 | 0.02 ± 0.00 | -2.64 ± 0.08 | 0.07 ± 0.01 | 2 |
| Gleaner | Brubru Brubru *(Nilaus afer)* | -2.11 ± 0.24 | -0.70 ± 0.31 | 0.03 ± 0.00 | -2.61 ± 0.10 | 0.08 ± 0.02 | 2 |
| Gleaner | Cape Penduline-Tit *(Anthoscopus minutus)* | -5.19 ± 01.20 | -1.20 ± 0.85 | 0.05 ± 0.01 | -3.52 ± 0.26 | 0.06 ± 0.04 | 2 |
| Gleaner | Cardinal Woodpecker *(Dendropicos fuscescens)* | -0.23 ± 0.14 | 0.20 ± 0.23 | 0.01 ± 0.00 | -2.96 ± 0.09 | 0.09 ± 0.01 | 2 |
| Gleaner | Chestnut-vented Tit-Babbler *(Parisoma subcaeruleum)* | -0.21 ± 0.10 | -0.44 ± 0.21 | 0.02 ± 0.00 | -1.91 ± 0.06 | 0.03 ± 0.01 | 2 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Gleaner | Chinspot Batis *(Batis molitor)* | -1.31 ± 0.16 | 0.21 ± 0.17 | 0.03 ± 0.00 | -2.23 ± 0.10 | 0.03 ± 0.01 | 2 |
| Gleaner | Common Scimitarbill *(Rhinopomastus cyanomelas)* | -1.46 ± 0.26 | 0.36 ± 0.57 | 0.01 ± 0.00 | -3.58 ± 0.17 | 0.09 ± 0.02 | 2 |
| Gleaner | Crimson-breasted Shrike *(Laniarius atrococcineus)* | -1.57 ± 0.18 | -0.16 ± 0.22 | 0.03 ± 0.00 | -2.20 ± 0.09 | 0.06 ± 0.02 | 2 |
| Gleaner | Desert Cisticola *(Cisticola aridulus)* | 0.14 ± 0.11 | -0.17 ± 0.34 | 0.00 ± 0.00 | -2.70 ± 0.09 | 0.02 ± 0.01 | 2 |
| Gleaner | Golden-tailed Woodpecker *(Campethera abingoni)* | -1.14 ± 0.18 | 0.25 ± 0.24 | 0.02 ± 0.00 | -3.01 ± 0.09 | 0.05 ± 0.01 | 2 |
| Gleaner | Greater Honeyguide *(Indicator indicator)* | -0.21 ± 0.19 | -0.09 ± 0.34 | 0.01 ± 0.00 | -3.61 ± 0.14 | 0.05 ± 0.01 | 2 |
| Gleaner | Green Wood-Hoopoe *(Phoeniculus purpureus)* | 0.74 ± 0.09 | -0.21 ± 0.23 | 0.00 ± 0.00 | -2.23 ± 0.07 | 0.09 ± 0.01 | 2 |
| Gleaner | Grey Penduline-Tit *(Anthoscopus caroli)* | -23.42 ± 33.78 | -4.53 ± 04.80 | 0.22 ± 0.34 | -4.09 ± 0.73 | 0.07 ± 0.05 | 2 |
| Gleaner | Grey-headed Bush-Shrike *(Malaconotus blanchoti)* | -1.85 ± 0.24 | 0.55 ± 0.28 | 0.02 ± 0.00 | -2.85 ± 0.10 | 0.04 ± 0.01 | 2 |
| Gleaner | Klaas's Cuckoo *(Chrysococcyx klaas)* | -1.45 ± 0.30 | -0.27 ± 0.38 | 0.02 ± 0.00 | -3.91 ± 0.18 | 0.04 ± 0.01 | 2 |
| Gleaner | Lesser Honeyguide *(Indicator minor)* | -0.14 ± 0.15 | -0.43 ± 0.33 | 0.01 ± 0.00 | -3.08 ± 0.10 | 0.06 ± 0.01 | 2 |
| Gleaner | Long-billed Crombec *(Sylvietta rufescens)* | -2.08 ± 0.23 | -0.54 ± 0.19 | 0.04 ± 0.00 | -2.55 ± 0.10 | 0.03 ± 0.01 | 2 |
| Gleaner | Rattling Cisticola *(Cisticola chiniana)* | -1.86 ± 0.20 | -0.53 ± 0.21 | 0.04 ± 0.00 | -2.11 ± 0.08 | 0.01 ± 0.01 | 2 |
| Gleaner | Red-headed Weaver *(Anaplectes melanotis)* | -9.83 ± 03.86 | -0.89 ± 0.77 | 0.09 ± 0.04 | -3.11 ± 0.25 | 0.23 ± 0.05 | 2 |
| Gleaner | Southern Black Tit *(Parus niger)* | -5.20 ± 0.80 | -0.25 ± 0.39 | 0.05 ± 0.01 | -2.00 ± 0.11 | 0.05 ± 0.02 | 2 |
| Gleaner | Southern Boubou *(Laniarius ferrugineus)* | -0.67 ± 0.11 | 0.89 ± 0.18 | 0.02 ± 0.00 | -1.44 ± 0.06 | 0.04 ± 0.01 | 2 |
| Gleaner | Tawny-flanked Prinia *(Prinia subflava)* | 0.38 ± 0.10 | 0.49 ± 0.17 | 0.01 ± 0.00 | -1.36 ± 0.09 | 0.05 ± 0.01 | 2 |
| Gleaner | Wing-snapping Cisticola *(Cisticola ayresii)* | 0.11 ± 0.12 | 1.01 ± 0.44 | -0.01 ± 0.00 | -2.74 ± 0.12 | 0.05 ± 0.02 | 2 |
| Gleaner | Yellow-bellied Eremomela *(Eremomela icteropygialis)* | -5.91 ± 02.75 | -0.37 ± 1.00 | 0.06 ± 0.03 | -5.06 ± 0.68 | 0.04 ± 0.03 | 2 |
| Gleaner | Zitting Cisticola *(Cisticola juncidis)* | 1.60 ± 0.08 | -0.29 ± 0.21 | 0.00 ± 0.00 | -2.38 ± 0.08 | 0.03 ± 0.01 | 2 |
| Granivore | African Firefinch *(Lagonosticta rubricata)* | -1.54 ± 0.30 | 0.59 ± 0.44 | 0.02 ± 0.00 | -4.02 ± 0.19 | 0.11 ± 0.03 | 3 |
| Granivore | African Quailfinch *(Ortygospiza atricollis)* | 1.18 ± 0.07 | -0.11 ± 0.28 | -0.01 ± 0.00 | -2.20 ± 0.07 | -0.01 ± 0.01 | 3 |
| Granivore | Black-faced Waxbill *(Estrilda erythronotos)* | -3.08 ± 0.42 | -0.87 ± 0.58 | 0.03 ± 0.01 | -2.88 ± 0.15 | 0.06 ± 0.02 | 3 |
| Granivore | Black-throated Canary *(Crithagra atrogularis)* | 1.65 ± 0.06 | -0.86 ± 0.23 | 0.00 ± 0.00 | -1.83 ± 0.06 | 0.03 ± 0.01 | 3 |
| Granivore | Blue Waxbill *(Uraeginthus angolensis)* | -0.83 ± 0.13 | -0.27 ± 0.15 | 0.03 ± 0.00 | -2.22 ± 0.08 | 0.03 ± 0.01 | 3 |
| Granivore | Bronze Mannikin *(Spermestes cucullatus)* | -0.80 ± 0.14 | -0.19 ± 0.32 | 0.01 ± 0.00 | -2.27 ± 0.08 | 0.03 ± 0.01 | 3 |
| Granivore | Cape Canary *(Serinus canicollis)* | -2.47 ± 0.36 | 2.37 ± 0.95 | -0.01 ± 0.01 | -2.67 ± 0.26 | 0.00 ± 0.07 | 3 |
| Granivore | Cape Sparrow *(Passer melanurus)* | 2.41 ± 0.07 | -1.45 ± 0.24 | -0.01 ± 0.00 | -1.65 ± 0.07 | 0.04 ± 0.01 | 3 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Granivore | Cape Turtle-Dove *(Streptopelia capicola)* | 1.92 ± 0.07 | -0.70 ± 0.19 | 0.00 ± 0.00 | -0.97 ± 0.08 | 0.07 ± 0.01 | 3 |
| Granivore | Chestnut-backed Sparrowlark *(Eremopterix leucotis)* | -1.32 ± 0.22 | -1.42 ± 01.11 | 0.00 ± 0.00 | -2.55 ± 0.25 | -0.03 ± 0.07 | 3 |
| Granivore | Cinnamon-breasted Bunting *(Emberiza tahapisi)* | -0.01 ± 0.12 | 0.61 ± 0.22 | 0.01 ± 0.00 | -2.86 ± 0.09 | 0.03 ± 0.01 | 3 |
| Granivore | Common Waxbill *(Estrilda astrild)* | 1.25 ± 0.08 | -0.06 ± 0.23 | 0.00 ± 0.00 | -2.55 ± 0.08 | 0.06 ± 0.01 | 3 |
| Granivore | Cuckoo Finch *(Anomalospiza imberbis)* | -1.02 ± 0.30 | 1.97 ± 0.72 | -0.01 ± 0.01 | -4.33 ± 0.31 | 0.14 ± 0.08 | 3 |
| Granivore | Dusky Indogobird *(Vidua funerea)* | -5.07 ± 1.78 | -1.11 ± 1.53 | 0.04 ± 0.02 | -4.4 ± 0.92 | 0.03 ± 0.06 | 3 |
| Granivore | Emerald-spotted Wood-Dove *(Turtur chalcospilos)* | -5.62 ± 1.00 | 0.50 ± 0.36 | 0.06 ± 0.01 | -2.71 ± 0.16 | 0.15 ± 0.03 | 3 |
| Granivore | Fan-tailed Widowbird *(Euplectes axillaris)* | -0.25 ± 0.13 | -0.89 ± 01.32 | -0.03 ± 0.01 | -2.24 ± 0.15 | 0.06 ± 0.03 | 3 |
| Granivore | Golden-breasted Bunting *(Emberiza flaviventris)* | -3.62 ± 0.41 | 0.42 ± 0.23 | 0.05 ± 0.00 | -2.30 ± 0.11 | 0.06 ± 0.02 | 3 |
| Granivore | Great Sparrow *(Passer motitensis)* | -6.28 ± 01.51 | 0.25 ± 0.55 | 0.06 ± 0.02 | -2.91 ± 0.18 | 0.02 ± 0.02 | 3 |
| Granivore | Green-winged Pytilia *(Pytilia melba)* | -1.16 ± 0.18 | -1.04 ± 0.41 | 0.02 ± 0.00 | -2.70 ± 0.11 | 0.07 ± 0.02 | 3 |
| Granivore | House Sparrow *(Passer domesticus)* | 1.37 ± 0.08 | -1.22 ± 0.27 | 0.00 ± 0.00 | -1.73 ± 0.07 | 0.02 ± 0.01 | 3 |
| Granivore | Jameson's Firefinch *(Lagonosticta rhodopareia)* | -1.17 ± 0.18 | 0.18 ± 0.26 | 0.02 ± 0.00 | -2.82 ± 0.10 | 0.06 ± 0.01 | 3 |
| Granivore | Long-tailed Paradise-Whydah *(Vidua paradisaea)* | -1.14 ± 0.20 | -0.82 ± 0.49 | 0.01 ± 0.00 | -2.94 ± 0.14 | 0.01 ± 0.02 | 3 |
| Granivore | Long-tailed Widowbird *(Euplectes progne)* | 2.04 ± 0.06 | -0.31 ± 0.32 | -0.02 ± 0.00 | -1.83 ± 0.07 | 0.05 ± 0.02 | 3 |
| Granivore | Namaqua Dove *(Oena capensis)* | 0.22 ± 0.10 | -0.86 ± 0.32 | 0.01 ± 0.00 | -2.34 ± 0.08 | 0.02 ± 0.01 | 3 |
| Granivore | Orange-breasted Waxbill *(Sporaeginthus subflavus)* | 0.45 ± 0.12 | -0.62 ± 0.56 | -0.01 ± 0.00 | -3.21 ± 0.12 | 0.11 ± 0.03 | 3 |
| Granivore | Pin-tailed Whydah *(Vidua macroura)* | 1.66 ± 0.08 | -0.30 ± 0.22 | 0.00 ± 0.00 | -2.50 ± 0.08 | 0.06 ± 0.01 | 3 |
| Granivore | Red-billed Firefinch *(Lagonosticta senegala)* | -1.94 ± 0.25 | -1.10 ± 0.42 | 0.03 ± 0.00 | -2.82 ± 0.11 | 0.03 ± 0.01 | 3 |
| Granivore | Red-billed Quelea *(Quelea quelea)* | 1.60 ± 0.07 | -1.05 ± 0.24 | 0.00 ± 0.00 | -2.16 ± 0.07 | 0.03 ± 0.01 | 3 |
| Granivore | Red-capped Lark *(Calandrella cinerea)* | 0.96 ± 0.08 | -1.55 ± 0.70 | -0.02 ± 0.00 | -2.09 ± 0.10 | -0.01 ± 0.02 | 3 |
| Granivore | Red-collared Widowbird *(Euplectes ardens)* | 0.58 ± 0.09 | 0.90 ± 0.25 | 0.00 ± 0.00 | -2.30 ± 0.08 | 0.05 ± 0.01 | 3 |
| Granivore | Red-eyed Dove *(Streptopelia semitorquata)* | 1.88 ± 0.07 | -0.08 ± 0.18 | -0.01 ± 0.00 | -1.18 ± 0.08 | 0.07 ± 0.01 | 3 |
| Granivore | Red-headed Finch *(Amadina erythrocephala)* | 0.49 ± 0.11 | -1.86 ± 0.64 | -0.01 ± 0.00 | -2.26 ± 0.09 | 0.06 ± 0.02 | 3 |
| Granivore | Scaly-feathered Finch *(Sporopipes squamifrons)* | -2.13 ± 0.21 | -1.93 ± 0.46 | 0.03 ± 0.00 | -1.41 ± 0.12 | -0.05 ± 0.03 | 3 |
| Granivore | Shaft-tailed Whydah *(Vidua regia)* | -3.52 ± 0.53 | -1.50 ± 0.70 | 0.03 ± 0.01 | -2.76 ± 0.22 | -0.02 ± 0.04 | 3 |
| Granivore | Southern Red Bishop *(Euplectes orix)* | 2.24 ± 0.10 | -0.62 ± 0.21 | -0.01 ± 0.00 | -1.68 ± 0.12 | 0.03 ± 0.01 | 3 |
| Granivore | Speckled Pigeon *(Columba guinea)* | 1.66 ± 0.17 | -0.57 ± 0.21 | -0.01 ± 0.00 | -1.30 ± 0.19 | 0.05 ± 0.01 | 3 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Granivore | Village Indigobird *(Vidua chalybeata)* | -2.20 ± 0.30 | -2.63 ± 0.87 | 0.02 ± 0.00 | -2.88 ± 0.15 | 0.05 ± 0.03 | 3 |
| Granivore | Violet-eared Waxbill *(Granatina granatina)* | -2.40 ± 0.29 | 0.03 ± 0.37 | 0.03 ± 0.00 | -2.58 ± 0.13 | 0.02 ± 0.01 | 3 |
| Granivore | White-browed Sparrow-Weaver *(Plocepasser mahali)* | 1.04 ± 0.06 | -0.96 ± 0.30 | 0.00 ± 0.00 | -1.37 ± 0.06 | 0.01 ± 0.01 | 3 |
| Granivore | White-winged Widowbird *(Euplectes albonotatus)* | 0.97 ± 0.08 | -0.31 ± 0.22 | 0.00 ± 0.00 | -2.20 ± 0.07 | 0.03 ± 0.01 | 3 |
| Granivore | Yellow Bishop *(Euplectes capensis)* | -2.36 ± 0.42 | 4.02 ± 1.68 | -0.03 ± 0.01 | -3.75 ± 0.42 | 0.14 ± 0.09 | 3 |
| Granivore | Yellow Canary *(Crithagra flaviventris)* | 0.63 ± 0.09 | -1.31 ± 0.49 | -0.01 ± 0.00 | -2.31 ± 0.08 | 0.03 ± 0.01 | 3 |
| Granivore | Yellow-crowned Bishop *(Euplectes afer)* | 1.48 ± 0.07 | -1.12 ± 0.37 | -0.01 ± 0.00 | -2.48 ± 0.07 | 0.02 ± 0.01 | 3 |
| Granivore | Yellow-fronted Canary *(Crithagra mozambicus)* | -0.36 ± 0.11 | 0.51 ± 0.17 | 0.02 ± 0.00 | -2.19 ± 0.07 | 0.04 ± 0.01 | 3 |
| Granivore | Yellow-throated Petronia *(Petronia superciliaris)* | -3.06 ± 0.42 | 0.69 ± 0.39 | 0.03 ± 0.01 | -2.92 ± 0.15 | 0.01 ± 0.02 | 3 |
| Ground-feeder | Abdim's Stork *(Ciconia abdimii)* | -1.81 ± 0.31 | 0.43 ± 0.57 | 0.01 ± 0.00 | -3.48 ± 0.22 | 0.03 ± 0.04 | 1 |
| Ground-feeder | African Grey Hornbill *(Tockus nasutus)* | -1.46 ± 0.17 | 0.48 ± 0.17 | 0.03 ± 0.00 | -2.01 ± 0.09 | 0.08 ± 0.02 | 1 |
| Ground-feeder | African Hoopoe *(Upupa africana)* | 0.47 ± 0.08 | 0.35 ± 0.23 | 0.00 ± 0.00 | -1.97 ± 0.06 | 0.07 ± 0.01 | 1 |
| Ground-feeder | African Pipit *(Anthus cinnamomeus)* | 1.91 ± 0.06 | -0.24 ± 0.21 | -0.01 ± 0.00 | -2.03 ± 0.06 | 0.04 ± 0.01 | 1 |
| Ground-feeder | African Sacred Ibis *(Threskiornis aethiopicus)* | 1.22 ± 0.07 | 0.02 ± 0.26 | -0.01 ± 0.00 | -1.31 ± 0.06 | 0.02 ± 0.01 | 1 |
| Ground-feeder | African Stonechat *(Saxicola torquatus)* | 2.28 ± 0.05 | 0.19 ± 0.21 | -0.02 ± 0.00 | -1.76 ± 0.06 | 0.05 ± 0.01 | 1 |
| Ground-feeder | Anteating Chat *(Myrmecocichla formicivora)* | 0.78 ± 0.07 | 0.49 ± 0.40 | -0.02 ± 0.00 | -1.73 ± 0.08 | 0.03 ± 0.02 | 1 |
| Ground-feeder | Arrow-marked Babbler *(Turdoides jardineii)* | -1.08 ± 0.15 | 0.52 ± 0.16 | 0.03 ± 0.00 | -2.20 ± 0.09 | 0.07 ± 0.01 | 1 |
| Ground-feeder | Black-crowned Tchagra *(Tchagra senegalus)* | -1.26 ± 0.18 | 1.29 ± 0.22 | 0.02 ± 0.00 | -2.55 ± 0.09 | 0.04 ± 0.01 | 1 |
| Ground-feeder | Black-headed Heron *(Ardea melanocephala)* | 2.01 ± 0.08 | -1.17 ± 0.29 | -0.01 ± 0.00 | -2.10 ± 0.08 | 0.06 ± 0.01 | 1 |
| Ground-feeder | Bokmakierie Bokmakierie *(Telophorus zeylonus)* | 1.05 ± 0.07 | 0.36 ± 0.29 | -0.01 ± 0.00 | -2.32 ± 0.08 | 0.08 ± 0.02 | 1 |
| Ground-feeder | Brown-crowned Tchagra *(Tchagra australis)* | -0.57 ± 0.14 | -0.29 ± 0.20 | 0.02 ± 0.00 | -2.91 ± 0.09 | 0.10 ± 0.01 | 1 |
| Ground-feeder | Brown-hooded Kingfisher *(Halcyon albiventris)* | -0.96 ± 0.14 | 0.23 ± 0.18 | 0.02 ± 0.00 | -2.39 ± 0.08 | 0.10 ± 0.02 | 1 |
| Ground-feeder | Buffy Pipit *(Anthus vaalensis)* | -0.84 ± 0.22 | 2.00 ± 0.42 | 0.00 ± 0.00 | -3.62 ± 0.17 | 0.04 ± 0.02 | 1 |
| Ground-feeder | Bushveld Pipit *(Anthus caffer)* | -6.95 ± 01.98 | -0.04 ± 0.70 | 0.06 ± 0.02 | -2.85 ± 0.23 | 0.07 ± 0.04 | 1 |
| Ground-feeder | Cape Crow *(Corvus capensis)* | -1.19 ± 0.19 | -1.05 ± 01.09 | -0.01 ± 0.00 | -1.85 ± 0.25 | -0.13 ± 0.07 | 1 |
| Ground-feeder | Cape Grassbird *(Sphenoeacus afer)* | -0.75 ± 0.15 | 1.88 ± 0.31 | 0.00 ± 0.00 | -2.35 ± 0.10 | 0.06 ± 0.02 | 1 |
| Ground-feeder | Cape Longclaw *(Macronyx capensis)* | 1.94 ± 0.06 | 0.26 ± 0.27 | -0.02 ± 0.00 | -1.81 ± 0.06 | 0.05 ± 0.01 | 1 |
| Ground-feeder | Cape Robin-Chat *(Cossypha caffra)* | 1.07 ± 0.07 | 0.60 ± 0.22 | -0.01 ± 0.00 | -1.52 ± 0.07 | 0.08 ± 0.01 | 1 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Ground-feeder | Cape Rock-Thrush *(Monticola rupestris)* | -2.36 ± 0.30 | 4.23 ± 0.56 | -0.01 ± 0.01 | -2.52 ± 0.18 | 0.10 ± 0.04 | 1 |
| Ground-feeder | Cape Wagtail *(Motacilla capensis)* | 1.38 ± 0.07 | 0.22 ± 0.21 | -0.01 ± 0.00 | -1.42 ± 0.07 | 0.05 ± 0.01 | 1 |
| Ground-feeder | Capped Wheatear *(Oenanthe pileata)* | 0.94 ± 0.09 | 1.06 ± 0.38 | -0.02 ± 0.00 | -2.17 ± 0.09 | 0.00 ± 0.02 | 1 |
| Ground-feeder | Cattle Egret *(Bubulcus ibis)* | 1.69 ± 0.08 | -0.73 ± 0.18 | 0.00 ± 0.00 | -1.60 ± 0.08 | 0.04 ± 0.01 | 1 |
| Ground-feeder | Cloud Cisticola *(Cisticola textrix)* | 1.06 ± 0.08 | -0.32 ± 0.44 | -0.02 ± 0.00 | -2.30 ± 0.09 | 0.05 ± 0.02 | 1 |
| Ground-feeder | Common Fiscal *(Lanius collaris)* | 2.53 ± 0.07 | -0.19 ± 0.18 | -0.01 ± 0.00 | -1.68 ± 0.07 | 0.03 ± 0.01 | 1 |
| Ground-feeder | Crowned Lapwing *(Vanellus coronatus)* | 1.88 ± 0.09 | -0.63 ± 0.19 | 0.00 ± 0.00 | -1.28 ± 0.10 | 0.06 ± 0.01 | 1 |
| Ground-feeder | Familiar Chat *(Cercomela familiaris)* | -0.43 ± 0.13 | 2.01 ± 0.24 | 0.00 ± 0.00 | -2.79 ± 0.09 | 0.13 ± 0.02 | 1 |
| Ground-feeder | Fiscal Flycatcher *(Sigelus silens)* | 1.11 ± 0.08 | 0.19 ± 0.25 | -0.01 ± 0.00 | -2.15 ± 0.06 | 0.04 ± 0.01 | 1 |
| Ground-feeder | Greater Kestrel *(Falco rupicoloides)* | -0.05 ± 0.14 | -1.48 ± 0.76 | -0.01 ± 0.00 | -3.05 ± 0.15 | 0.08 ± 0.03 | 1 |
| Ground-feeder | Groundscraper Thrush *(Psophocichla litsipsirupa)* | -1.07 ± 0.16 | 0.36 ± 0.21 | 0.02 ± 0.00 | -2.55 ± 0.08 | 0.07 ± 0.01 | 1 |
| Ground-feeder | Hadeda Ibis *(Bostrychia hagedash)* | 1.96 ± 0.07 | -0.27 ± 0.19 | -0.01 ± 0.00 | -1.21 ± 0.08 | 0.11 ± 0.02 | 1 |
| Ground-feeder | Kirrichane buttonquail *(Turnix sylvaticus)* | -1.87 ± 0.42 | 0.44 ± 0.85 | 0.00 ± 0.01 | -4.11 ± 0.32 | 0.03 ± 0.03 | 1 |
| Ground-feeder | Kurrichane Thrush *(Turdus libonyanus)* | -1.15 ± 0.16 | 0.63 ± 0.21 | 0.02 ± 0.00 | -2.56 ± 0.09 | 0.14 ± 0.02 | 1 |
| Ground-feeder | Lazy Cisticola *(Cisticola aberrans)* | -1.75 ± 0.26 | 1.97 ± 0.35 | 0.01 ± 0.00 | -3.20 ± 0.15 | 0.10 ± 0.03 | 1 |
| Ground-feeder | Lilac-breasted Roller *(Coracias caudatus)* | -3.37 ± 0.36 | -0.39 ± 0.26 | 0.05 ± 0.00 | -2.24 ± 0.11 | 0.06 ± 0.02 | 1 |
| Ground-feeder | Long-billed Pipit *(Anthus similis)* | -1.05 ± 0.20 | 1.67 ± 0.42 | 0.00 ± 0.00 | -3.12 ± 0.13 | 0.05 ± 0.02 | 1 |
| Ground-feeder | Magpie Shrike *(Corvinella melanoleuca)* | -7.34 ± 01.10 | -1.23 ± 0.30 | 0.09 ± 0.01 | -1.26 ± 0.09 | 0.04 ± 0.02 | 1 |
| Ground-feeder | Marico Flycatcher *(Bradornis mariquensis)* | -4.48 ± 0.54 | -0.11 ± 0.26 | 0.05 ± 0.01 | -2.06 ± 0.10 | 0.04 ± 0.02 | 1 |
| Ground-feeder | Mocking Cliff-Chat *(Thamnolaea cinnamomeiventris)* | -1.61 ± 0.22 | 1.42 ± 0.32 | 0.01 ± 0.00 | -2.76 ± 0.12 | 0.12 ± 0.02 | 1 |
| Ground-feeder | Mountain Wheatear *(Oenanthe monticola)* | 0.14 ± 0.11 | 1.62 ± 0.39 | -0.02 ± 0.00 | -2.86 ± 0.11 | 0.22 ± 0.03 | 1 |
| Ground-feeder | Neddicky Neddicky *(Cisticola fulvicapilla)* | 0.87 ± 0.08 | -0.04 ± 0.17 | 0.01 ± 0.00 | -1.85 ± 0.07 | 0.03 ± 0.01 | 1 |
| Ground-feeder | Pearl-spotted Owlet *(Glaucidium perlatum)* | -4.48 ± 0.64 | 0.04 ± 0.32 | 0.05 ± 0.01 | -2.65 ± 0.12 | 0.08 ± 0.02 | 1 |
| Ground-feeder | Pied Crow *(Corvus albus)* | 0.68 ± 0.07 | -0.38 ± 0.19 | 0.01 ± 0.00 | -1.45 ± 0.06 | 0.06 ± 0.01 | 1 |
| Ground-feeder | Pied Starling *(Spreo bicolor)* | 0.77 ± 0.08 | 0.18 ± 0.46 | -0.02 ± 0.00 | -1.93 ± 0.08 | 0.05 ± 0.02 | 1 |
| Ground-feeder | Plain-backed Pipit *(Anthus leucophrys)* | -0.76 ± 0.22 | 2.13 ± 0.47 | 0.00 ± 0.00 | -3.56 ± 0.18 | 0.04 ± 0.02 | 1 |
| Ground-feeder | Red-throated Wryneck *(Jynx ruficollis)* | 0.68 ± 0.10 | 0.71 ± 0.40 | -0.01 ± 0.00 | -2.70 ± 0.09 | 0.06 ± 0.02 | 1 |
| Ground-feeder | Rufous-naped Lark *(Mirafra africana)* | 1.31 ± 0.07 | 0.35 ± 0.18 | 0.00 ± 0.00 | -2.27 ± 0.07 | 0.06 ± 0.01 | 1 |

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|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Ground-feeder | Secretarybird Secretarybird *(Sagittarius serpentarius)* | -0.66 ± 0.17 | 0.65 ± 0.76 | -0.01 ± 0.00 | -2.54 ± 0.13 | 0.02 ± 0.02 | 1 |
| Ground-feeder | Sentinel Rock-Thrush *(Monticola explorator)* | -2.83 ± 0.42 | 3.56 ± 01.12 | -0.01 ± 0.01 | -2.52 ± 0.40 | -0.04 ± 0.13 | 1 |
| Ground-feeder | Southern Black Flycatcher *(Melaenornis pammelaina)* | -2.02 ± 0.23 | 1.00 ± 0.23 | 0.03 ± 0.00 | -2.45 ± 0.09 | 0.04 ± 0.01 | 1 |
| Ground-feeder | Southern White-crowned Shrike *(Eurocephalus anguitimens)* | -9.54 ± 03.90 | -0.23 ± 0.68 | 0.09 ± 0.04 | -3.24 ± 0.24 | 0.04 ± 0.03 | 1 |
| Ground-feeder | Southern Yellow-billed Hornbill *(Tockus leucomelas)* | -6.82 ± 01.10 | -0.19 ± 0.29 | 0.07 ± 0.01 | -1.53 ± 0.09 | 0.06 ± 0.02 | 1 |
| Ground-feeder | Spike-heeled Lark *(Chersomanes albofasciata)* | 0.09 ± 0.11 | 1.02 ± 0.57 | -0.02 ± 0.00 | -2.23 ± 0.11 | 0.01 ± 0.02 | 1 |
| Ground-feeder | Spotted Eagle-Owl *(Bubo africanus)* | -0.24 ± 0.17 | 0.70 ± 0.48 | 0.00 ± 0.00 | -3.29 ± 0.12 | 0.06 ± 0.02 | 1 |
| Ground-feeder | Spotted Thick-knee *(Burhinus capensis)* | 0.96 ± 0.09 | 0.08 ± 0.27 | -0.01 ± 0.00 | -2.39 ± 0.08 | 0.09 ± 0.01 | 1 |
| Ground-feeder | Striped Kingfisher *(Halcyon chelicuti)* | -4.37 ± 0.71 | -0.35 ± 0.60 | 0.04 ± 0.01 | -2.62 ± 0.15 | 0.03 ± 0.02 | 1 |
| Ground-feeder | Striped Pipit *(Anthus lineiventris)* | -2.27 ± 0.32 | 1.33 ± 0.44 | 0.01 ± 0.00 | -2.88 ± 0.13 | 0.04 ± 0.02 | 1 |
| Ground-feeder | Temminck's Courser *(Cursorius temminckii)* | -2.04 ± 0.31 | -0.22 ± 0.68 | 0.01 ± 0.00 | -3.40 ± 0.21 | 0.15 ± 0.04 | 1 |
| Ground-feeder | Wailing Cisticola *(Cisticola lais)* | -0.44 ± 0.13 | 1.39 ± 0.41 | -0.01 ± 0.00 | -2.59 ± 0.11 | 0.13 ± 0.02 | 1 |
| Ground-feeder | Wattled Starling *(Creatophora cinerea)* | 0.81 ± 0.09 | -1.97 ± 0.51 | -0.01 ± 0.00 | -2.51 ± 0.08 | 0.02 ± 0.01 | 1 |
| Ground-feeder | White Stork *(Ciconia ciconia)* | -0.26 ± 0.15 | 0.45 ± 0.44 | 0.00 ± 0.00 | -3.16 ± 0.12 | 0.01 ± 0.02 | 1 |
| Ground-feeder | White-browed Scrub-Robin *(Cercotrichas leucophrys)* | -3.31 ± 0.34 | 0.03 ± 0.19 | 0.05 ± 0.00 | -2.14 ± 0.10 | 0.02 ± 0.01 | 1 |
| Ground-feeder | White-throated Robin-Chat *(Cossypha humeralis)* | -4.02 ± 0.52 | 0.32 ± 0.24 | 0.05 ± 0.01 | -2.71 ± 0.14 | 0.03 ± 0.01 | 1 |
| Hawker | African Palm-Swift *(Cypsiurus parvus)* | 0.86 ± 0.08 | -0.04 ± 0.20 | 0.00 ± 0.00 | -1.58 ± 0.07 | 0.04 ± 0.01 | 1 |
| Hawker | Alpine Swift *(Tachymarptis melba)* | -1.63 ± 0.48 | 1.80 ± 0.56 | 0.01 ± 0.01 | -4.53 ± 0.40 | 0.01 ± 0.03 | 1 |
| Hawker | Common House-Martin *(Delichon urbicum)* | 0.24 ± 0.16 | -0.39 ± 0.40 | 0.00 ± 0.00 | -3.61 ± 0.14 | 0.05 ± 0.02 | 1 |
| Hawker | Fiery-necked Nightjar *(Caprimulgus pectoralis)* | -2.61 ± 0.42 | 0.81 ± 0.40 | 0.03 ± 0.01 | -3.66 ± 0.19 | 0.04 ± 0.01 | 1 |
| Hawker | Fork-tailed Drongo *(Dicrurus adsimilis)* | -1.35 ± 0.15 | 0.15 ± 0.15 | 0.03 ± 0.00 | -1.97 ± 0.08 | 0.06 ± 0.01 | 1 |
| Hawker | Lesser Striped Swallow *(Hirundo abyssinica)* | -0.41 ± 0.13 | 0.33 ± 0.16 | 0.02 ± 0.00 | -2.61 ± 0.08 | 0.06 ± 0.01 | 1 |
| Hawker | Little Bee-eater *(Merops pusillus)* | -1.39 ± 0.28 | 0.69 ± 0.46 | 0.01 ± 0.00 | -3.72 ± 0.19 | 0.05 ± 0.02 | 1 |
| Hawker | Little Swift *(Apus affinis)* | 1.02 ± 0.10 | -0.61 ± 0.25 | 0.00 ± 0.00 | -2.07 ± 0.09 | 0.03 ± 0.01 | 1 |
| Hawker | Pearl-breasted Swallow *(Hirundo dimidiata)* | -1.22 ± 0.19 | 0.45 ± 0.24 | 0.02 ± 0.00 | -2.83 ± 0.11 | 0.04 ± 0.01 | 1 |
| Hawker | Rock Martin *(Hirundo fuligula)* | 0.23 ± 0.11 | 0.87 ± 0.30 | 0.00 ± 0.00 | -2.47 ± 0.07 | 0.03 ± 0.01 | 1 |
| Hawker | White-fronted Bee-eater *(Merops bullockoides)* | -0.78 ± 0.13 | -0.20 ± 0.26 | 0.02 ± 0.00 | -2.09 ± 0.07 | 0.02 ± 0.01 | 1 |
| Predator | African Grass-Owl *(Tyto capensis)* | -1.66 ± 0.36 | 2.02 ± 01.77 | -0.03 ± 0.01 | -3.80 ± 0.47 | 0.11 ± 0.13 | 1 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Predator | African Harrier-Hawk *(Polyboroides typus)* | -0.59 ± 0.24 | 1.42 ± 0.43 | 0.00 ± 0.00 | -3.94 ± 0.18 | 0.02 ± 0.02 | 1 |
| Predator | African Hawk-Eagle *(Aquila spilogaster)* | -3.29 ± 0.66 | 1.25 ± 0.61 | 0.02 ± 0.01 | -4.01 ± 0.30 | 0.03 ± 0.02 | 1 |
| Predator | Barn Owl *(Tyto alba)* | -0.46 ± 0.17 | 0.50 ± 0.43 | 0.00 ± 0.00 | -3.33 ± 0.12 | 0.03 ± 0.01 | 1 |
| Predator | Black Sparrowhawk *(Accipiter melanoleucus)* | -0.08 ± 0.20 | 0.22 ± 0.65 | -0.01 ± 0.00 | -3.67 ± 0.15 | 0.05 ± 0.02 | 1 |
| Predator | Black-chested Snake-Eagle *(Circaetus pectoralis)* | -0.67 ± 0.17 | 0.49 ± 0.31 | 0.01 ± 0.00 | -3.10 ± 0.12 | 0.04 ± 0.01 | 1 |
| Predator | Black-shouldered Kite *(Elanus caeruleus)* | 1.76 ± 0.08 | -0.22 ± 0.20 | -0.01 ± 0.00 | -1.82 ± 0.09 | 0.05 ± 0.01 | 1 |
| Predator | Brown Snake-Eagle *(Circaetus cinereus)* | -2.13 ± 0.35 | 0.87 ± 0.43 | 0.02 ± 0.00 | -3.59 ± 0.20 | 0.03 ± 0.02 | 1 |
| Predator | Gabar Goshawk *(Melierax gabar)* | -1.49 ± 0.26 | 0.25 ± 0.38 | 0.02 ± 0.00 | -3.51 ± 0.17 | 0.03 ± 0.02 | 1 |
| Predator | Hamerkop Hamerkop *(Scopus umbretta)* | 0.30 ± 0.12 | -0.62 ± 0.29 | 0.01 ± 0.00 | -2.95 ± 0.10 | 0.03 ± 0.01 | 1 |
| Predator | Jackal Buzzard *(Buteo rufofuscus)* | -1.10 ± 0.23 | 1.96 ± 0.68 | -0.01 ± 0.00 | -3.59 ± 0.22 | 0.11 ± 0.05 | 1 |
| Predator | Lanner Falcon *(Falco biarmicus)* | -0.20 ± 0.24 | 0.01 ± 0.60 | 0.00 ± 0.00 | -4.16 ± 0.21 | 0.04 ± 0.02 | 1 |
| Predator | Little Sparrowhawk *(Accipiter minullus)* | -0.43 ± 0.21 | 0.39 ± 0.45 | 0.00 ± 0.00 | -3.65 ± 0.14 | 0.04 ± 0.01 | 1 |
| Predator | Marsh Owl *(Asio capensis)* | 0.39 ± 0.12 | -0.14 ± 0.62 | -0.02 ± 0.00 | -3.55 ± 0.14 | 0.20 ± 0.03 | 1 |
| Predator | Martial Eagle *(Polemaetus bellicosus)* | 1.08 ± 01.65 | 0.13 ± 01.14 | 0.01 ± 0.01 | -8.16 ± 01.52 | -0.10 ± 0.21 | 1 |
| Predator | Rock Kestrel *(Falco rupicolus)* | -0.50 ± 0.16 | 1.82 ± 0.43 | -0.01 ± 0.00 | -3.10 ± 0.16 | 0.06 ± 0.04 | 1 |
| Predator | Shikra Shikra *(Accipiter badius)* | -2.54 ± 0.73 | -1.00 ± 0.71 | 0.03 ± 0.01 | -4.87 ± 0.51 | 0.02 ± 0.03 | 1 |
| Predator | Tawny Eagle *(Aquila rapax)* | -6.89 ± 03.06 | 1.42 ± 01.21 | 0.05 ± 0.03 | -3.08 ± 01.01 | -0.27 ± 0.35 | 1 |
| Predator | Verreaux's Eagle *(Aquila verreauxii)* | -1.76 ± 0.25 | 1.41 ± 0.48 | 0.01 ± 0.00 | -2.85 ± 0.13 | 0.06 ± 0.03 | 1 |
| Vegivore | Blue Crane *(Anthropoides paradiseus)* | -1.81 ± 0.24 | 0.87 ± 01.38 | -0.02 ± 0.01 | -2.29 ± 0.20 | 0.13 ± 0.05 | 1 |
| Vegivore | Cape Bunting *(Emberiza capensis)* | -1.63 ± 0.23 | 2.40 ± 0.43 | 0.00 ± 0.00 | -2.64 ± 0.14 | 0.07 ± 0.03 | 1 |
| Vegivore | Cape Weaver *(Ploceus capensis)* | -0.26 ± 0.14 | 0.95 ± 0.33 | 0.00 ± 0.00 | -2.97 ± 0.10 | 0.08 ± 0.02 | 1 |
| Vegivore | Coqui Francolin *(Peliperdix coqui)* | -1.40 ± 0.19 | 0.40 ± 0.31 | 0.02 ± 0.00 | -2.65 ± 0.11 | 0.05 ± 0.02 | 1 |
| Vegivore | Crested Francolin *(Dendroperdix sephaena)* | -3.42 ± 0.35 | 0.24 ± 0.20 | 0.05 ± 0.00 | -2.15 ± 0.10 | 0.06 ± 0.02 | 1 |
| Vegivore | Egyptian Goose *(Alopochen aegyptiaca)* | 1.69 ± 0.07 | 0.45 ± 0.20 | -0.01 ± 0.00 | -1.13 ± 0.07 | 0.03 ± 0.01 | 1 |
| Vegivore | Grey Go-away-bird *(Corythaixoides concolor)* | -0.47 ± 0.09 | 0.36 ± 0.17 | 0.02 ± 0.00 | -1.07 ± 0.07 | 0.14 ± 0.03 | 1 |
| Vegivore | Helmeted Guineafowl *(Numida meleagris)* | 1.59 ± 0.07 | 0.24 ± 0.17 | 0.00 ± 0.00 | -1.34 ± 0.08 | 0.10 ± 0.01 | 1 |
| Vegivore | Natal Spurfowl *(Pternistis natalensis)* | -2.02 ± 0.21 | 1.22 ± 0.20 | 0.03 ± 0.00 | -2.33 ± 0.10 | 0.11 ± 0.02 | 1 |
| Vegivore | Orange River Francolin *(Scleroptila levaillantoides)* | 0.72 ± 0.09 | -3.34 ± 01.20 | -0.03 ± 0.00 | -2.24 ± 0.10 | 0.09 ± 0.02 | 1 |

| Guild | Species | Abundance (log scale) | | | Detection (logit scale) | | Group |
|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | Protected areas ($\hat{\beta}_1$) | Savanna ($\hat{\beta}_2$) | Intercept ($\hat{\alpha}_0$) | Log Hours ($\hat{\alpha}_1$) | |
| Vegivore | Red-winged Francolin *(Scleroptila levaillantii)* | -1.65 ± 0.27 | 2.21 ± 0.66 | -0.01 ± 0.01 | -3.71 ± 0.22 | 0.22 ± 0.05 | 1 |
| Vegivore | Shelley's Francolin *(Scleroptila shelleyi)* | -3.66 ± 0.67 | 0.63 ± 1.15 | 0.01 ± 0.00 | -3.27 ± 0.39 | 0.08 ± 0.07 | 1 |
| Vegivore | Southern Masked-Weaver *(Ploceus velatus)* | 2.72 ± 0.12 | -0.56 ± 0.14 | 0.00 ± 0.00 | -1.59 ± 0.13 | 0.03 ± 0.01 | 1 |
| Vegivore | Speckled Mousebird *(Colius striatus)* | 0.73 ± 0.08 | 0.05 ± 0.20 | 0.00 ± 0.00 | -1.64 ± 0.06 | 0.06 ± 0.01 | 1 |
| Vegivore | Spur-winged Goose *(Plectropterus gambensis)* | 1.28 ± 0.07 | 0.54 ± 0.27 | -0.01 ± 0.00 | -2.10 ± 0.06 | 0.02 ± 0.01 | 1 |
| Vegivore | Streaky-headed Seedeater *(Crithagra gularis)* | 0.18 ± 0.10 | 0.13 ± 0.28 | 0.00 ± 0.00 | -2.21 ± 0.07 | 0.05 ± 0.01 | 1 |
| Vegivore | Swainson's Spurfowl *(Pternistis swainsonii)* | 1.64 ± 0.07 | -0.25 ± 0.19 | 0.00 ± 0.00 | -1.94 ± 0.08 | 0.07 ± 0.01 | 1 |
| Vegivore | Village Weaver *(Ploceus cucullatus)* | -0.91 ± 0.19 | -0.77 ± 0.36 | 0.02 ± 0.00 | -3.25 ± 0.11 | 0.05 ± 0.01 | 1 |
| Vegivore | White-bellied Korhaan *(Eupodotis senegalensis)* | -3.43 ± 0.49 | -0.98 ± 01.41 | 0.01 ± 0.01 | -2.04 ± 0.35 | -0.02 ± 0.08 | 1 |

Chapter 3

# Why a landscape view is important: nearby urban and agricultural land affect bird abundances in protected area

Male African grey hornbill (*Lophoceros nasutus*) in the Kruger National Park, South Africa.

Photograph by Greg Duckworth

## 3.1 ABSTRACT

**AIM**: Protected areas are one of the primary conservation tools used worldwide. However, they are often imbedded in landscapes that are intensely used by people, such as for agriculture or urban development. The proximity of these land-use types to protected areas can potentially affect the degree to which protected areas conserve species and habitats (i.e., the ecological effectiveness). I examined to what degree areas of agricultural and urban land use near protected areas influenced the ecological effectiveness of protected areas. If protected areas were effective regardless of their surroundings, there would be no change in measures of ecological effectiveness within protected areas as urban or agricultural areas adjacent to or nearby protected areas increased in proportion.

**LOCATION**: Greater Gauteng region, South Africa.

**METHODS**: I analysed distribution data for 198 common, resident species, collected over regular grid cells (approximately 61 $km^2$ in area). For each species, I estimated how abundance varied as the proportion of protected area within a grid cell increased. I define this relationship as the proportion-abundance relationship, which I used as a measure of ecological effectiveness of protected area. A positive proportion-abundance relationship indicated that abundance increased as the proportion of protected area within a landscape increased, and the protected area was thus ecologically effective. A negative proportion-abundance relationship indicated the opposite. I then examined how the proportion-abundance relationship changed (either increased or decreased) as urban and agricultural area within the same grid cell increased in proportion. I assigned each species to one of seven guilds based on the type of food the species ate, and its primary mode of foraging. These included frugivores, gleaners, granivores, ground-feeders, hawkers, predators and vegivores. I examined whether the proportion-abundance relationship, as well as how overall bird abundance, was affected by agricultural and urban areas across guilds.

**RESULTS**: The proportion-abundance relationship increased, which led to an overall increase in bird abundance within protected areas, for 58% of species with an increase in the proportion of urban area near protected areas. The proportion-abundance relationship increased, which led to an overall increase in bird abundance within protected area, for 49% of species with an increase in the proportion of agricultural area near protected areas. The majority of the cases for which the overall bird abundance increased in protected areas, were due to a negative proportion-abundance relationship becoming more positive as urban / agricultural area near protected area sincreased. Increases in urban area near protected areas yielded a significant increase in the average proportion-abundance relationship for two guilds (granivores and ground-feeders), a significant decrease for one guild (frugivores), and no statistically significant changes in the remaining four guilds (vegivores, predators, gleaners, and hawkers). Increases in agricultural area adjacent to protected areas yielded a significant increase in the average proportion-abundance relationship for six guilds (frugivores, gleaners, ground-feeders, hawkers, predators, and vegivores), and no change for one guild (granivores).

**MAIN CONCLUSION**: My results show land-use type surrounding or near protected areas influences  the proportion-abundance relationship, and hence the ecological effectiveness of protected areas. The magnitude of this effect was more positive for agricultural area than for urban area. This suggests that most species were, on average, more dependent on protected areas for persistence when protected areas are neighboured by agricultural areas, compared to urban area neighbours protected area. I conclude that protected areas must be viewed as constituents within the landscape, rather than islands of protection.

**KEY WORDS**: Abundance estimation, protected area, avian conservation, landscape ecology, citizen science

## 3.2 INTRODUCTION

Protected area are one of the key strategies for conserving the earth's natural habitat and biodiversity (James et al., 1999; Parrish et al., 2003; Gaston et al., 2008). Although not a sole solution to conservation challenges, protected areas are generally considered effective at conserving biodiversity around the world (Chape et al., 2005; Gaston et al., 2006). Every year, large amounts of financial and human resources are allocated to maintain current protected areas, and develop new ones (James et al., 1999; Bruner et al., 2004; Naidoo et al., 2006; Rands et al., 2010). Protected areas are generally designed by conservation managers to conserve biodiversity, habitat, and to promote ecosystem functionality such as pollination and water purification (Gaston et al., 2008). In the last few decades these goals have broadened to include social aspects, such as national development and poverty reduction (Naughton-Treves et al., 2005).

In general, there is an expectation that protected areas are effective at conserving biodiversity (Gaston et al., 2008). However, a large body of literature shows that many protected areas are failing to conserve the flagship species they were intended to conserve (Western & Henry, 1979; Newmark, 1996; Brashares et al., 2001; Rodrigues et al., 2004; Craigie et al., 2010; Rands et al., 2010; Ogutu et al., 2011; Cantú-Salazar et al., 2013), and furthermore, biodiversity in general is declining in some protected areas (Hoekstra et al., 2002; Craigie et al., 2010; Watson et al., 2014). Consequently, despite the large allocation of resources invested in protected areas (Rodrigues et al., 2004; Hockings et al., 2006; Gaston et al., 2008), there is growing concern that they are not achieving the conservation goals set out for them (Newmark, 1996; Brashares et al., 2001; Hilton-taylor et al., 2004).

One major reason that the conservation goals set out for protected areas may not be achieved could be due to land-use types neighbouring protected areas, and in particular, urban and agricultural area (DeFries et al., 2007; Hansen & Defries, 2007; Leroux & Kerr, 2013). For example, the intensity of human settlements situated within or around protected area is strongly positively correlated with biodiversity declines, species extinction, fire frequency, poaching, and general habitat degradation within (or along the borders of) protected areas (Brashares et al., 2001; Herremans & Herremans-Tonnoeyr, 2001; Parks & Harcourt, 2002; Cardillo et al., 2004; Knapp et al., 2008). Additionally, the density of roads and other infrastructure correlates highly with biodiversity loss within and outside protected areas (Trollope et al., 2009). It appears that in general, people preferentially settle near protected areas; urban settlements are located outside or near protected areas at a higher rate than is expected by chance (Chown et al., 2003), and the population growth rate of human settlements just outside protected areas was almost double that of their rural counterparts for 306 protected areas within 45 Latin American and African countries (Wittemyer et al., 2008). Other studies report similar findings elsewhere in the world (Luck, 2007). Given the rapid projected growth rate of the global human population (Cohen, 2003), and the preferred location of human settlements near protected areas, it is apparent that the strain of human settlements on protected areas will not dissipate in the near future. It is therefore important to gain a mechanistic understanding of how the capacity of protected areas to conserve biodiversity and habitats (i.e., the ecological effectiveness of protected areas) is affected by adjacent urban area. With this information, protected areas managers can initiate suitable conservation action, if necessary.

The negative impacts of agriculture on biodiversity have been widely acknowledged and reported (Kleijn et al., 2001; Bengtsson et al., 2005; Tscharntke et al., 2005). Activities associated with agricultural practices such as drainage, tillage, run-off, and fertilizing (with artificial fertilizers) are harmful to biodiversity, and therefore, biodiversity in agricultural areas is often reported to be lower than in protected areas (Darkoh, 2003; Feehan et al., 2005). Furthermore, intensive farming can have negative long-term effects on biodiversity beyond the area that is actually farmed (Stoate et al., 2001, 2009). Consistent large-scale agricultural practices can decrease the quality of the soil, air, and water within entire landscapes, and consequently alter the shape and structure of the landscape (Stoate et al., 2001; Billeter et al., 2008). Rapid changes in landscape structure compromise important ecosystem processes such as pollination (Kremen & Ricketts, 2000; Potts et al., 2010), nutrient recycling (Alberola et al., 2008; Goulding et al., 2008; Pollock et al., 2008), and water purification (Pretty, 2008; Garnett et al., 2013). Because protected areas are imbedded within landscapes of multiple uses, including agriculture, they can be subject to cascading negative effects of large-scale agricultural practices, which may, in turn, negatively affect their ecological effectiveness.

Multiple studies have focussed on the effects of the surrounding landscape on protected areas (Craighead, 1978; DeFries et al., 2007, 2010; Turner et al., 2008; Chazdon et al., 2009; Greve et al., 2011; Leroux & Kerr, 2013). However, relatively few studies have explicitly studied how land-use types adjacent to, or near protected areas affect the ecological effectiveness of protected areas. I address this issue explicitly in this chapter, and using abundance as a proxy for ecological effectiveness, study how urban and agricultural area near protected areas affect the abundance of common, resident bird species within protected areas. Abundance is a good measure by which to assess the ecological status of species, as it is used as a measure of extinction risk (IUCN, 2000; Gaston, 2010). Birds are good environmental indicators of ecosystem health, easy to observe, and well monitored, making them an ideal choice for this type of study (Furness & Greenwood, 1993; Greenwood, 2004). I study common bird species as they have been shown to be important drivers of ecosystem patterns, and functions, such as primary productivity and nutrient cycling (Lennon et al., 2011; Winfree et al., 2015). A decline in abundances and diversity of common species can indicate drastic declines in ecosystem integrity (Gaston, 2011). Monitoring abundances of common birds within protected areas therefore gives a good representation of the ecological integrity of protected areas, and consequently, their ecological effectiveness.

I used atlas data collected from regular grid cells across the greater Gauteng area in South Africa to estimate how the abundance of common, resident bird species varied as the proportion of protected area within a grid cell increased. In the previous chapter, I examined the relationship between bird species' abundances and the proportion of protected area within the same grid cell. I defined this relationship as the proportion-abundance relationship, and I used it as a measure of ecological effectiveness of protected areas. A positive proportion-abundance relationship indicated that abundance increased as the proportion of protected area within a landscape increased; from this, I inferred that protected areas were ecologically effective for that species. Conversely, a negative proportion-abundance relationship indicated the opposite. Here, I examine how the proportion-abundance relationship changes with increasing proportion of urban and agricultural area in the same grid cell. My ecological focus was to determine the way in which the proportion-abundance relationship varied with increases in either urban or agricultural land-use types, rather than the proportion-abundance relationship itself.

In this chapter I address two key aims; 1) for what percentage of species does the proportion-abundance relationship increase or decrease with increasing proportions of urban and agricultural area in the same grid cell? 2) What is the average change in magnitude of the proportion-abundance relationship with increasing proportions of urban and agricultural area in the same grid cell. I expected a high degree of variation in the way the proportion-abundance relationship changed in response to increases in agricultural and urban area near protected areas. For example, agricultural areas have been shown to contain a lower abundance and diversity of insects, relative to natural habitat (Biesmeijer et al., 2006; Potts et al., 2010). Species that depend on insects for food are expected to be less abundant in agricultural areas, on average, compared to protected areas (in Chapter 2, I show this for guilds of birds that primarily feed on insects caught off the ground and in the air). Therefore, as the proportion of agricultural area near protected area increases, I expect the average proportion-abundance relationship for insectivorous guilds to become statistically more positive (more steep), as these species avoid agricultural area and persist in protected areas. Conversely, granivores (species that primarily feed on grains and seeds) can take advantage primarily of good conditions offered by both urban and agricultural land (Whittingham & Markland, 2002; Chace & Walsh, 2006). Thus, they can potentially be more abundant in urban and agricultural area (Sekercioglu, 2012), even when compared to protected areas (I show this in Chapter 2), although this depends on the type of agriculture (Newton, 2004). Thus, I hypothesise that the average proportion-abundance relationship for granivores will decrease as the proportion of both agricultural and urban land outside protected areas increases, as granivores preferentially persist in agricultural and urban areas. On the other hand, raptor species in southern Africa have been shown to respond negatively (by decreasing in abundance and range extent) to human-modified landscapes (Brandl et al., 1985; Herremans & Herremans-Tonnoeyr, 2000), in particular, to agricultural areas where they are actively persecuted by farmers (Boshoff, 1980; Anderson, 2000). Thus, I expect the average proportion-abundance relationship for predators to become significantly more positive as the proportion of both agricultural and urban areas outside protected areas increases.

## 3.3 METHODS

### *3.3.1 Study area*

I selected a heterogeneous landscape (a square with coordinates at the NW corner: 25S 27E, and SE corner: 27S 29E) that included the greater Gauteng Province of South Africa. It consisted of a rich mix of urban and other heavily human-modified land-use types, as well as protected areas (Fig. 1.2, Chapter 1). The study area included the cities of Pretoria and Johannesburg (Fig. 1.3, Chapter 1), which are two of the most densely populated cities in South Africa (Statistics South Africa, 2012). Moreover, this area was relatively homogeneous in terms of climate and the total number of potentially detectable species.

The study area was approximately 35 000 $km^2$, and comprised of eight land-use types (Fig. 1.2, Chapter 1): mines (0.80% of total land use); plantations (0.32%); waterbodies (2.80%); degraded (2.54%); protected area (6.40%); urban (8.13%); agriculture (28.71%); and natural land (50.30%). Here, natural land refers to land that is not primarily used for any of the other land uses. Therefore, in addition to representing naturally occurring land, it can also represent small holdings, open plots alongside roads or between agricultural area, and recreational land uses (such as sports-fields, parks and lawns).

Urban, agricultural, and natural land made up approximately 87% of the land-use cover over the study area, and are known to be influential in affecting bird distributions (Brandon et al., 1998; Knapp et al., 2008; Santos et al., 2008; Zhang et al., 2011). I therefore exclusively examined these land-use types in addition to protected area in this analysis. Land-use data were provided by the South African National Biodiversity Institute (South African National Biodiversity Institute (SANBI), 2009) at a 30 metre x 30 metre resolution.

### *3.3.2 Species detection / non-detection data*

I used bird detection data from the second Southern African Bird Atlas Project (SABAP 2) which started in June 2007 (Harebottle et al., 2007) and was on-going in 2018. SABAP 2 is a citizen science project whereby registered volunteers submit checklists of birds they observed during a fixed time period within a pre-defined area called a pentad, which is 5' x 5' in dimension (unit is arcminutes; approximately 61 $km^2$ in area). Volunteers must have spent at least two hours but not more than five days searching for birds within each pentad. Only the presence of bird species is recorded per pentad, not the number of birds seen. Observers were asked to sample all habitats within the pentad. Unusual records were scrutinized by a vetting committee, who either accepted or rejected the record based on supporting information (Harebottle et al., 2007).

I considered only common, resident birds within the study area, and omitted any nomadic, alien, and migratory species, totalling 200 species. I included bird atlas data that were collected and submitted to the project between the beginning of January 2014 and end of December 2015. The years 2014 and 2015 were the most data rich of SABAP 2, with enough data to support robust data analyses (see section 3.3.4 below). Because pentads within the study area were not surveyed the same number of times, like Broms et al. (2014), I randomly selected 100 checklists for pentads that had more than 100 checklists. The study area covers 576 pentads (a 24 pentad by 24 pentad grid), for which 10 400 checklists were submitted at an average of approximately 18 checklists per pentad (min. 1 and max. 468).

Each species was assigned to a guild based on information *sensu* Hockey et al. (2005). A species member ship of a guild is based on the type of food it preferentially eats, and its primary foraging mode. I distinguished between seven guilds, namely: frugivores (species that primarily consume fleshy fruit, totalling 9 species); gleaners (species that primarily consume insects and other invertebrates caught off plants, totalling 31 species); granivores (species that primarily consume seeds and grains, totalling 48 species); ground-feeders (species that primarily consume insects and invertebrates caught off the ground, totalling 63 species); hawkers (species that primarily consume insects and other invertebrates caught in the air, totalling 11 species); predators (birds of prey, species that primarily consume the flesh of vertebrates, totalling 19 species), and vegivores (vegetative herbivores; species that primarily consume vegetative parts of plants, totalling 19 species).

### *3.3.3 Land-use type covariate data*

I modelled the abundance of common bird species as a function of the major land-use types within the study area. A key assumption of the models used (and, indeed, for statistical modelling in general) was no high correlations amongst covariates. A high degree of correlation amongst model covariates would produce inaccurate beta estimates with large standard errors, and consequently, misleading inferences relating to the relationship between response variable and covariates (abundance and land-use types respectively). Approximately 94% of the study region comprised of agricultural (28.71%), natural (50.30%), protected area (6.40%) or urban (8.13%) land uses collectively. Given that these four land-use types constituted almost 100% of every grid cell within the study area, the proportion of any single land-use type can be calculated by summing the remaining land-use type proportions and subtracting this sum from 100%. Therefore, it was not necessary to include each as a covariate within the abundance component of the Royle-Nichols abundance model (specified in equation 5, see section 3.3.4 below); including all land-use types as covariates would confound the model and lead to inaccurate results. Because the ecological hypotheses I proposed related to land-use types agricultural, urban, and protected area, I omitted natural land as a covariate from the abundance component of the model (equation 5, see section 3.3.4 below). This also avoided natural land being negatively correlated with the remaining three covariates. Natural land was very common throughout the study area; the sum of the remaining proportions of land-use types agricultural, urban, and protected area was, on average, 43.24% over all pentads (Fig. A3.1, Appendix 3). Thus there was enough natural land within each pentad such that the remaining land-use types would not sum to 100% and confound the model. Furthermore, I tested for collinearity amongst the remaining three land-use types using Pearson's pair-wise correlation tests. None of the remaining land-use types was highly correlated with the other remaining land-use types (Table A3.1, Appendix 3). These two points ensured that I did not have any problem with multi-collinearity within the study.

### *3.3.4 Analyses*

To model the abundance of each species per pentad, I used an extension of traditional occupancy models, known as the Royle-Nichols model of abundance (Royle & Nichols, 2003). Briefly, occupancy models are a class of models which use detection / non-detection data to estimate the probability that a species occurs within a specified area (a pentad in this case). These models account for the fact that most species are not observed perfectly in each habitat in which they occur (MacKenzie & Kendall, 2002; Pellet & Schmidt, 2005). Failure to account for non-detection may bias parameter estimates (Boulinier et al., 1998; Nichols et al., 1998; MacKenzie et al., 2006).

### 3.3.4.1 Abundance models

The model exploits the relationship between the latent abundance at pentad $i$ ($N_i$), the probability of detecting the species at pentad $i$ during survey $j$ ($p_{ij}$), and the probability of detecting an individual ($r_{ij}$) by:

$$p_{ij} = 1 - (1 - r_{ij})^{N_i} \tag{1}$$

where, at pentad $i$ and survey $j$, $N_i$ is the latent abundance, $r_{ij}$ is the detection probability for an individual, and $p_{ij}$ is the pentad-specific detection probability.

The detection of an individual during survey $j$ at pentad $i$ is modelled using a binomial distribution:

$$w_{ij} \sim Binomial\ (r_{ij}) \tag{2}$$

I modelled the individual detection probability $r_{ij}$ with survey specific covariates using a logit link function in the form:

$$logit(r_{ij}) = \alpha_0 + \alpha_1 \times ћ_{ij} \tag{3}$$

where $ћ_{ij}$ is the logarithm of the number of hours spent birding during survey $j$ at pentad $i$, and the $\alpha$ are coefficients to be estimated by the model.

The latent abundance across pentads, $N_i$, was modelled using a Poisson distribution with rate parameter $\lambda$:

$$N_i \sim Poisson\ (\lambda_i) \tag{4}$$

and λ was modelled with pentad specific covariates using the log link function:

$$log(\lambda_i) = \beta_0 + \beta_1 \times PA_i + \beta_2 \times Urban_i + \beta_3 \times Agric_i + \beta_4 \times PA_i \times Urban_i +$$

$$\beta_5 \times PA_i \times Agric_i + \beta_6 \times Savanna_i \quad (5)$$

where the proportion of pentad $i$ occupied by protected area, urban area, agriculture area, and savanna vegetation is represented by $PA_i$, $Urban_i$, $Agric_i$, and $Savanna_i$ respectively, and the $\beta$ are the coefficients to be estimated by the model. Biome is a major driver of bird diversity in the study area, which consisted of savanna and grassland, present in almost equal proportions (savanna occupies the northern 50% of the study area, and grassland the southern 50%). Including $\beta_6$ accounted for abundances of birds within the savanna biome. Only savanna was included in the model, as a covariate since the proportion of grassland is given by subtracting the proportion of savanna from 100%; including both would confound the model.

A major assumption of the Royle-Nichols model is that the populations under study are closed (i.e. species abundance does not change markedly over the course of the study period). In reality, bird abundances do change over time, and thus, the closure assumption is usually violated to some degree. To satisfy this model assumption, I chose a relatively short time window of two years, over which these common, resident bird populations are relatively stable. My main results should further be robust to small violations of the closure assumption because they rely on comparing relative abundance estimates, and not absolute ones (Barker et al., 2018). I fitted abundance models to the data for each species separately, using package 'unmarked' (Fiske & Chandler, 2011) in program R (R Core development team, 2016).

#### 3.3.4.2 Interpretations of model beta coefficients

In the absence of urban and agricultural area, the relationship between the proportion of protected area and bird abundance in a pentad is represented by $\beta_1$ (proportion-abundance relationship). My primary aim was to examine how this relationship changed with increasing proportions of urban and agricultural area in the same pentad. Therefore, the model parameters $\beta_4$ and $\beta_5$ (equation 5), which estimate the effects of the interactions between the protected area ($\beta_1$) and urban ($\beta_4$) or agricultural ($\beta_5$) area within the same pentad were of most interest. They indicate the degree to which the slope for the linear proportion-abundance relationship changed when the proportion of urban ($\beta_4$) or agricultural ($\beta_5$) area within the same pentad changes. Species with a positive $\beta_4$ and $\beta_5$ value indicate that the slope of the proportion-abundance relationship increases (i.e., becomes more positive) as the amount of urban or agricultural area increases within the pentad, meaning that the effect of protected area on the abundance of birds becomes more positive when urban or agricultural area neighbours protected area. The opposite is true for negative $\beta_4$ and $\beta_5$ values. I further examined variation in $\beta_4$ and $\beta_5$ through guilds using simple data aggregation, and a hierarchical Bayesian analysis (see sections below).

*For what percentage of species does the proportion-abundance relationship increase or decrease with increasing proportions of urban and agricultural land in the same pentad?*

In response to increasing proportions of urban or agricultural area nearby protected area, the slope of the proportion-abundance relationship may become stronger (a significantly steeper slope describing the proportion-abundance relationship), weaker (a significantly less steep slope), remain the same (a slope with no significant change), or may even change sign completely (change from a positive slope to a negative slope, or vice versa). The type of change in the proportion-abundance relationship for each species is indicated by the estimates for the interaction coefficients ($\beta_4$ and $\beta_5$), specified in equation 5. Interpreting the estimates for these coefficients provides a good understanding of how bird abundances are projected to change within protected area with increasing proportions of agricultural and urban area near protected area. However, a more thorough understanding of how this occurs is gained from interpreting these interaction coefficients with the estimates for the other land-use type covariates that pertain to land-use types ($\beta_0 - \beta_3$, main effects in equation 5). Thus, I used the main and interaction effects that pertain to land-use types ($\beta_0 - \beta_5$), and conceived of eight conceptually defined unique hypothetical cases (or scenarios) of the ways in which urban and agricultural area near protected area could potentially modify the relationship between bird abundance and the proportion of protected area (Fig. 3.1 A-H). Each case is the result of a unique combination of conceptually derived relationships (either positive or negative) between the main and interaction effects and bird abundance. There are, of course, many more hypothetical cases that could be designed, but the ones I consider are those that best align with the ecological hypotheses I put forward. More information on the manner in which I designed the cases is contained in Appendix 3 (Table A3.2). Distinguishing between these cases allows for a better understanding of the overall fitted relationships of the main and interaction effects in equation 5 as estimated by the model.

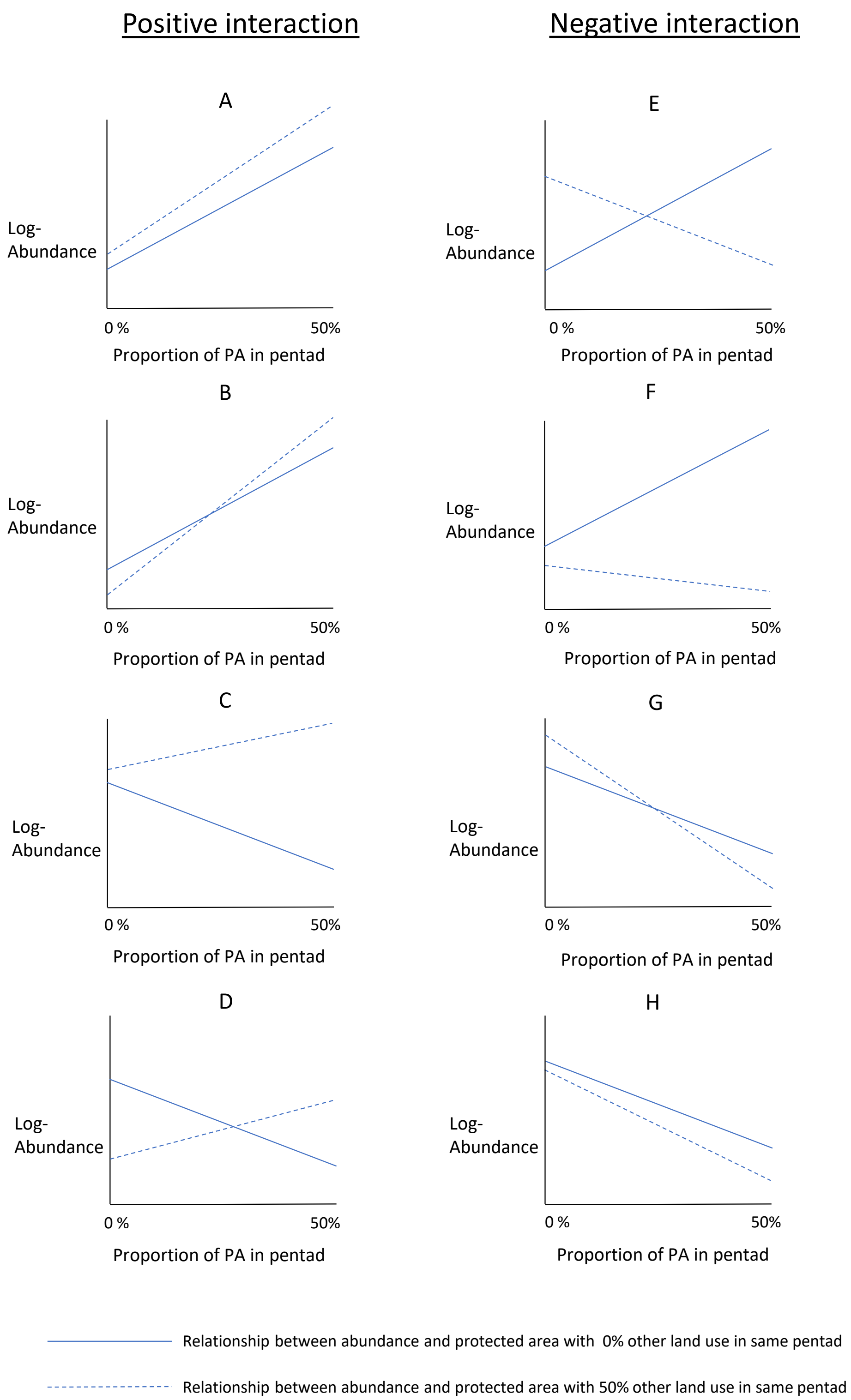



**Figure 3.1.** Conceptual cases showing the possible interactions between protected area, log-abundance of birds, and one of the land-use types (agriculture or urban) within the same pentad. The conceptual graphs are identical for urban and agricultural land-use type. Log-abundance (y-axis) is modelled as a linear function of the proportion of protected area ('PA' on the x-axis) within a pentad. This is the proportion-abundance relationship (the slope of this relationship is estimated by $\beta_1$

in equation 5), and is indicated by the solid line. The dotted line indicates how this relationship is modified when either agricultural or urban area occupy 50% of the pentad. Positive interactions, i.e., the proportion-abundance relationship becomes more positive as either agricultural or urban area increase, are in the left-hand column. Negative interactions, i.e., the proportion-abundance relationship becomes more negative as either agricultural or urban area increase, are in the right-hand column.

Fig. 3.1 is divided into two columns which show positive interactions (left-hand column) and negative interactions (right-hand column). With positive interactions, the proportion-abundance relationship becomes more positive as urban or agricultural area within the same pentad increase, as illustrated by the dotted line having a more positive slope than the solid one. With negative interactions, the proportion-abundance relationship becomes more negative as urban or agricultural area within the same pentad increase, as illustrated by the dotted line having a more negative slope than the solid one.

In cases where pentads are without protected area, local abundance is a function of the main effects of urban or agricultural area, illustrated by examining values of the y-intercepts, and relative to natural land. The intercept for the solid line indicates the average abundance for a land-use type scenario of 0% protected area, and 100% natural land. The intercept for the dotted line indicates the average abundance for a land-use type scenario of 0% protected area, and 50% either urban or agricultural area, and 50% natural land. Cases A, C, E, and G show situations where the species is more abundant in urban / agriculture area (dotted line y-intercept) than in natural land (solid line y-intercept – positive main effect); and in cases B, D, F, and H, species are less abundant (negative main effect).

After fitting a model to each species, I categorised each species based on the definitions described in Fig. 3.1 for its reaction to urban and agricultural land. As a single guild was assigned to each species, I counted the frequency of species within each guild that fell into each interaction case (A – H). This indicated the manner in which the proportion-abundance relationship for each guild is expected change given increases in urban / agricultural land near protected area (assuming all other factors in that relationship remain constant). Furthermore, for each guild, I counted the number of species that fell into the positive interaction cases (A, B, C, and D, Fig. 3.1), and calculated the percentage of species in each guild that are predicted to experience an increase in overall abundance with increases in urban / agricultural area. Similarly, I counted the number of species that fell into the negative interaction cases (E, F, G, and H, Fig. 3.1), and calculated the percentage of species in each guild that are predicted to experience an decrease in overall abundance with increases in urban / agricultural area. This analysis counts only the frequency with which species' proportion-abundance relationship is predicted to increase or decrease, rather than the magnitude of this change; this is considered in the next section below.

*What is the average change in magnitude of the proportion-abundance relationship with increasing proportions of urban and agricultural land in the same pentad?*

I used a hierarchical Bayesian analysis to estimate the average change in the magnitude of the average proportion-abundance relationship for each guild, along with associated credible intervals. This analysis used the species-specific mean and standard error estimates for the interaction terms $\hat{\beta}_4$ (urban) and $\hat{\beta}_5$ (agriculture) from equation 5 in the Royle-Nichols model of abundance to estimate a mean $\hat{\beta}_4$ and $\hat{\beta}_5$, and associated credible intervals, for each guild. The basic structure of this model was similar to a linear mixed-effects model, with guild as a random factor and normally distributed errors. However, instead of treating the mean interaction estimates as if they were observed values, I modelled them as coming from a normal distribution using the means and standard errors as estimated by the Royle-Nichols model of abundance. This approach is similar to the analysis described in McCarthy and Masters (2005; see also Lloyd et al., 2014). I used non-informative priors for the mean interaction response per guild. I implemented this in the program WinBUGS (Lunn et al., 2000) with 50 000 iterations and 25 000 burn in and 3 MCMC chains. The Gelman-Rubin diagnostic indicated that this model converged, and all R-hat values were < 1.01. The WinBUGS code for this model is provided in Appendix 3 (Model A3.1).

## 3.4 RESULTS

### 3.4.1 Royle-Nichols abundance models

Of the 200 models run, 2 did not converge, likely due to data sparsity, and were excluded from further analysis. These species were reported on < 0.5% of all checklists submitted over the study period (despite being widespread species, they were difficult to detect). The remaining 198 model results were further analysed, and comprised of the following guilds: frugivores (n = 9), gleaners (n = 30), granivores (n = 48), ground-feeders (n = 62), hawkers (n = 11), predators (n = 19), vegivores (n = 19). See Figure A3.2 (Appendix 3) for a visual summary of the mean model parameters across guilds, and Table A3.3 (Appendix 3) for model results for each species within each guild.

*For what percentage of species does the proportion-abundance relationship increase or decrease with increasing proportions of urban and agricultural land in the same pentad?*

The proportion-abundance relationship became more positive, and hence the overall abundance per pentad was expected to increase for 58% of species as urban area adjacent to or near protected areas increased in proportion, compared to 49% of species as agricultural area near protected area increased in proportion (Table A3.4, Appendix 3). Positive interaction cases C and D were observed most frequently across all guilds for increases in proportion of both agricultural and urban area (Fig. 3.2). Together, cases C and D comprise 82% of all the positive interaction cases as urban area increased (C: 33%, D: 49%), whilst they comprised 86% of all the positive interaction cases as agricultural area increased (C: 25%, D: 61%). On the other hand, negative interaction cases E and G were observed most frequently across all guilds for increases in proportion of both the agricultural and urban area (Fig. 3.2). Cases E and G made up 75% of all negative interaction cases as both urban and agricultural area increased (E: 33%, G: 49% for both urban and agricultural land use increases).

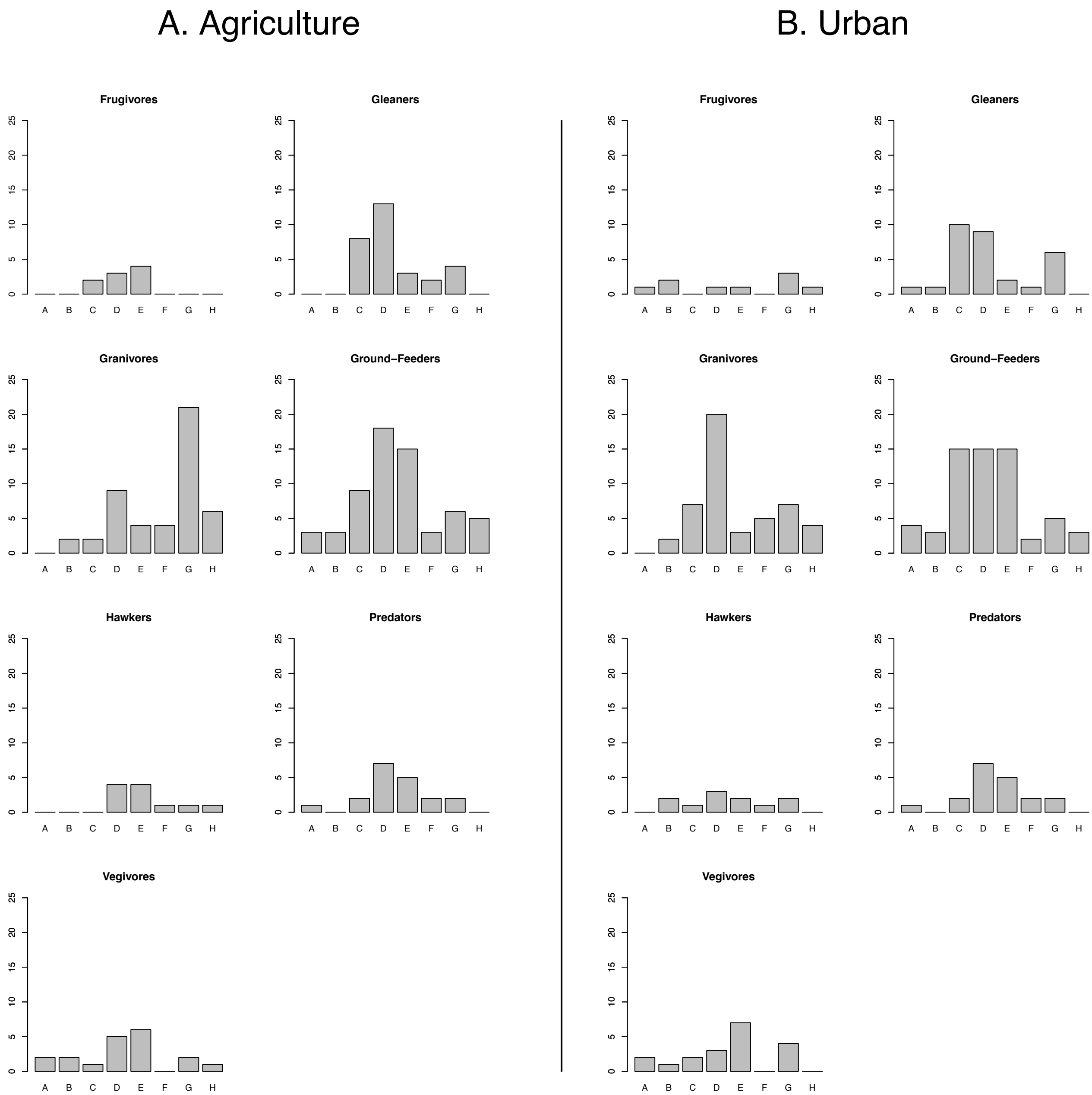



**Figure 3.2** Frequency counts of species within each guild falling into different possible interaction cases (A-H) per pentad, which illustrate how the proportion-abundance relationship changed with increasing proportion of agricultural (panel 'A' on the left of the figure) or urban (panel 'B' on the right of the figure) area. Cases A-H refer to those defined in Fig. 3.1. Cases A, B, C, and D indicate situations where the proportion-abundance relationship becomes more positive with increasing agricultural or urban area in the same pentad (termed 'positive interaction cases'). Cases E, F, G, and H indicate situations where the proportion-abundance relationship becomes more negative within increasing surrounding agricultural or urban area (termed 'negative interaction cases')

*What is the average change in magnitude of the proportion-abundance relationship with increasing proportions of urban and agricultural land in the same pentad?*

For the granivores and ground-feeder guilds, the average proportion-abundance relationship became significantly more positive with a higher proportion of urban area in the same pentad. For frugivores, this relationship became statistically more negative, whilst it became neither more positive nor more negative for the remaining guilds (gleaners, hawkers, predators, and vegivores; i.e., the confidence intervals for these guilds overlapped zero, Fig. 3.3)

As the proportion of agricultural area increased within pentads, the average proportion-abundance relationship became significantly more positive for six of the seven guilds: frugivores, vegivores, predators, gleaners, ground feeders, and hawkers. For the last guild, granivores, the average change in the proportion-abundance relationship was close to zero, and non-significant (Fig. 3.3).

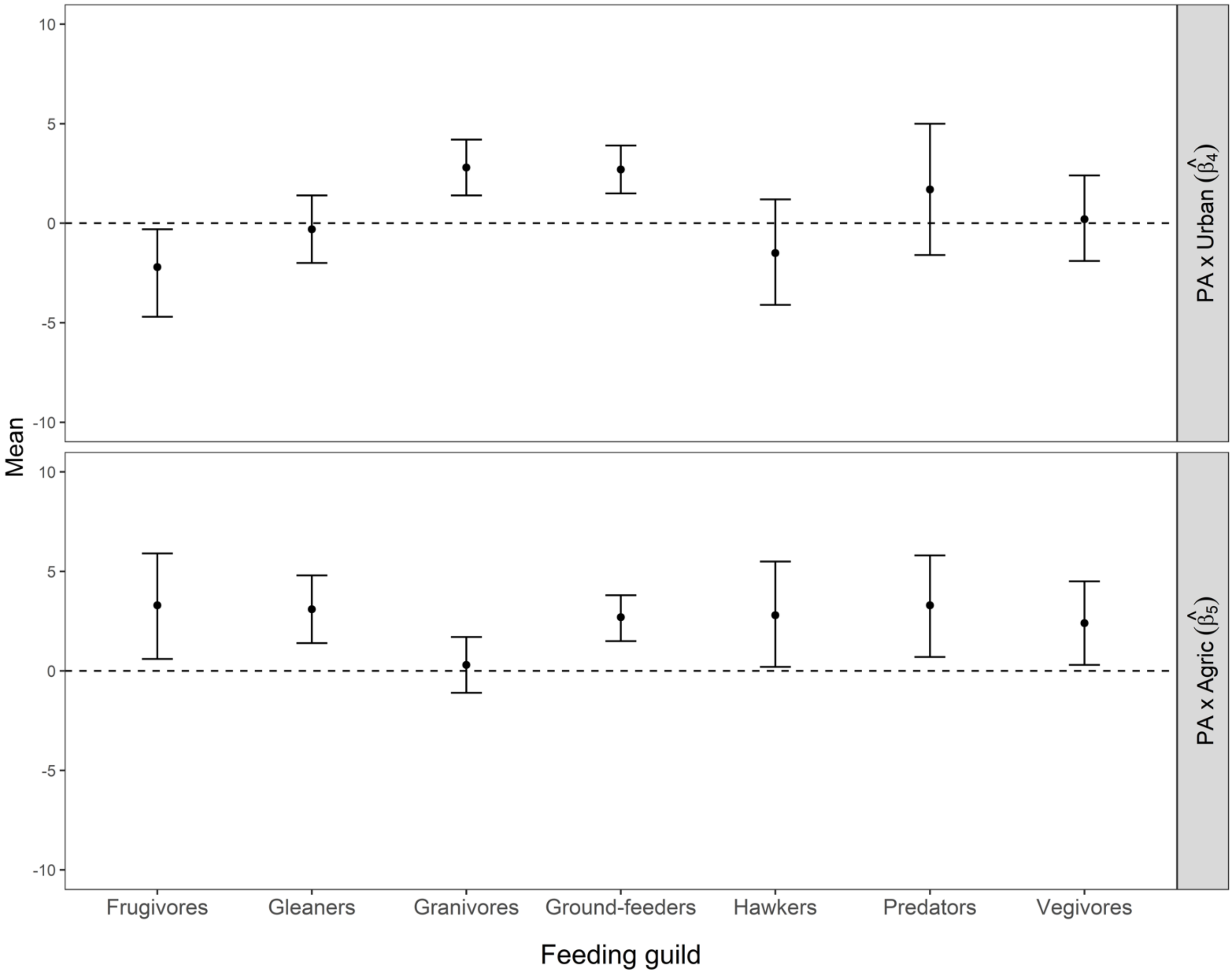



**Figure 3.3.** Mean and 95% credible interval indicating how the average proportion-abundance relationship for each guild is modified by an increasing proportion of urban ($\hat{\beta}_4$; top panel) and agricultural ($\hat{\beta}_5$; bottom panel) area, as estimated by the Bayesian hierarchical analysis. These are the interaction effects $\beta_4$ and $\beta_5$ specified in equation 5. Positive values indicated the proportion-abundance relationship becomes more positive for each guild, on average, as the proportion of urban or agricultural area in the pentad increases. Negative values indicated the opposite. $\beta_4$ and $\beta_5$ values estimated by the Royle-Nichols model of abundance fitted once for each of the 198 species. Confidence intervals that do not overlap zero indicate a statistically significant effect for either $\hat{\beta}_4$ or $\hat{\beta}_5$ whilst confidence intervals that overlap zero indicate no statistical significance.

## 3.5 DISCUSSION

Protected areas are a key tool for biodiversity conservation. However, there are concerns that the ecological effectiveness of protected areas is influenced by nearby land-use types in the landscape (Santos et al., 2008; DeFries et al., 2010; Thomas et al., 2012; Cottee-Jones et al., 2015). I examined to what degree this concern may apply to a large group of common species across many protected area over a heterogeneous landscape in the greater Gauteng region of South Africa. Using abundance models, which are an extension of occupancy models (Royle & Nichols, 2003), I modelled how urban and agricultural land-use types near in the same pentads affected the relationship between protected area and bird abundances (proportion-abundance relationship). My results suggest that urban and agricultural area near protected areas affect the proportion-abundance relationship, but that the magnitude and direction of this effect differs between land-use types and guilds. My results suggest that protected areas do not function in isolation, but rather, they must be considered as a constituent component of the greater landscape.

The average proportion-abundance relationship became more positive in response to increasing proportions of agricultural area within the same pentad for six of the seven guilds (frugivores, vegivores, predators, gleaners, ground-feeders, and hawkers), and none decreased significantly (Fig. 3.3). This result concurs with my initial hypothesis relating to insectivorous guilds (including gleaners, ground-feeders, and hawkers) and predators. This result could possibly be due to the activities associated with farming practices which decrease the quality of the soil, air, and water within entire landscapes, rendering agricultural area less suitable for a broad range of bird guilds (Billeter et al., 2008; Stoate et al., 2001). The change in the proportion-abundance relationship for granivores did not statistically differ from zero.

This is surprising, as I initially hypothesised that the proportion-abundance relationship would decrease as agricultural areas near protected areas increased in proportion, because granivores have been shown to adapt quickly to novel environments, and to take advantage of good conditions (for example, large amounts of food available year round) offered in these environments (Chace & Walsh, 2006). It has been shown that the type of crop farmed can have a significant influence on the ability of granivores to successfully adapt to new agricultural environments (Newton, 2004). It could be that in this case, the types of crops planted in agricultural land near protected areas is not suitable for consumption by granivores.

The effect of urban areas near protected areas on bird abundances was varied, because only granivorous and ground-feeding species became significantly more positive in their average proportion-abundance relationship, whilst it became more negative for frugivorous species (Fig. 3.3). Frugivores can take advantage of fruit-bearing trees planted in urban gardens (Shanahan et al., 2001), which is probably the case here. On the other hand, the negative factors associated with dense urban areas, such as persecution, predation, or pollution (Blair, 1996), or even the design and use of the urban areas by people (Paker et al., 2014) may explain the proportion-abundance relationship becomes, on average, more more positive as the area of urban land adjacent protected areas increased.

My results showed that agricultural area near protected areas resulted in a more positive proportion-abundance relationship, on average, compared to nearby urban land. This result has been found in some cases elsewhere throughout the world (Horsák et al., 2009; Gagné & Fahrig, 2011; Menon et al., 2016), and my results are consistent with these studies. Together, my study and the aforementioned show that protected areas are not isolated islands separated from the rest of the landscape, and that the ecological effectiveness of protected areas is dependent on the types of land use that surround them.

For most species, overall increases in the proportion-abundance relationship with concomitant increase in urban and agricultural area alongside protected area were best described by interaction cases C and D (Fig. 3.2). These refer to cases in which a negative proportion-abundance relationship becomes less negative as the proportion of agricultural area near protected area increases (Fig. 3.1). Of the 58% of species for which the proportion-abundance relationship increased as the proportion of urban area increased, 82% fell into cases C and D. Similarly, of the 49% of species for which the proportion-abundance relationship increased as the proportion of agricultural area increased, 86% fell into cases C and D. This is an important finding, as it shows that in isolation from other land-use types, protected areas would negatively affect a selection of species, and this relationship only becomes less negative (or, even positive) as considerable proportions of urban or agricultural areas are introduced into the landscape.

My results show that accounting for urban or agricultural land-use types modifies the abundance-proportion relationship (which was discussed in Chapter 2). For example, when examining the abundance of granivores as function of protected areas only (in Chapter 2), granivores were found to decrease in abundance as protected areas increased in proportion within the landscape (Table 2.1). In this chapter, I show that this observed decrease is due to agricultural land-use type: my analysis showed that granivores decrease in abundance within protected areas as agricultural areas increase in proportion (Table A3.4). Conversely, granivores increased in abundance within protected areas as the proportion of urban areas increased (Table A3.4). As another example, the predators guild exhibited the highest increase in abundance as the proportion of protected areas increased within a landscape (Table 2.1), when examining abundance as a function of protected areas. However, here I show that increases in the predators guild was largely due to increases in the proportion of urban area within the landscape, rather than increases in agricultural area (Table A3.4). This indicates a synergistic relationship between protected area and both urban and agricultural area, one in which urban, agricultural, and protected area complement each other in such a way that a negative relationship between bird abundance and proportion of protected area becomes less negative. These relationships are of considerable conservation importance, and the mechanisms that underpin it should be explored in detail in future studies.

My results also emphasise the importance of landscape heterogeneity to the ecological effectiveness of protected area. Although I didn't address landscape heterogeneity directly, my results indicate that if managed correctly, a heterogeneous landscape could deliver benefits to bird conservation, and thus conservation in general. A heterogeneous habitat consisting of urban, agricultural, natural, and protected area can result in increased abundance and biodiversity for many birds, as well as for many other classes of organism (MacArthur & Macarthur, 1961; Davidowitz & Rosenzweig, Michael, 1998; Benton et al., 2003; Gonzalez-Megias et al., 2011; Luo et al., 2012; Garnett et al., 2013; Skerratt, 2013). Birds are mobile species that can easily cross physical boundaries, and thus, use resources over a large proportion of the landscape. Bird diversity may therefore be affected by the characteristics of the greater landscape, rather than the ecological benefit provided by a single land use.

In conclusion, I found strong evidence that the ecological effectiveness of protected areas (proportion-abundance relationship) was affected by the proportion of urban and agricultural areas. Agricultural areas near protected areas affected more positively the ecological effectiveness than did urban areas near protected area; on average the proportion-abundance relationship of six guilds (frugivores, gleaners, ground-feeders, hawkers, predators, and vegivores) increased as the proportion of agriculture and protected area increased. Conversely, as urban area near protected area increased in proportion, only two guilds increased in their average proportion-abundance relationship (granivores and ground-feeders), whilst this relationship decreased in for frugivores. The major way in which near urban and agricultural land changed the bird abundance inside protected area was by a negative proportion-abundance relationship becoming less negative. A future research direction, therefore, is to reveal the exact mechanisms that underpin this transition. It must be noted, however, that I did not consider migratory or rare species, whose use of protected areas and the surrounding landscape is likely to differ substantially from that of the common, resident species I considered here. Nonetheless, my results indicate that a heterogeneous landscape which includes protected, urban, and agricultural areas, rather than uniform habitats of single use, may benefit biodiversity, and in doing so may increase the ecological effectiveness of protected areas.

## 3.6 APPENDIX: Supplementary material for Chapter 3.

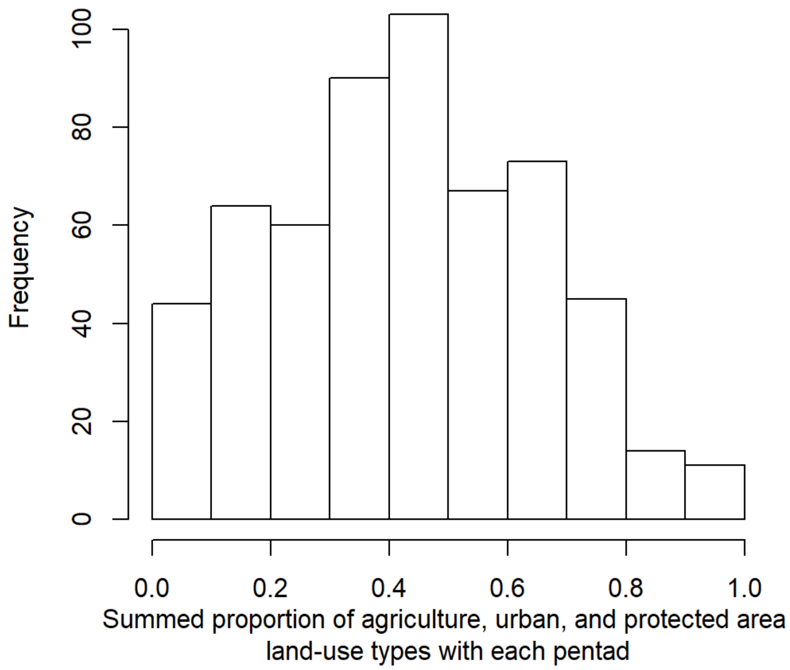



**Figure A3.1.** Histogram showing summed proportion of land-use types agriculture, urban, and protected area for each pentad over the study area.

**Table A3.1.** Pearson's pairwise correlation coefficients amongst land-use types agriculture, urban, and protected area per pentad. Land-use types agricultural, urban, protected, and natural area collectively occupy 94% of the land uses within the study area. Because these land-use types comprise of almost 100% of each grid cell, including each one as a covariate in the Royle-Nichols model of abundance would confound the model (see section 3.3.3 for more information). Natural land was omitted from the model, and the correlation coefficients for the remaining three land-use types shown here.

| | Agriculture | Urban | Protected areas |
|---|---|---|---|
| Agriculture | 1.00 | | |
| Urban | -0.28 | 1.00 | |
| Protected areas | -0.27 | -0.06 | 1.00 |

**Table A3.2.** Conceptual hypothetical interaction cases shown in Fig. 3.1. Each case (i.e., row) is a unique combination of the hypothetical relationship (either positive [+] or negative [-]) between bird abundance, and the main and interaction effects that pertain to land-use types, as specified in equation 5. Importantly, the sign for the land-use type main effect is relative to the sign of the proportion-abundance relationship (a '+' sign for the land-use type main effect indicated that this main effect was more positive than the proportion-abundance relationship, and a '-' sign the opposite).

| Interaction Case | Proportion-abundance relationship | Land-use type main effect | Interaction effect |
|---|---|---|---|
| A | + | + | + |
| B | + | - | + |
| C | - | + | + |
| D | - | - | + |
| E | + | + | - |
| F | + | - | - |
| G | - | + | - |
| H | - | - | - |

**Model A3.1.** WinBUGS model code for Bayesian analysis, describing the average $\beta_4$ and $\beta_5$ for each guild, along with associated error.

The model below codes the Bayesian analysis, the results of which produced figure 3.3. This model estimates the average $\hat{\beta}_4$ and $\hat{\beta}_5$ for each guild, along with standard error. $\hat{\beta}_4$ and $\hat{\beta}_5$ are the coefficients of the interaction terms in equation 5 in the methods text: $\hat{\beta}_4$ represents the protected areas × urban interaction, and $\hat{\beta}_5$ represents the protected areas × agriculture interaction. The model was fitted once for each beta (the model is identical for either beta).

```
# the data are the mean interaction effects (either β_4 for β_5;
#'interaction.beta'; the model is identical for both) and their associated
# standard error 'se'. 'n' is the number of species (198).'spp' indicates
# to which of the seven guild a species belongs. fg is the mean of the
# interaction effect for each of the seven guilds.


Model {


      # likelihood

      for(j in 1:n) {

            interaction.beta[j] ~ dnorm(mu[j], tau.observation.error[j])

            tau.observation.error[j] <- pow(se[j], -2)

            # the interaction betas come from a normal distribution of

            # mean 'mu', and  standard error 'se'

            mu[j] ~ dnorm(mu.a[j], tau.species)

            # This is assumed to come hierarchically from a normal

            # distribution, and heterogeneity between species must be

            # estimated.

            mu.a[j] <- fg[spp[j]]

            # Means for each guild

      } # likelihood




      # Priors
```

```
      sd.species ~ dunif(0, 100)
      tau.species <- pow(sd.species, -2)
      sd.fg ~ dunif(0, 100)
      tau.fg <- pow(sd.fg, -2)
      for(f in 1:7) {
      # 7 feeding guilds
      fg[f] ~ dnorm(0, tau.fg)
      } # guild prior
} # model
```

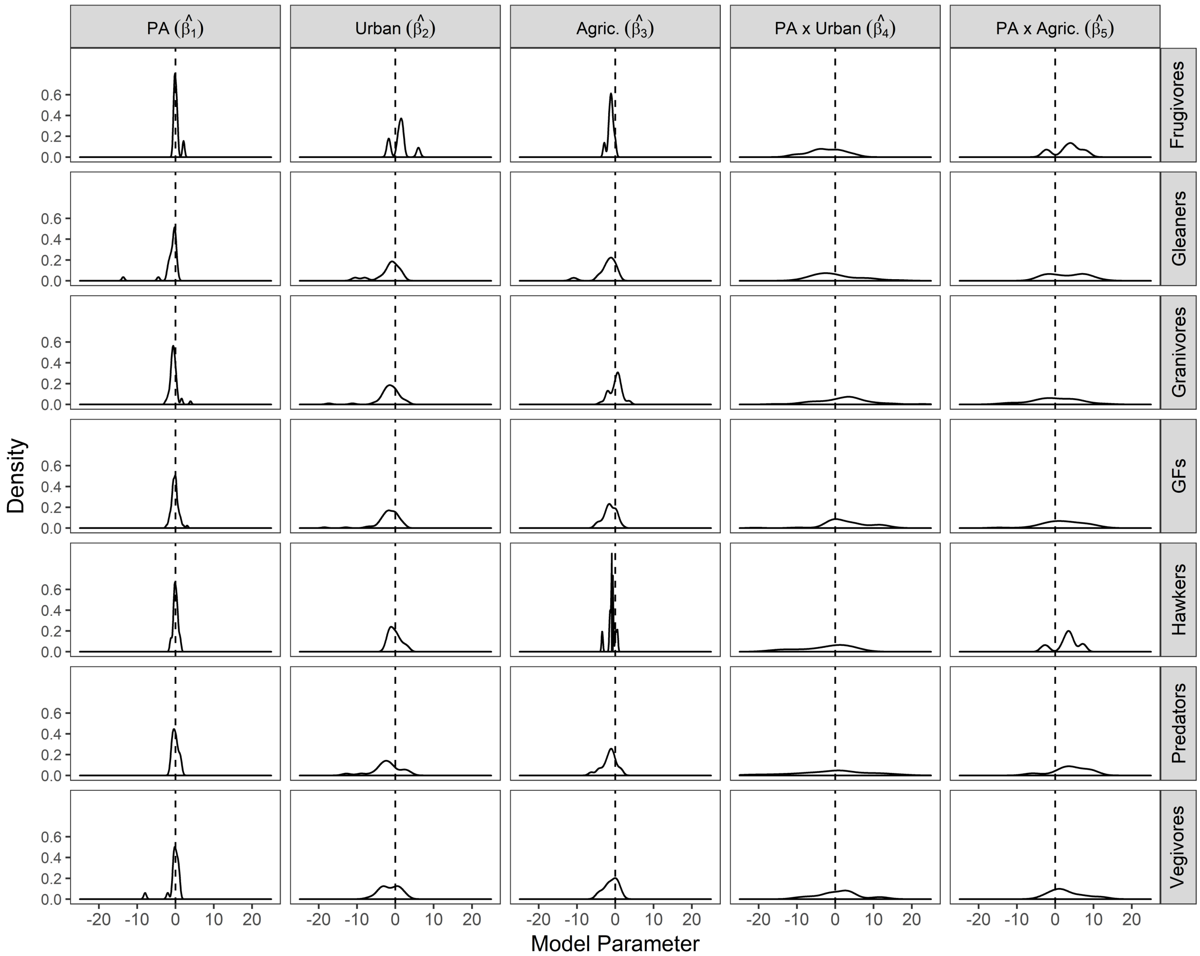



**Figure A3.2.** Density plots of model coefficients for 198 bird species as estimated by the Royle-Nichols model of abundance (equation 5, section 3.3.4.1; abundance component). Model parameters are labelled by columns, and the guild to which each species belongs is labelled by rows. Only mean model estimates are shown (standard deviations for each mean estimate are omitted). The model estimates abundance of birds per pentad as a function of the proportion of a pentad occupied by protected areas (‘PA’), agricultural land (‘Agric.’), urban land ‘(Urban’), and their interactions. A single model was fitted for each of the 198 species independently, and the study area was the greater Gauteng region in South Africa. ‘GF’ refers to the ground-feeding guild (see methods text for description of guilds).

**Table A3.3.** Mean and standard errors of model parameters estimated by the Royle-Nichols model of abundance, fitted independently for each of the 198 common, resident species. The estimated $\hat{\beta}$ here refer to those specified in equation 5 of the main methods text (section 3.3.4.1), and estimates are on the log scale (estimates for the detection components have been omitted). 'Agricultural interaction-case', and 'Urban interaction-case' refer to which of the interaction cases, as defined in Figure 3.2 of the main text, a species falls. 'Guild' refers to the guild which has been assigned to each species ('GF' refers to the guild ground-feeder). When fitting the models, all covariates were standardized to a mean of zero and a standard deviation of one, to ensure model convergence. 'PA' represents Protected Areas land-use type, and 'Agric. and 'Urb.' represent Agricultural and Urban land-use types respectively.

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| Frugivore | Acacia Pied Barbet (*Tricholaema leucomelas*) | 0.61 ± 0.20 | -0.42 ± 0.42 | -1.68 ± 0.48 | -0.87 ± 0.38 | 4.81 ± 3.42 | -2.21 ± 2.56 | 0.32 ± 0.15 | C | D |
| Frugivore | African Olive-Pigeon (*Columba arquatrix*) | -1.21 ± 0.30 | 2.11 ± 0.67 | 6.01 ± 0.37 | -0.03 ± 0.67 | -10.54 ± 5.20 | 4.99 ± 3.57 | -1.23 ± 0.24 | E | B |
| Frugivore | Black-collared Barbet (*Lybius torquatus*) | 1.22 ± 0.13 | -0.03 ± 0.26 | 0.82 ± 0.23 | -1.59 ± 0.27 | 0.27 ± 2.09 | 3.02 ± 1.46 | 0.29 ± 0.10 | D | H |
| Frugivore | Cape Glossy Starling (*Lamprotornis nitens*) | 1.51 ± 0.12 | -0.19 ± 0.24 | 0.72 ± 0.20 | -1.10 ± 0.22 | -4.13 ± 2.19 | -2.32 ± 1.54 | 0.30 ± 0.08 | C | G |
| Frugivore | Crested Barbet (*Trachyphonus vaillantii*) | 1.27 ± 0.12 | -0.27 ± 0.25 | 1.36 ± 0.20 | -1.05 ± 0.23 | -2.91 ± 2.19 | 4.43 ± 1.38 | 0.24 ± 0.09 | D | G |
| Frugivore | Dark-capped Bulbul (*Pycnonotus tricolor*) | 1.21 ± 0.11 | 0.39 ± 0.21 | 1.84 ± 0.18 | -1.25 ± 0.22 | -4.22 ± 1.90 | 3.99 ± 1.15 | 0.54 ± 0.08 | E | B |
| Frugivore | Red-faced Mousebird (*Urocolius indicus*) | 1.01 ± 0.14 | -0.27 ± 0.29 | 1.57 ± 0.21 | -0.54 ± 0.25 | -6.64 ± 2.66 | 2.16 ± 1.55 | 0.38 ± 0.09 | D | G |
| Frugivore | Red-winged Starling (*Onychognathus morio*) | 0.11 ± 0.22 | 0.44 ± 0.33 | 1.90 ± 0.33 | -2.88 ± 0.53 | 0.19 ± 2.51 | 8.33 ± 1.84 | 0.57 ± 0.17 | E | A |
| Frugivore | Yellow-fronted Tinkerbird (*Pogoniulus chrysoconus*) | -1.87 ± 0.33 | 0.19 ± 0.32 | -1.83 ± 0.73 | -1.66 ± 0.56 | 2.02 ± 3.63 | 7.20 ± 1.75 | 2.90 ± 0.30 | E | E |
| Gleaner | Ashy Tit (*Parus cinerascens*) | -1.80 ± 0.50 | -1.60 ± 1.13 | -0.74 ± 1.05 | -1.46 ± 1.02 | -2.07 ± 9.70 | 2.43 ± 6.16 | 1.56 ± 0.41 | C | C |
| Gleaner | Barred Wren-Warbler (*Calamonastes fasciolatus*) | -7.54 ± 2.14 | -1.23 ± 1.07 | -2.90 ± 1.75 | 0.76 ± 0.92 | 11.10 ± 7.76 | -2.78 ± 5.78 | 7.08 ± 2.13 | G | D |
| Gleaner | Bar-throated Apalis (*Apalis thoracica*) | 0.07 ± 0.23 | 0.55 ± 0.36 | 0.86 ± 0.41 | -1.80 ± 0.52 | 0.87 ± 3.15 | 7.72 ± 1.86 | 0.28 ± 0.18 | E | A |
| Gleaner | Black-backed Puffback (*Dryoscopus cubla*) | -0.51 ± 0.23 | -0.42 ± 0.31 | 0.46 ± 0.39 | -2.71 ± 0.50 | -5.33 ± 3.16 | 8.17 ± 1.69 | 2.08 ± 0.20 | D | G |
| Gleaner | Black-chested Prinia (*Prinia flavicans*) | 1.69 ± 0.12 | -1.14 ± 0.38 | -1.10 ± 0.26 | 0.16 ± 0.22 | 3.58 ± 2.85 | -2.49 ± 2.04 | -0.24 ± 0.09 | G | D |
| Gleaner | Black-headed Oriole (*Oriolus larvatus*) | 0.02 ± 0.23 | -0.16 ± 0.30 | -1.37 ± 0.51 | -2.54 ± 0.50 | -2.20 ± 3.52 | 7.16 ± 1.70 | 1.65 ± 0.19 | D | C |
| Gleaner | Brubru Brubru (*Nilaus afer*) | -0.67 ± 0.31 | -1.24 ± 0.40 | -4.54 ± 0.89 | -2.48 ± 0.55 | 7.58 ± 3.95 | -2.07 ± 2.92 | 2.63 ± 0.27 | C | D |
| Gleaner | Cape Penduline-Tit (*Anthoscopus minutus*) | -5.14 ± 1.31 | -1.48 ± 1.29 | -1.59 ± 1.62 | 0.59 ± 1.24 | 7.32 ± 9.11 | -1.39 ± 6.93 | 4.91 ± 1.27 | G | D |
| Gleaner | Cardinal Woodpecker (*Dendropicos fuscescens*) | 0.76 ± 0.21 | -0.57 ± 0.33 | 0.01 ± 0.38 | -3.10 ± 0.49 | -3.97 ± 3.31 | 6.03 ± 1.98 | 0.89 ± 0.16 | D | G |
| Gleaner | Chestnut-vented Tit-Babbler (*Parisoma subcaeruleum*) | 0.29 ± 0.17 | -0.20 ± 0.27 | -1.12 ± 0.37 | -0.89 ± 0.32 | -2.44 ± 3.03 | -3.81 ± 1.88 | 1.47 ± 0.13 | C | C |
| Gleaner | Chinspot Batis (*Batis molitor*) | -0.41 ± 0.21 | -0.25 ± 0.23 | -1.63 ± 0.42 | -1.77 ± 0.37 | 0.69 ± 2.43 | 1.22 ± 1.51 | 2.67 ± 0.18 | D | D |
| Gleaner | Common Scimitarbill (*Rhinopomastus cyanmelas*) | -1.11 ± 0.48 | 0.38 ± 0.74 | -0.35 ± 0.92 | -0.68 ± 1.05 | 1.38 ± 6.54 | -2.21 ± 5.09 | 0.56 ± 0.38 | F | E |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| Gleaner | Crimson-breasted Shrike (*Laniarius atrococcineus*) | -1.27 ± 0.24 | 0.02 ± 0.28 | -1.89 ± 0.54 | -0.19 ± 0.38 | -2.43 ± 3.44 | -3.11 ± 1.91 | 2.85 ± 0.21 | F | F |
| Gleaner | Desert Cisticola (*Cisticola aridulus*) | 0.66 ± 0.22 | -0.18 ± 0.43 | -2.69 ± 0.59 | -0.23 ± 0.43 | -0.33 ± 5.10 | -1.87 ± 2.69 | 0.20 ± 0.17 | C | C |
| Gleaner | Golden-tailed Woodpecker (*Campethera abingoni*) | -0.15 ± 0.26 | -1.06 ± 0.40 | -0.64 ± 0.50 | -2.71 ± 0.58 | 1.13 ± 3.40 | 10.11 ± 2.07 | 1.81 ± 0.22 | D | C |
| Gleaner | Green Wood-Hoopoe (*Phoeniculus purpureus*) | 1.04 ± 0.16 | -0.82 ± 0.36 | 1.52 ± 0.24 | -1.25 ± 0.30 | -4.67 ± 2.97 | 6.78 ± 1.80 | 0.15 ± 0.11 | D | G |
| Gleaner | Grey Penduline-Tit (*Anthoscopus caroli*) | -27.80 ± 76.32 | -13.64 ± 8.53 | -124.46 ± 72.42 | -10.40 ± 5.29 | -6.87 ± 107.50 | 46.14 ± 36.32 | 30.30 ± 76.32 | D | C |
| Gleaner | Grey-headed Bush-Shrike (*Malaconotus blanchoti*) | -0.86 ± 0.33 | -0.26 ± 0.41 | -0.08 ± 0.60 | -2.52 ± 0.71 | -3.29 ± 4.39 | 7.47 ± 2.35 | 1.91 ± 0.27 | D | C |
| Gleaner | Klaas's Cuckoo (*Chrysococcyx klaas*) | -1.56 ± 0.41 | -0.17 ± 0.51 | 1.93 ± 0.48 | -1.04 ± 0.85 | -4.83 ± 4.27 | 2.16 ± 3.30 | 2.63 ± 0.33 | D | G |
| Gleaner | Lesser Honeyguide (*Indicator minor*) | 0.36 ± 0.24 | -0.74 ± 0.45 | 0.79 ± 0.40 | -1.72 ± 0.52 | -9.29 ± 4.81 | 4.73 ± 2.53 | 0.84 ± 0.18 | D | G |
| Gleaner | Long-billed Crombec (*Sylvietta rufescens*) | -1.69 ± 0.26 | -0.52 ± 0.24 | -1.01 ± 0.39 | -1.08 ± 0.35 | -5.22 ± 2.79 | -0.58 ± 1.60 | 4.13 ± 0.25 | C | C |
| Gleaner | Rattling Cisticola (*Cisticola chiniana*) | -1.73 ± 0.24 | -0.11 ± 0.26 | -0.57 ± 0.40 | -0.08 ± 0.35 | -3.14 ± 2.83 | -4.35 ± 1.84 | 3.62 ± 0.22 | C | C |
| Gleaner | Red-headed Weaver (*Anaplectes melanotis*) | -8.22 ± 4.82 | -2.03 ± 0.82 | -7.85 ± 3.32 | -11.32 ± 2.39 | -6.60 ± 16.69 | 3.62 ± 10.20 | 9.67 ± 4.84 | C | C |
| Gleaner | Southern Black Tit (*Parus niger*) | -3.41 ± 0.92 | -1.82 ± 0.56 | -10.55 ± 2.35 | -4.38 ± 0.89 | 9.62 ± 8.46 | 6.43 ± 3.44 | 4.96 ± 0.91 | D | D |
| Gleaner | Southern Boubou (*Laniarius ferrugineus*) | -0.41 ± 0.18 | 0.10 ± 0.28 | 1.52 ± 0.29 | -1.22 ± 0.36 | -0.57 ± 2.36 | 8.94 ± 1.33 | 1.45 ± 0.14 | E | B |
| Gleaner | Tawny-flanked Prinia (*Prinia subflava*) | 0.77 ± 0.14 | -0.19 ± 0.26 | 1.35 ± 0.23 | -1.27 ± 0.27 | -0.86 ± 2.16 | 6.82 ± 1.35 | 0.60 ± 0.10 | D | G |
| Gleaner | White-crested Helmet-Shrike (*Prionops plumatus*) | -4.46 ± 1.68 | -2.07 ± 1.07 | -8.02 ± 3.84 | -4.36 ± 1.66 | 8.22 ± 13.69 | 12.20 ± 5.65 | 4.94 ± 1.65 | D | D |
| Gleaner | Wing-snapping Cisticola (*Cisticola ayresii*) | 0.62 ± 0.27 | 0.12 ± 0.65 | -3.84 ± 0.83 | -0.22 ± 0.51 | 16.44 ± 4.75 | 1.35 ± 3.45 | -1.28 ± 0.24 | E | E |
| Gleaner | Yellow-bellied Eremomela (*Eremomela icteropygialis*) | -3.52 ± 2.93 | -4.47 ± 2.75 | -10.56 ± 6.55 | -4.29 ± 2.96 | 36.44 ± 18.47 | 8.90 ± 15.21 | 4.58 ± 2.75 | C | D |
| Gleaner | Zitting Cisticola (*Cisticola juncidis*) | 1.81 ± 0.15 | -0.47 ± 0.29 | -1.84 ± 0.28 | 0.60 ± 0.22 | 4.37 ± 2.56 | 0.20 ± 1.52 | -0.24 ± 0.09 | G | D |
| Granivore | African Firefinch (*Lagonosticta rubricata*) | -0.95 ± 0.49 | 0.10 ± 0.59 | -0.59 ± 0.90 | -1.91 ± 1.09 | -5.74 ± 6.79 | 4.92 ± 3.62 | 1.37 ± 0.39 | E | F |
| Granivore | African Quailfinch (*Ortygospiza atricollis*) | 1.43 ± 0.15 | 0.00 ± 0.35 | -4.97 ± 0.57 | 0.79 ± 0.27 | 6.43 ± 4.11 | -3.24 ± 2.08 | -0.64 ± 0.12 | B | E |
| Granivore | Black-faced Waxbill (*Estrilda erythronotos*) | -3.24 ± 0.53 | -0.08 ± 0.68 | -2.51 ± 1.31 | 1.19 ± 0.73 | 3.98 ± 6.52 | -11.96 ± 5.97 | 3.21 ± 0.48 | G | D |
| Granivore | Black-throated Canary (*Crithagra atrogularis*) | 1.49 ± 0.12 | -0.86 ± 0.35 | -0.93 ± 0.25 | 0.91 ± 0.20 | 4.50 ± 2.58 | -0.35 ± 1.68 | -0.20 ± 0.09 | G | D |
| Granivore | Blue Waxbill (*Uraeginthus angolensis*) | -0.55 ± 0.17 | -0.69 ± 0.23 | -1.16 ± 0.33 | -0.40 ± 0.27 | 3.71 ± 1.99 | 2.16 ± 1.29 | 3.00 ± 0.14 | D | D |
| Granivore | Bronze Mannikin (*Spermestes cucullatus*) | -1.19 ± 0.25 | -0.68 ± 0.56 | 3.33 ± 0.33 | -0.58 ± 0.56 | 1.81 ± 3.19 | 6.62 ± 2.71 | 1.32 ± 0.19 | D | H |
| Granivore | Cape Canary (*Serinus canicollis*) | -1.82 ± 0.81 | 1.49 ± 1.32 | 0.20 ± 1.62 | -2.22 ± 1.96 | -7.34 ± 16.54 | 8.49 ± 6.65 | -1.08 ± 0.72 | E | B |
| Granivore | Cape Sparrow (*Passer melanurus*) | 1.79 ± 0.10 | -1.63 ± 0.40 | 1.44 ± 0.16 | 1.02 ± 0.17 | 4.29 ± 2.32 | 2.77 ± 1.74 | -0.77 ± 0.08 | G | H |
| Granivore | Cape Turtle-Dove (*Streptopelia capicola*) | 1.89 ± 0.11 | -0.31 ± 0.26 | 0.04 ± 0.19 | 0.19 ± 0.19 | 0.36 ± 2.24 | -3.31 ± 1.52 | -0.36 ± 0.07 | G | G |
| Granivore | Chestnut-backed Sparrowlark (*Eremopterix leucot*is) | -2.57 ± 0.49 | -0.53 ± 1.58 | -3.05 ± 1.73 | 3.84 ± 0.83 | 6.63 ± 13.64 | -4.72 ± 6.83 | 0.77 ± 0.37 | G | D |
| Granivore | Cinnamon-breasted Bunting (*Emberiza tahapisi*) | 1.17 ± 0.20 | 0.03 ± 0.28 | -2.62 ± 0.51 | -2.20 ± 0.43 | 3.91 ± 3.02 | -0.41 ± 2.00 | 0.67 ± 0.15 | F | E |
| Granivore | Common Waxbill (*Estrilda astrild*) | 1.14 ± 0.15 | -0.44 ± 0.36 | -1.06 ± 0.31 | 0.82 ± 0.26 | 7.30 ± 2.65 | 1.91 ± 1.72 | -0.14 ± 0.11 | H | D |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| Granivore | Cuckoo Finch (*Anomalospiza imberbis*) | -0.62 ± 0.65 | 0.40 ± 1.25 | -1.38 ± 1.36 | -1.84 ± 1.53 | 14.21 ± 8.19 | 11.38 ± 5.97 | -1.20 ± 0.53 | E | E |
| Granivore | Cut-throat Finch (*Amadina fasciata*) | -3.65 ± 0.52 | -0.41 ± 0.75 | 2.82 ± 0.56 | -0.34 ± 0.92 | 3.78 ± 4.35 | 4.08 ± 3.85 | 3.25 ± 0.46 | D | H |
| Granivore | Dusky Indogobird (*Vidua funerea*) | -4.51 ± 2.16 | -1.19 ± 2.12 | -1.68 ± 2.53 | 0.44 ± 2.49 | 15.61 ± 11.69 | -48.03 ± 40.99 | 3.97 ± 1.81 | G | D |
| Granivore | Emerald-spotted Wood-Dove (*Turtur chalcospilos*) | -5.45 ± 1.66 | -1.98 ± 0.66 | -17.36 ± 4.19 | -4.04 ± 1.05 | 22.78 ± 11.49 | 13.59 ± 3.29 | 6.71 ± 1.66 | D | D |
| Granivore | Fan-tailed Widowbird (*Euplectes axillaris*) | -1.53 ± 0.38 | -1.23 ± 2.49 | -1.46 ± 1.04 | 3.57 ± 0.64 | 4.05 ± 20.70 | 7.73 ± 7.59 | -2.21 ± 0.45 | H | D |
| Granivore | Golden-breasted Bunting (*Emberiza flaviventris*) | -2.70 ± 0.47 | 0.21 ± 0.28 | -3.31 ± 0.83 | -2.06 ± 0.56 | -0.45 ± 3.81 | -3.51 ± 2.23 | 4.43 ± 0.46 | F | F |
| Granivore | Great Sparrow (*Passer motitensis*) | -5.87 ± 1.02 | 1.69 ± 0.54 | -0.27 ± 1.29 | 2.82 ± 0.79 | -8.95 ± 9.06 | -14.82 ± 5.92 | 5.11 ± 0.98 | B | F |
| Granivore | Green-winged Pytilia (*Pytilia melba*) | -1.23 ± 0.28 | -0.82 ± 0.59 | -1.15 ± 0.64 | 0.64 ± 0.50 | 3.21 ± 4.94 | -3.33 ± 3.40 | 1.83 ± 0.23 | G | D |
| Granivore | House Sparrow (*Passer domesticus*) | 1.09 ± 0.13 | -0.88 ± 0.41 | 1.97 ± 0.19 | 0.43 ± 0.23 | 2.76 ± 2.40 | -2.10 ± 2.15 | -0.18 ± 0.09 | G | H |
| Granivore | Jameson's Firefinch (*Lagonosticta rhodopareia*) | -0.54 ± 0.27 | -0.65 ± 0.42 | -0.15 ± 0.47 | -1.81 ± 0.56 | 1.96 ± 3.24 | 5.74 ± 2.28 | 1.80 ± 0.22 | D | D |
| Granivore | Laughing Dove (*Spilopelia senegalensis*) | 2.03 ± 0.11 | -0.54 ± 0.22 | 0.55 ± 0.16 | 0.55 ± 0.17 | 1.02 ± 1.76 | -0.70 ± 1.18 | 0.05 ± 0.07 | G | G |
| Granivore | Long-tailed Paradise-Whydah (*Vidua paradisaea*) | -1.05 ± 0.34 | -0.10 ± 0.55 | -2.15 ± 0.88 | 0.83 ± 0.60 | -6.94 ± 8.51 | -6.62 ± 4.32 | 1.52 ± 0.26 | G | C |
| Granivore | Long-tailed Widowbird (*Euplectes* progne) | 2.40 ± 0.11 | -0.79 ± 0.49 | -3.44 ± 0.32 | 0.25 ± 0.20 | 9.88 ± 3.98 | 0.34 ± 2.18 | -2.30 ± 0.12 | G | D |
| Granivore | Namaqua Dove (*Oena capensis*) | -0.04 ± 0.18 | -0.71 ± 0.44 | -4.08 ± 0.69 | 1.77 ± 0.30 | 9.95 ± 3.84 | -2.91 ± 2.37 | 0.90 ± 0.14 | G | D |
| Granivore | Orange-breasted Waxbill (*Sporaeginthus subflavus*) | 0.12 ± 0.27 | -1.27 ± 0.98 | -0.15 ± 0.51 | 0.86 ± 0.51 | 6.96 ± 6.32 | 4.24 ± 4.13 | -0.77 ± 0.23 | H | D |
| Granivore | Pink-billed Lark (*Spizocorys conirostris*) | 0.33 ± 0.61 | -193.64 ± 58.73 | 11.21 ± 4.18 | -1.53 ± 1.12 | -5.96 ± 294.32 | -59.93 ± 152.61 | -4.06 ± 1.18 | C | C |
| Granivore | Pin-tailed Whydah (*Vidua macroura*) | 1.64 ± 0.15 | -0.35 ± 0.31 | -1.27 ± 0.27 | 0.79 ± 0.22 | 5.05 ± 2.54 | -0.86 ± 1.64 | -0.33 ± 0.09 | G | D |
| Granivore | Red-billed Firefinch (*Lagonosticta senegala*) | -1.63 ± 0.35 | -1.55 ± 0.65 | -2.06 ± 0.84 | 0.15 ± 0.56 | -4.33 ± 7.03 | 4.47 ± 3.19 | 2.59 ± 0.29 | H | C |
| Granivore | Red-billed Quelea (*Quelea quelea*) | 1.80 ± 0.11 | -1.00 ± 0.31 | -3.05 ± 0.32 | 1.08 ± 0.17 | 2.45 ± 3.11 | -0.12 ± 1.50 | 0.05 ± 0.08 | G | D |
| Granivore | Red-capped Lark (*Calandrella cinerea*) | 1.07 ± 0.20 | -0.57 ± 0.90 | -5.75 ± 0.81 | 1.64 ± 0.33 | -0.73 ± 12.15 | -5.36 ± 4.18 | -1.97 ± 0.21 | G | C |
| Granivore | Red-collared Widowbird (*Euplectes ardens*) | 1.47 ± 0.17 | -0.03 ± 0.38 | -0.74 ± 0.36 | -2.26 ± 0.38 | 6.16 ± 2.91 | 4.90 ± 2.07 | -0.92 ± 0.14 | D | D |
| Granivore | Red-eyed Dove (*Streptopelia semitorquata*) | 1.83 ± 0.11 | -0.39 ± 0.27 | 1.02 ± 0.18 | -0.01 ± 0.18 | -2.10 ± 2.28 | 4.35 ± 1.34 | -0.57 ± 0.08 | D | G |
| Granivore | Red-headed Finch (*Amadina erythrocephala*) | 0.27 ± 0.22 | -1.27 ± 0.97 | 2.53 ± 0.32 | -0.56 ± 0.46 | -0.18 ± 5.56 | -3.36 ± 5.52 | -0.95 ± 0.18 | C | G |
| Granivore | Scaly-feathered Finch (*Sporopipes squamifrons*) | -2.69 ± 0.30 | -1.06 ± 0.63 | 1.29 ± 0.49 | 0.97 ± 0.46 | -3.23 ± 5.17 | -5.29 ± 3.94 | 3.00 ± 0.26 | G | G |
| Granivore | Shaft-tailed Whydah (*Vidua regia*) | -3.90 ± 0.63 | -0.97 ± 0.93 | -2.93 ± 1.47 | 1.94 ± 0.72 | 11.71 ± 6.84 | -10.85 ± 6.14 | 3.76 ± 0.57 | G | D |
| Granivore | Southern Red Bishop (*Euplectes orix*) | 2.07 ± 0.12 | -0.95 ± 0.33 | 0.27 ± 0.18 | 0.46 ± 0.18 | 1.71 ± 2.45 | 3.09 ± 1.55 | -0.92 ± 0.08 | H | G |
| Granivore | Speckled Pigeon (*Columba guinea*) | 1.44 ± 0.13 | -0.29 ± 0.29 | 0.36 ± 0.20 | 0.72 ± 0.20 | 0.10 ± 2.42 | -1.26 ± 1.56 | -0.33 ± 0.08 | G | G |
| Granivore | Village Indigobird (*Vidua chalybeata*) | -1.89 ± 0.45 | -1.98 ± 1.13 | -2.33 ± 1.14 | 0.01 ± 0.80 | 3.24 ± 9.18 | -10.02 ± 7.87 | 2.12 ± 0.38 | G | C |
| Granivore | Violet-eared Waxbill (*Granatina granatina*) | -1.64 ± 0.39 | 0.51 ± 0.37 | -1.75 ± 0.82 | -0.81 ± 0.68 | -3.63 ± 4.99 | -11.79 ± 4.06 | 2.62 ± 0.34 | F | F |
| Granivore | White-browed Sparrow-Weaver (*Plocepasser mahali*) | 1.71 ± 0.13 | -2.55 ± 0.55 | -3.79 ± 0.44 | -0.81 ± 0.25 | 8.86 ± 4.28 | 6.84 ± 2.38 | -0.65 ± 0.11 | D | D |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| Granivore | White-winged Widowbird (*Euplectes albonotatus*) | 0.70 ± 0.14 | -0.35 ± 0.31 | -1.68 ± 0.35 | 1.63 ± 0.21 | 4.35 ± 2.78 | 0.77 ± 1.50 | 0.57 ± 0.09 | H | D |
| Granivore | Yellow Bishop (*Euplectes capensis*) | -2.35 ± 1.15 | 3.93 ± 2.25 | 0.22 ± 2.17 | -0.11 ± 2.47 | -15.76 ± 31.08 | 6.45 ± 9.07 | -3.18 ± 1.54 | E | B |
| Granivore | Yellow Canary (*Crithagra flaviventris*) | 0.76 ± 0.20 | -0.94 ± 0.68 | -2.49 ± 0.55 | 0.51 ± 0.37 | -10.42 ± 9.19 | -1.77 ± 3.57 | -0.68 ± 0.17 | G | C |
| Granivore | Yellow-crowned Bishop (*Euplectes afer*) | 1.31 ± 0.15 | -0.51 ± 0.49 | -2.04 ± 0.36 | 1.62 ± 0.25 | 4.28 ± 4.10 | -6.18 ± 2.60 | -0.75 ± 0.12 | G | D |
| Granivore | Yellow-fronted Canary (*Crithagra mozambicus*) | 0.50 ± 0.18 | -0.14 ± 0.25 | -0.57 ± 0.35 | -2.14 ± 0.37 | -1.38 ± 2.52 | 4.62 ± 1.50 | 1.33 ± 0.14 | D | C |
| Granivore | Yellow-throated Petronia (*Petronia superciliaris*) | -1.74 ± 0.55 | 0.35 ± 0.46 | -2.10 ± 1.15 | -3.27 ± 1.12 | -6.25 ± 6.51 | -1.98 ± 3.94 | 2.57 ± 0.50 | F | F |
| GF | African Grey Hornbill (*Tockus nasutus*) | -0.46 ± 0.21 | -0.45 ± 0.26 | -0.59 ± 0.39 | -2.69 ± 0.41 | -2.13 ± 2.64 | 7.37 ± 1.47 | 2.41 ± 0.18 | D | C |
| GF | African Hoopoe (*Upupa africana*) | 0.81 ± 0.16 | 0.10 ± 0.35 | 1.69 ± 0.26 | -1.55 ± 0.34 | 1.23 ± 2.43 | 1.49 ± 2.05 | -0.09 ± 0.12 | E | A |
| GF | African Pipit (*Anthus cinnamomeus*) | 2.12 ± 0.11 | 0.08 ± 0.26 | -2.28 ± 0.27 | 0.62 ± 0.18 | 5.89 ± 2.28 | -5.22 ± 1.58 | -0.74 ± 0.09 | B | E |
| GF | African Sacred Ibis (*Threskiornis aethiopicus*) | 0.89 ± 0.13 | 0.23 ± 0.41 | 2.45 ± 0.20 | 0.21 ± 0.26 | 2.24 ± 2.67 | 0.55 ± 2.14 | -0.98 ± 0.11 | A | A |
| GF | African Stonechat (*Saxicola torquatus*) | 2.29 ± 0.10 | -0.45 ± 0.34 | -1.77 ± 0.24 | 0.47 ± 0.18 | 9.62 ± 2.52 | 1.81 ± 1.56 | -1.59 ± 0.09 | H | D |
| GF | Anteating Chat (*Myrmecocichla formicivora*) | 1.69 ± 0.16 | -0.41 ± 0.60 | -6.78 ± 0.81 | -0.74 ± 0.33 | 12.86 ± 5.85 | 1.41 ± 2.98 | -2.01 ± 0.17 | D | D |
| GF | Arrow-marked Babbler (*Turdoides jardineii*) | -0.32 ± 0.19 | -0.12 ± 0.22 | -1.64 ± 0.41 | -1.29 ± 0.33 | -0.33 ± 2.42 | 4.48 ± 1.20 | 2.47 ± 0.16 | D | C |
| GF | Black-crowned Tchagra (*Tchagra* senegalus) | -0.57 ± 0.28 | 0.73 ± 0.31 | -1.78 ± 0.68 | -1.68 ± 0.58 | 2.85 ± 3.39 | 2.31 ± 1.96 | 1.47 ± 0.23 | E | E |
| GF | Black-headed Heron (*Ardea melanocephala*) | 1.29 ± 0.13 | -1.43 ± 0.50 | 0.78 ± 0.21 | 1.72 ± 0.20 | 2.94 ± 3.30 | 4.52 ± 1.96 | -0.85 ± 0.09 | H | H |
| GF | Blue Korhaan (*Eupodotis caerulescens*) | -0.07 ± 0.51 | -53.27 ± 82.41 | -18.52 ± 6.75 | -1.06 ± 0.93 | 0.09 ± 147.30 | -15.55 ± 223.89 | -3.36 ± 0.87 | C | C |
| GF | Bokmakierie Bokmakierie (*Telophorus zeylonus*) | 2.09 ± 0.14 | -0.74 ± 0.44 | -2.64 ± 0.39 | -1.73 ± 0.30 | 3.82 ± 3.98 | 4.26 ± 2.32 | -1.40 ± 0.13 | D | D |
| GF | Brown-crowned Tchagra (*Tchagra australis*) | 0.29 ± 0.19 | -0.58 ± 0.26 | -1.51 ± 0.40 | -1.70 ± 0.37 | -2.88 ± 2.92 | 0.33 ± 1.76 | 2.05 ± 0.16 | C | C |
| GF | Brown-hooded Kingfisher (*Halcyon albiventris*) | -0.34 ± 0.20 | -0.71 ± 0.29 | 0.19 ± 0.33 | -1.62 ± 0.38 | 4.66 ± 2.12 | 6.67 ± 1.54 | 2.18 ± 0.16 | D | H |
| GF | Buffy Pipit (*Anthus vaalensis*) | 0.74 ± 0.41 | 1.15 ± 0.50 | -3.51 ± 1.09 | -3.13 ± 0.98 | 9.50 ± 4.74 | -2.89 ± 4.18 | -0.54 ± 0.32 | F | E |
| GF | Bushveld Pipit (*Anthus caffer*) | -5.07 ± 2.19 | -0.57 ± 0.77 | -7.75 ± 4.02 | -4.78 ± 2.01 | 4.80 ± 13.26 | -8.49 ± 10.36 | 5.34 ± 2.18 | C | D |
| GF | Cape Crow (*Corvus capensis*) | -1.56 ± 0.46 | -0.55 ± 1.47 | -5.91 ± 2.35 | 1.90 ± 0.80 | -20.72 ± 35.97 | -3.86 ± 7.71 | -0.15 ± 0.39 | G | C |
| GF | Cape Grassbird (*Sphenoeacus afer*) | 0.06 ± 0.29 | 0.63 ± 0.48 | -3.08 ± 0.91 | -1.32 ± 0.61 | 10.86 ± 4.45 | 8.42 ± 2.27 | -0.46 ± 0.24 | E | E |
| GF | Cape Longclaw (*Macronyx capensis*) | 2.38 ± 0.11 | -0.37 ± 0.40 | -3.08 ± 0.30 | 0.12 ± 0.20 | 12.66 ± 2.97 | -0.58 ± 1.94 | -2.01 ± 0.11 | G | D |
| GF | Cape Robin-Chat (*Cossypha caffra*) | 1.33 ± 0.13 | -0.03 ± 0.34 | 2.00 ± 0.21 | -1.09 ± 0.26 | -1.85 ± 2.59 | 7.03 ± 1.66 | -0.91 ± 0.10 | D | G |
| GF | Cape Rock-Thrush (*Monticola rupestris*) | -1.23 ± 0.60 | 3.04 ± 0.80 | 0.89 ± 1.24 | -5.33 ± 2.02 | 8.08 ± 5.49 | 12.69 ± 3.78 | -1.61 ± 0.53 | E | A |
| GF | Cape Wagtail (*Motacilla capensis*) | 1.22 ± 0.13 | 0.13 ± 0.32 | 0.62 ± 0.23 | 0.20 ± 0.23 | 3.90 ± 2.43 | 0.19 ± 1.74 | -0.70 ± 0.10 | A | A |
| GF | Capped Wheatear (*Oenanthe pileata*) | 1.50 ± 0.18 | 1.28 ± 0.46 | -2.23 ± 0.45 | -0.39 ± 0.34 | 1.52 ± 4.88 | -4.95 ± 3.00 | -2.17 ± 0.19 | F | E |
| GF | Cattle Egret (*Bubulcus ibis*) | 1.50 ± 0.12 | -0.71 ± 0.26 | -0.18 ± 0.21 | 0.66 ± 0.18 | 0.33 ± 2.17 | 0.32 ± 1.37 | 0.24 ± 0.08 | G | C |
| GF | Cloud Cisticola (*Cisticola textrix*) | 1.61 ± 0.17 | -0.48 ± 0.59 | -3.89 ± 0.53 | 0.00 ± 0.32 | 4.34 ± 6.09 | -1.31 ± 3.12 | -1.71 ± 0.17 | G | D |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| GF | Common Fiscal (*Lanius collaris*) | 2.41 ± 0.09 | -0.65 ± 0.28 | -0.31 ± 0.18 | 0.17 ± 0.17 | 2.21 ± 2.27 | 3.42 ± 1.34 | -1.15 ± 0.08 | H | D |
| GF | Crowned Lapwing (*Vanellus coronatus*) | 1.75 ± 0.15 | -1.00 ± 0.30 | 0.19 ± 0.19 | 0.30 ± 0.18 | 1.34 ± 2.32 | 3.53 ± 1.47 | -0.33 ± 0.08 | H | G |
| GF | Familiar Chat (*Cercomela familiaris*) | 0.86 ± 0.24 | 1.38 ± 0.30 | -1.63 ± 0.56 | -3.18 ± 0.59 | 5.88 ± 2.89 | -0.56 ± 2.19 | -0.33 ± 0.20 | E | E |
| GF | Fiscal Flycatcher (*Sigelus silens*) | 1.85 ± 0.14 | -0.62 ± 0.39 | 0.18 ± 0.26 | -2.05 ± 0.30 | 2.72 ± 2.84 | 3.86 ± 2.09 | -0.96 ± 0.12 | D | H |
| GF | Greater Kestrel (*Falco rupicoloides*) | 0.24 ± 0.31 | -1.77 ± 1.17 | -3.65 ± 0.93 | 0.25 ± 0.59 | 12.60 ± 7.88 | -3.62 ± 6.23 | -0.67 ± 0.27 | G | D |
| GF | Groundscraper Thrush (*Psophocichla litsipsirupa*) | -0.53 ± 0.23 | -0.12 ± 0.30 | -0.26 ± 0.43 | -1.39 ± 0.44 | -3.28 ± 3.10 | 4.28 ± 1.71 | 2.05 ± 0.19 | D | C |
| GF | Hadeda Ibis (*Bostrychia hagedash*) | 1.77 ± 0.11 | -0.18 ± 0.27 | 1.46 ± 0.17 | 0.24 ± 0.18 | -1.47 ± 2.20 | 1.34 ± 1.45 | -0.70 ± 0.08 | H | G |
| GF | Kurrichane Thrush (*Turdus libonyana*) | -1.29 ± 0.79 | 0.75 ± 0.90 | 0.18 ± 1.32 | -1.47 ± 1.72 | -41.18 ± 29.89 | -0.85 ± 7.58 | 0.75 ± 0.59 | E | B |
| GF | Kurrichane Thrush (*Turdus libonyanus*) | -0.54 ± 0.23 | -0.23 ± 0.32 | 0.49 ± 0.40 | -1.89 ± 0.49 | -0.34 ± 2.81 | 8.11 ± 1.73 | 1.77 ± 0.19 | D | G |
| GF | Lazy Cisticola (*Cisticola aberrans*) | -0.60 ± 0.44 | 0.83 ± 0.52 | -0.46 ± 0.88 | -3.41 ± 1.14 | 5.60 ± 4.44 | 9.94 ± 2.89 | 0.40 ± 0.35 | E | E |
| GF | Lilac-breasted Roller (*Coracias caudatus*) | -2.54 ± 0.41 | -0.63 ± 0.34 | -2.49 ± 0.70 | -2.00 ± 0.52 | -0.22 ± 3.90 | -1.85 ± 2.46 | 4.29 ± 0.40 | C | C |
| GF | Long-billed Pipit (*Anthus similis*) | 0.60 ± 0.37 | 0.19 ± 0.62 | -1.60 ± 0.84 | -4.09 ± 1.01 | 5.56 ± 5.43 | 9.87 ± 3.47 | -0.76 ± 0.31 | E | E |
| GF | Magpie Shrike (*Corvinella melanoleuca*) | -7.98 ± 1.33 | -1.24 ± 0.43 | -1.71 ± 0.60 | -0.41 ± 0.41 | 0.32 ± 4.05 | -1.10 ± 2.57 | 9.37 ± 1.34 | C | C |
| GF | Marico Flycatcher (*Bradornis mariquensis*) | -4.72 ± 0.60 | 0.79 ± 0.29 | -0.28 ± 0.57 | 0.35 ± 0.46 | -1.43 ± 3.25 | -13.86 ± 3.21 | 5.66 ± 0.60 | B | E |
| GF | Mocking Cliff-Chat (*Thamnolaea cinnamomeiventris*) | 0.21 ± 0.35 | -0.05 ± 0.48 | -2.54 ± 0.93 | -4.62 ± 0.93 | 7.56 ± 4.33 | 8.23 ± 2.88 | 0.25 ± 0.29 | D | D |
| GF | Mountain Wheatear (*Oenanthe monticola*) | 1.05 ± 0.22 | 0.33 ± 0.63 | -0.44 ± 0.48 | -2.51 ± 0.53 | -8.27 ± 7.28 | 9.03 ± 3.03 | -1.94 ± 0.23 | E | F |
| GF | Neddicky Neddicky (*Cisticola fulvicapilla*) | 1.52 ± 0.13 | -0.62 ± 0.26 | -1.80 ± 0.31 | -1.41 ± 0.25 | -1.23 ± 2.74 | 2.59 ± 1.46 | 0.44 ± 0.10 | D | C |
| GF | Pearl-spotted Owlet (*Glaucidium perlatum*) | -3.64 ± 0.72 | -1.13 ± 0.51 | -4.72 ± 1.31 | -1.68 ± 0.72 | 12.29 ± 4.61 | 4.36 ± 2.85 | 4.83 ± 0.70 | D | D |
| GF | Pied Crow (*Corvus albus*) | 1.20 ± 0.14 | -0.23 ± 0.26 | 0.93 ± 0.22 | -1.50 ± 0.26 | -1.32 ± 2.23 | -2.31 ± 1.74 | 0.39 ± 0.10 | C | G |
| GF | Pied Starling (*Spreo bicolor*) | 1.22 ± 0.18 | -1.37 ± 0.87 | -1.07 ± 0.41 | -0.79 ± 0.37 | 13.92 ± 4.89 | 4.80 ± 3.82 | -2.09 ± 0.20 | D | D |
| GF | Plain-backed Pipit (*Anthus leucophrys*) | 0.67 ± 0.43 | 1.44 ± 0.56 | -2.91 ± 1.04 | -2.81 ± 1.01 | 10.71 ± 4.80 | -2.86 ± 4.40 | -1.12 ± 0.35 | E | E |
| GF | Red-throated Wryneck (*Jynx ruficollis*) | 1.69 ± 0.20 | -0.88 ± 0.70 | -1.57 ± 0.44 | -2.17 ± 0.44 | 10.52 ± 4.36 | 4.87 ± 3.45 | -1.86 ± 0.19 | D | D |
| GF | Rufous-naped Lark (*Mirafra africana*) | 2.19 ± 0.13 | 0.05 ± 0.23 | -2.57 ± 0.31 | -1.30 ± 0.24 | 4.83 ± 2.29 | -2.39 ± 1.52 | -0.31 ± 0.10 | F | E |
| GF | Secretarybird Secretarybird (*Sagittarius serpentarius*) | -0.04 ± 0.41 | 0.72 ± 0.89 | -12.90 ± 3.48 | 0.54 ± 0.71 | 12.11 ± 17.37 | -5.91 ± 5.88 | -1.45 ± 0.39 | B | E |
| GF | Sentinel Rock-Thrush (*Monticola explorator*) | -1.18 ± 0.84 | 2.06 ± 1.38 | -3.77 ± 3.00 | -4.00 ± 2.32 | 0.55 ± 17.62 | 8.83 ± 6.96 | -2.02 ± 0.87 | E | E |
| GF | Southern Black Flycatcher (*Melaenornis pammelaina*) | -0.70 ± 0.30 | -0.03 ± 0.32 | -2.76 ± 0.79 | -2.64 ± 0.61 | 2.88 ± 3.71 | 5.87 ± 1.94 | 2.16 ± 0.26 | D | D |
| GF | Southern White-crowned Shrike (*Eurocephalus anguitimens*) | -9.55 ± 4.65 | -1.42 ± 1.18 | -1.96 ± 1.94 | -2.38 ± 1.65 | 1.22 ± 10.39 | 6.86 ± 6.81 | 9.46 ± 4.67 | D | C |
| GF | Southern Yellow-billed Hornbill (*Tockus leucomelas*) | -7.80 ± 1.73 | -0.75 ± 0.39 | -3.76 ± 0.93 | -2.70 ± 0.61 | 6.42 ± 3.98 | -1.52 ± 2.93 | 9.16 ± 1.74 | C | D |
| GF | Spike-heeled Lark (*Chersomanes albofasciata*) | 1.09 ± 0.24 | -1.69 ± 1.18 | -3.46 ± 0.77 | -1.71 ± 0.53 | 15.82 ± 7.74 | 11.20 ± 4.97 | -2.43 ± 0.28 | D | D |
| GF | Spotted Eagle-Owl (*Bubo africanus*) | 0.13 ± 0.33 | 0.07 ± 0.72 | 1.41 ± 0.54 | -1.98 ± 0.78 | -10.86 ± 7.45 | 9.38 ± 3.76 | -0.59 ± 0.27 | E | B |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| GF | Spotted Thick-knee (*Burhinus capensis*) | 0.94 ± 0.17 | 0.10 ± 0.39 | 2.22 ± 0.23 | -0.46 ± 0.32 | -0.37 ± 2.80 | 1.32 ± 2.17 | -0.57 ± 0.12 | E | B |
| GF | Striped Kingfisher (*Halcyon chelicuti*) | -2.61 ± 0.84 | -0.94 ± 0.72 | -4.57 ± 2.17 | -4.35 ± 1.44 | 0.05 ± 10.48 | -2.21 ± 6.62 | 3.15 ± 0.80 | C | C |
| GF | Striped Pipit (*Anthus lineiventris*) | -0.84 ± 0.52 | 0.00 ± 0.67 | -0.79 ± 1.13 | -4.90 ± 1.43 | -1.77 ± 7.29 | 11.48 ± 3.88 | 0.64 ± 0.44 | D | C |
| GF | Wailing Cisticola (*Cisticola lais*) | 0.57 ± 0.26 | 0.15 ± 0.61 | -1.89 ± 0.71 | -2.15 ± 0.61 | -0.08 ± 6.63 | 7.69 ± 3.10 | -1.14 ± 0.24 | E | E |
| GF | Wattled Starling (*Creatophora cinerea*) | 0.85 ± 0.19 | -2.32 ± 0.86 | -0.35 ± 0.38 | 0.12 ± 0.36 | -1.34 ± 6.27 | 2.92 ± 3.93 | -0.50 ± 0.15 | G | C |
| GF | White Stork (*Ciconia ciconia*) | -0.50 ± 0.32 | 0.34 ± 0.67 | -0.15 ± 0.61 | 1.06 ± 0.61 | 0.53 ± 5.96 | 2.55 ± 3.30 | 0.15 ± 0.24 | A | E |
| GF | White-browed Scrub-Robin (*Cercotrichas leucophrys*) | -2.98 ± 0.37 | -0.12 ± 0.26 | -1.55 ± 0.51 | -0.44 ± 0.38 | 0.22 ± 2.87 | -0.40 ± 1.64 | 4.85 ± 0.36 | C | C |
| GF | White-throated Robin-Chat (*Cossypha humeralis*) | -3.97 ± 0.58 | 0.24 ± 0.34 | -0.48 ± 0.59 | -0.32 ± 0.54 | -1.05 ± 3.52 | 0.55 ± 2.06 | 5.19 ± 0.57 | E | F |
| Hawker | African Palm-Swift (*Cypsiurus parvus*) | 0.97 ± 0.13 | -0.40 ± 0.30 | 1.91 ± 0.20 | -0.64 ± 0.26 | 0.43 ± 2.17 | 4.01 ± 1.59 | 0.18 ± 0.10 | D | G |
| Hawker | Alpine Swift (*Tachymarptis melba*) | -1.12 ± 0.77 | 1.20 ± 0.77 | -1.51 ± 1.50 | -1.41 ± 1.68 | 3.94 ± 8.28 | 3.46 ± 4.94 | 0.81 ± 0.56 | E | E |
| Hawker | Common House-Martin (*Delichon urbicum*) | 0.42 ± 0.29 | -0.42 ± 0.54 | -1.20 ± 0.57 | 0.54 ± 0.51 | -12.53 ± 7.78 | 3.20 ± 2.87 | 0.42 ± 0.20 | H | C |
| Hawker | Fiery-necked Nightjar (*Caprimulgus pectoralis*) | -1.61 ± 0.57 | 0.28 ± 0.50 | -0.14 ± 0.95 | -3.43 ± 1.23 | -15.18 ± 7.57 | 4.70 ± 3.65 | 2.56 ± 0.51 | E | F |
| Hawker | Fork-tailed Drongo (*Dicrurus adsimilis*) | -0.81 ± 0.19 | -0.23 ± 0.20 | -1.21 ± 0.36 | -0.85 ± 0.30 | 1.98 ± 2.02 | 1.82 ± 1.25 | 3.18 ± 0.16 | D | D |
| Hawker | Lesser Striped Swallow (*Hirundo abyssinica*) | -0.17 ± 0.19 | 0.20 ± 0.23 | 0.40 ± 0.31 | -0.78 ± 0.34 | -7.71 ± 2.69 | 2.61 ± 1.33 | 2.11 ± 0.15 | E | B |
| Hawker | Little Bee-eater (*Merops pusillus*) | -0.61 ± 0.48 | -0.09 ± 0.66 | -2.17 ± 1.07 | -0.84 ± 1.02 | 4.11 ± 5.96 | 3.70 ± 3.88 | 0.91 ± 0.36 | D | D |
| Hawker | Little Swift (*Apus affinis*) | 0.87 ± 0.15 | -0.14 ± 0.33 | 0.86 ± 0.25 | 0.10 ± 0.27 | -4.13 ± 2.98 | -2.06 ± 1.97 | 0.15 ± 0.11 | G | G |
| Hawker | Pearl-breasted Swallow (*Hirundo dimidiata*) | -0.44 ± 0.29 | 0.42 ± 0.30 | -1.53 ± 0.60 | -1.37 ± 0.54 | -0.38 ± 3.33 | -3.26 ± 2.30 | 1.88 ± 0.23 | F | E |
| Hawker | Rock Martin (*Hirundo fuligula*) | 0.05 ± 0.22 | 0.63 ± 0.44 | 3.09 ± 0.31 | -0.87 ± 0.50 | -1.38 ± 3.23 | 6.89 ± 2.20 | -0.26 ± 0.17 | E | B |
| Hawker | White-fronted Bee-eater (*Merops bullockoides*) | -0.40 ± 0.21 | -1.21 ± 0.45 | -0.19 ± 0.44 | -0.87 ± 0.43 | 3.00 ± 3.32 | 7.56 ± 2.17 | 1.46 ± 0.17 | D | D |
| Predator | African Grass-Owl (*Tyto capensis*) | -0.68 ± 0.82 | 0.30 ± 3.02 | -2.96 ± 2.12 | -1.62 ± 1.87 | 8.91 ± 23.59 | 3.40 ± 15.14 | -3.09 ± 1.09 | E | E |
| Predator | African Harrier-Hawk (*Polyboroides typus*) | -1.16 ± 0.47 | 1.43 ± 0.64 | 2.63 ± 0.62 | 0.09 ± 1.03 | -0.17 ± 5.00 | 6.08 ± 3.30 | 0.45 ± 0.34 | A | A |
| Predator | African Hawk-Eagle (*Aquila spilogaster*) | -1.91 ± 0.89 | 0.30 ± 0.85 | -2.66 ± 2.13 | -3.07 ± 2.07 | 2.16 ± 9.07 | 5.55 ± 5.73 | 1.76 ± 0.76 | E | E |
| Predator | Barn Owl (*Tyto alba*) | 0.10 ± 0.33 | 0.90 ± 0.45 | -0.92 ± 0.68 | -0.97 ± 0.70 | -15.15 ± 8.53 | -6.80 ± 4.23 | 0.20 ± 0.26 | F | F |
| Predator | Black Sparrowhawk (*Accipiter melanoleucus*) | -0.26 ± 0.40 | -0.60 ± 1.14 | 2.36 ± 0.56 | -0.80 ± 0.89 | 0.44 ± 7.34 | 9.23 ± 5.36 | -0.86 ± 0.32 | D | G |
| Predator | Black-chested Snake-Eagle (*Circaetus pectoralis*) | 0.19 ± 0.31 | -0.17 ± 0.44 | -4.15 ± 0.94 | -0.98 ± 0.58 | 3.06 ± 5.06 | 2.89 ± 2.55 | 0.84 ± 0.23 | D | D |
| Predator | Black-shouldered Kite (*Elanus caeruleus*) | 1.37 ± 0.15 | -0.10 ± 0.29 | -0.75 ± 0.25 | 1.42 ± 0.20 | 2.70 ± 2.64 | -0.37 ± 1.49 | -0.36 ± 0.09 | G | D |
| Predator | Brown Snake-Eagle (*Circaetus cinereus*) | -0.90 ± 0.55 | -0.69 ± 0.72 | -9.00 ± 2.89 | -1.73 ± 1.10 | 16.19 ± 8.16 | 7.56 ± 3.78 | 1.58 ± 0.45 | D | D |
| Predator | Gabar Goshawk (*Melierax gabar*) | -0.58 ± 0.40 | 0.14 ± 0.44 | -2.31 ± 0.86 | -1.13 ± 0.76 | 0.82 ± 4.76 | -4.98 ± 3.74 | 1.77 ± 0.32 | F | E |
| Predator | Hamerkop Hamerkop (*Scopus umbretta*) | 0.65 ± 0.21 | -0.87 ± 0.43 | -0.88 ± 0.41 | -0.34 ± 0.38 | -6.02 ± 4.40 | 3.10 ± 2.25 | 0.85 ± 0.15 | D | C |
| Predator | Jackal Buzzard (*Buteo rufofuscus*) | 0.31 ± 0.48 | -0.12 ± 1.16 | -6.01 ± 1.93 | -2.40 ± 1.13 | 28.58 ± 7.06 | 4.00 ± 6.33 | -1.66 ± 0.43 | D | D |

| Guild | Species | Abundance model estimates (log scale) | | | | | | | Agric. interaction-case | Urban interaction-case |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept ($\hat{\beta}_0$) | PA ($\hat{\beta}_1$) | Urban ($\hat{\beta}_2$) | Agric. ($\hat{\beta}_3$) | PA × Urban ($\hat{\beta}_4$) | PA × Agric. ($\hat{\beta}_5$) | Savanna ($\hat{\beta}_6$) | | |
| Predator | Lanner Falcon (*Falco biarmicus*) | 0.64 ± 0.46 | -1.24 ± 1.00 | -3.78 ± 1.10 | -0.96 ± 0.86 | 12.18 ± 7.05 | 5.48 ± 4.95 | -0.42 ± 0.33 | D | D |
| Predator | Little Sparrowhawk (*Accipiter minullus*) | 0.60 ± 0.37 | -0.57 ± 0.66 | 1.22 ± 0.54 | -4.38 ± 0.98 | -11.19 ± 6.78 | 10.55 ± 3.86 | -0.07 ± 0.28 | D | G |
| Predator | Marsh Owl (*Asio* capensis) | 0.38 ± 0.29 | -0.79 ± 1.02 | -2.33 ± 0.68 | 1.38 ± 0.53 | 9.98 ± 7.34 | 1.48 ± 4.50 | -1.28 ± 0.26 | G | D |
| Predator | Martial Eagle (*Polemaetus bellicosus*) | 2.15 ± 1.15 | -0.30 ± 1.06 | -12.79 ± 7.63 | -6.31 ± 3.14 | -6.85 ± 38.78 | -46.92 ± 38.01 | 0.21 ± 0.99 | C | C |
| Predator | Rock Kestrel (*Falco rupicolus*) | 0.16 ± 0.36 | 1.35 ± 0.54 | -4.11 ± 1.17 | -0.10 ± 0.68 | -5.40 ± 9.64 | 2.80 ± 2.99 | -0.96 ± 0.30 | E | F |
| Predator | Shikra Shikra (*Accipiter badius*) | -1.08 ± 0.92 | -0.96 ± 0.84 | -1.17 ± 1.22 | -2.45 ± 1.46 | -21.60 ± 15.15 | 1.46 ± 6.61 | 2.77 ± 0.65 | C | C |
| Predator | Tawny Eagle (*Aquila rapax*) | -5.47 ± 3.51 | 0.48 ± 1.54 | -2.61 ± 6.05 | -4.25 ± 4.89 | -32.55 ± 46.74 | 9.41 ± 11.28 | 4.24 ± 3.37 | E | F |
| Predator | Verreaux's Eagle (*Aquila verreauxii*) | -2.13 ± 0.50 | 1.08 ± 0.77 | 3.74 ± 0.68 | -1.61 ± 1.29 | -0.44 ± 5.26 | 9.27 ± 3.89 | 0.58 ± 0.37 | E | A |
| Vegivore | Blue Crane (*Anthropoides paradiseus*) | -1.48 ± 0.61 | 1.00 ± 1.73 | -6.63 ± 3.28 | 0.32 ± 1.18 | 2.47 ± 28.46 | -3.26 ± 10.21 | -1.92 ± 0.69 | B | E |
| Vegivore | Cape Bunting (*Emberiza capensis*) | 0.03 ± 0.41 | 0.64 ± 0.66 | -3.26 ± 1.35 | -4.25 ± 1.11 | 3.44 ± 7.30 | 12.53 ± 3.25 | -0.91 ± 0.36 | E | E |
| Vegivore | Cape Weaver (*Ploceus capensis*) | 0.27 ± 0.27 | 0.18 ± 0.48 | 0.29 ± 0.49 | -1.76 ± 0.62 | 3.96 ± 3.84 | 5.51 ± 2.66 | -0.19 ± 0.22 | E | A |
| Vegivore | Coqui Francolin (*Peliperdix coqui*) | 0.43 ± 0.30 | -0.37 ± 0.38 | -4.13 ± 0.96 | -3.68 ± 0.67 | -3.32 ± 5.72 | 2.26 ± 2.80 | 1.06 ± 0.24 | D | C |
| Vegivore | Crested Francolin (*Dendroperdix sephaena*) | -2.96 ± 0.42 | -0.25 ± 0.27 | -3.36 ± 0.71 | -1.42 ± 0.43 | 1.43 ± 3.41 | 1.22 ± 1.72 | 4.78 ± 0.41 | D | D |
| Vegivore | Egyptian Goose (*Alopochen aegyptiaca*) | 1.34 ± 0.12 | 0.93 ± 0.26 | 0.81 ± 0.21 | 0.86 ± 0.20 | -1.29 ± 2.50 | -2.11 ± 1.53 | -0.95 ± 0.09 | B | A |
| Vegivore | Grey Go-away-bird (*Corythaixoides concolor*) | -0.07 ± 0.15 | 0.39 ± 0.24 | 2.25 ± 0.21 | -1.54 ± 0.31 | -7.40 ± 2.29 | 2.71 ± 1.36 | 1.58 ± 0.11 | E | B |
| Vegivore | Helmeted Guineafowl (*Numida meleagris*) | 1.65 ± 0.12 | 0.16 ± 0.24 | -0.71 ± 0.23 | 0.07 ± 0.20 | 1.67 ± 2.25 | -0.21 ± 1.39 | -0.38 ± 0.08 | A | E |
| Vegivore | Natal Spurfowl (*Pternistis natalensis*) | -1.00 ± 0.28 | 0.63 ± 0.27 | -2.94 ± 0.75 | -2.10 ± 0.52 | 5.41 ± 2.98 | 0.32 ± 1.81 | 2.35 ± 0.25 | E | E |
| Vegivore | Orange River Francolin (*Scleroptila levaillantoides*) | 1.44 ± 0.21 | -7.94 ± 2.68 | -4.50 ± 0.70 | -0.51 ± 0.40 | 39.31 ± 11.37 | 5.69 ± 8.21 | -2.78 ± 0.27 | C | D |
| Vegivore | Red-winged Francolin (*Scleroptila levaillantii*) | 0.11 ± 0.55 | 0.22 ± 1.05 | -3.58 ± 1.67 | -4.57 ± 1.56 | 12.73 ± 8.87 | 11.59 ± 5.37 | -1.57 ± 0.48 | E | E |
| Vegivore | Shelley's Francolin (*Scleroptila shelleyi*) | -3.54 ± 1.18 | 0.04 ± 1.85 | -0.05 ± 2.17 | -0.27 ± 2.50 | 10.56 ± 11.14 | 1.80 ± 10.52 | 1.16 ± 0.93 | E | E |
| Vegivore | Southern Masked-Weaver (*Ploceus velatus*) | 2.24 ± 0.13 | -0.56 ± 0.22 | 0.58 ± 0.16 | 0.28 ± 0.17 | -1.84 ± 1.91 | 1.80 ± 1.16 | -0.27 ± 0.07 | H | G |
| Vegivore | Speckled Mousebird (*Colius striatus*) | 0.90 ± 0.14 | -0.46 ± 0.31 | 2.53 ± 0.19 | -0.75 ± 0.26 | -5.70 ± 2.46 | 8.03 ± 1.48 | 0.27 ± 0.10 | D | G |
| Vegivore | Spur-winged Goose (*Plectropterus gambensis*) | 0.87 ± 0.15 | 0.91 ± 0.36 | -1.33 ± 0.37 | 1.52 ± 0.27 | 3.44 ± 3.63 | -1.78 ± 1.95 | -1.01 ± 0.13 | A | E |
| Vegivore | Streaky-headed Seedeater (*Crithagra gularis*) | 0.84 ± 0.18 | -0.30 ± 0.40 | 1.02 ± 0.31 | -2.26 ± 0.41 | -0.78 ± 3.16 | 2.56 ± 2.43 | -0.08 ± 0.14 | D | G |
| Vegivore | Swainson's Spurfowl (*Pternistis swainsonii*) | 1.85 ± 0.12 | -0.34 ± 0.25 | -3.00 ± 0.30 | 0.87 ± 0.18 | 3.17 ± 2.64 | -0.41 ± 1.30 | -0.14 ± 0.08 | G | D |
| Vegivore | Village Weaver (*Ploceus cucullatus*) | -1.23 ± 0.30 | -0.64 ± 0.52 | 1.00 ± 0.47 | 0.29 ± 0.58 | -1.23 ± 4.20 | 0.78 ± 2.90 | 1.98 ± 0.24 | G | G |
| Vegivore | White-bellied Korhaan (*Eupodotis senegalensis*) | -2.30 ± 0.84 | -2.02 ± 2.32 | -2.03 ± 2.34 | -2.67 ± 1.89 | -10.01 ± 30.59 | 7.63 ± 11.77 | 0.72 ± 0.70 | D | C |

**Table A3.4.** Percentage of total species per guild for which the proportion-abundance relationship increased or decreased, based on the definitions presented in Figure 3.1, with increasing proportions of either urban (A) or agricultural (B) area within the same pentad. Based on Figure 3.1, species defined as increasing their proportion-abundance relationship fell into interaction cases A, B, C, or D. Species defined as decreasing their proportion-abundance relationship fell into interaction cases E, F, G, or H. Estimates of abundances taken from the Royle-Nichols model of abundance, fitted for each species separately. Figures in parentheses refer to number of species within guild.

| Guild | A: Urban | | B: Agriculture | |
|---|---|---|---|---|
| | Increased (%) | Decreased (%) | Increased (%) | Decreased (%) |
| Frugivores (9) | 44 | 56 | 56 | 44 |
| Gleaners (30) | 70 | 30 | 70 | 30 |
| Granivores (48) | 60 | 40 | 27 | 73 |
| Ground-feeders (62) | 60 | 40 | 53 | 47 |
| Hawkers (11) | 55 | 45 | 36 | 64 |
| Predators (19) | 58 | 42 | 53 | 47 |
| Vegivores (19) | 42 | 58 | 53 | 47 |
| Overall | 58 | 42 | 49 | 51 |

Chapter 4

# The dynamic benefits of protected areas: occupancy and colonization probabilities of common bird species increase in areas with higher proportions of protected areas

Brown Snake Eagle (*Circaetus cinereus*) in the Kruger National Park, South Africa. Photograph by Allan Duckworth.

## 4.1 ABSTRACT

**AIM**: Protected areas are a key component of global conservation efforts, and it is critical to assess how effectively they conserve biodiversity. Most methods that assess protected areas' conservation effectiveness are static, whilst species' range dynamics are spatially and temporally dynamic. I use dynamic methods and test the effect of protected areas on the local occupancy, colonization, and extinction rates of 186 common, resident bird species. If protected areas were ecologically beneficial to avian biodiversity, I expect landscapes with a higher proportion of protected areas to be positively related to occupancy and colonization, and negatively related to extinction.

**LOCATION**: Greater Gauteng region of South Africa between 2008-2014

**METHODS**: I analysed bird detection / non-detection data over regular grid cells. For each species, I used dynamic occupancy models to estimate colonization and extinction probability as a function of the proportion of protected area per grid cell. Occupancy at year 2008 (initial occupancy at the first year of the study) was estimated as a function of the proportion of protected area, land-use type, and vegetation per grid cell. I also estimated equilibrium occupancy, which is the expected occupancy probability given the species is at (or heading towards) an equilibrium level of occupancy and is calculated using estimated colonization and extinction probabilities. I assigned species into guilds, based on the type of food a species preferentially ate and its mode of foraging. These included: frugivores, gleaners, granivores, ground-feeders, hawkers, predators, and vegivores. I used a Bayesian hierarchical analysis to estimate the average colonization and extinction estimates per guild.

**RESULTS**: As the proportion of protected area per grid cell increased, average colonization probability increased for all guilds, whilst average extinction probability increased for granivores and ground-feeders, and was unrelated in the remaining guilds. The average equilibrium occupancy was significantly higher in grid cells with full protection compared to cells of no protection, for all guilds except granivores. In comparison, average initial occupancy (at 2008), which was derived using static methods, was only slightly positively affected by the proportion of protected areas per pentad for all guilds. Dynamic occupancy models revealed the positive relationship between protected areas and occupancy probability, which would have otherwise gone undetected by static analyses.

**MAIN CONCLUSION**: In general, protected areas provided conservation benefit for bird species across the study area. The results highlight the power of dynamic methods for analysing dynamic processes.

**KEY WORDS:** Protected areas, common species, dynamic occupancy models, landscape ecology, atlas data.

## 4.1 INTRODUCTION

Protected areas are one of the key tools used to conserve biodiversity against the global threats of land-use and climate change (James et al., 1999; IUCN, 2000; Parrish et al., 2003; Naughton-Treves et al., 2005; Gaston et al., 2008). Currently, 12% of the earth's terrestrial surface is covered by protected areas, with a goal to reach 17% by the year 2020, as one of the Aichi targets (target 11, UNEP, 2011). The desired increase in terrestrial protected areas coverage is testament to their world-wide success (Hockings et al., 2006; Butchart et al., 2010; Geldmann et al., 2013). Many species occur in higher abundance inside protected areas, and biodiversity is generally higher in protected areas than outside (Walpole & Leader-Williams, 2002; Rodrigues et al., 2004; Owen-Smith et al., 2006; Dalerum et al., 2008; Watson et al., 2011; Geldmann et al., 2013). For example, in Chapter 2 of this thesis, I show that certain species are more abundant in landscapes with higher proportions of protected areas than others. Moreover, some species are only found in protected areas (Simberloff, 1998; Sergio et al., 2006). These examples illustrate the conservation benefit that protected areas are able to provide.

Given the heavy reliance of biological conservation on protected areas, it is critical to quantify just how effective protected areas are at conserving biodiversity. Most metrics used to assess protected areas' effectiveness are based on static analyses of protected areas (i.e., those that analyse "snapshots" of species' distributions and relate this to the environmental conditions at a single point in time), whilst species ranges are dynamic (Thomas et al., 2012). However, a general question asked about protected areas is 'How effective are protected areas' (Parrish et al., 2003), which further begs the questions 'do protected areas slow the rate of extinction?' and 'Do they facilitate colonization of new areas?' It is difficult to glean the answers to these questions from static analyses because protected areas may be placed in areas that already had high biodiversity, or, areas in which species naturally occurred (Gaston et al., 2006; Gaston & Fuller, 2008). Consequentially, inferences based on static analyses may potentially be inaccurate, if indeed a species' distribution is not in equilibrium with environmental conditions, which seldom is the case in reality (Yackulic et al., 2015). A more powerful test of the effectiveness of protected areas for biodiversity conservation is to examine the processes of species' range dynamics, for example the vital rates colonization and extinction.

Colonization is defined as the probability of a site unoccupied site at time $t$ to become occupied by time $t + 1$, and extinction is the probability of a site occupied at time $t$ to become unoccupied by time $t + 1$ (MacKenzie et al., 2003; Royle & Kéry, 2007). Occupancy, the probability that a species occupies an area at a given time, is therefore affected by changes in the dynamic components extinction and colonization. Examining dynamic components in relation to protected areas provides an understanding of how protected areas affect species throughout the landscape, and the nature of the benefit provided by protected areas to species. For example, Hiley et al. (2013) showed that protected areas act as establishment centres for birds that are newly colonizing an area; landscapes with more protected areas were more likely to be colonized. However, protected areas can still play a critical role in conservation long after a species has colonized the landscape; Gillingham et al. (2015a) found the abundance of birds in protected areas was higher than in the surrounding areas long after the landscape had been colonized. The successful colonization of the landscape by species appears to depend critically on their ability to colonize protected areas, and persist therein. This has considerable implications for birds shifting their ranges in response to climate and land-use change (Jetz et al., 2007; Peterson et al., 2011; Hannah et al., 2013). Quantifying the rates of colonization and extinction in relation to protected areas can provide useful insight into the ecological effectiveness, in terms of species conservation, of protected areas within landscapes.

Estimates of colonization and extinction for sites can be inferred from detection / non-detection data over multiple site visits. Observed extinction and colonization can be related to site-level characteristics (such as habitat or land-cover), for example with logistic regressions or similar binary response models (MacKenzie et al., 2006; Elith et al., 2009; Kéry, 2011). A notable caveat of these models is that they assume all species are observed perfectly. This is not the case in reality, as few species are ever detected perfectly in all the habitats they occupy (MacKenzie et al., 2002). This discrepancy between "real world" situations and model assumptions can lead to models with biased parameter estimates (Boulinier et al., 1998; Nichols et al., 1998). An alternate modelling framework, dynamic occupancy models, accounts for imperfect detection. This framework hierarchically models the detection and dynamic components (colonization and extinction) separately (MacKenzie et al., 2002). By accounting for imperfect detection, colonization and extinction can be estimated without bias (assuming the other model assumptions are met, Kéry, 2010; Kéry & Schaub, 2011; Maggini et al., 2011).

The key focus of this study was to examine how protected areas affect the occupancy, colonization, and extinction of common bird species within a heterogeneous area of South Africa. Birds are good biological indicators of ecosystem health (Lawton et al., 1998; Barlow et al., 2007). They are wide-spread and well-studied, making them a good class of organism with which to examine the effectiveness of protected areas (Furness & Greenwood, 1993). I consider common birds because ecosystem patterns and function, such as primary productivity and nutrient cycling, can be driven by common species, rather than rare ones (Lennon et al., 2011; Winfree et al., 2015). Furthermore, declines in abundance and species richness of common species can affect ecosystems negatively, and can potentially indicate severe declines in ecosystem health (Gaston, 2011). Monitoring the effect of protected areas on population dynamics of common bird species can potentially provide insight into the ecological effectiveness of protected areas.

I focused on two different types of occupancy; initial occupancy, and equilibrium occupancy. Initial occupancy is the average occupancy over the first period of the study. Equilibrium occupancy is calculated using colonization and extinction estimates, and is based on the concept that when occupancy is constant over time, extinction is balanced out by colonization. Therefore, equilibrium occupancy is the occupancy that would eventually be reached by the system, given extinction and colonization are constant over time (MacKenzie et al., 2006). Given the above considerations, I set out the following study questions:

a) How do protected areas affect the colonization, extinction, and initial occupancy rates of common bird species?

b) How do protected areas affect equilibrium occupancy rates?

As I do in Chapters 2 and 3, I use guilds as a stratifying group. I expect the guilds that were found to have a higher average abundances within protected areas in Chapter 2 (frugivores, ground-feeders, hawkers, predators and vegivores) will have a higher initial occupancy, equilibrium occupancy, and colonization probabilities in protected areas than outside protected areas. These guilds are also expected to have a lower extinction probability within protected areas.

## 4.3 METHODS

### *4.3.1 Study area and land-use types*

I selected a square area within the greater Gauteng Province in South Africa from 25 to 27°S, and from 27 to 29°E (Fig. 1.2B), which contained a combination of protected areas and heavily modified land uses. The study area was heterogeneous in its land use, and primarily consisted of seven land-use types, namely mines (making up 0.88% of the study area), plantations (0.32%), waterbodies (2.80%), degraded areas (2.54%), protected areas (6.40%), urban (8.13%), agriculture (28.71%), and natural land (50.30%), as taken from a national project mapping land-use types across South Africa (South African National Biodiversity Institute (SANBI), 2009). Natural, urban, agricultural, and protected areas land types made up 92% of the area, and were therefore exclusively examined in this study. Vegetation is a major driver of avian biodiversity in the study area (Hockey et al., 2005), which was dominated by two types: savanna in the northern half, and grasslands in the southern half. Together, savanna and grassland accounted for 99% of the vegetation types in the study area.

In this chapter, I used the same land-use proportion data in my modelling as I did in Chapter 3. Given that the data were proportions, there existed the risk of multicollinearity amongst the land-use proportion data, which were used as covariates in the models (see section 4.3.3.1 for the model equations). This is the same potential collinearity problem I encountered in Chapter 3. I refer the reader to section 3.3.3 of this thesis, in which I give a detailed description of how I avoided multicollinearity between the model covariates, as I give only a brief description here. Essentially, because all model covariates sum to nearly 100% of each pentad, including all of them as covariates will confound the model, leading to biased coefficient estimates. The proportion of any one covariate can be calculated by subtracting the sum of the remaining three from 100%. Thus, only three of the four land-use types need to be specified explicitly as covariates. I chose to omit natural land as a covariate from the model (specifically, in equation 3 described in section 4.3.3.1), to retain consistency with the methods presented in Chapter 3, and because my ecological hypotheses throughout this thesis relate to land-use types agricultural, urban, and protected area. Because natural land occupied 43.24% of the study area, enough natural land was present within each pentad such that the remaining land-use types don't sum to 100% and confound the model (Fig. A3.1, Appendix 3). I tested for collinearity amongst the remaining three land-use types using Pearson's correlation coefficient, and found no evidence of multicollinearity (Table A3.1, Appendix 3).

### *4.3.2 Species detection/non-detection data*

Species detection data were extracted from a national bird survey project, the second Southern African Bird Atlas Project (SABAP 2). This is a citizen science project, which began in 2007 (Harrison et al., 2008) and is presently on-going. Registered volunteers collect and submit checklists of bird species observed within a regular, pre-defined area called a pentad, which is 5' x 5' in dimension (unit is in arcminutes, approximately $61km^2$). For each checklist submitted, volunteers must have birded intensively for at least two hours during a period of up to but not more than five days. Volunteers may submit multiple checklists. Only species' presences were recorded, not a count of the birds observed. Irregular (or out of range) sightings were checked by a vetting committee. Volunteers were asked to visit all available habitats within a pentad (Harebottle et al., 2007; Underhill, 2016). As defined by Hockey et al. (2005), I considered only common, resident species within the region, and omitted any nomadic, alien, and migratory species, which totalled 200 species. For these species, detection data were collected between January 2008 and December 2014, and had been submitted to the project by December 2014 were included in the study.

The study area covered 576 pentads making up a 24 x 24 square pentad grid, covering approximately 35 000 $km^2$. Over the study duration, 23 665 checklists were submitted, at an average of 41 checklists per pentad, with a maximum of 974 and minimum of 7. Following Broms et al. (2014), I used at most 100 checklists per pentad. Where pentads had more than this, 100 were randomly selected.

### *4.3.3 Analyses*

#### 4.3.3.1 Dynamic Occupancy Models

Site-occupancy models recognise that a species can go undetected during surveys and account for this by allocating a separate component in the model specifically to estimate the probability of detection, which enables direct and unbiased modelling of the biological process, such as colonization and extinction (MacKenzie et al., 2003). Each process can depend on separate covariates, modelled on the logit scale. At its most basic level, occupancy models can estimate the probability that a species occupies a site, over a single time period (single season occupancy models, MacKenzie et al., 2003), whilst accounting for imperfect detection. A season is a specified period of time of any reasonable length during which the occupancy status of a grid cell is assumed to stay constant.

Dynamic occupancy models differ from single season occupancy models in that they allow for changes in occupancy over time (i.e., between seasons). This is done by estimating dynamic components, colonization and extinction (see below, equation 2). To estimate these components, it is necessary to collect repeated detection / non-detection data for each season over the duration of the study. The input data are in the form $y_{ijt}$, which indicate detection / non-detection $y$, for site $i$, during survey $j$, in season $t$.

Initial occupancy, which is the occupancy probability over the 1st season at site $i$ $(z_{i1})$, is estimated from a Bernoulli trial with a mean of $\Psi_{i1}$:

$$z_{i1} \sim Bernoulli\ (\Psi_{i1}) \tag{1}$$

For all later seasons, ($t$ = 2, 3, 4 … $T$) occupancy probabilities at site $i$ are a function of the previous season's occupancy probability, and the dynamic components colonization ($\gamma_i$) and persistence ($\phi_i$). Extinction is the complement of persistence ($1 - \phi$), and here, I focus explicitly on extinction, rather than persistence. Extinction probability refers to the probability a site goes unoccupied at time $t$, given it was occupied at time $t - 1$. Colonization probability refers to the probability a species occupies site $i$ at season $t$, given the site was unoccupied at season $t - 1$. These are linked through the following equation:

$$Z_{it} \sim Bernoulli\ (Z_{it-1} \times\ (1 - \phi_{it-1}) + (1 -\ Z_{it-1}) \times\ \gamma_{it-1}), \qquad \text{for t>1} \tag{2}$$

$\phi$ and $\gamma$ can depend on season- and site-specific covariates (MacKenzie et al., 2003). Sites remain either occupied or unoccupied over the duration of each season. The model allows for extinctions and colonization events between seasons (MacKenzie et al., 2006).

To answer the first question posed by this study ("How do protected areas affect the colonization, extinction, and initial occupancy rates of common bird species?"), I fitted separate multi-season occupancy models to the data for each of the 200 species considered. I regarded each calendar year (beginning January) as a season, resulting in 6 seasons (2008-2014). This period was long enough to ensure there were enough data, year on year, to robustly estimate the effect of protected areas on the dynamic components. Furthermore, the species I studied were resident, and common, meaning that they come from demographically stable populations, that were not likely to change markedly year on year. I used calendar years as seasons so that the split between seasons occurred after the breeding season for most birds in the species list. The months January and February constitute the hottest part of the year in South Africa, and many birds are inclined to breed during the winter and spring. For example, Golden-tailed Woodpecker (*Campethera abingoni*) breeds anywhere between August – December (Tarboton, 1994); Cape Crow (*Corvis capensis*) is likely to breed at any time between July (the middle of the South African winter) to January (Jenkins & Underhill, 1997); and Black-chested Prinia (*Prinia flavicans*) breeds at any time between August and May (Berruti, 1997). Other birds are able to breed at any time of the year if conditions are right, for example, Hadeda Ibis (*Bostrychia hagedash*; Duckworth & Altwegg, 2014). It follows that defining seasons by calendar years aligns with the biology for most of the species studied here.

Occupancy probability was estimated for the year 2008 (henceforth called: initial occupancy), and the dynamic components were derived for the remaining seasons.

For each of the 200 species considered, initial occupancy was modelled as:

$$\text{logit}(\Psi_{i1}) = \beta_0 + \beta_1 \times PA_i + \beta_2 \times Agriculture_i + \beta_3 \times Urban_i + \beta_4 \times Savanna_i \quad (3)$$

With colonization in the form:

$$\text{logit}(\gamma_i) = \beta_5 + \beta_6 \times PA_i \quad (4)$$

and extinction in the form:

$$\text{logit}(1 - \phi_i) = \beta_7 + \beta_8 \times PA_i \quad (5)$$

Detection was fit in the form

$$\text{logit}(\text{p}_{ijt}) = \beta_9 + \beta_{10} \times \text{ɦ}_{ijt} \tag{6}$$

where for pentad $i$, survey $j$, and season $t$, $p_{ijt}$ is the detection probability and $\text{ɦ}_{ijt}$ is the number of hours spent birding, $PA_i$ is the proportion of pentad $i$ occupied by protected areas, $Agriculture_i$ is the proportion occupied by Agricultural land, $Urban_i$ is the proportion occupied by Urban areas, and $Savanna_i$ is the proportion occupied by Savanna biome. Savanna and grasslands are the main biomes in the study area which occur in almost equal proportions; savanna makes up the vegetation in the northern half of the study area, and grasslands the south. For equations 4 and 5, $\text{PA}$ is constant through time across the study area. The relationship between colonization ($\gamma_i$ eqn. 4) and $PA_i$, as well as between extinction ($1 - \phi_i$ eqn. 5) and $PA_i$ varied spatially with the proportion of protected area per pentad across the study site, but not temporally. I therefore assume that the effect of protected areas on the colonization and extinction rates of species is constant over time.

The relationship between protected areas and initial occupancy, colonization, and extinction was addressed respectively in equation 3 ($\beta_1$), equation 4 ($\beta_6$), and equation 5 ($\beta_8$). The $\beta$ coefficients are estimated by the model, which is parameterised in a way that the occupancy component intercept ($\beta_0$) corresponds to the average occupancy probability for birds in natural land. $\beta_5$, $\beta_7$ and $\beta_9$ are intercepts for the colonization, extinction, and detection processes respectively. All models were fitted in program R (R Development Core Team, 2017) with add-on package "unmarked" (Fiske & Chandler, 2011).

#### 4.3.3.2 Avian guilds and Bayesian analysis of colonization and extinction probabilities

I assigned each species to one of seven guilds, based on the type of food the species preferentially consumes and its foraging mode, sensu Hockey et al. (2005). These were: frugivores (species that primarily consume fleshy fruit, totalling 9 species); gleaners (species that primarily consume insects and other invertebrates caught off plants, totalling 31 species); granivores (species that primarily consume seeds and grains, totalling 48 species); ground-feeders (species that primarily consume insects and invertebrates caught off the ground, totalling 63 species); hawkers (species that primarily consume insects and other invertebrates caught in the air, totalling 11 species); predators (birds of prey, species that primarily consume the flesh of vertebrates, totalling 19 species), and vegivores (vegetative herbivores; species that primarily consume vegetative parts of plants, totalling 19 species).

I used a Bayesian analysis to examine how the effects of protected areas on extinction ($\beta_6$ in equation 4) and colonization ($\beta_8$ in equation 5) varied amongst guilds. I adopted a framework similar to that of McCarthy & Masters (2005). This structure was similar to a linear mixed effects model, with guild as a normally distributed random factor. However, instead of treating guild-level mean extinction or colonization estimates as directly observed quantities, I modelled them as drawn from a normal distribution using the means and standard errors as estimated by the dynamic occupancy models. I specified the priors for the mean response per guild to come from a normal distribution with a mean of 0, and the standard deviation to come from a uniform distribution (min of 0, and max of 100). I implemented this in the program WinBUGS (Lunn et al., 2000) with 50 000 iterations, 25 000 burn in, and 3 MCMC chains. The Gelman-Rubin diagnostic indicated that this model converged, and all R-hat values were < 1.01 (This model is structurally similar to the one used in Chapter 3, except it is informed by differed beta coefficients. See Appendix 3, Model A3.1 for more information on the general structure of this model).

#### 4.3.3.3 Equilibrium occupancy

Equilibrium occupancy is the expected occupancy probability at which the net number of sites colonized equals the net number of sites lost to extinction each season. Equilibrium occupancy is defined by MacKenzie et al. (2006) as:

$$\Psi_{eq.s} = \frac{\gamma_s}{\gamma_s + 1 - \phi_s} \tag{7}$$

Where, for species $s$, $\Psi_{eq.s}$ is the equilibrium occupancy, $\gamma_s$ is the colonization probability, and $1 - \phi_s$ is the extinction probability (estimated in equations 4 and 5 respectively).

Finally, to answer the third question posed in this study ("How do protected areas affect equilibrium occupancy rates?"), I calculated two equilibrium occupancies for each of the 200 species using equation 7, but each differed in their specified *PA* covariate value. One calculation assumed a pentad is fully protected (i.e, the 'PA' covariates in equations 4 and 5 are set to 1) and the other assuming no protection ('PA' covariates set to 0). This enabled a comparison of equilibrium occupancy under a scenario of full protection, and of no protection, which was indicated by Δ equilibrium occupancy, and calculated as follows:

$$\widehat{\Delta\Psi}_{eq.s} = \hat{\Psi}_{eq.s.full\,protection} - \hat{\Psi}_{eq.s.no\,protection} \tag{8}$$

where for species $s$, Δ equilibrium occupancy ($\widehat{\Delta\Psi}_{eq.s}$) is the difference between estimated equilibrium occupancy for a fully protected pentad ($\hat{\Psi}_{eq.s.full\,protection}$) and estimated equilibrium occupancy for a pentad with no protection ($\hat{\Psi}_{eq.s.no\,protection}$). Δ equilibrium occupancy ($\widehat{\Delta\Psi}_{eq.s}$) can take values from -1 to +1, and a positive value implies that a higher occupancy is expected under full protection than under no protection. A negative value implies the opposite. I then calculated the average Δ equilibrium occupancy ($\widehat{\Delta\Psi}_{eq.s}$) and associated credible intervals for each guild using a hierarchical Bayesian analysis. This model was like the one used in section 4.3.3.2 to calculate the average extinction and colonization probabilities per guild, but the model was informed by Δ equilibrium occupancy for each species ($\widehat{\Delta\Psi}_{eq.s}$) rather than by the dynamics quantities colonization and extinction.

## 4.4 RESULTS

*Model convergence of multi-season occupancy models*

14 of the 200 individual species models fitted did not converge. These were species that were rarely sighted (reported on <0.5% of the checklists submitted, even though the species may be common, it was not easily detected) and my results are therefore based on the 186 species for which the models converged. This resulted in 9 frugivores, 29 gleaners, 45 granivores, 60 ground feeders, 11 hawkers, 17 predators, and 15 vegivores (Table A4.1, Appendix 4).

*How do protected areas affect the colonization, extinction, and initial occupancy rates of common bird species?*

Extinction and colonization

The relationship between the proportion of protected areas per pentad and average colonization probability was significantly positive for all seven guilds (Fig. 4.1, upper panel). This suggests that on average, pentads with a higher proportion of protected areas are more likely to be colonized by birds from the seven guilds considered here, compared to those with a lower proportion of protected areas. The average extinction probability for ground-feeders and granivores significantly increased as the proportion of protected areas within a pentad increased (Fig. 4.1, lower panel). For the remaining five guilds (namely frugivores, predators, vegivores, gleaners, and hawkers), the 95% credible intervals overlapped zero, indicating that there was no clear trend between the proportion of a pentad occupied by a protected area and the average extinction probability for these guilds. For guilds granivores and ground-feeders, an increase in the proportion of protected areas per pentad is expected to lead to a significant increase in average colonization probability, as well as in average extinction probability.

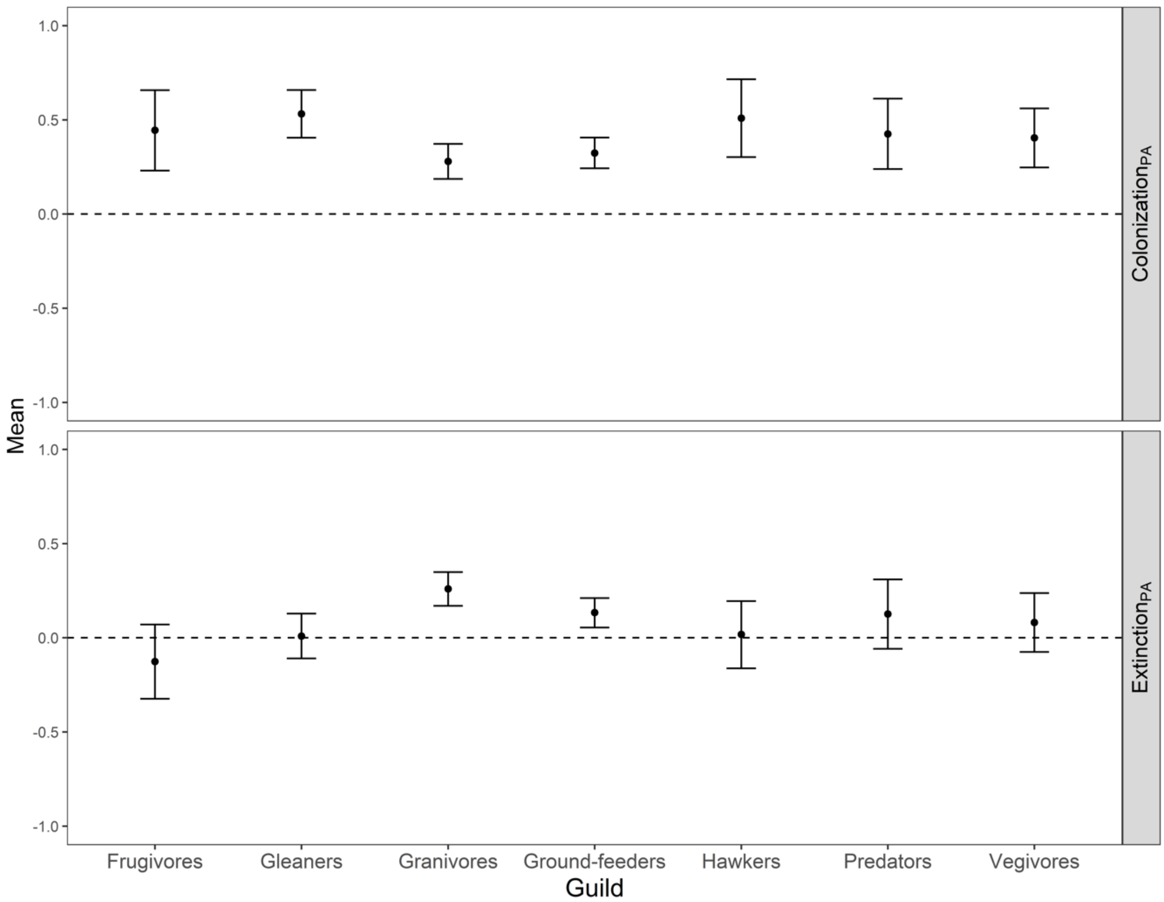



**Figure 4.1.** Mean and 95% credible intervals (black dots and error bars respectively) of a hierarchical Bayesian analysis summarising multi-state occupancy model dynamic components, colonization (upper panel, $\beta_6$ in equation 4) and extinction (lower panel, $\beta_8$ in equation 5) compared across seven guilds for 186 common bird species in the greater Gauteng region of South Africa. This analysis summarises results of 186 individual dynamic occupancy models, where colonization and extinction of each species were fit as a function of the proportion of a pentad occupied by protected areas. See the results text for the number of species within each guild.

Initial Occupancy

Initial occupancy (estimate for occupancy at 2008) varied widely as a function of the proportion of protected areas in a pentad (Fig. 4.2). Of the 186 species examined, 24 (13%) had positive estimates for $\hat{\beta}_1$ and associated confidence intervals, 15 (8%) had negative estimates for $\hat{\beta}_1$ and associated confidence intervals, and the remaining 147 (79%) had their confidence intervals overlap zero, which indicated that initial occupancy was not strongly related to the proportion of protected areas per pentad. I further estimated the weighted mean for the parameter $\hat{\beta}_1$. The weighted mean estimate for each species weights the mean estimate of $\hat{\beta}_1$ by the inverse of its standard error. This gives a higher weighting to observations with a small error, and less weighting to observations with a large error. The weighted $\hat{\beta}_1$ mean estimate was 0.04 on the logit scale, indicating that on average, the initial occupancy for the species considered here was very weakly positively related to the proportion of protected areas per pentad.

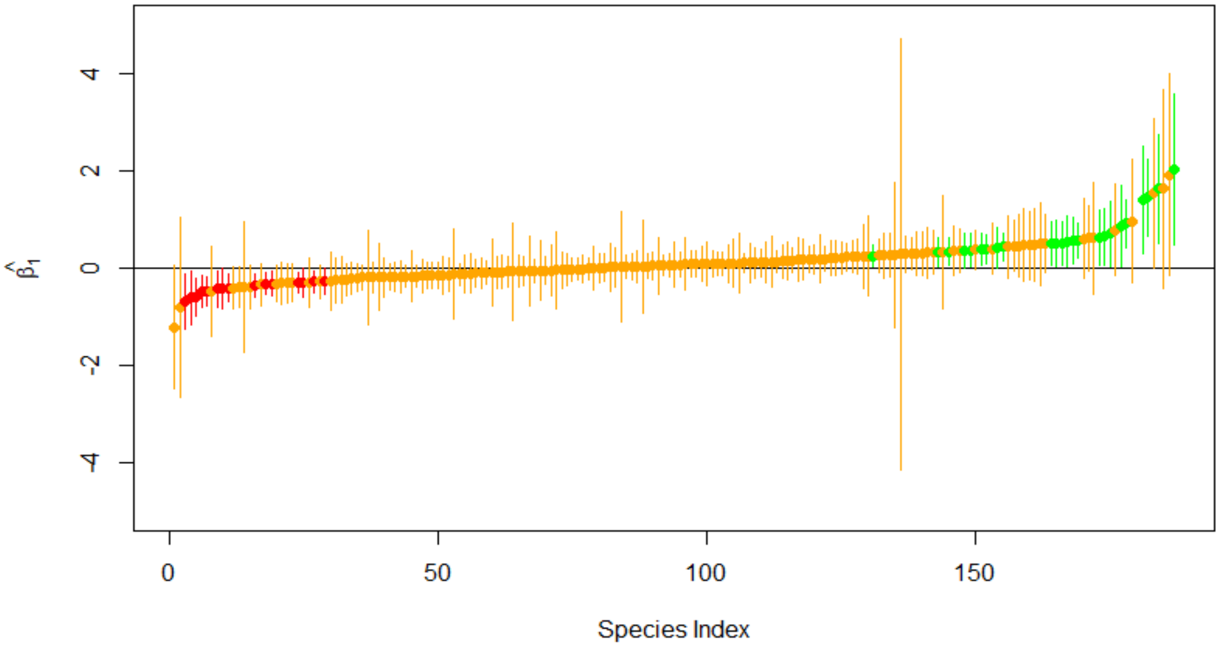



**Figure 4.2.** Estimated slope of the linear (on the logit scale) relationship between initial occupancy (in 2008) and proportion of protected area per pentad for 186 common bird species in the greater Gauteng area in South Africa (this is $\hat{\beta}_1$ in equation 3.) Species are sorted by magnitude of this slope, and the vertical lines are 95% confidence intervals. Red dots and lines represent species with mean and confidence intervals less than 0 (initial occupancy was negatively correlated to the area of protected areas within pentads). Green dots and lines represent species with mean and confidence intervals greater than 0 (initial occupancy was positively correlated to the area of protected areas within pentads). Orange dots and lines represent species with confidence intervals that overlapped zero, (initial occupancy was not significantly influenced by the proportion of protected areas within pentads). Species names, associated $\hat{\beta}_1$ values, and confidence intervals are shown in Table A4.1 of Appendix 4.

*How do protected areas affect equilibrium occupancy?*

Except for the granivores, average Δ equilibrium occupancy ($\widehat{\Delta\Psi}_{eq.s}$ ) was positive for all guilds and credible intervals did not overlap zero (Fig. 4.3). Fully protected pentads are therefore predicted, on average, to have significantly higher equilibrium occupancy probabilities compared to pentads with no protection, for guilds frugivores, gleaners, ground-feeders, hawkers, predators, and vegivores. Whilst the average Δ equilibrium occupancy for granivores was positive, the credible interval overlapped zero, indicating no significant difference between the average equilibrium occupancy in pentads with full protection and those with no protection.

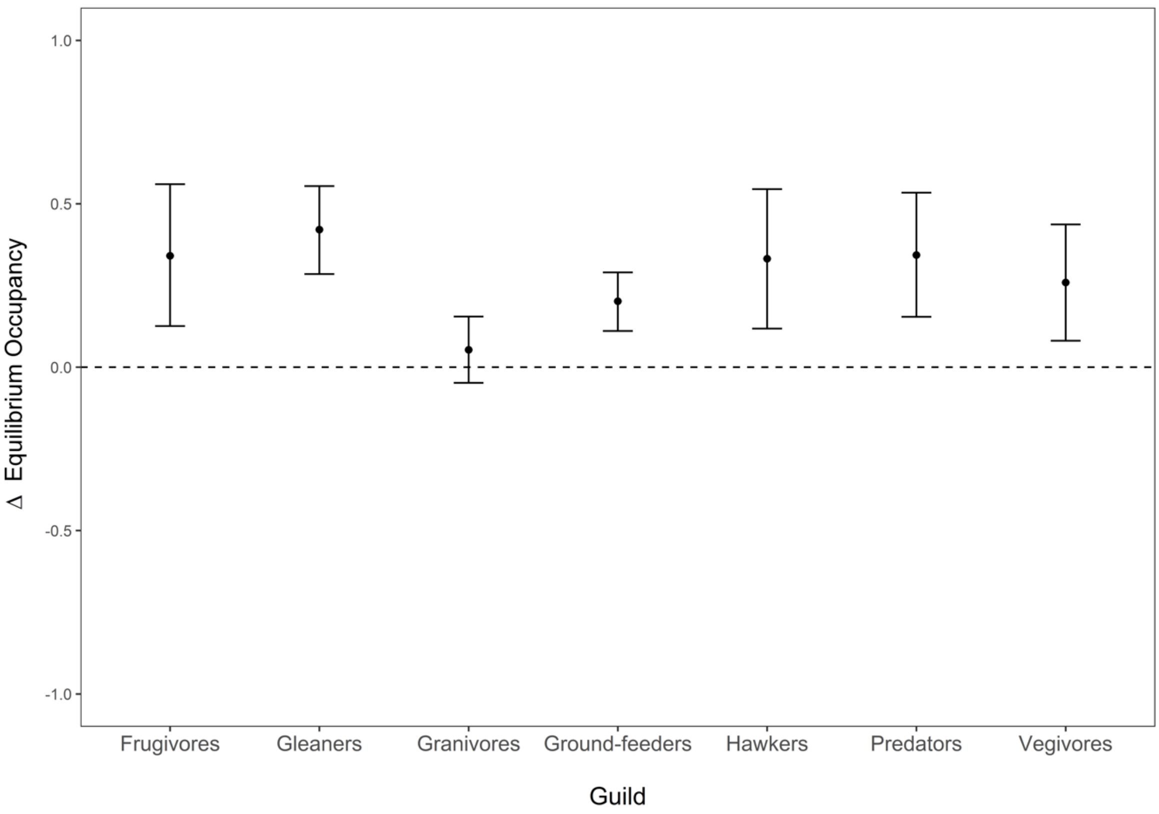



**Figure 4.3.** Average *Δ* equilibrium occupancy and 95% credible intervals for each guild. Equilibrium occupancy is the expected occupancy probability given the dynamic components colonization and equilibrium were at dynamic equilibrium with each other. Average *Δ* equilibrium occupancy is the average difference between equilibrium occupancy assuming a pentad is fully protected and the equilibrium occupancy assuming a pentad is not protected at all. A positive value indicates expected occupancy is higher in pentads with full protection, compared to pentads with no protection. I calculated the average *Δ* occupancy estimate for each species (using equation 8) and used a hierarchical Bayesian analysis to summarize the results into average guild responses (see results text for number of species within each guild). Estimates taken from the dynamic occupancy model results where extinction and colonization for each species are fit as a function of the proportion of protected area per pentad, run once for each of the 186 species.

## 4.5 DISCUSSION

I studied the degree to which protected areas affected the dynamic components of occupancy (colonization and extinction) for 186 common, resident bird species over a heterogeneous region of South Africa. I assigned each species to one of seven avian guilds, based on the type of food it preferentially ate, and its primary foraging mode, sensu Hockey et al. (2005). I analysed occupancy, equilibrium occupancy, extinction, and colonization probability through these guilds. My results show the average colonization probability for each guild was positively statistically correlated to the proportion of protected area per pentad. On the other hand, the average extinction probability for two guilds was also statistically positively correlated to the proportion of protected area per pentad, whilst it was unrelated for the remaining five guilds. For six guilds, the average estimated equilibrium occupancy was significantly higher in pentads assuming full protection compared to pentads assuming no protection, whilst no statistical difference was found for one guild. In contrast, however, the initial occupancy probability (which estimates the occupancy-environment relationship during the first year of the study, 2008) was only slightly positively related to protected areas. Therefore, the dynamic components colonization and extinction, as well as equilibrium occupancy, show that protected areas have a positive impact on occupancy for most guilds, something which the static analysis did not show. My study highlights the conservation benefit provided by protected areas to common species over the study region. It also highlights the value of using dynamic occupancy models as opposed to methods that estimate only static relationships.

My key results show that for all guilds the average colonization rate was strongly positively correlated to the proportion of protected area per pentad (Fig 4.1), and that for all guilds except granivores, the average equilibrium occupancy probability in fully protected pentads was higher than in those with no protection (Fig. 4.3). These findings agree with my initial hypothesis regarding equilibrium occupancy and colonization probability. This finding is also in agreement with my results in Chapter 2, in which found that granivores had higher average abundances in pentads with fewer protected areas (Figs. 2.2 & 2.3, Chapter 2). There is thus ample evidence to suggest that protected areas offer little benefit to the granivorous guild, on average. Nonetheless, because on average, six of the seven guilds occupied pentads of full protection at a higher rate than pentads of no protection, my results indicate that in general protected areas in the region were effective at providing conservation benefit to most of the species considered. These results here are congruent with studies which also found protected areas to be beneficial to common avian species world-wide (Rajasarkka et al., 1994; Carroll et al., 2004; Knapp et al., 2008; Santos et al., 2008; Thomas et al., 2012; Hiley et al., 2013), and more specifically, in South Africa (Child et al., 2009; Greve et al., 2011).

Protected areas did not reduce the average rate of extinction for common species, as originally hypothesised. Granivores and ground-feeders actually experienced increased extinction rates on average, with increasing proportion of protected areas (Fig. 4.1). This may be a function of the land-use types in the wider landscape. Here, urban and agricultural land-use types were the other dominant land-use type in the study region, and granivores and ground-feeders can adapt well to these land-use types (Benton et al., 2002; Newton, 2004; Chace & Walsh, 2006). Perhaps they actively seek out these habitats, on average, rather than protected areas, leading to my observed results. However, this finding necessitates further investigation.

Protected areas are of considerable importance to range dynamics of birds, primarily because birds are very mobile and can easily pass into and out of protected areas. Importantly, protected areas appear to play a very important role in bird species colonizing the greater landscape. For example, Hiley et al. (2013) and Thomas et al. (2012) found that birds were able to colonize protected areas more easily than other land-use types within the landscape. Once established in protected areas, birds colonised other areas throughout the greater landscape. The role of protected areas in bird conservation is not simply just to facilitate the colonization of the greater landscape. Long after colonizing the landscape, some bird species still prefer protected areas to other land-use types available within the landscape. For example, Gillingham et. al. (2015a) found that in areas that had been colonised for lengthy periods (approximately 30-40 years), the abundance of birds within protected areas was still higher compared to outside protected areas. This highlights the important role played by protected areas in the overall conservation of avian biodiversity over time. Since I show that a fully protected pentad is preferentially colonized over pentads of no protection on average across six of the seven guilds considered here (Fig. 4.3), and that because protected areas are expected to become preferentially colonised by alien species when colonizing landscapes (Thomas et al., 2012; Hiley et al., 2013; Thomas & Gillingham, 2015), protected areas will play an important conservation role for species shifting their ranges in response to climate change. This information is useful to conservation managers and groups, as they can prioritise the maintenance of protected areas already in optimal positions within the landscape, with the ultimate goal of mitigating avian biodiversity loss due to climate change. Additionally, since birds are good indicators of ecosystem health and functioning (Furness & Greenwood, 1993), and a relatively small decline in common birds can have a disproportionate impact on the ecological functioning of an area (Gaston, 2011), healthy populations of common species in protected areas can help overall conservation effectiveness of protected areas.

The sizes of the protected areas situated throughout the study area may have had some bearing on my results. Many small protected areas were situated throughout the study region, and not one single (or a few), large protected area. Larger protected areas do not necessarily convey greater conservation benefits. Frequent occurrences of protected areas within the landscape can be of more conservation significance than their overall size (this is essentially the Single Large Or Several Small debate: Simberloff & Abele, 1976; Wilcox & Murphy, 1985). A larger number of protected areas represents more opportunities for colonization by bird species (because the landscape is fragmented). An interesting experiment to consider is how the colonization probability of common bird species over this study area would be affected by a single, large protected area. These factors should be given due consideration when planning for biodiversity conservation, especially in the light of climate change. Birds are much more likely to occupy the greater landscape if they can travel easily between closely-situated protected areas (Gilroy et al., 2014), making landscape colonization a much more likely prospect for species shifting their ranges in response to climate change.

Examining species range dynamics with dynamic models allowed for inferences that would otherwise have been overlooked when using static analyses. The dynamic analyses showed a strong relationship between equilibrium occupancy probability and protected areas for most species. Equilibrium occupancy predictions using the rates of colonization and extinction showed that pentads with a higher proportion of protected areas also had higher average occupancy probabilities for all guilds except for granivores (Fig. 4.3). However, the static relationship between initial occupancy and proportion of protected area was only slightly positive (the weighted $\hat{\beta}_1$ estimate across all guilds showing the relationship between initial occupancy and the proportion of protected areas was 0.04; Fig. 4.2). Dynamic analyses therefore revealed a strong relationship between occupancy and protected areas that would not have been apparent using static analyses alone. This mismatch between dynamic and static analyses occurs because static analyses assume a species' relationship with the environment is in equilibrium. In reality, species are rarely in equilibrium with their environments which are constantly changing due to, for example, climate change, land-use change, and biological invasions (Yackulic et al., 2015). Added to this is a lag in response of species to changes in their environment. Often, species only react to environmental changes some time after the environment has changed (Warren et al., 2001; Walther et al., 2002). Together, these processes result in a constant change in the relationship between a species and the environment through time and space (Guillera-Arroita et al., 2014; Lahoz-Monfort et al., 2014; Yackulic & Ginsberg, 2016). These dynamic processes should optimally be analysed with dynamic methods for accurate inference.

As a caveat of my study, I assumed closure throughout the year, but in reality, colonization and extinction could happen at any time. The closure assumption is therefore violated to some degree. However, I expect my results to be robust to the closure assumption as long as colonization and extinction happen randomly throughout the study period, which is a reasonable expectation given I studied common, resident species. In fact, for many of these species, dispersal is not tied to any particular time of the year (Harrison et al., 1997). Dynamic occupancy models are similar to robust design capture-mark-recapture models, which have been shown to be robust to violation of the closure assumption under random movement in and out of the population (Kendall, 1999).

In conclusion, my key results indicated that protected areas within the study region were successful in the sense that they maintained a habitat of suitable quality to encourage colonization and support occupation by bird species, thus achieving a goal of the conservation of avian biodiversity. My analysis also shows that the positive relationship between protected areas and occupancy was only revealed through dynamic analysis, and not by the static analysis. Thus, in my case the dynamic processes of species' ranges (colonization and extinction) were more informative than relying on basic occupancy-environment relationships, as has been also been found by other authors (Kéry, 2011; Maggini et al., 2011; Yackulic et al., 2015). More specific to this study, conservationists should aim to understand how the dynamic processes of colonization and extinction vary through time and space as a function of protected areas.

## 4.6 APPENDIX: Supplementary material for Chapter 4.

**Table A4.1.** Dynamic occupancy model parameter estimates on the logit scale ± standard errors, for each species (n = 186). These are the results of the fitted model specified in equations 3-6 in the methods text. From these equations, $\hat{\beta}_0 - \hat{\beta}_4$ are estimated in columns 'Intercept', 'Protected areas', 'Agricultural', 'Urban', and 'Savanna', under the 'Initial Occupancy' section. $\hat{\beta}_5$ and $\hat{\beta}_6$ are estimated in columns 'Intercept' and 'Protected areas' under the 'Colonization' section. Similarly, $\hat{\beta}_7$ and $\hat{\beta}_8$ are represented in columns 'Intercept', and 'Protected areas', under the 'Extinction' section.

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Frugivore | African Olive-Pigeon (*Columba arquatrix*) | -2.75 ± 0.26 | 0.39 ± 0.17 | -0.79 ± 0.32 | 0.96 ± 0.16 | -0.90 ± 0.25 | -3.59 ± 0.16 | 0.47 ± 0.07 | -1.31 ± 0.18 | 0.50 ± 0.14 |
| Frugivore | Cape Glossy Starling (*Lamprotornis nitens*) | 02.10 ± 0.28 | -0.32 ± 0.19 | -0.56 ± 0.21 | 0.82 ± 0.36 | 0.90 ± 0.28 | -0.29 ± 0.12 | 0.12 ± 0.11 | -2.70 ± 0.11 | -0.05 ± 0.10 |
| Frugivore | Black-collared Barbet (*Lybius torquatus*) | 01.07 ± 0.16 | 0.21 ± 0.19 | -0.86 ± 0.20 | 0.26 ± 0.19 | -0.22 ± 0.19 | -1.25 ± 0.10 | 0.16 ± 0.16 | -1.98 ± 0.09 | -0.49 ± 0.14 |
| Frugivore | Red-winged Starling (*Onychognathus morio*) | -0.88 ± 0.16 | 0.43 ± 0.15 | -0.55 ± 0.19 | 0.61 ± 0.16 | 0.65 ± 0.17 | -2.60 ± 0.13 | 0.48 ± 0.13 | -1.62 ± 0.13 | -0.45 ± 0.15 |
| Frugivore | Yellow-fronted Tinkerbird (Pogoniulus chrysoconus) | -1.47 ± 0.21 | 0.29 ± 0.17 | -0.42 ± 0.20 | -0.02 ± 0.15 | 01.90 ± 0.22 | -3.59 ± 0.19 | 0.70 ± 0.11 | -2.24 ± 0.17 | 0.02 ± 0.09 |
| Frugivore | Dark-capped Bulbul (*Pycnonotus tricolor*) | 01.48 ± 0.23 | 0.79 ± 0.48 | -0.26 ± 0.17 | 0.83 ± 0.23 | 01.03 ± 0.19 | -0.86 ± 0.21 | 01.60 ± 0.56 | -2.97 ± 0.20 | -1.14 ± 0.55 |
| Frugivore | Crested Barbet (*Trachyphonus vaillantii*) | 02.26 ± 0.34 | 0.62 ± 0.59 | -0.54 ± 0.21 | 0.34 ± 0.26 | 0.78 ± 0.33 | -1.06 ± 0.17 | 0.24 ± 0.40 | -2.47 ± 0.12 | -0.66 ± 0.27 |
| Frugivore | Acacia Pied Barbet (*Tricholaema leucomelas*) | 0.42 ± 0.18 | -0.48 ± 0.16 | -0.60 ± 0.18 | -0.42 ± 0.14 | 0.85 ± 0.19 | -2.64 ± 0.17 | 0.47 ± 0.10 | -2.00 ± 0.13 | 0.14 ± 0.09 |
| Frugivore | Red-faced Mousebird (*Urocolius indicus*) | 02.38 ± 0.43 | -0.25 ± 0.23 | -0.79 ± 0.20 | 01.39 ± 0.73 | 01.00 ± 0.29 | -1.30 ± 0.14 | 0.50 ± 0.20 | -2.74 ± 0.13 | -0.07 ± 0.10 |
| Gleaner | Red-headed Weaver (*Anaplectes melanotis*) | -27.34 ± 19.79 | -0.41 ± 0.22 | -1.82 ± 0.59 | -0.70 ± 0.37 | 22.77 ± 17.61 | -5.26 ± 0.56 | 0.43 ± 0.20 | -2.00 ± 0.40 | -0.90 ± 0.73 |
| Gleaner | Cape Penduline-Tit (*Anthoscopus minutus*) | -7.73 ± 03.67 | -0.27 ± 0.31 | -0.51 ± 0.35 | -0.47 ± 0.31 | 06.16 ± 03.28 | -5.11 ± 0.58 | 0.23 ± 0.51 | -71.69 ± 153.99 | 18.77 ± 42.95 |
| Gleaner | Bar-throated Apalis (*Apalis thoracica*) | -0.51 ± 0.15 | 0.03 ± 0.14 | -0.46 ± 0.19 | 0.09 ± 0.14 | 0.48 ± 0.17 | -2.23 ± 0.12 | 0.16 ± 0.12 | -1.29 ± 0.13 | -0.54 ± 0.17 |
| Gleaner | Chinspot Batis (*Batis molitor*) | -0.10 ± 0.24 | 0.61 ± 0.42 | -0.74 ± 0.24 | -0.08 ± 0.21 | 02.63 ± 0.28 | -2.95 ± 0.17 | 0.75 ± 0.29 | -3.04 ± 0.19 | -0.29 ± 0.23 |
| Gleaner | Barred Wren-Warbler (*Calamonastes fasciolatus*) | -4.39 ± 0.98 | 0.04 ± 0.14 | 0.45 ± 0.22 | 0.20 ± 0.19 | 03.53 ± 0.90 | -4.83 ± 0.34 | 0.47 ± 0.13 | -1.82 ± 0.29 | 0.45 ± 0.15 |
| Gleaner | Golden-tailed Woodpecker (*Campethera abingoni*) | -0.86 ± 0.25 | 0.70 ± 0.34 | -1.43 ± 0.31 | 0.05 ± 0.19 | 01.61 ± 0.26 | -3.11 ± 0.19 | 0.39 ± 0.16 | -2.13 ± 0.18 | -0.06 ± 0.11 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Gleaner | Desert Cisticola (*Cisticola aridulus*) | 02.05 ± 0.53 | -0.70 ± 0.29 | -1.33 ± 0.40 | -1.08 ± 0.32 | 0.20 ± 0.30 | -1.59 ± 0.18 | 0.33 ± 0.26 | -1.52 ± 0.13 | -0.02 ± 0.14 |
| Gleaner | Wing-snapping Cisticola (*Cisticola ayresii*) | -0.09 ± 0.18 | -0.03 ± 0.12 | -0.03 ± 0.20 | -0.48 ± 0.17 | -0.63 ± 0.19 | -2.70 ± 0.23 | -0.72 ± 0.43 | -1.70 ± 0.18 | -0.32 ± 0.20 |
| Gleaner | Rattling Cisticola (*Cisticola chiniana*) | -0.69 ± 0.18 | -0.16 ± 0.14 | -0.27 ± 0.19 | 0.36 ± 0.16 | 02.26 ± 0.20 | -2.94 ± 0.13 | 0.79 ± 0.13 | -2.67 ± 0.15 | 0.15 ± 0.09 |
| Gleaner | Cardinal Woodpecker (*Dendropicos fuscescens*) | 0.09 ± 0.22 | 0.46 ± 0.38 | -0.87 ± 0.23 | 0.33 ± 0.16 | 01.19 ± 0.23 | -2.27 ± 0.19 | 01.49 ± 0.38 | -2.19 ± 0.18 | -0.15 ± 0.16 |
| Gleaner | Black-backed Puffback (*Dryoscopus cubla*) | -0.93 ± 0.19 | 0.40 ± 0.27 | -0.61 ± 0.21 | 0.63 ± 0.17 | 01.83 ± 0.23 | -3.39 ± 0.19 | 0.96 ± 0.16 | -2.17 ± 0.16 | -0.04 ± 0.11 |
| Gleaner | Yellow-bellied Eremomela (*Eremomela icteropygialis*) | -2.28 ± 0.72 | 01.54 ± 0.79 | -0.83 ± 0.48 | 0.07 ± 0.34 | 03.54 ± 0.80 | -36.11 ± 58.81 | 06.30 ± 10.57 | -2.78 ± 0.68 | 0.66 ± 0.23 |
| Gleaner | Greater Honeyguide (*Indicator indicator*) | 0.08 ± 0.22 | -0.16 ± 0.18 | -0.93 ± 0.26 | 0.41 ± 0.20 | 0.87 ± 0.24 | -3.06 ± 0.33 | 0.41 ± 0.24 | -7.50 ± 06.29 | -13.54 ± 16.46 |
| Gleaner | Lesser Honeyguide (*Indicator minor*) | -0.12 ± 0.18 | -0.06 ± 0.14 | -0.37 ± 0.19 | 0.35 ± 0.15 | 0.75 ± 0.19 | -2.77 ± 0.25 | 0.19 ± 0.14 | -28.74 ± 1095.90 | -6.35 ± 290.82 |
| Gleaner | Crimson-breasted Shrike (*Laniarius atrococcineus*) | -0.44 ± 0.17 | -0.07 ± 0.16 | -0.16 ± 0.20 | -0.03 ± 0.16 | 02.17 ± 0.20 | -3.23 ± 0.16 | 0.52 ± 0.15 | -2.50 ± 0.15 | -0.17 ± 0.15 |
| Gleaner | Southern Boubou (*Laniarius ferrugineus*) | -0.21 ± 0.14 | 0.37 ± 0.20 | -0.34 ± 0.16 | 0.33 ± 0.14 | 01.50 ± 0.16 | -2.60 ± 0.12 | 0.55 ± 0.15 | -2.12 ± 0.11 | -0.43 ± 0.14 |
| Gleaner | Grey-headed Bush-Shrike (*Malaconotus blanchoti*) | -1.62 ± 0.28 | 0.19 ± 0.26 | -0.49 ± 0.27 | 0.12 ± 0.24 | 02.01 ± 0.31 | -3.34 ± 0.21 | 0.49 ± 0.16 | -2.26 ± 0.28 | 0.04 ± 0.17 |
| Gleaner | Black-headed Oriole (*Oriolus larvatus*) | -0.46 ± 0.17 | 0.25 ± 0.18 | -0.52 ± 0.20 | 0.30 ± 0.15 | 01.39 ± 0.19 | -2.57 ± 0.14 | 0.74 ± 0.14 | -1.91 ± 0.14 | -0.26 ± 0.12 |
| Gleaner | Chestnut-vented Tit-Babbler (*Parisoma subcaeruleum*) | 0.44 ± 0.13 | -0.32 ± 0.13 | -0.66 ± 0.15 | -0.35 ± 0.12 | 01.09 ± 0.15 | -2.62 ± 0.14 | 0.41 ± 0.10 | -2.92 ± 0.14 | 0.08 ± 0.11 |
| Gleaner | Ashy Tit (*Parus cinerascens*) | -1.63 ± 0.18 | -0.40 ± 0.21 | -0.33 ± 0.20 | -0.25 ± 0.17 | 0.69 ± 0.18 | -4.09 ± 0.29 | 0.49 ± 0.11 | -1.76 ± 0.25 | 0.52 ± 0.16 |
| Gleaner | Southern Black Tit (*Parus niger*) | -4.16 ± 0.77 | -0.41 ± 0.14 | -1.18 ± 0.31 | -0.65 ± 0.21 | 03.41 ± 0.71 | -4.27 ± 0.26 | 0.58 ± 0.09 | -2.16 ± 0.23 | 0.18 ± 0.15 |
| Gleaner | Green Wood-Hoopoe (*Phoeniculus purpureus*) | 0.75 ± 0.18 | 0.35 ± 0.26 | -0.51 ± 0.20 | 0.45 ± 0.22 | 0.32 ± 0.20 | -1.03 ± 0.12 | 0.42 ± 0.16 | -1.74 ± 0.12 | -0.12 ± 0.09 |
| Gleaner | Black-chested Prinia (*Prinia flavicans*) | 02.46 ± 0.28 | -0.06 ± 0.37 | 0.28 ± 0.42 | 0.04 ± 0.25 | 0.35 ± 0.33 | 0.35 ± 0.68 | 01.79 ± 01.78 | -3.26 ± 0.19 | 0.44 ± 0.08 |
| Gleaner | Tawny-flanked Prinia (*Prinia subflava*) | 01.62 ± 0.35 | 02.03 ± 0.79 | -0.20 ± 0.18 | 01.19 ± 0.37 | 01.36 ± 0.21 | -1.83 ± 0.34 | 0.07 ± 0.90 | -2.67 ± 0.23 | -1.66 ± 0.63 |
| Gleaner | White-crested Helmet-Shrike (*Prionops plumatus*) | -4.92 ± 01.21 | -0.24 ± 0.25 | -0.99 ± 0.52 | -2.45 ± 01.50 | 02.37 ± 0.91 | -3.80 ± 0.29 | 0.58 ± 0.12 | -2.18 ± 0.55 | 0.48 ± 0.26 |
| Gleaner | Common Scimitarbill (*Rhinopomastus cyanomelas*) | -1.60 ± 0.32 | -0.32 ± 0.22 | -0.50 ± 0.36 | -0.16 ± 0.22 | 0.70 ± 0.31 | -2.48 ± 0.19 | -0.09 ± 0.16 | -0.57 ± 0.25 | -0.19 ± 0.19 |
| Gleaner | Long-billed Crombec (*Sylvietta rufescens*) | -0.75 ± 0.21 | -0.24 ± 0.16 | -0.36 ± 0.23 | 0.25 ± 0.19 | 02.79 ± 0.25 | -3.37 ± 0.18 | 01.15 ± 0.24 | -2.97 ± 0.17 | -0.04 ± 0.14 |
| Gleaner | Brubru Brubru (*Nilaus afer*) | -0.84 ± 0.18 | -0.18 ± 0.18 | -1.11 ± 0.23 | -0.63 ± 0.17 | 01.37 ± 0.18 | -3.59 ± 0.24 | 01.06 ± 0.28 | -2.43 ± 0.20 | 0.27 ± 0.11 |
| Gleaner | Klaas's Cuckoo (*Chrysococcyx klaas*) | -0.83 ± 0.26 | 0.10 ± 0.31 | -0.63 ± 0.30 | 0.24 ± 0.19 | 01.57 ± 0.25 | -4.05 ± 0.45 | 01.17 ± 0.27 | -1.88 ± 0.22 | 0.10 ± 0.13 |
| Granivore | Red-headed Finch (*Amadina erythrocephala*) | 0.41 ± 0.20 | -0.41 ± 0.21 | 0.80 ± 0.20 | 01.53 ± 0.40 | -0.64 ± 0.18 | -2.34 ± 0.14 | -0.10 ± 0.10 | -1.17 ± 0.11 | 0.62 ± 0.15 |
| Granivore | Cut-throat Finch (*Amadina fasciata*) | -6.94 ± 03.29 | -0.15 ± 0.20 | 0.63 ± 0.34 | 02.21 ± 01.19 | 06.68 ± 03.31 | -3.53 ± 0.19 | 0.35 ± 0.09 | -0.82 ± 0.19 | 0.00 ± 0.14 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Granivore | Cuckoo Finch (*Anomalospiza imberbis*) | -5.46 ± 01.91 | 0.49 ± 0.43 | -4.57 ± 02.51 | -1.41 ± 01.02 | -2.69 ± 01.35 | -2.46 ± 0.21 | 0.25 ± 0.13 | 0.14 ± 0.45 | 0.04 ± 0.23 |
| Granivore | Red-capped Lark (*Calandrella cinerea*) | -0.22 ± 0.18 | 0.09 ± 0.18 | 0.81 ± 0.23 | -0.93 ± 0.21 | -1.80 ± 0.22 | -2.90 ± 0.15 | 0.09 ± 0.10 | -2.25 ± 0.15 | 0.89 ± 0.15 |
| Granivore | Speckled Pigeon (*Columba guinea*) | 04.21 ± 0.96 | 01.92 ± 01.06 | 01.94 ± 0.83 | 01.58 ± 0.98 | -0.51 ± 0.49 | -0.63 ± 0.19 | 0.26 ± 0.12 | -3.83 ± 0.20 | 0.46 ± 0.09 |
| Granivore | Black-throated Canary (*Crithagra atrogularis*) | 07.96 ± 02.46 | 0.26 ± 0.24 | 05.75 ± 02.19 | -0.16 ± 0.24 | -0.07 ± 0.49 | -0.28 ± 0.23 | 0.02 ± 0.20 | -3.91 ± 0.23 | 0.30 ± 0.13 |
| Granivore | Yellow Canary (*Crithagra flaviventris*) | -0.57 ± 0.16 | 0.10 ± 0.12 | 0.22 ± 0.17 | -0.77 ± 0.21 | -0.68 ± 0.16 | -2.42 ± 0.13 | -0.39 ± 0.18 | -2.37 ± 0.17 | 0.30 ± 0.10 |
| Granivore | Yellow-fronted Canary (*Crithagra mozambicus*) | 0.88 ± 0.26 | 01.39 ± 0.57 | -0.35 ± 0.22 | 0.28 ± 0.15 | 01.84 ± 0.24 | -2.16 ± 0.20 | 01.16 ± 0.47 | -2.65 ± 0.20 | -0.82 ± 0.53 |
| Granivore | Golden-breasted Bunting (*Emberiza flaviventris*) | -1.87 ± 0.35 | -0.03 ± 0.17 | -0.91 ± 0.25 | -0.42 ± 0.18 | 02.73 ± 0.34 | -3.39 ± 0.18 | 0.85 ± 0.14 | -2.43 ± 0.18 | 0.07 ± 0.10 |
| Granivore | Cinnamon-breasted Bunting (*Emberiza tahapisi*) | 15.58 ± 05.83 | -0.40 ± 0.68 | -1.81 ± 0.44 | -1.38 ± 0.39 | 14.60 ± 05.51 | -2.24 ± 0.22 | 0.71 ± 0.27 | -2.44 ± 0.17 | -0.33 ± 0.18 |
| Granivore | Chestnut-backed Sparrowlark (*Eremopterix leucotis*) | -1.75 ± 0.29 | -1.22 ± 0.64 | 01.34 ± 0.24 | -0.73 ± 0.34 | 0.26 ± 0.21 | -3.68 ± 0.23 | 0.10 ± 0.13 | -1.36 ± 0.19 | 0.56 ± 0.27 |
| Granivore | Common Waxbill (*Estrilda astrild*) | 01.43 ± 0.25 | 0.03 ± 0.17 | -0.23 ± 0.32 | 0.02 ± 0.20 | -0.54 ± 0.27 | -0.56 ± 0.21 | 0.52 ± 0.28 | -2.78 ± 0.20 | -0.35 ± 0.27 |
| Granivore | Black-faced Waxbill (*Estrilda erythronotos*) | -1.91 ± 0.30 | -0.43 ± 0.20 | 0.04 ± 0.20 | -0.33 ± 0.21 | 01.60 ± 0.27 | -3.60 ± 0.26 | 0.36 ± 0.12 | -3.02 ± 0.44 | 0.51 ± 0.19 |
| Granivore | Yellow-crowned Bishop (*Euplectes afer*) | 02.24 ± 0.37 | 0.21 ± 0.19 | 01.34 ± 0.48 | -0.44 ± 0.17 | -0.92 ± 0.29 | -1.12 ± 0.15 | 0.02 ± 0.10 | -2.55 ± 0.15 | 0.41 ± 0.08 |
| Granivore | Red-collared Widowbird (*Euplectes ardens*) | 0.24 ± 0.14 | 0.50 ± 0.23 | -0.98 ± 0.19 | -0.08 ± 0.13 | -0.98 ± 0.17 | -1.94 ± 0.12 | 0.38 ± 0.09 | -1.91 ± 0.13 | 0.16 ± 0.08 |
| Granivore | Fan-tailed Widowbird (*Euplectes axillaris*) | -2.89 ± 0.37 | -0.07 ± 0.51 | 0.92 ± 0.22 | -0.05 ± 0.20 | -1.53 ± 0.36 | -3.93 ± 0.23 | 0.06 ± 0.16 | -2.52 ± 0.32 | 0.94 ± 0.29 |
| Granivore | Yellow Bishop (*Euplectes capensis*) | -5.26 ± 02.58 | -0.09 ± 0.36 | -1.05 ± 0.92 | -4.95 ± 04.80 | -0.93 ± 0.84 | -3.17 ± 0.23 | -0.28 ± 0.20 | 02.52 ± 01.15 | -2.37 ± 0.97 |
| Granivore | Southern Red Bishop (*Euplectes orix*) | 04.39 ± 01.15 | -0.02 ± 0.12 | 0.56 ± 0.31 | 0.88 ± 0.34 | -2.79 ± 01.05 | -1.26 ± 0.17 | 0.18 ± 0.08 | -3.43 ± 0.15 | 0.44 ± 0.08 |
| Granivore | Long-tailed Widowbird (*Euplectes progne*) | 02.15 ± 0.33 | -0.15 ± 0.13 | 0.11 ± 0.20 | -0.92 ± 0.22 | -3.19 ± 0.36 | -2.41 ± 0.13 | -0.06 ± 0.09 | -3.00 ± 0.12 | 0.59 ± 0.10 |
| Granivore | Violet-eared Waxbill (*Granatina granatina*) | -2.23 ± 0.45 | -0.17 ± 0.12 | -0.42 ± 0.20 | -0.35 ± 0.17 | 02.26 ± 0.41 | -4.06 ± 0.28 | 0.11 ± 0.26 | -2.92 ± 0.33 | 0.03 ± 0.19 |
| Granivore | Red-billed Firefinch (*Lagonosticta senegala*) | -1.40 ± 0.33 | -0.20 ± 0.15 | 0.17 ± 0.26 | -0.08 ± 0.19 | 02.39 ± 0.34 | -3.04 ± 0.18 | 0.38 ± 0.09 | -1.69 ± 0.17 | 0.29 ± 0.10 |
| Granivore | Namaqua Dove (*Oena capensis*) | 0.81 ± 0.17 | -0.19 ± 0.16 | 0.77 ± 0.23 | -0.78 ± 0.16 | 0.91 ± 0.20 | -2.31 ± 0.17 | 0.13 ± 0.09 | -2.26 ± 0.15 | 0.58 ± 0.09 |
| Granivore | African Quailfinch (*Ortygospiza atricollis*) | 01.04 ± 0.19 | -0.27 ± 0.13 | 0.38 ± 0.24 | -1.05 ± 0.18 | -0.83 ± 0.21 | -1.39 ± 0.13 | 0.11 ± 0.08 | -2.60 ± 0.15 | 0.24 ± 0.11 |
| Granivore | House Sparrow (*Passer domesticus*) | 02.94 ± 0.56 | 0.04 ± 0.13 | 0.57 ± 0.23 | 03.67 ± 01.07 | -0.55 ± 0.22 | -0.99 ± 0.13 | 0.01 ± 0.08 | -2.44 ± 0.12 | 0.27 ± 0.07 |
| Granivore | Cape Sparrow (*Passer melanurus*) | 03.84 ± 0.67 | 0.10 ± 0.12 | 0.89 ± 0.28 | 01.54 ± 0.49 | -2.14 ± 0.59 | -0.70 ± 0.13 | 0.18 ± 0.08 | -3.09 ± 0.12 | 0.55 ± 0.06 |
| Granivore | Great Sparrow (*Passer motitensis*) | -5.81 ± 02.02 | -0.28 ± 0.18 | 0.27 ± 0.35 | 0.10 ± 0.23 | 05.48 ± 01.86 | -5.61 ± 0.60 | 0.71 ± 0.21 | -1.91 ± 0.29 | -0.12 ± 0.20 |
| Granivore | Yellow-throated Petronia (*Petronia superciliaris*) | -1.74 ± 0.28 | -0.20 ± 0.13 | -1.32 ± 0.31 | -0.41 ± 0.18 | 0.84 ± 0.22 | -4.94 ± 0.62 | 0.46 ± 0.24 | -1.48 ± 0.21 | -0.18 ± 0.15 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Granivore | White-browed Sparrow-Weaver (*Plocepasser mahali*) | 0.28 ± 0.11 | -0.31 ± 0.11 | -0.12 ± 0.13 | -0.64 ± 0.13 | -0.22 ± 0.13 | -2.19 ± 0.12 | 0.33 ± 0.07 | -2.92 ± 0.14 | 0.56 ± 0.08 |
| Granivore | Green-winged Pytilia (*Pytilia melba*) | -0.69 ± 0.19 | -0.48 ± 0.15 | -0.12 ± 0.20 | -0.49 ± 0.17 | 01.73 ± 0.20 | -3.30 ± 0.22 | 0.44 ± 0.11 | -2.42 ± 0.20 | 0.32 ± 0.10 |
| Granivore | Red-billed Quelea (*Quelea quelea*) | 03.52 ± 0.65 | -0.47 ± 0.47 | 0.97 ± 0.53 | -0.90 ± 0.26 | 01.15 ± 0.54 | -0.90 ± 0.18 | 0.64 ± 0.21 | -3.08 ± 0.16 | 0.31 ± 0.09 |
| Granivore | Cape Canary (*Serinus canicollis*) | -3.60 ± 0.49 | 0.50 ± 0.31 | 0.48 ± 0.42 | 0.00 ± 0.37 | -0.70 ± 0.51 | -4.99 ± 0.37 | -0.22 ± 0.48 | -0.66 ± 0.54 | -1.77 ± 0.89 |
| Granivore | Bronze Mannikin (*Spermestes cucullatus*) | -2.06 ± 0.24 | -0.02 ± 0.14 | -0.34 ± 0.25 | 01.01 ± 0.17 | 01.27 ± 0.25 | -2.87 ± 0.12 | 0.27 ± 0.08 | -1.81 ± 0.17 | 0.03 ± 0.13 |
| Granivore | Orange-breasted Waxbill (*Sporaeginthus subflavus*) | -1.08 ± 0.25 | 0.11 ± 0.20 | 0.28 ± 0.32 | -0.06 ± 0.18 | -1.10 ± 0.29 | -1.84 ± 0.16 | -0.20 ± 0.13 | -1.64 ± 0.23 | 0.15 ± 0.26 |
| Granivore | Scaly-feathered Finch (*Sporopipes squamifrons*) | -1.37 ± 0.21 | -0.37 ± 0.12 | -0.06 ± 0.17 | 0.09 ± 0.14 | 01.79 ± 0.22 | -3.52 ± 0.18 | 0.25 ± 0.10 | -2.14 ± 0.15 | 0.24 ± 0.10 |
| Granivore | Cape Turtle-Dove (*Streptopelia capicola*) | 05.09 ± 01.21 | 0.25 ± 0.43 | -0.56 ± 0.35 | -0.39 ± 0.26 | -2.26 ± 01.10 | -0.09 ± 0.28 | 0.55 ± 0.40 | -4.32 ± 0.22 | 0.07 ± 0.19 |
| Granivore | Red-eyed Dove (*Streptopelia semitorquata*) | 03.99 ± 01.13 | 01.63 ± 01.05 | 0.52 ± 0.41 | 0.10 ± 0.25 | -1.75 ± 1.00 | 0.32 ± 0.21 | 0.57 ± 0.40 | -3.07 ± 0.13 | -0.02 ± 0.11 |
| Granivore | Laughing Dove (*Streptopelia senegalensis*) | 54.52 ± 33.52 | 0.46 ± 0.36 | 25.22 ± 17.68 | 31.51 ± 30.06 | -2.07 ± 15.21 | 05.93 ± 12.94 | 11.04 ± 33.99 | -51.00 ± 372.16 | -3.44 ± 296.69 |
| Granivore | Emerald-spotted Wood-Dove (*Turtur chalcospilos*) | -3.96 ± 0.69 | 0.18 ± 0.15 | -0.64 ± 0.26 | -1.95 ± 0.63 | 02.48 ± 0.58 | -4.22 ± 0.26 | 0.46 ± 0.12 | -2.12 ± 0.25 | 0.27 ± 0.10 |
| Granivore | Blue Waxbill (*Uraeginthus angolensis*) | 0.18 ± 0.15 | -0.19 ± 0.16 | -0.49 ± 0.17 | -0.10 ± 0.14 | 01.94 ± 0.18 | -2.81 ± 0.14 | 0.81 ± 0.14 | -2.83 ± 0.14 | -0.16 ± 0.13 |
| Granivore | Village Indigobird (*Vidua chalybeata*) | -1.56 ± 0.24 | -0.31 ± 0.20 | -0.01 ± 0.21 | -0.36 ± 0.21 | 01.16 ± 0.23 | -3.36 ± 0.26 | 0.50 ± 0.11 | -1.99 ± 0.34 | 0.95 ± 0.21 |
| Granivore | Dusky Indigobird (*Vidua funerea*) | -1.68 ± 0.29 | -0.12 ± 0.20 | -0.63 ± 0.31 | -0.39 ± 0.23 | 0.98 ± 0.26 | -123.28 ± 288.78 | 24.76 ± 57.92 | -2.01 ± 0.43 | 0.20 ± 0.23 |
| Granivore | Long-tailed Paradise-Whydah (*Vidua paradisaea*) | -0.50 ± 0.20 | -0.21 ± 0.17 | 0.03 ± 0.22 | -0.49 ± 0.20 | 01.64 ± 0.23 | -3.18 ± 0.23 | 0.50 ± 0.11 | -2.00 ± 0.20 | 0.29 ± 0.10 |
| Granivore | Shaft-tailed Whydah (*Vidua regia*) | -2.66 ± 0.58 | -0.30 ± 0.15 | -0.29 ± 0.23 | 0.02 ± 0.19 | 02.69 ± 0.54 | -4.09 ± 0.26 | 0.20 ± 0.17 | -2.34 ± 0.30 | 0.47 ± 0.15 |
| Granivore | African Firefinch (*Lagonosticta rubricata*) | -1.28 ± 0.43 | -0.61 ± 0.29 | -0.77 ± 0.42 | -0.19 ± 0.24 | 01.11 ± 0.36 | -2.54 ± 0.25 | 0.38 ± 0.13 | -1.28 ± 0.24 | 0.21 ± 0.23 |
| Granivore | Jamesons Firefinch (*Lagonosticta rhodopareia*) | -0.75 ± 0.26 | -0.60 ± 0.20 | -0.57 ± 0.27 | 0.14 ± 0.22 | 02.52 ± 0.33 | -2.79 ± 0.17 | 0.89 ± 0.15 | -2.34 ± 0.19 | 0.04 ± 0.13 |
| Ground-feeder | Bushveld Pipit (*Anthus caffer*) | -3.38 ± 0.66 | 0.28 ± 0.76 | -1.13 ± 0.45 | -2.13 ± 0.88 | 01.87 ± 0.54 | -28.12 ± 35.67 | 12.39 ± 17.05 | -8.78 ± 14.34 | -9.36 ± 35.88 |
| Ground-feeder | Plain-backed Pipit (*Anthus leucophrys*) | -0.85 ± 0.31 | 0.10 ± 0.20 | -2.50 ± 0.65 | -1.56 ± 0.39 | -2.11 ± 0.53 | -2.27 ± 0.19 | 0.12 ± 0.18 | -1.06 ± 0.20 | -0.43 ± 0.21 |
| Ground-feeder | Striped Pipit (*Anthus lineiventris*) | -2.65 ± 0.42 | 0.17 ± 0.23 | -1.21 ± 0.46 | 0.05 ± 0.22 | 0.86 ± 0.35 | -3.66 ± 0.30 | 0.74 ± 0.14 | -1.75 ± 0.37 | 0.29 ± 0.15 |
| Ground-feeder | Long-billed Pipit (*Anthus similis*) | -1.07 ± 0.19 | 0.21 ± 0.17 | -0.58 ± 0.24 | -0.29 ± 0.17 | -0.42 ± 0.22 | -2.77 ± 0.19 | 0.43 ± 0.10 | -1.19 ± 0.20 | 0.09 ± 0.11 |
| Ground-feeder | Buffy Pipit (*Anthus vaalensis*) | -0.98 ± 0.31 | -0.19 ± 0.21 | -1.29 ± 0.41 | -0.78 ± 0.27 | -0.09 ± 0.30 | -2.28 ± 0.25 | 0.28 ± 0.15 | -1.11 ± 0.33 | -0.35 ± 0.25 |
| Ground-feeder | Black-headed Heron (*Ardea melanocephala*) | 02.88 ± 0.44 | 0.07 ± 0.13 | 01.74 ± 0.47 | 0.75 ± 0.30 | -0.91 ± 0.37 | -1.10 ± 0.14 | 0.04 ± 0.07 | -2.84 ± 0.13 | 0.59 ± 0.08 |
| Ground-feeder | Hadeda Ibis (*Bostrychia hagedash*) | 31.50 ± 40.06 | 0.36 ± 0.23 | 01.07 ± 0.63 | 0.02 ± 0.24 | -26.18 ± 35.52 | -0.16 ± 0.17 | 0.57 ± 0.27 | -3.25 ± 0.14 | 0.03 ± 0.11 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Ground-feeder | Marico Flycatcher (Bradornis mariquensis) | -5.05 ± 01.13 | -0.10 ± 0.13 | -0.33 ± 0.19 | -0.22 ± 0.17 | 05.36 ± 01.04 | -4.46 ± 0.25 | 0.66 ± 0.12 | -2.84 ± 0.21 | 0.27 ± 0.10 |
| Ground-feeder | Spotted Eagle-Owl (*Bubo africanus*) | -1.16 ± 0.23 | 0.14 ± 0.18 | -0.40 ± 0.29 | 0.18 ± 0.17 | -0.22 ± 0.24 | -2.28 ± 0.18 | 0.15 ± 0.15 | -0.98 ± 0.21 | -0.01 ± 0.16 |
| Ground-feeder | Cattle Egret (*Bubulcus ibis*) | 23.41 ± 23.70 | -0.04 ± 0.19 | 07.35 ± 03.57 | 0.77 ± 0.57 | -11.49 ± 21.31 | -0.46 ± 0.31 | 0.17 ± 0.12 | -4.69 ± 0.35 | 0.62 ± 0.12 |
| Ground-feeder | Spotted Thick-knee (*Burhinus capensis*) | 0.25 ± 0.16 | 0.19 ± 0.13 | -0.19 ± 0.20 | 0.62 ± 0.21 | -0.68 ± 0.20 | -1.29 ± 0.10 | 0.08 ± 0.07 | -1.08 ± 0.10 | 0.07 ± 0.07 |
| Ground-feeder | Familiar Chat (*Cercomela familiaris*) | -0.98 ± 0.17 | 0.16 ± 0.12 | -0.76 ± 0.23 | -0.10 ± 0.14 | 0.09 ± 0.18 | -2.25 ± 0.12 | 0.12 ± 0.10 | -0.98 ± 0.15 | -0.51 ± 0.16 |
| Ground-feeder | White-browed Scrub-Robin (*Cercotrichas leucophrys*) | -1.73 ± 0.35 | 0.44 ± 0.33 | -0.15 ± 0.26 | -0.10 ± 0.22 | 03.70 ± 0.39 | -3.67 ± 0.19 | 01.46 ± 0.27 | -2.89 ± 0.17 | 0.09 ± 0.11 |
| Ground-feeder | Spike-heeled Lark (*Chersomanes albofasciata*) | -0.74 ± 0.19 | -0.12 ± 0.20 | -0.48 ± 0.28 | -0.95 ± 0.21 | -1.96 ± 0.29 | -3.40 ± 0.22 | 0.12 ± 0.13 | -2.11 ± 0.18 | 0.66 ± 0.17 |
| Ground-feeder | White Stork (*Ciconia ciconia*) | 0.13 ± 0.81 | -0.17 ± 0.27 | 01.11 ± 0.80 | -2.35 ± 01.50 | -1.26 ± 0.92 | -1.62 ± 0.24 | -0.12 ± 0.23 | -1.43 ± 0.29 | -0.23 ± 0.62 |
| Ground-feeder | Lazy Cisticola (*Cisticola aberrans*) | -1.03 ± 0.24 | 0.87 ± 0.43 | -0.17 ± 0.30 | 0.22 ± 0.17 | 0.56 ± 0.25 | -2.52 ± 0.20 | 0.57 ± 0.14 | -1.11 ± 0.24 | -0.05 ± 0.11 |
| Ground-feeder | Wailing Cisticola (*Cisticola lais*) | -1.49 ± 0.19 | 0.09 ± 0.14 | -0.79 ± 0.24 | -0.21 ± 0.16 | -1.03 ± 0.23 | -2.90 ± 0.16 | -0.22 ± 0.16 | -1.72 ± 0.19 | -0.27 ± 0.21 |
| Ground-feeder | Cloud Cisticola (*Cisticola textrix*) | 01.65 ± 0.37 | 0.09 ± 0.14 | 0.01 ± 0.22 | -1.52 ± 0.28 | -3.08 ± 0.44 | -2.81 ± 0.18 | 0.17 ± 0.09 | -2.56 ± 0.13 | 0.60 ± 0.09 |
| Ground-feeder | Lilac-breasted Roller (*Coracias caudatus*) | -3.34 ± 0.76 | -0.28 ± 0.11 | -0.50 ± 0.23 | -0.25 ± 0.16 | 03.54 ± 0.70 | -3.65 ± 0.16 | 0.29 ± 0.11 | -2.26 ± 0.15 | -0.13 ± 0.14 |
| Ground-feeder | Magpie Shrike (*Corvinella melanoleuca*) | -8.13 ± 02.01 | -0.33 ± 0.11 | -0.31 ± 0.19 | -0.26 ± 0.16 | 07.97 ± 01.82 | -4.46 ± 0.22 | 0.51 ± 0.10 | -3.27 ± 0.23 | 0.34 ± 0.12 |
| Ground-feeder | Pied Crow (*Corvus albus*) | 0.73 ± 0.14 | -0.19 ± 0.14 | -0.58 ± 0.17 | 0.54 ± 0.18 | 0.81 ± 0.16 | -1.36 ± 0.11 | 0.25 ± 0.11 | -2.66 ± 0.13 | -0.15 ± 0.17 |
| Ground-feeder | Cape Crow (*Corvus capensis*) | -2.02 ± 0.20 | -0.30 ± 0.26 | 0.04 ± 0.22 | -0.27 ± 0.21 | -0.10 ± 0.22 | -4.03 ± 0.26 | -0.05 ± 0.20 | -1.60 ± 0.25 | 0.09 ± 0.27 |
| Ground-feeder | Cape Robin-Chat (*Cossypha caffra*) | 0.33 ± 0.11 | 0.10 ± 0.10 | -0.18 ± 0.14 | 0.30 ± 0.14 | -0.46 ± 0.14 | -1.55 ± 0.09 | 0.16 ± 0.07 | -1.68 ± 0.09 | 0.11 ± 0.07 |
| Ground-feeder | White-throated Robin-Chat (*Cossypha humeralis*) | -2.02 ± 0.33 | 0.11 ± 0.16 | -0.10 ± 0.22 | 0.42 ± 0.23 | 03.18 ± 0.36 | -4.31 ± 0.27 | 0.81 ± 0.17 | -2.99 ± 0.25 | 0.01 ± 0.15 |
| Ground-feeder | Wattled Starling (*Creatophora cinerea*) | 0.42 ± 0.17 | 0.01 ± 0.14 | 0.77 ± 0.23 | -0.09 ± 0.13 | -0.14 ± 0.18 | -1.79 ± 0.14 | -0.01 ± 0.09 | -1.50 ± 0.13 | 0.63 ± 0.12 |
| Ground-feeder | Blue Korhaan (*Eupodotis caerulescens*) | -5.19 ± 01.06 | -0.81 ± 0.94 | -0.16 ± 0.24 | -3.33 ± 01.39 | -2.35 ± 0.69 | -5.36 ± 0.40 | -0.21 ± 0.43 | -1.43 ± 0.37 | 01.33 ± 0.85 |
| Ground-feeder | Southern White-crowned Shrike (*Eurocephalus anguitimens*) | -8.06 ± 03.18 | -0.11 ± 0.16 | -0.23 ± 0.25 | -0.38 ± 0.23 | 06.77 ± 02.86 | -36.37 ± 55.49 | 06.10 ± 09.95 | -2.68 ± 0.56 | 0.47 ± 0.20 |
| Ground-feeder | Greater Kestrel (*Falco rupicoloides*) | -0.84 ± 0.18 | -0.40 ± 0.23 | 0.36 ± 0.19 | -0.61 ± 0.22 | -0.17 ± 0.18 | -2.67 ± 0.16 | 0.09 ± 0.10 | -1.53 ± 0.17 | 0.39 ± 0.15 |
| Ground-feeder | Pearl-spotted Owlet (*Glaucidium perlatum*) | -3.81 ± 0.86 | 0.62 ± 0.35 | -0.82 ± 0.24 | -0.58 ± 0.19 | 04.03 ± 0.82 | -5.02 ± 0.42 | 1.00 ± 0.15 | -3.39 ± 0.34 | 0.56 ± 0.12 |
| Ground-feeder | Brown-hooded Kingfisher (*Halcyon albiventris*) | -0.20 ± 0.17 | 0.32 ± 0.27 | -0.76 ± 0.20 | 0.14 ± 0.14 | 01.79 ± 0.19 | -3.00 ± 0.16 | 0.80 ± 0.18 | -2.74 ± 0.16 | -0.33 ± 0.19 |
| Ground-feeder | Striped Kingfisher (*Halcyon chelicuti*) | -7.94 ± 03.17 | -0.14 ± 0.18 | -1.20 ± 0.41 | -0.75 ± 0.31 | 05.84 ± 02.84 | -5.07 ± 0.43 | 0.77 ± 0.13 | -1.74 ± 0.31 | 0.36 ± 0.13 |
| Ground-feeder | Red-throated Wryneck (*Jynx ruficollis*) | 0.27 ± 0.22 | -0.06 ± 0.16 | -0.46 ± 0.25 | 0.12 ± 0.17 | -1.81 ± 0.30 | -3.29 ± 0.31 | 0.21 ± 0.13 | -2.31 ± 0.17 | 0.37 ± 0.13 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Ground-feeder | Common Fiscal (*Lanius collaris*) | 10.81 ± 04.09 | 0.06 ± 0.12 | 01.10 ± 0.33 | 0.14 ± 0.18 | -8.57 ± 03.66 | -1.37 ± 0.15 | 0.28 ± 0.09 | -3.62 ± 0.14 | 0.34 ± 0.08 |
| Ground-feeder | Cape Longclaw (*Macronyx capensis*) | 01.87 ± 0.28 | -0.16 ± 0.13 | 0.09 ± 0.19 | -0.99 ± 0.21 | -2.84 ± 0.32 | -2.08 ± 0.13 | 0.08 ± 0.08 | -3.08 ± 0.14 | 0.67 ± 0.09 |
| Ground-feeder | Southern Black Flycatcher (*Melaenornis pammelaina*) | -2.14 ± 0.30 | 0.52 ± 0.23 | -0.52 ± 0.23 | -0.42 ± 0.18 | 02.04 ± 0.29 | -3.61 ± 0.20 | 01.05 ± 0.16 | -2.29 ± 0.21 | -0.04 ± 0.11 |
| Ground-feeder | Rufous-naped Lark (*Mirafra africana*) | 02.98 ± 0.36 | -0.19 ± 0.35 | -1.50 ± 0.31 | -1.12 ± 0.21 | 0.19 ± 0.26 | -1.57 ± 0.18 | 0.45 ± 0.19 | -2.98 ± 0.14 | 0.03 ± 0.12 |
| Ground-feeder | Sentinel Rock-Thrush (*Monticola explorator*) | -4.24 ± 0.77 | 0.46 ± 0.33 | -0.74 ± 0.63 | -0.54 ± 0.70 | -1.35 ± 0.69 | -4.93 ± 0.44 | -0.23 ± 0.44 | -0.71 ± 0.62 | -1.25 ± 0.66 |
| Ground-feeder | Cape Rock-Thrush (*Monticola rupestris*) | -3.01 ± 0.41 | 0.91 ± 0.25 | -0.50 ± 0.45 | 0.26 ± 0.21 | 0.22 ± 0.33 | -4.25 ± 0.29 | 0.69 ± 0.15 | -1.05 ± 0.32 | 0.05 ± 0.14 |
| Ground-feeder | Mountain Wheatear (*Oenanthe monticola*) | -1.31 ± 0.16 | -0.01 ± 0.16 | -0.56 ± 0.21 | -0.06 ± 0.14 | -1.30 ± 0.21 | -2.97 ± 0.15 | -0.36 ± 0.18 | -1.56 ± 0.16 | -0.14 ± 0.18 |
| Ground-feeder | Capped Wheatear (*Oenanthe pileata*) | 0.59 ± 0.26 | 0.18 ± 0.14 | 0.18 ± 0.22 | -0.67 ± 0.20 | -2.08 ± 0.30 | -2.88 ± 0.19 | -0.05 ± 0.16 | -2.17 ± 0.13 | 0.04 ± 0.11 |
| Ground-feeder | Groundscraper Thrush (*Psophocichla litsipsirupa*) | -0.51 ± 0.19 | 0.32 ± 0.23 | -0.37 ± 0.21 | 0.00 ± 0.17 | 01.76 ± 0.21 | -2.82 ± 0.15 | 0.67 ± 0.16 | -2.31 ± 0.16 | -0.20 ± 0.13 |
| Ground-feeder | Fiscal Flycatcher (*Sigelus silens*) | 0.14 ± 0.13 | -0.13 ± 0.12 | -0.55 ± 0.17 | 0.22 ± 0.14 | -0.40 ± 0.16 | -1.35 ± 0.10 | 0.30 ± 0.07 | -1.72 ± 0.10 | 0.35 ± 0.06 |
| Ground-feeder | Cape Grassbird (*Sphenoeacus afer*) | -1.30 ± 0.16 | 0.25 ± 0.12 | -0.29 ± 0.20 | -0.19 ± 0.16 | -0.23 ± 0.19 | -3.01 ± 0.15 | 0.15 ± 0.11 | -1.27 ± 0.16 | -0.46 ± 0.18 |
| Ground-feeder | Pied Starling (*Spreo bicolor*) | -0.39 ± 0.15 | 0.11 ± 0.15 | -0.20 ± 0.18 | 0.06 ± 0.14 | -1.76 ± 0.19 | -3.15 ± 0.18 | -0.01 ± 0.12 | -2.43 ± 0.16 | 0.66 ± 0.14 |
| Ground-feeder | Brown-crowned Tchagra (*Tchagra australis*) | 0.57 ± 0.21 | -0.06 ± 0.27 | -0.74 ± 0.21 | -0.29 ± 0.17 | 01.99 ± 0.24 | -2.81 ± 0.18 | 01.05 ± 0.26 | -2.75 ± 0.16 | -0.02 ± 0.12 |
| Ground-feeder | Black-crowned Tchagra (*Tchagra senegalus*) | -0.56 ± 0.21 | 0.55 ± 0.24 | -0.92 ± 0.31 | 0.00 ± 0.17 | 01.45 ± 0.20 | -3.72 ± 0.36 | -0.53 ± 0.85 | -2.94 ± 0.43 | -2.50 ± 01.17 |
| Ground-feeder | Mocking Cliff-Chat (*Thamnolaea cinnamomeiventris*) | -2.13 ± 0.23 | 0.32 ± 0.15 | -0.65 ± 0.26 | -0.38 ± 0.22 | 0.49 ± 0.23 | -3.44 ± 0.17 | 0.62 ± 0.10 | -1.30 ± 0.20 | -0.04 ± 0.11 |
| Ground-feeder | Southern Yellow-billed Hornbill (*Tockus leucomelas*) | -9.25 ± 02.59 | -0.17 ± 0.12 | -0.76 ± 0.21 | -0.33 ± 0.16 | 08.61 ± 02.33 | -4.46 ± 0.24 | 0.68 ± 0.11 | -2.87 ± 0.23 | 0.21 ± 0.13 |
| Ground-feeder | Kurrichane Thrush (*Turdus libonyanus*) | -0.92 ± 0.17 | 0.42 ± 0.21 | -0.44 ± 0.20 | 0.13 ± 0.15 | 01.44 ± 0.19 | -3.00 ± 0.14 | 0.64 ± 0.12 | -1.77 ± 0.14 | -0.14 ± 0.11 |
| Ground-feeder | Kurrichane Buttonquail (*Turnix sylvaticus*) | -1.46 ± 0.46 | 0.04 ± 0.29 | -1.08 ± 0.68 | -0.78 ± 0.53 | 0.11 ± 0.43 | -3.02 ± 0.32 | 0.33 ± 0.13 | 0.78 ± 0.57 | 0.07 ± 0.24 |
| Ground-feeder | African Grey Hornbill (*Tockus nasutus*) | -0.37 ± 0.17 | 0.64 ± 0.29 | -0.69 ± 0.19 | 0.08 ± 0.15 | 01.88 ± 0.18 | -3.58 ± 0.19 | 0.64 ± 0.24 | -3.12 ± 0.19 | -0.30 ± 0.20 |
| Ground-feeder | African Hoopoe (*Upupa africana*) | 01.81 ± 0.58 | 0.18 ± 0.22 | -0.42 ± 0.19 | 02.90 ± 01.06 | 0.69 ± 0.22 | -1.41 ± 0.12 | 0.74 ± 0.22 | -1.60 ± 0.10 | -0.06 ± 0.08 |
| Ground-feeder | African Pipit (*Anthus cinnamomeus*) | 03.24 ± 0.45 | 0.24 ± 0.18 | 01.81 ± 0.50 | -0.21 ± 0.16 | -0.64 ± 0.27 | -0.62 ± 0.17 | -0.10 ± 0.11 | -3.09 ± 0.15 | 0.33 ± 0.08 |
| Ground-feeder | African Sacred Ibis (*Threskiornis aethiopicus*) | 01.12 ± 0.18 | 0.05 ± 0.11 | 0.36 ± 0.18 | 0.88 ± 0.26 | -0.89 ± 0.18 | -1.62 ± 0.12 | -0.04 ± 0.08 | -2.23 ± 0.11 | 0.21 ± 0.09 |
| Ground-feeder | African Stonechat (*Saxicola torquatus*) | 02.54 ± 0.37 | 0.13 ± 0.11 | 0.57 ± 0.25 | -0.20 ± 0.16 | -2.34 ± 0.36 | -1.68 ± 0.12 | 0.40 ± 0.09 | -3.17 ± 0.13 | 0.52 ± 0.07 |
| Ground-feeder | Anteating Chat (*Myrmecocichla formicivora*) | -0.53 ± 0.14 | -0.11 ± 0.14 | -0.08 ± 0.16 | -1.10 ± 0.21 | -1.33 ± 0.17 | -2.71 ± 0.12 | -0.20 ± 0.13 | -2.03 ± 0.12 | 0.24 ± 0.12 |
| Ground-feeder | Arrow-marked Babbler (*Turdoides jardineii*) | -0.20 ± 0.19 | 01.45 ± 0.41 | -0.06 ± 0.22 | -0.09 ± 0.17 | 02.27 ± 0.23 | -2.96 ± 0.15 | 0.65 ± 0.23 | -2.78 ± 0.16 | -0.42 ± 0.18 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Ground-feeder | Bokmakierie (*Telophorus zeylonus*) | 0.34 ± 0.13 | -0.03 ± 0.12 | -0.72 ± 0.19 | -0.27 ± 0.13 | -1.64 ± 0.19 | -2.62 ± 0.14 | 0.28 ± 0.07 | -2.32 ± 0.12 | 0.39 ± 0.09 |
| Ground-feeder | Neddicky (*Cisticola fulvicapilla*) | 03.07 ± 0.43 | 0.02 ± 0.58 | -1.23 ± 0.26 | -0.52 ± 0.18 | 01.17 ± 0.38 | -0.66 ± 01.02 | 03.34 ± 02.87 | -3.48 ± 0.20 | -0.89 ± 0.44 |
| Ground-feeder | Secretarybird (*Sagittarius serpentarius*) | -1.15 ± 0.25 | 0.24 ± 0.17 | 0.19 ± 0.28 | -1.14 ± 0.36 | -0.54 ± 0.24 | -2.84 ± 0.27 | 0.03 ± 0.18 | -1.19 ± 0.27 | 0.04 ± 0.12 |
| Hawker | Little Swift (*Apus affinis*) | 01.64 ± 0.22 | -0.09 ± 0.17 | -0.12 ± 0.21 | 0.66 ± 0.37 | 0.12 ± 0.21 | -0.76 ± 0.16 | 0.59 ± 0.28 | -2.37 ± 0.14 | 0.27 ± 0.08 |
| Hawker | Fiery-necked Nightjar (*Caprimulgus pectoralis*) | -2.83 ± 0.65 | 0.28 ± 02.27 | -1.44 ± 0.55 | -0.34 ± 0.26 | 02.00 ± 0.66 | -3.66 ± 0.34 | 0.71 ± 01.91 | -2.07 ± 0.39 | 0.26 ± 0.93 |
| Hawker | Common House-Martin (*Delichon urbicum*) | 0.89 ± 0.50 | -0.13 ± 0.47 | -1.38 ± 0.70 | -0.61 ± 0.29 | -0.03 ± 0.43 | -0.20 ± 0.32 | 01.10 ± 0.65 | -1.12 ± 0.25 | -0.05 ± 0.17 |
| Hawker | Fork-tailed Drongo (*Dicrurus adsimilis*) | -0.14 ± 0.18 | 0.62 ± 0.29 | -0.08 ± 0.21 | 0.17 ± 0.17 | 02.43 ± 0.21 | -3.26 ± 0.17 | 0.84 ± 0.21 | -3.32 ± 0.17 | -0.23 ± 0.17 |
| Hawker | Lesser Striped Swallow *(Hirundo abyssinica*) | 0.90 ± 0.25 | 01.63 ± 0.57 | -0.19 ± 0.21 | 0.64 ± 0.17 | 02.20 ± 0.23 | -2.88 ± 0.19 | 01.07 ± 0.29 | -2.95 ± 0.17 | -0.23 ± 0.18 |
| Hawker | Pearl-breasted Swallow (*Hirundo dimidiata*) | -0.88 ± 0.21 | 0.10 ± 0.25 | -0.51 ± 0.24 | -0.48 ± 0.17 | 01.88 ± 0.22 | -3.16 ± 0.18 | 0.52 ± 0.14 | -2.76 ± 0.25 | 0.18 ± 0.11 |
| Hawker | Rock Martin (*Hirundo fuligula*) | -0.79 ± 0.16 | 0.34 ± 0.14 | -0.20 ± 0.20 | 0.80 ± 0.19 | 0.13 ± 0.19 | -2.07 ± 0.11 | 0.28 ± 0.08 | -1.07 ± 0.13 | 0.00 ± 0.09 |
| Hawker | White-fronted Bee-eater (*Merops bullockoides*) | -1.33 ± 0.18 | -0.06 ± 0.12 | -0.17 ± 0.19 | 0.04 ± 0.15 | 01.41 ± 0.19 | -2.81 ± 0.13 | 0.37 ± 0.08 | -2.17 ± 0.17 | 0.10 ± 0.11 |
| Hawker | Little Bee-eater (*Merops pusillus*) | -1.18 ± 0.32 | 0.24 ± 0.33 | -0.73 ± 0.37 | -0.71 ± 0.27 | 0.89 ± 0.27 | -3.19 ± 0.33 | 0.36 ± 0.19 | -1.53 ± 0.32 | 0.01 ± 0.15 |
| Hawker | African Palm-Swift (*Cypsiurus parvus*) | 01.31 ± 0.38 | 0.37 ± 0.18 | 0.20 ± 0.17 | 03.30 ± 0.77 | 0.69 ± 0.17 | -1.38 ± 0.10 | 0.44 ± 0.12 | -2.16 ± 0.12 | 0.03 ± 0.09 |
| Hawker | Alpine Swift (*Tachymarptis melba*) | -1.55 ± 0.43 | 0.97 ± 0.65 | -0.03 ± 0.44 | -0.19 ± 0.29 | 0.95 ± 0.40 | -2.97 ± 0.36 | 0.37 ± 0.18 | -0.74 ± 0.46 | -0.06 ± 0.18 |
| Predator | Little Sparrowhawk *(Accipiter minullus)* | -1.42 ± 0.29 | 0.30 ± 0.23 | -0.27 ± 0.36 | 01.14 ± 0.28 | 0.86 ± 0.32 | -3.01 ± 0.29 | 01.33 ± 0.28 | -1.78 ± 0.33 | 0.65 ± 0.18 |
| Predator | Marsh Owl (*Asio capensis*) | 0.11 ± 0.26 | 0.02 ± 0.21 | 0.48 ± 0.28 | -0.79 ± 0.24 | -1.59 ± 0.29 | -2.36 ± 0.19 | 0.11 ± 0.11 | -1.70 ± 0.16 | 0.41 ± 0.14 |
| Predator | Jackal Buzzard (*Buteo rufofuscus*) | -1.67 ± 0.36 | 0.45 ± 0.27 | -0.06 ± 0.37 | -0.76 ± 0.46 | -0.39 ± 0.33 | -3.01 ± 0.34 | 0.25 ± 0.23 | -0.90 ± 0.41 | -0.17 ± 0.17 |
| Predator | Brown Snake-Eagle (*Circaetus cinereus*) | -0.85 ± 0.29 | -0.06 ± 0.31 | -0.45 ± 0.26 | -1.23 ± 0.35 | 01.45 ± 0.28 | -3.72 ± 0.41 | 0.48 ± 0.41 | -2.80 ± 0.60 | -2.14 ± 01.49 |
| Predator | Lanner Falcon (*Falco biarmicus*) | 0.82 ± 0.30 | 0.10 ± 0.23 | 0.62 ± 0.36 | -0.13 ± 0.16 | 0.15 ± 0.23 | -31.91 ± 73.95 | 05.64 ± 13.26 | -55.51 ± 519.75 | 07.48 ± 163.49 |
| Predator | Rock Kestrel (*Falco rupicolus*) | -1.07 ± 0.38 | 0.15 ± 0.20 | 0.12 ± 0.31 | -2.32 ± 0.73 | -0.91 ± 0.32 | -2.50 ± 0.20 | 0.21 ± 0.13 | -1.15 ± 0.21 | -0.02 ± 0.19 |
| Predator | Gabar Goshawk (*Melierax gabar*) | -1.48 ± 0.36 | -0.34 ± 0.22 | -1.18 ± 0.38 | -0.40 ± 0.23 | 02.19 ± 0.36 | -3.29 ± 0.24 | 0.58 ± 0.15 | -2.08 ± 0.23 | 0.18 ± 0.13 |
| Predator | Martial Eagle (*Polemaetus bellicosus*) | -8.05 ± 05.67 | -0.05 ± 0.40 | -1.21 ± 01.10 | -13.26 ± 10.53 | -0.50 ± 01.03 | -3.59 ± 0.63 | 0.73 ± 0.35 | -0.80 ± 0.77 | -0.42 ± 0.53 |
| Predator | African Grass-Owl (*Tyto capensis*) | -1.50 ± 0.29 | 0.36 ± 0.18 | 0.11 ± 0.27 | -0.47 ± 0.25 | -0.85 ± 0.28 | -13.98 ± 199.69 | -0.94 ± 184.75 | -17.92 ± 30.41 | -40.32 ± 79.14 |
| Predator | African Harrier-Hawk (*Polyboroides typus*) | 0.11 ± 0.29 | 0.46 ± 0.38 | 0.13 ± 0.32 | 0.63 ± 0.24 | 0.86 ± 0.31 | -33.90 ± 111.00 | 13.87 ± 47.43 | -9.93 ± 07.47 | -20.28 ± 19.52 |
| Predator | African Hawk-Eagle (*Aquila spilogaster*) | -6.59 ± 02.48 | -0.31 ± 0.21 | -2.27 ± 0.81 | -0.36 ± 0.26 | 04.12 ± 02.19 | -4.67 ± 0.45 | -0.10 ± 0.43 | -1.65 ± 0.45 | -1.91 ± 01.06 |

| Guild | Species | Initial Occupancy | | | | | Colonization | | Extinction | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Intercept $\hat{\beta}_0$ | Protected areas $\hat{\beta}_1$ | Agriculture $\hat{\beta}_2$ | Urban $\hat{\beta}_3$ | Savanna $\hat{\beta}_4$ | Intercept $\hat{\beta}_5$ | Protected areas $\hat{\beta}_6$ | Intercept $\hat{\beta}_7$ | Protected areas $\hat{\beta}_8$ |
| Predator | Barn Owl (*Tyto alba*) | -0.48 ± 0.24 | 0.12 ± 0.22 | -0.31 ± 0.28 | -0.02 ± 0.16 | 0.55 ± 0.25 | -1.81 ± 0.15 | 0.14 ± 0.12 | -0.47 ± 0.17 | -0.15 ± 0.11 |
| Predator | Black Sparrowhawk (*Accipiter melanoleucus*) | -2.23 ± 0.32 | 0.29 ± 0.23 | -0.25 ± 0.39 | 0.37 ± 0.20 | -0.41 ± 0.34 | -2.66 ± 0.17 | 0.26 ± 0.13 | -0.94 ± 0.26 | 0.19 ± 0.26 |
| Predator | Black-chested Snake-Eagle (*Circaetus pectoralis*) | -1.17 ± 0.27 | -0.02 ± 0.23 | -0.41 ± 0.33 | -0.46 ± 0.20 | 01.52 ± 0.29 | -2.13 ± 0.17 | 0.74 ± 0.21 | -2.13 ± 0.31 | 0.21 ± 0.12 |
| Predator | Hamerkop (*Scopus umbretta*) | 01.14 ± 0.31 | 0.33 ± 0.59 | -0.44 ± 0.25 | -0.04 ± 0.17 | 0.79 ± 0.29 | 02.58 ± 02.09 | 12.15 ± 05.70 | -35.59 ± 619.07 | -12.40 ± 282.24 |
| Predator | Shikra (*Accipiter badius*) | -1.66 ± 0.40 | 0.01 ± 0.26 | -0.26 ± 0.31 | 0.17 ± 0.24 | 01.83 ± 0.38 | -3.81 ± 0.38 | 0.42 ± 0.24 | -1.97 ± 0.35 | 0.38 ± 0.25 |
| Predator | Verreauxs Eagle (*Aquila verreauxii*) | -2.93 ± 0.33 | 0.57 ± 0.18 | -0.19 ± 0.38 | 0.50 ± 0.19 | 0.25 ± 0.31 | -3.62 ± 0.18 | 0.63 ± 0.09 | -0.77 ± 0.24 | 0.10 ± 0.12 |
| Vegivore | Blue Crane (*Anthropoides paradiseus*) | -2.81 ± 0.35 | -0.19 ± 0.50 | 0.30 ± 0.32 | -0.34 ± 0.32 | -0.50 ± 0.36 | -4.70 ± 0.39 | 0.11 ± 0.23 | -1.66 ± 0.35 | 0.46 ± 0.41 |
| Vegivore | Speckled Mousebird (*Colius striatus*) | 0.83 ± 0.18 | 0.10 ± 0.14 | -0.21 ± 0.16 | 01.10 ± 0.30 | 0.39 ± 0.16 | -1.21 ± 0.10 | 0.67 ± 0.18 | -1.94 ± 0.10 | -0.15 ± 0.09 |
| Vegivore | Grey Go-away-bird (*Corythaixoides concolor*) | 0.26 ± 0.15 | 0.28 ± 0.19 | -0.40 ± 0.17 | 01.38 ± 0.22 | 01.94 ± 0.18 | -3.00 ± 0.14 | 0.60 ± 0.15 | -3.16 ± 0.15 | -0.23 ± 0.15 |
| Vegivore | Streaky-headed Seedeater (*Crithagra gularis*) | -0.32 ± 0.15 | 0.51 ± 0.24 | -0.93 ± 0.20 | 0.28 ± 0.15 | -0.10 ± 0.17 | -2.10 ± 0.11 | 0.54 ± 0.11 | -1.47 ± 0.12 | 0.07 ± 0.07 |
| Vegivore | Crested Francolin (*Dendroperdix sephaena*) | -1.66 ± 0.29 | 0.55 ± 0.27 | -0.17 ± 0.21 | 0.00 ± 0.19 | 02.97 ± 0.30 | -4.25 ± 0.25 | 01.02 ± 0.16 | -2.91 ± 0.20 | 0.07 ± 0.12 |
| Vegivore | Cape Bunting (*Emberiza capensis*) | -1.67 ± 0.19 | 0.23 ± 0.15 | -0.34 ± 0.24 | -0.29 ± 0.20 | 0.15 ± 0.21 | -3.40 ± 0.19 | 0.45 ± 0.09 | -0.81 ± 0.20 | 0.11 ± 0.10 |
| Vegivore | Coqui Francolin (*Peliperdix coqui*) | -0.75 ± 0.21 | 0.13 ± 0.27 | -1.42 ± 0.29 | -0.80 ± 0.20 | 0.97 ± 0.20 | -3.22 ± 0.21 | 0.59 ± 0.15 | -1.89 ± 0.18 | 0.14 ± 0.10 |
| Vegivore | Spur-winged Goose (*Plectropterus gambensis*) | 01.17 ± 0.21 | 0.03 ± 0.12 | 0.86 ± 0.26 | -0.52 ± 0.16 | -0.97 ± 0.22 | -1.47 ± 0.12 | -0.11 ± 0.09 | -2.14 ± 0.12 | 0.27 ± 0.08 |
| Vegivore | Cape Weaver (*Ploceus capensis*) | -0.99 ± 0.18 | 0.40 ± 0.15 | -0.31 ± 0.23 | 0.52 ± 0.16 | -0.13 ± 0.20 | -2.11 ± 0.13 | 0.14 ± 0.10 | -1.04 ± 0.18 | -0.26 ± 0.15 |
| Vegivore | Village Weaver (*Ploceus cucullatus*) | -1.26 ± 0.23 | -0.07 ± 0.16 | -0.26 ± 0.24 | 0.30 ± 0.19 | 01.47 ± 0.24 | -2.81 ± 0.17 | 0.42 ± 0.11 | -1.58 ± 0.19 | 0.25 ± 0.12 |
| Vegivore | Natal Spurfowl (*Pternistis natalensis*) | -1.57 ± 0.27 | 0.27 ± 0.23 | -0.79 ± 0.23 | -0.57 ± 0.17 | 02.16 ± 0.27 | -3.07 ± 0.15 | 0.62 ± 0.16 | -2.14 ± 0.16 | -0.33 ± 0.16 |
| Vegivore | Red-winged Francolin (*Scleroptila levaillantii*) | -2.66 ± 0.46 | 0.07 ± 0.23 | -1.95 ± 0.58 | -1.41 ± 0.51 | -1.81 ± 0.52 | -3.71 ± 0.28 | 0.19 ± 0.16 | -8.67 ± 08.78 | -22.12 ± 23.19 |
| Vegivore | Orange River Francolin (*Scleroptila levaillantoides*) | -0.48 ± 0.16 | -0.09 ± 0.18 | -0.27 ± 0.21 | -0.83 ± 0.17 | -1.98 ± 0.22 | -3.32 ± 0.20 | -0.01 ± 0.14 | -2.90 ± 0.21 | 0.62 ± 0.16 |
| Vegivore | Shelleys Francolin (*Scleroptila shelleyi*) | -4.00 ± 0.78 | 0.09 ± 0.28 | -0.76 ± 0.70 | 0.16 ± 0.30 | 0.79 ± 0.61 | -5.56 ± 0.78 | 0.34 ± 0.30 | -2.47 ± 01.87 | 0.42 ± 0.64 |
| Vegivore | Swainsons Spurfowl (*Pternistis swainsonii*) | 04.25 ± 0.82 | 0.04 ± 0.49 | 01.33 ± 0.76 | -0.83 ± 0.24 | 0.62 ± 0.59 | -0.62 ± 0.20 | 0.62 ± 0.25 | -3.34 ± 0.16 | 0.18 ± 0.10 |

Chapter 5

# Dynamic occupancy model reveals that Cape Rock-jumper (*Chaetops frenatus*) is disappearing from the hottest part of its range

Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. Photograph by Richard Flack.

## 5.1 ABSTRACT

**AIM**: Climate and land-use change pose extinction risks to species world-wide. Understanding how species' occupancy dynamics respond to climate and land-use change is essential to reduce the risk of extinction. In this chapter, I use dynamic occupancy models which account for two important aspects of species' ranges: (i) detection process in atlas project data collection; and (ii) the dynamic nature of species' distributions. I apply it to the Cape Rock-jumper (*Chaetops frenatus*), a species that has declined in abundance and range extent over recent decades due to its inability to cope with high temperatures, with specific emphasis on the extinction component of its range dynamics.

**METHODS**: I analysed Cape Rock-jumper detection / non-detection data collected from regular defined grid cells across the study area over two phases of the Southern African Bird Atlas Project (SABAP): 1987-1992 (SABAP 1) & 2007-2015 (SABAP 2). I developed a dynamic occupancy model to examine the range dynamics (occupancy and extinction probability) of the Cape Rock-jumper. I estimated occupancy probability at SABAP 1 as a function of mean temperature and precipitation over the warmest annual quarter, proportion of fynbos vegetation and protected area per grid cell. Extinction probability was estimated as a function of mean temperature and precipitation over the warmest annual quarter. Occupancy probability during SABAP 2 was estimated using the occupancy status (presence or absence of Cape Rock-jumper) during SABAP 1 and the extinction probability.

**RESULTS**: The dynamic occupancy model captured well the range contraction of the Cape Rock-jumper between SABAP 1 and SABAP 2. Occupancy probability during SABAP 1 increased significantly with the proportion of fynbos vegetation and protected area per grid cell, whilst it decreased with increases in mean temperature (significant relationship) and precipitation (non-significant) over the warmest annual quarter. Cape Rock-jumper extinction probability increased with increases in mean temperature (significant relationship) and precipitation over the warmest annual quarter (non-significant).

**MAIN CONCLUSIONS**: My results suggest Cape Rock-jumper's range contractions during the study was likely due to increasing extinction probability in response to increases in the mean temperature over the warmest annual quarter. Thus, climate change poses a significant extinction threat to the Cape Rock-jumper. This work suggests that dynamic occupancy models are a powerful tool to analyse species distributions and identify species in need of conservation action.

**KEY WORDS**: Cape Rock-jumper (*Chaetops frenatus*), fynbos birds, dynamic occupancy models, species distribution modelling, climate change

## 5.2 INTRODUCTION

A rapidly changing climate impacts biodiversity throughout the world. Climate change is thought to have contributed significantly to the extinction of species (Pounds et al., 1999; Waller et al. 2007), whilst many others are at risk (Parmesan & Yohe, 2003; Huntley et al., 2006; Jetz et al., 2007). In addition, some natural landscapes throughout the world are converted to land-use types that support the needs of an ever-increasing human population, such as urban or agricultural area (DeFries et al., 2007; United Nations, 2013b). Given such rapid changes in climate and land-use, it is of critical importance to quantify how these two processes affect species' distributions and population dynamics. This information can be used for biodiversity protection, and forms an important component to conservation strategies (Hannah et al., 2002; Araújo & Guisan, 2006).

A good way to measure how species are affected by climate and land-use change is to measure the suitability of a particular habitat for a species, with respect to these two variables. The suitability of habitats for a particular species can be estimated using site-occupancy models. Site-occupancy is the probability a species occupies a particular site (generally, a regular grid cell), given a suite of conditions, e.g. climatic (such as temperature, or rainfall amount), physical (such as land-use type, or habitat), and others (MacKenzie et al., 2003; Bailey et al., 2014). Typically, species distribution models (SDMs) have been used to model species' habitat suitability, and have been applied successfully over a wide range of disciplines (e.g., Elith & Graham, 2009; Morin et al., 2009). In these instances, SDMs relate species' known presences to associated environmental conditions, and use these relationships to project their ranges into the future (Araújo & Guisan, 2006; Dormann et al., 2007; Elith & Leathwick, 2009).

Most SDMs do not account for: (i) detection probability; and (ii) the dynamic nature of species' distributions. In reality, no species is detected perfectly within all the habitats it occupies (MacKenzie et al., 2002). Failure to account for detection probability can result in underestimates of occupancy as well as biased relationships between occupancy probability and environmental conditions (Altwegg et al., 2008; Kéry, 2011; Lahoz-Monfort et al., 2014). Traditional SDMs assume that a species is in equilibrium with its environment, and that the environment is suitable where the species occurs and unsuitable where it does not occur (Hirzel et al., 2001; Araújo & Townsend Peterson, 2012; Yackulic et al., 2012). The equilibrium assumption is violated where species lag behind the changing climate and can lead to biased inference about environmental suitability (Yackulic et al., 2015; Clement et al., 2016). Huntley et al. (2010) therefore called for a more mechanistic approach to modelling species distributions. They suggested modelling environmental suitability, population dynamics and dispersal as separate modules (Huntley et al 2010). Such an approach, however, requires detailed data that are not readily available for most species. A slightly less mechanistic approach is to examine range dynamics by taking a metapopulation view and studying colonisation and extinction at local sites (Altwegg et al., 2008; Bled et al., 2013; Yackulic et al., 2015) using dynamic occupancy models. Colonization probability is defined as the probability a previously unoccupied site becomes occupied, and extinction probability is the complement to persistence probability, where persistence is the probability a previously occupied site stays occupied (MacKenzie et al., 2002; Royle & Kéry, 2007). Dynamic occupancy models estimate extinction and colonization directly (MacKenzie et al., 2006; Royle & Kéry, 2007; Kéry, 2011). Modelling directly colonization and extinction allows researchers to unmask the dynamics that lead to observed species' ranges. This is incredibly powerful, and especially useful for species expanding or contracting their range.

The Cape Rock-jumper *(Chaetops frenatus)* is a medium-sized insectivorous bird, indigenous to the Western Cape of South Africa (Frazer, 1997), and is a good candidate species for distribution modelling. Firstly, Cape Rock-jumper actively avoids human-dominated land-use types such as urban and agricultural areas, and strictly inhabits the natural vegetation of the region (Frazer, 1997; Lee & Barnard, 2016). Land-use change of the natural habitat over its current range therefore poses a significant risk to the Cape Rock-jumper. Secondly, the Cape Rock-jumper has decreased markedly in abundance and range extent over recent decades, in response to a warmer and drier climate (Huntley et al., 2012; Milne et al., 2015; Lee & Barnard, 2016). The Cape Rock-jumper has shown to be vulnerable to increases in temperature caused by climate change (Milne et al., 2015); its threshold for increasing evaporative water loss at high temperatures is relatively low compared to other birds in the region. Species that lose water to the atmosphere will necessarily have to replenish water stores, presumably via accessible surface water (e.g., Lee et al., 2017). Given that climate over the last five decades has become drier in the Western Cape of South Africa (van Wilgen et al., 2016), less rainfall could limit the amount of surface water available. In turn, less surface water can limit the distribution of the Cape Rock-jumper, especially during periods when it experiences the highest rate of evaporative water loss (i.e., the warmest period of the year). Third, and finally, the Cape Rock-jumper's conservation status was recently uplisted to 'Near Threatened' in South Africa (Taylor et al., 2014). Thus, its persistence may be heavily dependent on protected areas. Together, the three abovementioned points demonstrate the importance of examining the Cape Rock-jumper's range dynamics, especially in relation to climate and land-use change.

The central aim of this chapter is to develop a dynamic occupancy model for the Cape Rock-jumper, and examine its range dynamics. I make use of Cape Rock-jumper detection data collected over two phases of the Southern African Bird Atlas Project (SABAP; Harebottle et al., 2007): SABAP 1 (1987-1992), and SABAP 2 (2007-2015). I estimate its occupancy probability at SABAP 1 as a function of temperature, rainfall, protected area, and natural vegetation. Because the Cape Rock-jumper's range has decreased in extent over the last few decades in response to a hotter and drier climate (Milne et al., 2015; Lee & Barnard, 2016), I examine the extinction processes between SABAP 1 and SABAP 2 as a function of temperature and rainfall (which affects the availability of surface water). Finally, I estimate its occupancy probability at SABAP 2. A secondary aim of this chapter is to assess how well the dynamic occupancy model captures the known decrease in range extent of the Cape Rock-jumper (Milne et al., 2015; Lee & Barnard, 2016).

## 5.3 METHODS

### *5.3.1 Study area*

My study area was situated in south-west South Africa, primarily in the Western Cape because this region encompasses the entire range of Cape Rock-jumper (Figs. 1.1 & 1.3). This area generally experiences a Mediterranean climate. Winters (June-August) are wet and cool, and summers (December-February) are dry and hot (Conradie, 2012). Mean annual rainfall ranges from 150mm in the driest of regions (Karoo desert, situated inland), to around 2000mm in the Kogelberg mountain range which is situated along the south-western coast of the study area (Maitre et al., 1996; Conradie, 2012). Temperatures are generally mild along the coast, and rarely exceed 40 °C or drop below freezing (Conradie, 2012). However, temperatures become more extreme inland and in the Klein Karoo desert, where average daily minimum temperatures in winter are -6 °C, whilst average maximum temperatures are in the mid-30s during summer, but can often exceed 40 °C (Bulpin, 1992). The landscape is characterised by extensive, rugged mountain ranges, composed of mostly granite and sandstone with large rocky outcrops (Trustwell, 1977). The vegetation in the region is characterised as fynbos, which is made up of sclerophyllous shrubs, and very few tall-growing endemic trees (Manning, 2008).

*5.3.2 Study species and detection/non-detection data*

The Cape Rock-jumper is a medium-sized bird (20-25cm in length), and primarily feeds on insects (Frazer, 1997).  It is a conspicuous bird with a far-carrying and unique call, making it readily detectable when present. Cape Rock-jumper is endemic to the fynbos region of the Western Cape of South Africa, and prefers to inhabit areas with shorter vegetation, and drier slopes of mountains or hills (Frazer, 1997; Lee & Barnard, 2016).

Cape Rock-jumper detection data were extracted from two atlas projects in Southern Africa. The first Southern African Bird Atlas Projects (SABAP) ran from 1987 to 1992 (SABAP 1), and the second (SABAP 2) from 2007 – present (still ongoing in 2018). Both projects employed similar protocols; volunteers surveyed pre-defined sampling areas over a fixed time period and submitted checklists of all bird species seen or heard. Only the presence of a species was recorded, not the number of birds seen or heard. During SABAP 1, data were collected across southern Africa on a quarter degree grid cell level (QDGC; 15’ × 15’ in resolution [unit is arcminutes], which is an area of approximately 550 $km^2$, Harrison et al., 1997). Data collection during SABAP 2 is on a pentad scale (a pentad is 5’ x 5’ (arcminutes), approximately 61 $km^2$ , nine pentads make up one QDGC). Most of the data were collected by volunteers birding intensely for a few hours on a single day, although volunteers were allowed to add species to their checklists for up to and including 30 days in SABAP 1, and five days in SABAP 2. The protocol for SABAP 2 further required volunteers to have birded intensely for at least two hours. In both projects the data were vetted by a committee (Frazer, 1997; Harebottle et al., 2007). For the data analysis, SABAP 2 data were pooled over the nine pentads that make up a QDGC in order to compare data at the same scale for the two atlas projects. My study area consisted of 354 QDGCs, which corresponded to an area of approximately 195 000 $km^2$. See Figure A5.1 in Appendix 5 for the sampling effort during each SABAP.

### *5.3.3 Climate data*

Lee and Barnard (2016) modelled the distribution of Cape Rock-jumper between 1987 and 2013 as a function of temperature and rainfall using SDMs. They found the mean temperature over the warmest annual quarter was the most significant temperature variable limiting the Cape Rock-jumper's range. Following Lee and Barnard, and given the inability of the species to cope with prolonged periods of high temperatures (Milne et al., 2015), I selected the mean temperature during the warmest annual quarter as a climate variable in my modelling framework. Higher mean temperatures brought about through climate changes means that species will lose more water to the environment via evaporative water loss, and this is particularly true for the Cape Rock-jumper (Milne et al., 2015). For this reason, I selected precipitation over the warmest annual quarter to represent water availability over the warmest period (when evaporation demands of Cape Rock-jumper the highest) as a covariate in my modelling framework.

I sourced daily data for rainfall and mean temperature from NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP) dataset, prepared by the Climate Analytics Group and NASA Ames Research Center using the NASA Earth Exchange, and distributed by the NASA Center for Climate Simulation (Thrasher et al., 2012). The data are derived from the General Circulation Model (GCM) runs performed under the Coupled Model Intercomparison Project

Phase 5 (CMIP5) for the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Taylor et al., 2012). These data are the result of a process of statistical downscaling to 0.25 degrees (approximately 25 km x 25 km) and bias-correction against historical data from Global Meteorological Forcing Dataset (GMFD) for Land Surface Modelling for the period 1950–2005 (Thrasher et al., 2012). To illustrate the development and application of my dynamic occupancy model, I selected one GCM that is deemed to perform well in South Africa (C. Lennard, personal communication), the GFDL-CM3 (Donner et al., 2011), and extracted the data for this model for the period between 1986 and 2005 (see Fig. 5.1).

To compute the mean temperature over the warmest annual quarter, I first identified the warmest annual quarter of the year: for each day within a calendar year, I first calculated the mean temperature as the mean of the daily maximum and minimum. I then calculated the monthly mean as the mean of the daily means. Thereafter, I scanned all monthly means within a calendar year and identified a single three-month period for which the three-monthly mean was highest; this was identified as the warmest annual quarter of the calendar year, and the mean value was used in the analysis. Because I allowed the warmest quarter of the year to constitute any three month period of the calendar year, the warmest quarter of the year may not constitute the same three-month period each calendar year. I used calendar years for both the climate and bird detection data because these data need to align for the analyses. Using a calendar year for the temperature data splits the southern-hemisphere summer (which generally runs from December to February), and potentially, risks missing the signal between the mean temperature of the warmest annual quarter and the key population demographics in this study. However, given the rate of global warming and climate change, climate throughout the year is expected to increase year on year, which would be picked up in my analysis. For precipitation, I summed the daily precipitation for each of those quarters to obtain total precipitation over the warmest quarter. For temperature, over each of the quarters, I then averaged the monthly means of daily minimum and maximum temperatures to obtain the mean temperature over the warmest quarter. I averaged monthly means in temperature as I was interested in mean temperature over prolonged periods, and not in extreme values, such as daily maximum or minimum (which daily data would better represent).

To allow for lagged (Roy et al., 2001; Pearce-Higgins et al., 2015) or indirect (Rotenberry & Wiens, 2009) species' responses to climate, I chose slightly earlier climate periods compared to the bird atlas data. I used environmental data for the period 1986–1991 for SABAP 1, and 1992–2005 for the SABAP 1–SABAP 2 transitional period (Fig. 5.1). Figures for mean temperature and precipitation over the warmest annual quarter are shown in Appendix 5 (Fig. A5.2 and Fig. A5.3 for mean temperature and precipitation respectively).

### *5.3.4 Land-use type data*

I further assessed the way in which land-use types affect the range dynamics of the Cape Rock-jumper. The Cape Rock-jumper is endemic to the fynbos region within the Western Cape of South Africa, and is a shy species that avoids human-mediated land-use change (Frazer, 1997). Its persistence could therefore potentially depend upon the amount of fynbos vegetation present within the study area. Thus, I included the percentage of each QDGC that is occupied by fynbos vegetation as a continuous covariate in my modelling framework. These data were obtained from Mucina & Rutherford (2006), who mapped potential vegetation, and were included as a continuous covariate in the model. Given that these data model potential (and not actual) vegetation, I thus acknowledge that the fynbos variable may not fully represent the current distribution of fynbos. However, given that my study examines the range of Cape Rock-jumper in relation to climate, the effects of fynbos was not of primary interest. Rather, I use it as a spatial variable because Cape Rock-jumper is an endemic species, and do not intend to draw strong ecological inferences from this variable.

The conservation status of Cape Rock-jumper has been uplisted as 'Near threatened' (Taylor et al., 2014; Lee & Barnard, 2016), and it may critically depend on protected areas for persistence. Thus, I included the proportion of a QDGC that is officially protected (private and public) as a covariate within my modelling framework. These data were obtained from the South African national land-cover dataset (South African National Biodiversity Institute (SANBI), 2009), and were included as a continuous covariate in the model.

### *5.3.5 Model Structure*

I used dynamic occupancy models to analyse the distribution of the Cape Rock-jumper. Dynamic occupancy models are explained in detail in the methods section of Chapter 4 of this thesis (section 4.3.3.1), and I refer the reader to that section for an explanation of the statistical methods I used, as I give only a brief description of the methods here.

During atlas surveys, a species in not always detected in areas where it really does occur (these cases are referred to as false negatives). Ignoring the issue of detection in species' distribution models can potentially produce inaccurate model results (Kéry, 2011). Dynamic occupancy models incorporate the detection process into the modelling framework by allocating a separate component to model the detection probability explicitly (MacKenzie et al., 2002). Incorporating the detection component into the modelling framework allows for unbiased analyses of species' distributions (MacKenzie et al., 2003).

Dynamic occupancy models differ from simpler single season occupancy models in that they can estimate the changes in species' occupancy probability over time (i.e., between seasons). A season can be a specified period of any reasonable length during which the occupancy status of a grid cell (or area) is assumed to stay constant. Changes in occupancy probability over time are calculated by estimating the dynamic components, colonization and persistence between each season (see below, equation 2). To estimate these components, it is necessary to collect repeated detection / non-detection data for each season over the duration of the study.

Initial occupancy, which is the occupancy probability over the 1st season at site $i$ $(z_{i1})$, is estimated from a Bernoulli trial with a mean of $\Psi_{i1}$:

$$Z_{i1} \sim Bernoulli\ (\Psi_{i1}) \qquad (1)$$

For all later seasons, ($t$ = 2, 3, 4 … $T$) occupancy probabilities at site $i$ are a function of the previous season's occupancy probability, and the dynamic components persistence ($\phi$) and colonization ($\gamma$). Extinction probability is the complement of persistence (1 – $\phi$), and here, I focus explicitly on extinction, rather than persistence. Extinction probability refers to the probability a site is unoccupied at time $t$ , given it was occupied at time $t-1$. Colonization probability is defined as the probability a species occupies site $i$ at season $t$, given the site was unoccupied at season $t-1$. These are linked by the following equation:

$$Z_{it} \sim Bernoulli\ (Z_{it-1} \times\ (1-\phi_{it-1}) + (1-\ Z_{it-1}) \times\ \gamma_{it-1}), \quad \text{for t>1} \qquad (2)$$

$1-\phi$ and $\gamma$ can depend on season- and site-specific covariates (MacKenzie et al., 2003). The model allows for extinctions and colonization events between seasons, but sites are assumed to remain either occupied or unoccupied during each season (MacKenzie et al., 2006).

Here, I model the distribution of the Cape Rock-jumper in two seasons; I consider SABAP 1 the first season, and SABAP 2 the second season. I assume demographic closure within each SABAP; the Cape Rock-jumper is a resident endemic to the region, generally occurs in groups, and can be territorial (Frazer, 1997; Hockey et al., 2005; Sinclair et al., 2011), suggesting relative stability from year to year (and potential lags behind climate change).

Occupancy during SABAP 1 was modelled in the following form:

$$\mathrm{logit}(\Psi_{i1}) = \beta_0 + \beta_1 \times PA_i + \beta_2 \times Fynbos_i + \beta_3 \times Mean\_temp_i + \beta_4 \times Precip_i \qquad (3)$$

where for QDGC $i$, $Mean\_temp_i$ is the mean temperature over the warmest annual quarter, and $Precip_i$ is the precipitation over the warmest annual quarter, both averaged over the period 1986-1991 (Fig. 5.1). $PA_i$ and $Fynbos_i$ represent the proportion of QDGC $i$ occupied by protected area and fynbos vegetation respectively.

Occupancy probability during SABAP 2 was modelled with the following equation:

$$Z_{i2} \sim Bernoulli\,(Z_{i1} \times (1 - \phi_{i1}) + (1 - Z_{i1}) \times \gamma_{i1}) \qquad (4)$$

where $Z_{i1}$ indicates the occupancy status during SABAP 1. Colonization was modelled in the following form:

$$\mathrm{logit}(\gamma_{i1}) = \beta_5 \qquad (5)$$

where $\beta_5$ is the colonization intercept.

Extinction was modelled in the following form:

$$\mathrm{logit}(1 - \phi_{i1}) = \beta_6 + \beta_7 \times Mean\_temp_i + \beta_8 \times Precip_i \qquad (6)$$

where for QDGC $i$, $Mean\_temp_i$ and $Precip_i$ represent the same climatic covariates as described in equation 3, except they were averaged during the period 1992-2005 (Fig. 5.1), and $\beta_6$ is the intercept.

And finally, detection was fitted in the form:

$$\text{logit}(\text{p}_{iy}) = \beta_9 + \beta_y \times Y_{iy} \quad (7)$$

where $\text{p}_{iy}$ is the detection probability at QDGC $i$ during year $y$. The $Y_{iy}$ are the year $y$ during which QDGC $i$ was surveyed. $\beta_9$ is the intercept, and $\beta_y$ is the $\beta$ coefficient representing detection for each year $y$ of the SABAPs. I included year as a categorical covariate on detection because the species is decreasing in abundance and range extent (Huntley et al., 2012; Lee & Barnard, 2016), and is likely to be more scarce over time, and thus more difficult to detect year on year.

No covariate was specified for the colonization probability of Cape Rock-jumper between SABAP 1 and SABAP 2. The colonization model was estimated with an intercept only (a single average over the whole study region). Since Cape Rock-jumper's range has shrunk significantly over the last few decades (Huntley et al., 2012; Milne et al., 2015; Lee & Barnard, 2016), few colonization events have occurred between SABAP 1 and SABAP 2. Thus, the relationship between mean colonization and the model covariates would not be well estimated, irrespective of the covariates chosen. Inaccurately specifying colonization events could generate imprecise model predictions for occupancy during SABAP 2, because of the hierarchical nature of dynamic occupancy models.

Implementation

All data preparation and analyses were performed in program R version 3.4.1 (R Development Core Team, 2017). The R package "dismo" (Hijmans et al., 2017) was used to compute the temperature and precipitation-based climatic variables. The R package "unmarked" (Fiske & Chandler, 2011) was used to run the dynamic occupancy models. Each model covariate was scaled to a mean of 0 and a standard deviation of 1 before being entered into the model.

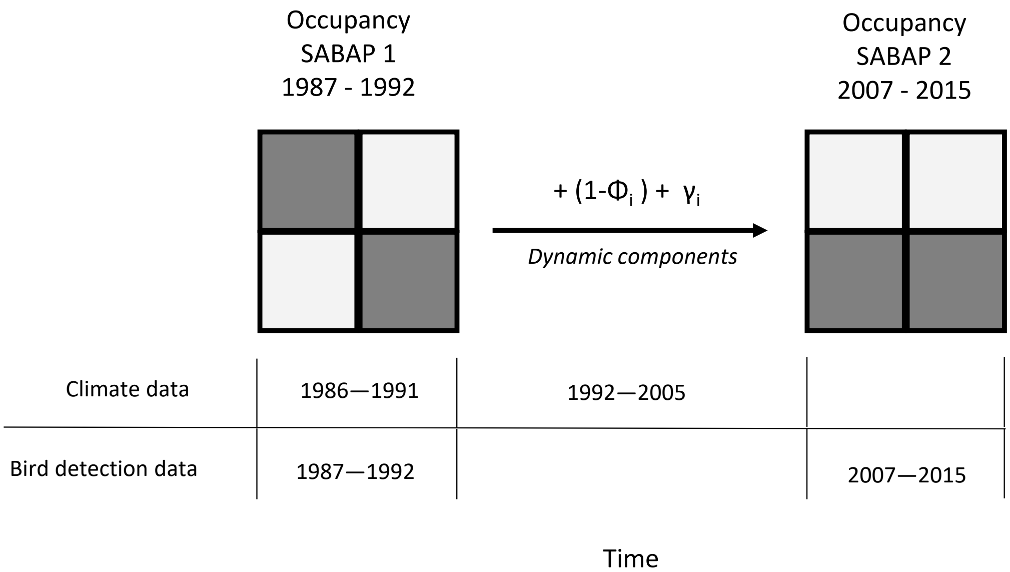



**Figure 5.1.** Diagram of the dynamic occupancy model used to examine the range dynamics of Cape Rock-jumper (*Chaetops frenatus*) in South Africa during the period 1987 – 2015. The four grid cells represent a simple spatial arrangement where Cape Rock-jumper may be present (dark grid cells), or absent (light grid cells). The spatial grids represent, from left to right, occupancy probability during SABAP 1 and SABAP 2. Occupancy status of SABAP 1 is directly estimated by the model. Occupancy status during SABAP 2 is derived from the occupancy status during SABAP 1 and the dynamic components extinction (1-$\Phi$) and colonization ($\gamma$) [see eqn. 4 for the model parameterization]. The time period below each model component indicates the duration of that component for the bird detection data, and the climate data which were averaged over the specified period.

## 5.4 RESULTS

*5.4.1 Estimates for occupancy probability during SABAP 1*

During SABAP 1, the Cape Rock-jumper's range was estimated to have occupied the south-western parts of the study area, along the western (up to approximately -31.5 degrees latitude) and south-eastern coastlines (up to approximately 26 degrees longitude), and was largely absent inland (Fig. 5.2A). The core (as defined by an occupancy probability >0.6 in this chapter, and identified by green-coloured QDGCs) of Cape Rock-jumper's range appeared to be split into two components; the western component extended north to south in the south-western part of its range at approximately 19 degrees longitude (indicated by solid-lined circle overlaid on the map, Fig. 5.2A). The second, south-eastern component was a cluster of QDGCs running west to east, along the south-eastern portion of its range at approximately 22 – 25 degrees longitude (indicated by the dash-lined circle overlaid on the map, Fig. 5.2A). The majority of the QDGCs that make up these two components of its core range overlapped protected areas and fynbos vegetation. For example, over its core range, protected areas occupied 45% of each grid cell, and fynbos vegetation constituted 94% of the vegetation. Cape Rock-jumper was predicted to have occurred at very low probabilities (<0.3) over the north-eastern, and eastern regions of the study area (Fig. 5.2A). The mean occupancy probability in study region during SABAP 1 was 0.22.

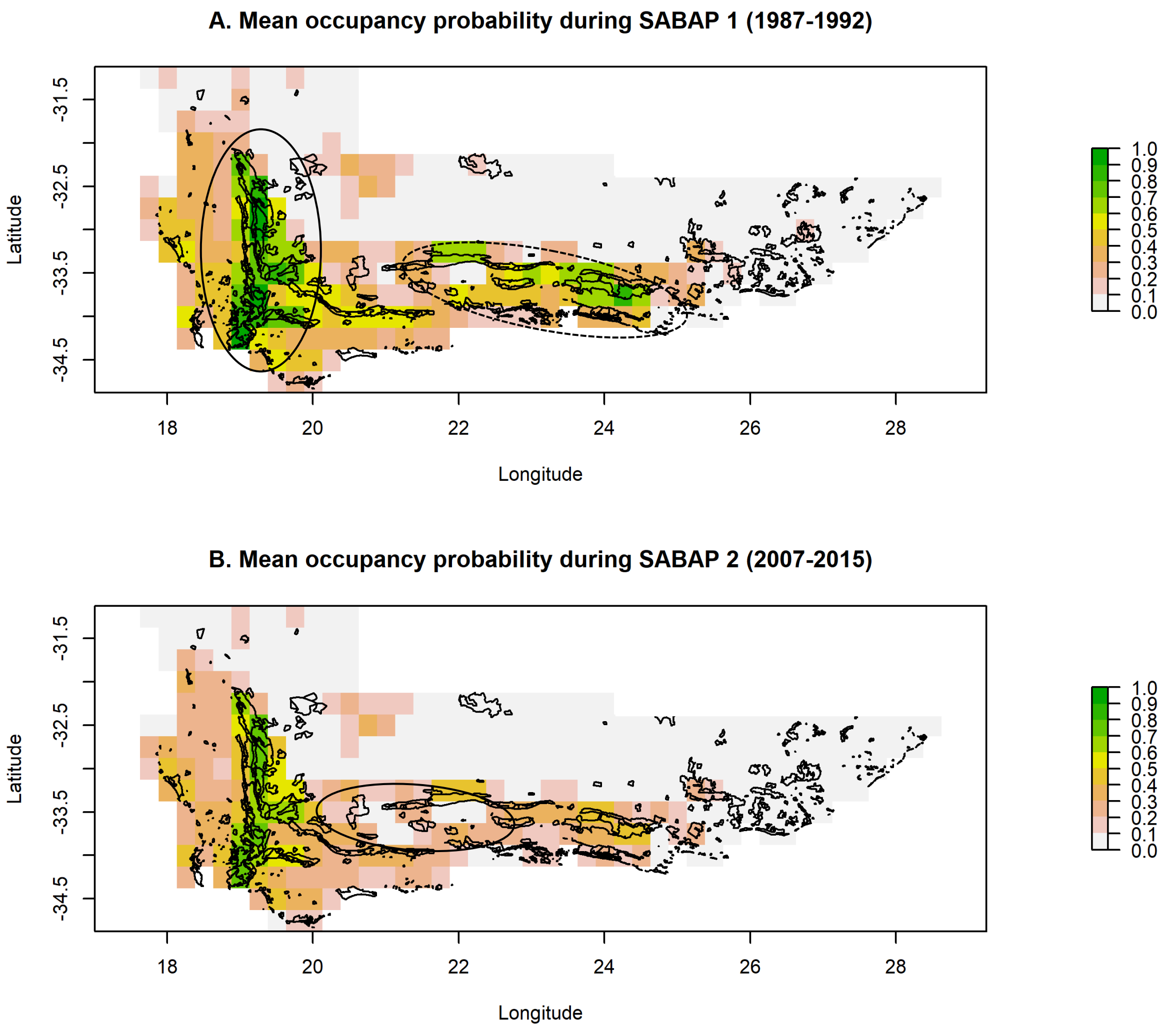



**Figure 5.2.** Predictions of mean occupancy probability for the endemic Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. A and B are mean estimates of occupancy based on checklists of detection or no detection during bird atlas projects running between 1987-1992 (A: SABAP 1), and 2007-2015 (B: SABAP 2), and refer to the gridded data on the coloured scale. Polygons represent protected areas, both private and public. Each grid cell represents a 15’ X 15’ regular square (unit is arcminutes), and the total area of the study region is approximately 195 000 km$^2$. See text for descriptions of circled areas for both panels A and B.

### *5.4.2 Mean relationships between the model covariates and mean occupancy during SABAP 1 (1987 – 1992)*

Occupancy probability during SABAP 1 increased significantly as proportions of both fynbos and protected area increased within a QDGC (Fig. 5.3A & B; mean estimates on the logit scale: 1.023 and 0.578 for protected area and fynbos respectively). As the mean temperature of the warmest annual quarter increased, occupancy probability significantly decreased (Fig. 5.3C, mean estimate on the logit scale -0.381). As the precipitation over the warmest annual quarter increased, occupancy probability during SABAP 1 decreased very slightly (Figs 5.3D, mean estimate on the logit scale: and -0.176), and this relationship was not statistically significant. See Table A5.1 in Appendix 5 for a full list of model covariates, standard errors, and significance values estimated for the relationships between SABAP 1 occupancy and model covariates.

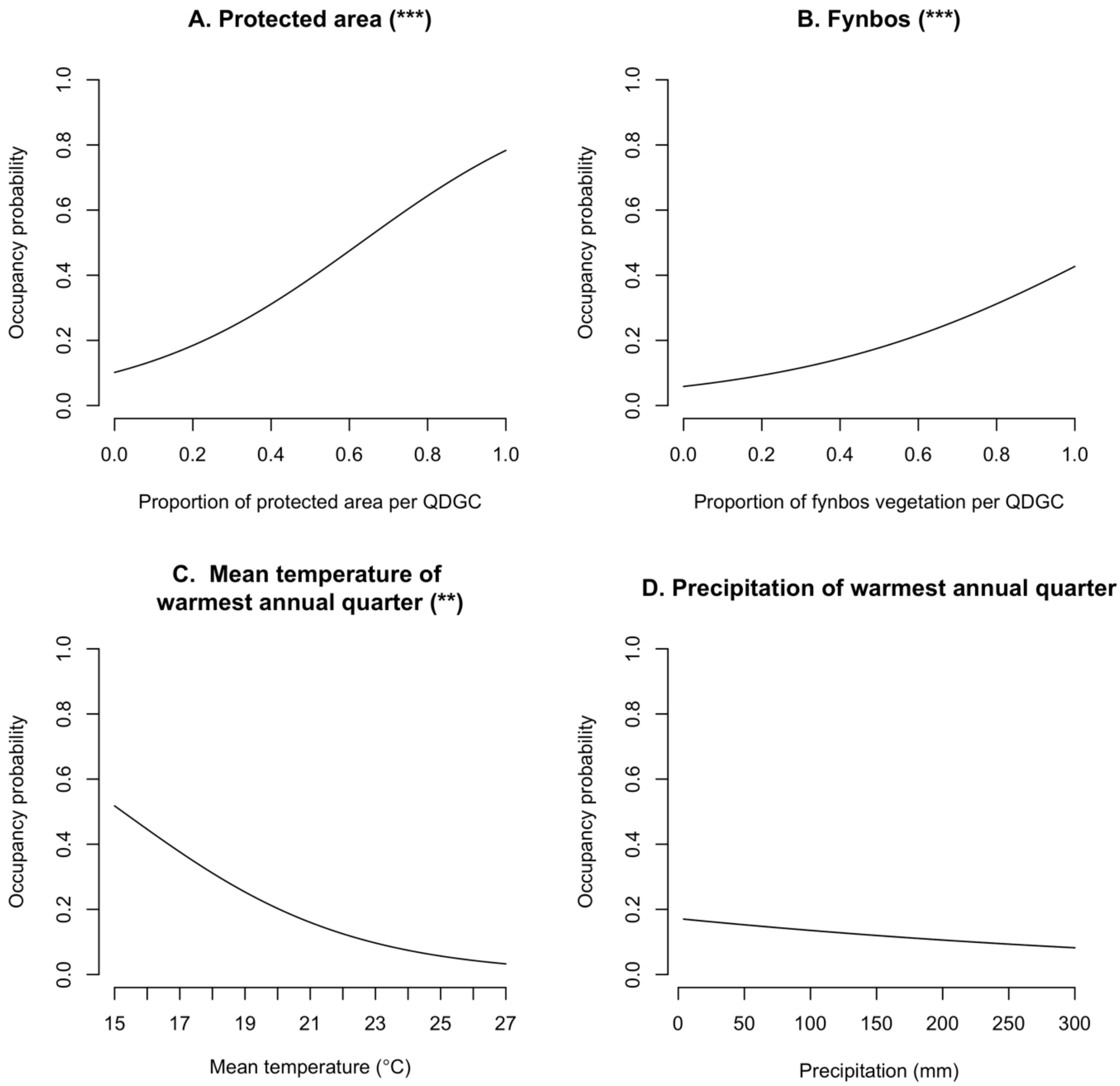



**Figure 5.3**. Estimated mean relationship between occupancy probability (y-axis) and the model covariates (x-axis) proportion of protected area (A), proportion of fynbos vegetation (B), mean temperature over warmest annual quarter (C) and precipitation over warmest annual quarter (D) during SABAP 1 (1987-1992) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. See equation 3 for the specification of the relationship between SABAP 1 occupancy and model covariates. Asterisks in brackets denote significance ('***' at the 0.001 level; '**' at the 0.01 level, and '*' at the 0.05 level. See Appendix 5, Table A5.1 for mean estimates, standard errors and significance levels for all model components).

### *5.4.3 Estimates for occupancy probability during SABAP 2*

For a selection of QDGCs situated in between the two components of Cape Rock-jumper's core SABAP 1 range (indicated by the solid circle in Fig 5.2B), occupancy probability during SABAP 2 appears to have decreased markedly relative to SABAP 1, and for some QDGCs it is predicted to be almost zero. This contrasts with relatively high estimates at SABAP 1 over the same area (mean occupancy probability in the study region during SABAP 1 was 0.22). The mean occupancy probability in the study region during SABAP 2 was 0.16.

Across the whole study area, the estimated occupancy probability of Cape Rock-jumper during SABAP 2 decreased markedly compared to the estimated occupancy probability during SABAP 1 (Fig. 5.2B). The two components making up Cape Rock-jumper's SABAP 1 core range experienced considerable declines in estimated occupancy probability during SABAP 2, relative to SABAP 1. Over the western component of its SABAP 1 core range (indicated by the solid-lined circle in Fig. 5.2A), a general decrease in occupancy probability was apparent in all QDGCs that make up the area. For example, in this region, occupancy probability was estimated to be 0.6 or higher for 22 QDGCs during SABAP 1, but for only 14 QDGCs during SABAP 2. This indicates a shrinking of Cape Rock-jumper's core range from SABAP 1 to SABAP 2.

The south-eastern component of its SABAP 1 core range (indicated by the dash-lined circle, Fig. 5.2A) has undergone severe decreases in occupancy probability between SABAP 1 and SABAP 2. Estimated occupancy probability for 11 QDGCs in this region was greater than 0.6 during SABAP 1. At SABAP 2, no QDGC in this region had an estimated occupancy probability of 0.5 of higher. At 2015 (and beyond), this region can no longer be considered a core part of the Cape Rock-jumper's range.

### *5.4.4 Estimates for mean extinction probability as a function of climate between SABAP 1 and SABAP 2*

As the mean temperature during the warmest annual quarter increased, extinction probability increased significantly (Fig. 5.4A, mean estimate on the logit scale: 0.403). As the mean precipitation during the warmest annual quarter increased, extinction probability was also expected to increase, but the increase was not significant (Fig. 5.4B, mean estimate on the logit scale: 0.744). See Table A5.1 in Appendix 5 for a full list of model covariates, standard error, and significance values estimated for the relationships between extinction probability and the climatic covariates.

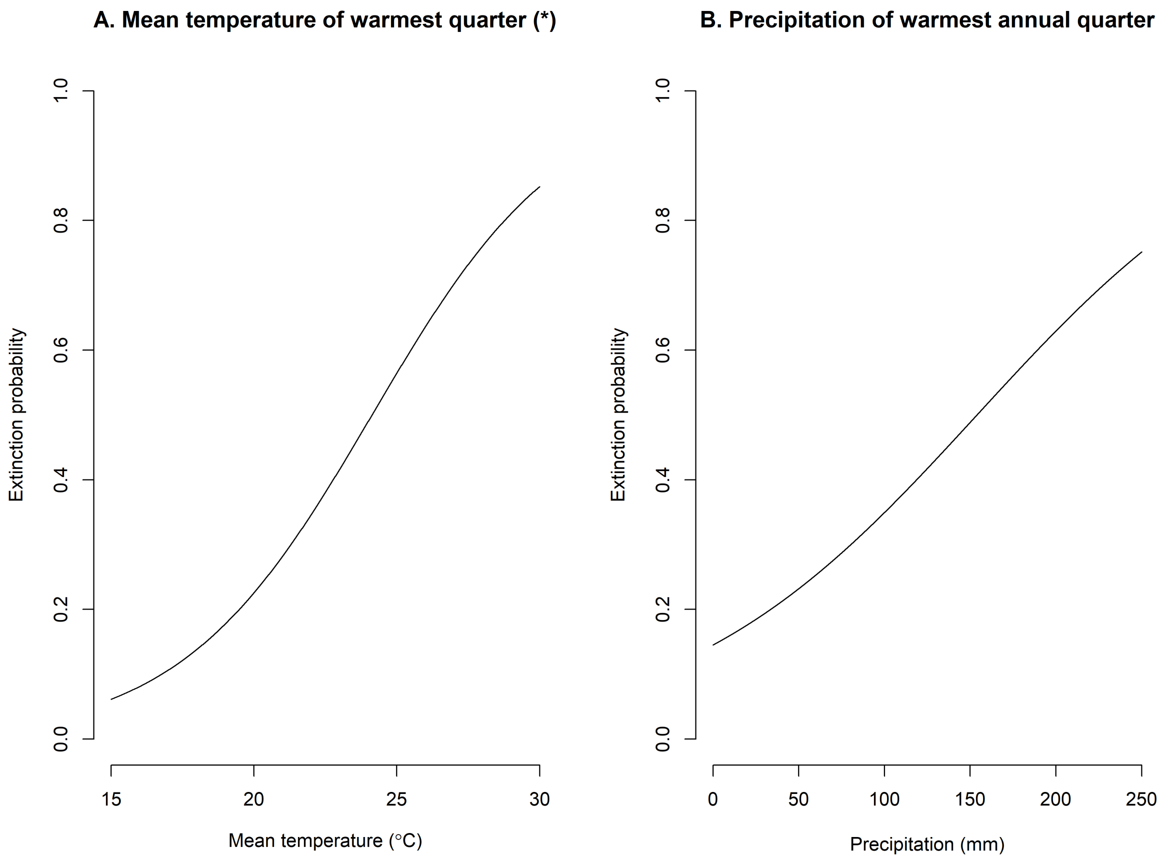



**Figure 5.4.** Estimated mean relationship between the extinction probability (y-axis) and the model covariates (x-axis), mean temperature of warmest annual quarter (A), and precipitation of the warmest annual quarter (B) between the periods 1987-1992 (SABAP 1) and 2007-2015 (SABAP 2) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa. See equation 6 for the specification of extinction probability. Asterisks in brackets denote significance ('***' at the 0.001 level; '**' at the 0.01 level, and '*' at the 0.05 level. See Appendix 5, Table A5.1 for mean estimates, standard errors and significance levels for all model components).

Mean extinction probability for Cape Rock-jumper increased from west to east, with the highest probabilities estimated at the eastern-most region of the study area (Fig. 5.5). Relatively low extinction probabilities were evident in the top half of the region making up the western component of Cape Rock-jumper's SABAP 1 core range (as indicated by the solid-lined circle in Fig. 5.2A).

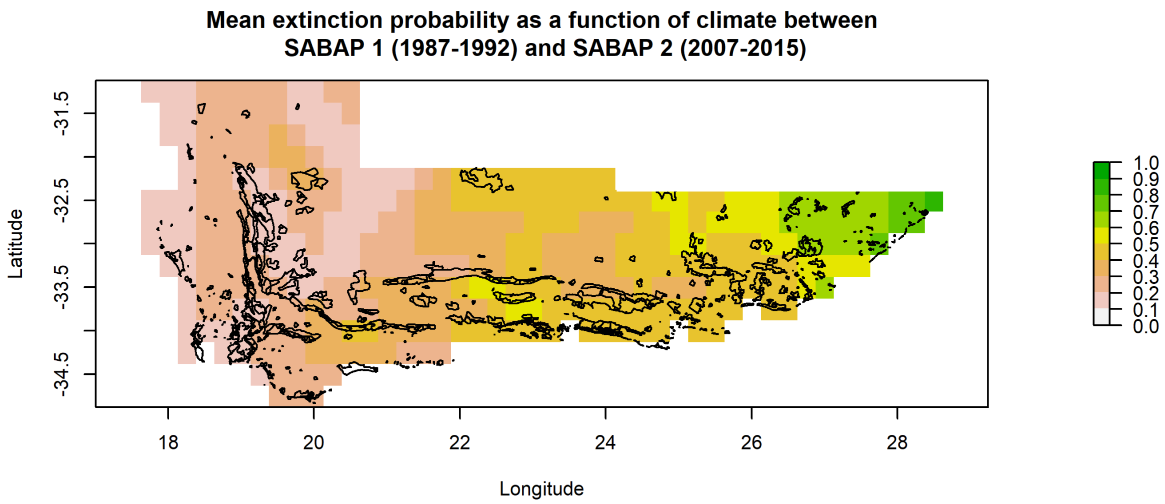



**Figure 5.5.** Realised mean extinction probability over the study area between SABAP 1 (1987-1992) and SABAP 2 (2007-2015) for the Cape Rock-jumper (*Chaetops frenatus*) in the Western Cape of South Africa, and refer to the gridded data on the coloured scale. See equation 6 for the structure of this model. Polygons represent protected areas, both private and public. Each grid cell represents a 15' X 15' regular square (unit is arcminutes), and the total area of the study region is approximately 195 000 km$^2$.

## 5.5 DISCUSSION

A key goal of this chapter was to develop a dynamic occupancy model and examine the range dynamics of the Cape Rock-jumper (*Chaetops frenatus*), endemic to the Western Cape of South Africa. I fitted a dynamic occupancy model to Cape Rock-jumper detection data collected during two phases of the Southern African Bird Atlas Project (SABAP), the first of which ran from 1987 – 1992 (SABAP 1), and the second from 2007 and is still ongoing (SABAP 2, although I used data only up to 2015). A secondary goal was to examine how well the occupancy model was able to capture the shrinking range of Cape Rock-jumper between SABAP 1 and 2, as shown by other studies (Milne et al., 2015; Lee & Barnard, 2016).

My key findings show that an increase in the mean temperature of the warmest annual quarter significantly decreased the occupancy probability of the Cape Rock-jumper during SABAP 1 (Fig. 5.3C), and significantly increased the extinction probability between SABAP 1 and 2 (Fig. 5.2A&B, and Fig. 5.4A). These results are congruent with others' findings that the species does not cope well with high temperatures (Huntley & Barnard, 2012; Milne et al., 2015; Lee & Barnard, 2016). I show that the key mechanisms underpinning range contractions of the Cape Rock-jumper over recent decades are likely linked to an increase in extinction events as mean temperature has increased (Fig. 5.4A). Mean temperatures over the Cape Rock-jumper's current range are predicted to increase in the future, as a consequence of continued climate change (van Wilgen et al., 2016). This is likely to lead to an increase in Cape Rock-jumper extinction events in the future, and ultimately, further shrinkage of its already contracted range. I further show that the contractions to the Cape Rock-jumper's range between SABAP 1 and 2 were captured well by the dynamic occupancy model. This highlights the benefits of using occupancy models to predict species distributions, and relationships with the environment.

Occupancy probability during SABAP 1 increased significantly with the proportion of fynbos and protected area per QDGC (Fig. 5.3A&B). This result is in agreement with what is known about the species; the Cape Rock-jumper actively avoids human-mediated land-use types (for example urban, and agriculture), and strictly inhabits fynbos vegetation (Frazer, 1997; Lee & Barnard, 2016). The Cape Rock-jumper's conservation status is currently listed as 'Near threatened' (Taylor et al., 2014), and this study highlights that its persistence depends, to some degree, on protected areas.

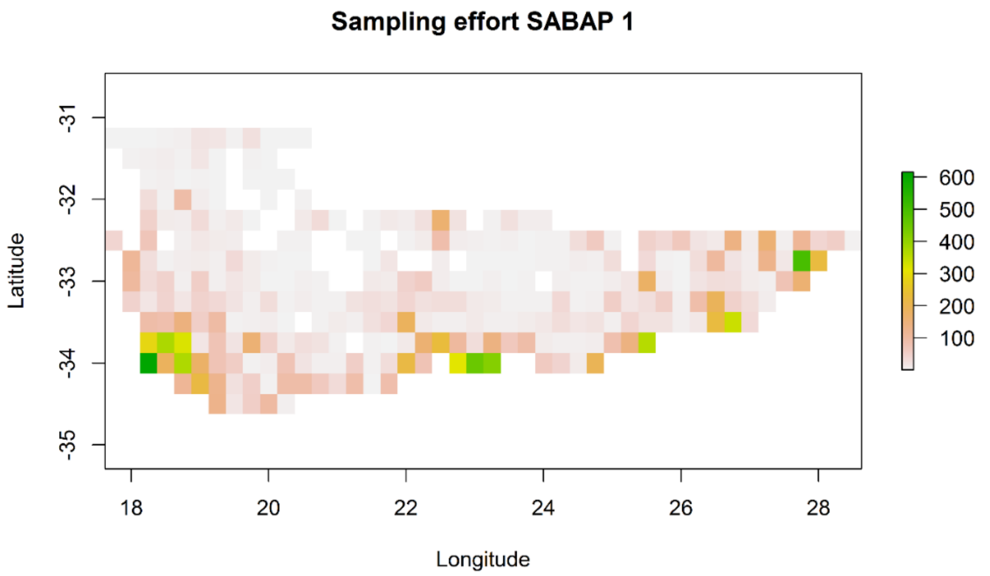
I found that an increase in precipitation during the warmest annual quarter led to a decrease in occupancy probability during SABAP 1 (Fig. 5.2D) and an increase in extinction probability between SABAP 1 and 2 (Fig. 5.4D), but these relationships were not statistically significant (Table A5.1, Appendix 5). Thus, it appears that an increase in precipitation could potentially limit this species, but not significantly so. This finding is corroborated by Lee and Barnard (2016), who studied climatic effects on the range dynamics of six species endemic to the fynbos vegetation (including the Cape Rock-jumper), and concluded that changes in the ranges of these species were largely due to changes in temperature, rather than in precipitation.

This chapter also demonstrates the power of dynamic occupancy models in modelling the distributions of species. The dynamic occupancy model simulated the known shrinkage of Cape Rock-jumper's range with good statistical confidence between SABAP 1 and 2 in a way that agreed with the raw SABAP detection data (Fig. 1.3, see Appendix 5 for the standard errors associated with estimates of mean occupancy [Fig. A5.4] and extinction [Fig. A5.5]) and other findings on the species (Milne et al., 2015; Lee & Barnard, 2016). Additionally, the dynamic occupancy model was able to estimate well the relationships between the range dynamics (occupancy and extinction probabilities) and the model covariates (climate and fynbos), in a way that was in agreement with previous findings (Frazer, 1997; Huntley & Barnard, 2012; Taylor et al., 2014; Milne et al., 2015; Lee & Barnard, 2016).

The modelling of species' distributions is an increasingly important field, given the ubiquitous influence of land-use and climate change on species and their distributions (Midgley et al., 2006; Jones, 2011; Huntley et al., 2012). It is important to understand the risk climate change poses to species, and how rapidly changes in climate affect species, in order to inform international policy and mitigate biodiversity loss as a result of climate change (Urban, 2015). A benefit of dynamic occupancy models is that they can model the dynamic components, colonization and extinction, directly. This allows researchers to model colonization and extinction of species under specific conditions, e.g., different suites of scenarios of climate change. Thus, it is possible to determine parts of the species' current range that are likely to go extinct first, or, regions that the species is likely to colonize first (e.g., Martin et al., 2010; Keane et al., 2012; Broms et al., 2014; Clement et al., 2016). Occupancy models therefore are suitably poised as methods to analyse the distribution of rare species, or those of conservation concern given climate change, and can be fitted with relative ease (e.g., Fiske & Chandler, 2011).

In conclusion, the dynamic occupancy model I used to examine the range dynamics of the Cape Rock-jumper captured the range contractions of the Cape Rock-jumper between SABAP 1 and 2 well. An increase in the mean temperature over the warmest annual quarter limits the range of the Cape Rock-jumper, specifically, by increasing the extinction probability. A hotter future climate, as is predicted for the region, is therefore expected to shrink further the already contracted range of the Cape Rock-jumper. I also show that dynamic occupancy models are a powerful tool by which to analyses species' distributions.

## **5.6 APPENDIX:** Supplementary material for Chapter 5



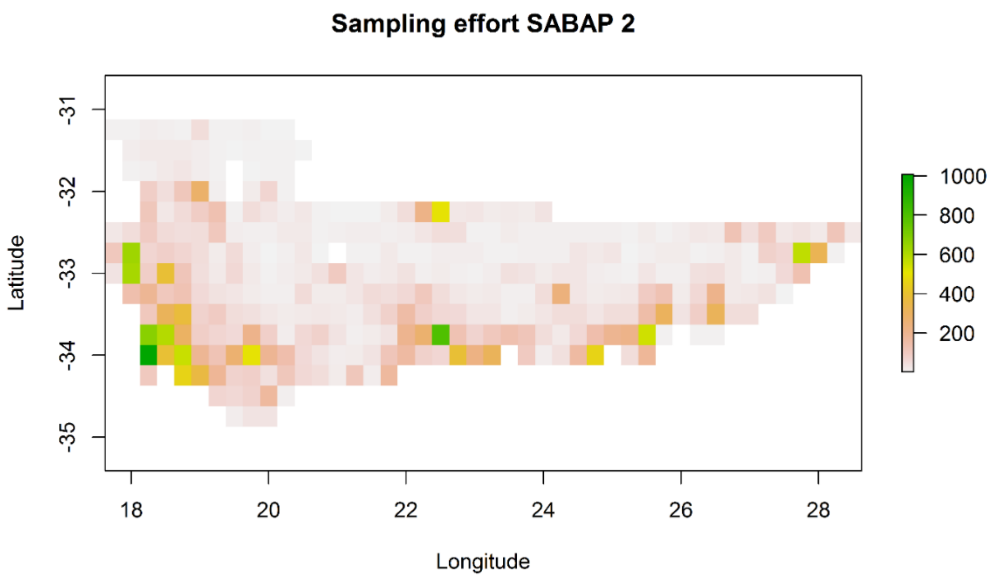




**Figure A5.1.** Sampling effort for SABAP 1 & 2. Each pentad is coloured by the number of checklists submitted. The study area comprises 354 pentads. 306 were sampled during SABAP 1, and 348 during SABAP 2.

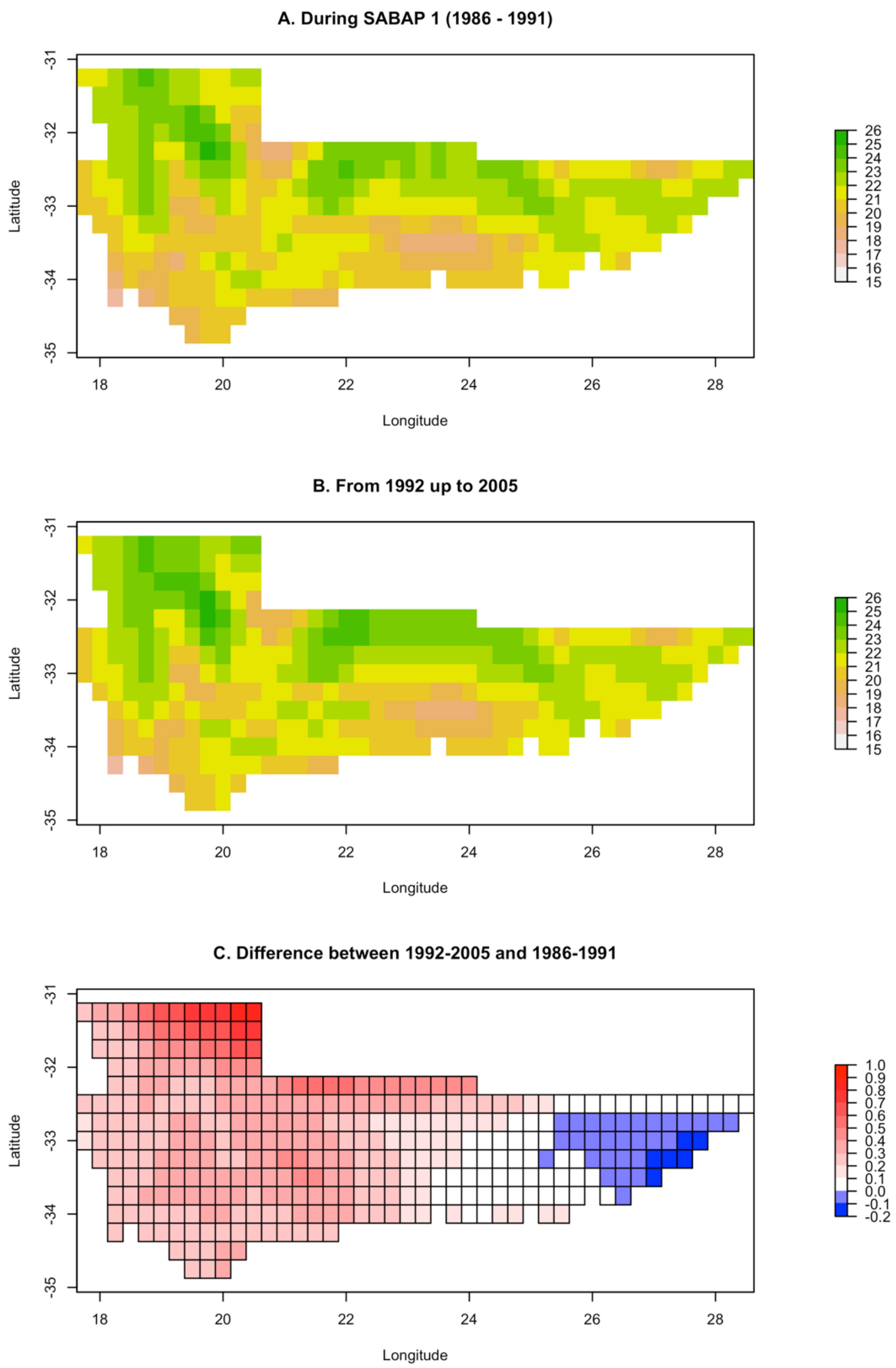



**Figure A5.2.** Mean temperature of the warmest annual quarter for each QDGC in the study area, during (A) SABAP 1 (1986-1991), (B) between SABAP 1 and SABAP 2 (1992-2005), and (C) the difference between these two periods (between 1992-2005 and 1986-1991). See section 5.3.3 for details on how these data were obtained.

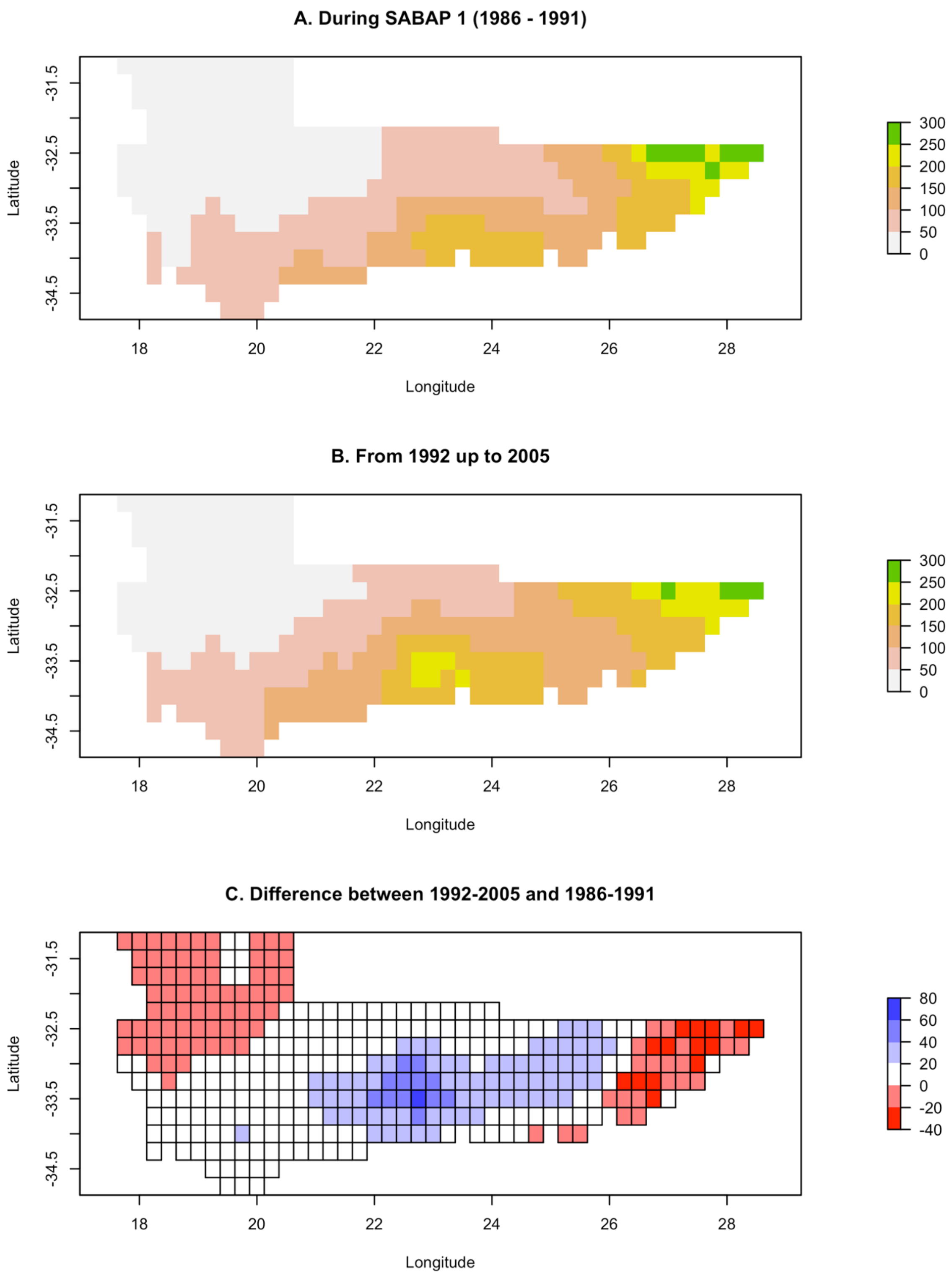
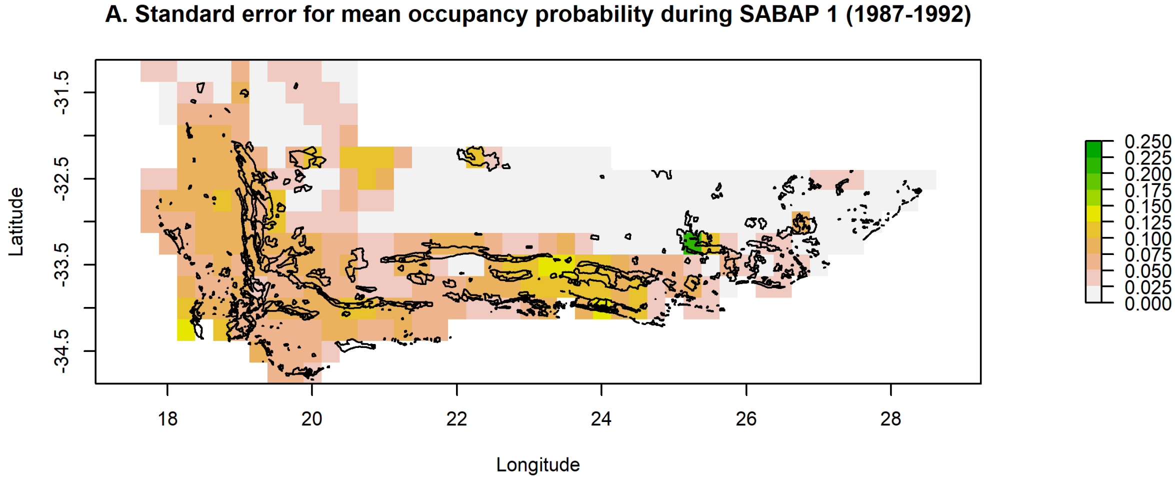



**Figure A5.3.** Mean precipitation of the warmest annual quarter for each QDGC in the study area, during (A) SABAP 1 (1986-1991), (B) between SABAP 1 and SABAP 2 (1992-2005), and (C) the difference between these two periods (between 1992-2005 and 1986-1991). See section 5.3.3 for details on how these data were obtained.

**Table A5.1.** Model estimates for the dynamic occupancy model, modelling the range dynamics of the Cape Rock-jumper during SABAP 1 (1987-1992) and SABAP 2 (2007-2015) over the Western Cape of South Africa. The model is made up of four components, psi (occupancy), gamma (colonization), epsilon (extinction), and p (detection). The term 'Mean temperature' refers to the mean temperature over the warmest annual quarter, and 'Precipitation' to the precipitation over the warmest annual quarter. 'Fynbos' and 'protected areas' refer to the proportion of a QDGC occupied by either.

| Model parameter | Mean Estimate | SE | p |
|---|---|---|---|
| ***Psi*** | | | |
| Intercept | -1.807 | 0.262 | < 0.001 |
| Temperature | -0.381 | 0.241 | < 0.01 |
| Precipitation | -0.176 | 0.267 | > 0.05 |
| Fynbos | 1.023 | 0.246 | < 0.001 |
| Protected areas | 0.578 | 0.193 | < 0.001 |
| | | | |
| ***Gamma*** | | | |
| Intercept | -37.4 | 171.2 | > 0.05 |
| | | | |
| ***Epsilon*** | | | |
| Intercept | -0.707 | 0.497 | > 0.05 |
| Temperature | 0.403 | 0.675 | < 0.05 |
| Precipitation | 0.744 | 0.508 | > 0.05 |
| | | | |
| ***p*** | | | |
| 1987 | -2.976 | 0.16 | < 0.001 |
| 1988 | -0.201 | 0.22 | < 0.05 |
| 1989 | 0.372 | 0.22 | < 0.05 |
| 1990 | 0.774 | 0.22 | < 0.001 |
| 1991 | 0.442 | 0.24 | < 0.05 |
| 1992 | 0.642 | 0.25 | < 0.05 |
| 2007 | 0.103 | 0.22 | < 0.05 |
| 2008 | -0.229 | 0.25 | < 0.05 |
| 2009 | -0.812 | 0.27 | < 0.05 |
| 2010 | -0.648 | 0.24 | < 0.05 |
| 2011 | -0.292 | 0.226 | > 0.05 |
| 2012 | -0.123 | 0.223 | > 0.05 |
| 2013 | -0.239 | 0.247 | > 0.05 |
| 2014 | -0.063 | 0.319 | > 0.05 |



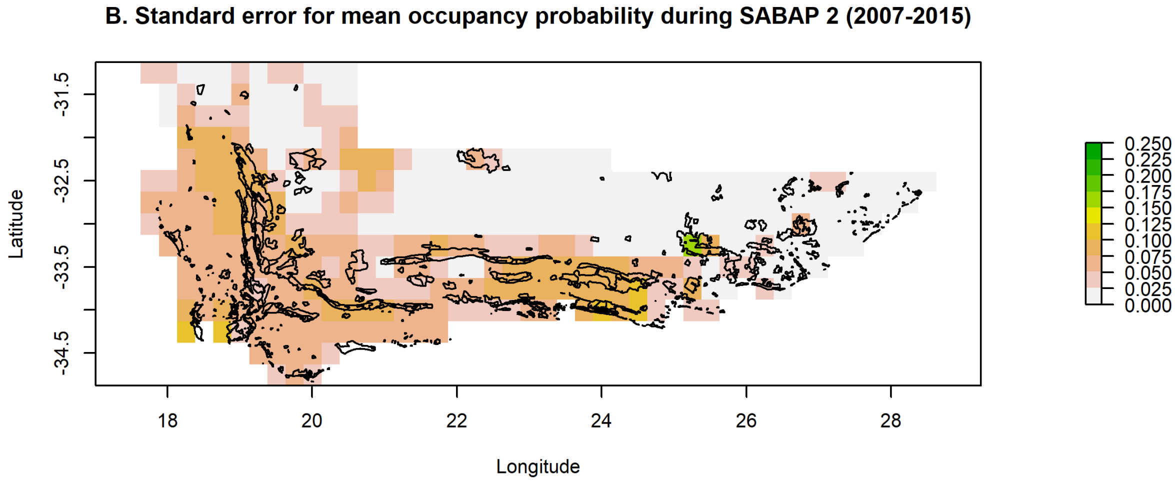




**Figure A5.4.** Standard error of the mean estimate of occupancy probability during SABAP 1 (A) and SABAP 2 (B).

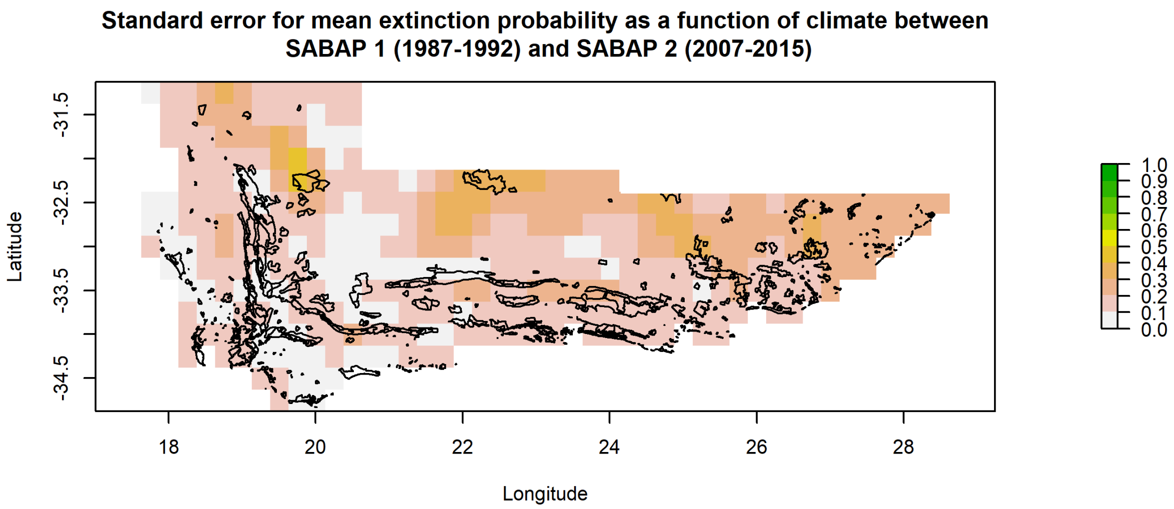



**Figure A5.5.** Standard error of the mean extinction probability between SABAP 1 and SABAP 2.

Chapter 6

# Synthesis and consolidation

Hamerkop (*Scopus umbretta)* in the Kruger National Park, South Africa. Photograph by Greg Duckworth

*6.1 Thesis overview*

Land-use and climate change over the recent few decades have caused a substantial loss of biodiversity world-wide (Vitousek et al., 1997; Chapin et al., 2000; Foley et al., 2005). In the future, the current rate of land-use and climate change is predicted to increase (UNEP, 2011), intensifying concerns around biodiversity. Protected areas are regarded as one of the major tools mitigating global biodiversity loss; they are large areas of land set aside specifically for the conservation of biodiversity, and to reduce the extinction rates of species (UNESCO, 1974; Gaston et al., 2008). However, despite the heavy reliance on protected areas world-wide for biodiversity conservation, the exact degree to which they provide a net conservation gain to biodiversity is largely unknown (Parrish et al., 2003; Gaston et al., 2006). Although information relating to the ecological effectiveness of protected areas is difficult to obtain in a general sense (Gaston et al., 2008), it is critical; working towards a balance between biodiversity conservation and meeting the needs of an increasing human population requires a mechanistic understanding of how general biodiversity is affected by protected areas (and, indeed, all other major land-use types).

The major aim of this thesis was to use dynamic occupancy models to assess the influence of protected areas and climate change on the occupancy dynamics of selected bird species within South Africa. Chapters 2 – 4 focussed on the effects of protected areas and other land-use types on the population dynamics of 200 common and resident bird species in the greater Gauteng region. Common bird species were studied because they tend to be abundant, widespread, and in general, drive patterns of biodiversity and ecosystem functionality (Gaston & Fuller, 2008; Lennon et al., 2011; Winfree et al., 2015). Even subtle declines in common species can have disproportionately negative effects on ecosystem functioning, and potentially lead to significant losses of ecosystem integrity (Gaston, 2010; Winfree et al., 2015). I therefore assessed the population dynamics of common bird species as a function of protected areas; this gave good insights into the ecological integrity of protected areas, as well as for the landscapes in which they are embedded (Devictor et al., 2007; Gaston & Fuller, 2008; Winfree et al., 2015). Chapter 1 was an introductory chapter, in which I introduced the reader to important topics that pertain to the data chapters that followed. In Chapter 2, I focused on how the average abundance of common birds varied as a function of the proportion of protected areas within an area (the proportion-abundance relationship). In Chapter 3, I assessed the relative changes to the proportion-abundance relationship for common birds as certain land-use types nearby protected areas increased in proportion. In Chapter 4 my focus was again on common species, and analysed how components of their population dynamics, colonization and extinction, varied with protected areas. Finally, in Chapter 5, I used dynamic occupancy models and focussed on the occupancy and extinction (the complement of persistence) probability of the endemic and near threatened (Taylor et al., 2014) Cape Rock-jumper (*Chaetops frenatus*), and how these quantities vary in relation to climate.

## *6.2 Key findings and directions for future research*

### On the conservation effectiveness of protected areas

My results indicated that in general, protected areas were effective at conserving common, resident bird species (Chapters 2 – 4). I also found that the occupancy probability of the endemic threatened Cape Rock-jumper (*Chaetops frenatus*) was significantly higher in protected areas than in non-protected areas. My consolidated findings therefore suggest that protected areas were effective at conserving avian biodiversity over the regions I studied. The results of this thesis therefore support other studies from around the world that found protected areas are effective conservation tools (Walpole & Leader-Williams, 2002; Rodrigues et al., 2004; Owen-Smith et al., 2006; Dalerum et al., 2008; Child et al., 2009; Greve et al., 2011; Watson et al., 2011; Geldmann et al., 2013).

For Chapters 2 - 4, I assigned each common species to one of seven guilds, which were defined by the type of food the species preferentially consumed and its primary mode of foraging. These were: frugivores, gleaners, granivores, ground-feeders, hawkers, predators, and vegivores (see section 1.2.6.1 in Chapter 1 for a precise definitions of these guilds). For each species, I calculated how the average abundance increased as the proportion of protected area within a pentad increased, and I called this the proportion-abundance relationship. I then accounted for the variance in each species' average proportion-abundance estimate, and calculated the average proportion-abundance relationship for each guild. Using a pattern recognition technique, I grouped together guilds that had a similar average proportion-abundance relationship. I found three distinct groups which differed in their average proportion-abundance relationship (Table 2.1 and Figure 2.3; Chapter 2). The first group consisted of frugivores, ground-feeders, hawkers, predators, and vegivores, and were, on average, more abundant in areas with a higher proportion of protected areas, than in areas with a lower proportion. The second group consisted only of gleaners, the average abundance for which did not vary at all with the proportion of protected areas. The last group consisted only of granivores, and the average abundance was higher in areas with a low proportion of protected areas, compared to areas of a higher proportion of protected areas. My results showed that five of the seven guilds were estimated to be on average, more abundant in pentads of a higher proportion of protected area, compared to pentads with a low proportion. I conclude that, because the average abundance for five of the seven guilds was predicted to be higher in areas with a higher proportion of protected areas than areas with a lower proportion, protected areas were effective at increasing the average abundance for most guilds.

I found evidence that land-uses surrounding, or nearby, protected areas can affect the conservation effectiveness of the protected area (i.e., the ability of protected areas to conserve successfully natural habitat and biodiversity; Gaston et al., 2008). Again, I used the seven guilds as stratifying groups, and calculated how the average proportion-abundance relationship varied for each guild as the proportion of either urban or agricultural land near protected areas increased. I found that on average, the proportion-abundance relationship became significantly more positive for the guilds frugivores, vegivores, predators, gleaners, ground-feeders, and hawkers as the proportion of agricultural area near protected areas increased (Fig. 3.3, Chapter 3). On average, these guilds are predicted to be more reliant on protected area for persistence as agricultural land near protected areas increases in proportion.  In contrast, as the proportion of urban area near protected areas increased, the average proportion-abundance became statistically more positive for only granivores and ground-feeders, whilst becoming statistically more negative for frugivores (Fig. 3.3, Chapter 3). Therefore, on average, the guilds granivores and ground-feeders were shown to be more reliant on protected areas for persistence as urban area near protected areas increases in proportion. On the contrary, frugivores were estimated to be less reliant on protected areas for persistence as urban area near protected areas increases in proportion.

Large tracts of land are required to meet the agricultural and development needs of an ever-increasing human population (UNEP, 2011; United Nations, 2013b). Consequently, a greater emphasis on protected areas for biodiversity conservation will be expected in the future

(DeFries et al., 2007; Uehara-pradol & Fonseca, 2007; Mcdonald et al., 2008). Understanding how biodiversity within protected areas is affected by land-uses nearby protected areas is thus of profound importance in successfully conserving biodiversity and ecosystems in the future. My results indicated that protected areas do not function in isolation; the natural surroundings of protected areas can influence the ecological effectiveness of protected areas, something that is increasingly becoming recognised (DeFries et al., 2007; Rayner et al., 2014). I showed here that more guilds will, on average, be reliant on protected areas for persistence as agricultural area is in proximity to protected areas, compared to when urban area is in proximity to protected area. This agrees with the findings of other studies which have investigated the negative effects of agricultural land-use on biodiversity in general (Bengtsson et al., 2005; Tscharntke et al., 2005; Billeter et al., 2008; Potts et al., 2010; Loecke et al., 2017; Scholtz et al., 2017). Mitigating the negative effects of agricultural land-use on biodiversity therefore appears to be an important first step in attaining a balance between biodiversity and the needs of the human population over the greater Gauteng region. It must be noted, however, that despite the generally negative effects of human modified land-use types on biodiversity (Burel et al., 1998; Chace & Walsh, 2006; Tscharntke et al., 2012; Gilroy et al., 2014), these land-use types can also benefit some species because they can provide additional resources, such as sustenance, and shelter, with less seasonal variation (Robinson et al., 2001; Chace & Walsh, 2006; Duckworth & Altwegg, 2014).

One key goal set for protected areas is to conserve natural habitat (Gaston et al., 2008; UNEP, 2011). This is of critical importance to the species confined to protected areas, because their survival depends on, to varying degrees, the natural habitat within protected areas (Geldmann et al., 2013; Phipps et al., 2013; Hatchwell, 2014). However, birds can be very mobile across landscapes, and are easily able to cross physical boundaries such as protected area borders. Therefore, common birds can be abundant in areas that other species, which typically occur in protected areas, are not, for example, in urban areas (Tweit & Tweit, 1986; Blair, 1996; Chace & Walsh, 2006). Thus, a good way to test if protected areas create good habitat is to measure if they increased the colonization and decrease the extinction probabilities of common bird species. I investigated this concept in Chapter 4. Again, I used guilds as a stratifying group and measured the average colonization and extinction probability of each guild. I found that an increase in the proportion of protected areas significantly increased the average colonization probability for all seven guilds (Fig. 4.1, Chapter 4). For each guild, I also considered the average equilibrium occupancy probability - this is the occupancy probability expected if a species was at dynamic equilibrium with its environment. I found that the average equilibrium occupancy probability for six of the seven guilds (frugivores, gleaners, ground-feeders, hawkers, predators, vegivores) was statistically higher in pentads that were fully protected, compared to pentads that were not protected at all (Fig. 4.3, Chapter 4). This suggests that on average, species from these guilds are estimated to occupy protected areas, rather than other areas within the landscape. Together, these results show clearly the conservation benefit protected areas provide to common bird species, thus deeming them successful.

In Chapter 5 I switched my focus to the Cape Rock-jumper, a near threatened species, endemic to the Western Cape of South Africa (Taylor et al., 2014). This species' range has drastically shrunk over the last few decades (Simmons et al., 2004; Lee & Barnard, 2016), reportedly due to its inability to cope with high temperatures (Milne et al., 2015). Simulations of its range by 2100 indicate that its current range is expected to shrink even further under future scenarios of climate change (Huntley et al., 2012). In this chapter, I fitted a dynamic occupancy model to Cape Rock-jumper distribution data, collected over two bird atlas projects (SABAP 1: 1987-1992, and SABAP 2 2007-2015). This analyses also examined how increases in temperature over Cape Rock-jumper's range, brought about by climate change, influenced its extinction probability. The dynamic occupancy model performed well, and estimated a dramatic decline in the range of Cape Rock-jumper during SABAP 2, relative to its SABAP 1 range (Fig. 5.2A & B, Chapter 5). This result was in agreement with the findings of other studies on the Cape Rock-jumper (Milne et al., 2015; Lee & Barnard, 2016). I found that extinction probability increased significantly with mean temperature over the warmest annual quarter (Fig. 5.4A). Given that temperature is projected to increase further under future climate change scenarios (IPCC, 2013) my findings suggest that the range of Cape Rock-jumper will continue to decline in future, as was estimated by Huntly et al (2012).

Chapters 4 & 5 highlight the value of studying the dynamic components, colonization and extinction, of species' ranges. Dynamic methods are quickly becoming acknowledged as useful methods for analysis of population dynamics (Elith & Leathwick, 2009; Bled et al., 2013; Yackulic et al., 2015). In Chapter 4, my dynamic occupancy models showed that for all common species studied, the average occupancy probability, at year 2008 (which was statically derived) did not have a strong relationship with the proportion of protected areas. On the contrary, the average equilibrium occupancy per guild, estimated using dynamic methods, revealed that equilibrium occupancy was significantly reliant on protected areas. This detail was not detected from a statically derived average occupancy probability at 2008. This chapter emphasized the importance of using dynamic methods to analyse dynamic processes.

Chapter 5 highlighted the use of dynamic occupancy models in analysing species' distributions. One exciting possibility of these models is that they enable the direct modelling of the colonization and extinction processes of a species' range dynamics. This approach has two main benefits from a conservation perspective. Firstly, they allow one to statistically relate colonization or extinction probabilities to appropriate covariates (for example, environmental, or temporal). This is useful in the prediction of a species' distribution in future, because colonization and extinction can be estimated under a suite of future climate scenarios. Thus, one may estimate from what parts of its range a species is likely to go extinct first, or in the case of colonization, identity areas which are predicted to be colonized first under different future climate projections. This can potentially allow for the implementation of appropriate management scenario, where possible (e.g., Dawson et al., 2011; Maclean & Wilson, 2011; Urban, 2015). Secondly, this approach doesn't assume the species is in equilibrium with its environment. Violation of the equilibrium assumption may lead to inaccurate model results and subsequent ecological inferences (Hirzel et al., 2001; Munguía et al., 2012; Yackulic et al., 2012, 2015). Equilibrium may, or may not, be a problem of concern for the analysis, but needs to be weighed up on a case by case basis for each species of study (Braidwood & Ellis, 2012). For example, if the interval between seasons (in the dynamic occupancy model) is longer that the average time taken by the species to respond to change in the environment, equilibrium will not be a problem. However, this is often difficult to know with certainty in practice. Given that dynamic occupancy models omit the need for assuming equilibrium, and the ease with which they can be fited to data, they may be applicable to a wide range of cases. For example, to datasets generated from citizen science projects, which collect large volumes of data over large geographic extents for a variety of organisms (Dickinson et al., 2012).

As a caveat of this work, I noted that my study was correlative in nature. I related presences of common birds to climate, proportions of the land-use types protected areas (agricultural, urban, and natural), and interpreted model outputs that estimated correlates within these data. Like all correlative studies, it does not demonstrate causation for the observed relationships, or unveil the underlying mechanisms by which these land-use types affected bird abundances or occupancy dynamics, which should be the focus of future research (see below). Nonetheless, this thesis provides valuable insight into the response of common species to landscape heterogeneity, and identified the role protected areas played in affecting the range dynamics of the species considered.

As a continuation of the themes presented in this thesis, I suggest that a valuable next step building on the work I present here is to assess the land-use types that make up the landscape. The core finding of this thesis confirms the ecological effectiveness of protected areas. However, natural land is increasingly being converted to land-use types which accommodate for the ever-increasing human population (United Nations, 2013b). Consequently, landscapes are becoming more dense and heterogeneous in land-use types. The reality is that species, and especially birds because they are very mobile, will encounter more frequently agricultural and urban land-uses, amongst others. A critical question to answer, then, is what is the optimal mix of land-use types within the study that conserves biodiversity but also caters for the needs of an increasing human population? For example, I found that granivores appear to favour agricultural to urban land adjacent to protected areas, whilst other guilds such as frugivores appear to favour urban land over agricultural land adjacent to protected areas (Chapter 3). What are the threshold percentages of each land-use that simultaneously conserve biodiversity, and meet the needs of a human populations? In answering these questions, more questions arise. For example, what mechanisms underpin an average increase in abundance of granivores in agricultural land-use types, and is it independent of the type of crop farmed? I propose that in addition to the abovementioned suggestions, further research should seek to discover the mechanisms responsible for the correlations I present here.

Another exciting application of dynamic occupancy models is analysing the range dynamics of rare or threatened species (e.g., Broms et al., 2017). Given that the detection process is an inherent component of dynamic occupancy models, it is possible to develop accurate distribution maps for rare species using sparse data over large regions. These distributions can be projected into the future under simulated climate change scenarios. Perhaps conservation tools can be included in the model outputs, to simulate probable outcomes given conservation input, rendering model outputs a variety of scenarios (e.g., De Wan et al., 2009).

*6.3 Concluding remarks*

Land-use and climate change pose extinction threats to biodiversity world-wide. The underlying mechanisms of how these processes affect biodiversity needs to be understood to conserve biodiversity, and implement effective plans that will continue to conserve biodiversity in future. Statistical modelling plays an increasingly important role in uncovering biological mechanisms and species' interactions with their environments. In this thesis, I used atlas data collected via a national citizen science project, and dynamic occupancy methods that account for the imperfect nature of atlas data, as well as the dynamic nature of species' ranges, to examine occupancy dynamics of common species. I showed that protected areas were generally ecologically effective; however, this appeared to be dependent on the guild to which a species belongs, and the land-use types in proximity to protected areas. Nearby agricultural and urban land-use types significantly affected the ecological effectiveness of protected areas, and hence the benefit provided by protected areas to species. Thus, the land-use types of the landscape in which protected areas are imbedded are of considerable conservation importance. The effect of climate change must also be incorporated into these plans. The range of the Cape Rock-jumper (*Chaetops frenatus*) has shrunk substantially over recent decades, and I show that increases in the mean temperature over the warmest annual quarter lead to increases in extinction probability. The continued rate of climate change suggests further shrinkages to its range in the near future. This work also indicates that climate change is an ever-present threat to biodiversity. In consolidating these findings, this thesis has provided critical insight into, and information about future conservation needs for general biodiversity.

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