UNGULATE COMMUNITIES AND THE ROLE OF ENVIRONMENTAL GRADIENTS IN THEIR SPATIAL AND TEMPORAL DYNAMICS

by

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DECLARATION

I, Zaara Kidwai, declare that “*Ungulate communities and the role of environmental gradients in their spatial and temporal dynamics”,* is my own work and that all the sources that I have used or quoted have been indicated and acknowledged by means of complete references. I further declare that I submitted the thesis/dissertation to originality checking software and that it falls within the accepted requirements for originality. I further declare that I have not previously submitted this work, or part of it, for examination at UNISA for another qualification or at any other higher education institution.

Kidwai

04/12/2023

(Zaara Kidwai) Date

DEDICATION

To my parents and my extraordinary SB

ACKNOWLEDGEMENTS

My sincere gratitude goes out to everyone who helped me in finishing my thesis. I would like to start by sincerely thanking my supervisor *Dr. Cornelius J. Louw,* for his immense patience and kindness towards my struggles and overall journey. I could not have found a better supervisor and an extremely supportive mentor especially for the specialization I chose. I would also like to thank my co-supervisor *Professor Jason P. Marshal,* for his guidance in the thesis. I am grateful for the collaboration of *Pieter H. Nel* and *Mpho Sekgarametso* (North West Parks and Tourism Board) in this study. I would also take this moment to thank Dr. José Jiménez and Dr. Jeffrey W. Doser, for their help, guidance and collaboration in my thesis.

My PhD journey gave me the opportunity to meet some very interesting colleagues in the University of Wits. I would like to thank *Jonathan Levin,* for always staying available to help, be it software help or simply brainstorming for ideas. Of course, our frequent ice cream runs did not hurt. I thank *Gina Walsh,* for being a great friend and playing a major part in helping me construct my thesis. I am thankful to *Elena Mariotti,* for relieving me with her quirky remarks in the time of stress. Thank you guys! for being the friends I needed in an unknown and unfamiliar country.

This study was absolutely not possible without the unwavering support of my family. I am grateful for the courage I got from my *Dad*, and the tenacity I got from my *Mom*, needed to complete my PhD. My sisters *Farina* and *Samien* inspired me to see this journey through. I thank my brother in laws *Imran Khan* and *Meraj Ahmad,* for their support and encouragement. I thank my nieces and nephews *Mihika, Izhaan, Zoey* and *Arzeb,* for being my lucky charms and comic relief. I thank *Baba,* who kept pushing me towards finishing my PhD. I hope he is proud of me, and is blessing me from the clouds. I also thank *Maa, Dada and Didi,* for their blessings, constant love and support.

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He is my lobster.

ABSTRACT

The African savanna supports a high diversity of ungulate species that have intrigued scientists for a long time. Fluctuating densities across space and time suggest ungulate populations are predominantly regulated by climatic conditions. In South Africa, most conservation areas are relatively small and likely impose limitations to resource acquisition by ungulates. The rationale of this thesis is to explore the variables causing population fluctuations in co-existing species, along with understanding the difference in their spatial distribution and segregation patterns in the North-West province of South Africa. The study includes 17 years (1999-2015) of data collected across 13 protected areas via aerial surveys during the dormant season. I used N-mixture models to improve estimation of population abundance of a rare species (black rhino) from replicated aerial surveys while accounting for imperfect detection. Generalized linear models and spatial occupancy models were used to determine factors affecting distribution and habitat partitioning of ungulates across the landscape. Ungulate habitat selection and occupancy was predominantly influenced by topography. For example, low-lying habitats were favoured by most ungulates during the dry season, probably because of the longer retention of soil moisture and higher forage quantity in areas lower down the catena during the dormant season. High heterogeneity in turn, were more important to mixed and bulk feeders e.g. impala, zebra. Spatial occupancy of ungulate groups was not directly related to the species richness in a feeder group. Pilanesberg had the lowest occupancy of all three groups despite having the highest number of species suggesting spatial avoidance or resource partitioning within each group. Spatial segregation was highest in sites with the highest species diversity. Within-group spatial segregation occurred within all three groups between similar sized along with between species of varying body size across all sites except Molopo. Species interactions within ungulate assemblages are complex and varies with changing environmental conditions. For the effective conservation of ungulate populations, the specific ecological context needs to be considered. Additional ecological factors e.g., predation, resource availability and management variables e.g., fire, water availability and fences are equally important influences on the viability of ungulate populations of small fenced conservation areas.

Key terms: Ungulates; Aerial surveys; N-mixture models; Abundance; Population dynamics; Distribution; Detection probability; Habitat partitioning; Spatial occupancy; North West Province.

PUBLICATIONS

The following work from this thesis has been published in peer-reviewed journal:

Chapter 2

Kidwai Z., Jimenez J, Louw C.J., Nel H.P. and Marshal J.P. 2019. Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (Diceros bicornis L.) populations from aerial counts. Global Ecology and Conservation: https://doi.org/10.1016/j.gecco.2019.e00687

My contribution to the paper included design of study, collection, extraction of sampled data from North West Parks and Tourism Board (NWPTB) for years between 1999 and 2015 and collection of meteorological data from NASA Prediction of Worldwide Energy Resources (POWER). I statistically analysed and interpreted the data, and drafted the abstract, introduction, methods, results, discussion and conclusion sections of the paper. Co-authors read, edited, and made suggestions to improve the overall paper.

IN PREPARATION

The following data chapters have not been submitted for publication.

Chapter 3

Kidwai Z., Louw C.J., Nel H.P. and Marshal J.P. Landscape scale predictors of ungulate habitat use in the North West Province, South Africa.

I designed the study, collected and extracted the field survey data from North West Parks and Tourism Board (NWPTB), Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectrometer (MODIS), land cover data from South African National Land cover Data and digital elevation models from USGS Science based catalog for years between 1999 and 2015. I statistically analysed and interpreted the data, and drafted the abstract, introduction, methods, results, discussion and conclusion sections of the paper. Co-authors read, edited, and made suggestions to improve the overall chapter.

Chapter 4

Kidwai Z., Doser J., Louw C.J., Nel H.P. and Marshal J.P. Spatial occupancies, community richness and spatial segregation patterns among ungulates in the North West Province, South Africa

I designed the study, collected the field survey data from North West Parks and Tourism Board (NWPTB). I also extracted Normalized Difference Vegetation Index (NDVI) from Moderate Resolution Imaging Spectrometer (MODIS), soil nutrients data from ISRIC World Soil Information, land cover data from South African National Land Cover Data and digital elevation models from USGS Science based catalogue for years between 1999 and 2015. I statistically analysed and interpreted the data, and drafted the abstract, introduction, methods, results, discussion and conclusion sections of the paper. Co-authors read, edited, and made suggestions to improve the overall chapter.

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CHAPTER 1. General Introduction

1.1. INTRODUCTION

The global rise in the human population over the last century have caused considerable declines in large herbivore populations throughout the African continent, largely due to progressive contraction of their natural habitats (Vrba & Schaller, 2000; Vié et al., 2009; Craigie et al., 2010; García-Marmolejo et al., 2013; Venter et al., 2014). However, species are not equally affected e.g. declines are most evident for roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*), tsessebe (*Damaliscus lunatus*), eland (*Taurotragus oryx*) (Ogutu & Owen-Smith, 2003; Dunham et al., 2004; Ogutu et al., 2011, Marshal et al., 2016), greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus elipsiprimnus*) and warthog (*Phacochoerus africanus*) (Ogutu & Owen-Smith, 2003) across different nature reserves in Africa. Numbers of other species remained stable, or increased e.g., zebra (*Equus burchelli*), impala (*Aepyceros melampus*), giraffe (*Giraffa camelopardalis*) and blue wildebeest (*Connochaetes taurinus*) (Ogutu & Owen-Smith, 2003). Studies aimed at understanding the drivers of ungulate population change are required to advance conservation decisions and to avoid population explosions or sudden population crashes. Furthermore, gaining insight into the habitat requirements of competition sensitive species could help maintain the integrity of the ungulate diversity in an ecosystem.

Contractions in geographical range are commonly associated with the decline of a species (Gaston, 1994; Gaston et al., 1998; Holt et al., 1997; Harnik, 2011). Establishing the ecological factors structuring spatial distributions is therefore inherently important from a conservation perspective. Ungulates are ecosystem architects as they provide some of the crucial ecological services including seed dispersal and nutrient recycling (Hobbs, 1996). Therefore, sustaining healthy ungulate populations is critical to health of the ecosystem they inhabit (Bro-Jørgensen, 2016). Several factors structure ungulate distribution and density (Illius & O'Connor, 2000; Maffei & Taber, 2003; Redfern et al., 2003; Rivero et al., 2005; Owen-Smith & Mills, 2006; Keuroghlian & Eaton, 2008). Amongst others, these factors include rainfall (Coe et al., 1976; Fritz & Duncan, 1994; Owen-Smith, 2000; Ogutu et al., 2008), soil nutrients (Bell, 1982), geology (Fritz et al., 2002), predation and of course, competition (Wang et al., 2006; Owen-Smith, 2006; 2008; Rotella et al., 2009; Bateman et al., 2012; Koons et al., 2015). Numerical responses of large ungulate populations to environmental conditions are not always similar across the species specturm, because foraging adaptations and adaptations to minimize predation risk differ among species (Sæther, 1997; Hopcraft et al., 2010). Furthermore, long-term data sets are required to compare factors influencing distributions of a species across the landscape (Eberhardt, 1988). Despite extensive research on ungulate populations, scientific archives lack in-depth research on ecological determinants of ungulate habitat partitioning and spatial segregation patterns in multi-species environments, other than for the species with any evident conservation or economic importance (Gaillard et al., 1998; Wittemyer et al., 2013).

1.1.1. Background

Global environmental changes, including those of climate, continental drift, and sea levels has influenced distribution patterns of a number of animal species, driving evolutionary change (Sepkoski, 1976), global changes in biodiversity patterns (Ricklefs, 2004; Harrison & Cornell, 2008; Thomas et al., 2008) and even mass extinction (Hallam & Wignall, 1999; Peters, 2008). Ungulates have been one of the most abundant herbivore mammals since the Cenozoic era (ca. 65 million years ago

(Ma) to present) found throughout the world except the continents of Antarctica and Australia (Saarinen, 2019). Ungulates include species from the orders Artiodactyla (even-toed; e.g., pigs, antelopes, hippos and giraffes) and Perissodactyla (odd-toed; e.g., rhinos, zebras and horses). Due to the presence of high skeletal material, fossil preservation of ungulates has been more reliable than other smaller animals resulting in a rich fossil record (Janis et al., 1998; Darroch et al., 2014). This is probably also the reason that they are taxonomically one of the better understood groups of terrestrial mammals (Alroy, 2003).

Being such a diverse group, it is hardly surprising that the ungulate taxonomic classification has been frequently updated and corrected, (Groves & Grubb, 2011). More than 250 species of modern ungulates are recognized globally (Wilson & Reeder, 2005) under the clade "*Ungulata*", out of which almost 90 ungulate species are found in Africa alone (Leuthold, 1977). The group cover a vast range in body-size, extending from a small buck weighing 3-4kg all the way up to hippos and rhinos, weighing more than 1000 kg (Estes, 1991), no doubt a consequence of the varied habitat across Africa (Leuthold, 1977). Co-existence and spatial segregation of this varied group has been the focus of many scientific studies for a while (see Li et al., 2022). This study therefore, aims to provide some new insights on co-existence and spatial segregation of ungulate populations within small fenced conservation areas (<10,000 km^2). Ungulate populations in these areas are also influenced by management interventions. Understanding the factors allowing co-existence and spatial segregation are therefore, important to develop objective based management strategies for ungulate species including harvests and species recovery strategies.

1.1.2. Foraging behavior in ungulates

Ungulates have undergone a series of adaptations over geological time, which enabled them to change their diet (Illius, 1997; Mendoza et al., 2002; Saarinen, 2019). Although most of the ungulates are herbivores (including grazers, browsers and mixed feeders), it also consists of some omnivorous groups such as *Suidae* (i.e. pigs) (Benton, 1993; Janis et al., 1998; Saarinen, 2019). Small sized ungulates space use is determined by predation risk and a more selective diet compared to large grazers (Hopcraft et al., 2012). Therefore, ungulate body size plays an important role in their spatial distribution across landscapes (Jarman, 1974; Botkin et al., 1981; Bell, 1982; Hopcraft et al., 2010) along with defining their group size (Jarman, 1974). Ungulates are heterogeneously distributed across landscapes according to the availability of resources (McNaughton, 1988). Recent studies suggested that the landscape changes also affect population dynamics of ungulates (Anderson et al., 2006; Hopcraft et al., 2010; Seydack et al., 2012; García-Marmolejo et al., 2015). It is therefore important to investigate species-specific and site-specific species responses to ecological factors for strategizing management interventions.

1.1.3. Ungulate distribution patterns

Ungulate species throughout the world are now restricted to ranges much smaller than their historical range, reportedly due to habitat fragmentation (Smith & Fowler, 1981; Vieira-Fragoso, 1999; Morris, 2002; García-Marmolejo et al., 2013). However, isolating all the factors responsible for ungulate population fluctuations is challenging because they often are interdependent or operate over varying temporal scales (Fowler, 1981). Studies concerned with the temporal dynamics of vertebrates range from being mainly descriptive to those exploring causal mechanisms of observed dynamics, the latter of which have much scope for future research (Caughley & Gunn, 1993; Owen-Smith, 2000; Turchin, 2003; Brotz et al., 2012; Chakraborty et al., 2013). Interspecific competitionhas received considerable attention as a potential driver of population regulation (Mccullough, 1999; Arsenault & Owen-Smith, 2002; Barabás et al., 2016; Deliberato, 2017). Even so, population level responses to competition remains sparse, possibly, because habitat modifications obscure any evidence related to competition (Mccullough, 1999). Furthermore, the population dynamics of wildlife populations are very context dependent, most notably linked to the species under consideration and the ecological conditions they are exposed to (Sæther, 1997; Hopcraft et al., 2010).

Although, temporal fluctuations in abundance in response to climatic fluctuations and growth rate should predominate in ungulate populations (Sæther, 1997; Gaillard et al., 1998; 2000), some previous studies suggested that predation is the most important determinant driving ungulate abundance and community structure (Jeffries & Lawton, 1984; McNaughton & Georgiadis, 1986; Shipley, 1999). Predation not only causes mortality, but also structure space use of prey species, and thus modify the extent of resource overlap. Predator presence therefore alters the intensity of competition between different species (Roughgarden & Feldman, 1975; Glasser, 1979; 1982; Holt, 1984).

Rainfall and associated primary production in vegetation largely dictates ungulate biomass (Coe et al., 1976; McNaughton et al., 1989; Mduma et al., 1999; Ogutu et al., 2008; 2014). Soil nutrients, seasonal fluctuations in resource availability and landscape barriers further impose limitations to ungulate distribution patterns (Bell, 1982; East, 1984; Seagle & McNaughton, 1992; Fritz & Duncan, 1994; Gaillard et al., 2000; Coulson et al., 2005; Anderson et al., 2006; 2010; Bleich et al., 2010; Bayarbaatar, 2016).

There is a dearth of literature on the response of large mammal population distributions to various ecological drivers (Craigie et al., 2010). Studies, aimed at identifying the main drivers of ungulate spatial distributions at landscape scales are important for the implementation of sound species- and site-specific management strategies (Tuljapurkar & Caswell, 1997; Gaillard et al., 1998).

The current study encorporates a range of study sites, with and without large predators, and a broad spectrum of environmental conditions across the North West province. Consequently, the spatial distribution of ungulates in predator free sites are driven by environmental factors and possibly competition. Research on some of the ungulate species found in the landscape were conducted in only a few of these study sites (e.g., Madikwe, Pilanesberg and Kgaswane) (see Brockett, 2002; Hrabar & du Toit, 2005; Marshal et al., 2016; Louw et al., 2019). However, most of the reserves in the landscape remain unexplored for multi species ungulate interactions. Additionally, most of the currently available African ungulate research was conducted in comparatively larger reserves (>10,000 km^2) such as Kruger National Park (see Redfern et al., 2003; Dunham et al., 2004; Seydack et al., 2012; Rigoudy et al., 2022) or from Serengeti National Park and Serengeti ecosystem (see Mduma et al., 1999; Anderson et al., 2010; Hopcraft et al., 2012; Hunninck et al., 2020). The study contributes towards filling gaps in existing literature on factors structuring the spatial distribution of ungulate communities in smaller reserves across a heterogeneous landscape, and hopefully contribute towards conservation practices involving ungulates in the North-West (NW) Province.

1.2. STUDY AREA

The study was conducted in the North-West Province of South Africa (between latitude of 24°15’S to 28°15’S and longitude of 22°30’E to 28°30’E) comprising of 13 Nature

Reserves (including three dams) namely (from east to west): Borakalalo National Park, Vaalkop Dam Nature Reserve, Pilanesberg National Park, Kgaswane Mountain Reserve, Madikwe Game Reserve, Boskop Dam Nature Reserve, Molemane Eye Nature Reserve, Botsalano Game Reserve, Mafikeng Game Reserve, Wolwespruit Nature Reserve, Bloemhof Dam Nature Reserve, SA Lombard Nature Reserve and Molopo Game Reserve (Figure 1.1). The landscape of the province changes from plains in the west to mountains in the east. The altitude of the region ranges from 1,000 m mean above sea level (masl) in the plains to 2,000 m masl in the mountains with mostly plains with pans in the center. Presence of flat terrain and undulating plains with scattered hills, lowlands, and parallel hills are characteristic features of the northeastern portion of the province (Goslar et al., 2008).

The entire area faces nearly year-round sunshine. August through March are the region's summer months, with sporadic afternoon thunderstorms. The area has a rainfall range of 300 mm to 700 mm annually due to which it is considered as an “arid region”. The rainfall gradient increases from west to east and south to north with a slight increased gradient at the central interior (Kruger & Nxumalo, 2017). Temperature in summer ranges between 22°C and 34°C while the average winter temperature ranges from 2°C to 20°C in a single day (Goslar et al., 2008) (Figure 1.2).

Three broad categories of vegetation are found across the region (Acocks, 1988) consisting of the 61 total vegetation types (Goslar et al., 2008). Bushveld is restricted to the north-eastern region that consists of Mixed, Sour and Sourish-mixed veld interspersed with Bankenveld and Turf Thornveld type. Central region is uniformly composed of mixed vegetation with equal proportion of dry and sandy *Cymbopogon-Themeda* veld having Sourish-mixed bushveld in the north. The most arid region of the province, the western region, mainly consists of Kalahari Thornveld (Spickett et al., 2011).

The NW Province is extremely rich in biodiversity. More than 130 mammals, 300 birds, 25 amphibians, 50 reptile species and 3,000 plant species are distributed across the province. To conserve these species, protected areas have been set up in different parts of the province which contributes to an area of about 2,833 km^2 and this figure amounts to a little over 2% to the total land area of the province (Goslar et al., 2008).

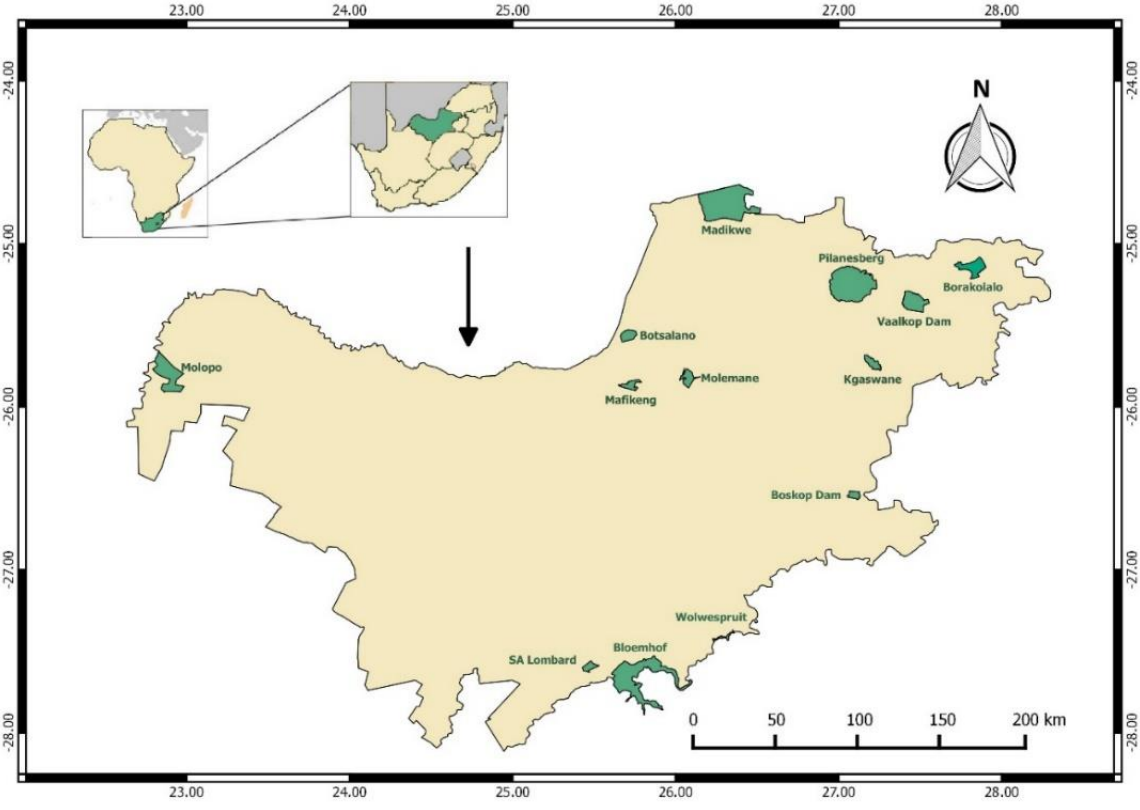

Figure 1.1: Map of North West Province highlighting the study sites

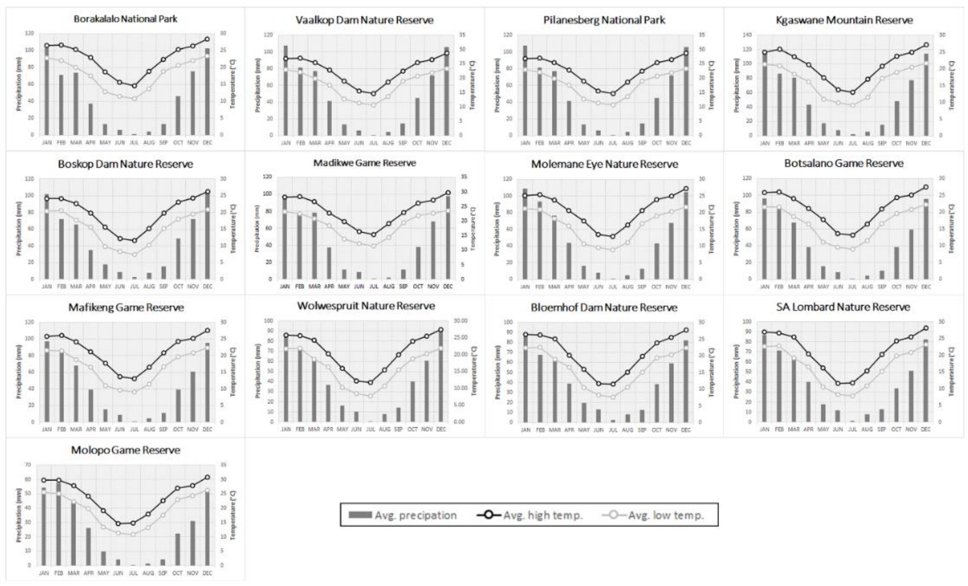

Figure 1.2: Average precipitation and minimum and maximum temperatures for the study areas in the NW Province (NASA POWER, 2020).

1.2.1. Study Sites

1.2.1.1. Borakalalo National Park

Borakalalo National Park (hereafter Borakalalo) is situated approximately 60 km north of Brits (27° 49’E latitude and 25° 9’S longitude). It consists of more than 140 km^2 of mixed and sourish mixed bushland (Brown et al., 1997). It lies along the banks of the Moretele River with 8 km^2 of Klipvoor Dam on one side (Greyling & Huntley, 1984; NW Read, 2015; Gordon-Cumming, 2017) and a riverine forest on the other (Brown et al., 1995). It encompasses plains to gentle slopes in the landscape (Brown et al., 1996) leading to an altitude averaging between 960 m to 1172 m mean above sea level (masl.) (Brown, 1998; Gordon-Cumming, 2017). Average monthly temperature ranges between 19°C to 31°C and average annual rainfall is 552 mm (NASA POWER, 2020). The reserve consists of a wide variety of antelopes, giraffe, white rhino (*Ceratotherium simum*), leopard (*Panthera pardus*) and numerous smaller mammalian species (North West Parks, 2015). Over 350 species of birds are recorded in this reserve, including the rare golden Plover (*Pluvialis fulva*) (Chittenden, 2007; NWPTB, 2020). The reserve is also home to the nationally threatened reptilian species of African python (*Python natalensis*) (NW READ, 2015).

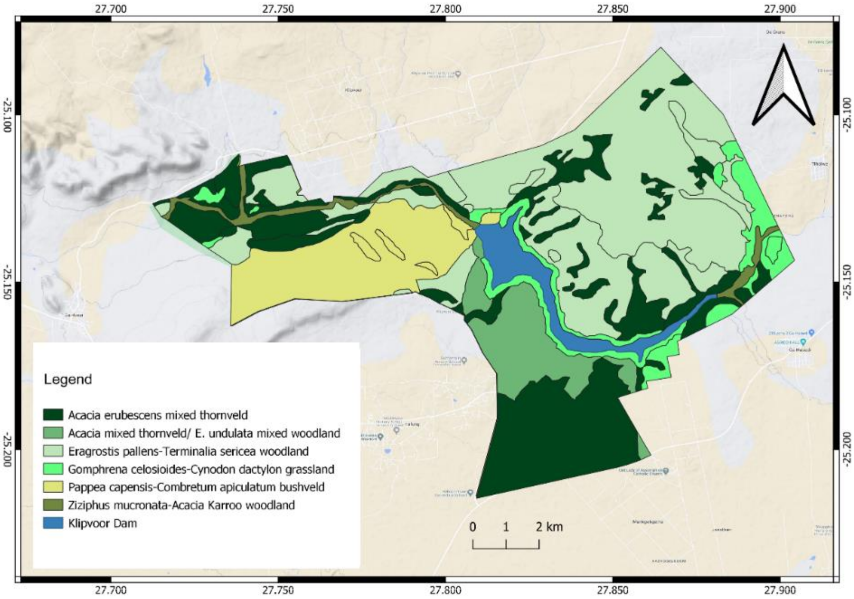

Figure 1.3: Major Vegetation types in Borakalalo Nature Reserve (NWPTB, 2020)

1.2.1.2. Vaalkop Dam Nature Reserve

This Dam (27° 25'E latitude, 25° 20'S longitude) is located 54 km north of Brits near Beestekraal and north-east of Rustenburg. The Vaalkop dam nature reserve (hereafter Vaalkop) with a size of 40 km^2 is made up of three parts, one of which (of an area 800ha) has been set aside as a bird sanctuary and is not open to general public. Vegetation of the reserve is typically bushveld comprising of mixed *Acacia* thornveld and broadleaf woodland (Birdlife, 2018). The average temperature in this area is 20°C (NASA POWER, 2020) with an elevation range of 969 m to 1,130 m masl. (Topographic maps, 2020) and average annual rainfall of 566 mm (NASA POWER, 2020). The reserve is usually an attraction for bird watchers and anglers (NWPTB, 2020). Over 300 bird species have been recorded from this area. Large mammalian species such as impala, red hartebeest and zebra are also reported from the nature reserve (Nel, 2018).

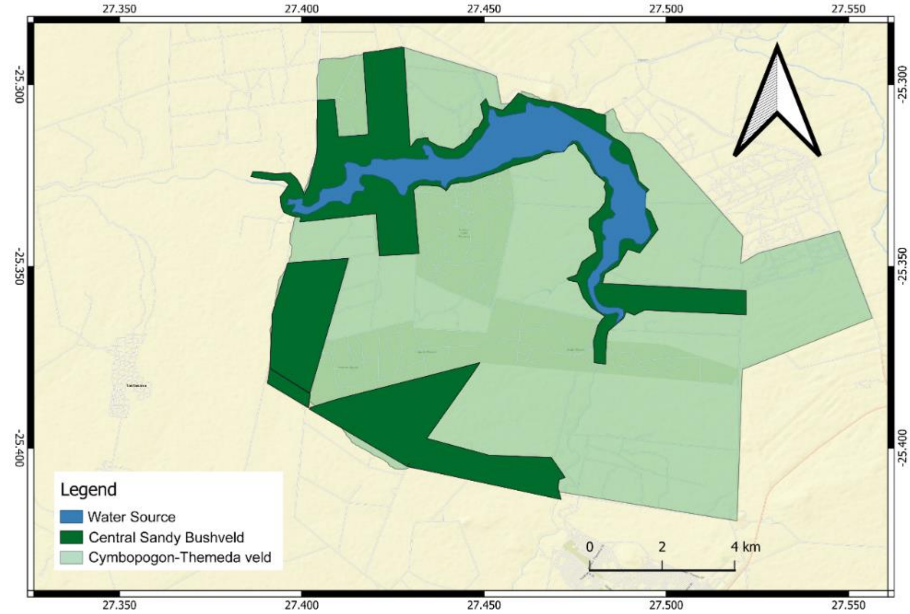

Figure 1.4: Major Vegetation types in Vaalkop Dam Nature Reserve (NWPTB, 2020)

1.2.1.3. Pilanesburg National Park

Pilanesberg National Park (hereafter Pilanesberg) is situated in the region of Bojanala in the North West Province and encompasses an area of about 550 km^2 (25° 15'S latitude, 27° 6'E longitude). The geological landscape was formed ca. 1,300 million years ago by a crater that was produced by volcanic eruptions (by a now-extinct volcano), and fringed by a group of concentric hills (Carruthers, 2011). The park lies between a transition zone of the Kalahari and sour bushveld (Acocks, 1988). The vegetation is a mix of open grassland to thickets of *Vachellia* and broad-leaf bushveld species (Hrabar & du Toit, 2005; Louw et al., 2019). The average annual rainfall received by the park lies in the range of 600-700 mm with the average annual temperature in the range of 15°C to 30°C (NWPTB, 2020). Nearly twenty-five species of the large mammals occur in Pilanesberg which includes lion, cheetah (*Acinonyx jubatus*), leopard, brown hyena (*Hyaena brunnea*), elephant, springbok (*Antidorcas marsupialis*), hippopotamus (*Hippopotamus amphibious*), black (*Diceros bicornis*) and white rhino, and crocodile (*Crocodylus niloticus*) (NWPTB, 2020).

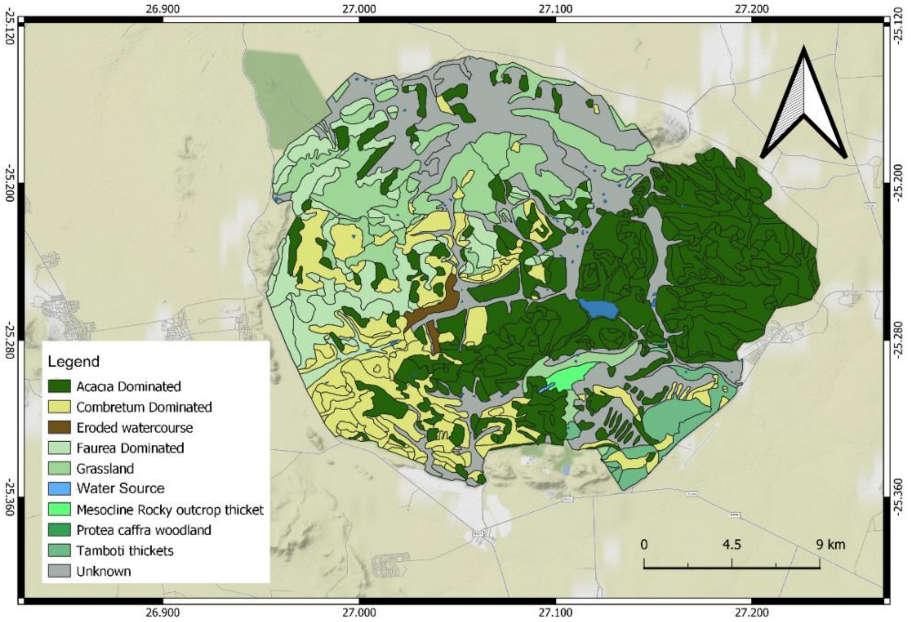

Figure 1 5: Major Vegetation types in Pilanesberg Nature Reserve (NWPTB, 2020)

1.2.1.4. Kgaswane Mountain Reserve

Kgaswane mountain reserve (27° 11' E latitude, 25° 43’S longitude), covers an area of 45 km^2 and is situated north of the the town of Rustenburg comprising of a varied habitat of quartzite mountain peaks along with *vleis* (wet grassland) on the northern slopes of the Magaliesberg. It has an elevation in the range of 1,230–1,660 m masl. The reserve (hereafter Kgaswane) consists of high-elevation plateaus descending towards an alluvial soil and marshland basin resulting in formation of a wetland (Nel, 2000; Marshal et al., 2016). Vegetation consists of a mixture of vleis, grassland, open shrubland and woodland (Parrini & Owen-Smith, 2010). The reserve is home to a number of large herbivores including antelopes such as kudu, blesbok (*Damaliscus pygargus*), duiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*), mountain reedbuck (*Redunca fulvorufula*), klipspringer (*Oreotragus oreotragus*), and waterbuck along with small to medium sized predators such as leopard, aardwolf (*Proteles cristata*), caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*) (Nel, 2018).

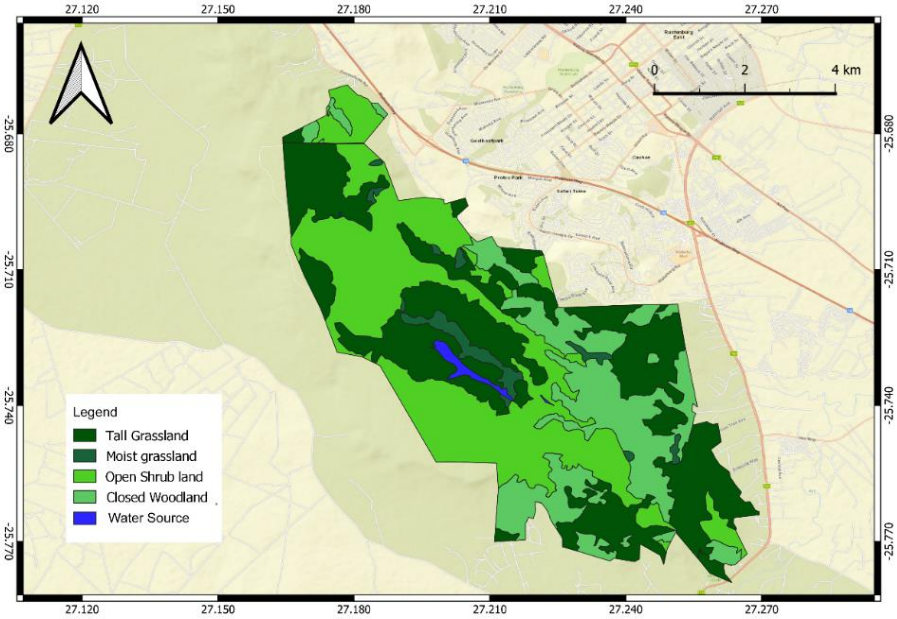

Figure 1.6: Major Vegetation types in Kgaswane Mountain Reserve (NWPTB, 2020)

1.2.1.5. Madikwe Game Reserve

The Madikwe game reserve (24° 45'S latitude 26° 16'E longitude) is known to be one of the biggest game reserves of South Africa with an area of more than 600 km^2. The reserve (hereafter Madikwe) is situated next to the Botswana border in the far north of North West Province (NWPTB, 2020). Madikwe is composed of a mixture of large open woodlands and grasslands which is divided in the middle by the rocky hills of “Rant van Tweedepoort” and bordered in the south by mountains of Dwarsberg. Majority of the vegetation of the reserve can be classified as Sourish Mixed Bushveld (Acocks, 1988) with the dominating *Vachellia* species in the tree-shrub layer from medium-low to tall-growing flora. The most peculiar feature of this area is the presence of scattered isolated hills otherwise known as “inselbergs” that has risen abruptly from the otherwise flat terrain (NWPTB, 2020). The area receives an average annual rainfall of around 500 mm per annum and the temperature here ranges from 3°C - 32°C (NASA POWER, 2020). More than 60 large mammalian species are found in this reserve that includes lion (*Panthera leo*), elephant (*Loxodonta africana*), both black and white rhinoceros, leopard and African buffalo (*Syncerus caffer*) (Nel, 2018).

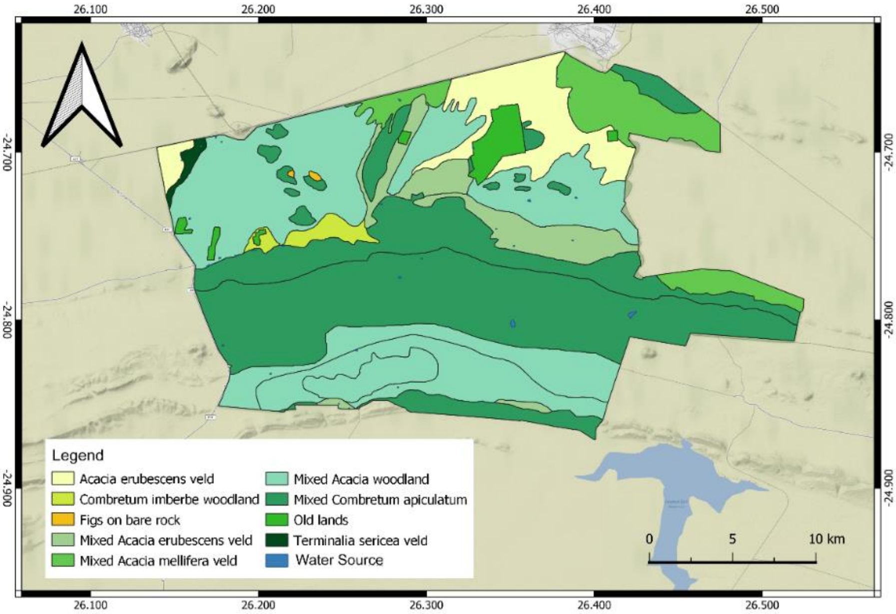

Figure 1.7: Major Vegetation types in Madikwe Game Reserve (NWPTB, 2020)

1.2.1.6. Boskop Dam Nature Reserve

This nature reserve (27° 08'E latitude, 26° 33'S longitude) has an area of 30 km^2 of continued mosaic of sour grasslands constituting Bankenveld (Acocks, 1988). It is located 20 km north of the Potchefstroom town in the valley of Moori river. The climate of the area usually ranges from having temperatures of -1°C (May – September) to 32°C (during October-January) with dry frosty winters and wet summers (Bredenkamp et al., 1994). Boskop dam nature reserve (hereafter Boskop) faces average annual rainfall of around 600 mm (Bezuidenhout & Bredenkamp, 1990) The reserve holds rocky, non-arable shallow soils (Louw, 1951) with a mixture of shale, lava, quartzite ridge, dolomitic limestone, few faults and a diabase dyke in its complex geology (Annandale & Nealer, 2011; Barnard et al., 2013). The reserve is home to large mammalian species such as springbok, black wildebeest (*Connochaetes gnou*), blesbok, red hartebeest and zebra (Nel, 2018).

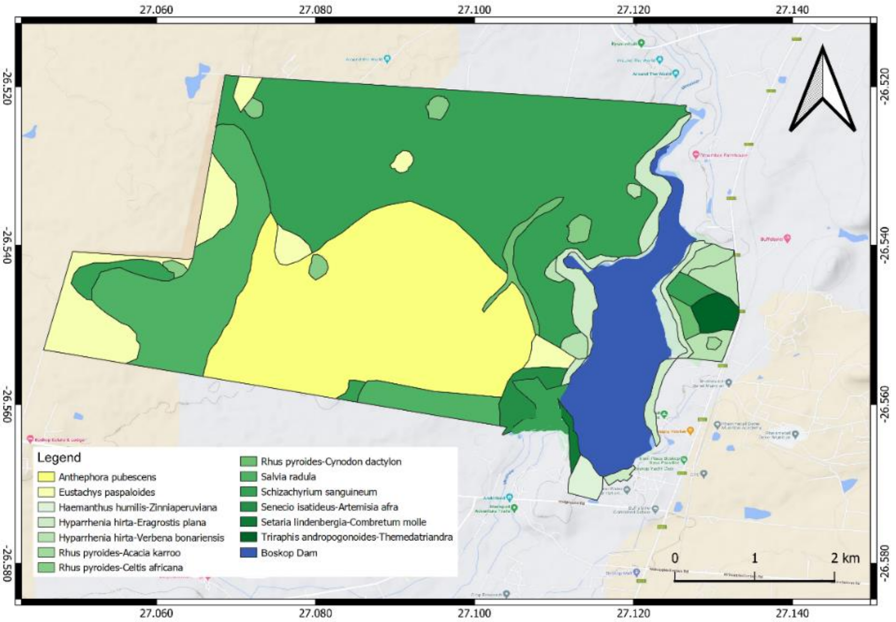

Figure 1.8: Major Vegetation types in Boskop Dam Nature Reserve (NWPTB, 2020)

1.2.1.7. Molemane Eye Nature Reserve

The Molemane eye nature reserve (27° 11'E latitude 25° 43'S longitude) is situated at an altitude range of 1,474-1,540 m masl on the Lichtenburg-Zeerust Road, around 10 km from Ottoshoop covering an area of almost 50 km^2 (Leitner, 2013; NWPTB, 2020). Vegetation in the Molemane eye nature reserve (Molemane) is composed of Kalahari grassland and acacia thorn scrub or sour mixed bushveld (Acocks, 1988; Newbery & van Heerden, 2002) over undulating terrain. The soil mainly consists of dolomite and chert (Mucina & Rutherford, 2006). Temperature of the reserve ranges from -5°C in the winters to 35°C in the summers. The average annual rainfall received by the area is around 600 mm (NASA POWER, 2020). The reserve has good numbers of ungulates such as zebra, blesbok, warthog and African buffalo (Knoop et al., 2009; Leitner, 2013).

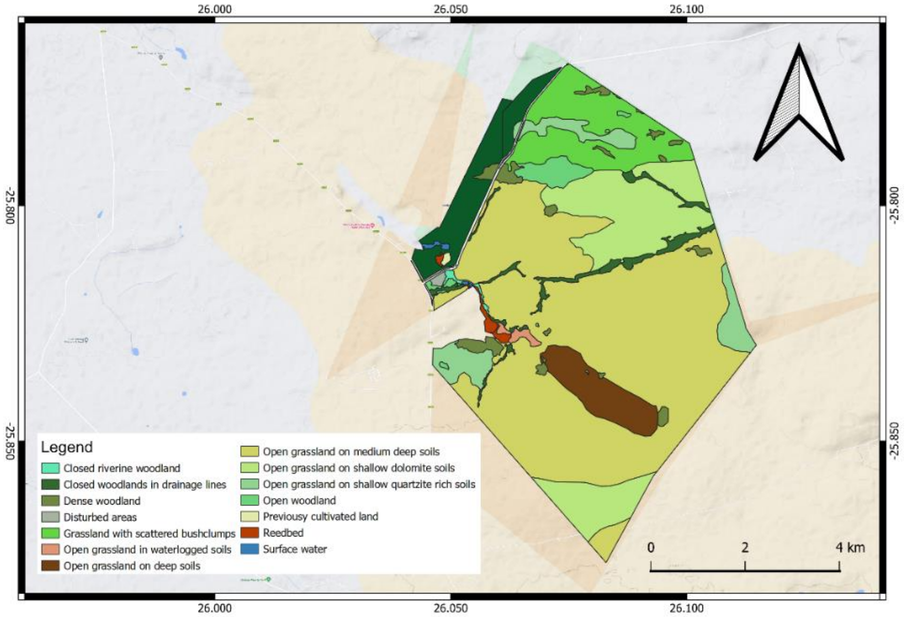

Figure 1.9: Major Vegetation types in Molemane Eye Nature Reserve (NWPTB, 2020)

1.2.1.8. Botsalano Game Reserve

Located at 18 km north of the Ramatlabama border post on Botswana border (to the west of Mafikeng), Botsalano game reserve (25° 42'E latitude, 25° 33'S longitude) covers an area of 58 km^2 (NWPTB, 2020) with an elevation range of 1,320 m to 1,440 m masl (Birdlife, 2015). Vegetation of Botsalano game reserve (hereafter Botsalano) is represented by a mix of wide-ranging grassland and *Vachellia* woodlands also called as Klerksdorp Thornveld (Mucina & Rutherford, 2006). Geology of the reserve comprises of rocky and shallow soils interspersed with deep sandy loam with quartz and limestone (Munyati & Moeng, 2015). The climate in this reserve is generally mild to very hot in summers with a possibility of winter nights being extremely cold. The area receives an annual average rainfall of around 500 mm (Birdlife, 2015). The Reserve is home to over 200 bird species with records of a few globally threatened species including Cape Vulture (*Gyps coprotheres*), Kori Bustard (*Ardeotis kori*), Secretary bird (*Sagittarius serpentarius*) (Birdlife, 2015). The major large mammalian species in the reserve include African buffalo, zebra, red hartebeest (*Alcelaphus caama*) and white rhinoceros (Nel, 2018).

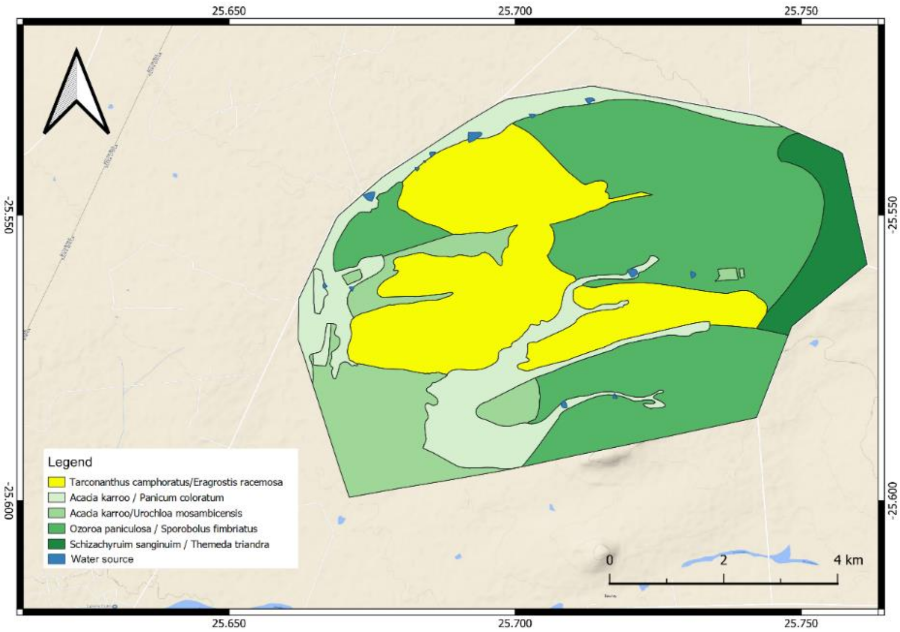

Figure 1.10: Major Vegetation types in Botsalano Game Reserve (NWPTB, 2020)

1.2.1.9. Mafikeng Game Reserve

With an area of 48 km^2, Mafikeng Game Reserve (25° 43' E Latitude, 25° 52' S longitude) established in 1992 (Brockett, 2002), is located almost in the upper middle part of North West Province (Seitlhamo, 2011). Elevation of the Mafikeng game reserve (hereafter Mafikeng) ranges form 1,260 – 1,420 m asl. with a flat terrain (Seitlhamo, 2002). An underlying layer of lava with andesitic composition (Mucina & Rutherford, 2006) features a considerable part of the reserve. The climate in this area is mild to hot (15°C - 35°C), with the possibility of winter nights being extremely cold (Seitlhamo, 2011). The average annual rainfall in the area is around 550 mm. The vegetation of this reserve is described as mixed bushveld by Acocks (1988), and dry *Cymbopogon-Themeda* veld by Mucina and Rutherford (2006) with dominant woodland species being *Rhus lancea* and *Vachellia* while *Cymbopogon plurinodis, Themeda triandra Enneapogon scoparius, Elionuris muticus, and Heteropogon* *contortus* being the dominant grass species (Adcock, 1991). The reserve comprises of a good populations of game animals including zebra, white rhino, gemsbok (*Oryx gazela*), African buffalo, ostrich (*Struthio camelus*) and giraffe (Nyirenda et al., 2016).

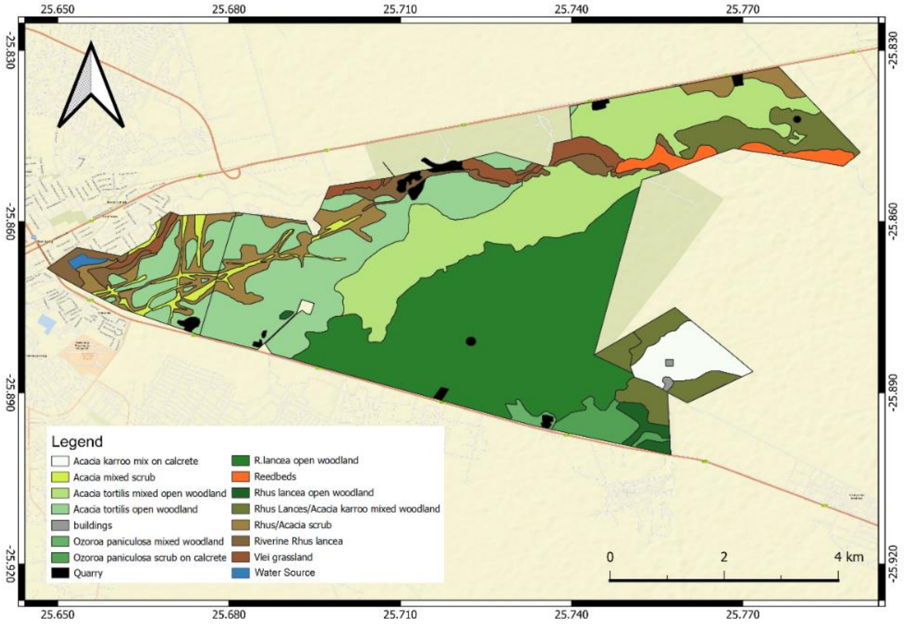

Figure 1.11: Major Vegetation types in Mafikeng Game Reserve (NWPTB, 2020)

1.2.1.10. Wolwespruit Dam Nature Reserve

This Wolwespruit dam nature reserve (26° 16'E latitude 27° 24'S longitude) is one of the least known nature reserves in the North West Province (NWPTB, 2020). Located upstream on the Vaal River, at a distance of 130 km from the Bloemhof Dam, the Wolwespruit dam nature reserve (hereafter Wolwespruit) has an area of 23 km^2 with an average elevation between 1,554 and 1,664 m masl. (Topographic maps, 2020). Temperature of the region ranges from 9°C - 26°C and the area receives an annual average rainfall of 490 mm (NASA POWER, 2020). The reserve comprises of a riverine bush habitat stretched throughout its length. Although small, the reserve comprises of a number of large herbivores such as kudu, impala, black wildebeest, red hartebeest, blesbok and zebra (Nel, 2018).

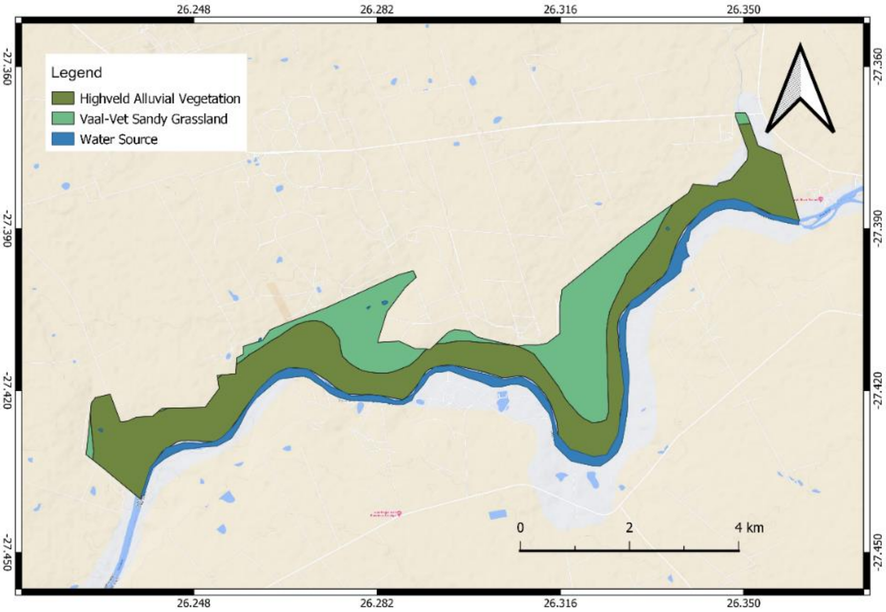

Figure 1.12:Major vegetation types in Wolwespruit Dam Nature Reserve (NWPTB, 2020)

1.2.1.11. Bloemhof Dam Nature Reserve

The Bloemhof dam nature reserve (25° 39'E latitude and 27° 40’S longitude) is located 320 km from Johannesburg and 4 km east of Bloemhof city. The size of the Bloemhof dam nature reserve (hereafter Bloemhof) is 250 km^{2} with an open Kalahari scrub vegetation called as Kimberly Thornveld (Mucina & Rutherford, 2006) and influx of water in the dam from Vall river (NWPTB, 2020). Climate in this reserve is usually mild to hot (12°C – 26°C) (Shafir & Oldewage, 1992) in summers but can be cold in winter nights (NASA POWER, 2020). The area receives an average annual rainfall of 480 mm (NASA POWER, 2020). Bloemhof comprises of a wide variety of game species such as springbok, black wildebeest, eland and gemsbok (Nel, 2018) and more than 250 species of birds including breeding colonies of White-backed Vultures (*Gyps africanus*) (Birdlife, 2018).

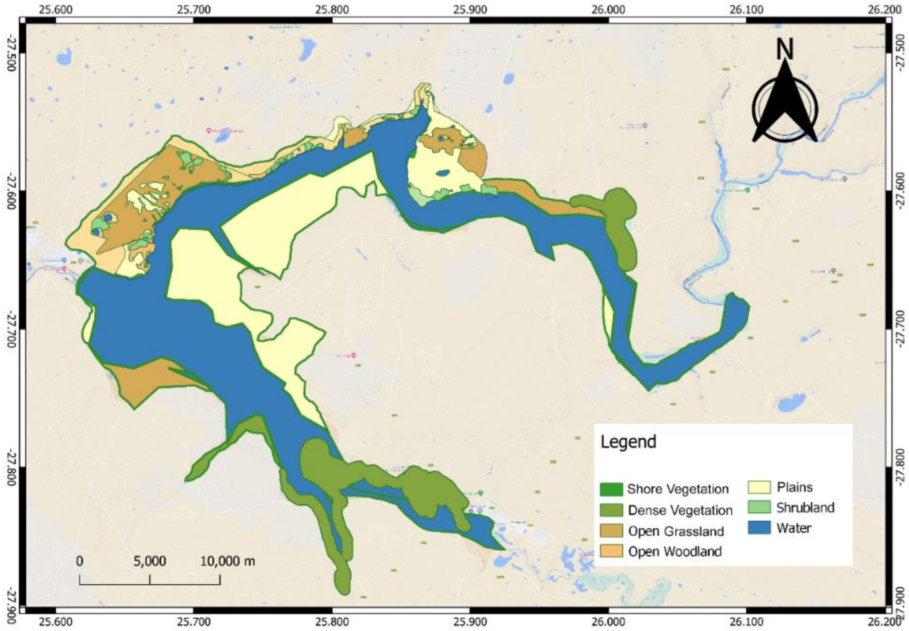

Figure 1.13: Major habitat types in Bloemhof Dam Nature Reserve (NWPTB, 2020)

1.2.1.12. S.A. Lombard Nature Reserve

This reserve (25° 30’E latitude, 27° 35’S longitude) is located at about 17 km west of Bloemhof with an area of approximately 42 km^2 (van Zyl, 1965; Buys & Dott, 1991) and an altitude of 1283 m (van Zyl, 1965; Rechav, 1986). The topography of the reserve (hereafter SA Lombard) consists of a small area of open Kalahari grassland on an undulating flood plain. Vegetation in some areas are represented by Kalahari thornveld dominated by trees and shrubs such as a few species of *Vachellia*, *Rhus lancea*, *Pentzia incana, Chrysocoma cenuifolia* and *Tarchonanthus camphoratus* while other areas by open *Cymbopogon-Themeda* grasslands (van Zyl, 1965; Rechav, 1986; Acocks, 1988; Buys & Dott, 1991). The area experiences wide fluctuations in temperature ranging from -10°C in winters to almost 40°C in summers. The reserve receives average annual rainfall in the range of 400-550 mm. The reserve hosts good population of ungulates including eland, black wildebeest, impala, red hartebeest, springbok and zebra (Rechav, 1986).

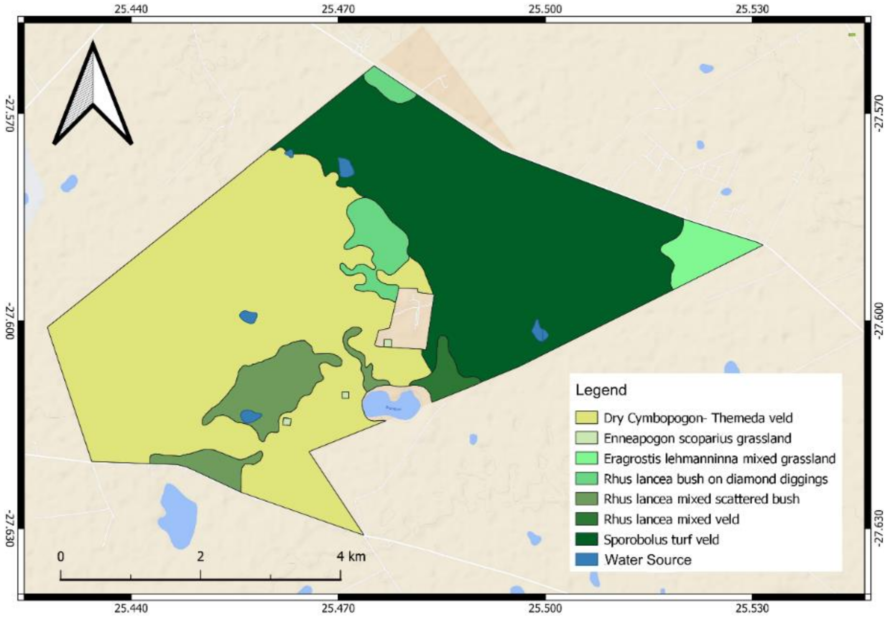

Figure 1.14: Major vegetation types in SA Lombard Nature Reserve (NWPTB, 2020)

1.2.1.13. Molopo Game Reserve

With an area of 240 km^2, the Molopo game reserve (22° 57'E latitude 25° 48'S longitude) is located in the far west side of the province, near Vostershoop and next to the Botswana border marked by a part of Molopo river (van Niekerk, 2011). The elevation of the reserve (hereafter Molopo) is 1,000 m masl (van Niekerk, 2014). This remote reserve has a unique arid savanna habitat with grassland and thornveld dunes named as Molopo Bushveld with dominant tree species of *Acacia* and *Boscia* tree species (Mucina & Rutherford, 2006). The climate in the area is characterized by extreme high and low temperatures with a range between -7°C to 35°C (van Niekerk, 2011) and average annual rainfall of 333 mm (Coleman & Downs, 2009). Deep red soils are found in the area with sand dunes near drainage valleys (van Niekerk, 2011). The reserve is home to a diverse group of mammals including Cheetah, caracal, blue wildebeest, eland, gemsbok, kudu, zebra, red hartebeest, impala, waterbuck, brown hyena and warthog (Nel, 2018). More than 120 species of birds have also been recorded from this reserve which includes breeding pairs of martial eagles, bateleur

(*Terathopius ecaudatus*), and tawny eagles (*Aquila rapax*). Two common vulture species in the reserve are lappet faced vultures (*Torgos tracheliotos*) and white-backed vultures (Birdlife, 2018).

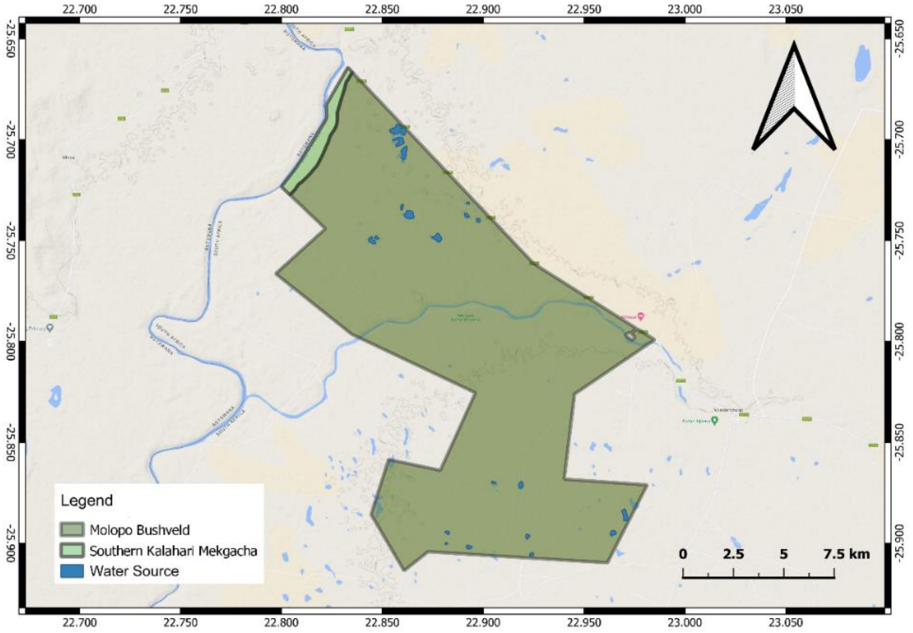

Figure 1.15: Major vegetation types in Molopo Game Reserve (NWPTB, 2020)

1.3. RATIONALE FOR THE RESEARCH

1.3.1. Research Focus

Co-existence in multi-species ungulate assemblages in African ecosystems has intrigued scientists for a long time and is an active area of ongoing research. Spatial distribution of resources, i.e., landscape heterogeneity has an overriding positive effect on the viability of wildlife populations (Hobbs & Gordon, 2010) because of the buffering effect of low quality patches. This can be further enhanced by frequent planned fires, as is regularly done by managers. The current research thesis will focus on identifying and evaluating various biotic and abiotic drivers influencing ungulate population dynamics and spatial distributions across a range of environmental settings in order to improve current knowledge. The study aims to investigate the factors structuring the spatial distribution of ungulate species. Spatial occupancy forms part of this goal and hopefully the findings from this study will facilitate the interpretation of the varied long-term growth rates of ungulate populations; across both species and sites in the NW Province to help the management establish informed harvesting protocols. Gradual population declines of habitat-specific species in smaller game reserves (Seydack et al., 2012) suggest inadequate knowledge persists throughout the conservation fraternity regarding the preferred microclimate of ungulate species within which they can persist. It is quite conceivable that some protected areas do not equally meet the spatial requirements for individual species, where species with large spatial requirements are likely to be impacted most.

The purpose of this research is to identify the ecological drivers of ungulate space use in smaller fenced conservation areas (<10,000 km^2) in South Africa, across ecological gradients. The objective, furthermore, is to compare habitat partitioning between ungulates and their occupancy patterns across the landscape, and in particular, to find plausible explanations for the disparities in spatial occupancies and segregation across sites. It is certainly possible that some protected areas do not optimally provide for the spatial requirements across all species, with some species normally inhabiting large home range sizes most likely to be impacted negatively.

1.3.2. Research Question and Objectives

The present study intends to identify important environmental drivers affecting changes in population distribution across NW landscape. Environmental drivers considered included rainfall, temperature, soil nutrients and landscape features. The study further aimed to use spatial data in GIS platforms to assess the importance of spatial segregation as a mechanism allowing coexistence in ungulate societies. Conservative management regimes keep populations at low densities, and thus limit investigations concerned with population performance to contributions from climatic fluctuations and environmental structure. Investigating spatial occupancy helps to identify factors limiting their spatial distribution, which ultimately impacts at the population level. It is difficult to establish whether current growth rates are linked to spatial constraints, a distinct possibility given the variability in growth rates, spatially and across the species spectrum. The major focus of the overall study is to determine the environmental drivers influencing distributions of co-existing ungulate populations.

The following objectives were accordingly formulated:

1. To estimate precise population abundance and detection probability of ungulates from aerial counts.
2. To evaluate the major environmental determinants of habitat partitioning for ungulates in the North-West Province.
3. To determine the major environmental variables driving spatial distributions, spatial occupancy levels, and segregation patterns of ungulate species across landscapes.

I formulated hypothesis for each objective based on previous literature and tested them through model selection by finding the most parsimonious descriptive model of ungulate distributions based on temporal and spatial factors. I expected species to respond more towards spatial factors than temporal factors. However, this might not be the case when ungulate density increases, at which point, species are likely to become less selective (Rosenzweig, 1991).

1.4. RESEARCH DESIGN AND METHODS

Various monitoring techniques are carried out for large mammals depending on the objectives of the study (McComb et al., 2010). These include some direct methods such as line transects (Buckland et al., 2001), aerial counts (Norton-Griffiths, 1978; Oswald, 1982; Gasaway et al., 1986; Unsworth et al., 1994), and indirect methods such as pellet/scat counts (Fuller, 1991) track counts (Wilson & Delahay, 2001). These methods are then associated with appropriate survey analysis software to get desired results (e.g. DISTANCE (Thomas et al., 2010)).

Aerial surveys have been carried out since the mid-1950s across the African continent (Jachmann, 2002). One of the downsides of using an aerial count against ground transects is the higher probability of inaccuracies in abundance estimation (Jachmann, 2001; 2002; Terrill Paterson et al., 2019), that can be corrected through the use of double counts based on the model of mark-recapture (Caughley, 1974) or using Peterson estimate (Seber, 1982; Caughley & Sinclair, 1994) and deriving a correction factor (Caughley & Grice, 1982; Graham & Bell, 1989; Caughley & Sinclair, 1994; Jachmann, 2001). Another cost-effective way is using unbiased population models (e.g. Peterson 2019; see Kidwai et al., 2019) that accounts for imperfect detections (Royle, 2004) by using the survey counts that are replicated both over time and space (Kéry et al., 2009).

Estimating the probability of a species using certain habitat features in a given area and time, by modelling landscape use, is a crucial and increasingly widespread approach in research and management (Nielson & Sawyer, 2013; Jarnevich et al., 2015; Wisdom et al., 2020; Li et al., 2022; Singh et al., 2022). Analyses at the species community scale have recently progressed due to statistical advancements and the growing availability of data from various taxa (Devarajan et al., 2020). One such widely applied class of community models is the hierarchical multi-species occupancy model. Multi-species occupancy modelling (MSOM) offers a way to measure biodiversity while taking into consideration various sources of uncertainty, inaccurate detections, and imperfect sampling methods (MacKenzie et al., 2002; Tyre et al., 2003; Dorazio & Royle, 2005, Gelfand et al., 2005). In MSOM, the community pool of capture histories as well as the species-specific capture histories in combination can be used to quantify effects of covariates at both the individual species and community-level. Additionally, it produces estimates (with fully propagated uncertainty) of occupancy probability that are species-specific as well as community-level summaries like species richness (Dorazio & Royle, 2005; Doser et al., 2022) that can be used to inform the modelled parameters for each species. Such an approach is particularly helpful for modelling rare or hard-to-detect species with lower detection probabilities, which are frequently found in non-invasive surveys (Zipkin et al., 2010).

The data in the current study was collected through Arial surveys each year in late July to August (late dry season) with a four-seater Bell Jet Ranger II helicopter (Nel, 2018). Survey counts spanned the years 1999-2015. A half strip width of 250 m (depending on the reserve and terrain), was surveyed, giving a total strip width of 500 m. The flying heights varied between 60 m to 100 m while the flying speed was maintained at an average of 90 kilometres per hour (Nel, 2018). The data includes the game audit data set consisting of harvest, removal and introduction figures across all the study sites over the study period.

Three replicate count sessions were conducted at the larger reserves e.g., Madikwe, Pilanesberg, Borakalalo, Kgaswane and Molopo under the management of the North West Parks and Tourism Board. For other reserves such as Boskop, Wolwespruit, Bloemhof, SA Lombard, Mafikeng, Botsalano, Molemane, and Valkop (Bultfontein & La Boheme areas) two replicates for the counts were carried out. This decision was taken by the executive management as a result of an agreement between the Board and Auditor-general. Surveys was not conducted in the years 2016 and 2017 due to funding constraints (Nel, 2018).

1.5. ORGANISATION OF THESIS

This thesis has been written as three separate scientific papers bookended by an introduction, and a conclusion with synthesis of key findings. **Chapter two** has been published in a peer reviewed journal, and **Chapter three** and **Chapter four** are written as stand-alone manuscripts which have not been submitted for publication.

Chapter one provides introduction to the study which includes the background of ungulate populations and previous similar studies carried out across the globe. This chapter also describes rationale, methodology and the objectives of the study along with descriptive account of the study area.

Chapter two explores the use of N-mixture models in estimating population abundance and detection probabilities of ungulate species from aerial counts. The chapter advocates on the precision of N-mixture models in estimating population abundance, and emphasizes on its use for determining harvest quota of ungulate species in the NW Province.

Chapter three focuses on assessing the important environmental factors driving habitat partitioning in ungulate groups across the NW Province. The chapter used generalized linear mixed models to explore relationships between ungulate detections and ecological drivers. Key factors were identified for each of the species and their relationships across the study sites were evaluated.

Chapter four describes the role of variables in spatial occupancy of ungulates in selected sites of NW Province with varying rainfall. Ungulate groups were created based on their feeding behaviour for carrying out the study. Multi-species occupancy modelling was used to draw conclusions of ungulate spatial occupancies and species richness in the study sites. The chapter also deals with identifying co-occurrence and segregation patterns between individual ungulate species across the study sites.

Finally, in **Chapter five** I synthesize the key findings of the thesis and the implications for the conservation and management of ungulates in the NW Province. I also highlight research gaps and considerations for management interventions of various ungulate groups in the thirteen conservation reserves of the NW Province.

1.6. REFERENCES

Acocks, J. (1988). Veld Types of South Africa, Third Edition. *Memoirs of the Botanical Survey of South Africa*, *57*.

Adcock, K. (1991). Vegetation map of Molopo Game Reserve. Bophuthatswana Parks Board, Pilanesberg National Park.

Alroy, J. (2003). Taxonomic inflation and body mass distributions in North American fossil mammals. *Journal of Mammalogy*, *84*(2). https://doi.org/10.1644/1545-1542(2003)084<0431:TIABMD>2.0.CO;2

Anderson, T. M., Dong, Y., & Mcnaughton, S. J. (2006). Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture and grazing. *Journal of Ecology*, *94*(6). https://doi.org/10.1111/j.1365-2745.2006.01148.x

Anderson, T. M., Hopcraft, J. G. C., Stephanie, E., Ritchie, M., Grace, J. B., & Olff, H. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, *91*(5). https://doi.org/10.1890/09-0739.1

Annandale, E., & Nealer, E. (2011). Exploring aspects of the water history of the Potchefstroom region and the local management of it. *New Contree*, *62*.

Arsenault, R., & Owen-Smith, N. (2002). Facilitation versus competition in grazing herbivore assemblages. In *Oikos* Vol. 97(3): 313-318. https://doi.org/10.1034/j.1600-0706.2002.970301.x

Barabás, G., Michalska-Smith, M. J., & Allesina, S. (2016). The effect Of intra- and interspecific competition on coexistence in multispecies communities. *American Naturalist*, *188*(1). https://doi.org/10.1086/686901

Barnard, S., Venter, A., & van Ginkel, C. E. (2013). Overview of the influences of mining-related pollution on the water quality of the Mooi River system's reservoirs, using basic statistical analyses and self organised mapping. *Water SA*, *39*(5). https://doi.org/10.4314/wsa.v39i5.10

Bateman, A. W., Ozgul, A., Coulson, T., & Clutton-Brock, T. H. (2012). Density dependence in group dynamics of a highly social mongoose, Suricata suricatta. *Journal of Animal Ecology*, *81*(3). https://doi.org/10.1111/j.1365-2656.2011.01934.x

Bayarbaatar, B. (2016). Distribution and Population Dynamics of Ungulates in the Mongolian Gobi. Doctoral Dissertations submitted to University of Massachusetts – Amherst.

Bell, R. H. V. (1982). *The Effect of Soil Nutrient Availability on Community Structure in African Ecosystems*. https://doi.org/10.1007/978-3-642-68786-0_10

Benton, M. J. (1993). The fossil record 2. Chapman and Hall, London

Bezuidenhout, H., & Bredenkamp, G. J. (1990). A reconnaissance survey of the vegetation of the dolomitic region in the Potchefstroom-Ventersdorp-Randfontein area, South Africa. *Phytocoenologia*, *18*(2–3). https://doi.org/10.1127/phyto/18/1990/387

Birdlife South Africa (2015). Botsalano Nature Reserve. Important Bird and Biodiversity Areas https://www.birdlife.org.za/what-we-do/important-bird-and-biodiversity-areas/what-we-do/iba-directory/botsalano-nature-reserve [Accessed on: 04/26/2020]

Birdlife South Africa (2018). Bloemhof Dam Nature Reserve and Surrounding areas including Sandveld Nature Reserve (OFS). https://www.birdlife.org.za/go-birding/birding-routes/birding-routes-north-west/wetlands-pans-and-dams/#1530131421505-aeeeb001-851c[Accessed on: 04/26/2020]

Birdlife South Africa (2018). Molopo Game Reserve. Important Bird and Biodiversity Areas https://www.birdlife.org.za/go-birding/birding-routes/birding-routes-north-west/kalahari/#1530131082455-62468e0c-55a1[Accessed on: 04/26/2020]

Birdlife South Africa (2018). Vaalkop Dam Nature Reserve. Important Bird and Biodiversity Areas https://www.birdlife.org.za/go-birding/birding-routes/birding-routes-north-west/kalahari/#1530131082455-62468e0c-55a1[Accessed on: 04/26/2020]

Bleich, V. C., Marshal, J. P., & Andrew, N. G. (2010). Habitat use by a desert ungulate: Predicting effects of water availability on mountain sheep. *Journal of Arid Environments*, *74*(6). https://doi.org/10.1016/j.jaridenv.2009.10.019

Botkin, D. B., Mellilo, J. M., & Wu, L. S. Y. (1981). How ecosystem processes are linked to large mammal population dynamics. *Dynamics of Large Mammal Populations*.

Bredenkamp, G. J., Bezuidenhout, H., Joubert, H., & Naude, C. (1994). The vegetation of the Boskop Dam Nature Reserve, Potchefstroom. *Koedoe*, *37*(1). https://doi.org/10.4102/koedoe.v37i1.323

Brockett, B. H. (2002). Accuracy, bias and precision of helicopter-based counts of black rhinoceros in Pilanesberg National Park, South Africa. *African Journal of Wildlife Research*, *32*(2).

Bro-Jørgensen, J. (2016). Our antelope heritage—Why the fuss? In J. Bro-Jørgensen & D. P. Mallon (Eds.), Antelope conservation (pp. 1–10). John Wiley & Sons Ltd.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E., & Pauly, D. (2012). Increasing jellyfish populations: Trends in Large Marine Ecosystems. *Hydrobiologia*, *690*(1). https://doi.org/10.1007/s10750-012-1039-7

Brown, L. R., Bredenkamp, G. J., & Van Rooyen, N. (1995). The phytosociology of the western section of Borakalalo Nature Reserve. *Koedoe*, *38*(2). https://doi.org/10.4102/koedoe.v38i2.314

Brown, L. R., Bredenkamp, G. J., & Van Rooyen, N. (1996). The phytosociology of the northern section of the Borakalalo Nature Reserve. *Koedoe*, *39*(1). https://doi.org/10.4102/koedoe.v39i1.279

Brown, L. R., Bredenkamp, G. J., & Van Rooyen, N. (1997). Phytosociological synthesis of the vegetation of the Borakalalo Nature Reserve, North-West Province. *South African Journal of Botany*, *63*(5). https://doi.org/10.1016/S0254-6299(15)30761-4

Brown, L. R. (1998). A plant ecological study and wildlife management plan of the Borakalalo Nature Reserve, North-West Province. PhD. thesis. University of Pretoria: Faculty of Natural & Agricultural Sciences.

Buckland, S. T. (2001). Introduction to distance sampling: Estimating abundance of biological populations. Oxford: Oxford University Press.

Buys, D., & Dott, H. M. (1991). Population fluctuations and breeding of eland Taurotragus oryx in a western Transvaal nature reserve. *Koedoe*, *34*(1). https://doi.org/10.4102/koedoe.v34i1.411

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1). https://doi.org/10.4102/koedoe.v53i1.1028

Caughley, G., & Sinclair, A. R. E. (1994). Wildlife ecology and management. Blackwell Scientific Publications.

Caughley, G. (1974). Bias in Aerial Survey. *The Journal of Wildlife Management*, *38*(4). https://doi.org/10.2307/3800067

Caughley, G., & Grice, D. (1982). A correction factor for counting emus from the air, and its application to counts in Western Australia. *Wildlife Research*, *9*(2). https://doi.org/10.1071/WR9820253

Caughley, G., & Gunn, A. (1993). Dynamics of Large Herbivores in Deserts: Kangaroos and Caribou. *Oikos*, *67*(1). https://doi.org/10.2307/3545094

Chakraborty, K., Das, K., & Kar, T. K. (2013). An ecological perspective on marine reserves in prey-predator dynamics. In *Journal of Biological Physics* (Vol. 39, Issue 4). https://doi.org/10.1007/s10867-013-9329-5

Chittenden, H. (2007). Roberts bird guide. Cape Town: John Voelcker Bird Book Fund.

Coe, M. J., Cumming, D. H., & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, *22*(4). https://doi.org/10.1007/BF00345312

Coleman, J. C., & Downs, C. T. (2009). Variation in urine concentrating ability and water balance of the Black-tailed Tree Rat Thallomys nigricauda, along an aridity gradient. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *154*(4). https://doi.org/10.1016/j.cbpa.2009.08.007

Coulson, T., Gaillard, J. M., & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *Journal of Animal Ecology*, *74*(4). https://doi.org/10.1111/j.1365-2656.2005.00975.x

Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, *143*(9). https://doi.org/10.1016/j.biocon.2010.06.007

Darroch, S. A. F., Webb, A. E., Longrich, N., & Belmaker, J. (2014). Palaeocene-Eocene evolution of beta diversity among ungulate mammals in North America. *Global Ecology and Biogeography*, *23*(7). https://doi.org/10.1111/geb.12156

Deliberato, H. G. (2017). Resources overlap and the distribution of grazer assemblages at Telperion and Ezemvelo Nature Reserves. Master's thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa.

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*, *43*(11). https://doi.org/10.1111/ecog.04957

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470). https://doi.org/10.1198/016214505000000015

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, *13*(8). https://doi.org/10.1111/2041-210X.13897

Dunham, K. M., Robertson, E. F., & Grant, C. C. (2004). Rainfall and the decline of a rare antelope, the tsessebe (Damaliscus lunatus lunatus), in Kruger National Park, South Africa. *Biological Conservation*, *117*(1). https://doi.org/10.1016/S0006-3207(03)00267-2

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, *22*(4). https://doi.org/10.1111/j.1365-2028.1984.tb00700.x

Eberhardt, L. L. (1988). Testing Hypotheses about Populations. *The Journal of Wildlife Management*, *52*(1). https://doi.org/10.2307/3801057

Estes, R. D. (1991). The behaviour guide to African mammals. Berkeley, University of California Press.

Fowler, C. W. (1981). Density Dependence as Related to Life History Strategy. *Ecology*, *62*(3). https://doi.org/10.2307/1937727

Fritz, H, Dallmeyer, D. R., Wallbrecher, E., Loizenbauer, J., Hoinkes, G., Neumayr, P., & Khudeir, A. A. (2002). Neoproterozoic tectonothermal evolution of the Central Eastern Desert, Egypt: a slow velocity tectonic process of core complex exhumation. *Journal of African Earth Sciences*, 34:137–155.

Fritz, H. (2002). Populations. John Wiley and Sons, New York.

Fritz, H., & Duncan, P. (1994). On the carrying capacity for large ungulates of African savanna ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, *256*(1345). https://doi.org/10.1098/rspb.1994.0052

Fuller, T. K. (1991). Do Pellet Counts Index White-Tailed Deer Numbers and Population Change? *The Journal of Wildlife Management*, *55*(3). https://doi.org/10.2307/3808966

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2). https://doi.org/10.1016/S0169-5347(97)01237-8

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toïgo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, *31*. https://doi.org/10.1146/annurev.ecolsys.31.1.367

García-Marmolejo, G., Chapa-Vargas, L., Huber-Sannwald, E., Weber, M., Rosas-Rosas, O. C., & Martínez-Calderas, J. (2013). Potential distributional patterns of three wild ungulate species in a fragmented tropical region of northeastern Mexico. *Tropical Conservation Science*, *6*(4). https://doi.org/10.1177/194008291300600407

García-Marmolejo, G., Chapa-Vargas, L., Weber, M., & Huber-Sannwald, E. (2015). Landscape composition influences abundance patterns and habitat use of three ungulate species in fragmented secondary deciduous tropical forests, Mexico. *Global Ecology and Conservation*, *3*. https://doi.org/10.1016/j.gecco.2015.03.009

Gasaway, W. C., Dubois, S. D., Reed, D. J., & Harbo, S. J. (1986). Estimating moose population parameters from aerial surveys. Biological Papers of the Univ. Alaska, Number 22, Institute of Arctic Biology.

Gaston, K. J. (1994). Rarity. In Rarity. https://doi.org/10.1007/978-94-011-0701-3

Gaston, K. J., Blackburn, T. M., & Lawton, J. H. (1998). Aggregation and Interspecific Abundance-Occupancy Relationships. Journal of Animal Ecology, 67(6), 995–999. http://www.jstor.org/stable/2647429

Gelfand, A. E., Schmidt, A. M., Wu, S., Silander, J. A., Latimer, A., & Rebelo, A. G. (2005). Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society. Series C: Applied Statistics*, *54*(1). https://doi.org/10.1111/j.1467-9876.2005.00466.x

Glasser, J. W. (1979). The Role of Predation in Shaping and Maintaining the Structure of Communities. *The American Naturalist*, *113*(5). https://doi.org/10.1086/283422

Glasser, J. W. (1982). A Theory of Trophic Strategies: The Evolution of Facultative Specialists. *The American Naturalist*, *119*(2). https://doi.org/10.1086/283906

Gordon-Cumming, I. (2017). Factors affecting local community attitudes towards conservation and protected areas at Borakalalo National Park, South Africa. Master's Thesis submitted to University of South Africa.

Goslar, A., Prosch, L., Ingle, S., Benedek, F., Hudson, K., Mampye, A., Tshivhase, N., & Lees, Z. (2008). North West Province Environment Outlook. A report on the state of the environment. Submitted to North West Department of Agriculture, Conservation and Environment.

Graham, A., & Bell, R. (1989). Investigating Observer Bias in Aerial Survey by Simultaneous Double-Counts. *The Journal of Wildlife Management*, *53*(4). https://doi.org/10.2307/3809603

Greyling, T., & Huntley, B. J. (1984). Diractory of the Southern African conservation areas. Pretoria: CSIR. (South African National Scientific Programmes Report 98).

Groves, C., & Grubb, P. (2011). Ungulate Taxonomy. Johns Hopkins University Press. Baltimore, Maryland, 317 pp.

Hallam, A., & Wignall, P. B. (1999). Mass extinctions and sea-level changes. *Earth Science Reviews*, *48*(4). https://doi.org/10.1016/S0012-8252(99)00055-0

Harnik, P. G., Simpson, C., & Payne, J. L. (2012). Long-term differences in extinction risk among the seven forms of rarity. Proceedings. Biological sciences, 279(1749), 4969–4976. https://doi.org/10.1098/rspb.2012.1902

Harrison, S., & Cornell, H. (2008). Toward a better understanding of the regional causes of local community richness. In *Ecology Letters* (Vol. 11, Issue 9). https://doi.org/10.1111/j.1461-0248.2008.01210.x

Hobbs, N. T. (1996). Modification of ecosystems by ungulates*. The Journal of Wildlife Management*, 60(4), 695–713. https://doi.org/10.2307/3802368

Hobbs, N. T. and Gordon, I. J. (2010). How does Landscape Heterogeneity Shape Dynamics of Large Herbivore Populations?. In Dynamics of Large Herbivore Populations in Changing Environments, N. Owen-Smith (Ed.). https://doi.org/10.1002/9781444318593.ch6

Holt, R. D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist*, *124*(3). https://doi.org/10.1086/284280

Holt, R. D., Lawton, J. H., Gaston, K. J., & Blackburn, T. M. (1997). On the Relationship between Range Size and Local Abundance: Back to Basics. Oikos, 78(1), 183–190. https://doi.org/10.2307/3545815

Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E., & Olff, H. (2012). Body size and the division of niche space: Food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, *81*(1). https://doi.org/10.1111/j.1365-2656.2011.01885.x

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. In *Trends in Ecology and Evolution* (Vol. 25, Issue 2). https://doi.org/10.1016/j.tree.2009.08.001

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (Diceros bicornis) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3). https://doi.org/10.1017/S1367943005002234

Hunninck, L., May, R., Jackson, C. R., Palme, R., Røskaft, E., & Sheriff, M. J. (2020). Consequences of climate-induced vegetation changes exceed those of human disturbance for wild impala in the Serengeti ecosystem. *Conservation Physiology*, *8*(1). https://doi.org/10.1093/conphys/coz117

Illius, A. W. (1997). Physiological adaptation in savanna ungulates. *Proceedings of the Nutrition Society*, *56*(3). https://doi.org/10.1079/pns19970108

Illius, A. W., & O'Connor, T. G. (2000). Resource heterogeneity and ungulate population dynamics. *Oikos*, *89*(2). https://doi.org/10.1034/j.1600-0706.2000.890209.x

Jachmann, H. (2001). Estimating abundance of African wildlife : an aid to adaptive management. *Kluwer Academic Publishers*.

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, *39*(5). https://doi.org/10.1046/j.1365-2664.2002.00752.x

Janis, C. M., Scott, K. M., & Jacobs, L. L. (1998). Evolution of Tertiary mammals of North America. Volume 1: terrestrial carnivores, ungulates, and ungulatelike mammals. In *Evolution of Tertiary mammals of North America. Volume 1: terrestrial carnivores, ungulates, and ungulatelike mammals*. https://doi.org/10.2307/3515443

Jarman, P. J. (1974). The Social Organisation of Antelope in Relation to Their Ecology. *Behaviour*, *48*(1–4). https://doi.org/10.1163/156853974X00345

Jarnevich, C. S., Stohlgren, T. J., Kumar, S., Morisette, J. T., & Holcombe, T. R. (2015). Caveats for correlative species distribution modeling. In *Ecological Informatics* (Vol. 29, Issue P1). https://doi.org/10.1016/j.ecoinf.2015.06.007

Jeffries, M. J., & Lawton, J. H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, *23*(4). https://doi.org/10.1111/j.1095-8312.1984.tb00145.x

Kéry, M., Dorazio, R. M., Soldaat, L., Van Strien, A., Zuiderwijk, A., & Royle, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, *46*(6). https://doi.org/10.1111/j.1365-2664.2009.01724.x

Keuroghlian, A., & Eaton, D. P. (2008). Importance of rare habitats and riparian zones in a tropical forest fragment: Preferential use by Tayassu pecari, a wide-ranging frugivore. *Journal of Zoology*, *275*(3). https://doi.org/10.1111/j.1469-7998.2008.00440.x

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis L.*) populations from aerial counts. *Global Ecology and Conservation*, *19*. https://doi.org/10.1016/j.gecco.2019.e00687

Knoop, M. C., Nel, H. P., Seitlhamo, W. S., & van Heerden, P. W. (2009). Report on animal population Estimates: 2009. North West Parks and Tourism Board, Mafikeng.

Koons, D. N., Colchero, F., Hersey, K., & Gimenez, O. (2015). Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics. *Ecological Applications*, *25*(4). https://doi.org/10.1890/14-0932.1

Kruger, A. C., & Nxumalo, M. P. (2017). Historical rainfall trends in South Africa: 1921–2015. *Water SA*, *43*(2). https://doi.org/10.4314/wsa.v43i2.12

Leitner, P. E. (2013). Key resource areas and management of buffalo (Syncerus caffer caffer) on Molemane Eye Nature Reserve. A research report submitted to the Faculty of Science, University of the Witwatersrand Johannesburg.

Leuthold, W. (1977). African Ungulates. A Comparative Review of Their Ethology and Behavioural Ecology. Germany: Springer Berlin Heidelberg.

Li, S., Zhao, Y., Xiao, W., Yellishetty, M., & Yang, D. (2022). Identifying ecosystem service bundles and the spatiotemporal characteristics of trade-offs and synergies in coal mining areas with a high groundwater table. *Science of the Total Environment*, *807*. https://doi.org/10.1016/j.scitotenv.2021.151036

Louw, C. J., Marshal, J. P., Nel, H. P., & Funston, P. J. (2019). Sex-Specific Predation Patterns on Kudu and Impala. *African Journal of Wildlife Research*, *49*(1). https://doi.org/10.3957/056.049.0077

Louw, W. J. (1951). An ecological account of the vegetation of the Potchefstroom are. Memoirs of the Botanical Survey of South Africa. Vol. 24: 1-106.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8). https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Maffei, L., & Taber, A. B. (2003). Area de acción de Mazama americana (Cervidae) en un bosque seco de Bolivia. *Ecología En Bolivia*, *38*(2).

Marshal, J. P., Rankin, C., Nel, H. P., & Parrini, F. (2016). Drivers of population dynamics in sable antelope: forage, habitat or competition? *European Journal of Wildlife Research*, *62*(5). https://doi.org/10.1007/s10344-016-1027-8

McComb, B., Zuckerberg, B., Vesely, D., & Jordan, C. (2010). Monitoring Animal Populations and Their Habitats: A Practitioner’s Guide. *New York*.

Mccullough, D. R. (1999). Density dependence and life-history strategies of ungulates. *Journal of Mammalogy*, *80*(4). https://doi.org/10.2307/1383164

McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature*, *334*(6180). https://doi.org/10.1038/334343a0

McNaughton, S. J., & Georgiadis, N. J. (1986). ECOLOGY OF AFRICAN GRAZING AND BROWSING MAMMALS. *Annual Review of Ecology and Systematics*, *17*(1). https://doi.org/10.1146/annurev.es.17.110186.000351

McNaughton, S. J., Oesterheld, M., Frank, D. A., & Williams, K. J. (1989). Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature*, *341*(6238). https://doi.org/10.1038/341142a0

Mduma, S. A. R., Sinclair, A. R. E., & Hilborn, R. (1999). Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology*, *68*(6). https://doi.org/10.1046/j.1365-2656.1999.00352.x

Mendoza, M., Janis, C. M., & Palmqvist, P. (2002). Characterizing complex craniodental patterns related to feeding behaviour in ungulates: A multivariate approach. *Journal of Zoology*, *258*(2). https://doi.org/10.1017/S0952836902001346

Morris, D. W. (2002). Measuring the Allee effect: Positive density dependence in small mammals. *Ecology*, *83*(1). https://doi.org/10.1890/0012-9658(2002)083[0014:MTAEPD]2.0.CO;2

Mucina, L., & Rutherford, M. C. (eds). 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Munyati, C., & Moeng, M. (2015). Geomatics in conservation: Mapping woody cover in Botsalano Game Reserve, North West Province. Geomatics Indaba Proceedings.

NASA POWER (2020). NASA Prediction of Worldwide Energy Resources. URL: https://power.larc.nasa.gov/ [Accessed August 7 2020]

Nel, H. P. (2018). Population estimates for large herbivores and predators in protected areas in the North West Parks Board. Unpublished Technical Report.

Nel, H.P. (2000). Ecological management objectives and monitoring procedures for Rustenburg Nature Reserve, North West Province. MSc thesis, University of Pretoria.

Newbery, R., & van Heerden, P. (2002). A Stocking Plan for Molemane Eye Nature Reserve. Internal North West Parks & Tourism Board report.

Nielson, R. M., & Sawyer, H. (2013). Estimating resource selection with count data. *Ecology and Evolution*, *3*(7). https://doi.org/10.1002/ece3.617

Norton-Griffiths, M. (1978). Counting animals. Handbook #1 Serengeti Ecological Monitoring Programme. Nairobi, Kenya. 2nd edition.

NW READ (2015) – see North West Department of Rural, Environment & Agricultural Development. Mahikeng: North West Provincial Government.

NWPTB (2020). North West Parks Board official website [WWW Document]. URL https://ho.org.za/parks/ [Accessed: 05/04/2020].

Nyirenda, M., Letlojane, L., & Syakalima, M. (2016). Prevalence of Brucella abortus in buffaloes of Mafikeng game reserve, North West province, South Africa: A retrospective study. *Indian Journal of Animal Research*, *50*(2). https://doi.org/10.18805/ijar.5923

Ogutu, J. O., & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters*, *6*(5). https://doi.org/10.1046/j.1461-0248.2003.00447.x

Ogutu, J. O., Owen-Smith, N., Piepho, H. P., & Said, M. Y. (2011). Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977-2009. *Journal of Zoology*, *285*(2). https://doi.org/10.1111/j.1469-7998.2011.00818.x

Ogutu, J. O., Piepho, H. P., Dublin, H. T., Bhola, N., & Reid, R. S. (2008). Rainfall influences on ungulate population abundance in the Mara-Serengeti ecosystem. *Journal of Animal Ecology*, *77*(4). https://doi.org/10.1111/j.1365-2656.2008.01392.x

Ogutu, J. O., Reid, R. S., Piepho, H. P., Hobbs, N. T., Rainy, M. E., Kruska, R. L., Worden, J. S., & Nyabenge, M. (2014). Large herbivore responses to surface water and land use in an East African savanna: Implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation*, *23*(3). https://doi.org/10.1007/s10531-013-0617-y

Oswald, K. (1982). A manual for aerial observers of moose. Ontario Min. of Nat. Res. Peterborough, ON. 103 pp.

Owen-Smith, N. (2000). Modeling the population dynamics of a subtropical ungulate in a variable environment: Rain, cold and predators. *Natural Resource Modeling*, *13*(1). https://doi.org/10.1111/j.1939-7445.2000.tb00028.x

Owen-Smith, N. (2006). Demographic determination of the shape of density dependence for three African ungulate populations. *Ecological Monographs*, *76*(1). https://doi.org/10.1890/05-0765

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, *117*(4). https://doi.org/10.1111/j.0030-1299.2008.16309.x

Owen-Smith, N., & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs*, *76*(1). https://doi.org/10.1890/04-1101

Parrini, F., & Owen-Smith, N. (2010). The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology*, *48*(2). https://doi.org/10.1111/j.1365-2028.2009.01143.x

Peters, S. E. (2008). Environmental determinants of extinction selectivity in the fossil record. *Nature*, *454*(7204). https://doi.org/10.1038/nature07032

Rechav, Y. (1986). Seasonal activity and hosts of the vectors of Crimean-Congo haemorrhagic fever in South Africa. *South African Medical Journal. Suid-Afrikaanse Tydskrif Vir Geneeskunde*, *69*(6).

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, *84*(8). https://doi.org/10.1890/01-0625

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. In *Ecology Letters* (Vol. 7, Issue 1). https://doi.org/10.1046/j.1461-0248.2003.00554.x

Rigoudy, N. L. A., Clinchy, M., Peel, M. J. S., Huebner S., Packer, C., & Zanette L. Y. (2022). Hierarchy of fear: experimentally testingungulate reactions to lion, African wild dog and cheetah. *Behav. Ecol.*, Volume 33(4): 789–797, https://doi.org/10.1093/beheco/arac04

Rivero, K., Rumiz, D. I., & Taber, A. B. (2005). Differential habitat use by two sympatric brocket deer species (Mazama americana and M. gouazoubira) in a seasonal Chiquitano forest of Bolivia. *Mammalia*, *69*(2). https://doi.org/10.1515/mamm.2005.015

Rosenzweig, M. L. (1991). Habitat Selection and Population Interactions: The Search for Mechanism. The American Naturalist, Vol. 137. Supplement: Habitat Selection. https://www.jstor.org/stable/2462286

Rotella, J. J., Link, W. A., Nichols, J. D., Hadley, G. L., Garrott, R. A., & Proffitt, K. M. (2009). An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals. *Ecology*, *90*(4). https://doi.org/10.1890/08-0971.1

Roughgarden, J., & Feldman, M. (1975). Species Packing and Predation Pressure. *Ecology*, *56*(2). https://doi.org/10.2307/1934982

Royle, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, *60*(1). https://doi.org/10.1111/j.0006-341X.2004.00142.x

Saarinen, J. (2019). *The Palaeontology of Browsing and Grazing*. https://doi.org/10.1007/978-3-030-25865-8_2

Sæther, B. E. (1997). Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. In *Trends in Ecology and Evolution* (Vol. 12, Issue 4). https://doi.org/10.1016/S0169-5347(96)10068-9

Seagle, S. W., & McNaughton, S. J. (1992). Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology*, *7*(4). https://doi.org/10.1007/BF00131254

Seber, G. A. F. (1982). The Estimation of Animal Abundance. Charles Griffin, London, UK. pp 588-643.

Seitlhamo, W. S. (2002). The spatial distribution of giraffe species inside Mafikeng Game Reserve. BSc Honours Thesis. University of the North West. Mafikeng.

Seitlhamo, W. S. (2011). Mapping and quantifying the impact of grazing around water points in a small semi-arid savanna game reserve. Master's thesis submitted to University of the Witwatersrand, Johannesburg.

Sepkoski, J. J. J. (1976). Species diversity in the Phanerozoic: Species-area effects. *Paleobiology*, *2*(4).

Seydack, A. H., Grant, C. C., Smit, I. P., Vermeulen, W. J., Baard, J., & Zambatis, N. (2012). Large herbivore population performance and climate in a South African semi-arid savanna. *Koedoe*, *54*(1). https://doi.org/10.4102/koedoe.v54i1.1047

Shafir, A., & Oldewage, W. H. (1992). Dynamics of a fish ectoparasite population: opportunistic parasitism in Argulus japonicus (Branchiura). *Crustaceana*, *62*(1). https://doi.org/10.1163/156854092X00046

Shipley, L. (1999). Grazers and browsers: how digestive morphology affects diet selection. *Grazing Behaviour of Livestock and Wildlife*.

Singh, H., Sharief, A., Joshi, B. D., Kumar, V., Mukherjee, T., Chandra, K., Bhardwaj, N., Thakur, M., & Sharma, L. K. (2022). Multi-species occupancy modeling suggests interspecific interaction among the three ungulate species. *Scientific Reports*, *12*(1). https://doi.org/10.1038/s41598-022-20953-7

Smith, T. D. & Fowler, C. W. (1981). An overview of the study of the population dynamics of large mammals. *Dynamics of Large Mammal Populations*.

Spickett, A. M., Heyne, I. H., & Williams, R. (2011). Survey of the livestock ticks of the North West province, South Africa. *The Onderstepoort Journal of Veterinary Research*, *78*(1). https://doi.org/10.4102/ojvr.v78i1.305

Terrill Paterson, J., Proffitt, K., Rotella, J., & Garrott, R. (2019). An improved understanding of ungulate population dynamics using count data: Insights from western Montana. *PLoS ONE*, *14*(12). https://doi.org/10.1371/journal.pone.0226492

Thomas, G. H., Orme, C. D. L., Davies, R. G., Olson, V. A., Bennett, P. M., Gaston, K. J., Owens, I. P. F., & Blackburn, T. M. (2008). Regional variation in the historical components of global avian species richness. *Global Ecology and Biogeography*, *17*(3). https://doi.org/10.1111/j.1466-8238.2008.00384.x

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B., Marques, T. A., & Burnham, K. P. (2010). Distance software: Design and analysis of distance sampling surveys for estimating population size. In *Journal of Applied Ecology* (Vol. 47, Issue 1). https://doi.org/10.1111/j.1365-2664.2009.01737.x

Topographic Maps (2020). Free topographic maps for visualization and sharing https://en-za.topographic-map.com/maps/e62k/Vaalkop-Dam/ [Accessed on: 05/05/2020]

Tuljapurkar, S., & Caswell, H. (1997). Structured-Population Models in Marine, Terrestrial, and Freshwater Systems. Chapman and Hall. https://doi.org/10.1007/978-1-4615-5973-3

Turchin, P. (2003). Complex Population Dynamics: A Theoretical/Empirical Synthesis. Princeton, NJ: Princeton University Press.

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. In *Ecological Applications* (Vol. 13, Issue 6). https://doi.org/10.1890/02-5078

Unsworth, J. A., Leban, F. A., Leptich, D. J., Garton, E. O., & Zager, P., eds. (1994). Aerial Survey: User's Manual, 2nd edn. Biose, ID: Idaho Department of Fish and Game.

van Niekerk, J. H. (2011). Observations of Red-billed Spurfowl (Pternistis adspersus) in the arid Molopo Nature Reserve, North West Province, South Africa. *CHINESE BIRDS*, *2*(3). https://doi.org/10.5122/cbirds.2011.0023

van Niekerk, J. H. (2014). Vocal behaviour of the Red-crested Korhaan , Lophotis ruficrista , in South Africa. *South African Journal of Wildlife Research*, *44*(April).

van Zyl, J. H. M. (1965). The vegetation of the SA Lombard Nature Reserve and its utilization by certain antelope. Zool. Afr. 1: 55-71.

Venter, J. A., Prins, H. H. T., Balfour, D. A., & Slotow, R. (2014). Reconstructing grazer assemblages for protected area restoration. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0090900

Vié, J.-C., Hilton-Taylor, C., & Stuart, S. N. (eds.) (2009). Wildlife in a Changing World – An Analysis of the 2008 IUCN Red List of Threatened Species. Gland, Switzerland: IUCN. 180 pp.

Vieira-Fragoso, J. M. (1999). Perception of scale and resource partitioning by peccaries: Behavioural causes and ecological implications. *Journal of Mammalogy*, *80*(3). https://doi.org/10.2307/1383270

Vrba, E. S, & Schaller, G. B. (2000). Antelopes, deer, and relatives : fossil record, behavioural ecology, systematics, and conservation. New Haven: Yale University Press.

Wang, G., Hobbs, N. T., Boone, R. B., Illius, A. W., Gordon, I. J., Gross, J. E., & Hamlin, K. L. (2006). Spatial and temporal variability modify density dependence in populations of large herbivores. *Ecology*, *87*(1). https://doi.org/10.1890/05-0355

Wilson, D. E., & Reeder, D. M. (eds.) (2005). Mammal Species of the World (3rd Edition). Johns Hopkins University Press, Baltimore, Maryland, 2142 pp.

Wilson, G. J., & Delahay, R. J. (2001). A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildlife Research*, *28*(2). https://doi.org/10.1071/WR00033

Wisdom, M. J., Nielson, R. M., Rowland, M. M., & Proffitt, K. M. (2020). Modeling Landscape Use for Ungulates: Forgotten Tenets of Ecology, Management, and Inference. In *Frontiers in Ecology and Evolution* (Vol. 8). https://doi.org/10.3389/fevo.2020.00211

Wittemyer, G., Daballen, D., & Douglas-Hamilton, I. (2013). Comparative Demography of an At-Risk African Elephant Population. *PLoS ONE*, *8*(1). https://doi.org/10.1371/journal.pone.0053726

Zipkin, E. F., Andrew Royle, J., Dawson, D. K., & Bates, S. (2010). Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, *143*(2). https://doi.org/10.1016/j.biocon.2009.11.016

Chapter 2. Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (Diceros bicornis l.) Populations from aerial counts

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2.1. ABSTRACT

Inaccurate estimates of animal populations may lead to flawed management interventions; therefore, it is essential to understand the status and population trend of a species in order to plan its management efficiently. Aerial surveys are considered a useful method for estimating the population size of large conspicuous animals inhabiting large areas, but raw count data from aerial surveys usually underestimate population sizes due to imperfect detection. The use of N-mixture models with aerial count data provides a useful tool to estimate the population sizes while taking detection probability into account. As a study case we used aerial surveys conducted for monitoring black rhinoceros (*Diceros bicornis*) in Madikwe Game Reserve and Pilanesberg Nature Reserve (South Africa) during 1999 - 2015, and we analysed data with a dynamic extension of the N-mixture model. We estimated 0.078 - 0.098 and 0.139 - 0.142 individuals/km^2, respectively, and we found evidence for density dependence in both reserves with a carrying capacity of 0.122 (0.102-0.142) individuals/100 km^2. Based on simulations used to assess precision of the estimates, root-mean-square error model (RMSE) estimates was significantly smaller than those for the raw maximum counts. The N-mixture models provide a promising approach to estimate population size, trends and demographic characteristics of large conspicuous mammals such as black rhinoceroses. Such analysis can provide estimates that are more accurate than raw counts. In addition, use of model covariates that affect a species' population parameters can provide useful information for their conservation and management.

Keywords: Aerial survey; black rhinoceros; dynamic N-mixture models; South Africa.

2.2. INTRODUCTION

Reliable information on the status of animal populations is essential to inform decision-making processes, assess the degree of compliance with planned conservation and management goals, or avoid undesirable outcomes from interventions (McCarthy & Possingham, 2007; Nichols & Williams, 2006). Inaccurate population estimates can lead to errors in establishing population status and setting conservation goals that limit the ability to determine the effects of management actions (Wiest et al., 2019). However, knowledge of the population sizes, especially for those that are elusive or distributed over large areas at low density, can be technically difficult to obtain or be expensive (Skalski, 1994). In such cases, given limited resources for monitoring wildlife populations, there is a need for both effective and cost-efficient survey methods (Parker et al., 2011).

Species of African rhinoceroses, the white rhino (*Ceratotherium simum*) and the black rhino (*Diceros bicornis*), are prime examples of this challenge. They typically occur at low density in protected areas administered by government and private owners (Walpole et al., 2001). The black rhinoceros, in particular, is among the ungulates that are threatened globally (Ferreira et al., 2017). The species is classified as “critically endangered” (Emslie, 2012) because of the demand for rhino horn, mainly from Far Eastern markets (Martin, 1991). Although intraspecific variation of black rhinoceros is still on debate (Moodley et al., 2017), of the 7-8 originally described subspecies, three have been declared “extinct” by the International Union for Conservation of Nature (IUCN) (Amin et al., 2006; Emslie, 2012). Over the last two decades, the remaining subspecies have been declining throughout the continent (Amin et al., 2006) despite the anti-poaching efforts (Cromsigt et al., 2002; Gakahu, 1993; Hrabar & du Toit, 2005).

The conservation status of the South African subspecies is still a key concern (Cromsigt et al., 2002; Ferreira et al., 2017). In 1930, there were an estimated 110 *D. b. minor* in South Africa in two populations of Hluhluwe-iMfolozi Park and Mkhuze Game Reserve of KwaZulu-Natal (KZN). With protection, active management and translocations to expand range and numbers, by the end of 2015 there were 54 breeding populations conserving an estimated 1,580 animals (Emslie & Adcock, 2016). However, after the most recent upsurge of poaching that started in 2008, from 2010-17 *D. b. minor* has actually suffered the highest poaching (551 reported) compared to 260 for the approximately equally numerous *D.b.bicornis* and 134 for the rarer *D. b. michaeli* (Southern African Development Community Rhino Management Group (SADC RMG), personal communication, April 4, 2019).

Continued monitoring of black rhino populations need not only evaluate the efficiency of anti-poaching efforts, but also provide information on population dynamics. In black rhinos, density-dependent social constraints such as territorial and antagonist behaviours (Adcock, 1994) contribute to population regulation (Hanski, 1990; Lundberg et al., 2000; Sæther, 1997). Resource availability per individual is reduced at high population densities, affecting survival, natality and age at maturity (Hrabar & du Toit, 2005; Sæther, 1997). In addition, many rhino populations are small and fragmented: ca. 75% of the reserves in Kenya, Namibia, and South Africa have <50 animals (Berger, 1994) such that genetic diversity loss and environmental stochasticity are serious threats (Hrabar & du Toit, 2005; Mduma et al., 1999; Owen-smith, 1990; Sinclair et al., 1985). Black rhino conservation practices typically seek to maximise the population growth by relying on a meta-population structure (Ferreira et al., 2017; Foose et al., 1993; Hrabar & du Toit, 2005). This requires detailed knowledge of population size, trend and demographic rates.

The status of populations is usually monitored by individual identification (ID) based monitoring by SADC RMG (e.g. to provide information on mortalities, calving, removals, poaching, individuals missing and presumed dead). ID based monitoring is recommended for black rhino given the additional value of demographic data that can be obtained. However, intensive helicopter block counts are more common for population estimation of large mammals in areas where ID-based monitoring is not logistically feasible (Caughley, 1977; Brockett, 2002; Ferreira et al., 2011; 2017, (Williams et al., 2017). Detection probability of animals, however, can be highly variable and is always lower than one. Use of raw count data from aerial surveys, therefore, usually underestimates population size (Caughley, 1977; Steinhorst & Samuel, 1989). Many authors have developed procedures for estimating visibility bias and corrections to population estimators (Hone, 2008; Jachmann, 2002; King et al., 1985; Ottichilo, 1999), and these are also used in aerial surveys of black rhinos (Ferreira et al., 2011; Mackie et al., 2013). Moreover, overestimation of abundance can occur from double counting or false positives (Schmidt, 2005) which can also underestimate survival probabilities in relation to environmental covariates (Gimenez et al., 2008; MacKenzie et al., 2017; Martin et al., 1995; Nichols & Williams, 2006; Tyre et al., 2003) while overestimating the extinction and turnover rates (Moilanen, 2002; Nichols et al., 1998).

In this study, we used data from aerial surveys of black rhinos, conducted in two reserves, Pilanesberg and Madikwe, South Africa, to estimate the population sizes and temporal trends between 1999 and 2015. To accommodate imperfect detection, we used N-mixture models that estimate abundance and detection probability simultaneously without identification of individuals in the populations (Royle, 2004). N-mixture models are rarely used with aerial count data in South Africa to estimate wildlife abundance (but see Lyet et al., 2016). The objective of this study was to demonstrate the use of N-mixture models to improve precision of abundance estimates, and comparing those results with established estimates from RMG ID based monitoring methods.

2.3. MATERIAL AND METHODS

2.3.1. Study Sites

Madikwe Game Reserve (henceforth Madikwe) is approximately 60 000 ha in extent and is one of the largest game reserves in South Africa. It is situated close to the Botswana border in the far north of North West Province (24° 45'S 26° 16'E). The vegetation of the reserve is composed of large open woodlands and grasslands, divided by the "Rant van Tweedepoort" Hills in the middle of the reserve, and bordered by the Dwarsberg Mountains in the south (NWPTB, 2018). The majority of the reserve is "Sourish Mixed Bushveld" (Acocks, 1988), with a tree-shrub layer of medium-low to medium-high growth and tall-growing *Vachellia* (previously *Acacia*) species being the most dominant (Figure 2.1). The main features of this area are the scattered inselbergs or isolated hills abruptly rising from otherwise flat plains (NWPTB, 2018). The climate in this region can be divided into the rainy season (October – April) and the dry season (May – September). The area receives rainfall of <500 mm per annum and temperature in the reserve vary from 3°C - 32°C (NWPTB, 2018). The reserve is a home to around 66 large mammalian species including lion (*Panthera leo*), leopard (*Panthera pardus*), rhinoceros (both black, and white), elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*); along with more than 300 species of resident and migrant birds. Black rhinos were reintroduced in the area in 1992.

Pilanesberg Nature Reserve (henceforth Pilanesberg; 25° 15' 42.12"S, 27° 6' 2.88"E) covers an area of 55,000 ha and is situated in the Bojanala Region of the North West

Province. Geologically, the area is formed by a crater of a long-extinct volcano that was produced by volcanic eruptions *ca.* 1,300 million years ago and fringed by a few concentric ridges or rings of hills (Carruthers, 2011). The park is in the transition zone between the dry Kalahari and wetter low-veld vegetation, commonly referred to as "Sour Bushveld" (Acocks, 1975). The habitat comprises of *Vachellia* and broad-leaf bushveld, varying from open grassland to thickets (Hrabar & du Toit, 2005) (Figure 2.1). The reserve receives annual rainfall in the range of 600 – 700 mm, with most of that falling during a dominant rainy season (October - April) followed by dry season from May to September. Highly variable annual rainfall can produce frequent droughts in some years (Farrell et al., 1978; McCarthy & Rubidge, 2006; Mucina & Rutherford, 2006; Carruthers, 2011). The average annual temperature in the area ranges from 15°C - 30°C (NWPTB, 2018). About 24 species of the larger mammals occur in Pilanesberg including lion, leopard, elephant, black and white rhino, buffalo, springbok (*Antidorcas marsupialis*), brown hyena (*Hyaena brunnea*), impala (*Aepyceros melampus*), cheetah (*Acinonyx jubatus*), sable antelope (*Hippotragus niger*), giraffe (*Giraffa camelopardalis*), zebra (*Equus quagga*) and hippo (*Hippopotamus amphibious*). Nineteen black rhinos were reintroduced to Pilanesberg from 1981 to 1983 and a further five animals were added in 1989 (Adcock et al., 1998). A recent increase in rhino poaching has been described in this area (NWPTB, 2015).

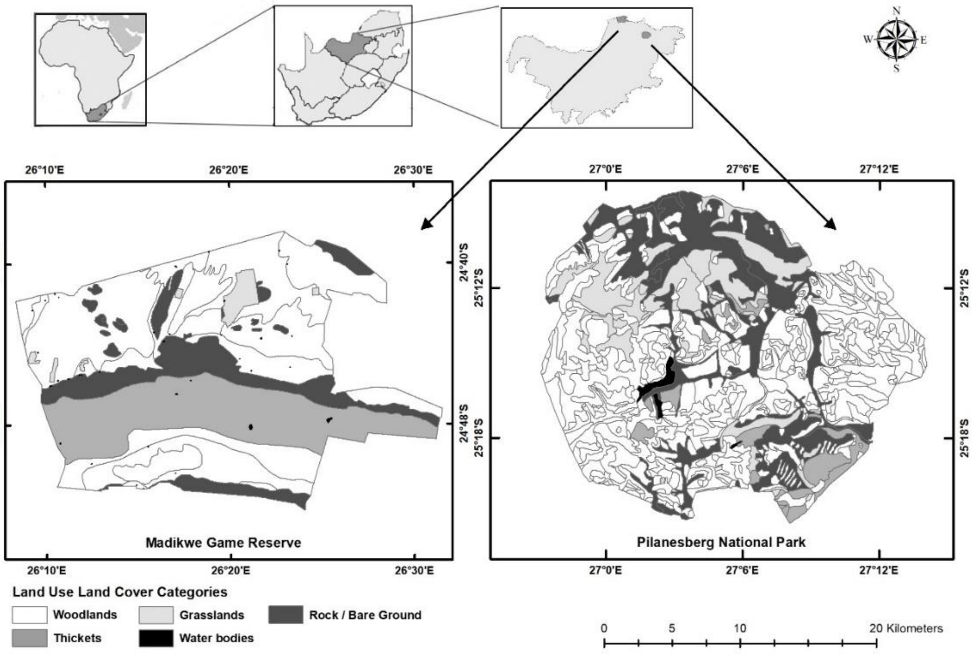

Figure 2.1: Details of geographic locations and land use land cover (LULC) categories in the study sites (NWPTB, 2018)

The black rhino populations in Madikwe and Pilanesberg both are considered by the IUCN “Key”: critical for the survival of the species, in the type “Key 2”: population increasing or stable and N = 51-100 (Emslie & Brooks, 1999).

2.3.2. Data collection

Three annual replicate aerial surveys were conducted from 1999-2015 during the late dry period (July to October) by using a four-seat Bell Jet Ranger II helicopter with all doors removed. The time between two replicate surveys varied between 1-7 days. The survey team consisted of a pilot, a data recorder and one observer on each side. The survey covered the entire area of both the reserves by flying 500 m wide transects at 90 km/h and 60-100 m above ground (Nel, 2015). Data recorded included locations of all observed individuals, date and time of each observation, and flight time of the survey summed over by year (sum of the three replicate surveys).

Figure 2.2: Black rhino group sighted in the bushveld during the aerial counts in Madikwe Game Reserve (Source: NWPTB, 2015)

2.3.3. Data analysis

We used an N-mixture model to estimate species abundance from count data while accounting for imperfect detection (Royle, 2004). This model depends on data from survey counts that are replicated both in space and over time (Kéry et al., 2009) which are necessary to enabled estimation of detection probability. This information was used to get the real abundance (λ) from a local variation in the abundance (N_i) at *i* sites using *j* temporal counts. There are two linked processes:

1. Ecological. The species has a local abundance in *i* sites (N_i) with latent abundance λ that is described by a Poisson distribution

$$N_i \sim \text{Poisson}(\lambda)$$

2. Observation. We observed y_{ij} (counts) from the N_i (individuals in each *i* sites) in each *j* temporal replicates with a detection probability *p*, which is described by a binomial distribution:

$$y_{i,j} \mid N_i \sim \text{Binomial}(N_i, p)$$

Thus, the N-mixture model simply consist of two linked generalized linear models. Inputs to the model are the replicate counts, which then yields estimates of the parameters of the ecological (abundance) and the observation processes (detection probability) (Kéry & Schaub, 2012). In this study we used a dynamic N-mixture or multi-season model that is a robust-design generalized form of N-mixture model (Royle, 2004) for open populations (Dail & Madsen, 2011). The covariates we used in the model are those that could influence the detection process: survey effort (total flight duration per year), Julian date (with a quadratic term), site (as a factor, characterizing different reserves) and the interaction terms. For population growth rate, we used climate covariates: annual rainfall and temperature (NASA, 2018) (Table 1).

Table 2.1. Covariates used to model abundance, recruitment, survival (or growth rate) and probability of detection using a binomial mixture model in Pilanesberg and Madikwe (South Africa), 1999–2015.

Covariate	Sample-unit specific measurement	Mean	Range	Rationale
Site	Factor	-	-	We can expect different detection probability between sites, due to vegetation cover and geomorphological attributes
Climate	Average annual rainfall (mm)	547.8	268.5-835.8	Inter-calving intervals decreased with an increase in rainfall (Berkeley & Linklater, 2010; Hrabar & du Toit, 2005). We can expect changes in recruitment
	Average annual temperature (ºC)	20.8	19.0-22.6	A positive relationship was observed between the percentage of calves born each month and mean monthly temperature (Freeman et al., 2014)
Fly time	Hours of flight (site by year)	19.6	14.1-24.0	As time of flight increase, we can expect the detection of black rhino also increase
Julian date	Ordinal day of the year	235	205-287	We can expect a variation in detection in the time of year counts were conducted (Brockett, 2002)

We began by assessing the assumptions of the N-mixture model. The first is that the population is geographically and demographically closed within the replicates in a year and a given site (in this case, a reserve). In our study, primary periods were years, over which the population was assumed to be open to gains and losses, while the three annual replicate surveys (secondary periods) were obtained within a sufficiently short time that the local population was assumed to be closed to births, deaths and movement. The second assumption is that individuals are counted only once per survey. Third, animal detections are independent of each other; otherwise, this issue must be addressed using a beta-binomial rather than a binomial observation model (Martin et al., 2011) that account for correlated detections of individuals. Finally, density dependence in vital rates, if present, must be explicitly modelled (Bellier et al., 2016) to consider this specific dynamic. Based on the biology of black rhinos, the fenced nature of the reserves, and methods of data capture, the first three assumptions are likely reasonable, although limited double-counting could lead to the estimation (Link et al., 2018). Moreover, we considered density dependence that could potentially exist (Hanski, 1990; Hrabar & du Toit, 2005; Lundberg et al., 2000; Sæther, 1997). Bellier et al. (2016) described the bias that may occur with density dependence and environmental stochasticity when estimating survival and recruitment, and they compared the use of four Dail-Madsen models in a Bayesian approach: 1) no density dependence (DM), 2) density dependence on survival (DDS), 3) density dependence on recruitment (DDR) and 4) density-dependence on both survival and recruitment (DDSR). To assess these models, they performed simulations, and adjusted the four models using cross-simulations. Bellier et al. (2016) concluded that accurate estimates of abundance and detection probability were possible without accounting for density dependence, but that recruitment, growth rate, or survival would be biased without explicitly modelling the density-dependent process.

To fit the N-mixture model, we used the unmarked package (Fiske & Chandler, 2011) in R (R Core Team, 2018), which provides a unified modelling framework for hierarchical models. It has been developed to separately model explanatory variables of both a latent abundance or occurrence, as well as on a conditional detection process. Unmarked also including tools for data exploration, model fitting, model criticism, post-hoc analysis, and model comparison (Fiske & Chandler, 2011). The computational cost of analysing models using unmarked is significantly lower than using the Bayesian approach.

Data were modelled using maximum likelihood methods with the function pcountOpen, specifically written to handle the Dail and Madsen model in unmarked (Chandler & King, 2011). For model selection, we followed a three-step process (Hostetler & Chandler, 2015) using the Akaike Information Criteria (AIC) (Akaike, 1974) corrected for small sample sizes (AICc) for model selection (Burnham & Anderson, 2002). First, we selected three models of initial abundance for the response variable (count data) by comparing the performance of Poisson, zero-inflated Poisson and Negative Binomial models. Second, we compared a set of candidate models with covariates that might affect the detection process. Third, we compared between four possible models with different population dynamics from unmarked: constant, trend, auto-regressive and Ricker and Gompertz models. Ricker and Gompertz models allowed us to evaluate density dependence (Hostetler and Chandler, 2015), although the authors warn about the need for additional studies on their validity in certain cases. The Ricker model (Ricker, 1954; 1958) is a discrete population model that gives the expected number (or density) of individuals $N_{t,}$ in year t as a function of the number of individuals in the previous year:

$$N_{[i,t]} = N_{[i,t-1]} \cdot e^{\gamma(1-\frac{N_{[i,t-1]}}{\omega})}$$

Where gamma (*γ*) is the maximum instantaneous population growth rate. Omega (ω) is either a parameter that describe the apparent survival rate (deaths and emigrations) in constant, trend and autoregressive models, or the equilibrium abundance (carrying capacity) in density-dependent models. The models require an integer value specifying the upper bound used in the integration (*K*). In our study, this upper bound was set at *K*=130, large enough so that it did not affect the models results.

We estimated annual abundance using empirical Bayes methods (ranef) from unmarked and demographic parameters using the best-supported models (based on AIC comparisons) following the rules of ΔAIC< 2 asserted by Burnham and Anderson (2002) to make a multi-model inference on coefficients. We used the predict function from unmarked to produce plots of estimated relationships with the predictors for each covariate. We used the parametric bootstrap approach to obtain *p*-values from sums of squares (SSE), Chi-square and Freeman-Tukey fit statistics that quantify the fit of a model to a data set, and as a measure of the goodness of fit of the N-mixture selected model. We simulated 1,000 bootstrap samples for each fit assessment. A dispersion parameter (ĉ) was calculated as the ratio of the observed fit statistic to the mean of the simulated distribution. Because the evidence of different density-dependence types, we compared our results in unmarked with the approach from Bellier et al (2016). Based on the previous knowledge from black rhino, we can expect density-dependent survival and recruitment (DDSR) (Hanski, 1990; Sæther, 1997; Hrabar & du Toit, 2005; Lundberg et al., 2000). We fitted this specific model using Nimble (de Valpine et al., 2017; NIMBLE Development Team, 2018) to compare results in DDSR model and in unmarked.

We also used N-mixture simulations to test the reliability of our results, show the relationship between the number of spatial replicates (sites) and accuracy of parameters estimates, and to compare the model outputs with the raw data (maximum counts). We employed modified versions of the original scripts from Chandler (2018). To simulate populations we used similar parameters to those obtained from the null models using our data in two different population dynamics scenarios: Ricker (λ=62; γ=0.2; ω=88; p=0.6) and constant (λ=58; γ=21; ω=0.73; p=0.6) with 2, 5 and 10 spatial replicates (sites). We also compared the population average from 1999-2015 in Madwike and Pilanesberg using the N-mixture approach and the ID monitoring from SADC RMG (personal communication, April 4, 2019), assuming those ID estimates were not biased. In the results, we present estimates and 95% confidence intervals (CI), unless otherwise stated.

2.4. RESULTS

2.4.1. Model selection

For initial abundance, the negative binomial distribution was more strongly supported than the Poisson and zero-inflated Poisson (Table 2.2A). The best-supported models for detection included the covariates Site, Julian Date (including the quadratic term) and the interaction term Site x Julian Date (Table 2.2B). Models with density-dependent dynamics were better supported than constant, trend, or autoregressive models. The best-supported full model was a Ricker model with Rainfall as covariate for growth rate (Table 2.2C). All models of Table 2.2C were used for multimodel inference on coefficients (Table 2.3). Complete R codes and data are in Appendices A and B.

Table 2.2: Model selection results. A) Initial abundance; B) Detection probability and C) Dynamics selection. Number of sites = 2. Number of years=17 Covariates

considered: Rainfall (R), Temperature (T), Site (Site), Fly time (Ft) and Julian Date (Jd). Model selection based on Akaike's Information Criterion (AIC), number of parameters (nPars), the difference AICc from the best fit models (ΔAICc<2), model weights (AICwt), and cumulative model weights (cltvWt).

	nPars	AIC	ΔAICc	AICwt	cltvWt
A. Initial Abundance					
Negative Binomial $\lambda(.)\gamma(.)\omega(.)$ [Const.]$p(.)$	5	684.37	0	0.95	0.95
Poisson $\lambda(.)\gamma(.)\omega(.)$[Const.]$p(.)$	4	690.74	6.37	0.04	0.99
ZIP $\lambda(.)\gamma(.)\omega(.)$[Const.]$p(.)$	5	692.75	8.38	0.01	1
B. Detection Probability					
$\lambda(.)\gamma(.)\omega(.)$[Const.]$p$(Site+Jd+I(Jd^2)+Site*Jd)	9	645.09	0	0.71	0.71
$\lambda(.)\gamma(.)\omega(.)$[Const.]$p$(Site+Jd+I(Jd^2)+Site*Jd+Ft)	10	646.90	1.81	0.29	0.99
$\lambda(.)\gamma(.)\omega(.)$[Const.]$p$(Site+Jd+I(Jd^2)	8	655.09	10.01	0.01	1
C. *Dynamics*					
$\lambda(.)\gamma(R)\omega(.)$[Ricker]$p$(Site+Jd+I(Jd^2)+Site*Jd)	10	642.70	0.00	0.46	0.46
$\lambda(.)\gamma(R+T)\omega(.)$[Ricker]$p$(Site+Jd+I(Jd^2)+Site*Jd)	11	644.47	1.77	0.19	0.65
$\lambda(.)\gamma(.)\omega(.)$[Const]$p$(Site+Jd+I(Jd^2)+Site*Jd)	9	644.62	1.92	0.18	0.83
$\lambda(.)\gamma(.)\omega(.)$[Ricker]$p$(Site+Jd+I(Jd^2)+Site*Jd)	9	644.64	1.93	0.17	1

Table 2.3: Model averaged parameter estimates for each covariate and the associated standard errors (*) Growth rate and carrying capacity are estimated using the Ricker models.

	Mean	SE
Detection		
Intercept p(.)	0.10	0.21
p(SiteB)	1.16	0.23
p(Julian date)	0.14	0.07
p(Julian date^2)	-0.10	0.04
p(Julian date*SiteB)	-0.43	0.15
Growth Rate:		
Intercept γ(.)	-0.96	0.56
γ(Rain)	0.67	0.63
γ(Temp)	-0.06	0.19
Carrying Capacity:		
Intercept ω(.)	4.29	0.08

2.4.2. Detection, population size and trend

The relation between Julian date and detection probability shows that detection declines in September and October, during early green-up of woody vegetation. Detectability was close to one in Pilanesberg for the earliest dates, while it was approximately 0.8 in Madikwe at the same time and diminished thereafter. There was a difference in detectability between both reserves: at the end of September, detectability decreased in both areas, although more markedly in Pilanesberg (Figure 2.3 and Table 2.3).

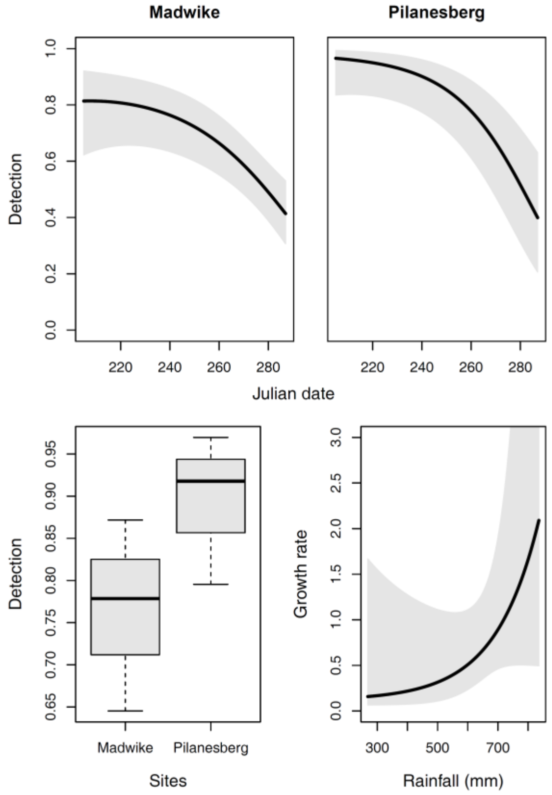

Figure 2.3: Predictions using model averaging from the best-fit models (ΔAICc<2). Top: probability of detecting black rhino in Madikwe and Pilanesberg depending on Julian date. Bottom left: detection probability by Site. Bottom right: growth rate vs. rainfall. Mean estimates are in black and their 95% confidence intervals are in grey

There is some support for effects of precipitation and temperature on growth rate, although it is weak (Table 2.3). Population size in Madikwe and Pilanesberg showed similar dynamics (Figure 2.4), with a density range of 0.078 - 0.098 and 0.139 - 0.142

individuals/km^2, respectively. Carrying capacity based on the Ricker model in unmarked (Figure 2.4 and Table 2.3) was estimated as 73.07 (60.99 - 85.14) individuals, or a density of ca. 0.122 (0.102 - 0.142) individuals/100 km^2. The population size estimates using the model DDSR in a Bayesian approach (Bellier et al. 2016) are somewhat similar to those obtained using the unmarked model (Results in Appendix C vs Abundance in Appendix A). The average difference in estimates between Bayesian vs unmarked approaches was 2.2 (1.57 - 6.84) individuals (positive) for Madikwe, and 1.80 (4.45 - 0.07) individuals for Pilanesberg (negative).

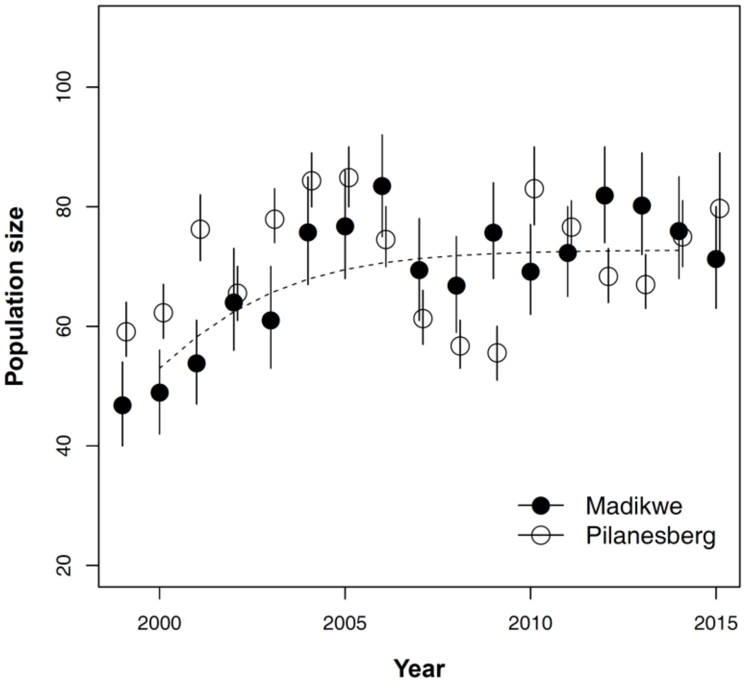

Figure 2.4: Average estimated abundance of Black Rhinoceros Diceros bicornis in Madikwe and Pilanesberg in 1999-2015 and Ricker model fit (dashed). Bars represent 95% confidence intervals on abundance estimates

2.4.3. Goodness of fit

The bootstrap p-values for the best-fit model based on the SSE, Freeman-Tukey, and Chi-square statistics were 0.66, 0.69 and 0.67, respectively, suggesting that our model provided an adequate fit to the data (Figure A.2 in Appendix A). The value of ĉ (ratio of observed/expected) was 0.73, indicating a slight under-dispersion.

2.4.4. Simulations

Using a simulated time span of 20 years (Table 2.4 and Appendix C), the estimate of initial abundance (λ) using N-mixture models had root-mean-square error (RSME) values substantially lower than using maximum yearly counts. For density-dependent and constant dynamics, the RMSE was reduced by half if we used ten spatial replicates instead of two. The accuracy of the detection probability estimate was high in both the constant and the Ricker models; however, in the simulation with density dependence, the accuracy of growth rate was lower than for the constant model.

Table 2.4: Root-mean-square error (RMSE) from the population parameter estimates through simulations. Simulations are based on our parameters estimates from the null models for Ricker and constant dynamics, for M ∈ {2, 5, 10} spatial replicates (sites). We also compare the RMSE from estimates and from raw count data (using the maximum from three yearly replicates). One hundred simulations of each case were conducted. Parameters: lambda: initial abundance; gamma: recruitment rate (constant) or growth rate (Ricker); omega: apparent survival probability (constant) or equilibrium abundance (Ricker) and p: detection probability.

		RICKER			**CONSTANT**		
M	Parameter	Simulated	RMSE		Simulated	RMSE	
			Estimates	Counts		Estimates	Counts
2	*lambda (λ)*	62.00	6.75	22.36	58.00	7.38	23.19
	gamma (γ)	0.20	0.15		21.00	8.93	
	omega (ω)	88.00	10.23		0.73	0.12	
	P	0.60	0.05		0.60	0.09	
5	*lambda (λ)*	62.00	5.12	20.74	58.00	6.16	17.10
	gamma (γ)	0.20	0.08		21.00	5.11	
	omega (ω)	88.00	6.71		0.73	0.06	
	P	0.60	0.04		0.60	0.04	
10	*lambda (λ)*	62.00	4.00	21.93	58.00	3.58	21.00
	gamma (γ)	0.20	0.05		21.00	3.07	
	omega (ω)	88.00	5.44		0.73	0.04	
	P	0.60	0.03		0.60	0.03	

2.4.5. Comparison RMG ID and N-mixture estimates

The range in RMG ID estimates for Madikwe was 27 - 82 with an average (1999-2015) of 56.5. For the N-mixture estimates, the minimum was 46.8 (40-54), the maximum was 83.5 (75-92), and the average (1999-2015) was 69.0 (53-85). The N-mixture average estimate was 22.2% higher. The RMG estimates for Pilanesberg ranged from 48 to 66 with an average of 56.0. The N-mixture estimates had a minimum of 55.6 (51-60), a maximum of 84.9 (80-90), and an average (1999-2015) of 71.09 (61-81). N-mixture average estimate was 26.7% higher than of RMG.

2.5. DISCUSSION

The density estimates we obtained from this study were between 0.078 and 0.154 rhinos/km^2 which are similar to the density estimates reported in Pilanesberg (0.076 individuals/km^2) by Adcock et al. (1998), who also pointed out that this population was then still below its ecological carrying capacity. Model selection of the N-mixture model also allowed us to confirm that density-dependent processes were evident for these populations of black rhino. AIC supported density-dependent models, with three of the four best models including Ricker distributions (Table 2.3). This selected distribution described a rapidly growing population with a horizontal asymptote of 0.122 (0.102 - 0.142) individuals/km^2 (Figure 2.4). The estimates of population size and support for density dependence that we obtained using the DDSR model were similar (see Figure 2.4 and Figure C1 from Appendix C) to those based on model selection in unmarked.

While the growth rate estimates from our model require cautious interpretation (Bellier et al., 2016), we found evidence that rainfall has had a positive effect on the growth rate (Figure 2.3, Table 2.3). Therefore, it is expected that rainfall positively influences black rhino populations. For instance, Berkeley and Linklater (2010) indicated that rainfall and, therefore, range conditions around conception influence seasonal conception rates and seasonal and annual progeny sex ratios.

In general, estimates from N-mixture models could be improved by using more spatial replicates (Knape & Korner-Nievergelt, 2015), although short time series from many sites can yield estimates of similar accuracy as long series from few sites (Bellier et al., 2016), as in our study. This is consistent with the results of our simulations (Table 2.4 and Appendix C). Furthermore, the use of more covariates would give further insights on the population responses to different observational and environmental conditions.

The use of N-mixture models with aerial count data may provide an instrumental framework for species management, which would allow managers to obtain better population estimates. Even in complex situations like those involving density dependence and environmental stochasticity, abundance and detection probability can be more accurately estimated, as demonstrated by our simulation. To improve the accuracy of vital rates estimates we could use a Bayesian N-mixture approach, select the appropriate type of density-dependence (DDR, DDS or DDSR) (Bellier et al., 2016) and also use informative priors. Vital rate estimates could be also addressed using identification-based models or even integrated population models (e.g. combining spatial capture-recapture and count models) that have important advantages compared to conventional analyses (Schaub et al., 2007) to obtain unbiased estimates.

About the differences of detection probability between reserves, SDAC RMG using ID monitoring (personal communication, April 4, 2019) found that a greater proportion of the population is counted in Pilanesberg than Madikwe, as we found using N-mixture model (Figure 2.3). In contrast, the differences in abundance between RMG ID and N-mixture estimates were unexpected. If we assume RMG ID are unbiased, the differences could lie in the execution of the aerial surveys. Accidental double-counts can lead to overestimation because a substantial bias arises with only a slight violation of model assumptions (Link et al., 2018). Another cause of bias could be an unmodeled source of variation in detection (e.g. observer experience). In the future, such biases could be minimized through proper planning, training and execution. Furthermore, integrated population models (IPM) or N-mixture models that incorporate false positives and false-negatives could reduce the effect of double-counting (Chambert et al., 2016). The use of those models is an attractive and simple approach to estimate densities of large mammals besides black rhino in the region, and they facilitate working at scales that are relevant for conservation and management. Aerial counts of large mammals, and the application of N-mixture models, would improve population size estimates, and provide more accurate knowledge of population trends and uncertainty of estimates. It should be noted that according our simulations (Table 2.4) even with high detection probability, the use of raw counts could mask substantial fluctuations in population sizes. In our simulations, using a detection probability of 0.6 and three replicates, maximum counts are biased at a 30%. Furthermore, an additional advantage of using dynamic N-mixture models is the possibility to include covariates as potential predictors of recruitment, survival and species abundance. Evaluating the relationship between potential covariates and demographic vital rates could provide more comprehensive information, which could aid in identifying threats to a species and could be targeted by the policy-making authorities.

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2.7. REFERENCES

Acocks, J. (1988). Veld Types of South Africa, Third Edition. *Memoirs of the Botanical Survey of South Africa*, *57*.

Adcock, K. (1994). The relevance of "territorial" behaviour in black rhino to their population management. In *Proceedings of a symposium on rhinos as game ranch animals.*

Adcock, K., Hansen, H. B., & Lindemann, H. (1998). Lessons from the introduced black rhino population in Pilanesberg National Park. Pachyderm 40–51.

Akaike, H. (1974). A New Look at the Statistical Model Identification. *IEEE Transactions on Automatic Control*, *19*(6). https://doi.org/10.1109/TAC.1974.1100705

Amin, R., Thomas, K., Emslie, R. H., Foose, T. J., & Van Strien, N. V. (2006). An overview of the conservation status of and threats to rhinoceros species in the wild. *International Zoo Yearbook*, *40*(1). https://doi.org/10.1111/j.1748-1090.2006.00096.x

Bellier, E., Kéry, M., & Schaub, M. (2016). Simulation-based assessment of dynamic N-mixture models in the presence of density dependence and environmental stochasticity. *Methods in Ecology and Evolution*, *7*(9). https://doi.org/10.1111/2041-210X.12572

Berger, J. (1994). Science, conservation, and black rhinos. *Journal of Mammalogy*, *75*(2). https://doi.org/10.2307/1382548

Berkeley, E. V., & Linklater, W. L. (2010). Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *African Journal of Wildlife Research*, *40*(1). https://doi.org/10.3957/056.040.0102

Brockett, B. H. (2002). Accuracy, bias and precision of helicopter-based counts of black rhinoceros in Pilanesberg National Park, South Africa. *African Journal of Wildlife Research*, *32*(2).

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A practical Information-theoretic Approach (2nd ed). Library of Congress Cataloging-in-Publication Data. In *Ecological Modelling* (Vol. 172).

Carruthers, J. (2011). Pilanesberg National Park, North West Province, South Africa: Uniting economic development with ecological design – A history, 1960s to 1984. *Koedoe*, *53*(1). https://doi.org/10.4102/koedoe.v53i1.1028

Caughley, G. (1977). Sampling in Aerial Survey. *The Journal of Wildlife Management*, *41*(4). https://doi.org/10.2307/3799980

Chambert, T., Hossack, B. R., Fishback, L. A., & Davenport, J. M. (2016). Estimating abundance in the presence of species uncertainty. *Methods in Ecology and Evolution*, *7*(9). https://doi.org/10.1111/2041-210X.12570

Chandler R. B. (2018). Unmarked. GitHub Repos. [WWW Document] URL: https://github.com/rbchan/unmarked/blob/master/inst/unitTests/sim.pcountOpen.r#L742 (accessed 20.12.18)

Chandler, R. B., & King, D. I. (2011). Habitat quality and habitat selection of golden-winged warblers in Costa Rica: An application of hierarchical models for open populations. *Journal of Applied Ecology*, *48*(4). https://doi.org/10.1111/j.1365-2664.2011.02001.x

Cromsigt, J. P. G. M., Hearne, J., Heitkönig, I. M. A., & Prins, H. H. T. (2002). Using models in the management of Black rhino populations. *Ecological Modelling*, *149*(1–2). https://doi.org/10.1016/S0304-3800(01)00524-5

Dail, D., & Madsen, L. (2011). Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. *Biometrics*, *67*(2). https://doi.org/10.1111/j.1541-0420.2010.01465.x de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Lang, D. T., & Bodik, R. (2017). Programming With Models: Writing Statistical Algorithms for General Model Structures With NIMBLE. *Journal of Computational and Graphical Statistics*, *26*(2). https://doi.org/10.1080/10618600.2016.1172487

Emslie, R. H. (2012). Diceros bicornis ssp. minor [WWW Document]. IUCN Red List Threat. Species. https://doi.org/http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T39321A16981557.en (accessed 1.12.18)

Emslie, R., & Adcock, K. (2016). A Conservation Assessment of Diceros bicornis. *The Red List of Mammals of South Africa, Swaziland and Lesotho.*

Emslie, R., & Brooks, M. (1999). Status Survey and Conservation Action Plan African Rhino. In *IUCN/SSC African Rhino Specialist Group*.

Farrell, V. R., & Tinley K. L. (1978). Pilanesberg National Park, Bophuthatswana: Planning and management proposals for Department of Agriculture, Republic of Bophuthatswana, August 1978, unpublished report.

Ferreira, S. M., Bissett, C., Cowell, C. R., Gaylard, A., Greaver, C., Hayes, J., Hofmeyr, M., Moolman-van der Vyver, L., & Zimmermann, D. (2017). The status of rhinoceroses in South African National Parks. *Koedoe*, *59*(1). https://doi.org/10.4102/koedoe.v59i1.1392

Ferreira, S. M., Greaver, C. C., & Knight, M. H. (2011). Assessing the population performance of the black rhinoceros in Kruger National Park. *African Journal of Wildlife Research*, *41*(2). https://doi.org/10.3957/056.041.0206

Fiske, I. J., & Chandler, R. B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*(10), 1–23. https://doi.org/10.18637/jss.v043.i10

Foose, T. J., Lacy, R. C., Brett, R., & Seal, U. S. (1993). Kenya Black Rhino Metapopulation Workshop part 2. IUCN/SSC Captive Breeding Specialist Group (CBSG), Apple Valley.

Freeman, E. W., Meyer, J. M., Bird, J., Adendorff, J., Schulte, B. A., & Santymire, R. M. (2014). Impacts of environmental pressures on the reproductive physiology of subpopulations of black rhinoceros (Diceros bicornis bicornis) in Addo Elephant

National Park, South Africa. *Conservation Physiology*, *2*(1). https://doi.org/10.1093/conphys/cot034

Gakahu, C. G. (1993). African rhinos: current numbers and distribution, in: Proceedings of an International Conference. Zoological Society, San Diego, U.S.A., pp. 161–165.

Gimenez, O., Viallefont, A., Charmantier, A., Pradel, R., Cam, E., Brown, C. R., Anderson, M. D., Brown, M. B., Covas, R., & Gaillard, J. M. (2008). The risk of flawed inference in evolutionary studies when detectability is less than one. *American Naturalist*, *172*(3). https://doi.org/10.1086/589520

Hanski, I. (1990). Density dependence, regulation and variability in animal populations. Philos. Trans. R. Soc. London. Biol. Sci. 330, 141–150. https://doi.org/10.1098/rstb.1990.0188

Hone, J. (2008). On bias, precision and accuracy in wildlife aerial surveys. *Wildlife Research*, *35*(4). https://doi.org/10.1071/WR07144

Hostetler, J. A., & Chandler, R. B. (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, *96*(6). https://doi.org/10.1890/14-1487.1

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (Diceros bicornis) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3). https://doi.org/10.1017/S1367943005002234

Jachmann, H. (2002). Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology*, *39*(5). https://doi.org/10.1046/j.1365-2664.2002.00752.x

Kéry, M., & Schaub, M. (2012). Bayesian population analysis using WinBUGS. A hierarchical perspective. Academic Press / Elsevier. https://doi.org/10.1016/B978-0-12-387020-9.00014-6

Kéry, M., Dorazio, R. M., Soldaat, L., Van Strien, A., Zuiderwijk, A., & Royle, J. A. (2009). Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, *46*(6). https://doi.org/10.1111/j.1365-2664.2009.01724.x

King, J. M., Sayers, A. R., Chara, P., de Leeuw, P. N., & Peacock, C. P. (1985). Improving aerial counts of Maasai livestock. *Agricultural Systems*, *16*(4). https://doi.org/10.1016/0308-521X(85)90062-9

Knape, J., & Korner-Nievergelt, F. (2015). Estimates from non-replicated population surveys rely on critical assumptions. *Methods in Ecology and Evolution*, *6*(3). https://doi.org/10.1111/2041-210X.12329

Link, W. A., Schofield, M. R., Barker, R. J., & Sauer, J. R. (2018). On the robustness of N-mixture models. *Ecology*, *99*(7). https://doi.org/10.1002/ecy.2362

Lundberg, P., Ranta, E., Ripa, J., & Kaitala, V. (2000). Population variability in space and time. In *Trends in Ecology and Evolution* (Vol. 15, Issue 11). https://doi.org/10.1016/S0169-5347(00)01981-9

Lyet, A., Slabbert, R., Versfeld, W. F., Leslie, A. J., Beytell, P. C., & du Preez, P. (2016). Using a binomial mixture model and aerial counts for an accurate estimate of Nile crocodile abundance and population size in the Kunene River, Namibia. *African Journal of Wildlife Research*, *46*(2). https://doi.org/10.3957/056.046.0071

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L., & Hines, J. E. (2017). Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence: Second Edition. In *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence: Second Edition*. https://doi.org/10.1016/C2012-0-01164-7

Mackie, C. S., Dunham, K. M., & Ghiurghi, A. (2013). Current status and distribution of the Vulnerable common hippopotamus *Hippopotamus amphibius* in Mozambique. In *ORYX* (Vol. 47, Issue 1). https://doi.org/10.1017/S0030605311001554

Martin T. E., Clobert, J., & Anderson, D. R. (1995). Return rates in studies of life history evolution: Are biases large? *Journal of Applied Statistics*, *22* (863–876). https://doi.org/10.1080/02664769524676

Martin, E. B. (1991). The present-day trade routes and markets for rhinoceros products, in: Proceedings of International Conference Rhinoceros Biological Conservation San Diego, pp. 1–10.

Martin, J., Royle, J. A., Mackenzie, D. I., Edwards, H. H., Kéry, M., & Gardner, B. (2011). Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Methods in Ecology and Evolution*, *2*(6). https://doi.org/10.1111/j.2041-210X.2011.00113.x

McCarthy, M. A., & Possingham, H. P. (2007). Active adaptive management for conservation. *Conservation Biology*, *21*(4). https://doi.org/10.1111/j.1523-1739.2007.00677.x

McCarthy, T., & Rubidge, B. (2006). The Story Of Earth & Life. Struik Publishers (Pty) Ltd, Cape Town, South Africa.

Mduma, S. A. R., Sinclair, A. R. E., & Hilborn, R. (1999). Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology*, *68*(6). https://doi.org/10.1046/j.1365-2656.1999.00352.x

Moilanen, A. (2002). Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos*, *96*(3). https://doi.org/10.1034/j.1600-0706.2002.960313.x

Moodley, Y., Russo, I. R. M., Dalton, D. L., Kotzé, A., Muya, S., Haubensak, P., Bálint, B., Munimanda, G. K., Deimel, C., Setzer, A., Dicks, K., Herzig-Straschil, B., Kalthoff, D. C., Siegismund, H. R., Robovský, J., O'Donoghue, P., & Bruford, M. W. (2017). Extinctions, genetic erosion and conservation options for the black rhinoceros (Diceros bicornis). *Scientific Reports*, *7*. https://doi.org/10.1038/srep41417

Mucina, L., & Rutherford, M. C. (2006). The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, Strelitzia.

NASA (2018). Prediction of Worldwide Energy Resources [WWW Document] URL https://power.larc.nasa.gov/ (accessed 10.22.18)

Nel, H. P. (2015). Population estimates for large herbivores and predators in protected areas in the North West Parks Board.

Nichols, J. D., & Williams, B. K. (2006). Monitoring for conservation. *Trends in Ecology and Evolution*, *21*(12). https://doi.org/10.1016/j.tree.2006.08.007

Nichols, J. D., Boulinier, T., Hines, J. E., Pollock, K. H., & Sauer, J. R. (1998). Inference Methods for Spatial Variation in Species Richness and Community Composition

When Not All Species Are Detected. Conservation Biology, 12(6), 1390–1398. http://www.jstor.org/stable/2989858

NIMBLE Development Team, (2018). NIMBLE User Manual. [WWW Document]. URL https://r-nimble.org/html_manual/ (accessed 10.11.18).

NWPTB (2015). Pilanesberg National Park Management Plan. Draft for discussion.

NWPTB (2018). North West Parks Board official website [WWW Document]. URL https://www.northwestparks.org.za (accessed 9.22.18).

Ottichilo, W. K. (1999). Comparison of sample and total counts of elephant and buffalo in Masai Mara, Kenya. *African Journal of Ecology*, *37*(4). https://doi.org/10.1046/j.1365-2028.1999.00199.x

Owen-smith, N. (1990). Demography of a Large Herbivore, the Greater Kudu Tragelaphus strepsiceros, in Relation to Rainfall. *The Journal of Animal Ecology*, *59*(3). https://doi.org/10.2307/5021

Parker, G., Sundaresan, S., Chege, G., & O'Brien, T. (2011). Using sample aerial surveys to estimate the abundance of the endangered Grevy's zebra in northern Kenya. *African Journal of Ecology*, *49*(1). https://doi.org/10.1111/j.1365-2028.2010.01232.x

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Ricker, W. E. (1954). Stock and Recruitment. *Journal of the Fisheries Research Board of Canada*, *11*(5). https://doi.org/10.1139/f54-039

Ricker, W. E. (1958). A handbook of computations for biological statistics of fish populations. Fish. Res. Board Can. Bull. 1, 119.

Royle, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, *60*(1). https://doi.org/10.1111/j.0006-341X.2004.00142.x

Sæther, B. E. (1997). Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. In *Trends in Ecology and Evolution* (Vol. 12, Issue 4). https://doi.org/10.1016/S0169-5347(96)10068-9

Schaub, M., Gimenez, O., Sierro, A., & Arlettaz, R. (2007). Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conservation Biology*, *21*(4). https://doi.org/10.1111/j.1523-1739.2007.00743.x

Schmidt, B. R. (2005). Monitoring the distribution of pond-breeding amphibians when species are detected imperfectly. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*(6). https://doi.org/10.1002/aqc.740

Sinclair, A. R. E., Dublin, H., & Borner, M. (1985). Population regulation of Serengeti Wildebeeest: a test of the food hypothesis. *Oecologia*, *65*(2). https://doi.org/10.1007/BF00379227

Skalski, J. R. (1994). Estimating Wildlife Populations Based on Incomplete Area Surveys. Wildlife Society Bulletin (1973-2006), 22(2), 192–203. http://www.jstor.org/stable/3783246

Steinhorst, R. K., & Samuel, M. D. (1989). Sightability Adjustment Methods for Aerial Surveys of Wildlife Populations. Biometrics, 45(2), 415–425. https://doi.org/10.2307/2531486

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. In *Ecological Applications* (Vol. 13, Issue 6). https://doi.org/10.1890/02-5078

Walpole, M. J., Morgan-Davies, M., Milledge, S., Bett, P., & Leader-Williams, N. (2001). Population dynamics and future conservation of a free-ranging black rhinoceros (Diceros bicornis) population in Kenya. *Biological Conservation*, *99*(2). https://doi.org/10.1016/S0006-3207(00)00219-6

Wiest, W. A., Correll, M. D., Marcot, B. G., Olsen, B. J., Elphick, C. S., Hodgman, T. P., Guntenspergen, G. R., & Shriver, W. G. (2019). Estimates of tidal-marsh bird densities using Bayesian networks. *Journal of Wildlife Management*, *83*(1). https://doi.org/10.1002/jwmg.21567

Williams, P. J., Hooten, M. B., Womble, J. N., & Bower, M. R. (2017). Estimating occupancy and abundance using aerial images with imperfect detection. *Methods in Ecology and Evolution*, *8*(12). https://doi.org/10.1111/2041-210X.12815

2.8. SUPPLEMENTARY MATERIAL

Supplementary information for "Using N-mixture model to accurately estimate abundance and population trend of black rhinoceros (*Diceros bicornis* L.) from aerial counts"

Appendix A: R + unmarked script

Zaara Kidwai, José Jiménez, Cornelius J. Louw, H. P. Nel and Jason P. Marshal

Table of Contents

Set working directory

```
setwd('C:/…/')
```

Load packages

```
library(unmarked)
## Loading required package: reshape
## Loading required package: lattice
## Loading required package: parallel
## Loading required package: Rcpp
```

Read data

```
# Replicated aerial counts data
ymat<-read.table('BlackRhino.txt', header=FALSE)
```

Naive estimate

```
y<-matrix(0,ncol=17, nrow=2)
for(i in 1:2){
  for(j in 1:17){
    y[i,j]<-max(ymat[i,(j+(j-1)*2)],ymat[i,(j+1+(j-1)*2)],ymat[i,(j+2+(j-1)*2)])
  }
}

plot(1999:2015,y[1,],pch=16, ylim=c(0,80), cex=1.25, type='b',
  xlab="Year", ylab="Naive population estimate")
points(1999:2015, y[2,], cex=1.25, type='b')
legend(2009.5,18, lty=1, lwd=c(2,1), pt.cex = 1.25, pch=c(16,1), col=c('black','black'),
  cex=1.25, legend=c('Madikwe','Pilanesberg'), bty='n')
```

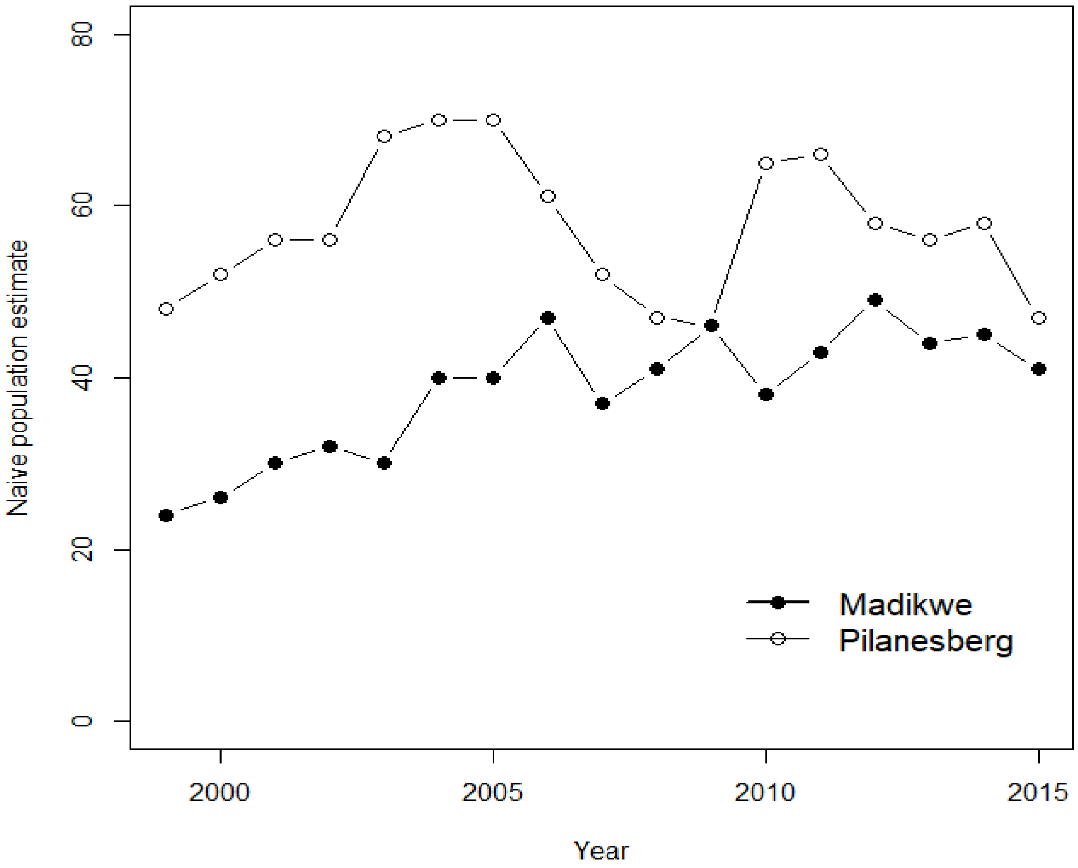


Figure A.1: Evolution of black rhino in Madikwe and Pilanesberg using the maximum yearly counts.

Covariates

```
Ft<-data.matrix(read.table('flyTimeRhino.txt', header=FALSE))
Jd<-data.matrix(read.table('julianDate.txt', header=FALSE))
Rm<-data.matrix(read.table('removal.txt', header=FALSE))
Rainfall<-data.matrix(read.table('rainfall.txt', header=FALSE))
temp<-data.matrix(read.table('temp.txt', header=FALSE))
```

Model in unmarked

Site-specific covariates

```
sc <- data.frame(Site = c('A','B'))  # A: Madikwe; B: Pilanesberg
```

Observation-specific covariates

```
oc <- list(
    Obs = matrix(1:51, nrow=2, ncol=51, byrow=TRUE),
    Jd = Jd)        # Julian date
```

Yearly-site covariates

```
ysc <- list(
    Ft = Ft,        # Fly time
    Rainfall = Rainfall,
    temp=temp,
    Rm=Rm)          # Removal
```

Setting data

```
umf <- unmarkedFramePCO(y=ymat,
                        siteCovs=sc,
                        obsCovs=oc,
                        numPrimary=17,
                        yearlySiteCovs=ysc)
```

Standardize covariates

```
yearlySiteCovs(umf) <- scale(yearlySiteCovs(umf))
obsCovs(umf) <- scale(obsCovs(umf))
```

Take a look

```
summary(umf)
## unmarkedFrame Object
##
## 2 sites
## Maximum number of observations per site: 51
## Mean number of observations per site: 51
## Number of primary survey periods: 17
## Number of secondary survey periods: 3
## Sites with at least one detection: 2
##
## Tabulation of y observations:
## 20 22 23 24 26 27 28 29 30 31 32 34 35 36 37 38 39 40 41 42 43 44 45 46 47
##  1  1  1  2  5  1  3  2  3  1  3  1  1  2  3  5  1  2  5  2  3  4  2  4  3
## 48 49 50 51 52 53 54 55 56 57 58 59 61 62 63 65 66 68 70
##  6  1  1  1  6  2  2  1  3  1  2  3  1  1  1  1  3  3  2
##
## Site-level covariates:
##  Site
##  A:1
##  B:1
##
## Observation-level covariates:
##       Obs                  Jd
##  Min.   :-1.6901   Min.   :-1.6193
##  1st Qu.:-0.8619   1st Qu.:-0.7576
##  Median : 0.0000   Median :-0.2999
##  Mean   : 0.0000   Mean   : 0.0000
##  3rd Qu.: 0.8619   3rd Qu.: 0.7906
##  Max.   : 1.6901   Max.   : 2.7966
##
## Yearly-site-level covariates:
##        Ft              Rainfall              temp               Rm
##  Min.   :-2.4017   Min.   :-2.20460   Min.   :-2.1972   Min.   :-0.5465
##  1st Qu.:-0.6145   1st Qu.:-0.66175   1st Qu.:-0.6620   1st Qu.:-0.5465
##  Median :-0.2780   Median : 0.08646   Median :-0.1920   Median :-0.5465
##  Mean   : 0.0000   Mean   : 0.00000   Mean   : 0.0000   Mean   : 0.0000
```

```
##   3rd Qu.: 0.4061   3rd Qu.: 0.71364   3rd Qu.: 0.7604   3rd Qu.: 0.2981
##   Max.   : 1.8936   Max.   : 2.27295   Max.   : 2.2267   Max.   : 2.8318
```

Fit open models for abundance: lambda (= abundance), gamma (= gains or recruitment), omega (= survival), p (= detect)

```
# Null model
fm.0.P <- pcountOpen(~1, ~1, ~1, ~1, data=umf,
  mixture='P', K=130, control=list(trace=TRUE), start=c(4,3.1,1,1))
fm.0.ZIP <- pcountOpen(~1, ~1, ~1, ~1, data=umf,
  mixture='ZIP', K=130, control=list(trace=TRUE), start=c(4,3.1,1,1,0))
fm.0.NB <- pcountOpen(~1, ~1, ~1, ~1, data=umf,
  mixture='NB', K=130, control=list(trace=TRUE), start=c(4,3.1,1,1,0))


brm0<- fitList('Poisson'             =fm.0.P,
               'ZIP'                 =fm.0.ZIP,
               'Negative Binomial'   =fm.0.NB)
modSel(brm0)
##                     nPars    AIC delta AICwt cumltvWt
## Negative Binomial       5 684.37  0.00 0.946     0.95
## Poisson                 4 690.74  6.37 0.039     0.99
## ZIP                     5 692.75  8.38 0.014     1.00
(lam <- exp(coef(fm.0.NB, type='lambda')))
## lam(Int)
## 57.82012
(gam <- exp(coef(fm.0.NB, type='gamma')))
## gamConst(Int)
##      20.46591
(om <- plogis(coef(fm.0.NB, type='omega')))
## omega(Int)
##   0.732117
(p <- plogis(coef(fm.0.NB, type='det')))
##   p(Int)
## 0.601168

fm.1 <- pcountOpen(~1, ~1, ~1, ~Site, umf,
  dynamics="constant",
  mixture='NB', start=c(4,0,0,0,0,2), K=130)
fm.2 <- pcountOpen(~1, ~1, ~1, ~Jd+I(Jd^2), umf,
  dynamics="constant",
  mixture='NB', start=c(4,0,0,0,0,0,2), K=130)
fm.3 <- pcountOpen(~1, ~1, ~1, ~Site+Jd+I(Jd^2), umf,
  dynamics="constant",
  mixture='NB', start=c(4,3.5,0,0,1,0,0,20), K=130)
fm.4 <- pcountOpen(~1, ~1, ~1, ~Site+Jd+I(Jd^2)+Site*Jd, umf,
  dynamics="constant",
  mixture='NB', start=c(4,0,0,0,0,0,0,0,2), K=130)
fm.5 <- pcountOpen(~1, ~1, ~1, ~Site*Jd+Site+Jd+I(Jd^2)+Ft, umf,
  dynamics="constant",
  mixture='NB', start=c(4,0,0,0,0,0,0,0,0,2), K=130)
```

Model selection. Detection

```
brm1<- fitList('lam(.)gam(.)om(.)p(.)'                         = fm.0.NB,
               'lam(.)gam(.)om(.)p(Site)'                      = fm.1,
               'lam(.)gam(.)om(.)p(Jd+I(Jd^2)'                 = fm.2,
               'lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)'            = fm.3,
               'lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)+Site*Jd)'   = fm.4,
               'lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)+Site*Jd+Ft)' = fm.5)


modSel(brm1)
```

```
##                                                nPars    AIC delta   AICwt   cuml
tvWt
## lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)+Site*Jd)        9 644.62  0.00 7.0e-01     0.
70
## lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)+Site*Jd+Ft)    10 646.36  1.74 3.0e-01     1.
00
## lam(.)gam(.)om(.)p(Site+Jd+I(Jd^2)                 8 657.01 12.39 1.4e-03     1.
00
## lam(.)gam(.)om(.)p(Site)                           6 669.67 25.05 2.6e-06     1.
00
## lam(.)gam(.)om(.)p(Jd+I(Jd^2)                      7 670.54 25.91 1.7e-06     1.
00
## lam(.)gam(.)om(.)p(.)                              5 684.37 39.75 1.6e-09     1.
00
```

Model selection. Abundance

```
brmD<- fitList(# No covariates in gamma
               'lam(.)gam(.)om(.)[Const]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.6,
               'lam(.)gam(.)om(.)[Trend]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.7,
               'lam(.)gam(.)om(.)[Autoreg]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.8,
               'lam(.)gam(.)om(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.9,
               # Rainfall as covariate in gamma
               'lam(.)gam(Rainfall)om(.)[Const]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.10,
               'lam(.)gam(Rainfall)om(.)[Trend]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.11,
               'lam(.)gam(Rainfall)om(.)[Autoreg]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.12,
               'lam(.)gam(Rainfall)om(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.13,
               # Rainfall and Temperature as covariates in gamma
               'lam(.)gam(Rainfall+temp)om(.)[Const]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.14,
               'lam(.)gam(Rainfall+temp)om(.)[Trend]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.15,
               'lam(.)gam(Rainfall+temp)om(.)[Autoreg]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.16,
               'lam(.)gam(Rainfall+temp)om(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)'
= fm.17)


modSel(fitList(fm.6,fm.7,fm.8,fm.9,fm.10,fm.11,fm.12,fm.13,fm.14,fm.15,fm.16,fm.17)
)

##
##       nPars    AIC delta   AICwt cumltvWt
## fm.13    10 642.70  0.00 0.38874     0.39
## fm.17    11 644.47  1.77 0.16068     0.55
## fm.6      9 644.62  1.92 0.14883     0.70
## fm.9      9 644.64  1.93 0.14799     0.85
## fm.14    11 645.90  3.20 0.07853     0.92
## fm.10    10 646.14  3.43 0.06983     0.99
## fm.7      8 653.24 10.54 0.00200     1.00
## fm.11     9 653.92 11.22 0.00142     1.00
## fm.8      9 655.25 12.54 0.00073     1.00
## fm.15    10 655.92 13.22 0.00052     1.00
## fm.12    10 655.95 13.25 0.00052     1.00
## fm.16    11 657.93 15.23 0.00019     1.00
## Warning message:
## In fitList(fm.6, fm.7, fm.8, fm.9, fm.10, fm.11, fm.12, fm.13, fm.14,  :
```

```
##  Your list was unnamed, so model names were added as object names
```

backtransform:

```
gamma_int    <- backTransform(linearComb(fm.13, type="gamma", coefficients=c(1,0)))
; gamma_int
## Backtransformed linear combination(s) of Growth Rate estimate(s)
##
##  Estimate    SE LinComb (Intercept) Rainfall
##     0.348 0.212   -1.05           1        0
##
## Transformation: exp
gamma_rain   <- backTransform(linearComb(fm.13, type="gamma", coefficients=c(0,1)))
; gamma_rain
## Backtransformed linear combination(s) of Growth Rate estimate(s)
##
##  Estimate   SE LinComb (Intercept) Rainfall
##      2.52 1.33   0.924           0        1
##
## Transformation: exp
p_int     <- backTransform(linearComb(fm.13, type="det", coefficients=c(1,0,0,0,0))
); p_int
## Backtransformed linear combination(s) of Detection estimate(s)
##
##  Estimate     SE LinComb (Intercept) SiteB Jd I(Jd^2) SiteB:Jd
##     0.528 0.0518   0.113           1     0  0       0        0
##
## Transformation: logistic
p_Site    <- backTransform(linearComb(fm.13, type="det", coefficients=c(0,1,0,0,0))
); p_Site
## Backtransformed linear combination(s) of Detection estimate(s)
##
##  Estimate     SE LinComb (Intercept) SiteB Jd I(Jd^2) SiteB:Jd
##     0.757 0.0417    1.14           0     1  0       0        0
##
## Transformation: logistic
p_Jd      <- backTransform(linearComb(fm.13, type="det", coefficients=c(0,0,1,0,0))
); p_Jd
## Backtransformed linear combination(s) of Detection estimate(s)
##
##  Estimate     SE LinComb (Intercept) SiteB Jd I(Jd^2) SiteB:Jd
##     0.534 0.0183   0.136           0     0  1       0        0
##
## Transformation: logistic
p_Jd2     <- backTransform(linearComb(fm.13, type="det", coefficients=c(0,0,0,1,0))
); p_Jd2
## Backtransformed linear combination(s) of Detection estimate(s)
##
##  Estimate     SE LinComb (Intercept) SiteB Jd I(Jd^2) SiteB:Jd
##     0.475 0.0107 -0.0987           0     0  0       1        0
##
## Transformation: logistic
p_SiteXJd <- backTransform(linearComb(fm.13, type="det", coefficients=c(0,0,0,0,1))
); p_SiteXJd
## Backtransformed linear combination(s) of Detection estimate(s)
##
##  Estimate     SE LinComb (Intercept) SiteB Jd I(Jd^2) SiteB:Jd
##     0.393 0.0348  -0.435           0     0  0       0        1
##
## Transformation: logistic
```

Abundance

```
black.rhino<-ranef(fm.13)  # To get all
bup(black.rhino)
```

```
##          [,1]     [,2]     [,3]     [,4]     [,5]     [,6]     [,7]
## [1,] 46.82095 48.92527 53.82453 64.01512 61.00254 75.75705 76.74588
## [2,] 59.13389 62.31687 76.27861 65.56049 77.92541 84.36233 84.91844
##          [,8]     [,9]    [,10]    [,11]    [,12]    [,13]    [,14]
## [1,] 83.51075 69.45007 66.84770 75.70615 69.17260 72.30242 81.91210
## [2,] 74.55045 61.33134 56.74073 55.61481 83.05397 76.64556 68.38189
##         [,15]    [,16]    [,17]
## [1,] 80.25660 75.97449 71.29647
## [2,] 67.01282 74.99584 79.76157
```

Confidence intervals

```
# To get confindence intervals
low.Mad<-confint(black.rhino)[1,1,]
hig.Mad<-confint(black.rhino)[1,2,]
low.Pil<-confint(black.rhino)[2,1,]
hig.Pil<-confint(black.rhino)[2,2,]
```

Goodness of fit

```
fitstats <- function(fm) {
    observed <- getY(fm@data)
    expected <- fitted(fm)
    resids <- residuals(fm)
    sse <- sum(resids^2)
    chisq <- sum((observed - expected)^2 / expected, na.rm=TRUE)
    freeTuke <- sum((sqrt(observed) - sqrt(expected))^2)
    out <- c(SSE=sse, Chisq=chisq, freemanTukey=freeTuke)
    return(out)
}

(pb <- parboot(fm.13, fitstats, nsim=1000, report=2, parallel=FALSE))
 chisquare test statistic
(c.hat <- pb@t0[2] / mean(pb@t.star[,2])) # c-hat as ratio of observed/expected
load("pb.RData")

par(mfrow=c(2,2))
par(mar = c(5.00,
            5.00,
            2.00,
            1.00))
hist(pb@t.star[,1], xlab="SSE", col="lightgrey",
  font.lab=2, cex.lab=1, main="")
abline(v=pb@t0[1], lty=2, lwd=2)
par(mar = c(5.00,
            1.00,
            2.00,
            2.00))
hist(pb@t.star[,2], xlab="Chisq", col="lightgrey",
  font.lab=2, cex.lab=1, main="")
abline(v=pb@t0[2], lty=2, lwd=2)
par(mar = c(5.00,
            5.00,
            1.00,
            0.00))
hist(pb@t.star[,3], xlab="freemanTukey", col="lightgrey", breaks=15,
  font.lab=2, cex.lab=1, main="")
abline(v=pb@t0[3], lty=2, lwd=2)
```

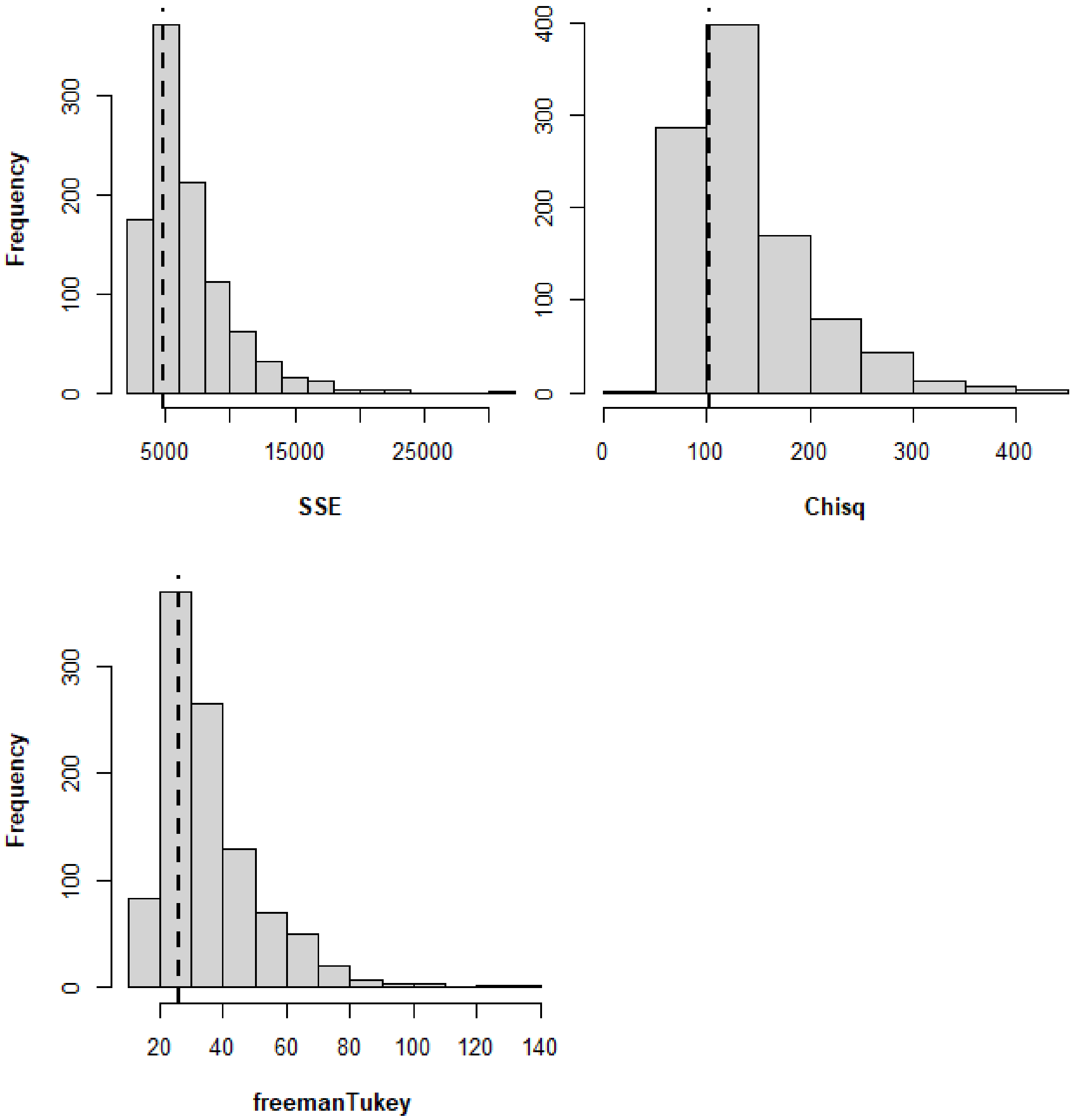


Figure A.2: Graphical assessment of model fit by parametric bootstrapping. The dashed line is the observed statistic. The histogram approximates the expected sampling distribution

Supplementary information for “Using N-mixture model to accurately estimate abundance and population trend of black rhinoceros (*Diceros bicornis* L.) from aerial counts”

Appendix B: Data

Zaara Kidwai, José Jiménez, Cornelius J. Louw, H. P. Nel and Jason P. Marshal

	Counts		Date	
	Madikwe	Pilanesberg	Madikwe	Pilanesberg
1999	24	48	10/08/1999	18/08/1999
1999	23	46	12/08/1999	19/08/1999
1999	20	48	15/08/1999	21/08/1999
2000	26	50	08/08/2000	12/08/2000
2000	22	48	09/08/2000	14/08/2000
2000	24	52	10/08/2000	15/08/2000
2001	28	52	04/09/2001	10/09/2001
2001	26	54	05/09/2001	11/09/2001
2001	30	56	07/09/2001	12/09/2001
2002	30	52	03/08/2002	10/08/2002
2002	26	56	04/08/2002	12/08/2002
2002	32	48	06/08/2002	14/08/2002
2003	28	63	04/08/2003	07/08/2003
2003	26	68	05/08/2003	09/08/2003
2003	30	59	06/08/2003	11/08/2003
2004	40	68	04/08/2004	12/08/2004
2004	38	66	06/08/2004	14/08/2004
2004	36	70	07/08/2004	15/08/2004
2005	40	68	09/08/2005	17/08/2005
2005	38	66	10/08/2005	20/08/2005
2005	36	70	11/08/2005	21/08/2005
2006	45	59	20/08/2006	13/08/2006
2006	43	61	22/08/2006	18/08/2006
2006	47	57	24/08/2006	21/08/2006
2007	29	48	25/07/2007	11/08/2007
2007	31	52	07/08/2007	13/08/2007
2007	37	46	09/08/2007	16/08/2007
2008	41	43	22/08/2008	12/08/2008
2008	27	44	24/08/2008	16/08/2008
2008	28	47	25/07/2008	21/08/2008
2009	41	46	14/09/2009	26/08/2009
2009	35	44	20/09/2009	30/08/2009
2009	46	32	25/09/2009	05/09/2009

2010	38	65	29/08/2010	18/09/2010
2010	34	42	02/09/2010	23/09/2010
2010	38	51	06/09/2010	26/09/2010
2011	42	66	30/08/2011	25/07/2011
2011	43	59	01/09/2011	27/07/2011
2011	32	62	08/09/2011	30/07/2011
2012	39	53	06/09/2012	31/07/2012
2012	49	54	08/09/2012	04/08/2012
2012	48	58	14/09/2012	11/08/2012
2013	44	56	09/09/2013	07/08/2013
2013	41	52	14/09/2013	12/08/2013
2013	44	53	17/09/2013	19/08/2013
2014	45	58	16/09/2014	28/08/2014
2014	38	52	17/09/2014	08/09/2014
2014	37	55	18/09/2014	14/09/2014
2015	37	41	23/09/2015	05/10/2015
2015	29	47	26/09/2015	08/10/2015
2015	41	26	30/09/2015	15/10/2015

Supplementary information for “Using N-mixture model to accurately estimate abundance and population trend of black rhinoceros (*Diceros bicornis* L.) from aerial counts”

Appendix C: DDSR approach-R + Nimble model

Zaara Kidwai, José Jiménez, Cornelius J. Louw, H. P. Nel and Jason P. Marshal

Table of Contents

Set working directory

```
setwd('C:/…/')
```

Read data

```
# Replicated aerial counts data
ymat<-read.table('BlackRhino.txt', header=FALSE)

ymat1<-data.matrix(ymat[,c(seq(1,51, by=3))])
ymat2<-data.matrix(ymat[,c(seq(2,51, by=3))])
ymat3<-data.matrix(ymat[,c(seq(3,51, by=3))])

y<-array(0,c(2,17,3))
y[,,1]<-ymat1
y[,,2]<-ymat2
y[,,3]<-ymat3

# Julian date
Jd<-data.matrix(read.table('julianDate.txt', header=FALSE))

Jd1<-data.matrix(Jd[,c(seq(1,51, by=3))])
Jd2<-data.matrix(Jd[,c(seq(2,51, by=3))])
Jd3<-data.matrix(Jd[,c(seq(3,51, by=3))])

JD<- array(0,c(2,17,3))
JD[,,1]<-Jd1
JD[,,2]<-Jd2
JD[,,3]<-Jd3

JD<-(JD-mean(JD))/sd(JD)

# Rainfall
```

```
Rainfall<-data.matrix(read.table('rainfall.txt', header=FALSE))
Rainfall<- (Rainfall-mean(Rainfall))/sd(Rainfall)
```

Model

```
library(nimble)
## nimble version 0.6-13 is loaded.
## For more information on NIMBLE and a User Manual,
## please visit http://R-nimble.org.
##
## Attaching package: 'nimble'
## The following object is masked from 'package:stats':
##
##     simulate
## define the model
code <- nimbleCode({
  # Priors and constraints
  alpha1 ~ dnorm(0,.01)
  alpha2 ~ dnorm(0,.01)
  alpha3 ~ dnorm(0,.01)
  gamma0 ~ dnorm(0,0.01)
  gamma1 ~ dnorm(0,0.01)

  for(g in 1:G) {
    for(t in 1:T){
      log(mean.r[g,t])<- gamma0 + gamma1*Rain[g,t]
    }
  }

  beta1 ~ dunif(-1, 1)
  sigma1 ~ dunif(0, 2)
  tau1 <- 1/pow(sigma1, 2)
  mean.phi ~ dunif(0, 1)
  mphi <- log(mean.phi/(1-mean.phi))
  beta2 ~ dunif(-1, 1)
  sigma2 ~ dunif(0, 2)
  tau2 <- 1/pow(sigma2, 2)

  for(g in 1:G) {
    p0[g] ~ dunif(0, 1)
    for(t in 1:T) {
      for(k in 1:K) {
        logit(p[g,t,k]) <- p0[g] + alpha1*JD[g,t,k] +
                           alpha2*p0[g]*JD[g,t,k] +
                           alpha3*JD[g,t,k]*JD[g,t,k]
      }
    }
  }

  lambda ~ dunif(0.1, 200)
  # Likelihood
  # Initial population size
  for (g in 1:G){
    N[g,1] ~ dpois(lambda)

    # State process
    for (t in 1:(T-1)){
      S[g,t] ~ dbin(phi[g,t], N[g,t])
      R[g,t] ~ dpois(N[g,t] * r[g,t])
      N[g,t+1] <- S[g,t] + R[g,t]
      # Density-dependence and environmental stochasticity in recruitment
      lr[g,t] <- log(mean.r[g,t]) + beta1*(N[g,t]-Nm)+ eps1[g,t]
      r[g,t] <- exp(lr[g,t])
      eps1[g,t] ~ dnorm(0, tau1)
      # Density-dependence and environmental stochasticity in survival
      lphi[g,t] <- mphi + beta2*(N[g,t]-Nm) + eps2[g,t]
      phi[g,t] <- 1/(1+exp(-lphi[g,t]))
      eps2[g,t] ~ dnorm(0, tau2)
```

```
    }
    # Observation process
    for (t in 1:T) {
      for(k in 1:K) {
        y[g,t,k] ~ dbin(p[g,t,k], N[g,t])
      }
    }
  } # g
})
```

Bundle data

```
y: count at site i and time t (3 replica)
T: nb of years
G: nb of sites
```

Data

```
data <- list(y = y, JD=JD, Rain=Rainfall)
```

Constants

```
constants<-list(T = dim(y)[2], G = dim(y)[1], K=dim(y)[3],
                Nm=mean(as.matrix(y)))
```

Inits

```
# Initial values for recruits R
ya<-apply(y, c(1,2), sum)
R1<-as.matrix(ya)[,-1]


inits  <-  list(mean.phi=runif(1,0.6,1),
                beta1 =runif(1,-1,-.1),
                beta2 =runif(1,-1,-.1),
                sigma1=runif(1,0.01,0.5),
                sigma2=runif(1,0.01,0.5),
                gamma0=runif(1, -1, 1),
                gamma1=runif(1, -1, 1),
                p0=runif(2,0.5,1),
                alpha1=runif(1,0.1,1),
                alpha2=runif(1,0.1,1),
                alpha3=runif(1,0.1,1),
                lambda = runif(1,20,200),
                R=R1+2)
```

Parameters monitored

```
params <- c('N')
```

Running the model

```
Rmodel <- nimbleModel(code=code, constants=constants,
  data=data, inits=inits)
## defining model...
## building model...
## setting data and initial values...
## running calculate on model (any error reports that follow may simply reflect mis
sing values in model variables) ...
## checking model sizes and dimensions... This model is not fully initialized. This
is not an error. To see which variables are not initialized, use model$initializeIn
fo(). For more information on model initialization, see help(modelInitialization).
## model building finished.
Cmodel <- compileNimble(Rmodel)
## compiling... this may take a minute. Use 'showCompilerOutput = TRUE' to see C++
compiler details.
## compilation finished.
```

```
mcmcspec<-configureMCMC(Rmodel, monitors=params, thin=10)

pumpMCMC <- buildMCMC(mcmcspec)
CpumpMCMC <- compileNimble(pumpMCMC, project = Rmodel)
## compiling... this may take a minute. Use 'showCompilerOutput = TRUE' to see C++
compiler details.
## compilation finished.
## Output:
library(coda)
library(lattice)


samplesList <- runMCMC(CpumpMCMC, niter = 1000000,
                     nburnin = 50000, nchains = 3)
## runMCMC's handling of nburnin changed in nimble version 0.6-11. Previously, nbur
nin samples were discarded *post-thinning*.  Now nburnin samples are discarded *pre
-thinning*.  The number of samples returned will be floor((niter-nburnin)/thin).
## running chain 1...
## |-------------|-------------|-------------|-------------|
## |-------------------------------------------------------|
## running chain 2...
## |-------------|-------------|-------------|-------------|
## |-------------------------------------------------------|
## running chain 3...
## |-------------|-------------|-------------|-------------|
## |-------------------------------------------------------|
samples<-rbind(as.matrix(samplesList[1][[1]]),
               as.matrix(samplesList[2][[1]]),
               as.matrix(samplesList[3][[1]]))

summary(mcmc.list(as.mcmc(samplesList[[1]]),
                  as.mcmc(samplesList[[2]]),
                  as.mcmc(samplesList[[3]])))
##
## Iterations = 1:95000
## Thinning interval = 1
## Number of chains = 3
## Sample size per chain = 95000
##
## 1. Empirical mean and standard deviation for each variable,
##    plus standard error of the mean:
##
##                   Mean       SD  Naive SE Time-series SE
## N[1, 1]     48.996800 4.016824 7.524e-03      2.454e-02
## N[2, 1]     64.991228 3.529405 6.611e-03      1.814e-02
## N[1, 2]     52.196811 4.444757 8.326e-03      2.564e-02
## N[2, 2]     70.089498 4.000707 7.494e-03      2.195e-02
## N[1, 3]     53.725337 4.364536 8.176e-03      2.948e-02
## N[2, 3]     81.633632 4.707205 8.817e-03      2.527e-02
## N[1, 4]     63.695375 5.784458 1.084e-02      2.819e-02
## N[2, 4]     73.479151 4.335836 8.122e-03      2.386e-02
## N[1, 5]     65.004863 6.075275 1.138e-02      3.052e-02
## N[2, 5]     87.113344 4.826542 9.041e-03      2.609e-02
## N[1, 6]     79.492274 6.420902 1.203e-02      3.238e-02
## N[2, 6]     93.773807 4.924628 9.225e-03      2.841e-02
## N[1, 7]     79.815589 6.042792 1.132e-02      3.155e-02
## N[2, 7]     93.900175 4.691508 8.788e-03      2.718e-02
## N[1, 8]     84.594228 5.565000 1.042e-02      3.334e-02
## N[2, 8]     82.098046 4.379125 8.203e-03      2.413e-02
## N[1, 9]     73.585109 6.472541 1.212e-02      3.194e-02
## N[2, 9]     67.960025 3.964758 7.427e-03      2.071e-02
## N[1, 10]    69.394747 5.310787 9.948e-03      2.990e-02
## N[2, 10]    62.891789 3.664322 6.864e-03      1.898e-02
## N[1, 11]    75.828298 6.461543 1.210e-02      4.615e-02
## N[2, 11]    62.418639 3.869993 7.249e-03      2.261e-02
## N[1, 12]    69.835744 5.124600 9.599e-03      3.527e-02
## N[2, 12]    88.754253 5.715589 1.071e-02      3.127e-02
## N[1, 13]    73.959053 5.240570 9.816e-03      3.674e-02
```

```
## N[2, 13]    86.464414 6.229117 1.167e-02      3.166e-02
## N[1, 14]    82.426519 5.967147 1.118e-02      4.333e-02
## N[2, 14]    76.584337 4.865995 9.115e-03      2.602e-02
## N[1, 15]    79.824007 6.431038 1.205e-02      4.809e-02
## N[2, 15]    75.181126 4.356704 8.161e-03      2.375e-02
## N[1, 16]    75.376225 6.698769 1.255e-02      4.793e-02
## N[2, 16]    82.322088 4.647306 8.705e-03      2.490e-02
## N[1, 17]    71.054639 7.839797 1.469e-02      5.494e-02
## N[2, 17]    85.082228 8.976498 1.681e-02      3.572e-02
##
## 2. Quantiles for each variable:
##
##                   2.5%       25%       50%       75%      97.5%
## N[1, 1]     41.000000 46.000000 49.000000 52.000000  5.700e+01
## N[2, 1]     59.000000 63.000000 65.000000 67.000000  7.300e+01
## N[1, 2]     44.000000 49.000000 52.000000 55.000000  6.100e+01
## N[2, 2]     63.000000 67.000000 70.000000 72.000000  7.900e+01
## N[1, 3]     45.000000 51.000000 54.000000 57.000000  6.200e+01
## N[2, 3]     74.000000 78.000000 81.000000 84.000000  9.200e+01
## N[1, 4]     53.000000 60.000000 64.000000 67.000000  7.600e+01
## N[2, 4]     66.000000 70.000000 73.000000 76.000000  8.300e+01
## N[1, 5]     53.000000 61.000000 65.000000 69.000000  7.700e+01
## N[2, 5]     79.000000 84.000000 87.000000 90.000000  9.800e+01
## N[1, 6]     67.000000 75.000000 79.000000 84.000000  9.200e+01
## N[2, 6]     86.000000 90.000000 93.000000 96.000000  1.050e+02
## N[1, 7]     68.000000 76.000000 80.000000 84.000000  9.200e+01
## N[2, 7]     86.000000 91.000000 93.000000 96.000000  1.050e+02
## N[1, 8]     73.000000 81.000000 85.000000 88.000000  9.500e+01
## N[2, 8]     75.000000 79.000000 82.000000 85.000000  9.200e+01
## N[1, 9]     61.000000 69.000000 73.000000 78.000000  8.700e+01
## N[2, 9]     61.000000 65.000000 68.000000 70.000000  7.700e+01
## N[1, 10]    59.000000 66.000000 69.000000 73.000000  8.000e+01
## N[2, 10]    57.000000 60.000000 63.000000 65.000000  7.100e+01
## N[1, 11]    64.000000 71.000000 76.000000 80.000000  8.900e+01
## N[2, 11]    56.000000 60.000000 62.000000 65.000000  7.100e+01
## N[1, 12]    60.000000 66.000000 70.000000 73.000000  8.000e+01
## N[2, 12]    79.000000 85.000000 88.000000 92.000000  1.010e+02
## N[1, 13]    64.000000 70.000000 74.000000 77.000000  8.400e+01
## N[2, 13]    76.000000 82.000000 86.000000 90.000000  1.000e+02
## N[1, 14]    71.000000 78.000000 82.000000 86.000000  9.400e+01
## N[2, 14]    69.000000 73.000000 76.000000 79.000000  8.800e+01
## N[1, 15]    67.000000 75.000000 80.000000 84.000000  9.300e+01
## N[2, 15]    68.000000 72.000000 75.000000 78.000000  8.500e+01
## N[1, 16]    63.000000 71.000000 75.000000 80.000000  8.900e+01
## N[2, 16]    74.000000 79.000000 82.000000 85.000000  9.300e+01
## N[1, 17]    57.000000 66.000000 71.000000 76.000000  8.700e+01
## N[2, 17]    69.000000 79.000000 84.000000 91.000000  1.040e+02
```

Plot

```
ps.dep.mat1 <- samples[,c(seq(1,34,by=2))]
ps.N1 <- ps.dep.mat1[,grep("N", colnames(ps.dep.mat1))]

ps.dep.mat2 <- samples[,c(seq(2,34,by=2))]
ps.N2 <- ps.dep.mat2[,grep("N", colnames(ps.dep.mat2))]

Years<-1999:2015
par(mar = c(5.50,
            5.00,
            5.00,
            3.00))
plot(Years, colMeans(ps.N1), type="p", ylim=c(20, 120), pch=16, cex=2,
     font.lab=2, cex.lab=1.25,
     xlab="Year", ylab="Population size")
segments(Years, apply(ps.N1, 2, quantile, prob=0.025),
         Years, apply(ps.N1, 2, quantile, prob=0.975))
points(Years+.1, colMeans(ps.N2), type="p", ylim=c(15, 150),
```

```
     xlab="Year", ylab="Population size", pch=1, cex=2)
segments(Years+.1, apply(ps.N2, 2, quantile, prob=0.025),
         Years+.1, apply(ps.N2, 2, quantile, prob=0.975))

legend(2009.5,35, lty=1, lwd=c(1,1), pt.cex = 2, pch=c(16,1),
  col=c('black','black'),
  cex=1.25, legend=c('Madikwe','Pilanesberg'), bty='n')
```

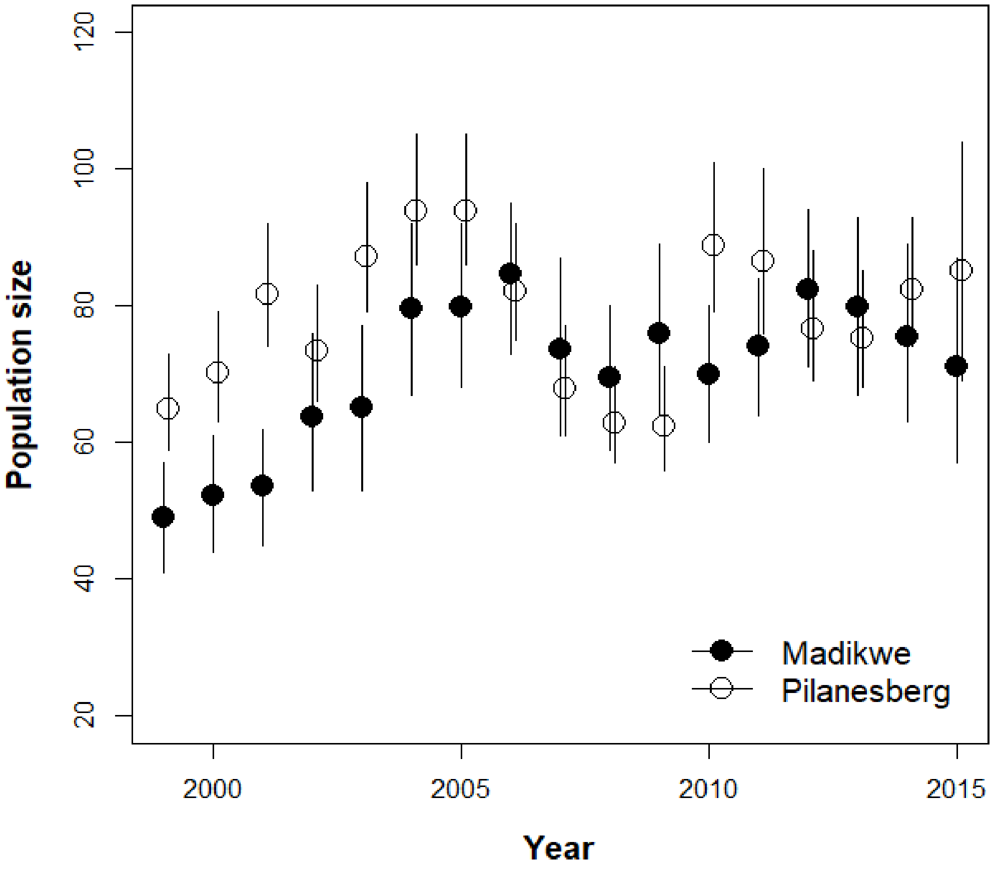


Figure C.1: Average estimated abundance of Black Rhinoceros Diceros bicornis in Madikwe and Pilanesberg in 1999-2015 using DDSR. Bars represent 95% Bayesian credible intervals on abundance estimates

Supplementary information for “Using N-mixture models to estimate abundance and temporal trends of ungulate populations from aerial counts: a case study of black rhinoceros (*Diceros bicornis* L.)”

Appendix D: Simulations

Zaara Kidwai, José Jiménez, Cornelius J. Louw, H. P. Nel and Jason P. Marshal

Table of Contents

Constant

```
# Simulate constant model with M=2 (sites) J=3 (secondary samples),
# T=20 (primary periods) and detection probability p=0.7

sim <- function(lambda=50, gamma=0.5, omega=0.8, p=0.7, M=10, T=20, J=3)
{
    y <- matrix(NA, M, J*T)
    N <- matrix(NA, M, T)
    S <- G <- matrix(NA, M, T-1)
    N[,1] <- rpois(M, lambda)
    for(t in 1:(T-1)) {
        S[,t] <- rbinom(M, N[,t], omega)
        G[,t] <- rpois(M, gamma)
        N[,t+1] <- S[,t] + G[,t]
        }
    N <- N[,rep(1:T, each=J)]
    y[] <- rbinom(M*J*T, N, p)
    y<-list(y,N)
    return(y)
}



library(unmarked)
## Loading required package: reshape
## Loading required package: lattice
## Loading required package: parallel
## Loading required package: Rcpp
nsim <- 100
simout <- matrix(NA, nsim, 5)
colnames(simout) <- c('lambda', 'gamma', 'omega', 'p', 'count')
```

```
for(i in 1:nsim)
  cat("sim:", i,
  lambda <-
  gamma <- 21     # Recruitment
  omega <- 0.73   # Apparent survival
  p <-
  T <-
  y.sim <- sim(lambda, gamma, omega, p,
  umf <- unmarkedFramePCO(y = y.sim[[1]],
```

```
  m <- pcountOpen(~1, ~1, ~1, ~1, umf,
    starts=c(log(lambda), log(gamma), plogis(omega),
    se=TRUE
  e <-
  simout[i, 1:2] <-
  simout[i, 3:4] <-
  simout[, 5] <-
  cat("mle = ", simout[i,],
```

Ricker

```
# Simulate Ricker model with M=2 (sites) J=3 (secondary samples),
# T=20 (primary periods) and detection p=0.7
# detection probability 0.7
library(unmarked)
sim <- function(lambda=1, gamma=0.1, omega=1.5, p=0.7, M=5, T=20, J=3)
{
    y <- N <- matrix(NA, M, J*T)
    N[,1] <- rpois(M, lambda)
    for(t in 2:T) {
        N[,t] <- rpois(M, N[,t-1]*exp(gamma*(1-N[,t-1]/omega)))
    }
    N <- N[,rep(1:T, each=J)]
    y[] <- rbinom(M*J*T, N, p)
    y<-list(y,N)
    return(y)
}


nsim <- 100
simout <- matrix(NA, nsim, 5)
colnames(simout) <- c('lambda', 'gamma', 'omega', 'p', 'count')
for(i in 1:nsim) {
    cat("sim:", i, "\n")
    lambda <- 62
    gamma <- 0.2
    omega <- 88
    p <- 0.6
    y.sim <- sim(lambda, gamma, omega, p)
    umf <- unmarkedFramePCO(y = y.sim[[1]], numPrimary=20)
    m <- pcountOpen(~1, ~1, ~1, ~1, umf, K=120, dynamics="ricker",
        starts=c(log(lambda), log(gamma), log(omega), plogis(p)),
        se=TRUE)
    e <- coef(m)
    simout[i, 1:3] <- exp(e[1:3])
    simout[i, 4] <- plogis(e[4])
    simout[, 5] <-  apply(cbind(y.sim[[1]][,1],y.sim[[1]][,2],y.sim[[1]][,3]),1,max)
    cat("  mle =", simout[i,], "\n")
    }
```

CHAPTER 3. Landscape scale predictors of ungulate habitat use in the North West Province, South Africa.

3.1. ABSTRACT

Ungulate space use is generally focused towards optimizing resource acquisition, and minimizing predation risk. Considering the broad spectrum of environmental conditions, including varying size of study sites, investigation into habitat selection responses is warranted. These might differ across sites depending on resource availability. Forage quantity and quality are key components structuring habitat partitioning by ungulates, yet there are multiple additional factors to be considered. Locations across the landscape of eleven species of grazing ungulate were recorded from 2000-2015 across 13 study sites during the dry season. Environmental variables were fitted to 16 models to investigate their effect on ungulate habitat use and partitioning. Zebra and red hartebeest were among the most widely distributed species. Habitat partitioning between ungulates was found to be structured mainly by differences in preference for forage quality (e.g., sable vs impala), heterogeneity (e.g., wildebeest vs red hartebeest), elevation (e.g., springbok vs buffalo), difference in habitat type (e.g., eland vs blesbok), reliance on surface water (e.g., zebra vs gemsbok) and avoidance of roads (e.g., zebra vs black wildebeest). Multiple ecological variables influence ungulate landscape use in the North West Province of South Africa, and their importance are perhaps amplified within the confines of small protected areas. Examining their contribution towards habitat use across the species spectrum provides insight into niche partitioning and coexistence among multi-species communities.

3.2. INTRODUCTION

Ungulates utilize space in order to optimize resource acquisition (including mitigating intra- and interspecific competition) and to minimize predation risk (Thaker et al., 2011). Doing so requires balancing nutritional gains with energetic costs e.g., thermoregulation, and energy expenditure related to foraging activities at landscape scales (Maloiy et al., 2009; Cain et al., 2006). Ungulate space use is structured by multiple biotic and abiotic factors (Milner et al., 1999; Maffei et al., 2002; Maffei & Taber, 2003; Rivero et al., 2005; Keuroghlian & Eaton, 2008; García-Marmolejo et al., 2013) but are generally considered to be dictated by resource availability (Senft et al., 1987; Macandza et al., 2004; 2012; Treydte et al., 2013). Seasonal variation in forage biomass and quality in African Savannas are considerable, with resource limitations reaching annual bottlenecks during the late dormant season (Owen-Smith, 2002). Resource heterogeneity in turn is shaped largely by landscape attributes (Stilwell et al., 2020) e.g., elevation (Anderson et al., 2006; Cromsigt & Olff, 2006), slope gradient (Bailey et al., 1996), fire (Allred et al., 2011), edaphic factors (soil depth, fertility, and pH), and are further modified by foraging activities of ungulates themselves (Anderson et al., 2006).

Co-existence among multispecies assemblages is achieved through niche partitioning and are most evident in the adaptive radiation into grazers, browsers, and mixed feeders (East, 1984; Holt, 1984; Prins & Olff, 1998; Voeten & Prins, 1999; García-Marmolejo et al., 2013; Deliberato, 2017). Further niche partitioning within each feeder type occurs through morpho-physiological adaptations e.g., dental structure (Mendoza et al., 2002) and gut anatomy (Illius, 1997; Janis, 2008), and digestive physiology. High spatial variation in grass biomass and quality exists across landscapes (Waide et al., 1999; Adler et al., 2011; Grace et al., 2016; Chen et al., 2018). For example, in bottomlands, grass is more plentiful and stays greener for longer into the dormant season (Bell, 1971; Wilmshurst et al., 1999) compared to areas higher up the catena. Slope gradient (Bailey et al., 1996) and surface water requirements (Redfern et al., 2003; Ogutu et al., 2014) also shape the habitat partitioning of ungulate populations (Solomon & Leak 1994; Lee et al., 2005). Certain species may furthermore only be found in areas with a favorable microclimate, to a large extent determined by slope and aspect in particular (Hennenberg & Bruelheide, 2003; Bennie et al., 2008).

Competition is minimized through spatial segregation (Kröger & Rogers, 2005; Odadi et al., 2011; Mariotti et al., 2020a). Ungulate species preferring medium to tall grass communities are at a disadvantage wherever consumer biomass is relatively high (Duncan et al., 2012). For example, red hartebeest and blue wildebeest commonly avoid zebra (Clutton-Brock et al., 1982; Mishra et al., 2004; Deliberato, 2017; Mariotti et al., 2020a; Mariotti et al., 2020b). Therefore, obligate grazers within the ungulate guild require large tracts of land to mediate resource limitation at local scales, when considering the above arguments, rendering them particularly susceptible to habitat fragmentation (see Skarpe, 1991; Kiffner & Lee, 2019). Anthropogenic factors have restricted ungulate movements and affected their distribution across a range of spatial scales (Feldhamer et al., 1986; Rooney, 2001; Licona et al., 2011), mainly due to the fencing in of protected areas, which means that resource availability is limited in both space and time (Hayward & Kerley, 2009). Studies aimed at identifying factors driving habitat use and resource partitioning are important in order to make informed management decisions (Tuljapurkar & Caswell, 1997; Gaillard et al., 1998) especially in South Africa where small protected areas predominate, and are commonly well below 100,000 ha (some < 5,000 ha) in size.

My objective was to estimate the major environmental determinants influencing resource partitioning of the ungulate populations in the North-West province. Small area size in dormant season conceivably could impose foraging limitations that would otherwise be absent in more open systems (Macandza et al., 2012). Findings that contradict expectations would then serve as motivation for further exploration. I therefore predict that 1) NDVI would be the major determinant of habitat partitioning for selective feeders e.g., wildebeest, red hartebeest (Mariotti et al., 2020a), blesbok (Furstenburg, 2016b) and sable (Owen-Smith et al., 2013), while, it will be less evident for bulk feeders such as zebra and buffalo (Seydack et al., 2012) or mixed feeders such as eland (Jarman, 1974), gemsbok (Lehmann et al., 2013), impala (Dunham, 1982), and springbok (Jarman, 1974). In parallel, 2) spatial distribution across the species spectrum negatively correlates with elevation and slope, driven largely by the longer retention time of soil moisture and forage biomass in bottom lands during the dry season (Frank et al., 1998; Hopcraft et al., 2010; Fynn et al., 2015; Bell, 1971; Wilmshurst et al., 1999). Higher biomass would suit tall grass feeders e.g., red hartebeest (Mariotti et al., 2020a), bulk feeders e.g., zebra and buffalo (Seydack et al., 2012) 3). Species considered sensitive to competition e.g., red hartebeest (Deliberato, 2017), sable (Marshal et al., 2016) are expected to utilize areas farther from surface water where foraging impact on vegetation is lower. Gemsbok and eland should follow this prediction due to their low surface water requirements (Skinner & Chimimba, 2005; Lehmann et al., 2013; Furstenburg, 2016a). For species highly dependent on surface water e.g., wildebeest, zebra (Macandza et al., 2012) and blesbok (Furstenburg, 2016b), we expect their distribution to negatively correlate with distance from surface water. 4) It was further expected that ungulate distribution correlate negatively with distance from roads due to the perceived risk that humans pose to ungulate species.

5) Considering the aridity of the study region, aspect is expected to influence soil moisture content and hence, areas with western aspects will be avoided by ungulate species in general. 6) Finally, we predict that species presence generally conforms to habitat preferences as reported in literature.

Soil nutrient availability was not considered for analysis. While this might be a limitation, elevation, slope, and NDVI arguably captures environmental heterogeneity adequately for the purposes of the investigation.

3.3. MATERIAL AND METHODS

3.3.1. Study Area

The study was carried out in 13 protected areas in South Africa's North-West (NW) Province (lat: 24°15’- 28°15’ S, long: of 22°30’ - 28°30’ E) (Figure 3.1). Altitude in the area ranges from 1,000 m to 2,000 m masl (Goslar et al., 2008). The temperature stays within a consistent range of 22°C to 34°C in the summer, to 2°C to 20°C from May to July (Goslar et al., 2008). The region is considered “arid” due to its annual rainfall range of 300 mm to 700 mm from west to east (Kruger & Nxumalo, 2017).

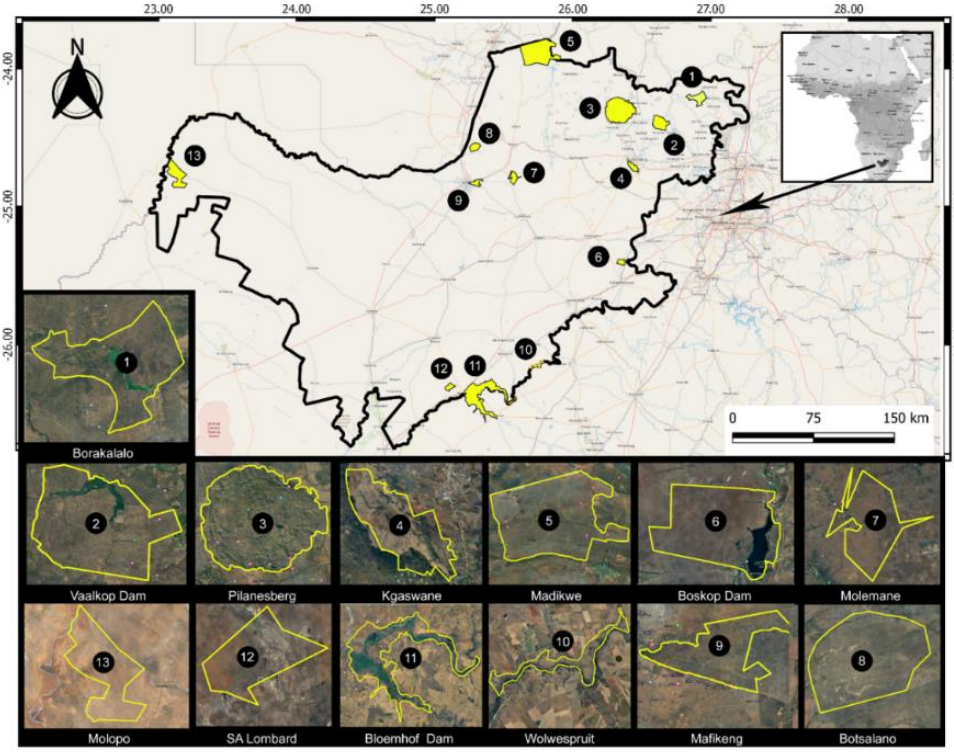


Figure 3.1: Map of North West Province highlighting the study sites

The region is characterized by a broad spectrum of vegetation types from Bankenveld and Turf Thornveld bushveld with scattered Sourish-Mixed veld in the north-east, to uniformly mixed in the center with an equal amount of dry and sandy *Cymbopogon-Themeda* veld and Kalahari Thornveld dominating in the western and driest region (Spickett et al., 2011).

The region is incredibly diverse with about 70 species of the large mammals including elephant (*Loxodonta Africana*), black rhinoceros (*Diceros bicornis*), white rhinoceros (*Ceratotherium simum*), hippopotamus (*Hippopotamus amphibious*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), plains zebra (*Equus quagga*), sable antelope (*Hippotragus niger*), springbok (*Antidorcas marsupialis*), impala (*Aepyceros melampus*), lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and brown hyena (*Hyaena brunnea*) to name a few (Goslar et al., 2008; Power et al., 2019).

3.3.2. Data Collection

Data in the current study was collected by conducting three yearly replicated aerial surveys with a four-seat Bell Jet Ranger II helicopter (with all doors removed) from 1999 to 2015 during the late dry season (July to October). The total strip width of each survey was 500 m at 90 km/hr. with a flying height between 60-100 m. The GPS coordinates of ungulate sightings, date and time of each observation, and survey effort was recorded for each flight every year. Aerial estimations conducted in dry season not only increase counting precision, but also helps with understanding the effect of resource partitioning between species due to limited resource availability (Chase et al., 2015).

3.2.2.1. Habitat variables:

I used Normalized Difference Vegetation Index (NDVI) as a proxy to variability in food quality (Hunninck et al., 2020). To add the NDVI as one of the covariates, I acquired the freely available raster file from MODIS13Q1 NDVI with a spatial resolution of 250 m x 250 m from the U.S. Geological Survey website (earthexplorer.usgs.gov). Moreover, I downloaded the images for the specific months (August to October) and years (1999–2015) of the study, georeferenced to overlay them directly in ArcGIS Desktop 10.8 (ESRI, 2020) and extract values for the specific sites. Heterogeneity was calculated by using MODIS NDVI image for each year. Raster was created with a spatial resolution of 250 m through computing the average difference in absolute values between the NDVI value of each pixel and the NDVI values of the eight pixels surrounding it (see Mariotti et al., 2020a) for each year by using QGIS 3.16.1 (QGIS, 2020). Habitat type raster was collected from open source 2020 South African National Land Cover Data (www.egis.environment.gov.za). The Digital Elevation Model (DEM) for the province was acquired from USGS Science based catalog

(Verdin, 2017). ‘Spatial analysis’ tool of ArcGIS Desktop 10.8 was used to create raster files for slope and aspect data from the DEM files. The extracted Aspect values was then converted into eight main directions (North, North-East, East, South-East, South, South West, West, North-West) in Microsoft Excel following Burrough and McDonell (1998). GPS location of the perennial water sources and GPS tracks of the internal roads was provided in the form of shapefiles by the NWPTB management for calculating distance from water and roads.

Each study area was divided into 2 x 2 km grids to gather the presence/ absence data of each species from each grid, each year (Figure 3.2). To reduce observational bias, I introduced a 400 m buffer at each GPS location of each species sightings (or group center) for every year (following Deliberato, 2017). After data extraction through ‘spatial join’ in ArcGIS 10.8, each grid came up with total sightings or blank records (no sightings). The final data was transformed into presence/absence (0/1) format by setting blanks to ‘zero’ and sighting totals to ‘one’The grid for each location was also used to extract the raster data for all covariates using ‘zonal statistics’ in ArcGIS Desktop 10.8. Distance from water and distance from road for each study site was calculated from the grid center with “Near” analysis tool in ArcGIS Desktop 10.8. Each returning ‘0’ or ‘1’ data for each species in the dataset for each replicate, each year was eventually fed in the model with corresponding covariates.

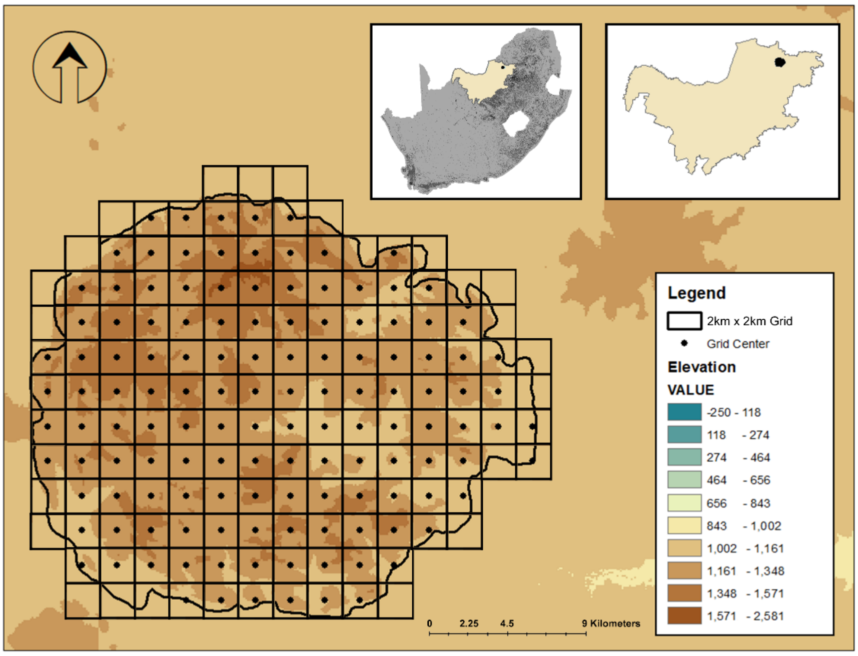


Figure 3.2: Map showing spatial grid placement on Pilanesberg National Park

3.3.3. Data Analysis:

To investigate the effect of environmental variables on ungulate habitat partitioning at a landscape scale, 16 generalized linear mixed models (GLMMs) with a binomial error distribution was fitted to spatial distributions of each species. The analysis was done using ‘lme4’ package (Bates et al., 2014) in software R (R Core Team, 2020). The response variable was the presence/ absence data of ungulates. Eight independent factors (fixed effects) were considered for the analysis after conducting a collinearity test to ensure non-collinearity. Two factors were categorical (habitat type and aspect) and six continuous (NDVI, heterogeneity, slope, elevation, distance from water source and distance from the road). Study sites and grids were used as the random effect that were integrated out using the Laplace approximation. Interactions between factors were also tested for e.g., between geographical factors (slope, elevation and aspect), NDVI with heterogeneity and heterogeneity with habitat type.

I scaled all the continuous variables to have a mean of zero and a standard deviation of one in order to make them comparable (Burnham & Anderson, 2002). The "AICcmodavg" package (Mazerolle & Mazerolle, 2017) was used to conduct model selection corrected for small sample bias (AICc). The best model was selected on the basis of the lowest AICc value (Anderson, 2008). For the best model, I calculated the predicted log odds ratios and associated 95% confidence intervals for each significant variable. Model's goodness of fit was also evaluated using log likelihood values (van Opheusden et al., 2020). The 'jtools' package in R was used to create predictions and plots (Long & Long, 2017).

3.4. RESULTS

A total number of 11 species of grazing ungulates was recorded from 902 grids during the aerial survey from 2000-2015 across the 13 study sites. Zebra and red hartebeest were the only species found on all sites. The maximum number of sightings were recorded for zebra (n = 4196) followed by impala (n = 3459) and blue wildebeest (n = 3107), while, the lowest number were for the sable (n = 352) (Table 3.1). The most parsimonious models included NDVI (in interaction with heterogeneity for blesbok and sable), elevation (in interaction with slope for five species), distance to water, and distance to road as the major influencing factors for habitat partitioning of ungulates. An interaction between habitat type and heterogeneity was found in the most parsimonious habitat partitioning models for six species.

Table. 3.1. AICc model results of the three best predictive models for the probability of presence of ungulate species across the North West Province, South Africa.

#	*Model*	*k*	*logLik*	*AIC*	*ΔAIC*	*df*	w_i
	Black Wildebeest *Connochaetes gnou (obs. = 11,405)*						
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-545	1138	0	18	0.917

m11	NDVI + Slope*Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	18	-546.4	1142.8	4.8	25	0.083
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from water + Distance from the road	23	-565.2	1156.4	18.4	13	<0.001
	Blesbok *Damaliscus pygargus (obs. = 5,660)*						
m13	NDVI*Heterogeneity + Elevation + Habitat + Distance from the road	12	-845	1736	0	14	0.850
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-847.5	1741	5	26	0.070
m2	NDVI*Heterogeneity + Slope + Elevation + Habitat + Aspect + Distance from water + Distance from the road	21	-849.5	1742.9	6.9	23	0.026
	Blue Wildebeest *Connochaetes taurinus (obs. = 23,271)*						
m5	NDVI + Slope*Elevation + Heterogeneity + Aspect + Distance from water	14	-2360.5	4761	0	16	0.947
m2	NDVI*Heterogeneity + Slope + Elevation + Habitat + Aspect + Distance from water + Distance from the road	21	-2364.5	4766.9	5.9	23	0.049
m4	Slope + Elevation + Habitat + Heterogeneity + Aspect + Distance from water + Distance from the road	19	-2363.8	4771.7	10.7	22	0.005
	Buffalo *Syncerus caffer (obs. = 13,609)*						
m5	NDVI + Slope*Elevation + Heterogeneity + Aspect + Distance from water	14	-1826.5	3685.1	0	16	0.998
m6	NDVI + Slope + Elevation + Aspect + Distance from water*Distance from the road	14	-1833.2	3698.4	13.4	16	0.001
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-1823.9	3699.8	14.7	26	<0.001
	Eland *Taurotragus oryx (obs. = 14,023)*						
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-2530	5114.1	0	27	0.850
m7	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road	24	-2532.7	5117.5	3.4	26	0.150
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-2546.5	5132.9	18.9	20	<0.001
	Gemsbok *Oryx gazela (obs. = 6,868)*						
m11	NDVI + Slope*Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	18	-2106.5	4257	0	22	0.880
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-2109.6	4263.3	6.3	27	0.120
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-2116.7	4273.4	16.5	20	<0.001
	Red Hartebeest *Alcelaphus caama (obs. = 16,691)*						
m4	Slope + Elevation + Habitat + Heterogeneity + Aspect + Distance from water + Distance from the road	19	-3023.1	6092.2	0	21	0.680
m2	NDVI*Heterogeneity + Slope + Elevation + Habitat + Aspect + Distance from water + Distance from the road	21	-3025.8	6093.7	1.5	23	0.320
m6	NDVI + Slope + Elevation + Aspect + Distance from water*Distance from the road	14	-3050.6	6133.3	41.1	16	<0.001
	Impala *Aepyceros melampus (obs. =50,929)*						
m11	NDVI + Slope*Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	18	-2597.6	5239.2	0	22	0.898
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-2602.8	5245.6	6.4	20	0.037
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from water + Distance from the road	23	-2595.9	5245.7	6.5	27	0.035
	Sable *Hippotragus niger (obs. = 1,609)*						
m9	NDVI*Heterogeneity + Elevation + Habitat + Distance from water	10	-566.8	1177.7	0	22	0.740

m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-577.3	1180	2.3	12	0.200
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-574.8	1183.6	5.9	15	0.060
	Springbok *Antidorcas marsupialis (obs. = 10,168)*						
m11	NDVI + Slope*Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	18	-1685	3414	0	22	0.996
m2	NDVI*Heterogeneity + Slope + Elevation + Habitat + Aspect + Distance from water + Distance from the road	21	-1689.5	3425.1	11.1	23	0.004
m4	Slope + Elevation + Heterogeneity + Habitat + Aspect + Distance from water + Distance from the road	19	-1698	3438	23.9	21	<0.001
	Zebra *Equus burchelli (obs. = 34,156)*						
m1	NDVI + Elevation + Habitat*Heterogeneity + Aspect + Distance from the road + Distance from water	23	-3190.4	6430.7	0	25	0.935
m3	NDVI + Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	16	-3200.6	6437.3	6.6	18	0.035
m11	NDVI + Slope*Elevation + Habitat*Heterogeneity + Distance from water + Distance from the road	18	-3199.1	6438.3	7.6	20	0.021

= Model identification number; obs. = no. of individuals observed; k = number of parameters in the model; logLik = log Likelihood estimate; AICc = Akaike's information criterion corrected for small-sample bias; ΔAICc = difference between model AICc and that of the lowest model; w_i= model probability (Akaike weight); * = interaction with main effects; NDVI = normalized difference vegetation index; Habitat = Habitat type.

3.4.1. NDVI, heterogeneity and habitat types

Black wildebeest, blue wildebeest, gemsbok, and springbok were all drawn to greener vegetation, while this was not apparent for buffalo, Impala and zebra (Figure 3.3). The other species that showed weak and non-significant positive response to NDVI were blesbok, eland and sable (Table S3.1). Blue wildebeest, eland, impala and sable used areas with higher heterogeneity, while red hartebeest preferred areas with lower heterogeneity. Although weak ($p>0.05$), black wildebeest showed a preference for heterogeneity, interacting with "grassland" habitat type (log odds = 0.44 ± 0.28). Gemsbok showed a weak avoidance of highly heterogeneous habitat, while, buffalo, springbok and zebra showed a weak preference for heterogeneous habitat.

Blesbok preferred 'grassland' (log-odds = 0.60 ± 0.18) over other habitat types. Eland and springbok preferred 'open woodland' habitat type (log-odds = 0.42 ± 0.06 and 1.43 ± 0.39 respectively), while gemsbok preferred 'shrubland' and avoided 'barren land' (log-odds = 0.39 ± 0.07 and -19.26 ± 6.27 respectively). There was weak evidence (p>0.05) of zebra preferring “open woodland”, “shrubland” and “grassland” habitat to the others (log-odds = 0.68 ± 0.44, 0.88 ± 0.67 and 0.36 ± 0.24 respectively). Similarly, sable showed a weak preference (p>0.05) to “open woodland” (log-odds = 4.43 ± 1.88), “grassland” (log-odds = 3.45 ± 1.90) and “waterbodies” (log-odds = 4.27 ± 2.45). Red hartebeest showed a weak positive preference (p>0.05) for “grassland” (log-odds = 0.33 ± 0.12). Evidence of weak (p>0.05) preference for “grassland” habitat (log-odds = 0.99 ± 0.55) was also found for impala (Table S3.1).

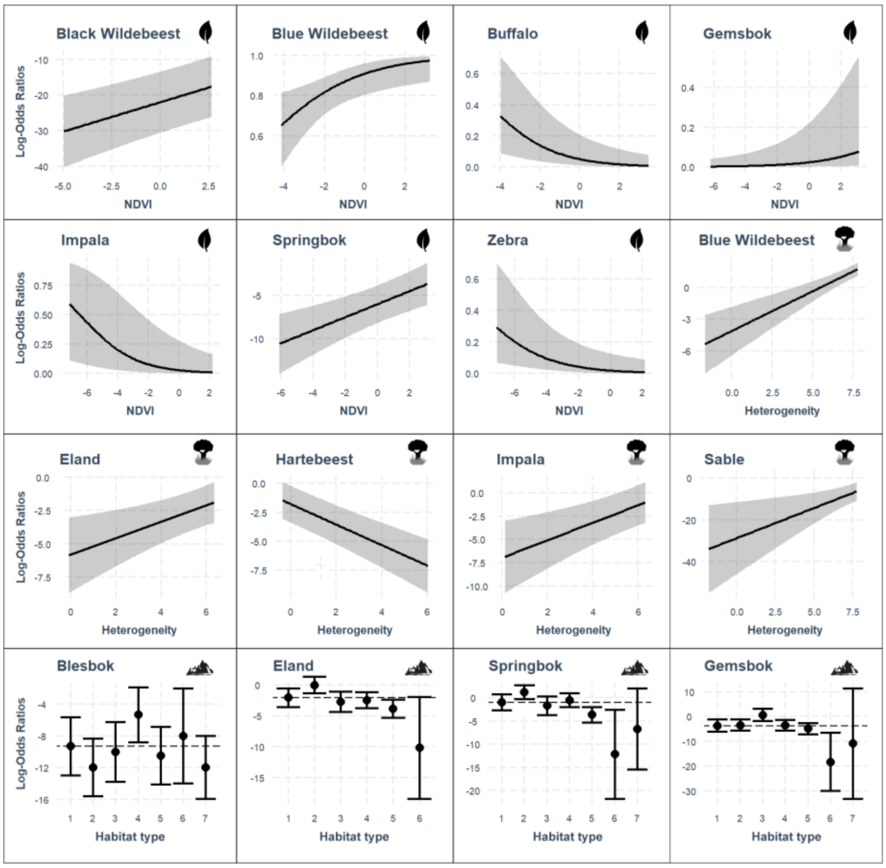


Figure 3.3: Predicted estimates (± 95% confidence interval) of ungulate habitat use in relation to the site variables: NDVI, heterogeneity and habitat type, across the study sites in the NW Province, South Africa. Only significant relations (<0.001) are graphed. The dashed line indicates the reference level ‘Closed woodland’. The covariates in each species-specific plot are represented by symbols: 🍃 = NDVI, 🌳 = Heterogeneity, ⛰ = Habitat Type. Habitat type codes: 1 = Closed woodland, 2 = Open woodland, 3 = Shrubland, 4 = Grassland, 5 = Water bodies (rivers, dams, wetlands) 6 = Barren Land, 7 = Cultivated areas

3.4.2. Elevation, slope and aspect

Eland, gemsbok and sable utilized higher elevations, while blesbok, buffalo and zebra favored lower elevations. Red hartebeest preferred lower elevations with reduced slopes. Impala and springbok showed a weak positive relation to elevation (p>0.05), while weak evidence of black- and blue wildebeest avoiding high elevation was found. Springbok preferred areas with lower slopes. There was weak evidence of blue wildebeest, impala and buffalo avoiding slopes. However, slopes had a weak positive influence on habitat use of gemsbok. Blue wildebeest, eland and zebra avoided the northwest aspect (log odds = -2.23 ± 0.91, -4.15 ± 1.42 and -2.81 ± 1.05 respectively), while buffalo and red hartebeest preferred areas with a southeast aspect (log odds = 0.87 ± 0.28 and 0.40 ± 0.27 respectively) (Figure 3.4; Table S3.1).

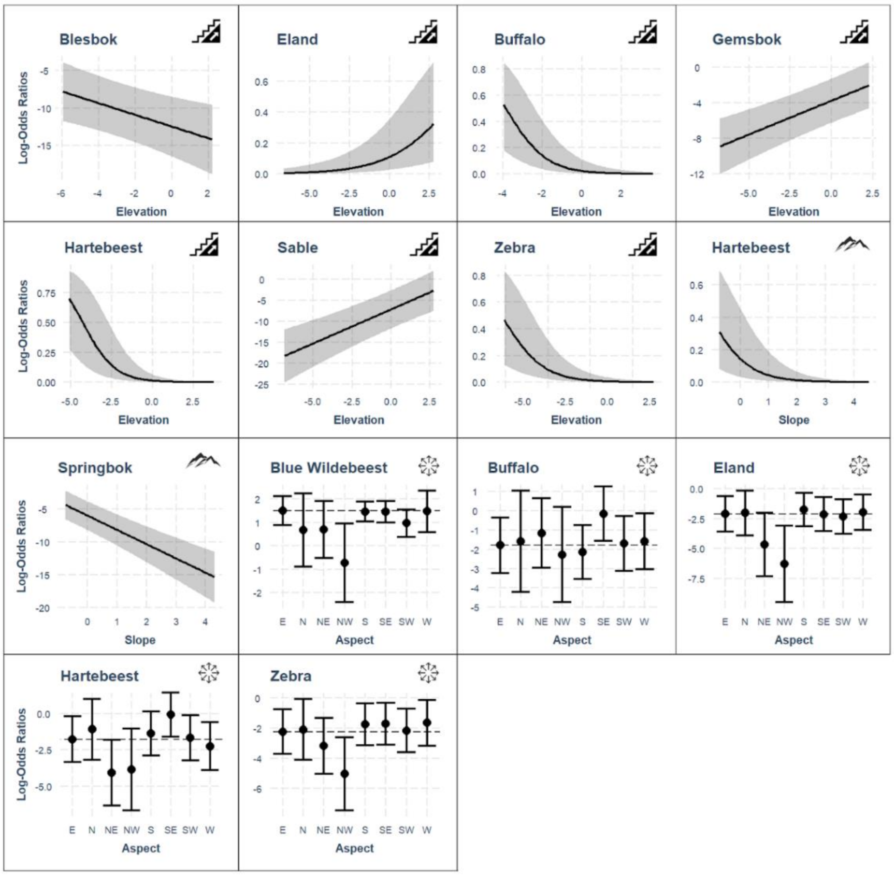


Figure 3.4: Predicted estimates (± 95% confidence interval) of ungulate habitat use in relation to the site variables: elevation, slope and aspect, across the study sites in the NW Province, South Africa. Only significant relations (<0.001) are graphed. The dashed line indicates the

reference level ‘East (ern)’ aspect. The covariates in each species-specific plot are represented by symbols: ▟= Elevation, ⛰ = Slope, ✥ = Aspect. Aspect codes: ‘E’= East, ‘N’=North, ‘NE’=Northeast, ‘NW’=Northwest, ‘S’=South, ‘SE’=Southeast, ‘SW’=Southwest, ‘W’=West.

3.4.3. Distance from surface water and roads

Both the species of wildebeest along with red hartebeest, impala, springbok and zebra preferred to stay close to the water sources. However, gemsbok distribution correlated negatively with distance from surface water (Figure 3.5). Buffalo and eland showed a weak negative relation with distance to surface water. Distance from roads appeared to be important in habitat selection, and influenced eight species: black wildebeest, blesbok, gemsbok and red hartebeest avoided roads while eland, springbok and zebra, preferred areas closer to the roads. Impala showed a weak preference ($p>0.05$) towards habitats near roads (Table S3.1).

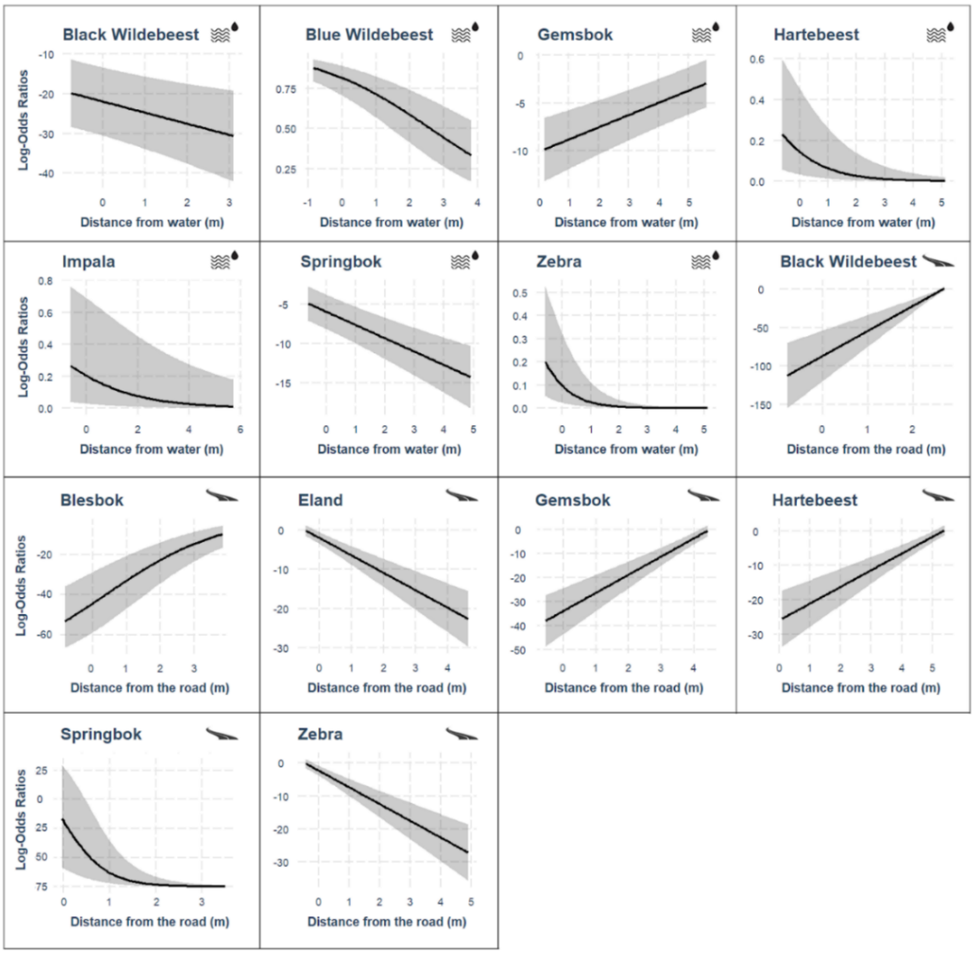


Figure 3.5: Predicted estimates (± 95% confidence interval) of ungulate habitat use in relation to the site variables: distance from water and distance from the road across the study sites in the NW Province, South Africa. Only significant relations (<0.001) are graphed. The covariates in each species-specific plot are represented by symbols: ≋ = Distance from water, ⟍ = Distance from road.

3.5. DISCUSSION

The findings of the study highlight important differences in habitat selection across the species spectrum. The importance of NDVI varied across the species spectrum and possibly reflects on low levels of productivity during the dormant season. Low-lying areas (bottomlands) where preferred by the majority of species, where forage abundance and greenness persisted for longer into the dormant season. Yet, there were exceptions, suggesting habitat varied sufficiently across the landscape, and feeding adaptations were sufficient across the species spectrum to allow the spatial segregation of species. Distance from surface water appears to be important in structuring spatial partitioning and our findings are broadly consistent with species-specific surface water dependence from literature. Proximity to roads appears to further structure habitat partitioning of species.

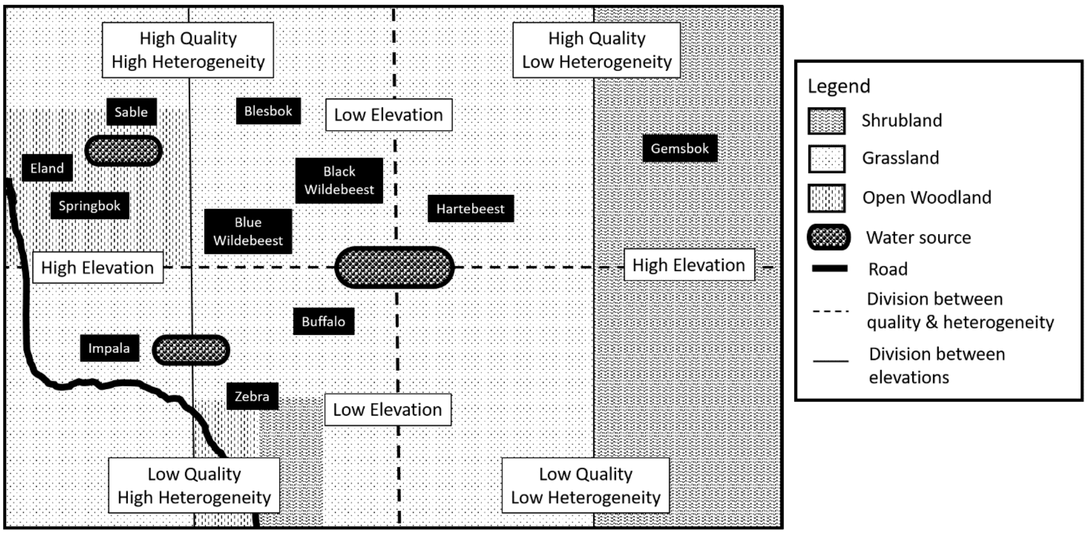


Figure 3.6: Graphical representation of habitat partitioning between ungulate species

In general, selective species favored green forage while mixed and bulk feeders traded off quality with quantity. Mixed feeders were found in habitats closer to roads and they partitioned habitats with other mixed feeders through difference in elevation and habitat type.

3.5.1. NDVI, heterogeneity and habitat types

Our results suggest the relative importance of greenness varied among species. It was identified as important for both wildebeest species, gemsbok and springbok (Figure 3.3), a result consistent with earlier studies where short, green grasses i.e., grazing lawns are preferred by black wildebeest (Cromsigt & Olff, 2006; Codron & Brink, 2007; Seydack et al., 2012; Deliberato, 2017; Mariotti et al., 2020b; McNaughton, 1984; Skead, 1980; Skinner & Chimimba, 2005; Martin et al., 2015). Furthermore, even though the relation was not significant (p>0.05), the only habitat type that black wildebeest preferred according to the best-fit model was “grassland” habitat, with heterogeneity as an interaction term. Blue wildebeest have a more flexible diet by comparison, despite being morphologically similar (Deliberato, 2017; Mariotti et al., 2020b). They similarly preferred greener vegetation, and heterogeneous environments. However, in this study, heterogeneity was calculated from NDVI values at a 250 m scale of resolution, and NDVI values depend on both the biomass of the vegetation as well as the degree of greenness. Therefore, pixels with greater tree cover have higher values than pixels with more grass cover (Pettorelli et al., 2005; van Bommel et al., 2006; Mariotti et al., 2020a). This could be explained by the greater dependence on shade by blue wildebeest (Lease et al., 2014). Blesbok favored grassland habitat with weak evidence of grass greenness and heterogeneity structuring their distribution. Similar to blue wildebeest, blesbok are shade dependent, which appears to be important for its survival and reproduction (Furstenburg, 2016b). Red hartebeest prefers habitat with limited disturbance through foraging activities from con-specifics i.e., medium to tall grassland (Venter & Child, 2016) and our results are consistent with these notions. NDVI was not identified as important for buffalo and zebra, and is consistent with their bulk feeding strategy (Seydack et al., 2012; Mariotti et al., 2020a; Mariotti et al., 2020b) requiring trade-offs between forage quantity and quality. Springbok and eland preferred open woodland habitats with forage of high NDVI and heterogeneity, a finding consistent with earlier studies (Jarman, 1974; Cerling et al., 2003; Codron et al., 2005; Wallington et al., 2007; Hein et al., 2008; Furstenburg, 2012), especially in the late dry season (D’Ammando et al., 2015) when browse becomes an important component in their diet. Consistent with literature, NDVI was not identified as important in impala distribution. Space use correlates with heterogeneity though, which similarly aligns with their status as mixed feeders

(Jarman, 1974; Dunham, 1982) and ability to switch to lower quality mixed diet during the dry season (Hunninck et al., 2020). Sable preferred heterogeneous open woodlands, grasslands and waterbodies in the study sites with greener forage, as predicted, which is consistent with earlier studies (Estes, 1991; Skinner & Chimimba, 2005; Magome et al., 2008). Gemsbok, contrastingly, selected for high NDVI, preferring shrubland habitat, while their occurrence negatively correlated with heterogeneity. This finding is not consistence with earlier studies (Relton, 2016; Lehmann et al., 2020). This may be due to the opportunistic foraging strategies by gemsbok (Lehmann et al., 2015).

3.5.2. Elevation, slope and aspect

Bottomlands generally have higher forage biomass than areas higher up the catena during the dormant season (see Wilmshurst et al., 1999). Higher biomass in turn means a higher proportion of the grass layer consists of fiber (Bell, 1971) assuming grazing lawns have not established. Considering the conservative management policies maintained in North West Parks, the finding that species most dependent on forage quantity (buffalo and zebra) prefer bottom lands during the dry season is not surprising and in agreement with my hypothesis. The finding is consistent with those of Bell (1971) and Wilmshurst et al. (1999). There was weak evidence of both species of wildebeest preferring low-lying areas as expected. Blesbok also preferred grazing lawns as it an extremely selective grazer, and avoid slopes and rocky terrain (see Furstenburg, 2016b). Earlier studies indicate red hartebeest prefer lower elevations and plains near mountain slopes with tall grass communities (see Mariotti et al., 2020a; Furstenburg, 2009). Gemsbok distribution, contrastingly, correlated with elevation and slope, suggesting a competition avoidance strategy. Gemsbok switches between suitable habitats, in response to temporal variations in resource availability, and are not slope or elevation sensitive (Lehmann et al., 2020; Furstenburg, 2022). The current finding therefore further suggests their foraging strategy involves reduced dependence on the grass layer during the dormant season (see Selebatso et al., 2018). Sable preferred higher elevations, possibly to avoid competition from conspecifics. However, previous studies have also reported sable avoiding high fiber content in bottomland foliage (Bell, 1971; 1984; le Roux, 2010). Different elevations support different forage types (Zhang et al., 2021), which allows mixed feeders to adaptively forage along elevation gradients (Furstenburg, 2012). Therefore, preference for higher elevations by eland further reflect on a reduced dependence on grass during the dormant season. Springbok avoided steep slopes in the current study, which contrasts with earlier studies (Furstenburg, 2023). A plausible explanation is that slope aspect has an overriding influence on greenness (Kumari et al., 2020) and potentially increase thermoregulatory costs in ungulates. Generally, across arid regions, the eastern and western slopes get equal sunlight but the afternoon sun in the western aspect makes it much warmer than the eastern one. Similarly, during the late dry season in the southern hemisphere, the sun’s east-west trajectory occurs through the northern aspect and thus the southern aspect is much cooler (Obiwulu et al., 2022). Therefore, as predicted buffalo and red hartebeest distribution were concentrated around the southeast aspect of the NW Province. Blue wildebeest, eland and zebra similarly avoided the northwestern aspect.

3.5.3. Distance from surface water and roads

As predicted, black wildebeest, blue wildebeest, red hartebeest, impala, springbok and zebra preferred areas close to surface water. Previous studies have suggested that proximity to water sources increase predation risk (De Boer et al., 2010; Louw et al., 2022). However, most of the study sites in the current study are devoid of large predators (Nel, 2018) which could explain the current findings. Results for springbok were rather surprising considering their low water requirements (Nagy & Knight, 1994). However, a plausible explanation is their preference for shorter grass swards that are commonly found near surface water (see Smit et al., 2007). Gemsbok are well adapted for arid environments (Smithers, 1983; Harris et al., 2015; Cain et al., 2017) and have developed a number of physiological and behavioral adaptations, voluntarily raising body temperature, slowing metabolic rate to reduce frequent water requirement and selective foraging (Lehmann et al., 2013; 2015; Harris et al., 2015; Cain et al., 2017; Furstenburg, 2022). This explains their negative association with surface water. Eland distribution weakly correlated with surface water proximity, which was rather surprising. Intake of dietary water compensates for water loss but has a seasonal component (see Kihwele et al., 2020). The contradictory findings about surface water and eland space use in earlier studies (see Western, 1975; Woodall & Skinner, 1993; Taylor, 1968; Kihwele et al., 2020) perhaps reflect on seasonal shifts in water dependence of eland, which in turn depends on the site-specific plant phenology.

We predicted all species to avoid roads due to human presence or traffic (Leblond et al., 2013; Gaynor et al., 2018). Our results suggest mixed feeders (eland, springbok, impala and zebra) favor habitat closer to roads, while selective feeders (wildebeest, blesbok, gemsbok, sable and red hartebeest) preferred areas away from roads. Water runoff from roads may generate greener vegetation along the roadside attracting herbivores towards the road (Trombulak & Frissell, 2000; Tsalyuk et al., 2019) but this depends on some early precipitation during the late dry season. We could find no plausible explanation for this disparity between mixed feeders and selective grazers. The results might well be spurious.

3.6. CONCLUSION

The study confirms that ungulate space utilization is structured by multiple environmental factors. The results of this study broadly correspond with current knowledge of the biology of the spectrum of species considered. The reader is reminded that census data were collected during the dormant season and results reflect on resource limitations most likely to affect resource partition between species. Even though high-quality grass and water source proximity should act as a key resource for attracting large herbivores (Parrini & Owen-Smith, 2010; Fynn et al., 2015), other factors sometimes play a bigger role in species distribution across a landscape. Although some species in the current study shared common behavioral attributes, the relative importance of environmental factors on their distribution pattern varied. While the same best model largely applies to most species, the relative importance of factors differed. As predicted, NDVI was selected as a significant predictor for habitat use in the best model of species foraging selectively. Species more dependent on forage biomass relied on mixed, low-quality forage, and accordingly selected areas with lower NDVI. Similarly, heterogeneity significantly influenced habitat preference of species commonly found in large herds, which is in accordance with earlier research (Murray & Illius, 1996). As predicted, red hartebeest occurrence negatively correlated with heterogeneity. Gemsbok, a species well adapted to drier environments (Lehmann et al., 2013), was the only species where occurrence negatively correlated with distance from water. Considering the study sites are situated in an arid region, the significance of slope aspect to ungulate distributions is most interesting. Further studies are required to determine if food or thermoregulatory costs ultimately drives avoidance of northwest aspects.

Habitat selection is a hierarchical process and predominantly occur at landscape scales (see Wilmshurst et al., 2000). The relation between habitat selection and population density is well established (Rosenzweig, 1991). Spatial distribution in conservatively managed populations is reflects on the extent of competition, with intra-specific competition promoting dispersal, and interspecific competition promoting spatial segregation (and potentially reduced space use). Interpreting the effects of various variables are challenging and can seldom be evaluated in isolation and can also be obscured by confounding effects. For example, habitat comprised of trees and grass, complicates NDVI estimation, while less so when consisting of a grass layer only. Ultimately, the current results suggest a combination of ecological variables determines ungulate space use in the North West Province, most notably NDVI and slope. Predation risk and competition from conspecifics were not considered in the current study and should be given due consideration in similar studies where large predators occur.

3.7. REFERENCES

Adler, P. B., Seabloom, E. W., Borer, E. T., et al. (2011). Productivity is a poor predictor of plant species richness. *Science*, *333*(6050). https://doi.org/10.1126/science.1204498

Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength: Of fire-grazing interaction. *Ecology and Evolution*, *1*(2). https://doi.org/10.1002/ece3.12

Anderson, D. R. (2008). Model based inference in the life sciences: A primer on evidence. In *Model Based Inference in the Life Sciences: A Primer on Evidence*. https://doi.org/10.1007/978-0-387-74075-1

Anderson, T. M., Dong, Y., & Mcnaughton, S. J. (2006). Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture and grazing. *Journal of Ecology*, *94*(6). https://doi.org/10.1111/j.1365-2745.2006.01148.x

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, *49*(5). https://doi.org/10.2307/4002919

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823. https://cran.r-project.org/package=lme4.

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American. Vol. 225: 86–93.

Bell, R. H. V. (1984). Majete game reserve: Report of an ulendo and suggestions for management and utilisation. Department of National Parks and Wildlife.

Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., & Baxter, R. (2008). Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, *216*(1). https://doi.org/10.1016/j.ecolmodel.2008.04.010

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: A practical Information-theoretic Approach (2nd ed). Library of Congress Cataloging-in-Publication Data. In *Ecological Modelling* (Vol. 172).

Burrough, P.A., & McDonnell, R. (1998). Principles of geographical information systems. Oxford University Press, New York: 190.

Cain, J. W., Krausman, P. R., Rosenstock, S. S., & Turner, J. C. (2006). Mechanisms of Thermoregulation and Water Balance in Desert Ungulates. *Wildlife Society Bulletin*, *34*(3). https://doi.org/10.2193/0091-7648(2006)34[570:motawb]2.0.co;2

Cain III, J. W., Avery, M. M, Caldwell, C. A., Abott, L. B., & Holechek, J. L. (2017). Diet composition, quality and overlap of sympatric American pronghorn and gemsbok. *Wildl. Biol.*, *2017(1*). https://doi.org/10.2981/wlb.00296

Cerling, T. E., Harris, J. M., & Passey, B. H. (2003). Diets of East African Bovidae based on stable isotope analysis. J. Mammal. Vol. 84: 456–470.

Chase, M., Frederick, H., Mukeka, J., & Ngene, S. (2015). Dry season fixed-wing aerial survey of elephants and other large mammals in the Tsavo and Amboseli Ecosystems, Kenya. Report. Elephants without Borders, Kasane, Botswana, and Kenya Wildlife Service, Nairobi, Kenya.

Chen, S., Wang, W., Xu, W., et al. (2018). Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(16). https://doi.org/10.1073/pnas.1700298114

Clutton-Brock, T.H., Guinness, F.E., & Albon, S. (1992). Red Deer: Behaviour and Ecology of Two Sexes. University of Chicago Press, Chicago.

Codron, D., & Brink, J. S. (2007). Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. *European Journal of Wildlife Research*, *53*(2). https://doi.org/10.1007/s10344-006-0070-2

Codron, D., Codron, J., Lee-Thorp, J. A., Sponheimer, M., & de Ruiter, D. (2005). Animal diets in the Waterberg based on stable isotopic composition of faeces. *African Journal of Wildlife Research*, *35*(1).

Cromsigt, J. P. G. M., & Olff, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. *Ecology*, *87*(6). https://doi.org/10.1890/0012-9658(2006)87[1532:RPASGM]2.0.CO;2

D'Ammando, G., Parrini, F., Attorre, F., & Boitani, L. (2015). Observations on dry season grazing by eland in a Magaliesberg Nature Reserve, South Africa. *African Journal of Ecology*, *53*(1). https://doi.org/10.1111/aje.12164

de Boer, W. F., Vis, M. J. P., De Knegt, H. J.,et al. (2010). Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy*, *91*(5). https://doi.org/10.1644/09-MAMM-A-392.1

Deliberato, H. G. (2017). Resources overlap and the distribution of grazer assemblages at Telperion and Ezemvelo Nature Reserves. Master's thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa.

Duncan, C., Chauvenet, A. L. M., McRae, L. M., & Pettorelli, N. (2012). Predicting the Future Impact of Droughts on Ungulate Populations in Arid and Semi-Arid Environments. *PLoS ONE*, *7*(12). https://doi.org/10.1371/journal.pone.0051490

Dunham, K. (1982). The foraging behaviour of impala *Aepyceros melampus*. *Wildl. Res. Tydskr. Natuurnav*, *12*(12).

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, *22*(4). https://doi.org/10.1111/j.1365-2028.1984.tb00700.x

Environmental Systems Research Institute (ESRI), (2020). ArcGIS Desktop 10.8 Geostatistical Analyst.

Estes, R. D. (1991). The behaviour guide to African mammals, including hoofed mammals, carnivores, primates. – Univ. of California Press.

Feldhamer, G. A., Gates, J. E., Harman, D. M., Loranger, A. J., & Dixon, K. R. (1986). Effects of Interstate Highway Fencing on White-Tailed Deer Activity. *The Journal of Wildlife Management*, *50*(3). https://doi.org/10.2307/3801112

Frank, D. A., McNaughton, S. J., & Tracy, B. F. (1998). The ecology of the earth’s grazing ecosystems: Profound functional similarities exist between the Serengeti and Yellowstone. *BioScience*, *48*(7). https://doi.org/10.2307/1313313

Furstenburg, D. (2016b). Blesbok & Bontebok Damaliscus pygargus Management. In: Eds. Pamela Oberem, The New Game Rancher. BRIZA Publisher, Pretoria. 196-204. ISBN 978-1-920217-62-4.

Furstenburg, D. (2016a). Eland (*Tragelaphus oryx*) Management. In: Eds. Pamela Oberem, The New Game Rancher. BRIZA Publisher, Pretoria. p 173-179. ISBN 978-1-920217-62-4

Furstenburg, D. (2022). Wildlife & Game southern Africa PART 5 - The Gemsbok as a Species Oryx *Gazella gazella*. Veteran-SA: 17-25

Furstenburg, D. (2009). Focus on the red hartebeest (*Alcelaphus buselaphus caama*). S A Hunter 05028: 60-64

Furstenburg, D. (2012). Eland facts (*Tragelaphus oryx*). S A Hunter 08067: 32-34.

Furstenburg, D. (2023). Wildlife & Game southern Africa PART 10 - The Springbok as a Species *Antidorcas marsupialis* (Zimmerman, 1780). Veteran_SA: 18-26.

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, *23*(4). https://doi.org/10.1007/s11273-015-9430-6

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2). https://doi.org/10.1016/S0169-5347(97)01237-8

García-Marmolejo, G., Chapa-Vargas, L., Huber-Sannwald, E., Weber, M., Rosas-Rosas, O. C., & Martínez-Calderas, J. (2013). Potential distributional patterns of three wild ungulate species in a fragmented tropical region of northeastern Mexico. *Tropical Conservation Science*, *6*(4). https://doi.org/10.1177/194008291300600407

Gaynor, K. M., Branco, P. S., Long, R. A., Gonçalves, D. D., Granli, P. K., & Poole, J. H. (2018). Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology*, *56*(4). https://doi.org/10.1111/aje.12552

Goslar, A., Prosch, L., Ingle, S., Benedek, F., Hudson, K., Mampye, A., Tshivhase, N., & Lees, Z. (2008). North West Province Environment Outlook. A report on the state of the environment. Submitted to North West Department of Agriculture, Conservation and Environment.

Grace, J. B., Anderson, T. M., Seabloom, E. W., et al. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, *529*(7586). https://doi.org/10.1038/nature16524

Harris, G., Sanderson, J. G., Erz, J., Lehnen, S. E., & Butler, M. J. (2015). Weather and prey predict mammals' visitation to water. *PLoS ONE*, *10*(11). https://doi.org/10.1371/journal.pone.0141355

Hayward, M. W., & Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? In *Biological Conservation* (Vol. 142, Issue 1). https://doi.org/10.1016/j.biocon.2008.09.022

Hein, K. A., Jaeger, S. R., Tom Carr, B., & Delahunty, C. M. (2008). Comparison of five common acceptance and preference methods. *Food Quality and Preference*, *19*(7). https://doi.org/10.1016/j.foodqual.2008.06.001

Hennenberg, K. J., & Bruelheide, H. (2003). Ecological investigations on the northern distribution range of Hippocrepis comosa L. in Germany. *Plant Ecology*, *166*(2). https://doi.org/10.1023/A:1023280109225

Holt, R. D. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist*, *124*(3). https://doi.org/10.1086/284280

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. In *Trends in Ecology and Evolution* (Vol. 25, Issue 2). https://doi.org/10.1016/j.tree.2009.08.001

Hunninck, L., May, R., Jackson, C. R., Palme, R., Røskaft, E., & Sheriff, M. J. (2020). Consequences of climate-induced vegetation changes exceed those of human disturbance for wild impala in the Serengeti ecosystem. *Conservation Physiology*, *8*(1). https://doi.org/10.1093/conphys/coz117

Illius, A. W. (1997). Physiological adaptation in savanna ungulates. *Proceedings of the Nutrition Society*, *56*(3). https://doi.org/10.1079/pns19970108

Janis, C. (2008). *An Evolutionary History of Browsing and Grazing Ungulates*. https://doi.org/10.1007/978-3-540-72422-3_2

Jarman, P. J. (1974). The Social Organisation of Antelope in Relation to Their Ecology. *Behaviour*, *48*(1–4). https://doi.org/10.1163/156853974X00345

Keuroghlian, A., & Eaton, D. P. (2008). Importance of rare habitats and riparian zones in a tropical forest fragment: Preferential use by *Tayassu pecari*, a wide-ranging frugivore. *Journal of Zoology*, *275*(3). https://doi.org/10.1111/j.1469-7998.2008.00440.x

Kiffner, C., & Lee, D. E. (2019). Population Dynamics of Browsing and Grazing Ungulates in the Anthropocene. https://doi.org/10.1007/978-3-030-25865-8_6

Kihwele, E. S., Mchomvu, V., Owen-Smith, N., Hetem, R. S., Hutchinson, M. C., Potter, A. B., Olff, H., & Veldhuis, M. P. (2020). Quantifying water requirements of African ungulates through a combination of functional traits. *Ecological Monographs*, *90*(2). https://doi.org/10.1002/ecm.1404

Kröger, R., & Rogers, K. H. (2005). Roan (Hippotragus equinus) population decline in Kruger National Park, South Africa: Influence of a wetland boundary. *European Journal of Wildlife Research*, *51*(1). https://doi.org/10.1007/s10344-004-0070-z

Kruger, A. C., & Nxumalo, M. P. (2017). Historical rainfall trends in South Africa: 1921–2015. *Water SA*, *43*(2). https://doi.org/10.4314/wsa.v43i2.12

Kumari, N., Saco, P. M., Rodriguez, J. F., Johnstone, S. A., Srivastava, A., Chun, K. P., & Yetemen, O. (2020). The Grass Is Not Always Greener on the Other Side: Seasonal Reversal of Vegetation Greenness in Aspect-Driven Semiarid Ecosystems. *Geophysical Research Letters*, *47*(15). https://doi.org/10.1029/2020GL088918

le Roux E. (2010). Habitat and forage dependency of sable antelope (*Hippotragus niger*) in the pretorius kop region of the Kruger National Park (Master’s Degree Thesis). University of the Witwatersrand, Johannesburg, South Africa.

Lease, H. M., Murray, I. W., Fuller, A., & Hetem, R. S. (2014). Black wildebeest seek shade less and use solar orientation behaviour more than do blue wildebeest. *Journal of Thermal Biology*, *45*. https://doi.org/10.1016/j.jtherbio.2014.08.008

Leblond, M., Dussault, C., & Ouellet, J. P. (2013). Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology*, *289*(1). https://doi.org/10.1111/j.1469-7998.2012.00959.x

Lee, T. D., Barrett, J. P., & Hartman, B. (2005). Elevation, substrate, and the potential for climate-induced tree migration in the White Mountains, New Hampshire, USA. *Forest Ecology and Management*, *212*(1–3). https://doi.org/10.1016/j.foreco.2005.03.007

Lehmann, D., Mfune, J. K. E., Gewers, E., Brain, C., & Voigt, C. C. (2015). Individual variation of isotopic niches in grazing and browsing desert ungulates. *Oecologia*, *179*(1). https://doi.org/10.1007/s00442-015-3335-1

Lehmann, D., Mfune, J. K. E., Gewers, E., Cloete, J., Aschenborn, O. H. K., Mbomboro, L., Kasaona, S., Brain, C., & Voigt, C. C. (2020). Spatiotemporal responses of a desert dwelling ungulate to increasing aridity in North-eastern

Namibia. *Journal of Arid Environments*, *179*. https://doi.org/10.1016/j.jaridenv.2020.104193

Lehmann, D., Mfune, J. K. E., Gewers, E., Cloete, J., Brain, C., & Voigt, C. C. (2013). Dietary Plasticity of Generalist and Specialist Ungulates in the Namibian Desert: A Stable Isotopes Approach. *PLoS ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0072190

Licona, M., Mccleery, R., Collier, B., Brightsmith, D. J., & Lopez, R. (2011). Using ungulate occurrence to evaluate community-based conservation within a biosphere reserve model. *Animal Conservation*, *14*(2). https://doi.org/10.1111/j.1469-1795.2010.00416.x

Long, J. A., & Long, M. J. A. (2017). Package ‘jtools’. https://cran.r-project.org/package=jtools. [Accessed 18 March 2021].

Louw, C. J., Ferreira, S. M., & Marshal, J. P. (2022). Water dependence structures predation risk for large herbivores in insular protected areas. *Mammalian Biology*, *102*(5–6). https://doi.org/10.1007/s42991-022-00278-8

Macandza, V. A., Owen-Smith, N., & Cain, I. W. (2012). Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *Journal of Zoology*, *287*(3). https://doi.org/10.1111/j.1469-7998.2012.00900.x

Macandza, V. A., Owen-Smith, N., & Cross, P. C. (2004). Forage selection by African buffalo in the late dry season in two landscapes. *African Journal of Wildlife Research*, *34*(2).

Maffei, L., Cuéllar, E., & Noss, A. J. (2002). Uso de Trampas-Cámara para la Evaluación de Mamíferos en el Ecotono Chaco-Chiquitanía. *Revista Boliviana de Ecología y Conservación Ambiental*, *11*.

Maffei, L., & Taber, A. B. (2003). Area de acción de *Mazama americana* (Cervidae) en un bosque seco de Bolivia. *Ecología En Bolivia*, *38*(2).

Magome, H., Cain, J. W., Owen-Smith, N., & Henley, S. R. (2008). Forage selection of sable antelope in pilanesberg game reserve, South Africa. *African Journal of Wildlife Research*, *38*(1). https://doi.org/10.3957/0379-4369-38.1.35

Maloiy, G. M. O., Rugangazi, B. M., & Rowe, M. F. (2009). Energy expenditure during level locomotion in large desert ungulates: The one-humped camel and the domestic donkey. *Journal of Zoology*, *277*(3). https://doi.org/10.1111/j.1469-7998.2008.00535.x

Mariotti, E., Parrini, F., Louw, C. J., & Marshal, J. P. (2020a). Habitat Use by a Large Herbivore Guild in a Fenced South African Protected Area. *African Journal of Wildlife Research*, *50*(1). https://doi.org/10.3957/056.050.0086

Mariotti, E., Parrini, F., Louw, C. J., & Marshal, J. P. (2020b). What grass characteristics drive large herbivore feeding patch selection? A case study from a South African grassland protected area. *African Journal of Range and Forage Science*. https://doi.org/10.2989/10220119.2020.1768146

Marshal, J. P., Rankin, C., Nel, H. P., & Parrini, F. (2016). Drivers of population dynamics in sable antelope: forage, habitat or competition? *European Journal of Wildlife Research*, *62*(5). https://doi.org/10.1007/s10344-016-1027-8

Martin, J., Benhamou, S., Yoganand, K., & Owen-Smith, N. (2015). Coping with spatial heterogeneity and temporal variability in resources and risks: Adaptive movement behaviour by a large grazing herbivore. *PLoS ONE*, *10*(2). https://doi.org/10.1371/journal.pone.0118461

Mazerolle, M. J., & Mazerolle, M. M. J. (2017). Package ‘AICcmodavg’. https://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf.

McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, *124*(6). https://doi.org/10.1086/284321

Mendoza, M., Janis, C. M., & Palmqvist, P. (2002). Characterizing complex craniodental patterns related to feeding behaviour in ungulates: A multivariate approach. *Journal of Zoology*, *258*(2). https://doi.org/10.1017/S0952836902001346

Milner, J. M., Elston, D. A., & Albon, S. D. (1999). Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology*, *68*(6). https://doi.org/10.1046/j.1365-2656.1999.00366.x

Mishra, C., Van Wieren, S. E., Ketner, P., Ignas M. A. Heitkönig, & Herbert H. T. Prins. (2004). Competition between Domestic Livestock and Wild Bharal *Pseudois* *nayaur* in the Indian Trans-Himalaya. Journal of Applied Ecology, 41(2), 344–354. http://www.jstor.org/stable/3505966

Murray, M. G. & Illius, A. W. (1996). Multispecies grazing in the Serengeti. [In: The Ecology and Management of Grazing. J. Hodgson and A. W. Illius, eds]. CAB International, Wallingford: 247–272.

Nagy, K. A., & Knight, M. H. (1994). Energy, water, and food use by springbok antelope (*Antidorcas marsupialis*) in the Kalahari Desert. *Journal of Mammalogy*, *75*(4). https://doi.org/10.2307/1382468

Nel, H. P. (2018). Population estimates for large herbivores and predators in protected areas in the North West Parks Board. Unpublished Technical Report.

Obiwulu, A. U., Erusiafe, N., Olopade, M. A., & Nwokolo, S. C. (2022). Modeling and estimation of the optimal tilt angle, maximum incident solar radiation, and global radiation index of the photovoltaic system. *Heliyon*, *8*(6). https://doi.org/10.1016/j.heliyon.2022.e09598

Odadi, W. O., Jain, M., Van Wieren, S. E., Prins, H. H. T., & Rubenstein, D. I. (2011). Facilitation between bovids and equids on an African savanna. *Evolutionary Ecology Research*, *13*(3).

Ogutu, J. O., Reid, R. S., Piepho, H. P., Hobbs, N. T., Rainy, M. E., Kruska, R. L., Worden, J. S., & Nyabenge, M. (2014). Large herbivore responses to surface water and land use in an East African savanna: Implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation*, *23*(3). https://doi.org/10.1007/s10531-013-0617-y

Owen-Smith, N., Le Roux, E., & Macandza, V. (2013). Are relatively rare antelope narrowly selective feeders? A sable antelope and zebra comparison. *Journal of Zoology*, *291*(3). https://doi.org/10.1111/jzo.12058

Owen-Smith, R. N. (2002). Adaptive Herbivore Ecology. In *Adaptive Herbivore Ecology*. https://doi.org/10.1017/cbo9780511525605

Parrini, F., & Owen-Smith, N. (2010). The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology*, *48*(2). https://doi.org/10.1111/j.1365-2028.2009.01143.x

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. In *Trends in Ecology and Evolution* (Vol. 20, Issue 9). https://doi.org/10.1016/j.tree.2005.05.011

Power, R. J., Van Straaten, A., Schaller, R., Mooke, M., Boshoff, T., & Nel, H. P. (2019). An inventory of mammals of the North West Province. South Africa. *Annals of the Ditsong National Museum of Natural History*, *8*.

Prins, H. H. T., & Olff, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In *Dynamics of tropical communities*.

QGIS Development Team, (2020). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team, (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, *84*(8). https://doi.org/10.1890/01-0625

Relton, C. E. (2016). Movement ecology of gemsbok in the central Kalahari in response to vegetation greenness as assessed by satellite imagery. Master's thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa.

Rivero, K., Rumiz, D. I., & Taber, A. B. (2005). Differential habitat use by two sympatric brocket deer species (*Mazama americana* and *M. gouazoubira*) in a seasonal Chiquitano forest of Bolivia. *Mammalia*, *69*(2).

Rosenzweig, M. L. (1991). Habitat Selection and Population Interactions: The Search for Mechanism. The American Naturalist, Vol. 137. Supplement: Habitat Selection. https://www.jstor.org/stable/2462286

Rooney, T. P. (2001). Deer impacts on forest ecosystems: A North American perspective. *Forestry*, *74*(3). https://doi.org/10.1093/forestry/74.3.201

Selebatso, M., Maude, G., & Fynn, R. W. S. (2018). Adaptive Foraging of Sympatric Ungulates in the Central Kalahari Game Reserve, Botswana. *African Journal of Wildlife Research*, *48*(2). https://doi.org/10.3957/056.048.023005

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, *37*(11). https://doi.org/10.2307/1310545

Seydack, A. H., Grant, C. C., Smit, I. P., Vermeulen, W. J., Baard, J., & Zambatis, N. (2012). Large herbivore population performance and climate in a South African semi-arid savanna. *Koedoe*, *54*(1). https://doi.org/10.4102/koedoe.v54i1.1047

Skarpe, C. (1991). Impact of grazing in savanna ecosystems. *Ambio*, *20*(8).

Skead, C. J. (1980). Historical mammal incidence in the Cape Province, 1. The Western and Northern Cape. In *Order* (Vol. 1).

Skinner, J. D., & Chimimba, C. T. (2005). The Mammals of the Southern African Sub-region. In *The Mammals of the Southern African Sub-region*. https://doi.org/10.1017/cbo9781107340992

Smit, I. P. J., Grant, C. C., & Devereux, B. J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, *136*(1). https://doi.org/10.1016/j.biocon.2006.11.009

Smithers, R. H. N. (1983). The Mammals of the Southern African Subregion. Pretoria, South Africa: University of Pretoria Press.

Solomon, D. S., & Leak, W. B. (1994). Migration of tree species in New England based on elevational and regional analysis, in Northeastern Forest Experiment Station. Research Paper NE-688. U.S. Department of Agriculture, Forest Service

Spickett, A. M., Heyne, I. H., & Williams, R. (2011). Survey of the livestock ticks of the North West province, South Africa. *The Onderstepoort Journal of Veterinary Research*, *78*(1). https://doi.org/10.4102/ojvr.v78i1.305

Stilwell, P., O'Brien, S., Hesse, E., Lowe, C., Gardner, A., & Buckling, A. (2020). Resource heterogeneity and the evolution of public goods cooperation. In *Evolution Letters* (Vol. 4, Issue 2). https://doi.org/10.1002/evl3.158

Taylor, C. R. (1968). The minimum water requirements of some East African bovids. Symposium of the Zoological Society of London 21: 195–206.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M., & Slotow, R. (2011). Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology*, *92*(2). https://doi.org/10.1890/10-0126.1

Treydte, A. C., Baumgartner, S., Heitkönig, I. M. A., Grant, C. C., & Getz, W. M. (2013). Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African savanna. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082831

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, *14*(1). https://doi.org/10.1046/j.1523-1739.2000.99084.x

Tsalyuk, M., Kilian, W., Reineking, B., & Getz, W. M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. *Ecological Monographs*, *89*(2). https://doi.org/10.1002/ecm.1348

Tuljapurkar, S., & Caswell, H. (1997). Structured-Population Models in Marine, Terrestrial, and Freshwater System, Chapman and Hall.

van Bommel, F. P. J., Heitkönig, I. M. A., Epema, G. F., Ringrose, S., Bonyongo, C., & Veenendaal, E. M. (2006). Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana. *Journal of Tropical Ecology*, *22*(1). https://doi.org/10.1017/S0266467405002932

van Opheusden, B., Acerbi, L., & Ma, W. J. (2020). Unbiased and efficient log-likelihood estimation with inverse binomial sampling. *PLoS Computational Biology*, *16*(12 December). https://doi.org/10.1371/journal.pcbi.1008483

Venter, J., & Child, M. F. (2016). A conservation assessment of *Alcelaphus buselaphus caama*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Verdin, K. L. (2017). Hydrologic Derivatives for Modeling and Applications (HDMA) database: U.S. Geological Survey data release, https://doi.org/10.5066/F7S180ZP.

Voeten, M. M., & Prins, H. H. T. (1999). Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia*, *120*(2).

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G. P., & Parmenter, R. (1999). The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, *30*. https://doi.org/10.1146/annurev.ecolsys.30.1.257

Wallington, B. P., McKechnie, A. E., Owen-Smith, N., & Woodborne, S. (2007). Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the suikerbosrand nature reserve. *African Journal of Wildlife Research*, *37*(2). https://doi.org/10.3957/0379-4369-37.2.127

Western, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, *13*(3–4). https://doi.org/10.1111/j.1365-2028.1975.tb00139.x

Wilmshurst, J. F., Fryxell, J. M., & Bergman, C. M. (2000). The allometry of patch selection in ruminants. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1441). https://doi.org/10.1098/rspb.2000.1007

Wilmshurst, J. F., Fryxell, J. M., Farm, B. P., Sinclair, A. R. E., & Henschel, C. P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, *77*(8). https://doi.org/10.1139/z99-088

Woodall, P. F., & Skinner, J. D. (1993). Dimensions of the intestine, diet and faecal water loss in some African antelope. *Journal of Zoology*, *229*(3). https://doi.org/10.1111/j.1469-7998.1993.tb02648.x

Zhang, J., Jiang, F., Li, G., Qin, W., Wu, T., Xu, F., Hou, Y., Song, P., Cai, Z., & Zhang, T. (2021). The four antelope species on the Qinghai-Tibet plateau face habitat loss and redistribution to higher latitudes under climate change. *Ecological Indicators*, *123*. https://doi.org/10.1016/j.ecolind.2021.107337

3.8. SUPPLEMENTARY MATERIAL

Table S3.1. The most parsimonious generalized linear models representing the coefficients that were used to determine the log-odd ratios for landscape selection by ungulates at the NW Province, South Africa, 2018.

Black Wildebeest *m3*

Coefficients				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-21.963	4.366	-5.031	0.000
NDVI	1.646	0.421	3.910	<0.001
Elevation	-0.468	0.283	1.655	0.098
HB2	-2.885	1.298	-2.223	0.026
HB3	-0.855	1.235	-0.692	0.489
HB4	0.443	0.979	0.452	0.651
HB5	-2.960	1.169	-2.533	0.011
HB7	-37.345	15.884	-2.351	0.019
HT	-1.691	0.699	-2.417	0.016
DW	-2.803	1.055	-2.656	<0.001
DR	32.483	6.286	-5.167	<0.001
HB2:HT	-1.748	0.758	2.305	0.021
HB3:HT	-1.346	0.873	1.543	0.123
HB4:HT	0.449	0.287	3.043	0.002
HB5:HT	-0.928	1.462	-0.634	0.526
HB7:HT	-85.466	37.778	-2.262	0.024

Blesbok m*13*

Coefficients				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-9.322	1.859	-5.015	0.000
NDVI	0.431	0.368	1.172	0.241
Elevation	-0.784	0.281	2.788	<0.001
HT	-0.508	0.431	-1.179	0.239
HB2	-2.675	0.959	-2.789	0.005
HB3	-0.743	1.066	-0.697	0.486
HB4	0.605	0.186	0.740	<0.001
HB5	-1.182	0.983	-1.202	0.230
HB6	-1.302	2.558	0.509	0.611
HB7	-2.672	1.292	-2.067	0.039
DR	15.338	2.692	-5.698	<0.001
NDVI:HT	0.334	0.200	1.670	0.095

Blue Wildebeest *m5*

Coefficients				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.497	0.312	4.795	0.000
NDVI	0.403	0.151	-2.668	<0.001
Slope	-0.812	0.174	-4.665	0.122
Elevation	-0.363	0.157	2.307	0.021
HT	0.753	0.151	-4.972	<0.001
Aspect N	-0.833	0.814	-1.023	0.306
Aspect NE	-1.808	0.602	-3.003	0.003
Aspect NW	-2.233	0.905	-2.467	<0.001
Aspect S	0.037	0.277	-0.135	0.893
Aspect SE	0.048	0.266	-0.180	0.857

Buffalo *m5*

Coefficients				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.796	0.733	-2.451	0.014
NDVI	-0.551	0.178	3.093	<0.001
Slope	-0.106	0.209	-0.507	0.612
Elevation	-0.981	0.216	4.549	<0.001
HT	0.473	0.343	-1.380	0.168
Aspect N	0.207	1.195	0.173	0.862
Aspect NE	0.635	0.625	1.016	0.310
Aspect NW	-0.488	1.088	-0.448	0.654
Aspect S	-0.346	0.291	-1.189	0.234
Aspect SE	0.873	0.282	-3.094	<0.001

Aspect SW	-0.534	0.338	-1.580	0.114
Aspect W	-0.031	0.473	-0.065	0.948
DW	-0.574	0.084	-6.798	<0.001
Slope:Elevation	-0.374	0.118	-3.177	0.001

Aspect SW	-0.084	0.351	0.240	0.810
Aspect W	-0.200	0.408	0.490	0.624
DW	-0.182	0.103	-1.761	0.078
Slope:Elevation	0.569	0.176	3.226	0.001

Eland *m1*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.093	0.758	-2.760	0.006
NDVI	0.211	0.122	1.725	0.085
Elevation	0.490	0.120	4.070	<0.001
HB2	0.428	0.060	-1.320	<0.001
HB3	-0.669	0.639	-1.047	0.295
HB4	-0.437	0.416	-1.049	0.294
HB5	-1.850	0.564	-3.284	<0.001
HB6	-7.867	11.962	-0.658	0.511
HB7	-8.231	4.246	-1.938	0.053
HT	0.630	0.220	-2.865	<0.001
Aspect N	0.127	0.712	0.178	0.859
Aspect NE	-2.494	1.101	-2.266	0.023
Aspect NW	-4.151	1.415	-2.933	<0.001
Aspect S	0.427	0.268	1.593	0.111
Aspect SE	0.022	0.268	0.083	0.934
Aspect SW	-0.183	0.317	-0.578	0.563
Aspect W	-0.178	0.397	0.449	0.653
DW	-0.430	0.184	-2.333	0.020
DR	-4.461	0.672	-6.642	<0.001
HB2:HT	-0.005	0.252	-0.021	0.983
HB3:HT	0.123	0.347	0.355	0.722
HB4:HT	0.538	0.210	2.557	0.011
HB5:HT	-2.500	1.201	-2.081	0.037
HB6:HT	-18.565	41.846	-0.444	0.657
HB7:HT	-23.639	14.938	-1.583	0.114

Gemsbok m*11*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.814	1.264	-3.018	0.003
NDVI	0.424	0.159	2.672	<0.001
Slope	-0.308	0.221	-1.394	0.163
Elevation	0.761	0.153	4.979	<0.001
HB2	0.254	0.628	0.404	0.686
HB3	0.396	0.071	-0.507	<0.001
HB4	0.208	0.606	0.343	0.732
HB5	-1.182	0.727	-1.626	0.104
HB6	-19.260	6.273	-2.122	<0.001
HB7	-7.218	11.359	-0.635	0.525
HT	-0.690	0.265	-2.605	0.009
DW	1.273	0.235	-5.409	<0.001
DR	7.589	1.079	-7.030	<0.001
Slope:Elevation	0.671	0.148	4.531	0.000
HB2:HT	-0.279	0.320	-0.873	0.383
HB3:HT	0.584	0.428	1.364	0.173
HB4:HT	0.704	0.268	2.627	0.009
HB5:HT	-1.019	0.706	-1.444	0.149
HB6:HT	-38.644	20.176	-1.915	0.055
HB7:HT	-11.212	38.748	-0.289	0.772

Red Hartebeest *m4*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.770	0.810	-2.186	0.029
Slope	-1.319	0.171	-7.709	<0.001
Elevation	-1.020	0.143	7.129	<0.001
HT	-0.888	0.146	-6.079	<0.001
HB2	0.813	0.447	-1.819	0.069

Impala m*11*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.358	1.105	-1.229	0.219
NDVI	-0.550	0.185	2.980	<0.001
Slope	-0.457	0.196	-2.339	0.019
Elevation	0.383	0.158	2.425	0.015
HB2	-0.050	0.578	-0.087	0.930

HB3	-0.783	0.659	-1.188	0.235
HB4	0.325	0.123	-0.769	0.442
HB5	-1.914	0.550	-3.480	0.001
HB6	-0.119	1.551	0.077	0.939
HB7	-1.465	0.773	-1.895	0.058
Aspect N	0.680	0.803	0.848	0.397
Aspect NE	-2.301	0.871	-2.642	0.008
Aspect NW	-2.102	1.234	-1.703	0.089
Aspect S	0.400	0.279	1.435	0.151
Aspect SE	0.403	0.273	0.744	<0.001
Aspect SW	-0.081	0.336	0.241	0.810
Aspect W	-0.487	0.413	-1.177	0.239
DW	-0.922	0.194	-4.743	<0.001
DR	4.844	0.780	-6.210	<0.001

HB3	-0.827	1.094	-0.756	0.450
HB4	0.991	0.557	1.780	0.075
HB5	0.491	0.832	0.591	0.555
HB6	-58.240	1463.947	-0.040	0.968
HB7	-4.419	13.097	-0.337	0.736
HT	0.934	0.298	-3.131	<0.001
DW	-0.569	0.196	-2.902	<0.001
DR	-1.838	0.812	-2.263	0.024
Slope:Elevation	-0.116	0.143	-0.815	0.415
HB2:HT	0.154	0.340	0.454	0.649
HB3:HT	1.868	1.984	0.942	0.346
HB4:HT	0.220	0.286	0.771	0.441
HB5:HT	-2.047	1.751	-1.169	0.242
HB6:HT	-204.649	4758.156	-0.043	0.966
HB7:HT	-15.174	46.093	-0.329	0.742

Sable *m9*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-7.145	2.306	-3.099	0.002
NDVI	0.385	0.258	1.490	0.136
Elevation	1.621	0.319	5.085	<0.001
HB2	4.437	1.887	2.351	0.019
HB4	3.459	1.907	1.814	0.070
HB5	4.272	2.452	1.742	0.081
HB6	-11.218	1.760	-0.001	0.999
HT	2.868	1.092	-2.626	<0.001
DW	-0.312	0.149	-2.095	0.036
NDVI:HT	-0.488	0.228	-2.136	0.033

Springbok m*11*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-1.027	0.864	-1.188	0.235
NDVI	0.456	0.184	2.485	<0.001
Slope	-2.050	0.333	-6.157	<0.001
Elevation	0.463	0.218	2.119	0.034
HB2	1.429	0.396	-2.491	<0.001
HB3	-0.712	0.884	-0.806	0.420
HB4	-0.519	0.495	1.050	0.294
HB5	-2.638	0.629	-4.195	<0.001
HB6	-11.192	4.887	-2.290	<0.001
HB7	-5.742	4.446	-1.291	0.197
HT	0.686	0.285	-2.410	0.016
DW	-0.166	0.262	-0.634	<0.001
DR	-1.159	0.288	-4.022	<0.001
Slope:Elevation	0.025	0.240	0.105	0.916
HB2:HT	0.121	0.348	0.348	0.728
HB3:HT	0.285	0.495	0.575	0.565
HB4:HT	0.613	0.284	2.156	0.031
HB5:HT	-0.892	0.798	-1.119	0.263
HB6:HT	-25.584	16.889	-1.515	0.130
HB7:HT	-1.660	17.073	-0.097	0.923

Zebra *m1*

	Coefficients			
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.235	0.756	-2.956	0.003

NDVI	-0.437	0.167	2.611	<0.001
Elevation	-0.823	0.172	4.776	<0.001
HB2	0.676	0.449	-1.505	0.132
HB3	0.881	0.675	-1.306	0.192
HB4	0.365	0.244	-0.861	0.390
HB5	-1.271	0.603	-2.107	0.035
HB7	-1.900	0.957	-1.985	0.047
HT	0.430	0.258	-1.668	0.095
Aspect N	0.150	0.796	0.188	0.851
Aspect NE	-0.931	0.652	-1.428	0.153
Aspect NW	-2.810	1.050	-2.676	<0.001
Aspect S	0.482	0.289	1.670	0.095
Aspect SE	0.524	0.284	1.845	0.065
Aspect SW	-0.078	0.342	0.229	0.819
Aspect W	-0.588	0.415	1.416	0.157
DW	-1.395	0.200	-6.972	<0.001
DR	-5.084	0.816	-6.234	<0.001
HB2:HT	-0.553	0.303	-1.826	0.068
HB3:HT	0.157	0.416	0.376	0.707
HB4:HT	0.356	0.251	1.418	0.156
HB5:HT	-0.424	0.447	-0.947	0.343
HB7:HT	-4.372	3.179	-1.375	0.169

NDVI = Normalized difference vegetation index; HB2 = habitat type open woodland; HB3 = shrubland; HB4 = grassland; HB5 = waterbodies; HB6 = barren lands; HB7 = mines/quarries; HT = heterogeneity; Aspect N = aspect north; NE = northeast; NW = northwest; S = south; SE = southeast; SW = southwest; W = west; DW = distance from water source; DR = distance from road.

CHAPTER 4. Spatial occupancies, community richness and spatial segregation patterns among ungulates in the North West Province, South Africa

4.1. ABSTRACT

Spatial distributions of ungulates are influenced by resource availability, predation risk and species interactions, which in turn escalates to demographic processes driving population trajectories. In turn, population trajectories, negative or otherwise, essentially drive conservation decision processes. Most multi-species occupancy studies have included two or more interacting species. I assessed ungulate spatial occupancies, community richness and spatial segregation patterns of 26 species from aerial surveys in the North-West province of South Africa from 2000-2015 using multi species occupancy modelling through spOccupancy package in R. For the purpose of the study, ungulate feeder types were partitioned into ruminant grazers, ruminant browsers, and non-ruminants. Slope and elevation were found to be the major contributing factors of ungulate occupancy. Spatial occupancy varied across sites from 52% to 66% across all feeder types. Spatial occupancy within feeder types also varied across sites, with ruminant grazers displaying the widest occupancy range across sites. Spatial segregation between species was directly associated with species richness irrespective of the size of the study area, suggesting competition avoidance i.e., resource partitioning. Spatial segregation occurred among browsers of similar body size only in Pilanesberg and Mafikeng. Bloemhof and Molopo showed high co-occurrence among most species from all groups. This suggests interspecific competition is not important in driving space use, possibly because feeding strategies differ sufficiently to allow co-existence.

4.2. INTRODUCTION

Ungulate spatial distributions across the landscape are fundamentally influenced by resource availability, predation risk (Coleman & Hill, 2014; McHugh et al., 2019), and mating opportunities (Spritzer et al., 2005; Herfindal et al., 2009; van Beest et al., 2013; Ofstad et al., 2016). Space use is shaped further by the species interactions (Pollock et al., 2014; Rota et al., 2016) most notably competition and facilitation, the latter of which appears to be more relevant within ungulate societies (see Arsenault & Owen-Smith, 2011). Due in part to the growing concern over the potential impact of climate change on ungulate communities globally (Veldhuis et al., 2019; Devarajan et al. 2020), species persistence has received considerable attention in literature (see Duncan et al., 2012). In parallel, wildlife populations are commonly reintroduced to wildlife sanctuaries (Venter et al., 2014), rendering species assemblages to artificial constructs (Simenstad et al., 2006; Venter et al., 2014). Incomplete information on the habitat requirements and historical range of species may result in unsuccessful reintroductions (Novellie & Knight, 1994; Castley et al., 2001). For these reasons, the mechanisms allowing coexistence, and the environmental factors influencing spatial occupancies of wild ungulate species, is of great importance, and acknowledged globally (see Li et al., 2022).

African ungulate feeder types are commonly differentiated on the basis of the adaptive radiations in their feeding ecology. The anatomical structure of the digestive system naturally partitions large herbivores into ruminants (foregut fermenters) and non-ruminants (hind-gut fermenters). Differences in feeding strategy associated with a range of morphological and physiological adaptations (Demment & van Soest, 1985) warrants a further distinction between grazers and browsers (Kiffner & Lee, 2019). Non-ruminant grazer ungulates e.g., zebra *Equus quagga* consume large quantities of forage, are tolerant towards low-quality grass as their digestive systems, which allows a rapid passage of ingesta (Demment & van Soest, 1985; Duncan et al., 1990; Mariotti et al., 2020). This furthermore allows them to utilize landscapes more extensively compared to ruminant species aside from any contributions related to body mass (McNaughton, 1988; 1990; Owen-Smith, 1988; Duncan et al. 1990; Sinclair, 2000). Ruminants, contrastingly, are reliant on forage of relatively high nutritional value, due to their limiting capacity to ingest large quantities of forage (Duncan et al., 1990; Mariotti et al., 2020)

Seasonal variation in primary productivity (Illius and O'Connor, 2000; Owen-Smith, 2002) and landscape attributes influencing resource heterogeneity (Owen-Smith, 2002; Cromsigt & Olff, 2006) and soil nutrients (Anderson et al., 2006) also shapes spatial distributions and spatial associations in ungulate assemblages. Bottomlands remain greener and forage more plentiful into the dormant season, leading to high grazer assemblages in the low-lying areas (Bell 1971; Wilmshurst et al., 1999; Selebatso et al., 2018). Contrastingly, the nutrient content of the browse layer is less affected by elevation, allowing browsers to occupy a range of habitats (Jarman, 1974; McNaughton & Georgiadis, 1986). Ungulates generally prefer habitat close to surface water (Solomon & Leak, 1994; Lee et al., 2005). High densities of prey near surface water, also attracts predators (Louw et al., 2022), while, the consumptive activities of high concentrations of ungulates near water modify vegetation structure (Murray & Illius, 2000). Selective feeders therefore tend to prefer habitat farther from surface water (Redfern et al., 2003; Ogutu et al., 2014). Ungulates also avoid roads due to the disturbance imposed by human activities (Leblond et al., 2013; Venter & Child, 2016).

Body mass has an overriding influence on ungulate resource use (Prins & Olff, 1998; Kleynhans et al., 2011). Theory suggests spatial segregation to be commonly more distinct between species of similar body mass (Sinclair, 1985; Hibert et al., 2010; Venter et al., 2014). Contrastingly, the indirect competition hypothesis (Clutton-Brock et al., 1982; 1987) predicts that ‘interspecific’ segregation occurs between different sized species while ‘intraspecific’ segregation occurs between males and females of sexually dimorphic species. Yet another viewpoint is that species interaction patterns change in response to changing metabolic requirements towards maturity (juvenile, sub-adult, adult) in their life cycle (Ruel & Ayres, 1999; Hart et al., 2016). With these opposing views on the importance of body mass contributing towards species co-existence and spatial segregation, the relative importance of body mass in structuring spatial distributions at landscape scales most likely varies across space.

Recent statistical breakthroughs and the expanding accessibility of data from many taxa have made analyses at the species community scale possible (Devarajan et al., 2020). The hierarchical multi-species occupancy model (MSOM) is one of these frequently used classes of community models. Multi-species occupancy modelling provides an approach for measuring biodiversity that accounts for various sources of uncertainty, imperfect detection, and inaccurate sampling methods (MacKenzie et al., 2002; Tyre et al., 2003; Gelfand et al., 2005). With fully propagated uncertainty, the community pool as well as species-specific capture histories can be used in MSOM to quantify the effects of covariates on both the individual species level and the community as a whole, while generating species-specific occupancy probability estimates, and estimate community-level summaries e.g., species richness. (Dorazio & Royle, 2005; Doser et al., 2022). Such an approach is particularly helpful for modelling rare or hard-to-detect species, which are frequently found in non-invasive surveys (Zipkin et al., 2010).

In the current study, I assessed ungulate spatial occupancies, community richness and spatial segregation patterns of species using data from the replicated aerial surveys conducted from 2000-2015 in four protected areas in the North-West (NW) province of South Africa. My study focusses on the late dry season when competition for resources is expected to be highest and spatial segregation is most evident (Macandza et al., 2012). Survey count data included 26 species of ungulates that were divided into grazers, browsers, and non-ruminants.

Following the above-mentioned concepts, the objectives of the study were 1) to determine major environmental drivers influencing the spatial occupancy patterns of ungulate groups in the NW Province, where covariates considered were topography (slope and elevation), soil nutrients (soil nitrogen and pH), NDVI, heterogeneity, survey effort (length of a flight path), distance from water sources and from roads. 2) To identify species co-occurrence patterns across different study sites. The following hypothesis were formulated: 1) ruminant species select areas of high NDVI, soil nutrients and lower heterogeneity relative to non-ruminant species; 2) grazing and non-ruminant species select areas of low elevation and avoid slopes while browsers prefer high elevation and slopes; 3) Survey efforts positively affect detections of large sized species across all feeder groups since longer flight paths in a grid would result in higher detection of larger ungulates; 4) ungulates generally prefer areas closer to surface water, and 5) avoid dirt roads. Furthermore, 6) species diversity within a feeder group correlates with level of occupancy 7) species diversity promotes spatial segregation, 8) within their respective groups; grazer and browser species spatially segregate, and this segregation is most distinct among species of similar body size.

4.3. MATERIAL AND METHODS

4.3.1. Study Sites

The study was conducted in four protected areas in the NW Province of South Africa (between latitude of 24°15’S to 28°15’S and longitude of 22°30’E to 28°30’E) (Figure 4.1). The province's landscape changes from plains to mountains from west to east. With largely plains and pans in the middle, the region's altitude ranges from 1,000 m mean above sea level (masl) to 2,000 m masl from plains to the mountains. The annual rainfall range of 300 mm to 700 mm classifying it as an ‘arid’ region (Mucina & Rutherford, 2006), with mean annual rainfall generally declining from east to west and from north to south (Kruger & Nxumalo, 2017). In contrast to the typical winter temperature, which can vary in a single day from 2°C to 20°C, the summer temperature maintains its steady range between 22°C and 34°C. (Goslar et al., 2008).

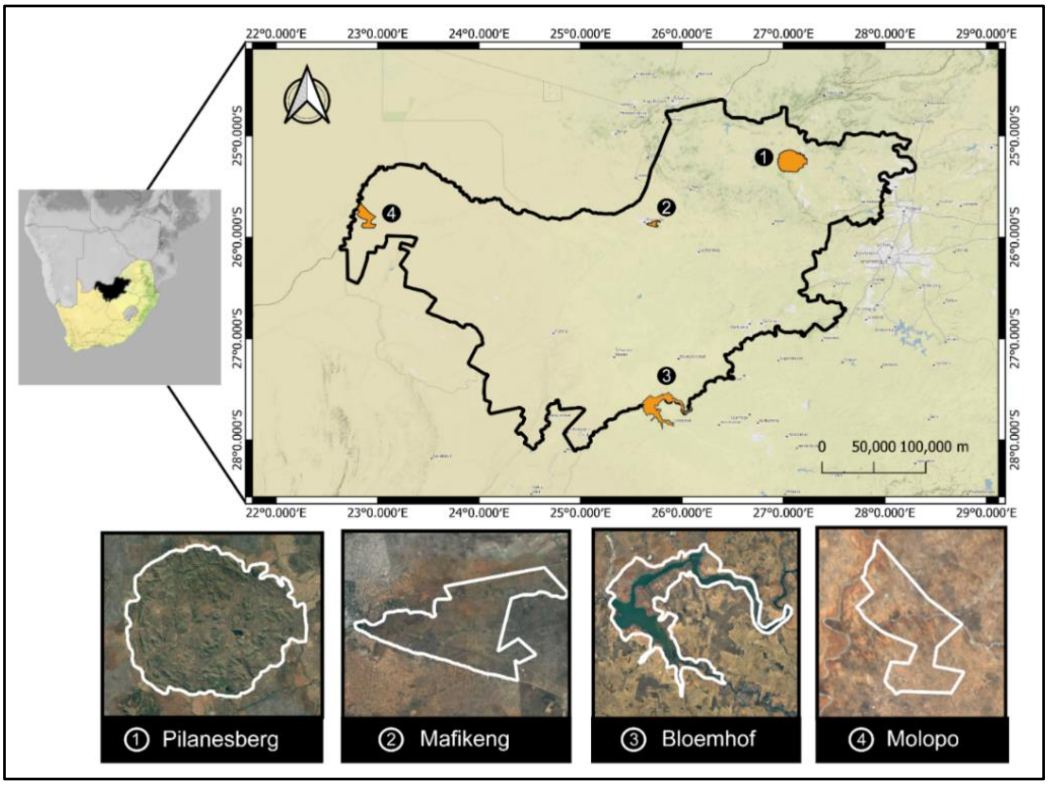


Figure 4.1: Map of North West Province highlighting the study sites

4.3.1.1. Pilanesberg National Park

At 25°15'S latitude and 27°6'E longitude, the park (henceforth ‘Pilanesberg’) is located in the Bojanala region of the province between the arid Kalahari and the wetter low-veld vegetation or "Sour Bushveld" (Acocks, 1988) and covers an area of around 550 km^2. The vegetation composition characterizes a mix of open grassland to thickets of *Vachellia* and broad-leaf bushveld species (Hrabar & du Toit, 2005; Kidwai et al., 2019; Louw et al., 2019). Pilanesberg is home to nearly thirty different species of large mammals, including the lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), African buffalo, elephant (*Loxodonta Africana*), springbok (*Antidorcas marsupialis*), sable antelope (*Hippotragus niger*), black rhinoceros (*Diceros bicornis*) and hippopotamus (*Hippopotamus amphibious*) among others (NWPTB 2020).

4.3.1.2. Mafikeng Game Reserve

The Reserve (henceforth ‘Mafikeng’; 25° 43' E Latitude, 25° 52' S Longitude) was founded in 1992 and encompasses an area of 48 km^2 (Brockett, 2002). It is located almost in the upper middle part of North West Province (Seitlhamo 2011). An underlying layer of andesitic lava characterizes a significant portion of the reserve (Mucina & Rutherford 2006). The vegetation of the park is described as dry *Cymbopogon-Themeda* veld (Adcock, 1991; Mucina & Rutherford, 2006). The reserve is home to healthy populations of game species including gemsbok (*Oryx gazela*), African buffalo, ostrich (*Struthio camelus*), and giraffe (*Giraffa camelopardalis*) (Nyirenda et al., 2016).

4.3.1.3 Bloemhof Dam Nature Reserve

The Bloemhof Dam Nature Reserve (henceforth ‘Bloemhof’) is situated 4 km east of Bloemhof town and 320 kilometres from Johannesburg, at latitudes 25° 39'E and 27°

40'S. The reserve is 250 km^2 in size and comprises of “Kimberly Thornveld”, an open Kalahari scrub vegetation (Mucina & Rutherford, 2006) with an inflow of Vall river water in the dam (NWPTB 2020). Numerous game species including blesbok (*Damaliscus pygargus*), black wildebeest (*Connochaetes gnou*), eland (*Taurotragus oryx*), and gemsbok are found here (Nel, 2018).

4.3.1.4. Molopo Game Reserve

The 240 km^2 Molopo game reserve (22° 57'E latitude, 25° 48'S longitude) is in the province's extreme west, next to the Botswana boundary, which is demarcated by a portion of the Molopo River (van Niekerk, 2011). This remote reserve has a characteristic arid savanna habitat called ‘Molopo Bushveld’ featuring grassland and thornveld dunes with dominant tree species of *Vachellia* and *Boscia* tree species (Mucina & Rutherford 2006). Sand dunes and deep, red soils can be found nearby the reserve’s drainage valleys. The reserve is home to a wide variety of mammalian species, including cheetah, caracal (*Caracal caracal*), blue wildebeest (*Connochaetes taurinus*), red hartebeest and waterbuck (*Kobus elipsiprimnus*) (Nel, 2018).

4.3.2. Data Collection

From 2000 through 2015, during the late dry season (July to October), data for the current study were gathered by undertaking three yearly replicated aerial surveys utilizing a four-seat Bell Jet Ranger II helicopter (with all doors removed). Survey total strip width was 500 m, with a flying height range of 60 m to 100 m and a speed of 90 km/h. The survey count data comprised of 26 species of ungulates. In every survey, flight's survey effort (GPS path in kilometres), GPS locations for ungulate sightings, and the time and date of each observation were recorded.

Ungulate species in the survey were divided into grazer (GZ), browser (BW) and non-ruminant (NR) feeding group for each study site. The groups were created only to simplify the analysis and find broad patterns in richness and occupancies knowing that the broad distinction is too simplistic from morphological and evolutionary perspective (Codron et al., 2019; Kiffner & Lee, 2019). The ruminant ungulates were categorized according to their diet composition i.e., grazers (≥50% grass), browsers (≥50% dicots) (see Kiffner & Lee, 2019). While, all the ungulates outside of "Ruminantia" sub-order (Clauss & Rössner, 2014) were considered as non-ruminants (Table 4.1).

Table 4.1. Ungulate species categorisation into groups of grazer, browser and non-ruminants based on foraging behaviour reported in previous research studies.

Category	Species	Body Mass (kg)*	Literature Reference
BW	**Bushbuck** *(Tragelaphus scriptus)*	43	Fischer & Linsenmair, 2001; Kiffner et al., 2017
BW	**Duiker** *(Sylvicapra grimmia)*	16	Fischer & Linsenmair, 2001; Pettorelli et al., 2009
BW	**Eland** *(Taurotragus oryx)*	560	Kiffner et al., 2016; Furstenburg, 2016[a]
BW	**Giraffe** *(Giraffa camelopardalis)*	800	Kiffner et al., 2017
BW	**Greater Kudu** *(Tragelaphus strepsiceros)*	220	Pettorelli et al., 2009
BW	**Klipspringer** *(Oreotragus oreotragus)*	12	Bireda & Yihune, 2020
BW	**Steenbok** *(Raphicerus campestris)*	12	Furstenburg, 2008[a]
GZ	**Black Wildebeest** *(Connochaetes gnou)*	130	Bukombe et al., 2016; Schuette et al., 2016; M'soka et al., 2017; Mariotti et al., 2020;
GZ	**Blesbuck** *(Damaliscus pygargus)*	70	Furstenburg, 2016b
GZ	**Blue Wildebeest** *(Connochaetes taurinus)*	290	Seydack et al., 2012; Mariotti et al., 2020
GZ	**Buffalo** *(Syncerus caffer)*	325	Rodgers, 1996; Waltert et al., 2008; Seydack et al., 2012; Kasiringua et al., 2019
GZ	**Common Reedbuck** *(Redunca arundinum)*	58	Waltert et al., 2008
GZ	**Gemsbok** *(Oryx gazela)*	260	Harris et al., 2015; Lehmann et al., 2013
GZ	**Impala** *(Aepyceros melampus)*	50	Gaidet & Gaillard, 2008; Pettorelli et al., 2009; Hempson et al., 2015; Bukombe et al., 2016; Schuette et al., 2016
GZ	**Mountain reedbuck** *(Redunca fulvorufula)*	29	Taylor & Skinner, 2006
GZ	**Red Hartebeest** *(Alcelaphus caama)*	170	Rodgers, 1996; Fischer & Linsenmair, 2001; Mariotti et al., 2020; Deliberato, 2017
GZ	**Sable** *(Hippotragus niger)*	235	Pettorelli et al., 2009; Chirima et al., 2013; Kasiringua et al., 2019
GZ	**Springbok** *(Antidorcas marsupialis)*	38	Furstenburg, 2023; Hein et al., 2008

GZ	**Tsessebe** *(Damaliscus lunatus)*	110	Furstenburg, 2016c
GZ	**Waterbuck** *(Kobus elipsiprimnus)*	250	Fischer & Linsenmair, 2001;Waltert et al., 2008
NR	**Black Rhino** (*Diceros bicornis*)	1100	Bian et al., 2013
NR	**Bushpig** *(Potamochoerus larvatu)*	69	Kihwele et al., 2020
NR	**Hippopotamus** *(Hippopotamus amphibious)*	1650	Bempah et al., 2022
NR	**Warthog** *(Phacochoerus africanus)*	75	Treydte et al., 2006; Kihwele et al., 2020
NR	**White Rhino** (*Ceratotherium simum*)	2300	Bian et al., 2013
NR	**Zebra** *(Equus burchelli)*	250	Deliberato, 2017; Kihwele et al., 2020

* Average female body mass information was obtained from Estes (1991); GZ = Grazer; BW = Browser, NR = Non-ruminants

Covariates: As a proxy for the variability in food quality, I employed the Normalized Difference Vegetation Index (NDVI) (Hunninck et al., 2020) for the survey months and years (2000–2015) of the study. From the U.S. Geological Survey website, I downloaded the freely available MODIS13Q1 NDVI raster file (earthexplorer.usgs.gov). MODIS (modis.gsfc.nasa.gov) uses images with a temporal resolution of 16 days and a spatial resolution of 250 m. High NDVI values describes continuous green vegetation (woodlands, cultivated grass fields) and low NDVI levels describe vegetation gaps, areas with brown vegetation, or places without vegetation (like water holes and bare soil) (van Bommel et al., 2006; Boyers, 2011; Deliberato, 2017). I created heterogeneity raster files with a spatial resolution of 250 m from NDVI of each year by calculating the difference between absolute NDVI values of each pixel and average of eight pixels surrounding it (following Mariotti et al., 2020). ISRIC World Soil Information provided raster dataset of soil nutrients for each site, including organic carbon, calcium, sodium, potassium, nitrogen and soil pH, at a spatial resolution of 250 m and a depth range of 0 to 30 cm (Hengl et al., 2015). North West Tourism and Parks Board (NWTPB) provided shape files for the perennial water sources and dirt roads inside the protected areas. The province's Digital Elevation Model (DEM) was acquired from the USGS Science-based catalogue (Verdin, 2017). Using the 'spatial analysis' tool in ArcGIS Desktop 10.8 (ESRI, 2020), raster files for slope were generated from the DEM files of each site.

Each study site was divided into 2 x 2 km grids to gather the presence/ absence data of the species from each replicate survey. In order to reduce observational bias, I introduced a 400 m buffer to each GPS location of the species sightings (following Deliberato, 2017). If a buffer would overlap in two adjoining cells, presence was marked for both of those cells through the 'spatial join' tool of ArcGIS Desktop 10.8. Once the data was extracted, each grid would come up with an entry of total sightings or blank records (no sightings). By setting blanks to zero and sighting totals to one, the final data was transformed into a presence/absence format. The grid for each location was also used to extract the data for soil nutrients, NDVI, heterogeneity, slope and elevation using 'zonal statistics' and length of flight path (survey effort) by 'intersect' tool in ArcGIS Desktop 10.8. The grid centre was used to calculate distance from water and dirt roads in each study site through "Near" analysis tool in ArcGIS Desktop 10.8. Due to strong collinearity between soil nutrients (>0.8), only nitrogen and pH were used in the final models.

To estimate predictions for group richness and species occupancy for each species across each site, finer grids of 100 x 100 meters were created to extract coordinates and site covariate data (soil nutrients, NDVI, heterogeneity, slope and elevation) demonstrating the "available" sites where the species occurrence could be predicted.

4.2.3. Data Analysis

I used multispecies occupancy modelling (MSOM) (Dorazio & Royle, 2005; Doser et al., 2023) to estimate the probability of the species (*i*) occurring within an area (*j*) sampled during our survey period/replicates (k), while accounting for the imperfect detection of the species (MacKenzie et al., 2002). I fit a separate multi-species occupancy model for each of the four nature reserves. Considering $z_{i,j}$ as the true presence (1) or absence (0) of a species *i* at site *j*, with $j = 1, . . . , J$ and $i = 1, . . . , N$., the true species-specific occupancy process arises from a Bernoulli distribution following:

$$z_{i,j} \sim \mathrm{Bernoulli}(\psi_{i,j}),$$

$$\mathrm{logit}(\psi_{i,j}) = \mathrm{x}_j^{\top}\beta_i + \mathrm{w}_{i,j}^{*}$$

where $\psi_{i,j}$ is the occurrence probability of species *i* at site *j*. I modelled $\psi_{i,j}$ as a function of a set of site-specific covariates (including an intercept), x_j, a set of species-specific effects of the covariates (β_i), and species-specific spatial random effect $\mathrm{w}_{i,j}^{*}$. The species-specific regression coefficients (β_i) are treated as random effects arising from a common distribution at the community level:

$$\beta i \sim \mathrm{Normal}\ (\mu_\beta, T_\beta),$$

where community-level mean effects for each occurrence covariate effect (including the intercept) is represented by a vector μ_β, while, T_β is a diagonal matrix whose diagonal elements (τ_β^2) represent the variability of each occurrence covariate effect among species within the community.

I modelled the species-specific spatial random effect $\mathrm{w}_{i,j}^{*}$ using the spatial factor modeling approach described by Doser et al., 2023, which allows us to account for both spatial autocorrelation and species correlations after accounting for the effects of the covariates included in the model. In this approach, I model $\mathrm{w}_{i,j}^{*}$as a linear combination of *q* of latent variables (i.e., factors) and their associated species-specific coefficients (i.e., factor loadings). More specifically, I had

$$\mathrm{w}_{i,j}^{*} = \lambda_{i_j}{}^{\top \mathrm{w}},$$

where λ_i is a vector of species-specific coefficients from an N x q matrix Λ, and w_j is a vector of spatial factors at site j. I modelled the spatial factors w_j using a Nearest Neighbor Gaussian Process (NNGP; Datta et al., 2016), a computationally efficient approach for modeling spatial autocorrelation. This approach inherently accounts for residual correlations between species, and I can derive a residual interspecies co-occurrence matrix $\Sigma = \Lambda\Lambda^T$, which can be used to provide insight on residual species co-occurrence patterns.

Finally, I explicitly accounted for imperfect detection by modeling the detection-non-detection data conditional on the true species-specific occupancy process. Let $y_{i,j,k}$ be the detection (1) or nondetection (0) of species *i* at site *j* during repeat visit *k*. I modelled $y_{i,j,k}$ according to:

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} z_{i,j}),$$

$$\text{logit}(p_{i,j,k}) = v_{i,j,k}^T \alpha_i,$$

where $p_{i,j,k}$ is the probability of detecting species *i* at site *j* during replicate *k* (provided it is present at site *j*). It is calculated as a function of site and replicate-specific covariates (V) and a vector of species-specific regression coefficients (α_i). Similar to the occurrence regression coefficients, the species-specific detection coefficients are also conceptualized as random effects generated from a common community-level distribution

$$\alpha_i \sim \text{Normal}(\mu_\alpha, T_\alpha),$$

where community-level mean effects for each detection covariate effect (including the intercept) is represented by a vector μ_α, while, T_α is a diagonal matrix whose diagonal elements (τ_α^2) represents the variability of each effect of detection covariate among species within the community (Doser et al., 2022).

I fitted the multi-species occupancy model with the spOccupancy package (Doser et al., 2022; 2023) in R (R Core Team, 2020). I used the default, vague prior distributions, details of which are available in Doser et al., 2022 and Doser et al., 2023. After checking for collinearity among covariates, six site-level covariates (slope, elevation, NDVI, heterogeneity, soil nitrogen, soil pH) with their quadratic terms and four detection covariates (survey effort, Julian date, distance from water and distance from road) and their quadratic terms were used for running a total of 25 models. I used backward-elimination strategy for model development. For the Markov chain Monte Carlo (MCMC) analysis, I ran three chains each with 10,000 iterations to achieve adequate convergence for each candidate model. I performed a posterior predictive check summarized with a Bayesian p-value as an assessment of model fit, where values around 0.5 indicated that the model fit adequately, and values less than 0.1 or greater than 0.9 suggested that the model did not fit the data well (Hooten & Hobbs, 2015). Model selection was performed using the Widely Applicable Information Criterion also known as Watanabe Akaike Information Criterion (WAIC) with the best-performing model having the lowest WAIC value (Watanabe, 2010). After fitting the models, I subsequently predicted occurrence probability of each species across each of the four protected areas through ‘predict’ function in spOccupancy. Along with calculating the probability of richness per group in a study site, occupancy with uncertainty for each individual species within a group was also calculated for each site. Finally, I generated and plotted the residual species covariance matrices to investigate the co-occurrence and segregation patterns between ungulate species per study site as a co-occurring species in the same locations (positive relation) or different locations (negative relation).

To investigate the influence of body mass on spatial segregation of ungulates in the most spatially segregated study sites, I conducted one-way analysis of variance (ANOVA). Body mass data was log transformed and difference in body mass was calculated between each species in each study site. The spatial correlation coefficient obtained from MSOM for each relation was then compared with the body mass difference for every group interaction and individual species interaction to find any patterns. This method was carried out to see if there are any visible patterns for species or groups of different body masses to co-exist or spatially segregate. The analysis was conducted between the groups ("Grazer - Browser", "Browser - Non-Ruminants" and "Grazer - Non-Ruminants") and within the groups for a better understanding of spatial distribution patterns. Three class of body mass difference were created to view the graphs: "Smaller" (if the difference value is between -6.0 and -2.0), "Comparable" (if the difference value is between -2.0 and 2.0) and "Larger" (if the difference value is between 2.0 and 6.0). Tukey's Honest Significant Difference (HSD) test was conducted as a post hoc analysis to examine the results between various groups.

4.4. RESULTS

The 2 km x 2 km grid size resulted in 156 grids for Pilanesberg, 26 grids for Mafikeng, 203 grids for Bloemhof and 90 grids for Molopo. The highest number of species (24) were recorded from Pilanesberg (GZ = 11; BW = seven; NR = six) followed by Mafikeng (18; GZ = ten, BW = five; NR = three), Molopo (13; GZ = six; BW = five; NR = two) and Bloemhof (11; GZ = six; BW = three; NR = two).

4.4.1. Environmental factors influencing ungulate spatial occupancy

According to the best-selected model for each feeding group, slope, elevation (along with their quadratic term), NDVI and heterogeneity were the selected site covariates, while survey efforts (along with its quadratic term), distance from water and distance from road, were the selected detection covariates significantly influencing species occupancies in the NW Province (Table 4.2).

The grazer group from all sites strongly avoided slopes. The browser group occupancy was positively influenced by slope, NDVI and heterogeneity across sites. The non-ruminant group occupied low-lying areas with high heterogeneity and areas closer to roads and water across the landscape (Table 4.3; Figure S4.1). Soil nutrients (nitrogen and pH) were not selected in the best-fit models for any groups.

Table 4.2. Model results of three best predictive models from spOccupancy with 10,000 MCMC iterations for spatial distribution of three ungulate groups across four sites in the NW Province, South Africa.

Site	Groups	#	Best model	WAIC	ΔWAIC	k	FT
Pilanesberg							
	Grazer	6	Elevation + Slope + Slope^2 + Efforts + Efforts^2	2965.468	0	48	0.41
		10	Slope + NDVI + Efforts + Efforts^2 + JD + DW	2974.921	9.453	49	
		12	Elevation + Slope + Slope^2 + NDVI + Nitrogen + Efforts+ Efforts^2 + JD	2983.691	18.22	55	
	Browser	7	Elevation + Slope + Efforts + DR	2463.315	0	22	0.49
		9	Elevation + Slope + Slope^2 + Efforts + Efforts^2 + JD	2469.712	6.39	32	
		11	Elevation + Heterogeneity + DW + DR	2477.109	13.79	22	
	Non-ruminant	13	Elevation + Slope + Slope^2 + Efforts + Efforts^2 + DR	1751.734	0	46	0.44
		12	Elevation + Slope + Slope^2 + NDVI + Nitrogen + Efforts + Efforts^2 + JD	1758.110	6.37	55	
		2	Slope + NDVI + Heterogeneity + Efforts + DW + JD	1763.677	11.94	36	
Mafikeng							
	Grazer	22	Elevation + Elevation^2 + Slope + Efforts	612.117	0	17	0.28
		10	Slope + NDVI + Efforts + Efforts^2 + JD + DW	617.405	5.29	18	
		2	Slope + NDVI + Heterogeneity + Efforts + DW + JD	621.132	9.01	22	
	Browser	24	Elevation + Slope + Efforts	361.188	0	26	0.32
		8	Elevation + Slope + Slope^2 + Efforts + Efforts^2	364.899	3.71	28	
		5	Elevation + Slope + NDVI + Efforts + JD	367.161	5.97	32	
	Non ruminant	15	Elevation + Slope + NDVI + Heterogeneity + DR	181.290	0	14	0.46
		4	Slope + Heterogeneity + Efforts + DW + DR	184.817	3.52	16	
		12	Elevation + Slope + Slope^2 + NDVI + Nitrogen + Efforts + Efforts^2 + JD	193.779	12.49	18	
Bloemhof							
	Grazer	16	Elevation + Elevation^2 + Slope + Efforts + Efforts^2	775.861	0	24	0.36
		14	Elevation + Elevation^2 + NDVI + Efforts + DW	782.575	6.71	31	

	4	Slope + Heterogeneity + Efforts + DW + DR	786.664	10.80	28	
Browser	11	Elevation + Heterogeneity + DW + DR	497.221	0	23	0.44
	8	Elevation + Slope + Slope^2 + Efforts + Efforts^2	505.513	8.29	15	
	3	Slope + Nitrogen + NDVI + NDVI^2 + Efforts + Efforts^2 + JD + JD^2	508.312	11.091	49	
Non ruminant	17	Slope + Slope^2 + DW + DR	398.371	0	18	0.36
	1	Elevation + Slope + Heterogeneity + NDVI + Efforts + DW + DR	401.286	2.92	26	
	12	Elevation + Slope + Slope^2 + NDVI + Nitrogen + Efforts + Efforts^2 + JD	404.211	5.84	32	
Molopo						
Grazer	18	Elevation + Slope + Efforts + DW	953.024	0	31	0.35
	16	Elevation + Elevation^2 + Slope + Efforts + Efforts^2	957.022	3.99	35	
	4	Slope + Heterogeneity + Efforts + DW + DR	965.134	12.11	44	
Browser	20	Elevation + NDVI + DW + DR	959.381	0	35	0.25
	17	Slope + Slope^2 + DW + DR	963.856	4.47	33	
	16	Elevation + Elevation^2 + Slope + Efforts +Efforts^2	967.538	8.15	28	
Non ruminant	21	Elevation + Slope + Efforts + Efforts^2 + DW + DR	539.623	0	24	0.37
	16	Elevation + Elevation^2 + Slope + Efforts + Efforts^2	541.821	2.19	31	
	5	Elevation + Slope + NDVI + Efforts + JD	548.410	8.78	48	

= model identification number; NDVI = normalized difference vegetation index; JD = Julian Date; Efforts = Survey Efforts; DW = Distance from water; DR = Distance from road; k = effective number of parameters in the model; WAIC = Widely Applicable Information Criterion; ΔWAIC = difference between model WAIC and that of the best model; FT = Freeman Tukey Statistic for the best model.

Table 4.3. Best-selected model's community-level estimates (95% credible intervals). $\mu_{\beta 0}$ is the community-level intercept of site covariates (slope, elevation, NDVI, heterogeneity). μα0 is community-level intercept of detection covariates (survey efforts, distance from water, and distance from roads). $\mu_{\beta 1}$, $\mu_{\beta 2}$, $\mu_{\beta 3}$, $\mu_{\beta 4}$ are the linear and quadratic effects of elevation, slope; $\mu_{\beta 5}$, $\mu_{\beta 6}$ are the linear effects of NDVI and heterogeneity. $\mu_{\alpha 1}$, $\mu_{\alpha 2}$ are the linear and quadratic effects of survey efforts; $\mu_{\alpha 3}$, $\mu_{\alpha 4}$ are the linear effects of distance from water and distance from road respectively. $\tau^2_{\beta,0}$,$\tau^2_{\beta,1}$,$\tau^2_{\beta,3}$, $\tau^2_{\beta,4}$ and $\tau^2_{\beta,5}$ are community-level variances for site covariates and $\tau^2_{\alpha,0}$, $\tau^2_{\alpha,1}$ and $\tau^2_{\alpha,2}$ are community-level variances for the detection covariates for the three ungulate groups across four sites in NW Province.

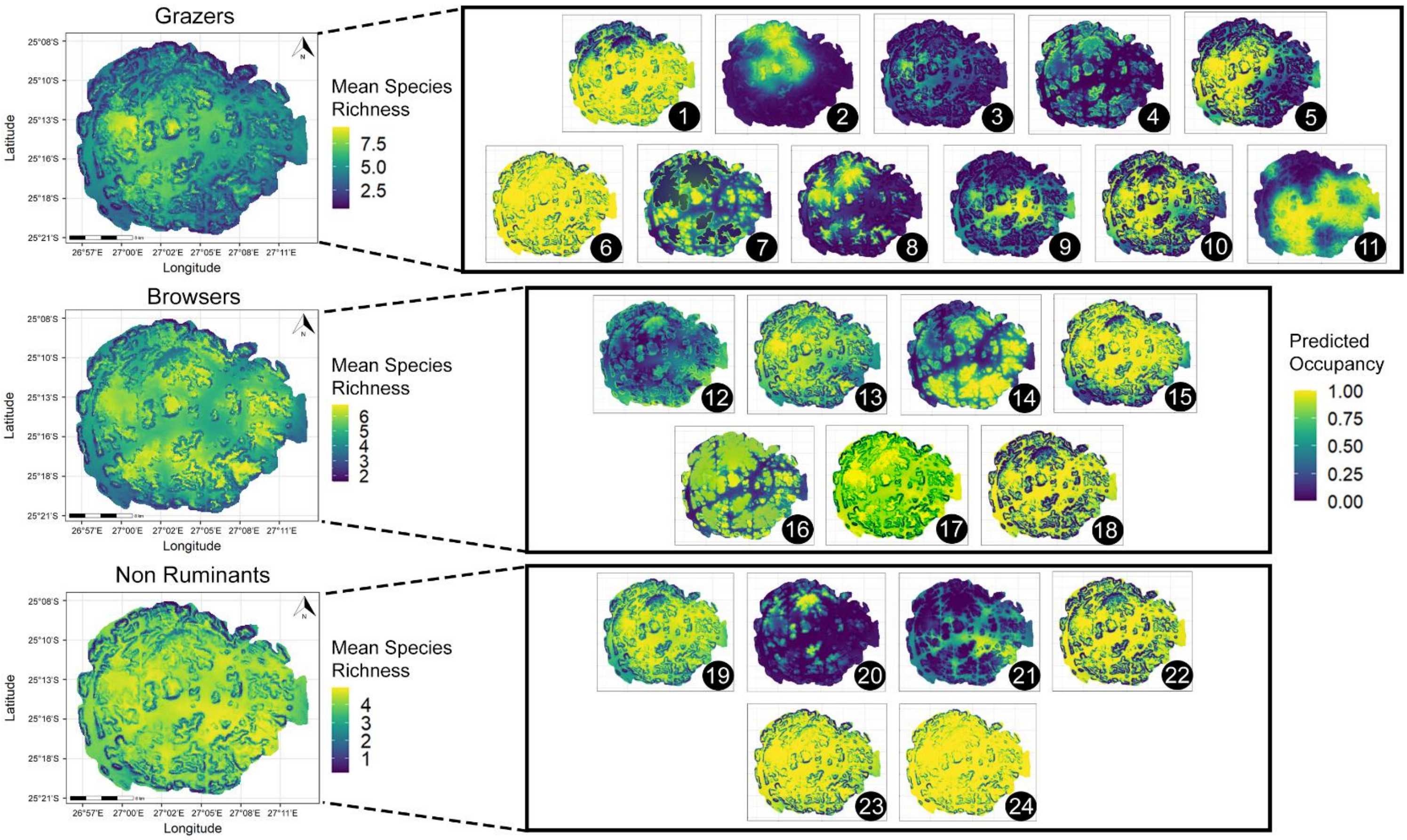
	Pilanesberg			***Mafikeng***			***Bloemhof***			***Molopo***		
Occurrence												
	GZ	*BW*	*NR*	*GZ*	*BW*	*NR*	*GZ*	*BW*	*NR*	*GZ*	*BW*	*NR*
$\mu_{\beta 0}$	-0.75 (-2.50, 1.16)	1.55 (-0.78, 3.58)	0.59 (-2.19, 3.28)	2.05 (0.09, 4.02)	1.88 (-0.61, 3.85)	1.27 (-2.3, 4.62)	1.37 (-0.58, 3.02)	1.03 (-1.42, 3.25)	0.03 (-3.03, - 2.07)	1.01 (-1.63, 3.43)	3.16 (-0.77, 5.62)	3.21 (0.89, 4.02)

$\mu_{\beta 1}$	1.19 (0.39, 1.99)	-1.63 (0.63, 2.68)	0.97 (-0.79, 2.64)	-1.58 (-2.19, -0.04)	-0.05 (-1.24, 1.83)	0.08 (-2.30, 2.19)	-0.65 (-2.02, -0.66)	0.09 (-0.06, -0.12)	-	-0.46 (-1.98, 1.23)	0.95 (0.57, 1.33)	0.52 (-0.67, 2.31)
$\mu_{\beta 2}$	-	-	-	-0.46 (-1.71, 0.96)	-	-	1.16 (-0.07, -3.05)	-	-	-	-	-
$\mu_{\beta 3}$	-1.08 (-1.85, -0.32)	0.73 (0.31, 1.15)	-1.28 (-2.63, -0.07)	-1.06 (-2.43, 0.26)	-1.85 (-3.67, 0.28)	-0.09 (-1.55, 1.34)	-0.08 (-0.85, 0.71)	-	-1.16 (-2.35, -0.12)	-1.67 (-2.04, -0.68)	-	0.07 (-1.06, 1.19)
$\mu_{\beta 4}$	-0.33 (-0.69, 0.01)	-	-0.48 (-1.17, 0.21)	-	-	-	-	-	1.82 (-2.08, -3.87)	-	-	-
$\mu_{\beta 5}$	-	-	-	-	-	-1.13 (-3.77, 2.22)	-	-	-	-	2.76 (0.28, 3.83)	-
$\mu_{\beta 6}$	-	-	-	-	-	2.27 (0.68, 4.79)	-	0.78 (0.18, 1.91)	-	-	-	-
Detection												
$\mu_{\alpha 0}$	1.12 (0.33, 3.06)	0.02 (-1.38, 1.29)	0.68 (-0.78, 1.97)	1.15 (0.11, 2.18)	0.55 (-0.54, 1.68)	1.35 (-0.45, 2.68)	0.44 (-1.30, 0.48)	-0.31 (-2.76, 1.92)	0.35 (-1.31, 1.78)	1.25 (0.26, 2.53)	1.23 (-0.18, 2.80)	-0.65 (-1.22, 0.68)
$\mu_{\alpha 1}$	0.37 (0.11, 0.63)	-0.41 (-0.89, -0.07)	-0.19 (-0.57, 0.39)	0.03 (0.03, 0.41)	-0.57 (-0.85, -0.19)	-	0.51 (0.19, 1.31)	-	-	-0.08 (-0.66, 0.53)	-	0.39 (-0.84, 1.21)
$\mu_{\alpha 2}$	-0.07 (0.02, 0.21)	-	-0.33 (-1.23, 0.33)	-	-	-	0.03 (-0.35, 0.02)	-	-	-	-	0.69 (-0.25, 1.34)
$\mu_{\alpha 3}$	-0.06 (-0.22, 0.34)	-	-	-	-	-	-	1.10 (-0.23, 2.39)	-1.25 (-1.38, -1.12)	-0.02 (-0.40, 0.55)	-0.06 (-0.64, 0.62)	-1.75 (-2.22, -0.68)
$\mu_{\alpha 4}$	-	-	-0.55 (-0.82, -0.13)	-	-	-0.86 (-1.48, -0.12)	-	0.72 (0.12, 1.82)	-1.78 (-2.77, -0.17)	-	0.48 (0.08, 0.88)	-0.44 (-0.13, -0.75)
Spatial Variance												
$\tau^2_{\beta,0}$	13.24 (4.76, 32.87)	11.65 (0.43, 67.15)	25.81 (8.04, 43.57)	9.28 (0.19, 37.22)	11.12 (0.13, 71.14)	9.57 (0.16, 16.76)	4.15 (0.09, 1.69)	23.15 (0.07, 65.41)	17.71 (7.88, 35.05)	29.60 (4.78, 51.11)	33.11 (0.11, 249.17)	36.22 (0.12, 64.01)
$\tau^2_{\beta,1}$	0.61 (0.058, 2.18)	0.78 (0.05, 0.20)	5.73 (0.72, 22.15)	0.69 (0.05, 2.99)	3.41 (0.07, 20.66)	9.50 (0.06, 47.48)	1.69 (0.05, 2.53)	22.05 (0.06, 64.39)	-	2.43 (0.08, 12.74)	1.40 (0.04, 10.15)	5.90 (0.06, 43.43)
$\tau^2_{\beta,2}$	-	-	-	2.63 (0.05, 15.08)	-	-	2.25 (0.05, 0.55)	-	-	-	-	-
$\tau^2_{\beta,3}$	1.20 (0.26, 3.78)	3.67 (0.73, 3.78)	1.28 (0.06, 6.19)	2.41 (0.06, 12.88)	2.33 (0.05, 13.23)	3.41 (0.05, 6.77)	0.41 (0.03, 0.19)	-	3.05 (0.05, 23.98)	0.16 (0.03, 0.65)	-	2.47 (0.06, 13.12)
$\tau^2_{\beta,4}$	0.14 (0.03, 0.49)	-	0.26 (0.03, 1.08)	-	-	-	-	-	13.51 (0.08, 53.99)	-	-	-
$\tau^2_{\beta,5}$	-	-	-	-	-	21.86 (0.08, 56.61)	-	-	-	-	1.43 (0.04, 8.22)	-
$\tau^2_{\beta,6}$	-	-	-	-	-	3.73 (0.06, 25.07)	-	35.70 (0.08, 62.87)	-	-	-	-
$\tau^2_{\alpha,0}$	1.12 (0.33, 3.06)	3.80 (0.78, 11.61)	2.97 (0.58, 11.47)	0.64 (0.47, 1.72)	1.46 (0.13, 6.21)	3.07 (0.07, 18.11)	5.96 (0.97, 20.93)	3.26 (0.22, 14.70)	2.82 (0.05, 15.55)	3.95 (0.88, 14.96)	3.40 (0.64, 13.41)	34.61 (0.04, 50.30)
$\tau^2_{\alpha,1}$	0.07 (0.02, 0.20)	0.16 (0.03, 0.56)	0.19 (0.03, 0.71)	0.13 (-0.29, 0.37)	0.31 (0.03, 1.29)	-	0.24 (0.03, 1.03)	-	-	0.42 (0.06, 1.56)	-	1.47 (0.04, 10.78)
$\tau^2_{\alpha,2}$	0.07 (0.02, 0.21)	-	1.06 (0.06, 5.67)	-	-	-	0.18 (0.03, 0.78)	-	-	-	-	4.76 (0.04, 17.81)
$\tau^2_{\alpha,3}$	2.07 (1.22, 3.02)	-	-	-	-	-	-	0.28 (-0.17, 0.76)	2.19 (0.05, 12.54)	0.29 (0.03, 1.42)	0.04 (-1.41, 1.33)	0.43 (0.04, 2.09)
$\tau^2_{\alpha,4}$	-	-	0.15 (0.03, 0.60)	-	-	0.75 (0.04, 5.07)	-	0.15 (-0.28, 0.61)	2.14 (0.03, 13.08)	-	24.64 (0.06, 49.06)	0.69 (0.03, 3.89)

GZ = Grazer, BW = Browser and NR = Non-ruminant; - = the parameter was not included in the best fit model. β0 and α0 = intercept; β1= elevation; β2 = elevation^2; β3 = slope; β4 = slope^2; β5 = NDVI; β6 = heterogeneity; α1 = survey efforts; α2 = survey efforts^2; α3 = distance from water; α4 = distance from the road. ^2 = quadratic term of the covariate.

4.4.2. Average ungulate group and species occupancies

Average occupancy (±) Standard Error (SE) of the grazer group was highest in Bloemhof (0.72 ± 0.09) and lowest in Pilanesberg (0.42 ± 0.08). Average occupancy of the browser group was comparable throughout the landscape being relatively high in Molopo (0.65 ± 0.09) and lowest in Pilanesberg (0.60 ± 0.05). Average occupancy of the non-ruminant group was highest in Mafikeng (0.73 ± 0.13) and lowest in Bloemhof (0.53 ± 0.08) (Figure 4.2-4.5). Zebra had the highest occupancy in Pilanesberg (0.92-0.94), while the lowest occupancy was of gemsbok (0.01-0.15). Warthog (0.90-0.96), eland (0.92-0.94) and gemsbok (0.88-0.90) had the highest occupancies in Mafikeng, Bloemhof and Molopo respectively (Table 4.4; Figure 4.2-4.4).



a) **b)**

Figure 4.2: Estimate of species richness and the associated uncertainty of the community of grazer, browser and non-ruminant groups across the Pilanesberg National Park from a spatial MSOM. Panel (a) shows posterior richness means and panel (b) shows predicted occurrence probability for ungulates in each group. 1=blue wildebeest, 2=buffalo, 3=common reedbuck, 4=gemsbok, 5=red hartebeest, 6=impala,7=mountain reedbuck, 8=sable, 9=springbok, 10=tsessebe, 11=waterbuck, 12=bushbuck, 13=duiker, 14=eland, 15=giraffe, 16=klipspringer, 17=greater kudu, 18=steenbok, 19=black rhino, 20=bush pig, 21=hippopotamus, 22=warthog, 23=white rhino, 24=zebra

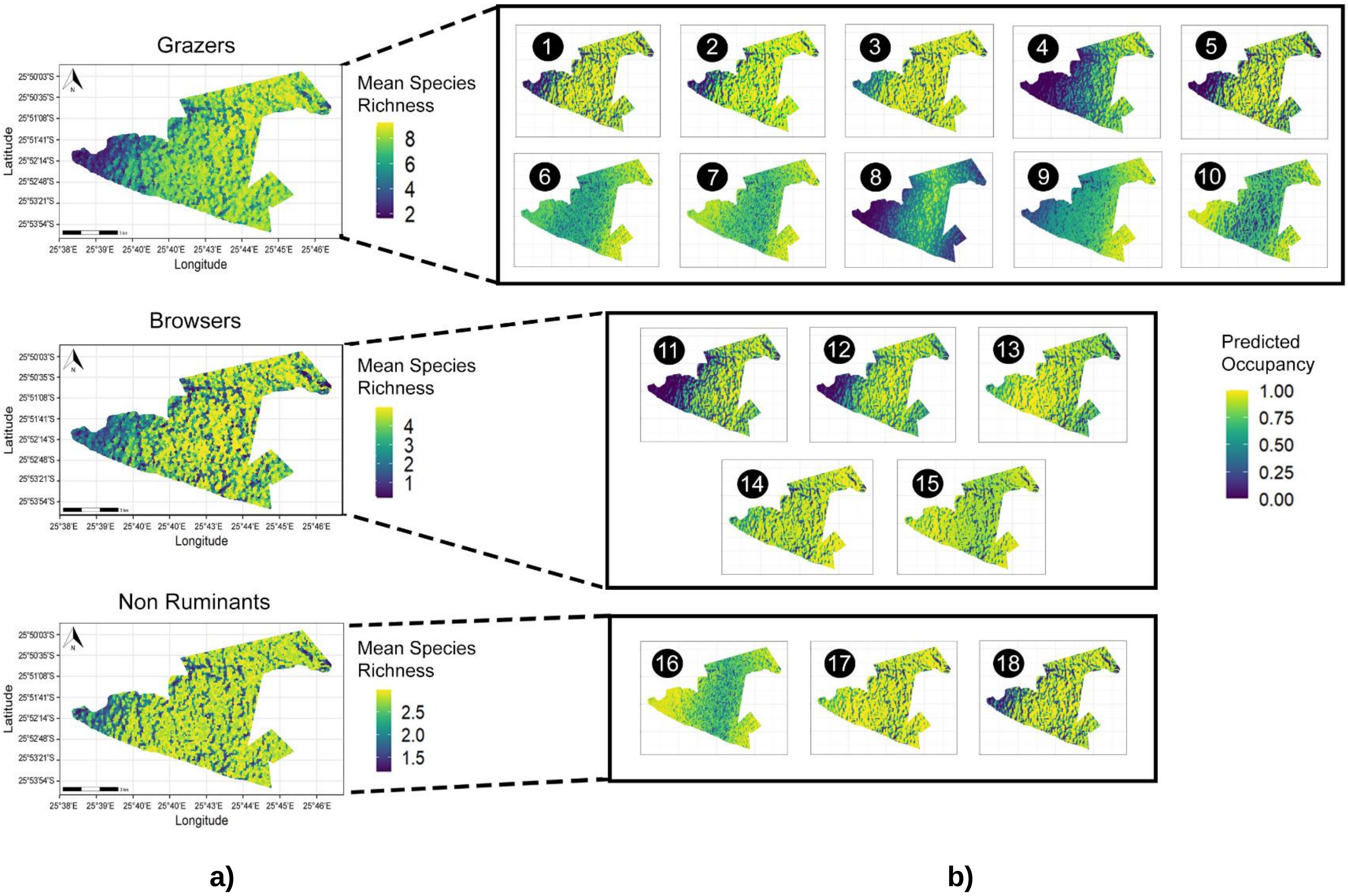


Figure 4.3: Estimate of species richness and the associated uncertainty of the community of grazer, browser and non-ruminant groups across the Mafikeng Game Reserve from a spatial MSOM. Panel (a) shows posterior richness means and panel (b) shows predicted occurrence probability for ungulates in each group. 1=black wildebeest, 2=blesbok, 3=buffalo, 4=common reedbuck, 5=gemsbok, 6=red hartebeest, 7=impala, 8=mountain reedbuck, 9=springbok, 10=waterbuck, 11=duiker, 12=eland, 13=giraffe, 14=greater kudu, 15=steenbok, 16=warthog, 17=white rhino, 18=zebra

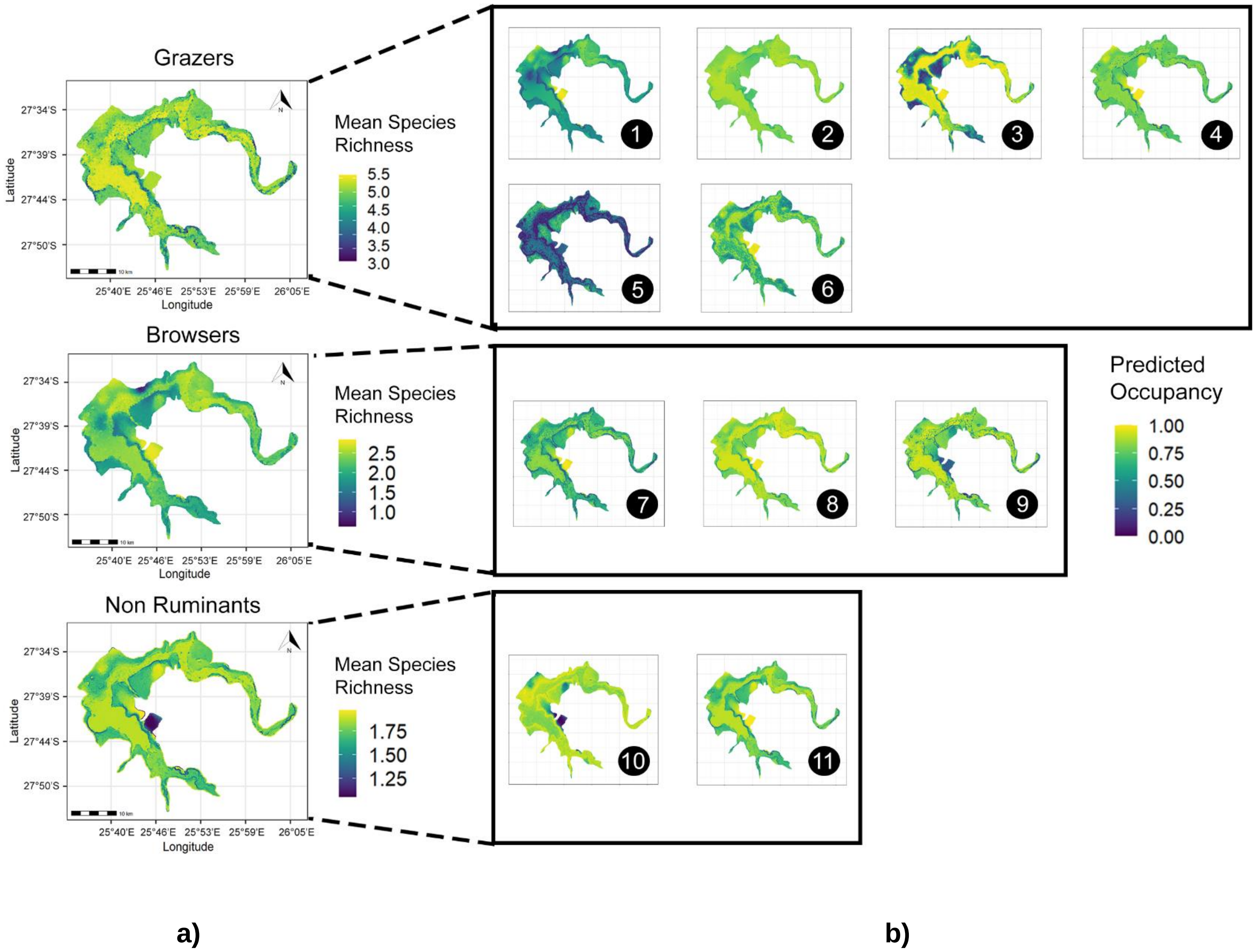


Figure 4.4: Estimate of species richness and the associated uncertainty of the community of grazer, browser and non-ruminant groups across the Bloemhof Dam Nature Reserve from a spatial MSOM. Panel (a) shows posterior richness means and panel (b) shows predicted occurrence probability for ungulates in each group. 1=black wildebeest, 2=blesbok, 3=gemsbok, 4=red hartebeest, 5=impala, 6=springbok, 7=duiker, 8=eland, 9=steenbok, 10=warthog, 11=zebra

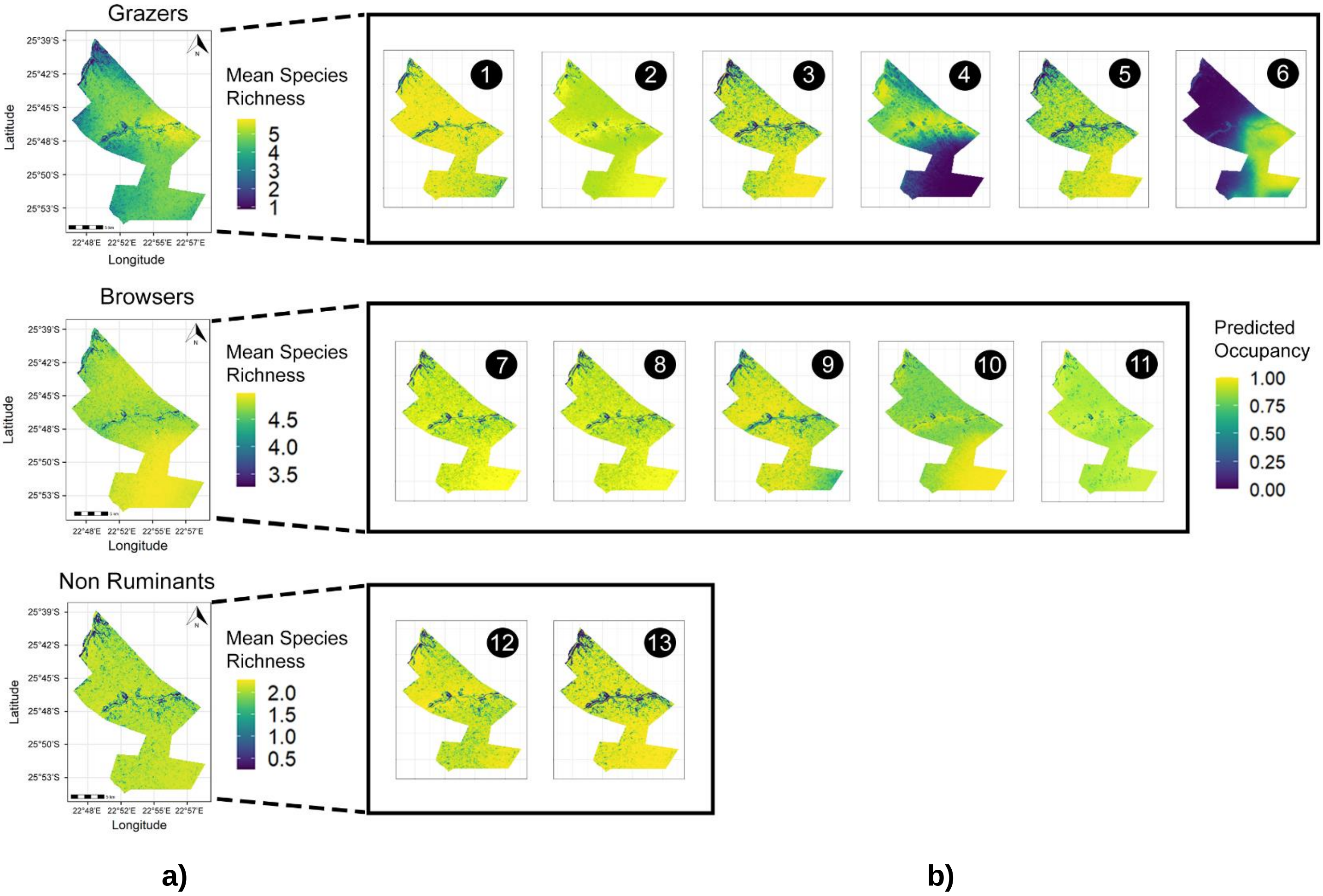


Figure 4.5: Estimate of species richness and the associated uncertainty of the community of grazer, browser and non-ruminant groups across the Molopo Game Reserve from a spatial MSOM. Panel (a) shows posterior richness means and panel (b) shows predicted occurrence probability for ungulates in each group. 1=blue wildebeest, 2=gemsbok, 3=red hartebeest, 4=impala, 5=springbok, 6=waterbuck, 7=duiker, 8=eland, 9=giraffe, 10= greater kudu, 11=steenbok, 12=warthog, 13=zebra

Table 4.4. Candidate model species-level occupancy estimates (95% credible intervals) for ungulate species in the three groups (grazer, browser and non-ruminant) across NW Province, South Africa. Ψ (Psi) = is the probability of occurrence of species *i* at site *j*.

	Pilanesberg		**Mafikeng**		**Bloemhof**		**Molopo**	
	Ψ	*95% CI*	*Ψ*	*95% CI*	*Ψ*	*95% CI*	*Ψ*	*95% CI*
Grazer	***n = 1349***		***n = 350***		***n = 457***		***n = 833***	
Black Wildebeest	–	–	0.75	(0.69-0.80)	0.76	(0.74-0.79)	–	–
Blesbok	–	–	0.78	(0.74-0.83)	0.84	(0.82-0.86)	–	–
Blue Wildebeest	0.76	(0.74-0.78)	–	–	–	–	0.84	(0.83-0.85)
Buffalo	0.28	(0.24-0.33)	0.77	(0.71-0.83)	–	–	–	–
Common Reed	0.09	(0.04-0.14)	0.38	(0.28-0.48)	–	–	–	–
Gemsbok	0.08	(0.01-0.15)	0.63	(0.56-0.71)	0.86	(0.84-0.88)	0.89	(0.88-0.90)
Red Hartebeest	0.44	(0.39-0.48)	0.69	(0.66-0.63)	0.74	(0.70-0.77)	0.84	(0.84-0.85)
Impala	0.89	(0.88-0.90)	0.90	(0.87-0.93)	0.23	(0.03-0.43)	0.28	(0.28-0.34)
Mount Reed	0.50	(0.48-0.52)	0.20	(0.03-0.38)	–	–	–	–
Sable	0.16	(0.08-0.25)	–	–	–	–	–	–
Springbok	0.30	(0.25-0.35)	0.82	(0.78-0.87)	0.86	(0.84-0.89)	0.53	(0.53-0.55)
Tsessebe	0.50	(0.47-0.54)	–	–	–	–	–	-
Waterbuck	0.57	(0.53-0.60)	0.54	(0.50-0.59)	–	–	0.28	(0.28-0.34)
Browser	***n = 1094***		***n = 157***		***n = 147***		***n = 901***	
Bushbuck	0.25	(0.11-0.39)	–	–	–	–	–	–
Duiker	0.37	(0.31-0.42)	0.37	(0.28-0.48)	0.35	(0.31-0.40)	0.44	(0.39-0.49)
Eland	0.72	(0.68-0.76)	0.64	(0.58-0.70)	0.93	(0.92-0.94)	0.83	(0.82-0.84)
Giraffe	0.59	(0.46-0.62)	0.73	(0.65-0.80)	–	–	0.63	(0.60-0.65)
Klipspringer	0.68	(0.65-0.70)	–	–	–	–	–	–
Greater Kudu	0.75	(0.74-0.76)	0.67	(0.63-0.72)	–	–	0.66	(0.65-0.67)
Steenbok	0.86	(0.83-0.89)	0.71	(0.65-0.77)	0.67	(0.62-0.72)	0.69	(0.68-0.70)
Non-Ruminant	***n = 1076***		***n = 139***		***n = 147***		***n = 328***	
Black Rhino	0.71	(0.69-0.74)	–	–	–	–	–	–
Bush pig	0.11	(0.03-0.19)	–	–	–	–	–	–
Hippo	0.24	(0.20-0.28)	–	–	–	–	–	–
Warthog	0.82	(0.80-0.85)	0.93	(0.90-0.96)	0.62	(0.60-0.65)	0.61	(0.60-0.62)
White Rhino	0.44	(0.43-0.46)	0.55	(0.50-0.60)	–	–	–	–
Zebra	0.93	(0.92-0.94)	0.73	(0.66-0.80)	0.53	(0.52-0.54)	0.80	(0.78-0.81)

n = number of detections (sighting of a group of animals together was counted as one detection); – = species not recorded from the study site

4.4.3. Spatial associations across the species spectrum

Although spatial segregation between feeder types was not very distinct in the study sites, it was more prevalent in the most species diverse sites (Pilanesberg and

Mafikeng). Bloemhof and Molopo, however, showed maximum species co-occurrence (Figure 4.6).

Evidence of spatial segregation within feeder groups was not consistent for grazers and browsers. For example, gemsbok spatially segregated from other grazers across the study sites, except at Bloemhof. Among browsers, duiker spatially segregated but not at Molopo. Impala and springbok spatially segregated from black wildebeest and gemsbok at Mafikeng but shared their spatial range with other grazing species elsewhere. Within the non-ruminant group, spatial segregation occurred between black rhino and white rhino, black rhino and hippo and black rhino and bush pig only in Pilanesberg (Figure 4.6).

Results from one-way ANOVA (Figure 4.7) did not reveal many significant relations ($p>0.05$) amongst body mass difference and spatial correlation coefficient within groups in the study sites. Although weak, spatial segregation within browsers, between comparable sized species (e.g., duiker and steenbok) and between large and small sized non-ruminants (white rhino and bush pig) was found in Pilanesberg. Among grazers, spatial segregation by sable and gemsbok from other grazers of all body sizes was found ($p<0.001$). Furthermore, in Mafikeng, spatial segregation was found between browsers of similar size (e.g., duiker and steenbok) and between large-sized and small-sized grazers (e.g., waterbuck and common reedbuck), browsers (e.g., giraffe and steenbok) and non-ruminants (e.g., white rhino and zebra). Similarly, at Bloemhof, large sized browsers spatially segregate with small sized browsers (e.g., eland and duiker). However, at Molopo, spatial segregation was not evident within the three groups (Figure 4.7; Figure S4.4).

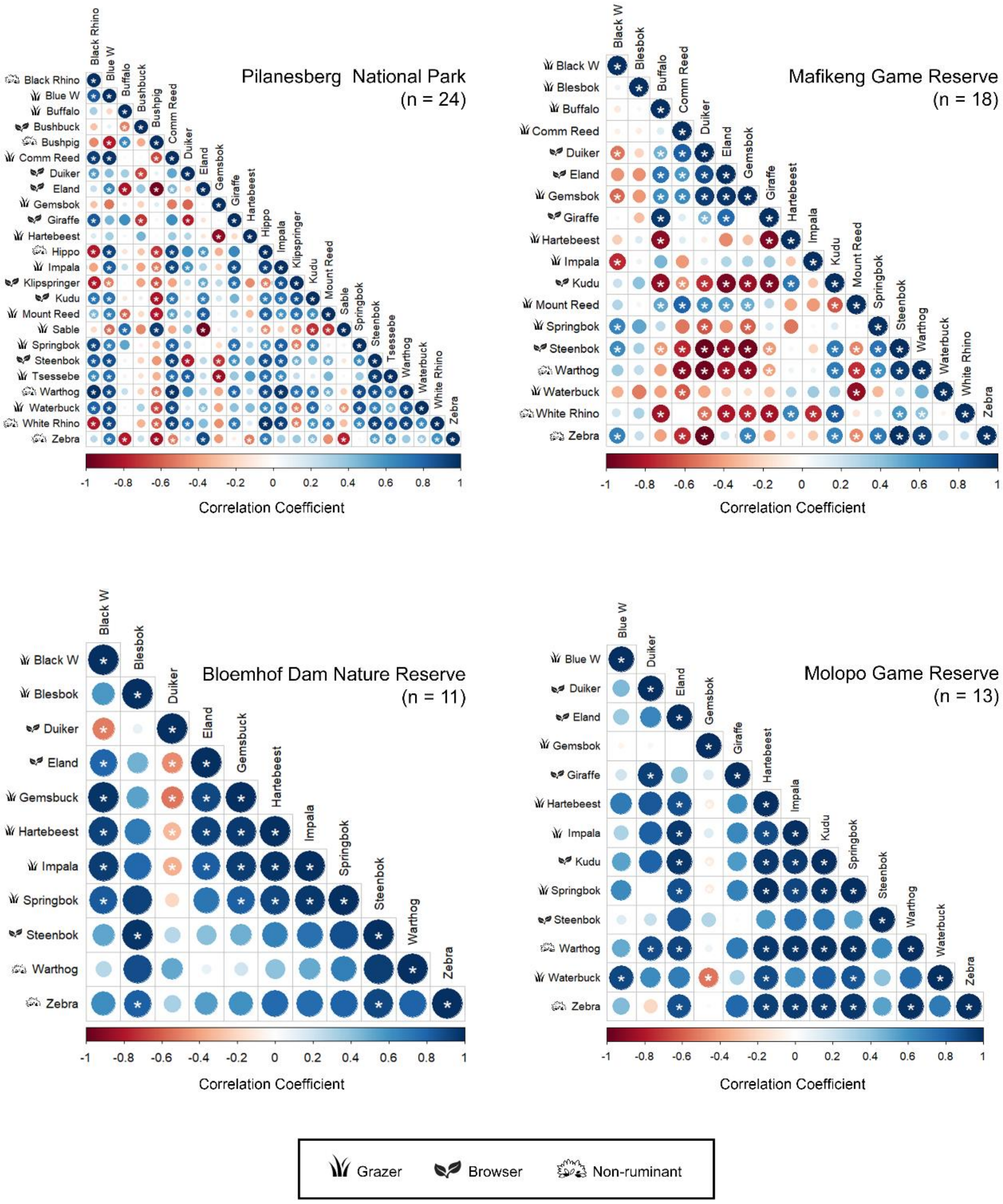


Figure 4.6: Residual covariance matrix for individual species spatial co-ocurrence in the four study sites. Star (*) represents significant level p<0.001. Comm Reed = Common Reedbuck, Black W = Black Wildebeest, Blue W = Blue Wildebeest, Mount Reed = Mountain Reedbuck. Colored band on the x-axis represents correlation coefficient gradient ranging from -1 to +1 with zero being no relation. Size and transparency of the circles represent strength of the spatial co-occurence. Blank squares indicate no relation.

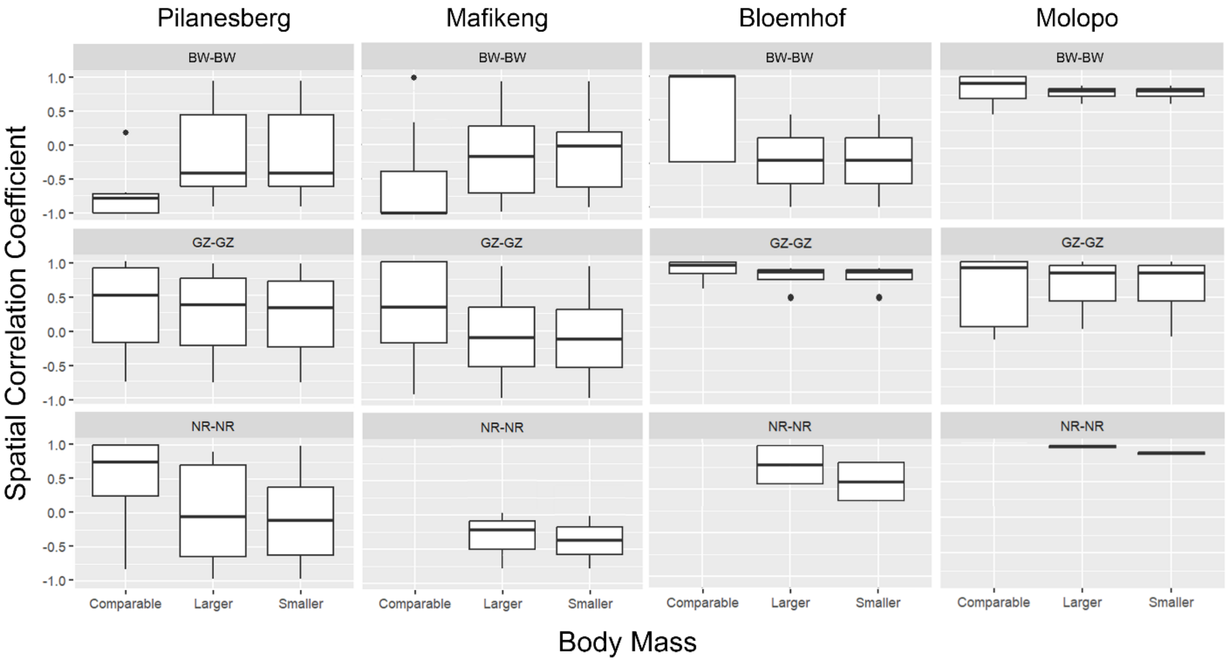


Figure 4.7: Relation between spatial correlation coefficients and body mass of ungulate groups from Pilanesberg, Mafikeng, Bloemhof and Molopo. Within-groups relations of difference in body mass and spatial correlation coefficient for grazers, browsers and non-ruminants are shown. GZ = grazers, BW = browsers and NR = non-ruminants. “Comparable”, “Larger” and “Smaller” refers to the different body mass class within group (GZ, BW or NR)

4.5. DISCUSSION

Spatial occupancy modelling confirmed that grazer species occupied areas of lower elevation, avoiding steep slopes, and close proximity to surface water. As expected, browser species occupied areas of varying elevations, varying slopes and high-quality forage. Non-ruminants were found across a range of elevations, away from steep slopes and in heterogeneous sites, as expected. Survey effort increased detection of grazers and non-ruminants, while it decreased detection of browsers due to the presence of small-sized cryptic species in the browser group. Average spatial occupancy of all feeder groups was the lowest in Pilanesberg despite the fact that diversity for each feeder type (grazer = 11, browser = seven, non-ruminant = six) was the highest. Although weak, evidence of spatial segregation between similar sized browsers were found only for Pilanesberg and Mafikeng. Bloemhof and Molopo showed no such spatial segregation patterns.

4.5.1. Factors affecting spatial distribution of ungulates

4.5.1.1. Hypothesis: Ruminant species select areas of high NDVI, soil nutrients and lower heterogeneity relative to non-ruminant species

The distribution of ungulates across NW Province was mainly influenced by the topography of the study sites, contrary to suggestions by earlier studies that NDVI, distance from water source and soil nutrients are important environmental determinants (East, 1984; Deliberato, 2017; Mariotti et al., 2020; Reece et al., 2023). Similarly, heterogeneity was selected as an influencing factor for ungulate occupancy only for non-ruminants in Mafikeng and for browsers in Bloemhof. Aerial counts were conducted in the late dry season, when NDVI, heterogeneity and soil nutrient content may not vary much spatially, so that their importance most likely declines during the dormant season. Therefore, the importance of NDVI and heterogeneity to ruminants in comparison to non-ruminants could not be thoroughly established.

4.5.1.2. Hypothesis: Grazing and non-ruminant species select areas of low elevation and avoid slopes while browsers prefer high elevation and slopes

Slope and elevation were the principal factors affecting ungulate distributions in the four study sites. As predicted, grazer’s occupancy was negatively related to the slope, as grazer species prefer open low elevation habitat (Fryxell et al., 2005; Kiffner & Lee, 2019; Mariotti et al., 2020). For example, buffalo and red hartebeest were generally found on lower elevations, while impala, a mixed feeder (Jarman, 1974; Dunham, 1982; Hunninck et al., 2020), occupied areas at both high and low elevations. Giraffe and steenbok were also found at low elevations in Pilanesberg and Mafikeng, suggesting soil moisture differences across the elevation gradient also structure spatial distribution of dicotyl species, all of which are not equally preferred by browsers. A number of species, for example, were not very selective of elevation: greater kudu and eland were found across a range of elevations and duiker occurred at higher elevations. A plausible explanation is that the root systems of grass species are shallow in comparison to those of dicotyls and hence the latter could persist across a range of elevations i.e., at least some species are less sensitive to moisture in the upper layers of soil (Lehmann et al., 2013; O'Brien et al., 2019). Slope had a negative influence on the distribution of non-ruminants across all sites (Figure S4.1, S4.2). My findings agree with previous studies that suggested non-ruminants and grazing ruminants mainly prefer feeding on open plains at low elevations with low-gradient slopes (Owen-Smith, 1988; Estes, 1991; Shrader & Perrin, 2006; Deliberato, 2017).

4.5.1.3. Hypothesis: Survey efforts positively affect detections of large sized species across all feeder groups

Longer flight paths resulted in higher detection of species across all groups. However, browser species showed lower detections with longer flight paths in Pilanesberg. The browser group in Pilanesberg included small-bodied cryptic species e.g., bushbuck, duiker and steenbok that may be difficult to spot through aerial surveys in the areas with complex vegetation cover and closed habitats of Pilanesberg (Jarman, 1974; Janis, 2008; Mucina & Rutherford, 2006). Across all groups, small-bodied species detection (common reedbuck, mountain reedbuck, duiker and steenbok) correlated negatively with survey efforts (Figure S4.3), yet there were no consistent results for detection of species of large body size with longer flight paths, and the hypothesis was therefore rejected.

4.5.1.4. Hypothesis: Ungulates prefer areas closer to surface water

Distance from water was not selected as an important covariate for ruminant ungulate distribution except with weak evidence for Bloemhof and Molopo. At Bloemhof, only the browser and non-ruminant groups preferred areas close to surface water (630.11 ± 59.27 m and 746.35 ± 60.34 m respectively). At Molopo, distance from surface water was an important determinant for all three feeder types (browser: 2510.67 ± 64.03 m, grazer: 2321.43 ± 48.32 m, non-ruminant: 1422 ± 86.54 m). Eland occupied areas farther from surface water in Bloemhof (5910.13 ± 67.23 m), while, it occupied areas close to surface water in Molopo (2358.61 ± 78.91 m). They have comparatively low surface water requirements (Skinner & Chimimba, 2005; Furstenburg, 2016a) but this is likely climate dependent hence the contrasting findings between Bloemhof and Molopo (the most arid study site).

4.5.1.5. Hypothesis: Ungulates generally prefer areas away from dirt roads

Distance from dirt roads contributed to the spatial occupancy of only browser and non-ruminant groups. Contrary to predictions, browsers were detected closer to the dirt roads, but only at Pilanesberg (509.80 ± 34.32 m) and Molopo (367.36 ± 36 m). Disturbance imposed by tourism activities therefore do not seem to be an important determinant, at least at the frequency of tourists visiting these two study sites. Eland and zebra occupied areas closer to dirt roads (698.75 ± 44.66 m and 318.58 ± 57.84 m respectively). During the dormant season, occasional rainfall and associated run-off provides green forage near roads (Ndibalema et al., 2008) and thus provides a plausible explanation why some ungulate species are attracted to roads. Why this was found for only two species is uncertain and additional investigations are needed to more thoroughly assess the influence of roads.

4.5.2. Group richness and occupancies

4.5.2.1. Hypothesis: Species diversity within a feeder group correlates with level of occupancy

Species richness within feeder groups was highest at Pilanesberg and lowest in Bloemhof. While the importance of rainfall and habitat heterogeneity as proximate factors contributing to species richness cannot be argued under ideal-free distribution scenarios, earlier introductions of game species into Pilanesberg (Anderson, 1986) might explain the high ungulate diversity at Pilanesberg. Despite the highest total number of species (24) and highest species richness within groups (grazer = 11, browser = seven, non-ruminant = six). Pilanesberg, had the lowest average across site occupancy of all the ungulate groups, indicating that occupancy of feeder groups did not correlate with species richness. The hypothesis was therefore rejected. Landscape structure, and a potentially strong link with predation risk, most likely explains much of this low occupancy in Pilanesberg (see Campos et al., 2013). Another plausible explanation is the spatial segregation amongst species of the same group (inter-specific competition) which limited the distribution of individual species (Reece et al., 2023) resulting in a lower occupancy level of individual species. Similarly, high occupancies in Bloemhof could be due to lower species richness, allowing larger landscape coverage and distribution of each species.

4.5.3. Spatial associations across feeder types

4.5.3.1. Hypothesis: Species diversity promotes spatial segregation

In the study sites with high species diversity (Pilanesberg and Mafikeng), spatial segregation between species was most distinct, irrespective of the feeder group examined. The classical view is that landscape structure complexities contribute towards species diversity (Hanski, 1998; Rainey & Travisano, 1998; Amarasekare, 2003; Geyrhofer & Brenner, 2020). The history of species reintroductions aside, the findings is consistent with earlier views that suggests high landscape heterogeneity promotes species diversity. Classical views further suggest spatial segregation among species reduces competition and promotes species diversity (Chesson, 2000; 2013; Chen et al., 2020).

4.5.3.2. Hypothesis: Within their respective groups; grazer and browser species spatially segregate, and this segregation is most distinct among species of similar body size

Our results showed no consistent patterns of spatial segregation among species within any feeder group, and thus our hypothesis was rejected. Gemsbok spatially segregates from most other grazers due to their specific habitat requirements in drier environment (Harris et al., 2015). Among browsers, duiker was the only species spatially segregating from other browsing species across the study sites. Duiker is found in grasslands only when adequate forbs and/or scatted woody shrubs are present with the grasslands (Furstenburg, 2008b). As they are highly selective, spatial segregation is probably a competition avoidance strategy. Non-ruminants spatially co-existed in all sites except Pilanesberg, where black rhino, the only browsing non-ruminant (Estes, 1991, Kiffner & Lee, 2019) spatially segregated from other grazing non-ruminants (Jarman, 1974; Kiffner & Lee, 2019).

Evidence of spatial segregation within feeding groups was detected for a number of species of comparable body size. These include duiker and bushbuck, blue wildebeest and gemsbok, gemsbok and waterbuck. However, spatial segregation was also evident among white rhino and species with large differences in body size. Also, they co-occurred with hippo, a non-ruminant of similar body size. At Bloemhof, duiker displayed negative co-occurrence with other species regardless of their body size or feeder group, possibly a reflection of its highly selective foraging strategy (Furstenburg, 2008b). Evidence of the importance of body size in spatial segregation within feeder groups was not as strong compared to earlier studies studies (see Prins & Olff, 1998; Kleynhans et al., 2011), which suggests, other factors (life cycle stage, sex of the species etc.) may have contributed to spatial occupancy and segregation patterns (Ruel & Ayres, 1999; Hart et al., 2016).

While the results of this study suggest spatial segregation as a mechanism of resource partitioning (Tilman, 1982) facilitates ungulate co-existence, occupancy of ungulates may change seasonally and with changing environmental conditions (Charles-Dominique et al., 2016). It is interesting to note however, that no relation between reserve size and spatial segregation patterns was found. Other mechanisms need to be explored to advance our knowledge of community ecology such as niche separation through differing preferences for plant species, plant parts, and predation risk related to body size of the prey species (Hopcraft et al., 2010; du Toit & Olff, 2014).

4.6. CONCLUSION

The current study focussed on the environmental factors affecting ungulate species distribution across the NW Province and the spatial associations among species. Aerial surveys were conducted only in the late dry season each year, and hence the importance of elevation and slope should be interpreted within this context. Similarly, the irrelevance of NDVI throughout simply links to a lack of photosynthetic activities during the dormant season. Flight path, distance from surface water and dirt roads affected occupancy of ungulates. Despite the highest species diversity in the grazer group for all study sites, average occupancy of grazers was highest only in Bloemhof. This suggests that resources for grazers are generally more aggregated than for browsers during the dormant season. Lowest average occupancies across all groups were found in Pilanesberg, despite the highest species diversity across all groups, suggesting individual spatial avoidance and/or resource partitioning among species within each functional group. Spatial segregation between species was closely associated with species richness irrespective of study area size. Mafikeng, for example, is one-fifth the size of Bloemhof, yet demonstrated high spatial segregation compared to Bloemhof, with its lower species diversity. No consistent patterns of spatial segregation among species within any feeder group was found. However, spatial segregation within similar sized browsers was observed only in Pilanesberg and Mafikeng. Consistent with earlier views (see Tilman, 1982), this study demonstrates that co-existence with high ungulate diversity is possibly achieved through spatial segregation. However, occupancy data spanning annual cycles can provide further insights into co-existence and competition among ungulates. Furthermore, coexistence among species is highly context dependent so should be the management decisions aimed at promoting integrity of ungulate assemblages (see Champagne et al., 2021).

4.7. REFERENCE

Acocks, J. (1988). Veld Types of South Africa, Third Edition. *Memoirs of the Botanical Survey of South Africa*, *57*.

Adcock, K. (1991). Vegetation map of Molopo Game Reserve. Bophuthatswana Parks Board, Pilanesberg National Park.

Amarasekare, P. (2003). Competitive coexistence in spatially structured environments: A synthesis. In *Ecology Letters* (Vol. 6, Issue 12). https://doi.org/10.1046/j.1461-0248.2003.00530.x

Anderson, J. L. (1986). Restoring a wilderness: the reintroduction of wildlife to an African national park. *International Zoo Yearbook*, *24*(1). https://doi.org/10.1111/j.1748-1090.1985.tb02538.x

Anderson, T. M., Dong, Y., & Mcnaughton, S. J. (2006). Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture and grazing. *Journal of Ecology*, *94*(6). https://doi.org/10.1111/j.1365-2745.2006.01148.x

Arsenault, R., & Owen-Smith, N. (2011). Competition and coexistence among short-grass grazers in the Hluhluwe-iMfolozi Park, South Africa. *Canadian Journal of Zoology*, *89*(10). https://doi.org/10.1139/z11-067

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American. Vol. 225: 86–93.

Bempah, G., Afrifa, J. K., Nartey, M. A., & Lu, C. (2022). Variations in Patch Use by Ruminant and Non-ruminant Herbivores in a Tropical Wildlife Reserve, Ghana. *Journal of Resources and Ecology*, *13*(6). https://doi.org/10.5814/j.issn.1674-764x.2022.06.018

Bian, G., Ma, L., Su, Y., & Zhu, W. (2013). The Microbial Community in the Feces of the White Rhinoceros (*Ceratotherium simum*) as Determined by Barcoded Pyrosequencing Analysis. *PLoS ONE*, *8*(7). https://doi.org/10.1371/journal.pone.0070103

Bireda, M., & Yihune, M. (2020). Foraging Ecology and Diurnal Activity Patterns of Klipspringer (*Oreotragus oreotragus*) in Yetefet Woyenat Forest, East Gojjam, Ethiopia. *International Journal of Zoology*, *2020*. https://doi.org/10.1155/2020/4930915

Boyers, M. F. (2011). Do Zebra (*Equus Quagga*) select for greener grass within the foraging area? In *October*.

Brockett, B. H. (2002). Accuracy, bias and precision of helicopter-based counts of black rhinoceros in Pilanesberg National Park, South Africa. *African Journal of Wildlife Research*, *32*(2).

Bukombe, J., Senzota, R. B., Fryxell, J. M., Kittle, A., Kija, H., Hopcraft, J. G. C., Mduma, S., & Sinclair, A. R. E. (2016). Do animal size, seasons and vegetation type influence detection probability and density estimates of Serengeti ungulates? *African Journal of Ecology*, *54*(1). https://doi.org/10.1111/aje.12255

Campos, P. R. A., Rosas, A., de Oliveira, V. M., & Gomes, M. A. F. (2013). Effect of Landscape Structure on Species Diversity. *PLoS ONE*, *8*(6). https://doi.org/10.1371/journal.pone.0066495

Castley, J. G., Boshoff, A. F., & Kerley, G. I. H. (2001). Compromising South Africa's natural biodiversity–inappropriate herbivore introductions. South African Journal of Science 97: 344–348.

Champagne, E., Royo, A. A., Tremblay, J., & Raymond, P. (2021). Tree assisted migration in a browsed landscape: Can we predict susceptibility to herbivores? Forest Ecology and Management, 498, 119576. https://doi.org/10.1016/j.foreco.2021.119576

Charles-Dominique, T., Davies, T. J., Hempson, G. P., Bezeng, B. S., Daru, B. H., Kabongo, R. M., Maurin, O., Muasya, A. M., Van Der Bank, M., & Bond, W. J. (2016). Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(38). https://doi.org/10.1073/pnas.1607493113

Chen, D., Liao, J., Bearup, D., & Li, Z. (2020). Habitat heterogeneity mediates effects of individual variation on spatial species coexistence. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1919). https://doi.org/10.1098/rspb.2019.2436

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chesson, P. (2013). Species competition and predation. In Ecological systems: selected entries from the encyclopedia of sustainability science and technology (ed. R Leemans), pp. 223–256. New York, NY: Springer.

Chirima, G. J., Owen-Smith, N., Erasmus, B. F. N., & Parrini, F. (2013). Distributional niche of relatively rare sable antelope in a South African savanna: Habitat versus biotic relationships. *Ecography*, *36*(1). https://doi.org/10.1111/j.1600-0587.2012.07333.x

Clauss, M., & Rössner, G. E. (2014). Old world ruminant morphophysiology, life history, and fossil record: Exploring key innovations of a diversification sequence. *Annales Zoologici Fennici*, *51*(1–2). https://doi.org/10.5735/086.051.0210

Clutton-Brock, T. H., & Ball, M. E. (1987). Rhum: the natural history of an island. Edinburgh University Press, Edinburgh.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. (1982). Red Deer: Behaviour and Ecology of Two Sexes. University of Chicago Press, Chicago

Codron, D., Hofmann, R. R., & Clauss, M. (2019). *Morphological and Physiological Adaptations for Browsing and Grazing*. https://doi.org/10.1007/978-3-030-25865-8_4

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*. https://doi.org/10.1016/j.anbehav.2013.11.027

Cromsigt, J. P. G. M., & Olff, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. *Ecology*, *87*(6). https://doi.org/10.1890/0012-9658(2006)87[1532:RPASGM]2.0.CO;2

Datta, A., Banerjee, S., Finley, A. O., & Gelfand, A. E. (2016). Hierarchical Nearest-Neighbor Gaussian Process Models for Large Geostatistical Datasets. *Journal of the American Statistical Association*, *111*(514). https://doi.org/10.1080/01621459.2015.1044091

Deliberato, H. G. (2017). Resources overlap and the distribution of grazer assemblages at Telperion and Ezemvelo Nature Reserves. Master's thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa.

Demment, M. W., & Van Soest, P. J. (1985). A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. The American Naturalist, 125, 641 - 672.

Devarajan, K., Morelli, T. L., & Tenan, S. (2020). Multi-species occupancy models: review, roadmap, and recommendations. *Ecography*, *43*(11). https://doi.org/10.1111/ecog.04957

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470). https://doi.org/10.1198/016214505000000015

Doser, J. W., Finley, A. O., & Banerjee, S. (2023). Joint species distribution models with imperfect detection for high-dimensional spatial data. *Ecology*, *104*(9). https://doi.org/10.1002/ecy.4137

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, *13*(8). https://doi.org/10.1111/2041-210X.13897

Duncan, C., Chauvenet, A. L. M., McRae, L. M., & Pettorelli, N. (2012). Predicting the Future Impact of Droughts on Ungulate Populations in Arid and Semi-Arid Environments. *PLoS ONE*, *7*(12). https://doi.org/10.1371/journal.pone.0051490

Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G., & Lloyd, M. (1990). Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence. *Oecologia*, *84*(3). https://doi.org/10.1007/BF00329768

du Toit, J. T., & Olff, H. (2014). Generalities in grazing and browsing ecology: Using across-guild comparisons to control contingencies. In *Oecologia* (Vol. 174, Issue 4). https://doi.org/10.1007/s00442-013-2864-8

East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, *22*(4). https://doi.org/10.1111/j.1365-2028.1984.tb00700.x

Estes, R. D. (1991). The behaviour guide to African mammals, including hoofed mammals, carnivores, primates. – Univ. of California Press.

Environmental Systems Research Institute (ESRI) (2020). ArcGIS Desktop 10.8 Geostatistical Analyst.

Fischer, F., & Linsenmair, K. E. (2001). Decreases in ungulate population densities. Examples from the Comoé National Park, Ivory Coast. *Biological Conservation*, *101*(2). https://doi.org/10.1016/S0006-3207(00)00130-0

Fryxell, J. M., Wilmshurst, J. F., Sinclair, A. R. E., Haydon, D. T., Holt, R. D., & Abrams, P. A. (2005). Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*, *8*(3). https://doi.org/10.1111/j.1461-0248.2005.00727.x

Furstenburg, D. (2008a). Focus on the steenbok (Raphicerus campestris). S A Hunter 10021:40-42.

Furstenburg, D. (2008b). Fokus op die gewone / Grysduiker (Sylvicapra grimmia). S A Hunter 11022:38-41.

Furstenburg, D. (2016a). Eland (Tragelaphus oryx) Management. In: Eds. Pamela Oberem, The New Game Rancher. BRIZA Publisher, Pretoria. pp 173-179. ISBN 978-1-920217-62-4

Furstenburg, D. (2016b). Blesbok & Bontebok Damaliscus pygargus Management. In: Eds. Pamela Oberem, The New Game Rancher. BRIZA Publisher, Pretoria. pp 196-204. ISBN 978-1-920217-62-4

Furstenburg, D. (2016c). Tsessebe (Damaliscus lunatus lunatus) Management. In: Eds. Pamela Oberem, The New Game Rancher. BRIZA Publisher, Pretoria. pp 205-210. ISBN 978-1-920217-62-4

Furstenburg, D. (2023). Wildlife & Game southern Africa PART 10 - The Springbok as a Species Antidorcas marsupialis (Zimmerman, 1780). Veteran_SA.: pp 18-26.

Gaidet, N., & Gaillard, J. M. (2008). Density-dependent body condition and recruitment in a tropical ungulate. *Canadian Journal of Zoology*, *86*(1). https://doi.org/10.1139/Z07-111

Gelfand, A. E., Schmidt, A. M., Wu, S., Silander, J. A., Latimer, A., & Rebelo, A. G. (2005). Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society. Series C: Applied Statistics*, *54*(1). https://doi.org/10.1111/j.1467-9876.2005.00466.x

Geyrhofer, L., & Brenner, N. (2020). Coexistence and cooperation in structured habitats. *BMC Ecology*, *20*(1). https://doi.org/10.1186/s12898-020-00281-y

Goslar, A., Prosch, L., Ingle, S., Benedek, F., Hudson, K., Mampye, A., Tshivhase, N and Lees, Z. (2008). North West Province Environment Outlook. A report on the state of the environment. Submitted to North West Department of Agriculture, Conservation and Environment.

Hanski, I. (1998). Metapopulation dynamics. In *Nature* (Vol. 396, Issue 6706). https://doi.org/10.1038/23876

Harris, G., Sanderson, J. G., Erz, J., Lehnen, S. E., & Butler, M. J. (2015). Weather and prey predict mammals' visitation to water. *PLoS ONE*, *10*(11). https://doi.org/10.1371/journal.pone.0141355

Hart, S. P., Schreiber, S. J., & Levine, J. M. (2016). How variation between individuals affects species coexistence. *Ecology Letters*, *19*(8). https://doi.org/10.1111/ele.12618

Hein, K. A., Jaeger, S. R., Tom Carr, B., & Delahunty, C. M. (2008). Comparison of five common acceptance and preference methods. *Food Quality and Preference*, *19*(7). https://doi.org/10.1016/j.foodqual.2008.06.001

Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J., & Vickers, K. J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, *90*(3). https://doi.org/10.1111/brv.12145

Hengl, T., Heuvelink, G. B. M., Kempen, B., Leenaars, J. G. B., Walsh, M. G., Shepherd, K. D., Sila, A., MacMillan, R. A., De Jesus, J. M., Tamene, L., & Tondoh, J. E. (2015). Mapping soil properties of Africa at 250 m resolution: Random forests significantly improve current predictions. *PLoS ONE*, *10*(6). https://doi.org/10.1371/journal.pone.0125814

Herfindal, I., Tremblay, J. P., Hansen, B. B., Solberg, E. J., Heim, M., & Sæther, B. E. (2009). Scale dependency and functional response in moose habitat selection. *Ecography*, *32*(5). https://doi.org/10.1111/j.1600-0587.2009.05783.x

Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouché, P., Ipavec, A., Convers, A., Ombredane, D., & de Visscher, M. N. (2010). Spatial avoidance of invading pastoral cattle by wild ungulates: Insights from using point process statistics. *Biodiversity and Conservation*, *19*(7). https://doi.org/10.1007/s10531-010-9822-0

Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. Ecological Monographs, 85, 3-28.

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. In

Trends in Ecology and Evolution (Vol. 25, Issue 2). https://doi.org/10.1016/j.tree.2009.08.001

Hrabar, H., & du Toit, J. T. (2005). Dynamics of a protected black rhino (Diceros bicornis) population: Pilanesberg National Park, South Africa. *Animal Conservation*, *8*(3). https://doi.org/10.1017/S1367943005002234

Hunninck, L., May, R., Jackson, C. R., Palme, R., Røskaft, E., & Sheriff, M. J. (2020). Consequences of climate-induced vegetation changes exceed those of human disturbance for wild impala in the Serengeti ecosystem. *Conservation Physiology*, *8*(1). https://doi.org/10.1093/conphys/coz117

Janis, C. (2008). *An Evolutionary History of Browsing and Grazing Ungulates*. https://doi.org/10.1007/978-3-540-72422-3_2

Jarman, P. J. (1974). The Social Organisation of Antelope in Relation to Their Ecology. *Behaviour*, *48*(1–4). https://doi.org/10.1163/156853974X00345

Kasiringua, E., Procheş, & Kopij, G. (2019). Population structure of ungulates in Waterberg National Park, Namibia. *Vestnik Zoologii*, *53*(1). https://doi.org/10.2478/vzoo-2019-0004

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (Diceros bicornis L.) populations from aerial counts. *Global Ecology and Conservation*, *19*. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., & Lee, D. E. (2019). *Population Dynamics of Browsing and Grazing Ungulates in the Anthropocene*. https://doi.org/10.1007/978-3-030-25865-8_6

Kiffner, C., Nagar, S., Kollmar, C., & Kioko, J. (2016). Wildlife species richness and densities in wildlife corridors of Northern Tanzania. *Journal for Nature Conservation*, *31*. https://doi.org/10.1016/j.jnc.2016.02.006

Kiffner, C., Rheault, H., Miller, E., Scheetz, T., Enriquez, V., Swafford, R., Kioko, J., & Prins, H. H. T. (2017). Long-term population dynamics in a multi-species assemblage of large herbivores in East Africa. *Ecosphere*, *8*(12). https://doi.org/10.1002/ecs2.2027

Kihwele, E. S., Mchomvu, V., Owen-Smith, N., Hetem, R. S., Hutchinson, M. C., Potter, A. B., Olff, H., & Veldhuis, M. P. (2020). Quantifying water requirements of African ungulates through a combination of functional traits. *Ecological Monographs*, *90*(2). https://doi.org/10.1002/ecm.1404

Kleynhans, E. J., Jolles, A. E., Bos, M. R. E., & Olff, H. (2011). Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos*, *120*(4). https://doi.org/10.1111/j.1600-0706.2010.18712.x

Kruger, A. C., & Nxumalo, M. P. (2017). Historical rainfall trends in South Africa: 1921–2015. *Water SA*, *43*(2). https://doi.org/10.4314/wsa.v43i2.12

Leblond, M., Dussault, C., & Ouellet, J. P. (2013). Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology*, *289*(1). https://doi.org/10.1111/j.1469-7998.2012.00959.x

Lee, T. D., Barrett, J. P., & Hartman, B. (2005). Elevation, substrate, and the potential for climate-induced tree migration in the White Mountains, New Hampshire, USA. *Forest Ecology and Management*, *212*(1–3). https://doi.org/10.1016/j.foreco.2005.03.007

Lehmann, D., Mfune, J. K. E., Gewers, E., Cloete, J., Brain, C., & Voigt, C. C. (2013). Dietary Plasticity of Generalist and Specialist Ungulates in the Namibian Desert: A Stable Isotopes Approach. *PLoS ONE*, *8*(8). https://doi.org/10.1371/journal.pone.0072190

Li, S., Zhao, Y., Xiao, W., Yellishetty, M., & Yang, D. (2022). Identifying ecosystem service bundles and the spatiotemporal characteristics of trade-offs and synergies in coal mining areas with a high groundwater table. *Science of the Total Environment*, *807*. https://doi.org/10.1016/j.scitotenv.2021.151036

Louw, C. J., Ferreira, S. M., & Marshal, J. P. (2022). Water dependence structures predation risk for large herbivores in insular protected areas. *Mammalian Biology*, *102*(5–6). https://doi.org/10.1007/s42991-022-00278-8

Louw, C. J., Marshal, J. P., Nel, H. P., & Funston, P. J. (2019). Sex-Specific Predation Patterns on Kudu and Impala. *African Journal of Wildlife Research*, *49*(1). https://doi.org/10.3957/056.049.0077

Macandza, V. A., Owen-Smith, N., & Cain, I. W. (2012). Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *Journal of Zoology*, *287*(3). https://doi.org/10.1111/j.1469-7998.2012.00900.x

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8). https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Mariotti, E., Parrini, F., Louw, C. J., & Marshal, J. P. (2020). What grass characteristics drive large herbivore feeding patch selection? A case study from a South African grassland protected area. *African Journal of Range and Forage Science*. https://doi.org/10.2989/10220119.2020.1768146

McHugh, D., Goldingay, R. L., Link, J., & Letnic, M. (2019). Habitat and introduced predators influence the occupancy of small threatened macropods in subtropical Australia. *Ecology and Evolution*, *9*(11). https://doi.org/10.1002/ece3.5203

McNaughton, S. J. (1988). Mineral nutrition and spatial concentrations of African ungulates. *Nature*, *334*(6180). https://doi.org/10.1038/334343a0

McNaughton, S. J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature*, *345*(6276). https://doi.org/10.1038/345613a0

McNaughton, S. J., & Georgiadis, N. J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, *17*(1). https://doi.org/10.1146/annurev.es.17.110186.000351

M’soka, J., Creel, S., Becker, M. S., & Murdoch, J. D. (2017). Ecological and anthropogenic effects on the density of migratory and resident ungulates in a human-inhabited protected area. African Journal of Ecology, 55, 618-631.

Mucina, L., & Rutherford, M. C. (2006). The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, Strelitzia.

Murray, M. G., & Illius, A. W. (2000). Vegetation modification and resource competition in grazing ungulates. *Oikos*, *89*(3). https://doi.org/10.1034/j.1600-0706.2000.890309.x

Ndibalema, V. G., Mduma, S., Stokke, S., & Røskaft, E. (2008). Relationship between road dust and ungulate density in Serengeti National Park, Tanzania. *African Journal of Ecology*, *46*(4). https://doi.org/10.1111/j.1365-2028.2007.00898.x

Nel, H. P. (2018). Population estimates for large herbivores and predators in protected areas in the North West Parks Board. Unpublished Technical Report.

Novellie, P. A., & Knight, M. (1994). Repatriation and translocation of ungulates into South African national parks: an assessment of past attempts. Koedoe 37: 115–119.

NWPTB (2020). North West Parks Board official website [WWW Document]. URL https://ho.org.za/parks/ [Accessed: 05/04/2020].

Nyirenda, M., Letlojane, L., & Syakalima, M. (2016). Prevalence of Brucella abortus in buffaloes of Mafikeng game reserve, North West province, South Africa: A retrospective study. *Indian Journal of Animal Research*, *50*(2). https://doi.org/10.18805/ijar.5923

O'Brien, T. G., Ahumada, J., Akampurila, E., et al. (2019). Camera trapping reveals trends in forest duiker populations in African National Parks. Remote Sensing in Ecol. Conserv. Vol. 6 (2):168–180. doi: 10.1002/rse2.132

Ofstad, E. G., Herfindal, I., Solberg, E. J., & Sæther, B. E. (2016). Home ranges, habitat and body mass: Simple correlates of home range size in ungulates. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 283, Issue 1845). https://doi.org/10.1098/rspb.2016.1234

Ogutu, J. O., Reid, R. S., Piepho, H. P., Hobbs, N. T., Rainy, M. E., Kruska, R. L., Worden, J. S., & Nyabenge, M. (2014). Large herbivore responses to surface water and land use in an East African savanna: Implications for conservation and human-wildlife conflicts. *Biodiversity and Conservation*, *23*(3). https://doi.org/10.1007/s10531-013-0617-y

Owen-Smith, R. N. (1988). Megaherbivores. In *Megaherbivores*. https://doi.org/10.1017/cbo9780511565441

Owen-Smith, R. N. (2002). Adaptive Herbivore Ecology. In *Adaptive Herbivore Ecology*. https://doi.org/10.1017/cbo9780511525605

Pettorelli, N., Bro-Jorgensen, J., Durant, S. M., Blackburn, T., & Carbone, C. (2009). Energy availability and density estimates in African ungulates. *American Naturalist*, *173*(5). https://doi.org/10.1086/597379

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., & Mccarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5). https://doi.org/10.1111/2041-210X.12180

Prins, H. H. T., & Olff, H. (1998). Species richness of African grazer assemblages: towards a functional explanation. In *Dynamics of tropical communities*.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rainey, P. B., & Travisano, M. (1998). Adaptive radiation in a heterogeneous environment. *Nature*, *394*(6688). https://doi.org/10.1038/27900

Redfern, J. V., Grant, R., Biggs, H., & Getz, W. M. (2003). Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, *84*(8). https://doi.org/10.1890/01-0625

Reece, S. J., Tambling, C. J., Leslie, A. J., & Radloff, F. G. T. (2023). Patterns and predictors of ungulate space use across an isolated Miombo woodland reserve. *Journal of Zoology*, *320*(2). https://doi.org/10.1111/jzo.13059

Rodgers, W. A. (1996). The Miombo woodlands. In East African Ecosystems and their conservation (eds. McClanaham, T.R., Young, T.P.), Oxford University, Oxford

Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., Parsons, A. W., & Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, *7*(10). https://doi.org/10.1111/2041-210X.12587

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. In *Trends in Ecology and Evolution* (Vol. 14, Issue 9). https://doi.org/10.1016/S0169-5347(99)01664-X

Schuette, P., Creel, S., & Christianson, D. (2016). Ungulate distributions in a rangeland with competitors, predators and pastoralists. *Journal of Applied Ecology*, *53*(4). https://doi.org/10.1111/1365-2664.12610

Seitlhamo, W. S. (2011). Mapping and quantifying the impact of grazing around water points in a small semi-arid savanna game reserve. Master's thesis submitted to University of the Witwatersrand, Johannesburg.

Selebatso, M., Maude, G., & Fynn, R. W. S. (2018). Adaptive Foraging of Sympatric Ungulates in the Central Kalahari Game Reserve, Botswana. *African Journal of Wildlife Research*, *48*(2). https://doi.org/10.3957/056.048.023005

Seydack, A. H., Grant, C. C., Smit, I. P., Vermeulen, W. J., Baard, J., & Zambatis, N. (2012). Large herbivore population performance and climate in a South African semi-arid savanna. *Koedoe*, *54*(1). https://doi.org/10.4102/koedoe.v54i1.1047

Shrader, A. M., & Perrin, M. R. (2006). Influence of density on the seasonal utilization of broad grassland types by white rhinoceroses. *African Zoology*, *41*(2). https://doi.org/10.1080/15627020.2006.11407370

Simenstad, C., Reed, D., & Ford, M. (2006). When Is Restoration Not? Ecol. Eng.26, 27–39. doi:10.1016/j.ecoleng.2005.09.007

Sinclair, A. R. E. (1985). Does Interspecific Competition or Predation Shape the African Ungulate Community? *The Journal of Animal Ecology*, *54*(3). https://doi.org/10.2307/4386

Sinclair, A. R. E. (2000). Adaptation, niche partitioning and coexistence of African Bovidae. Clues to the past. In (Eds.) Antelopes, deer and relatives edited by E.S. Vrba and G.B. Schaller. New York.

Skinner, J. D., & Chimimba, C. T. (2005). The Mammals of the Southern African Sub-region. In *The Mammals of the Southern African Sub-region*. https://doi.org/10.1017/cbo9781107340992

Solomon, D.S., & Leak, W.B. (1994). Migration of tree species in New England based on elevational and regional analyses. Forest Service research paper (Final).

Spritzer, M. D., Solomon, N. G., & Meikle, D. B. (2005). Influence of scramble competition for mates upon the spatial ability of male meadow voles. *Animal Behaviour*, *69*(2). https://doi.org/10.1016/j.anbehav.2004.03.015

Taylor, W. A., & Skinner, J. D. (2006). A review of the social organisation of mountain reedbuck, Redunca fulvorufula, and grey rhebok, Pelea capreolus, in relation to their ecology. *Transactions of the Royal Society of South Africa*, *61*(1). https://doi.org/10.1080/00359190609519188

Tilman, G. D. 1982. Resource Competition and Community Structure (Princeton University Press).

Treydte, A. C., Bernasconi, S. M., Kreuzer, M., & Edwards, P. J. (2006). Diet of the common warthog (*Phacochoerus africanus*) on former cattle grounds in a Tanzanian savanna. *Journal of Mammalogy*, *87*(5). https://doi.org/10.1644/05-MAMM-A-336R2.1

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. In *Ecological Applications* (Vol. 13, Issue 6). https://doi.org/10.1890/02-5078

van Beest, F. M., Vander Wal, E., Stronen, A. V., Paquet, P. C., & Brook, R. K. (2013). Temporal variation in site fidelity: Scale-dependent effects of forage abundance and predation risk in a non-migratory large herbivore. *Oecologia*, *173*(2). https://doi.org/10.1007/s00442-013-2647-2

van Bommel, F. P. J., Heitkönig, I. M. A., Epema, G. F., Ringrose, S., Bonyongo, C., & Veenendaal, E. M. (2006). Remotely sensed habitat indicators for predicting distribution of impala (Aepyceros melampus) in the Okavango Delta, Botswana. *Journal of Tropical Ecology*, *22*(1). https://doi.org/10.1017/S0266467405002932

van Niekerk, J. H. (2011). Observations of Red-billed Spurfowl (Pternistis adspersus) in the arid Molopo Nature Reserve, North West Province, South Africa. *CHINESE BIRDS*, *2*(3). https://doi.org/10.5122/cbirds.2011.0023

Veldhuis, M. P., Kihwele, E. S., Cromsigt, J. P. G. M., Ogutu, J. O., Hopcraft, J. G. C., Owen-Smith, N., & Olff, H. (2019). Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. *Ecology Letters*, *22*(10). https://doi.org/10.1111/ele.13350

Venter, J., & Child, M. F. (2016). A conservation assessment of Alcelaphus buselaphus caama. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Venter, J. A., Prins, H. H. T., Balfour, D. A., & Slotow, R. (2014). Reconstructing grazer assemblages for protected area restoration. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0090900

Verdin, K. L. (2017). Hydrologic Derivatives for Modeling and Applications (HDMA) database: U.S. Geological Survey data release, https://doi.org/10.5066/F7S180ZP.

Waltert, M., Meyer, B., Shanyangi, M. W., Balozi, J. J., Kitwara, O., Qolli, S., Krischke, H., & Mühlenberg, M. (2008). Foot Surveys of Large Mammals in Woodlands of Western Tanzania. *Journal of Wildlife Management*, *72*(3). https://doi.org/10.2193/2006-456

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, *11*.

Wilmshurst, J. F., Fryxell, J. M., Farm, B. P., Sinclair, A. R. E., & Henschel, C. P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, *77*(8). https://doi.org/10.1139/z99-088

Zipkin, E. F., Andrew Royle, J., Dawson, D. K., & Bates, S. (2010). Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, *143*(2). https://doi.org/10.1016/j.biocon.2009.11.016

4.8. SUPPLEMENTARY MATERIAL

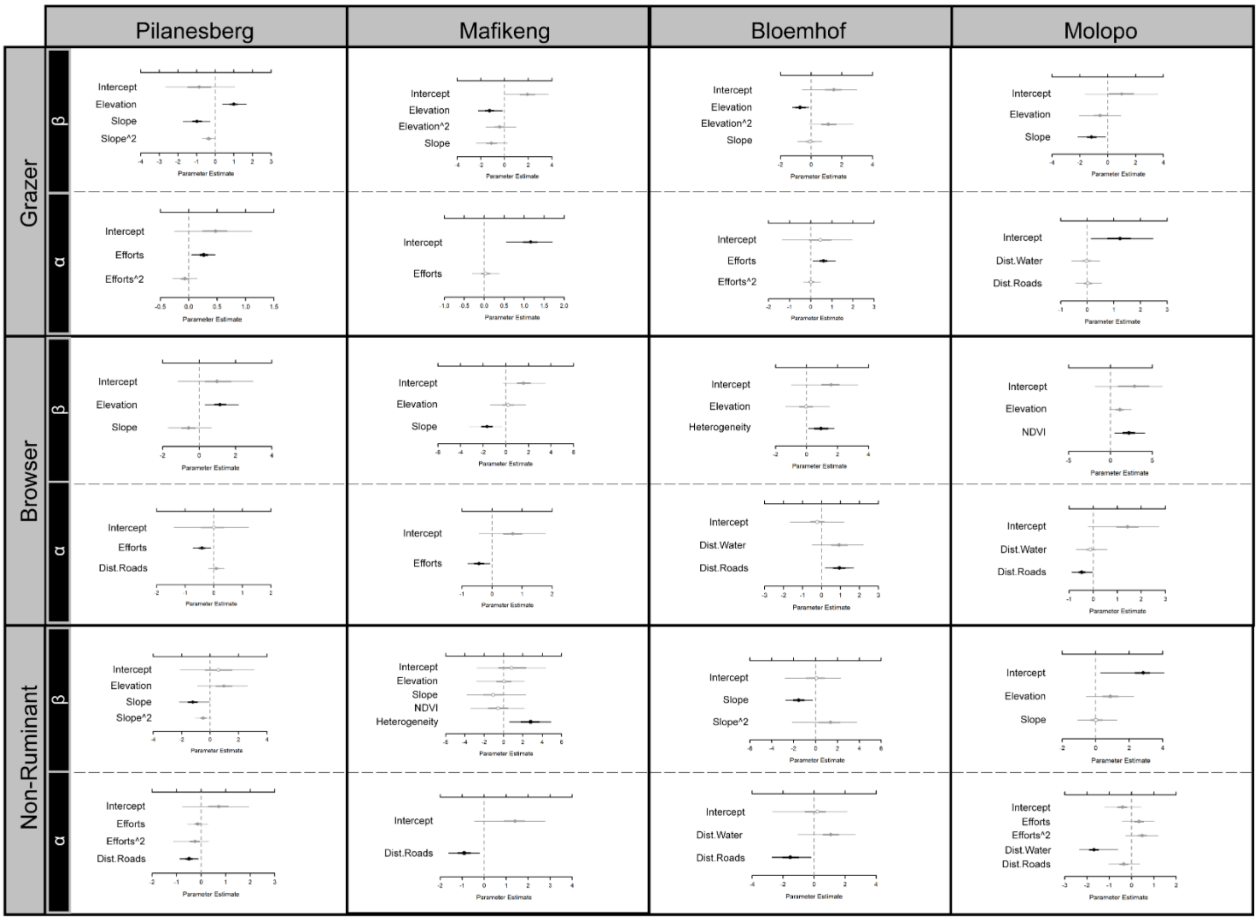


Figure S4.1: Candidate model community-level (for grazer, browser and non-ruminant groups) posterior median estimates with 95% credible intervals for site (β) and detection (α) covariates in the four study sites. Dashed line represents the reference level “0”. ○ = no influence; ◍ = weak influence; ● = significant influence

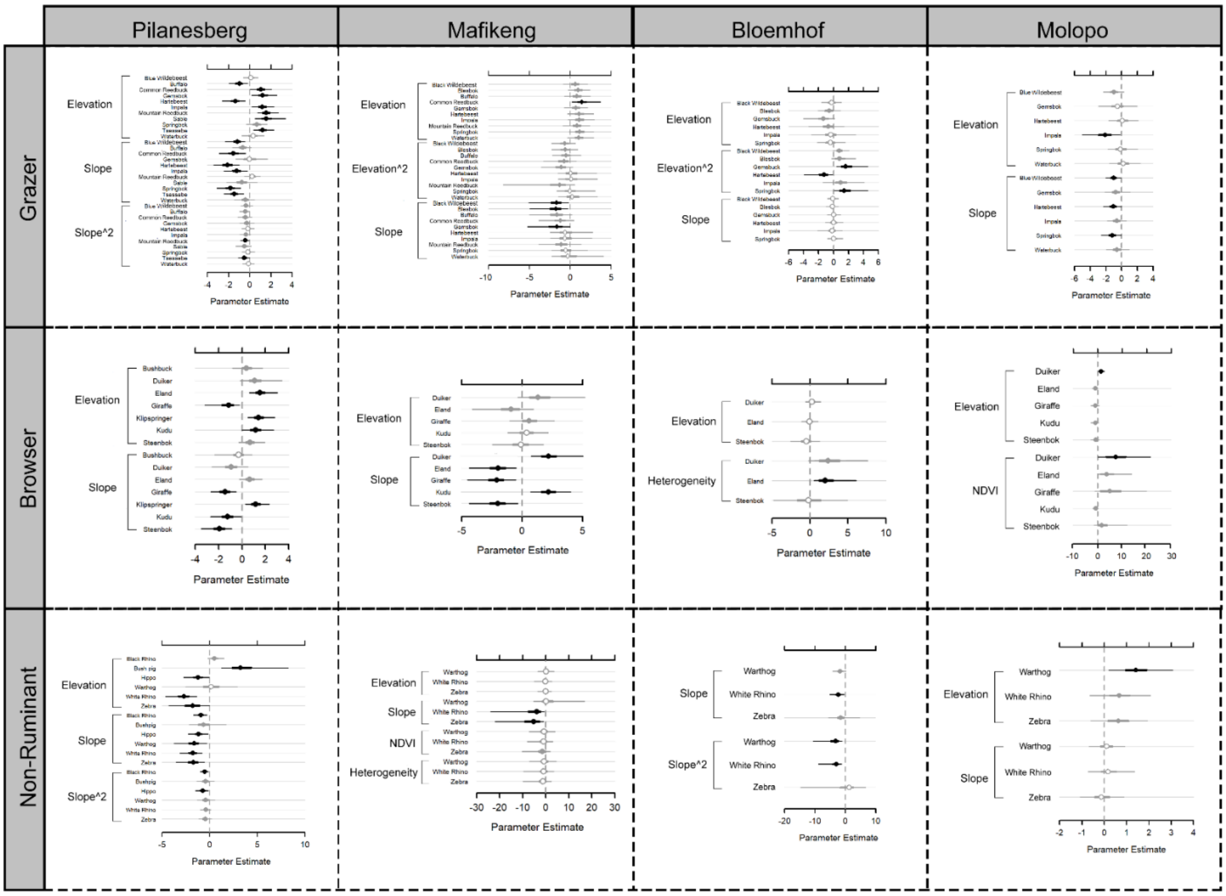


Figure S4.2: Candidate model species-level (within grazer, browser and non-ruminant groups) posterior median estimates with 95% credible intervals for site (β) covariates in the four study sites. Dashed line represents the reference level “0”. ○ = no influence; ◍ = weak influence; ● = significant influence.

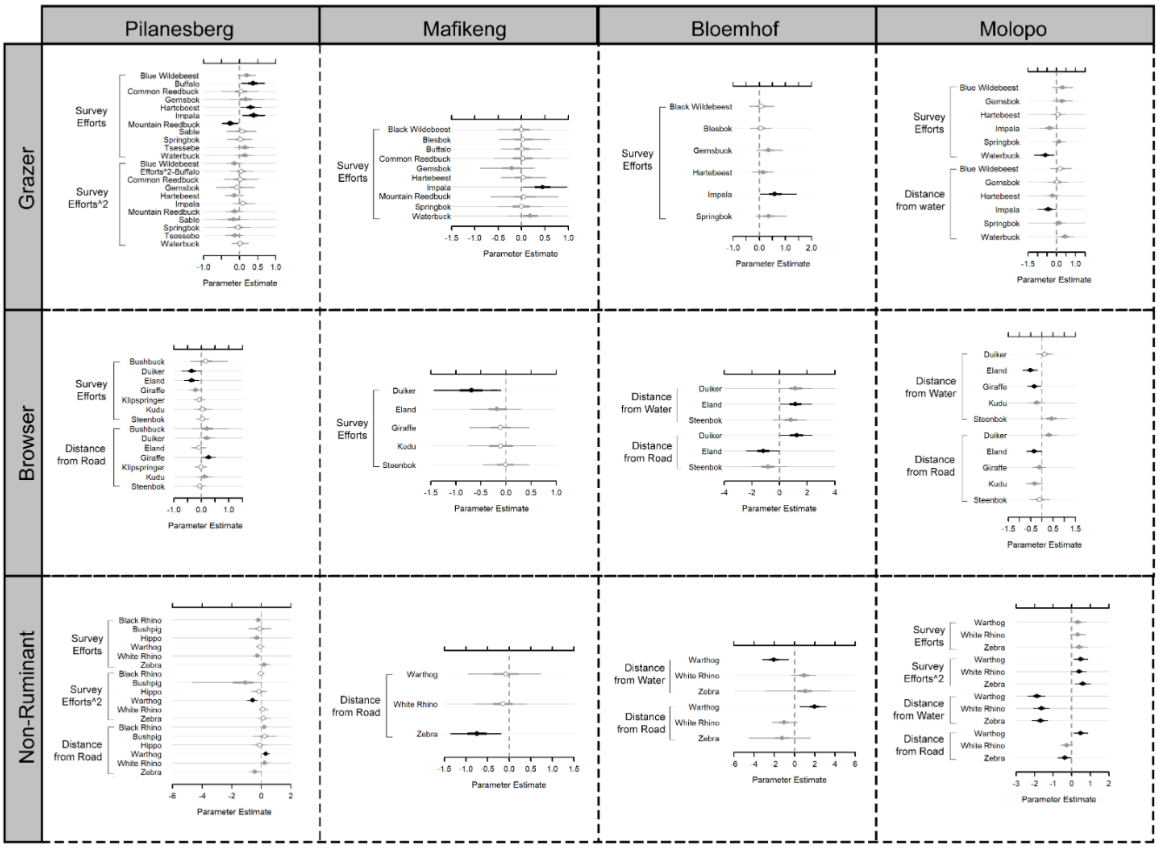


Figure S4.3: Candidate model species-level (within grazer, browser and non-ruminant groups) posterior median estimates with 95% credible intervals for detection (α) covariates in the four study sites. Dashed line represents the reference level “0”.

○ = no influence; ◍ = weak influence; ● = significant influence.

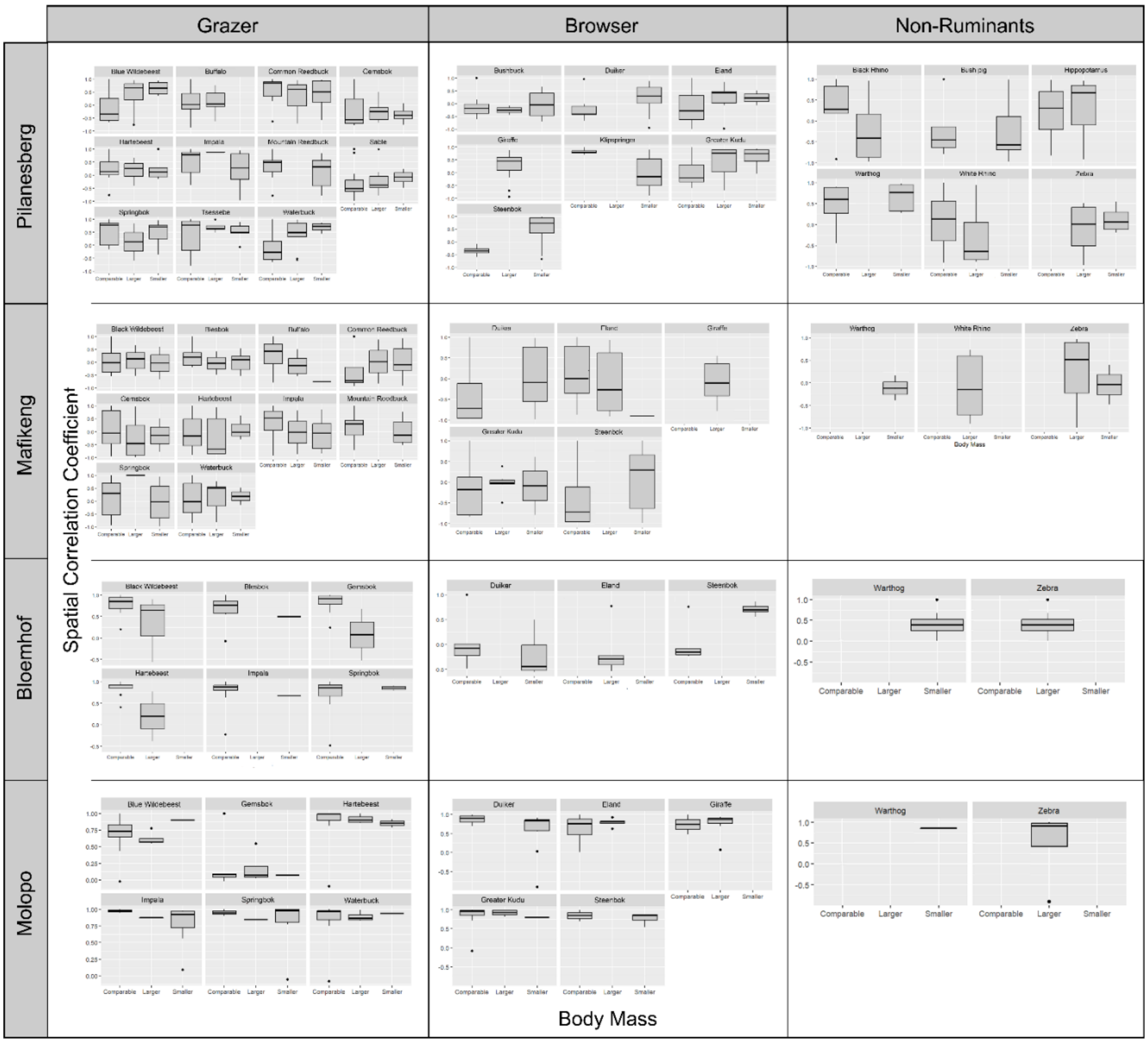


Figure S4.4: Relation between spatial correlation coefficients and body mass of ungulate species within groups from Pilanesberg, Mafikeng, Bloemhof and Molopo. Comparable”, “Larger” and “Smaller” refers to the body mass of the species mentioned on the top (red hartebeest, duiker, zebra etc.) in relation to all others within the group

CHAPTER 5. Synthesis and conclusion

This chapter presents a synthesis of the research presented in empirical chapters two through four. The rationale for embarking on these regional ecological studies is two-fold. Firstly, a sound understanding of ungulate population ecology is required to develop required strategies and policies to effectively manage and conserve ungulates and their associated biodiversity, as most ungulate species are poorly understood except the species of economic importance (Gaillard et al., 1998; Wittemyer et al., 2013; Li et al., 2022). Secondly, ungulate behaviour changes with the changing environmental conditions (Champagne et al., 2021), which may indicate a requirement of specific policies for the same species in different management reserves. This suggests a critical need for an increased ecosystem specific knowledge in the light of changing environmental conditions across landscape.

In an attempt to mitigate this knowledge gap, my objectives broadly included the design and implementation of multiple analytical studies in a relatively unexplored area of the North West (NW) province of South Africa. The aim was to: (1) explore the ways for precisely estimating ungulate population size from aerial counts (**chapter two**), (2) to understand the varying importance of environmental factors in structuring habitat utilization and partitioning at landscape scales (**chapters three**), and (3) to compare key spatial drivers of ungulate occupancies and co-occurrence patterns within different study sites across the landscape (**chapter four**). Space use by ungulates is governed by multiple drivers. While chapter 2 addressed the issue of observation error, chapter three aimed to identify environmental factors shaping distribution patterns. Chapter four aimed to look at spatial occupancy at a broad spatial scale and provide insight into the pervasive influences of competition and resource distribution.

Reducing observation error is essential in order to more accurately quantify population responses. Identifying variables important in habitat selection sheds light on fine-scaled selection processes and provide clues on which variables might be limiting during the dormant season. Spatial occupancy sheds light on how resource availability, and competition shape spatial occupancy. This ultimately links with population trends, and future research should aim to establish how strong these links are. In this concluding section, I will summarize the results of my thesis and highlight a few insights that address some unmet research needs in the North West Province of South Africa.

5.1. Contributions

5.1.1. Novel approach for the methods used in ungulate ecology

My study has contributed to the base knowledge of using N-mixture model for aerial counts while accounting for imperfect detection (**chapter two**) through package ‘unmarked’ in RStudio (R Core Team, 2020). It also serves as a pioneer study for using multi species occupancy modelling approach through ‘spOccupancy’ package in R with aerial count data from multiple study sites across a landscape (**chapter four**) with which I uncovered unique patterns of regional ungulate occupancies and species co-occurrence patterns.

Inaccuracy in abundance estimates, which could be due to species size or GPS accuracy, may lead to errors in assessing the status of a species, which in turn could negatively influence improper setting of conservation goals (Wiest et al., 2019). Wildlife population estimates inherently have two constraints – errors associated with statistical estimation and practical difficulties of counting all the individual animals in a population (Thompson, 1992; Skalski, 1994; Thompson, 2004; Dail & Madsen, 2011). Additionally, population estimates for species that are elusive or spread over larger areas with low ecological densities may turn out to be quite costly (Skalski, 1994; Morellet et al., 2009), as repeated surveys might be required to gather reliable data from a study area (Dail & Madson, 2011; Schmidt & Rattenbury, 2018). Furthermore, success of a monitoring technique has become a contributing factor for funding allocation to different conservation agencies (Stem et al., 2005; Torres et al., 2018). Population monitoring techniques are also affected by inadequacy of data, flawed study design, inappropriate use of statistics, unclear goals and lack of funds (Legg & Nagy, 2006; Nuno et al., 2013) along with environmental stochasticity (Harwood & Stokes, 2003). It is, therefore, extremely important to consider multiple possible limitations when designing a population monitoring study (Nuno et al., 2013). Cost effective survey methods for population monitoring is currently one of the major requirements in wildlife management (Parker et al., 2011). Therefore, finding a statistical tool to improve precision of species abundance estimates by addressing the errors associated with aerial counts would be extremely beneficial for monitoring and predicting species population trends for management interventions (Royle, 2004; Kidwai et al., 2019).

Given the challenges of estimating population size from aerial counts, I developed N-mixture models to accurately estimate ungulate populations and their detection probabilities from aerial counts and compared it with simulated data to check the reliability of the models. I also used multi-species occupancy modelling (MSOM) that takes various sources of uncertainty, inaccurate detections, and imperfect sampling methods into consideration (MacKenzie et al., 2002; Tyre et al., 2003; Dorazio & Royle, 2005; Gelfand et al., 2005) to determine occupancy of ungulates and their co-occurrence patterns in the NW Province. Both of these approaches are considerably novel in the field of ungulate ecology and provided useful insights for future research use.

I found that negative binomial N-mixture models are a better fit for aerial count data of ungulates (**chapter two**). Even though the chapter focusses on black rhino case study, population estimation of 27 seven ungulate species was carried out using N-mixture model (Appendix S5). Black rhino data was used as a case study due to the availability of individual ID monitoring data obtained from Southern African Development Community's Rhino Management Group (SADC RMG) for model result comparison and reliability testing. Removal through harvest, live sale or death however considered as a variable, was not selected in the best-fit models for any of the study species (Table S5.1). In general, seven species of ungulates showed increasing population trends, while 12 species demonstrated more or less stable trends, and eight species had declining population trends (Figure S5.1). Using MSOM I found variability in occupancy of ungulates in relation to study sites (**chapter four**). Although the number of ruminant grazing species was highest in each study site, their average occupancy was lower than the other two groups in most locations due to some species occurring in extremely small scale at each site. Occupancy of browsers remained comparable in all study sites with a little higher occupancy in drier settings as browser species have to cover more ground in search of high-quality forage in drier environments (Hopcraft et al., 2010; Morellet et al., 2013; Fynn et al., 2015). Despite having the most diverse non-ruminant group, Pilanesberg had the lowest average spatial occupancy of non-ruminants mainly because, bush pigs made up only 11% of the overall non-ruminant population. Furthermore, I found that sites with the highest species diversity had the most distinctive spatial segregation patterns between species irrespective of the ungulate groups they belonged. I also found that the species segregation was not only dependent on body size, but also relates to feeding behaviour.

Using N-mixture models for aerial count data to derive population estimates, could provide a statistically guided framework for species management (Kidwai et al., 2019). Another advantage of using N-mixture model is to include predictive covariates to suitably describe the population trend in terms of species abundance, recruitment and survival. By providing better insights on the potential predictors of recruitment, survival, abundance and detection in these models, policy makers are able to plan management strategies of the species accordingly. Similarly, in MSOM, the species capture histories can be used to quantify effects of covariates at both the individual species, and community-level, generate species-specific estimates of occupancy probability, and estimate community-level summaries such as species richness, all with fully propagated uncertainty (Dorazio & Royle, 2005; Doser et al., 2022). Such an approach is particularly helpful for modelling rare or hard-to-detect species with lower detection probabilities, which are frequently found in non-invasive surveys (Zipkin et al., 2010). Managers face a challenge in comprehending the nature of individual species and group interactions with one another in various settings and scales at which those interactions become crucial for strategic management. These modelling techniques therefore, provide an innovative approach to estimate such interactions.

5.1.2. Identification of factors affecting ungulate distributions and habitat use

My study has contributed towards a better understanding of the factors affecting ungulate detection probabilities (**chapter two**) habitat use (**chapter three**) and distribution (**chapter four**). My study has also contributed to the base knowledge of understudied regions in the NW Province in regards to ungulate population dynamics and habitat use.

I found that detection probabilities of ungulate species were affected by duration of the survey flight, body size, along with site and Julian dates (Figure S5.2 - S5.4). Interestingly all the species affected positively by duration of the flight, were either species with large groups (warthog and impala) or had a body mass of >190 kg or both (**chapter two**). Detections of most species declined in September and October, which is the start of greenery in the woody vegetation (Figure S5.2). However, detection probability for a few browsing species were comparatively high during that period due to their dependence on high quality nutrients available in those months (Jarman, 1974; Seydack et al., 2012). Rainfall was the only covariate selected for affecting growth rate of ungulates (Figure S5.5) as rainfall and range conditions around breeding seasons, may affect seasonal recruitment rates and the sex ratios of the young (Berkeley & Linklater, 2010).

Although ungulate space use is controlled by numerous biotic and abiotic factors (Maffei et al., 2002; Maffei & Taber, 2003; Rivero et al., 2005; Keuroghlian & Eaton, 2008; García-Marmolejo et al., 2013), they are generally considered to be constrained by resource availability (Senft et al., 1987; Macandza et al., 2004; 2012; Treydte et al., 2013). African savannas exhibit significant seasonal variation in forage quantity and quality, with resource scarcities leading to annual bottlenecks during the dormant season (Owen-Smith, 2002). The landscape attributes also greatly impact resource heterogeneity (Stilwell et al., 2020) e.g., elevation (Anderson et al., 2006; Cromsigt & Olff, 2006), slope gradient (Bailey et al., 1996), fire (Allred et al., 2011), edaphic factors (soil depth, fertility, and nutrients), and are further altered by the feeding behavior of ungulates on the landscape (Anderson et al., 2006).

I explored the extent to which topographical-vegetation interactions could plausibly explain divergent habitat use patterns in population performance of grazing ungulates with diverse forage requirements in a semi-arid savanna system (**chapter three**). The results of this study are broadly consistent with what is currently known about the biology of the grazing ungulates being studied. Ungulates that were more reliant on high forage biomass and relied on a mixed diet of low-quality forage chose habitats with lower NDVI rather than areas with higher forage greenness. Species with preference for a selective habitat type preferred areas with low heterogeneity. Similarly, species well adapted to drier environments were found to avoid close proximity to water sources. All the species that selected aspect as an influencing factor for their habitat use, selected eastern aspects while avoiding western aspects entirely, due to the sun's trajectory in the southern hemisphere causing the western aspect to be the hottest among the others. Most ungulate species were attracted to the bottomlands. This finding is consistent with the view that bottomlands retain their buffer resources during the dormant season to sustain ungulate populations (Bell, 1971; Wilmshurst et al., 1999).

Habitat selections result in specific occupancy pattern in a species. **Chapter four** provides insight on the spatial occupancy of ungulate groups (grazer, browser and non-ruminants) and their co-occurrence patterns in four selected sites of the NW Province. I found that grazing and non-ruminant ungulate group occupancy largely depended on presence of open, low-lying habitats away from the slopes as suggested by previous studies (Jarman, 1974; Janis, 2008; Stewart et al., 2002; Fryxell et al., 2005; Kiffner & Lee, 2019; Mariotti et al., 2020; Bempah et al., 2022). However, browser species were found to occupy lower elevations in the areas of high annual average rainfall because those locations have more productive sites during the dormant season to sustain populations most dependent on high quality forage (Frank et al., 1998; Hopcraft et al., 2010; Fynn et al., 2015). I demonstrated support for browser and non-ruminant ungulates occupying areas closer to the dirt roads in the protected areas. Most species that were found to occupy patches closer to roads were either large bodied or are short grass specialists. As the rainfall run-offs provide nutritious roadside vegetation during the dormant season (Ndibalema et al., 2008), this finding is not surprising.

High spatial segregation is directly related to high species diversity. Spatial segregation between ungulate groups did not show any specific pattern except within browsers in Mafikeng and Pilanesberg. There was weak evidence that body size differences between species promotes spatial segregation but not systematically based on similarity in size. Spatial avoidance was found within the browser group with species of similar size (e.g., Duiker and steenbok) in Pilanebsberg and Mafikeng. Large sized grazer species spatially segregated from small-sized grazers (e.g., Black wildebeest and impala) in Mafikeng. Similarly, large bodied browsers and non-ruminants spatially segregated from small-sized browsers (e.g., Kudu and duiker) and non-ruminants (Hippopotamus and bush pig) respectively. Molopo did not show such influence of body mass on spatial segregation, while spatial co-occurrences of species was most distinct in areas with lower ungulate diversity.

5.2. Implications

The results of my research demonstrate that regional ungulate conservation strategies require site-specific considerations that (1) are scale dependent, (2) incorporate topographical factors into their strategies, and (3) consider the species interactions in their approach. Additionally, (4) it has demonstrated that site occupancies are species and site specific across the landscape.

In **chapter two,** I showed that precise populations estimates could be derived from inexpensive methods such as population modelling. The method could be extremely helpful for management authorities that are actively carrying out yearly aerial counts. In general, using more spatial replicates could improve estimates from N-mixture models (Knape & Korner-Nievergelt, 2015). However, my simulation results suggest that estimates from short time series from many spatial sites return similar results as those from longer time series from a select few sites. Moreover, the addition of more variables might provide new insights into how the population reacts to various environmental conditions and how detection probability is affected. Simulations in the study revealed that using raw counts could conceal significant variations in population sizes even with high detection probabilities. Maximum counts revealed 30% biasness in our simulations with three replicates and a detection probability of 0.6. The script of the analysis and model codes were made publicly available, so that the management may easily incorporate them for estimating ungulate population using their future survey counts. As my study revealed that the detection probabilities of ungulate species in the NW Province decrease with the onset of wet season (September-October), the aerial surveys should be planned accordingly to avoid detection related obstructions from the greener vegetation contributing to ‘observation error’.

Currently, most wild ungulates in South Africa are found in fenced protected areas (Hayward & Kerley, 2009). Therefore, resource availability is constrained by the spatial constraints imposed by fences. However, due to the east-west precipitation gradient across the NW Province (Goslar et al., 2008), ungulates rely on different combinations of habitat variables across the study sites. My study (**chapter three** and **chapter four**) showed that the occupancy and habitat use of ungulates with even similar foraging requirements might vary depending on other available topographical and habitat variables. Most species were found to utilize grasslands, open woodland and habitats close to water sources. Furthermore, few grazing ungulates preferred heterogeneous grasslands suggesting that the management decisions for prescribed fire should keep that in mind. My research identified species-specific and community-specific habitat requirements, both on-site and across landscapes, which might be incredibly useful in developing "species within a site" management frameworks.

Species interactions appears to be another important determinant of species distribution, where spatial segregation was found between certain species. Increased species diversity was associated with a higher degree of segregation. Furthermore, while previous studies suggest similar body size drives spatial segregation (Sinclair, 1985; Hibert et al., 2010; Venter et al., 2014), results from **chapter four** suggest species composition and diversity is more important i.e., spatial segregation might vary among species depending on the ecological context.

5.3. Research needs/gaps identified

This doctoral thesis provides some of the first comprehensive data on the ungulate ecology in the protected areas of NW Province. However, much work remains to be done in order to more comprehensively uncover the factors shaping ungulate population dynamics and diversity in the region.

5.3.1. Growth rate and Demographic studies

Firstly, along with covering population counts, demographic data also contribute towards a better understanding of population trajectories in the multi species environment (Raithel et al., 2007; Harris et al., 2008). Demographic data can be extremely helpful in determining the “health” of an ecosystem (Terrill Paterson et al., 2019) and therefore, provide valuable insights to management interventions required at each site. Of key importance is time series of infant/ juvenile survival, the demographic rate(s) affected most when environmental conditions deteriorate. (Raithel et al., 2007; White et al., 2010; Eacker et al., 2017).

Although the use of N-mixture models provided population counts and growth rates of species, further research is warranted to uncover the drivers of growth rate variation of a species, both spatially and temporally. A critical assessment of growth rate is one of the cornerstone practices in conservation ecology (Petzoldt, 2017). Increased accuracy of yearly population growth provides scope for demographic inferences driving fluctuations in population abundance.

5.3.2. Additional covariates inclusion

Although the environmental variables included in this thesis provide sufficient support of their effect on spatial occupancy and habitat use of ungulates, some crucial ecological variables were not considered for the study. Across the African continent, rainfall and forage availability are perceived as the major limiting factors for ungulate population dynamics (Owen-Smith, 2008). However, my thesis could not find any apparent role of rainfall or temperature on population trends or patterns of ungulate distribution. The NW Province receives a gradient in average annual rainfall that decreases from east to west (Mucina & Rutherford, 2006), the effect of which is worth consideration for future studies.

NW Province has only a few protected areas with large predators (NWPTB, 2020). Moreover, the degree to which a predator regulates a prey species is reliant on the size of the ungulate species relative to the size of the predator (Hopcraft et al., 2010; 2012). In the areas where predators are absent, or at low densities, temporal fluctuations in resource availability is the most likely driver of fluctuations in densities, apart from occasional removals. Thus, I did not consider predation pressure in the current research. However, adding predator pressure could be an important aspect to compare in understanding ungulate distribution in predator rich and predator free environments.

5.3.3. Change in land use land cover (LULC) studies

LULC change analysis is important to advance our understanding of the consequences of such change on the other components of the environment, including temporal changes in species composition (Giri et al., 2005; Anil et al., 2011). Irreversible land cover changes occur throughout the world (Foley et al., 2005) including South Africa (Meadows & Hoffman, 2002) due to increase in agricultural practices, deforestation, residential encroachment, and over grazing among many other reasons (Gillson et al., 2012). Therefore, fine-scale resolution landscape analysis using GIS and remotely sensed data (Urban et al., 1987; Turner, 1989; Prendergast et al., 1993; Anil et al., 2011) plays an important role in understating changing patterns. Therefore, it is of interest to conservation practitioners to detect changes in spatial occupancy of ungulates in response to changing land cover, seasonally as well as over larger temporal scales. This information could also feed into the knowledge base required to effectively conserve and manage ungulate species across the landscape of NW Province.

5.4. REFERENCE

Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. (2011). Ungulate preference for burned patches reveals strength: Of fire-grazing interaction. *Ecology and Evolution*, *1*(2). https://doi.org/10.1002/ece3.12

Anderson, T. M., Dong, Y., & Mcnaughton, S. J. (2006). Nutrient acquisition and physiological responses of dominant Serengeti grasses to variation in soil texture and grazing. *Journal of Ecology*, *94*(6). https://doi.org/10.1111/j.1365-2745.2006.01148.x

Anil, N., Sankar, G., Rao, M., & Sailaja, U. (2011). Studies on land use/land cover and change detection from parts of South West Godavari District , A . P – using Remote Sensing and GIS techniques. *J.Ind.Geophys.Union*, *15*(4).

Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, *49*(5). https://doi.org/10.2307/4002919

Bell, R. H. V. (1971). A grazing ecosystem in the Serengeti. Scientific American. Vol. 225: 86–93.

Bempah, G., Afrifa, J. K., Nartey, M. A., & Lu, C. (2022). Variations in Patch Use by Ruminant and Non-ruminant Herbivores in a Tropical Wildlife Reserve, Ghana. *Journal of Resources and Ecology*, *13*(6). https://doi.org/10.5814/j.issn.1674-764x.2022.06.018

Berkeley, E. V., & Linklater, W. L. (2010). Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *African Journal of Wildlife Research*, *40*(1). https://doi.org/10.3957/056.040.0102

Champagne, E., Royo, A. A., Tremblay, J. P., & Raymond, P. (2021). Tree assisted migration in a browsed landscape: Can we predict susceptibility to herbivores? *Forest Ecology and Management*, *498*. https://doi.org/10.1016/j.foreco.2021.119576

Cromsigt, J. P. G. M., & Olff, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. *Ecology*, *87*(6). https://doi.org/10.1890/0012-9658(2006)87[1532:RPASGM]2.0.CO;2

Dail, D., & Madsen, L. (2011). Models for Estimating Abundance from Repeated Counts of an Open Metapopulation. *Biometrics*, *67*(2). https://doi.org/10.1111/j.1541-0420.2010.01465.x

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470). https://doi.org/10.1198/016214505000000015

Doser, J. W., Finley, A. O., Kéry, M., & Zipkin, E. F. (2022). spOccupancy: An R package for single-species, multi-species, and integrated spatial occupancy models. *Methods in Ecology and Evolution*, *13*(8). https://doi.org/10.1111/2041-210X.13897

Eacker, D. R., Lukacs, P. M., Proffitt, K. M., & Hebblewhite, M. (2017). Assessing the importance of demographic parameters for population dynamics using Bayesian integrated population modeling. *Ecological Applications*, *27*(4). https://doi.org/10.1002/eap.1521

Festa-Bianchet, M., Gaillard, J. M., & Côté, S. D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology*, *72*(4). https://doi.org/10.1046/j.1365-2656.2003.00735.x

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. (2005). Global consequences of land use. In *Science* (Vol. 309, Issue 5734). https://doi.org/10.1126/science.1111772

Forsyth, D. M., & Caley, P. (2006). Testing the irruptive paradigm of large-herbivore dynamics. *Ecology*, *87*(2). https://doi.org/10.1890/05-0709

Frank, D. A., McNaughton, S. J., & Tracy, B. F. (1998). The ecology of the earth’s grazing ecosystems: Profound functional similarities exist between the Serengeti and Yellowstone. *BioScience*, *48*(7). https://doi.org/10.2307/1313313

Fryxell, J. M., Wilmshurst, J. F., Sinclair, A. R. E., Haydon, D. T., Holt, R. D., & Abrams, P. A. (2005). Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*, *8*(3). https://doi.org/10.1111/j.1461-0248.2005.00727.x

Fynn, R. W. S., Murray-Hudson, M., Dhliwayo, M., & Scholte, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores. *Wetlands Ecology and Management*, *23*(4). https://doi.org/10.1007/s11273-015-9430-6

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2). https://doi.org/10.1016/S0169-5347(97)01237-8

García-Marmolejo, G., Chapa-Vargas, L., Huber-Sannwald, E., Weber, M., Rosas-Rosas, O. C., & Martínez-Calderas, J. (2013). Potential distributional patterns of three wild ungulate species in a fragmented tropical region of northeastern Mexico. *Tropical Conservation Science*, *6*(4). https://doi.org/10.1177/194008291300600407

Gelfand, A. E., Schmidt, A. M., Wu, S., Silander, J. A., Latimer, A., & Rebelo, A. G. (2005). Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society. Series C: Applied Statistics*, *54*(1). https://doi.org/10.1111/j.1467-9876.2005.00466.x

Gillson, L., Midgley, G. F., & Wakeling, J. L. (2012). Exploring the significance of land-cover change in South Africa. *South African Journal of Science*, *108*(5–6). https://doi.org/10.4102/sajs.v108i5/6.1247

Giri, C., Zhu, Z., & Reed, B. (2005). A comparative analysis of the Global Land Cover 2000 and MODIS land cover data sets. *Remote Sensing of Environment*, *94*(1). https://doi.org/10.1016/j.rse.2004.09.005

Goslar, A., Prosch, L., Ingle, S., Benedek, F., Hudson, K., Mampye, A., Tshivhase, N and Lees, Z. (2008). North West Province Environment Outlook. A report on the state of the environment. Submitted to North West Department of Agriculture, Conservation and Environment.

Harris, N. C., Kauffman, M. J., & Mills, L. S. (2008). Inferences About Ungulate Population Dynamics Derived From Age Ratios. *Journal of Wildlife Management*, *72*(5). https://doi.org/10.2193/2007-277

Harwood, J., & Stokes, K. (2003). Coping with uncertainty in ecological advice: Lessons from fisheries. *Trends in Ecology and Evolution*, *18*(12). https://doi.org/10.1016/j.tree.2003.08.001

Hayward, M. W., & Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? In *Biological Conservation* (Vol. 142, Issue 1). https://doi.org/10.1016/j.biocon.2008.09.022

Hibert, F., Calenge, C., Fritz, H., Maillard, D., Bouché, P., Ipavec, A., Convers, A., Ombredane, D., & de Visscher, M. N. (2010). Spatial avoidance of invading pastoral cattle by wild ungulates: Insights from using point process statistics. *Biodiversity and Conservation*, *19*(7). https://doi.org/10.1007/s10531-010-9822-0

Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E., & Olff, H. (2012). Body size and the division of niche space: Food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, *81*(1). https://doi.org/10.1111/j.1365-2656.2011.01885.x

Hopcraft, J. G. C., Olff, H., & Sinclair, A. R. E. (2010). Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. In *Trends in Ecology and Evolution* (Vol. 25, Issue 2). https://doi.org/10.1016/j.tree.2009.08.001

Janis, C. (2008). *An Evolutionary History of Browsing and Grazing Ungulates*. https://doi.org/10.1007/978-3-540-72422-3_2

Jarman, P. J. (1974). The Social Organisation of Antelope in Relation to Their Ecology. *Behaviour*, *48*(1–4). https://doi.org/10.1163/156853974X00345

Keuroghlian, A., & Eaton, D. P. (2008). Importance of rare habitats and riparian zones in a tropical forest fragment: Preferential use by Tayassu pecari, a wide-ranging frugivore. *Journal of Zoology*, *275*(3). https://doi.org/10.1111/j.1469-7998.2008.00440.x

Kidwai, Z., Jimenez, J., Louw, C. J., Nel, H. P., & Marshal, J. P. (2019). Using N-mixture models to estimate abundance and temporal trends of black rhinoceros (*Diceros bicornis L.*) populations from aerial counts. *Global Ecology and Conservation*, *19*. https://doi.org/10.1016/j.gecco.2019.e00687

Kiffner, C., & Lee, D. E. (2019). *Population Dynamics of Browsing and Grazing Ungulates in the Anthropocene*. https://doi.org/10.1007/978-3-030-25865-8_6

Knape, J., & Korner-Nievergelt, F. (2015). Estimates from non-replicated population surveys rely on critical assumptions. *Methods in Ecology and Evolution*, *6*(3). https://doi.org/10.1111/2041-210X.12329

Legg, C. J., & Nagy, L. (2006). Why most conservation monitoring is, but need not be, a waste of time. *Journal of Environmental Management*, *78*(2). https://doi.org/10.1016/j.jenvman.2005.04.016

Li, S., Zhao, Y., Xiao, W., Yellishetty, M., & Yang, D. (2022). Identifying ecosystem service bundles and the spatiotemporal characteristics of trade-offs and synergies in coal mining areas with a high groundwater table. *Science of the Total Environment*, *807*. https://doi.org/10.1016/j.scitotenv.2021.151036

Macandza, V. A., Owen-Smith, N., & Cain, I. W. (2012). Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *Journal of Zoology*, *287*(3). https://doi.org/10.1111/j.1469-7998.2012.00900.x

Macandza, V. A., Owen-Smith, N., & Cross, P. C. (2004). Forage selection by African buffalo in the late dry season in two landscapes. *African Journal of Wildlife Research*, *34*(2).

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8). https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

Maffei, L., Cuéllar, E., & Noss, A. J. (2002). Uso de Trampas-Cámara para la Evaluación de Mamíferos en el Ecotono Chaco-Chiquitanía. *Revista Boliviana de Ecología y Conservación Ambiental*, *11*.

Maffei, L., & Taber, A. B. (2003). Area de acción de *Mazama americana* (Cervidae) en un bosque seco de Bolivia. *Ecología En Bolivia*, *38*(2).

Mariotti, E., Parrini, F., Louw, C. J., & Marshal, J. P. (2020). What grass characteristics drive large herbivore feeding patch selection? A case study from a South African grassland protected area. *African Journal of Range and Forage Science*. https://doi.org/10.2989/10220119.2020.1768146

McShea, W. J., Underwood, H. B., & Rappole, J. H. (1997). The science of overabundance. Smithsonian, Washington DC.

Meadows, M. E., & Hoffman, M. T. (2002). The nature, extent and causes of land degradation in South Africa: Legacy of the past, lessons for the future? *Area*, *34*(4). https://doi.org/10.1111/1475-4762.00100

Morellet, N., Bonenfant, C., Börger, L., Ossi, F., Cagnacci, F., Heurich, M., Kjellander, P., Linnell, J. D. C., Nicoloso, S., Sustr, P., Urbano, F., & Mysterud, A. (2013). Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. *Journal of Animal Ecology*, *82*(6). https://doi.org/10.1111/1365-2656.12105

Morellet, N., Verheyden, H., Angibault, J. M., Cargnelutti, B., Lourtet, B., & Hewison, M. A. J. (2009). The effect of capture on ranging behaviour and activity of the European roe deer Capreolus capreolus. *Wildlife Biology*, *15*(3). https://doi.org/10.2981/08-084

Mucina, L., & Rutherford, M. C. (2006). The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, Strelitzia.

Ndibalema, V. G., Mduma, S., Stokke, S., & Røskaft, E. (2008). Relationship between road dust and ungulate density in Serengeti National Park, Tanzania. *African Journal of Ecology*, *46*(4). https://doi.org/10.1111/j.1365-2028.2007.00898.x

Nuno, A., Bunnefeld, N., & Milner-Gulland, E. J. (2013). Matching observations and reality: Using simulation models to improve monitoring under uncertainty in the Serengeti. *Journal of Applied Ecology*, *50*(2). https://doi.org/10.1111/1365-2664.12051

NWPTB (2020). North West Parks Board official website [WWW Document]. URL https://ho.org.za/parks/ [Accessed: 05/04/2020].

Owen-Smith, N. (2006). Demographic determination of the shape of density dependence for three African ungulate populations. *Ecological Monographs*, *76*(1). https://doi.org/10.1890/05-0765

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, *117*(4). https://doi.org/10.1111/j.0030-1299.2008.16309.x

Owen-Smith, N., Mason, D. R., & Ogutu, J. O. (2005). Correlates of survival rates for 10 African ungulate populations: Density, rainfall and predation. *Journal of Animal Ecology*, *74*(4). https://doi.org/10.1111/j.1365-2656.2005.00974.x

Owen-Smith, N. (2002). Adaptive Herbivore Ecology. In *Adaptive Herbivore Ecology*. https://doi.org/10.1017/cbo9780511525605

Parker, G., Sundaresan, S., Chege, G., & O'Brien, T. (2011). Using sample aerial surveys to estimate the abundance of the endangered Grevy's zebra in northern Kenya. *African Journal of Ecology*, *49*(1). https://doi.org/10.1111/j.1365-2028.2010.01232.x

Petzoldt, T. (2017). Estimation of growth rates with package growthrates. 1–8. Available at: https://cran.r-project.org/web/packages/growthrates/vignettes/Introduction.html.

Prendergast, J. R., Quinn, R. M., Lawton, J. H., Eversham, B. C., & Gibbons, D. W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, *365*(6444). https://doi.org/10.1038/365335a0

Prins, H. H. T., & Iason, G. R. (1989). Dangerous Lions and Nonchalant Buffalo. *Behaviour*, *108*(3–4). https://doi.org/10.1163/156853989X00330

Prins, H. H. T., & Weyerhaeuser, F. J. (1987). Epidemics in Populations of Wild Ruminants: Anthrax and Impala, Rinderpest and Buffalo in Lake Manyara National Park, Tanzania. *Oikos*, *49*(1). https://doi.org/10.2307/3565551

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raithel, J. D., Kauffman, M. J., & Pletscher, D. H. (2007). Impact of Spatial and Temporal Variation in Calf Survival on the Growth of Elk Populations. *Journal of Wildlife Management*, *71*(3). https://doi.org/10.2193/2005-608

Rivero, K., Rumiz, D. I., & Taber, A. B. (2005). Differential habitat use by two sympatric brocket deer species (Mazama americana and M. gouazoubira) in a seasonal Chiquitano forest of Bolivia. *Mammalia*, *69*(2). https://doi.org/10.1515/mamm.2005.015

Royle, J. A. (2004). N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics*, *60*(1). https://doi.org/10.1111/j.0006-341X.2004.00142.x

Schmidt, J. H., & Rattenbury, K. L. (2018). An open-population distance sampling framework for assessing population dynamics in group-dwelling species. *Methods in Ecology and Evolution*, *9*(4). https://doi.org/10.1111/2041-210X.12932

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, *37*(11). https://doi.org/10.2307/1310545

Seydack, A. H., Grant, C. C., Smit, I. P., Vermeulen, W. J., Baard, J., & Zambatis, N. (2012). Large herbivore population performance and climate in a South African semi-arid savanna. *Koedoe*, *54*(1). https://doi.org/10.4102/koedoe.v54i1.1047

Sinclair, A. R., & Arcese, P. (1995). Population consequences of predation-sensitive foraging: The Serengeti wildebeest. *Ecology*, *76*(3). https://doi.org/10.2307/1939353

Sinclair, A. R. E. (1985). Does Interspecific Competition or Predation Shape the African Ungulate Community? *The Journal of Animal Ecology*, *54*(3). https://doi.org/10.2307/4386

Skalski, J. R. (1994). Estimating wildlife populations based on incomplete area surveys. *Wildlife Society Bulletin*, *22*(2).

Stem, C., Margoluis, R., Salafsky, N., & Brown, M. (2005). Monitoring and evaluation in conservation: A review of trends and approaches. In *Conservation Biology* (Vol. 19, Issue 2). https://doi.org/10.1111/j.1523-1739.2005.00594.x

Stewart, K. M., Bowyer, R. T., Kie, J. G., Cimon, N. J., & Johnson, B. K. (2002). Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. *Journal of Mammalogy*, *83*(1). https://doi.org/10.1644/1545-1542(2002)083<0229:TDOEMD>2.0.CO;2

Stilwell, P., O'Brien, S., Hesse, E., Lowe, C., Gardner, A., & Buckling, A. (2020). Resource heterogeneity and the evolution of public goods cooperation. In *Evolution Letters* (Vol. 4, Issue 2). https://doi.org/10.1002/evl3.158

Terrill Paterson, J., Proffitt, K., Rotella, J., & Garrott, R. (2019). An improved understanding of ungulate population dynamics using count data: Insights from western Montana. *PLoS ONE*, *14*(12). https://doi.org/10.1371/journal.pone.0226492

Thompson, S. K. (1992). Sampling. New York: John Wiley.

Thompson, W. L. (2004). Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. *Population English Edition*, *34*(3).

Torres, A., Fernández, N., zu Ermgassen, S.O., et al. (2018). Measuring rewilding progress. Philosophical Transactions of the Royal Society B: Biological Sciences, 373.

Treydte, A. C., Baumgartner, S., Heitkönig, I. M. A., Grant, C. C., & Getz, W. M. (2013). Herbaceous forage and selection patterns by ungulates across varying herbivore assemblages in a South African savanna. *PLoS ONE*, *8*(12). https://doi.org/10.1371/journal.pone.0082831

Turner, M. G. (1989). Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics. Vol. 20*. https://doi.org/10.1146/annurev.es.20.110189.001131

Tyre, A. J., Tenhumberg, B., Field, S. A., Niejalke, D., Parris, K., & Possingham, H. P. (2003). Improving precision and reducing bias in biological surveys: Estimating false-negative error rates. In *Ecological Applications* (Vol. 13, Issue 6). https://doi.org/10.1890/02-5078

Urban, D. L., O'Neill, R. V, & Shugart, H. H. J. (1987). Landscape Ecology: A hierarchical perspective can help scientists understand spatial patterns. *BioScience*, *37*(2).

Venter, J. A., Prins, H. H. T., Balfour, D. A., & Slotow, R. (2014). Reconstructing grazer assemblages for protected area restoration. *PLoS ONE*, *9*(3). https://doi.org/10.1371/journal.pone.0090900

White, C. G., Zager, P., & Gratson, M. W. (2010). Influence of Predator Harvest, Biological Factors, and Landscape on Elk Calf Survival in Idaho. *Journal of Wildlife Management*, *74*(3). https://doi.org/10.2193/2007-506

Wiest, W. A., Correll, M. D., Marcot, B. G., et al. (2019). Estimates of tidal-marsh bird densities using Bayesian networks. *Journal of Wildlife Management*, *83*(1). https://doi.org/10.1002/jwmg.21567

Wilmshurst, J. F., Fryxell, J. M., Farm, B. P., Sinclair, A. R. E., & Henschel, C. P. (1999). Spatial distribution of Serengeti wildebeest in relation to resources. *Canadian Journal of Zoology*, *77*(8). https://doi.org/10.1139/z99-088

Wittemyer, G., Daballen, D., & Douglas-Hamilton, I. (2013). Comparative Demography of an At-Risk African Elephant Population. *PLoS ONE*, *8*(1). https://doi.org/10.1371/journal.pone.0053726

Zipkin, E. F., Andrew Royle, J., Dawson, D. K., & Bates, S. (2010). Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, *143*(2). https://doi.org/10.1016/j.biocon.2009.11.016

5.5. SUPPLEMENTARY MATERIAL

Table S5.1. Abundance estimates (±95% CIs) of 27 species of ungulates in NW Province obtained through the best model in N-mixture models. Where Nmax is the maximum number of individuals of a species detected in one survey session.

SPECIES	BEST MODEL*	NMAX	N-MIXTURE MODEL	
			Abundance	±95% CI
BLACK RHINO	λ(.)γ(R)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	54	67	53-81
BLACK WILDEBEEST	λ(.)γ(R)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	310	372	356-388
BLESBOK	λ(.)γ(R+T)ω(.)[Ricker]p(Site)	116	161	151-171
BLUE WILDEBEEST	λ(.)γ(R)ω(.)[Ricker]p(Jd+I(Jd^2)	963	1138	1035-1242
BUFFALO	λ(.)γ(R)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	140	167	161-173
BUSHBUCK	λ(.)γ(.)ω(.)[Const.]p(Site)	15	29	21-38
BUSHPIG	λ(.)γ(.)ω(.)[Const.]p(Site)	10	33	17-49
COMMON REEDBUCK	λ(.)γ(.)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd)	23	24	21-27
DUIKER	λ(.)γ(R)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd)	9	14	9-18
ELAND	λ(.)γ(R)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	140	167	150-185
GEMSBOK	λ(.)γ(.)ω(.)[Ricker]p(Site)	243	256	241-270
GIRAFFE	λ(.)γ(R)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	61	72	71-74
GREATER KUDU	λ(.)γ(.)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	152	176	172-180
RED HARTEBEEST	λ(.)γ(R)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd)	169	205	170-241
HIPPO	λ(.)γ(.)ω(.) [Const]p(Site+Jd+I(Jd^2)+Site*Jd)	56	59	52-65
IMPALA	λ(.)γ(.)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	575	659	621-697
KLIPSPRINGER	λ(.)γ(.)ω(.)[Trend]p(Site+Jd+I(Jd^2)+Site*Jd)	43	69	65-74
MOUNTAIN REEDBUCK	λ(.)γ(.)ω(.)[Const.]p(.)	43	52	48-56
NYALA	λ(.)γ(.)ω(.)[Const]p(Site+Jd+I(Jd^2)+Site*Jd)	53	33	9-57
SABLE	λ(.)γ(.)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	34	39	37-40
SPRINGBOK	λ(.)γ(R)ω(.)[Ricker]p(.)	242	278	254-302
STEENBOK	λ(.)γ(.)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	18	24	18-30
TSESSEBE	λ(.)γ(R)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	76	78	76-80
WARTHOG	λ(.)γ(R)ω(.)[Const.]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	99	140	100-179
WATERBUCK	λ(.)γ(.)ω(.)[Const.]p(Site)	89	115	91-139
WHITE RHINO	λ(.)γ(R)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd)	96	98	92-103
ZEBRA	λ(.)γ(R+T)ω(.)[Ricker]p(Site+Jd+I(Jd^2)+Site*Jd+Ft)	426	467	425-509

* R = Rainfall; T = temperature; JD = julian date, JD^2 = quadratic term of julian date

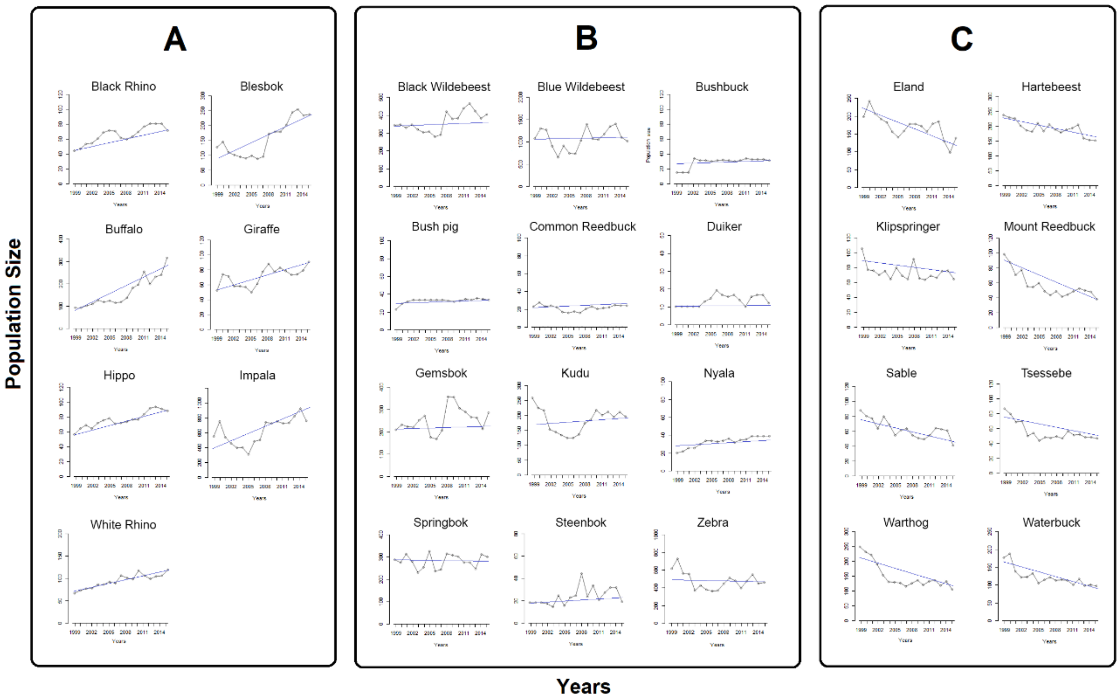


Fig S5.1: Changes in species abundance from the years 1999-2015 based on ‘N_i’ values from the best-fit N-mixture models (ΔAICc<2). A: Species with increasing populations; B: Species with comparatively stable populations; C: Species with decreasing populations

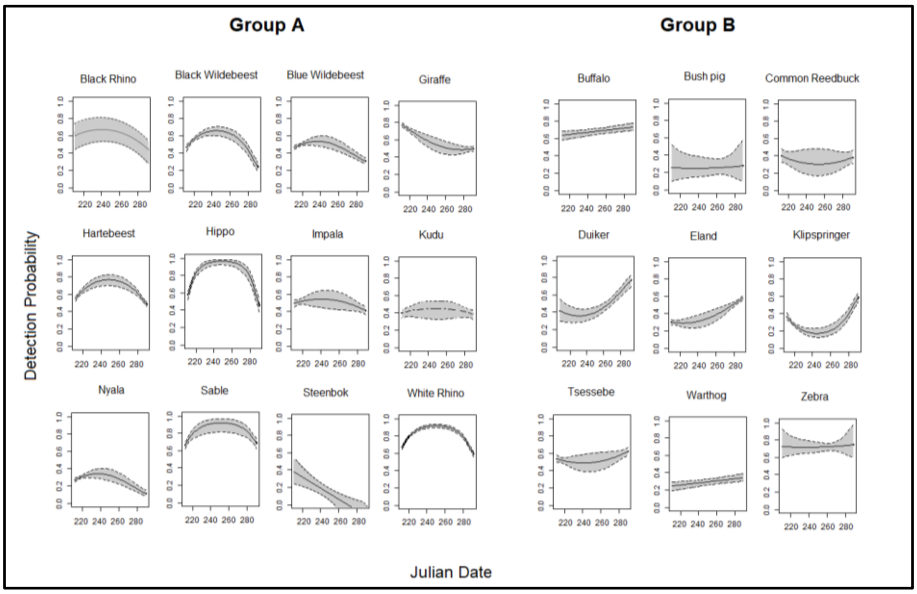


Fig S5.2: Predictions using model averaging from the best-fit models (ΔAICc<2). Probability of detecting ungulates in 13 study sites depending on Julian date. Estimates of 95% confidence intervals are in grey constructed from the model using the function ‘predict’ in unmarked. Group A: the species with decreasing detection probabilities with changing Julian Date. Group B: The species with increasing detection probabilities with changing Julian Date

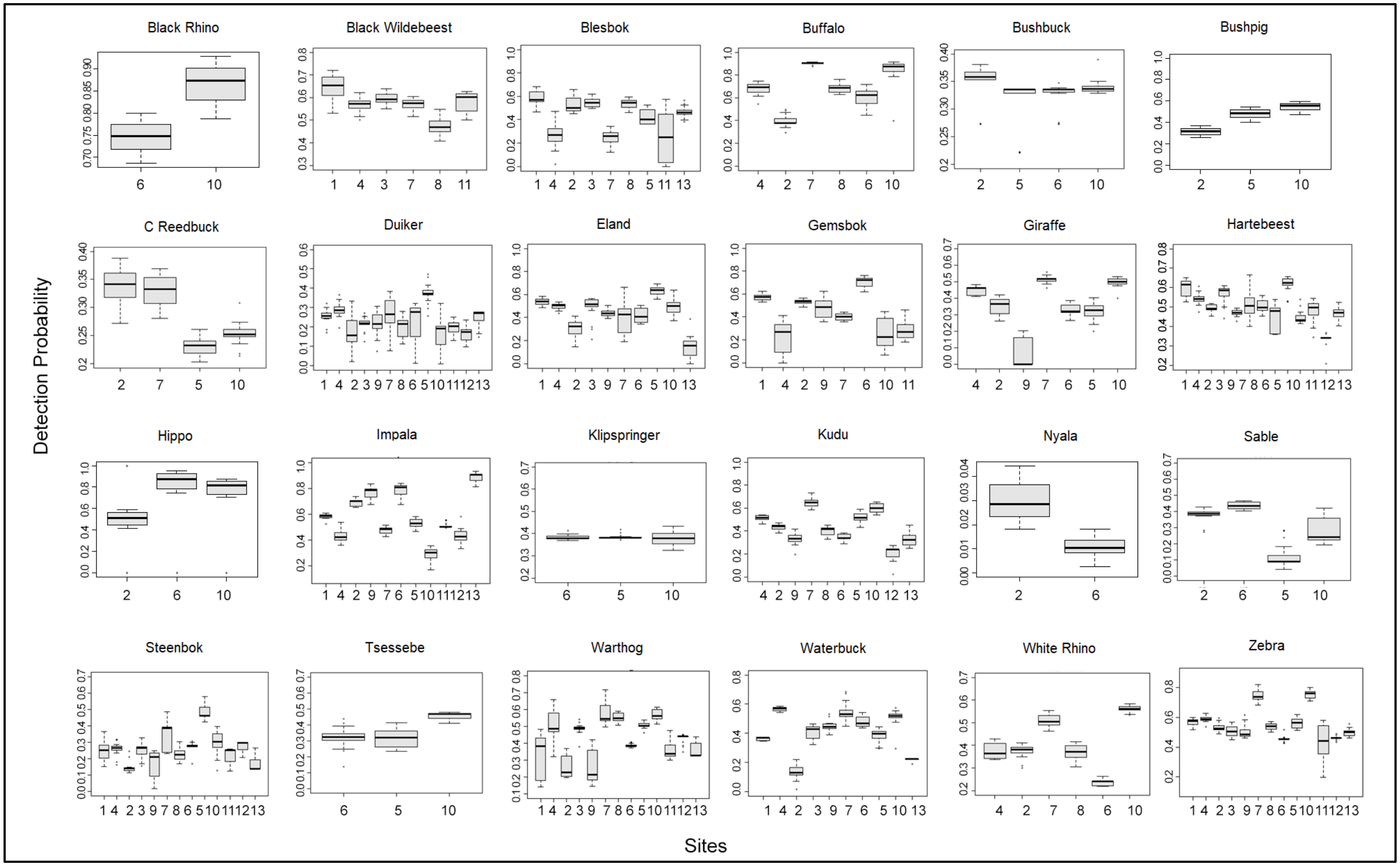
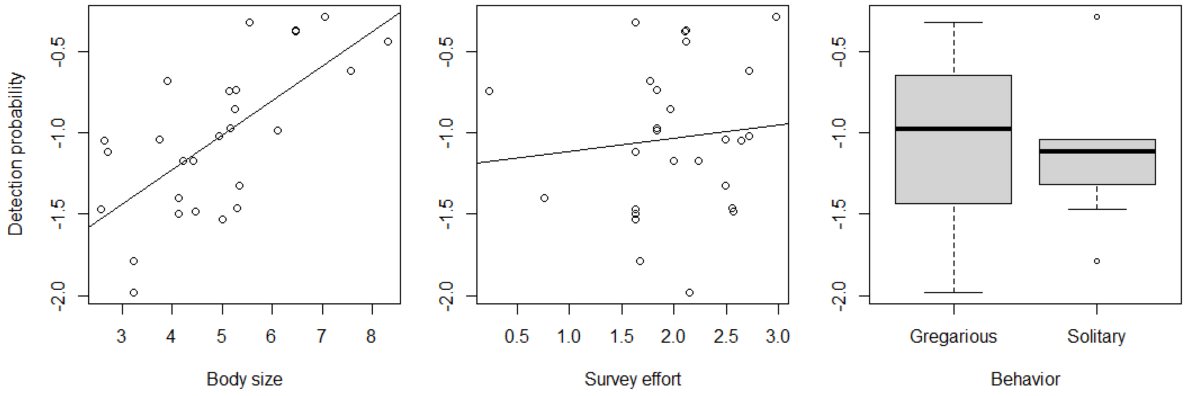


Fig S5.3: Predictions using model averaging from the best-fit models (ΔAICc<2). Probability of detecting ungulates by site with 95% confidence intervals using the function ‘predict’ in unmarked. 1=Bloemhof, 2=Borakalalo, 3=Boskop, 4=Botsalano, 5=Kgaswane, 6= Madikwe, 7=Mafikeng, 8=Molemane, 9=Molopo, 10=Pilanesberg, 11=SA Lombard, 12=Vaalkop, 13=Wolwespruit



a) b) c)

Fig S5.4: Relation between detection probability and a) Body Size, b) Survey effort and c) social behaviour of 27 ungulate species across 13 study sites of the NW Province. Overall, the regression model accounts for 92.92% of variance in species detection probability and is a significant fit to the data (F (4, 22) = 9.73, p < 0.001)

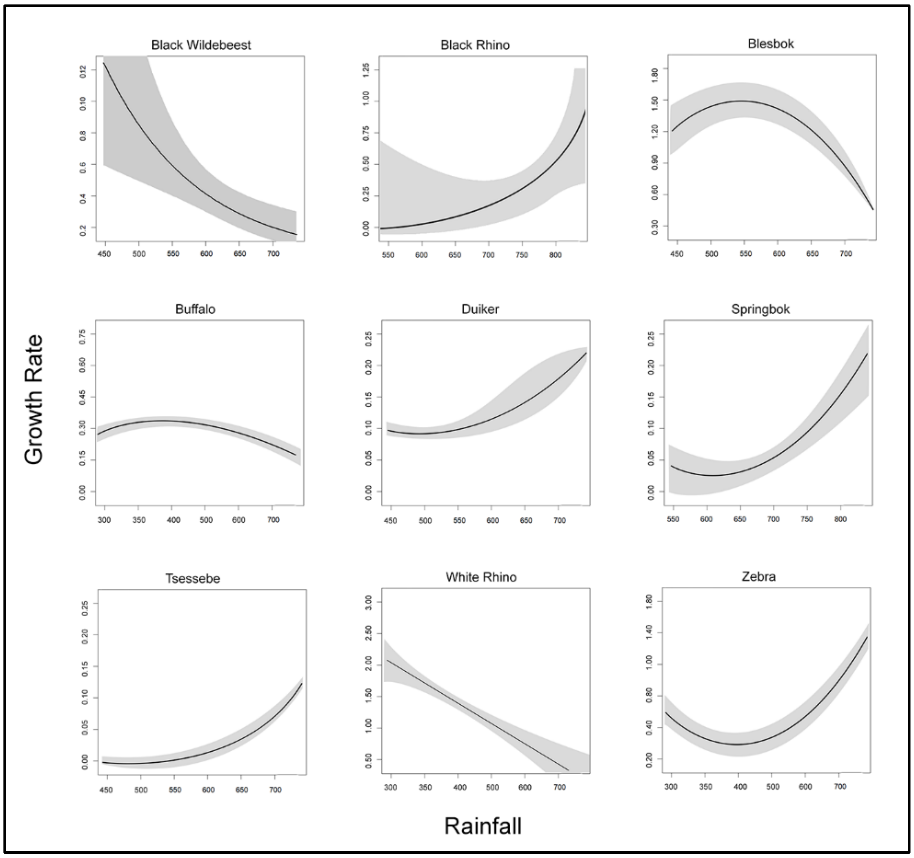


Fig S5.5: Growth vs rainfall predictions using model averaging from the best-fit models (ΔAICc<2) using the function 'predict' in unmarked. Mean estimates are in black and their 95% confidence intervals are in grey.