THE IMPACTS OF BOTTOM-UP AND TOP-DOWN DRIVERS IN SHAPING THE HERBIVORE COMMUNITY IN PAFURI, KRUGER NATIONAL PARK, SOUTH AFRICA

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

Department of Zoology and Entomology

by

Gareth Walker

June 2023

Supervisor: Prof. D.M. Parker

Co-supervisor: Dr L. Minnie

ABSTRACT

Globally, terrestrial mammal populations are facing critical population declines and range contractions owing to habitat fragmentation and destruction, wildlife overexploitation, and climate change driven by expansion of the human population. Mammalian herbivores are integral for maintaining ecosystem structure and functionality. They do this this through herbivory, by acting as prey and cycling soil nutrients. The impacts of herbivores on ecosystems, however, vary with their spatial occupancy which is influenced by interacting bottom-up and top-down factors. Modelling the drivers of herbivore communities is no trivial task given the myriad of potential bottom-up and top-down factors, and the interactions between the two, as well as the species-specific variations in intrinsic functional traits (e.g., foraging strategy, body size, metabolic rate, etc.) influencing herbivore responses (e.g., social structure, space-use, activity patterns, etc.) to these drivers. Consequently, few studies have attempted to model both bottom-up and top-down drivers in structuring herbivore communities, particularly in an African context where predator-prey guilds include multiple species, exposed to high levels of human activity. Therefore, the overarching aim of my research was to quantify the relative effects of both bottom-up and top-down factors driving the herbivore community in the northern Pafuri region of Kruger National Park, South Africa. I utilized a combination of field (i.e., camera trap and vegetation surveys) and analytical (i.e., stable carbon isotopes from faeces and plants) techniques in conjunction with geospatial data to evaluate the impacts of bottom-up (i.e., forage quantity, quality, and water availability) and top-down (i.e., predation and anthropogenic risks) factors on herbivore spatial occupancy and activity patterns. Herbivore responses to bottom-up and top-down factors were species-specific, even among members of the same feeding guild. Specifically, I found that herbivores (varying in body size and foraging strategy) displayed temporal, spatial and in some instances, dietary shifts that reflect species-specific, ecological trade-offs between resource acquisition, and predator and human avoidance. For example, kudu (*Tragelaphus strepsiceros*) displayed temporal and spatial avoidance of predators and humans, and exhibited previously undocumented levels of seasonal dietary shifts which suggests that the species traded forage acquisition for reduced predation and anthropogenic risks. Further, high levels of human activity appeared to eclipse the risks associated with natural predators resulting in human induced landscapes of fear. For example, warthogs (*Phacochoerus africanus*) and zebra (*Equus quagga*) occupied habitats with higher predation risks, but displayed spatial avoidance of nature reserve boundaries which were synonymous with high levels of bushmeat poaching. Most studies focussing on the impacts of bottom-up and top-down drivers neglect to consider the roles that humans play in structuring ecological communities. The results of my thesis, however, emphasize the importance of including anthropogenic drivers when investigating the roles that various bottom-up and top-down factors play in shaping ecological communities.

ACKNOWLEDGEMENTS

There is little doubt that the achievement of a doctorate degree extends way past the efforts of the candidate alone. In this regard, I count myself formidably fortunate to have had a tremendous team of people without whom, completion would not have been possible. Words themselves cannot express the gratitude that I have for every single one of you who so tirelessly supported me over the last three and a bit years in my pursuit of completing the marathon that is a PhD.

- First and foremost, to my supervisors Prof. Dan Parker and Dr Liaan Minnie. Your undying support, patience, encouragement, and enthusiasm proves that you are both by far the best supervisors that any student could wish for. I count myself incredibly privileged to have learnt from the "best in the business" and for that, I will forever be grateful to you both. Your mentorship exceeds what is to be expected of a supervisor and I have no doubt that past and future students will share the same sentiments. For good measure though, "this," "unclear antecedent," "succinct," and "NO," has to be added here for no reason.
- To Schalk van Dyk. I have no idea where to begin… The majority of this project is dedicated to you! Without you, I have little doubt that this study would barely have left the starting blocks. Your interest in the project coupled with your willingness to assist still astounds me. From helping service camera traps to collecting fresh dung samples – all the while ensuring our protection – word themselves cannot express my gratitude. I started off this project with a team member and concluded it with a friend. Thank you so very much Schalk!!!!!

- To Prof. Brian Reilly at Tshwane University of Technology. Thank you for recommending me for enrolment in this project and for your surreptitious interest in its completion. I am looking forward to hearing what you think!!
- To the State Veterinary Offices in Skukuza and in particular, to Dr Lin-Marie De-Klerk Lorist, thank you for all of your assistance! From transport permits to storage of dung samples and most importantly, for prioritizing my work, I am formidably grateful.
- To Sandra Visagie and her team of rangers, thank you for allowing us to share in the unrivalled beauty that is the Pafuri.
- To Marina Visser. Thank you for your assistance in helping identify vegetation samples. I think that without you, Schalk and I would still be paging through "Trees of Kruger."
- To Dr Grant Hall from the Stable Isotope Laboratory at the University of Pretoria. Thank you for your assistance in processing my vegetation and dung samples in record times. Your input in this project has been immense and I look forward to collaborating with you on publications going forward.
- To Dr Danny Govender, Judith Botha, Chenay Simms, Nikisha Singh, Patricia Khoza and Sharon Thompson from SANParks Scientific Services. Thank you for all of your assistance throughout the course of my study.
- To Dr Wendy Turner from the University of Wisconsin-Madison, USA. Thank you for securing funding for my and other EEID members' projects. Furthermore, thank you for your enthusiasm and continual support throughout the duration of my project.
- To Prof. Henriette van Heerden from the Department of Veterinary Tropical Diseases at the University of Pretoria. Thank you for your support and input during the initial stages of my project's inception.

- This study was funded by NSF Grant DEB-1816161/DEB-2106221 through the NSF-NIH-USDA Ecology and Evolution of Infectious Diseases program to Wendy Turner, Pauline Kamath, and Henriette van Heerden. Opinions expressed and conclusions arrived at are those of the author and are not necessarily reflective of the NSF.
- Thank you to Rhodes University, Nelson Mandela University (NMU), the University of Mpumalanga (UMP), and the Wildlife and Reserve Management Research group at Rhodes University for additional financial support and supplying of field equipment.
- To my friends and extended family who have stood by and supported me throughout the course of this study. You guys are absolute legends and I count myself so unbelievably lucky to have you all in my life. Specific mention goes to Steph Grobler and Chani Gillespie from Skukuza. Thank you for sharing your house with me for large parts of the previous three years.
- To my beautiful banana Carys Corry-Roberts. Where do I even begin???? You have stood by and supported me through times where I was unable to see the wood for the trees. I am the luckiest guy in the world to have you by my side. Thank you for your love, patience, and constant belief in me! I love you.
- To my brother Noons. Thank you for your encouragement and support not only during the course of this study but throughout the course of our lives. You are not only my brother, but my best friend too. Love you boy!!!!
- To my magnificent parents. Mom, Dad, thank you for absolutely everything that you have done for me and made possible over the years. I am beyond lucky to have the best ballies in the world. Dad… I swear I am finished studying now!!! Love you guys!!

TABLE OF CONTENTS

PREFACE

Each chapter in this thesis is prepared as a stand-alone manuscript with the study site description (Chapter 2) and references amalgamated into single sections. The contents of this thesis are structured as follows:

CHAPTER 1: General introduction that describes the rationale for my study.

CHAPTER 2: An extensive description of the study site

CHAPTER 3: Data chapter that explores seasonal dietary flexibility and spatiotemporal occupancy patterns of herbivore feeding guilds in the northern Pafuri region of Kruger National Park (Pafuri). Camera trapping methodology used across all the data chapters are described in detail here.

CHAPTER 4: Data chapter that assesses seasonal and habitat-specific responses by individual herbivore species to bottom-up, resource regulated effects.

CHAPTER 5: Data chapter that quantifies temporal and spatial responses by herbivores to seasonal and habitat-specific variations in predator- and human-related top-down effects.

CHAPTER 6: Synthesis chapter that discusses the impacts and interactions between bottom-up and top-down drivers regulating the herbivore community in Pafuri.

REFERENCES: Amalgamated references for the entire thesis.

APPENDICES: Includes all the additional information pertinent to topics addressed in the contents of my thesis.

Chapter 1: General introduction

Globally, terrestrial mammal populations are facing critical population declines and range contractions owing to habitat fragmentation and destruction, wildlife overexploitation and climate change driven by expansion of the human population (Ogutu et al. 2011, Bhola et al. 2012, Ripple et al. 2015, Steinbeiser et al. 2019, Vinks et al. 2020). Consequently, deriving reliable estimates on the space-use and behavioural responses of species to spatiotemporal variability in natural and anthropogenic drivers are required to advance science and facilitate biodiversity assessments over time, leading to more informed conservation and management decisions (Ripple et al. 2017, Palmer et al. 2018, Doser et al. 2022). Although single species assessments are important, quantifying the status and dynamics of entire communities is critical to better understand global change effects on biodiversity (Doser et al. 2022).

Of the 74 extant largest (≥ 100kg) terrestrial herbivores globally, 44 are listed as threatened with extinction, with 43 species experiencing widespread population declines (Ripple et al. 2015). Population declines undoubtedly have ecosystem-level impacts, as herbivores are fundamental to maintaining ecosystem structure and function through soil nutrient cycling, herbivory, and acting as prey (Pringle et al. 2011, Balfour et al. 2021). However, their impacts within ecosystems vary with their spatial occupancy at local and landscape scales which is driven by complex interplays between a myriad of drivers including resource availability, predators and humans (Bailey et al. 1996, Hopcraft et al. 2010, O'Kane & Macdonald 2018). Moreover, intrinsic functional traits such as body size and foraging strategy interact with species-specific habitat requirements and competition, influencing herbivore responses to these drivers (Cromsigt & Olff 2006, Young et al. 2020). Some of the drivers responsible for regulating herbivore populations are classified as bottom-up and top-down factors (Grange & Duncan 2006, Turkington 2009, Gandiwa 2013a).

Bottom-up factors regulate herbivore populations through resource restrictions from lower trophic levels (Dorresteijn et al. 2015). These bottom-up drivers, including forage availability and quality, and water availability, drive herbivore habitat selection (i.e., habitat selection theory; Rosenzweig 1981) and thus spatial occupancy (Coe et al. 1976, Gripenberg & Roslin 2007, Weterings et al. 2018). Ultimately, variation in habitat selection and occupancy impact reproduction, survival, and growth of herbivore populations and communities (Schmitz 2008, Gandiwa 2013a, Fryxell et al. 2022). For example, significant decreases in forage availability attributed to consecutive drought and extreme winter seasonal events drove mass mortality in 30% of Mongolia's terrestrial herbivore species, resulting in substantial population declines (Dangal et al. 2017). Similarly, in the absence of predators, mortality rates of zebra foals in Kenya increased during the dry season owing to significant reductions in the availability of suitable graze, resulting in population declines (Georgiadis et al. 2003). At the landscape scale, reductions in herbivore populations driven by resource limitations can have cascading impacts on the populations of predators at higher trophic levels, resulting in ecosystem instability (Schmitz 2008). As a result, bottom-up drivers may be relatively more important in regulating herbivore populations than top-down factors including predation and anthropogenic risks (e.g., Slobodkin 1960, Owen-Smith & Mills 2006, Riginos & Grace 2008, Gandiwa 2013b, Wenda et al. 2023).

Whereas bottom-up factors regulate herbivore populations from lower trophic levels, top-down factors impact the survival of species through risks attributed to predators and humans at higher trophic levels (Gandiwa 2013a, Gaynor 2019). Predators alter the population size, demography, and vital processes of herbivores through direct predation (i.e., consumption), as well as altering habitat selection, activity patterns, behaviour, diet and physiology through perceived predation risks (i.e., landscape of fear; Laundré et al. 2001). Consequently, herbivores face constant trade-offs between forage acquisition and avoiding periods and habitats with higher predation risks (i.e., optimal foraging theory; MacArthur & Pianka 1966, Riginos 2015, Davies et al. 2016b). Despite the obvious lethal effects associated with predation, perceived predation risks can have stronger effects on the dynamics of herbivore populations than direct predation itself (Winnie & Creel 2017, Gaynor 2019). As a result, herbivores are often required to expend more energy on costly antipredator behaviour (e.g., vigilance) which can limit foraging success and consequently impact survival, population growth and reproduction (Creel & Christianson 2008, Gaynor et al. 2019). For example, elk (*Cervus elaphus*) and bison (*Bison bison*) increased vigilance behaviour following the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park, USA, resulting in reduced foraging and decreased reproductive success and juvenile survival (Laundré et al. 2001). Similarly, in response to the reintroduction of cheetah (*Acinonyx jubatus*) in Bellebenno game reserve, Namibia, medium-sized herbivores increased vigilance around waterholes resulting in reduced levels of water intake impacting thermo- and osmoregulation (Ruble et al. 2022).

Although top-down pressures exerted by predators are important in regulating herbivore populations, anthropogenic top-down pressures are increasing – owing to human population growth and expansion – and may be stronger than pressures exerted by natural predators (Everatt et al. 2019b, Smith et al. 2021). Humans are keystone species that impact herbivore populations by acting as generalist, non-selective “super predators” (Gandiwa 2013a). Excessive wildlife offtakes (often illegal) has resulted in substantial population declines and even local extirpation of species (Dorresteijn et al. 2015, Suraci et al. 2019, Mills & Harris

2020). For example, excessive poaching in Kafue National Park, Zambia, between 1970 and 1980 lead to the local extinction of black rhinoceros (*Diceros bicornis*; Chomba & Matandiko 2011). Analogous to the landscapes of fear generated by perceived predation risks, indirect or non-lethal anthropogenic effects linked to human activities such as infrastructure development, human encroachment of nature reserve boundaries and unregulated tourism can in some instances be stronger than direct or lethal anthropogenic effects (Schuette et al. 2016, Mills & Harris 2020, Smith et al. 2021). Increased anthropogenic activities have caused herbivore range contractions accompanied by reduced foraging success which consequently impacts reproduction, survival, and population growth (Lindsey et al. 2013, Suraci et al. 2019, Mills & Harris 2020). For example, high levels of bushmeat poaching along the boundaries of Kafue National Park induced shifts in habitat selection by impala (*Aepyceros melampus*) resulting in increased spatial overlap with other herbivore species, invoking increased levels of competition and consequentially, reduced foraging success (Matandiko 2016).

According to optimal foraging (MacArthur & Pianka 1966) and habitat selection (Rosenzweig 1981) theories, herbivores adjust resource acquisition, activity patterns and space-use to optimise foraging opportunities while simultaneously reducing threats attributed to predators and humans. However, adopting a “one size fits all” interpretation of how herbivores balance resource acquisition and predator and human avoidance is naïve, given that herbivore responses to spatiotemporal variations in bottom-up and top-down factors differ according to body size and foraging strategy (Cromsigt & Olff 2006, Young et al. 2020). Specifically, body size determines species-specific trade-offs between foraging on large amounts of low-quality food (i.e., bulk foragers such as buffalo (*Syncerus caffer*) and kudu) versus foraging on small amounts of high-quality food (i.e., selective foragers such as common duiker (*Sylvicapra grimmia*) and warthogs; Illius & Gordon 1992, Wilmshurst et al. 2000). Furthermore, herbivore body size determines predation vulnerability, with predation risks decreasing with increasing body size (Olff et al. 2002, Hopcraft et al. 2010). For example, the occupancy of larger-bodied herbivores (≥ 150kg) in Serengeti National Park, Tanzania, was predominantly regulated by resources (i.e., bottom-up control), whereas the occupancy of smaller-bodied species was predominantly regulated by predation risks (i.e., top-down control; Anderson et al. 2016). Moreover, foraging strategy and dietary selection shape herbivore space-use and habitat selection that vary in response to spatiotemporal variations in predation and anthropogenic risks (Hebblewhite & Merrill 2009, Burkepile et al. 2013, Nicholson et al. 2014). For instance, browsers in Hwange National Park, Zimbabwe, shifted occupancy to open habitats with reduced browsing opportunities in response to increased predation risks from lions (*Panthera leo*) in closed, woodland habitats (Valeix et al. 2009a).

Although species-specific body sizes remain fairly constant across Africa (Clements et al. 2014), seasonal dietary flexibility of herbivore species driven by site-specific variations in forage availability and quality remain poorly studied (Sponheimer et al. 2003, Botha & Stock 2005, Codron et al. 2007a). For example, six herbivore species displayed undocumented seasonal dietary flexibilities in Punda Maria, Kruger National Park (KNP), owing to site-specific variations in forage quality and availability (Codron et al. 2007a). Moreover, Spitzer *et al.* (2020) found that the diets of roe deer (*Capreolus capreolus*) contained more than 25% grass owing to land use and climatic changes in Europe, despite the species being a presumed browser. Site-specific, seasonal fluctuations in forage availability and quality drives spatiotemporal variations in herbivore habitat selection and occupancy, which could result in species shifting among feeding guilds seasonally (Bubnicki et al. 2019). However, to my knowledge, no studies have accounted for the possible roles that site-specific, seasonal shifts in diet play in shaping herbivore responses to spatiotemporal variations in bottom-up and top-down factors.

Africa supports numerous biodiversity hotspots that include approximately 25% of the world's total mammal diversity (Agha et al. 2018, Comley 2019). The Pafuri triangle (hereafter Pafuri) in northern KNP, South Africa, is one such biodiversity hotspot with intact predator-prey guilds including multiple species (Deacon 2007, Ferreira & Funston 2020). Moreover, high levels of human activity attributed to tourism and infrastructure (Deacon 2007), and poaching (SANParks unpublished data 2022) make the Pafuri the ideal study site to contrast the impacts of bottom-up and human/natural predator top-down drivers regulating the herbivore community.

Given the complex interplay between the myriad of potential bottom-up and top-down drivers, the effects of which may not be mutually exclusive (Jedrzejewska & Jedrzejewski 2005, Gandiwa 2013a, Burkepile et al. 2013, Panebianco et al. 2022), few studies quantify both bottom-up and top-down drivers in structuring herbivore communities. Further, few studies assess the influence of bottom-up and top-down factors on herbivores in an African context with predator-prey guilds that include multiple species, exposed to high-levels of human activity (Gandiwa 2013b, Dorresteijn et al. 2015, Matandiko 2016). Therefore, the main aim of my research was to measure the relative effects of bottom-up and top-down factors driving the herbivore community in Pafuri, KNP. To address this, I first delineated herbivores according to feeding guild using a stable carbon isotopic faecal approach, on a seasonal basis. Thereafter, I assessed season- and habitat-specific variations in the occupancy patterns of each herbivore feeding guild (Chapter 3). Secondly, I evaluated the impacts of season- and habitat-specific variation in various bottom-up factors driving the occupancy of herbivores species (Chapter

4). Thirdly, I evaluated spatiotemporal responses by herbivores to season- and habitat-specific variation in predation and anthropogenic top-down risks (Chapter 5). Finally, I discuss the relative importance and possible interactions between bottom-up and top-down drivers regulating the herbivore community in Pafuri (Chapter 6).

Overall, I hypothesized that body size (Cromsigt & Olff 2006) and foraging strategy (Young et al. 2020) would be important determinants regulating spatiotemporal responses by herbivores to variations in bottom-up and top-down factors (Figure 1.1). Specifically, I predicted that larger herbivores such as elephants (*Loxodonta africana*) would be predominantly bottom-up, resource regulated (Hopcraft et al. 2012) and increase occupancy in habitats with increased quantities of available forage. In contrast, I predicted that smaller herbivores such as common duiker and warthogs would be predominantly top-down regulated (Hopcraft et al. 2012) and decrease occupancy in habitats with higher predation risks. Moreover, I predicted that herbivores, irrespective of body size, would be affected by anthropogenic risks and decrease occupancy in habitats synonymous with high levels of human activity. Further to body size, I predicted that foraging strategy would impact herbivore space-use, with browsers occupying closed woodland habitats, grazers occupying open grassland habitats, and mixed feeders shifting occupancy between the two habitats seasonally.

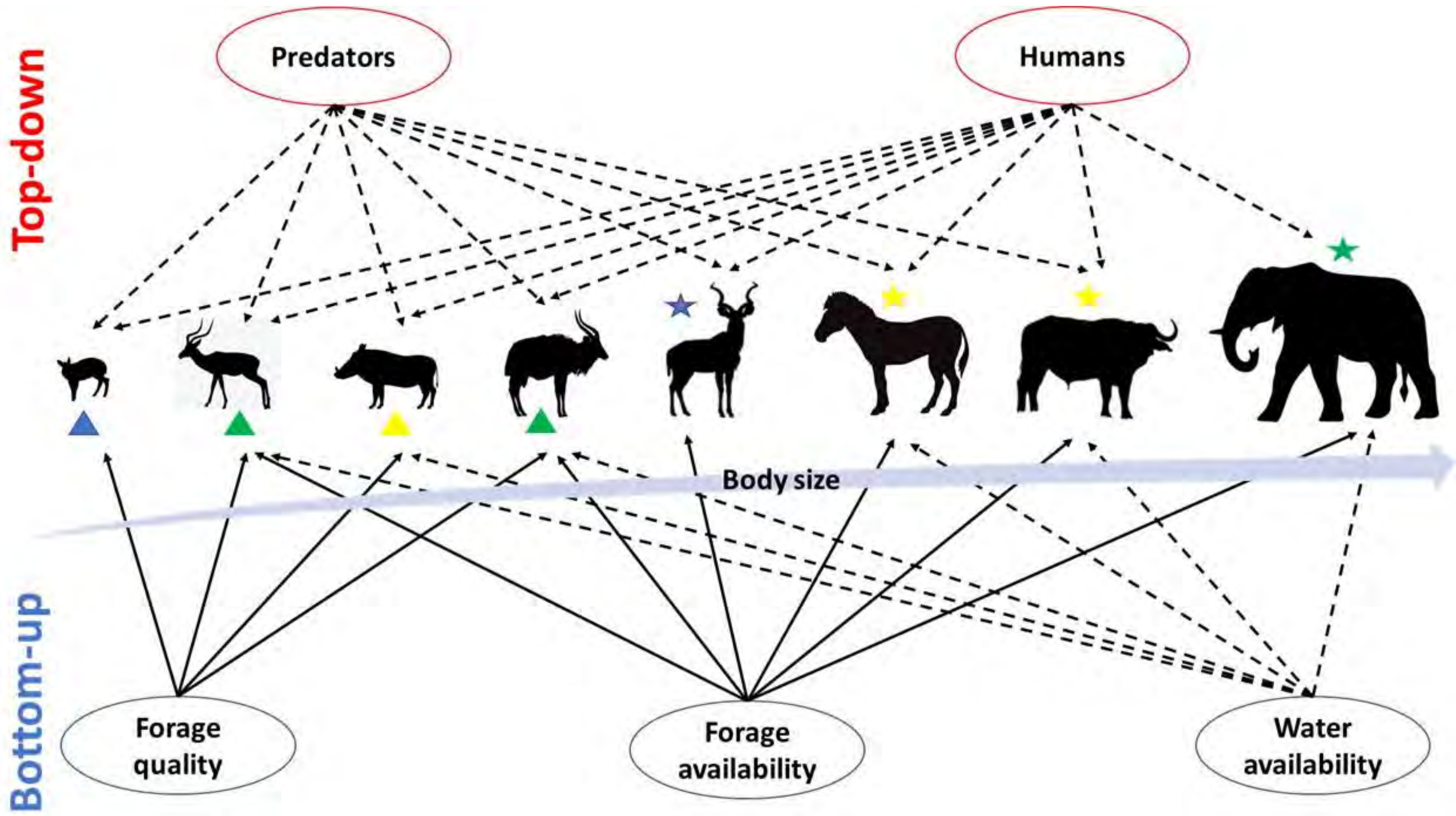


Figure 1.1: Hypothesised bottom-up and top-down drivers regulating the activity and space-use patterns of the focal species within the herbivore community in Pafuri, Kruger National Park. Solid lines represent directly proportional effects and dashed lines represent inversely proportional effects. Species are arranged in ascending order of body size from smallest (common duiker) to largest (elephant). Triangles and stars represent selective and bulk feeders respectively with colours illustrating feeding guilds (i.e., blue: browsers; yellow: grazers; green: mixed feeders).

Chapter 2: Study site

Study site

In November 2000, the Great Limpopo Transfrontier Park (GLTP) was established (Wolmer 2003). The area, covering almost 99 800 km², incorporates the KNP in South Africa, Gonarezhou National Park in Zimbabwe, and the Limpopo, Zinave and Banhine National Parks in Mozambique (Wolmer 2003, Chiutsi & Saarinen 2017). The Pafuri triangle (hereafter Pafuri) is at the centre of the GLTP (Figure 2.1a) and boasts a high abundance of plants and animal species (Wolmer 2003).

The establishment of the GLTP has, however, resulted in limited cross border control protocols, promoting high levels of human traffic from Mozambique and Zimbabwe into northern KNP (Hoogendoorn et al. 2019). The result thereof has been an increase in poaching incidences (SANParks unpublished data 2002, Reid 2018). However, the Communal Property Association (CPA), formed after land rights of the Pafuri were returned to the Makuleke community in 1996, have since devised a strategy aimed at the protection of land and all endemic wildlife species (Robins & Waal 2008). The monitoring and surveillance activities of the anti-poaching units have led, in part, to the recovery of predator and herbivore populations (Spenceley 2006). Furthermore, the implementation of an initiative called the 'Makuleke Large Mammal Reintroduction Project,' in 2005 has further facilitated the growth of the mammal community within the Pafuri (Lindsey et al. 2013).

The Pafuri (centred at 22˚24'05" S, 31˚11'49" E) is a 24 000-ha area of land that includes the section South of the Luvuvhu River and the Makuleke contractual park (North of the Luvuvhu River; South of the Limpopo River) (Figure 2.1b). Pafuri is bordered by Zimbabwe to the North and Mozambique to the East. Although only accounting for approximately 1% of the KNP's surface area (Steenkamp et al. 2013), Pafuri is associated with high levels of biodiversity that include approximately 70% of KNP's bird, mammal, fish, amphibian, reptile and tree species (Nortjé et al. 2012).

Climate

Pafuri has a hot, arid steppe climate (Kottek et al. 2006) and falls within the Tropical Premontane Arid Thorn Woodland climatic region (Schulze & McGee 1978). Climatic conditions vary from warm, wet summers (October to April) to mild, dry winters (May to September). Mean annual rainfall in the KNP decreases from South to North and from West to East with an average of 423.6 mm in Pafuri (Deacon 2007). The least amount of rain falls during July/August (3.2 mm) with the highest amount being recorded during February/March (87.2 mm; Figure 2.2a). The average daily temperatures during the summer range between 22.5°C and 31.8°C, with winter temperatures ranging between 12.9°C and 25.3°C (Figure 2.2b).

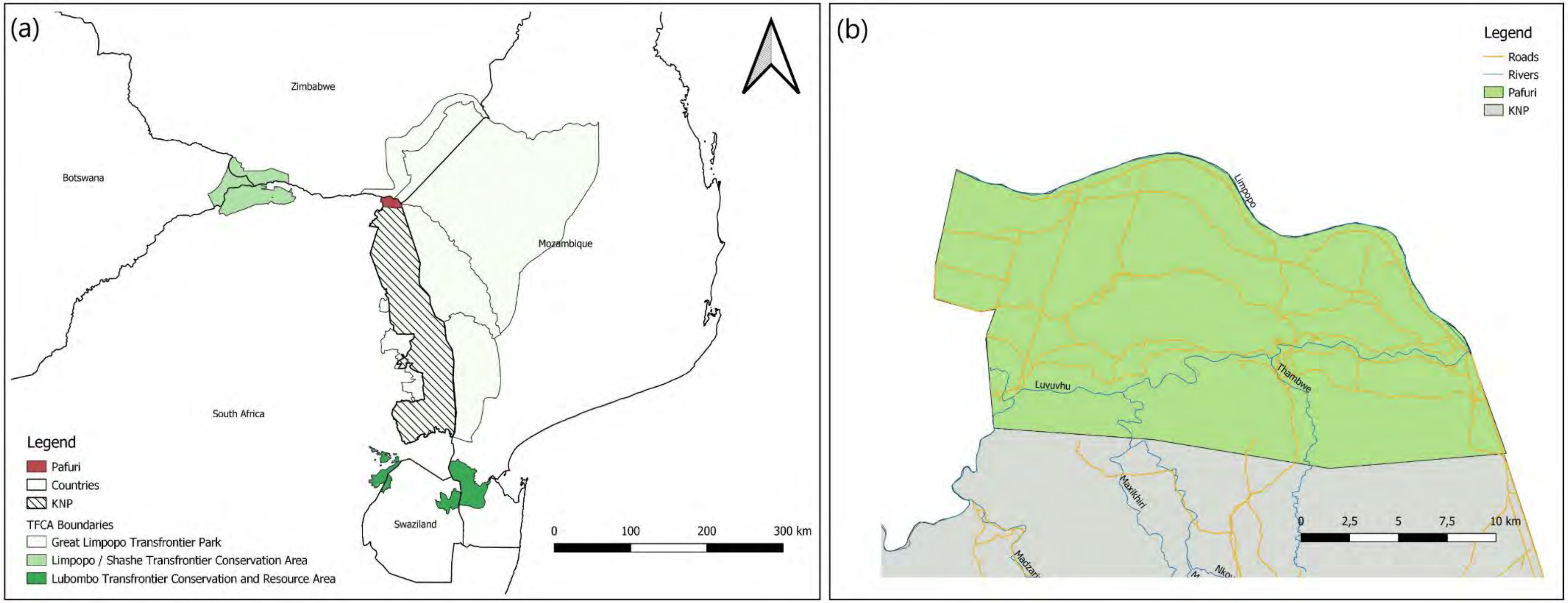


Figure 2.1: Three Transfrontier Conservation Areas (TFCA's) in southern Africa showing the Great Limpopo Transfrontier Park (GLTP). Pafuri is located at the centre of the GLTP (a) with the study site encompassing both the Makuleke contractual park and Pafuri region of KNP (b).

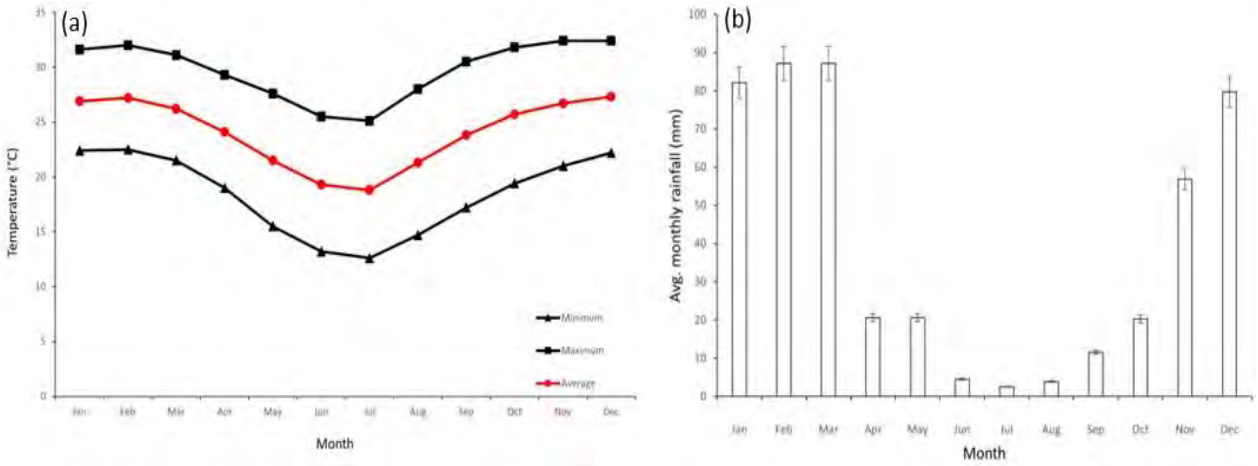


Figure 2.2: Average monthly temperatures (°C; a) and rainfall (mm; b) for Pafuri between 2016 and 2021.

Geology and soil

Nine geological features, each with contrasting rock types, are responsible for the habitat and corresponding vegetation heterogeneity associated with the Pafuri (Venter 1986, 1990). The main rock types that occur include quartzite, sandstone, mudstone, shale and basic (Deacon 2007). Marls, ferricrete, calcrete, unconsolidated sand and boulder beds occur in the eastern portions of the Pafuri whereas extensive areas of floodplain alluvium occur north of the Limpopo/Luvuvhu confluence (Venter 1990). Floodplains ensure a constant water supply for the mammal community in the Pafuri. Rounded basaltic rocky-outcrops protrude from the alluvium with some being capped by quartzitic boulders and cobblestones (Deacon 2007).

Soils surrounding the Luvuvhu River consist predominantly of deep red, calcareous, neocutanic clay of the Oakleaf form whereas soils flanking the Limpopo River consist mainly of deep brown, neocutanic and stratified, loam or fine sand; also, of the Oakleaf form (Tinley 1981, Venter 1986, Deacon 2007). Oakleaf soils retain water and absorb nutrients easily and are thus ideal substrates for vegetation growth (Nortjé 2018). Soil associated with the outer fringes of the Luvuvhu River floodplain are characterized by deep to moderately deep red and brown, paraduplex calcareous clay of the Valsrivier form with Limpopo River floodplain soil being dominated by very deep, brown calcareous and sodic, neocutanic and paraduplex clay of the Oakleaf and Valsrivier form (Venter 1990, Deacon 2007). Unlike Oakleaf soils, soils of the Valsrivier form are strong in structure and have a high clay content preventing easy water and nutrient absorption (Nortjé 2018). As such, vegetation growth will be limited to grass and shrub species with shallow root systems (Bezuidenhout 2009).

Vegetation

Eight vegetation types (Figure 2.3), dispersed through five bioregions, occur in the Pafuri (Mucina & Rutherford 2006). These include 1) ironwood dry forest; 2) Limpopo ridge bushveld; 3) lowveld riverine bushveld; 4) Makuleke sandy bushveld; 5) mopane basalt shrubland; 6) Musina mopane bushveld; 7) subtropical alluvial vegetation; and 8) subtropical salt pans. Soil nutrient levels and overall vegetation palatability vary between vegetation types. The subtropical alluvial vegetation, Limpopo ridge bushveld, Makuleke sandy bushveld, mopane basalt shrubland and Musina mopane bushveld all have higher soil nutrient levels and corresponding vegetation palatability in comparison to lowveld riverine forest, subtropical salt pans, and ironwood dry forests (Skarpe 1992, Mucina & Rutherford 2006). The heterogeneity in vegetation nutritional quality and quantity likely influence the movement of ungulate species that select areas with vegetation of high nutritional quality and quantity (Turkington 2009).

More than 256 plant taxa have been recorded throughout each of the eight vegetation types in the Pafuri (Joubert 2007). Moderately dense to dense mopane (*Colophospermum mopane*) thickets are dominant throughout the landscape with the species acting as an important food source during times of drought due to its water retaining capabilities (Siebert et al. 2003). Its ecological importance is further emphasized by its ability to retain dominance in a community when exposed to increased browsing pressure by large herbivores (Styles & Skinner 2000). Rare species such as the common corkwood (*Commiphora pyracanthoides*) and baobab trees (*Adansonia digitata*) occur in high densities throughout the Pafuri (Mucina & Rutherford 2006, Deacon 2007). Lowveld cluster-leaf (*Terminalia prunoides*) and Lebombo euphorbias (*Euphorbia confinalis*) occur in areas with shallow, calcareous soils and on rocky-outcrops. Ana trees (*Faidherbia albida*), common cluster figs (*Ficus sycomorus*) and nyala trees (*Xanthocercis zambesiaca*) are found throughout riverine forests on the banks of the Limpopo and Luvuvhu rivers with tall fever trees (*Vachellia xanthophloea*) occurring in clusters on the banks of pans.

In addition to the woody vegetation, a high diversity of grass species occur throughout the Pafuri. Common grass species such as nine-awn grass (*Enneapogon cenchroides*), tassel three-awn grass (*Aristida congesta*) and feather finger grass (*Chloris virgata*) occur in high densities throughout the Pafuri and provide high nutritional value for grazers and mixed feeders (O’Connor 1991).

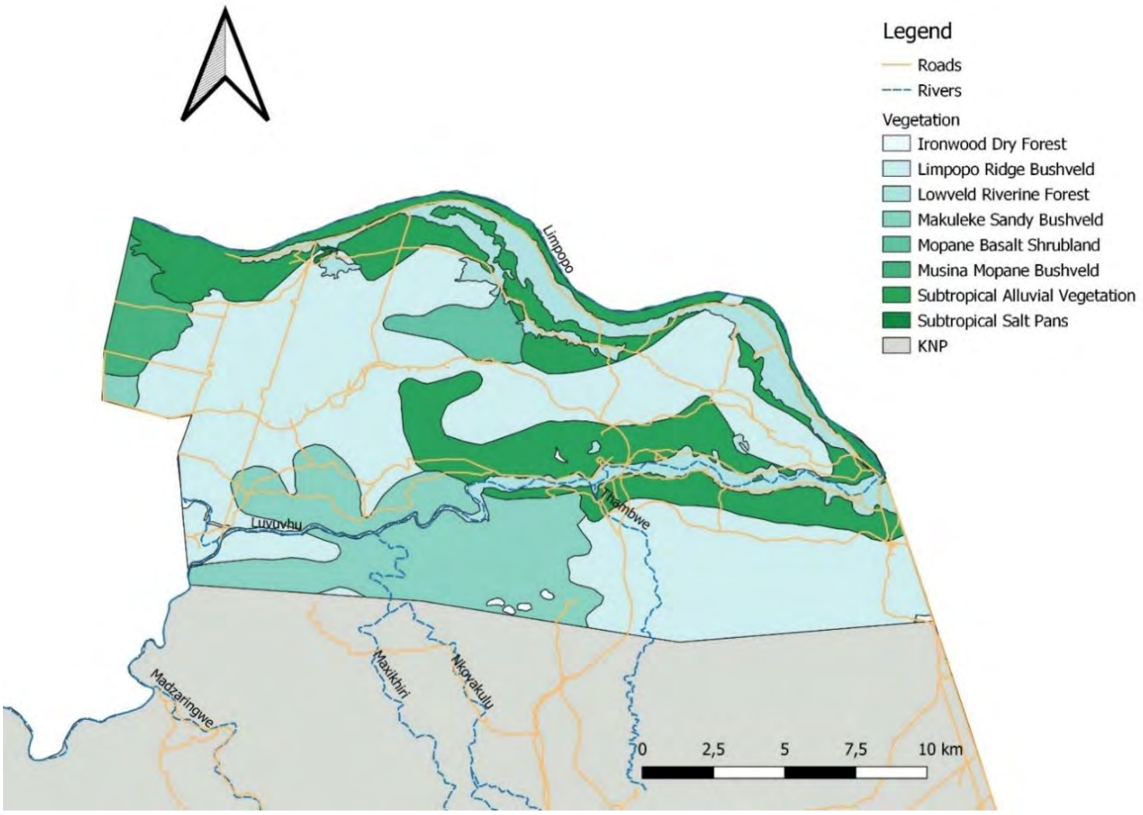


Figure 2.3: The eight vegetation types within the Pafuri according to Mucina and Rutherford (2006).

Mammal community

High-levels of mammal diversity have been documented in the Pafuri (Deacon 2007), with the aerial censuses of July 2017 recording 15 large (> 5 kg) mammal species (SANParks unpublished data, 2017). Certain species, including the Sharpe's grysbok (*Raphicerus sharpei*) and Samango/Syke's monkey (*Cercopithecus albogularis*), are locally endemic to the region. Moreover, large buffalo and elephant herds congregate along the banks of the Luvuvhu river in winter, with Pafuri serving as a vital point along the historical South Africa to Zimbabwe migration route of elephants. Although several large carnivores have been recorded in the region, including lions and spotted hyaena (*Crocuta Crocuta*) (Ferreira & Viljoen 2022), the densities of predators in Pafuri are unknown.

Chapter 3: Season- and habitat-specific variation in occupancy of a savanna herbivore community: a guild-level approach.

INTRODUCTION

Habitat fragmentation and destruction, wildlife overexploitation and climate change, driven by expansion of the human population, has induced global decreases in biodiversity (Ripple et al. 2015, Steinbeiser et al. 2019). Consequently, reliable estimates on the occurrence and behavioural patterns of species driven by spatiotemporal variability in natural and anthropogenic drivers are required to track biodiversity changes over time, and inform effective conservation and management decisions (Ripple et al. 2017, Palmer 2018, Doser et al. 2022). Although various studies have focussed on single species assessments (Williams et al. 2018, Runge et al. 2019, Edossa et al. 2022), few have quantified the status and dynamics of entire communities, required to facilitate an improved understanding of global change effects on biodiversity (Doser et al. 2022).

Mammalian herbivores influence terrestrial ecosystem structure and functioning through direct effects on vegetation structure and indirect effects on soil nutrient cycling (Hempson et al. 2015, Young et al. 2020, Davies et al. 2021). However, their impacts within ecosystems fluctuate with their spatial occupancy which varies among different functional groups of herbivores (Bubnicki et al. 2019). Specifically, spatial variation in occupancy is driven primarily by spatiotemporal variability of factors including resource availability (i.e., bottom-up factors), predators and humans (i.e., top-down factors) in combination with life-history traits, such as herbivore foraging strategy and body mass (Drouilly et al. 2018, Bubnicki et al. 2019, Kawamura et al. 2019, Boron et al. 2019).

The relative importance of bottom-up drivers, as reflected in forage availability, quality and water availability, vary spatiotemporally and thus drive herbivore space-use via resource limitations (Coe et al. 1976, Gripenberg & Roslin 2007, Weterings et al. 2018) and habitat selection (i.e., habitat selection theory, Rosenzweig 1981). Importantly, spatiotemporal variation in bottom-up factors impact reproduction, survival, and population growth of herbivore communities (Schmitz 2008, Gandiwa 2013b, Fryxell et al. 2022). For example, the nutritional condition of moose (*Alces alces*) decreased during periods of resource limitations, impacting pregnancy, parturition, and overwinter survival rates (Oates et al. 2021). Moreover, Hopcraft *et al*. (2010) showed that seasonal and habitat-specific variation in bottom-up factors, including forage availability and quality, are the predominant drivers of space-use of herbivore communities throughout Africa.

Irrespective, bottom-up drivers are not solely responsible for structuring herbivore communities (Gripenberg & Roslin 2007, Gandiwa 2013a, Welti et al. 2020), as they operate in concert with top-down processes. Top-down drivers, including risks attributed to predators and humans at higher trophic levels, affect the survival of herbivores (Gandiwa 2013a, Gaynor 2019). Specifically, predators and humans alter the population size, demography, and vital processes of herbivores through direct predation (i.e., consumption) and perceived predation risks (i.e., landscape of fear; Chapter 1; Laundre et al. 2010, Everatt et al. 2019a, Gaynor et al. 2019). For example, zebra responded to the presence of lions by occupying sub-optimal, closed habitats with reduced grazing opportunities (Fischhoff et al. 2007). Thus, trading forage acquisition for lower predation risks. Similarly, impala and warthogs avoided boundaries and roads in Kafue National Park presumably to avoid high levels of bushmeat poaching (Matandiko 2016).

According to the optimal foraging (MacArthur & Pianka 1966) and habitat selection theories (Rosenzweig 1981), herbivores need to maximise energetic gain by selecting habitats with ample foraging opportunities (i.e., bottom-up factors) while simultaneously limiting risks attributed to predators (Laundre et al. 2010) and humans (i.e., top-down factors; Gandiwa 2013a). However, herbivore responses to bottom-up and top-down factors vary interspecifically according to intrinsic functional traits such as body size and foraging strategy (Cromsigt & Olff 2006, Young et al. 2020, Davies et al. 2021). Specifically, larger herbivores (e.g., buffalo) are less at risk from predation and tend to occupy habitats with large quantities of low-quality forage (Macandza et al. 2004, Ryan et al. 2006, Veldhuis et al. 2019), whereas smaller herbivores (e.g., common duiker) are at a greater risk from predation and tend to occupy habitats with higher quality forage (Furstenburg 2008, Abu Baker & Brown 2014). Moreover, foraging strategy and diet influence herbivore habitat selection and spatial occupancy that vary in response to spatiotemporal variations in predation and anthropogenic risks (Hebblewhite & Merrill 2009, Burkepile et al. 2013, Nicholson et al. 2014). For example, African savanna browsers were more responsive to predation risks from ambush-hunting lions, in contrast to grazers, resulting in shifts in habitat selection from preferred woodland areas with abundant browse, to open habitats with fewer foraging opportunities when predation risks increased (Valeix et al. 2009a).

Traditionally, spatiotemporal variation in herbivore occupancy and space-use have been estimated using aerial and ground-based transects. However, these methods tend to be implemented infrequently and at coarse spatial scales resulting in inaccurate measurements and underestimations of herbivore abundance and distribution (Jachmann 2002). A methodological shift from aerial and ground surveys to motion sensor cameras has occurred over the last two to three decades (Kucera & Barrett 2011, Wearn & Glover-Kapfer 2019) with camera traps being the preferred, ubiquitous tool used in ecological and conservation studies (Karranth & Nichols 1998, O'Connell et al. 2011, Trolliet et al. 2014). Camera traps provide a non-invasive approach to wildlife detection and monitoring that has been made more accessible through advancements in camera trap technologies and cost efficiencies (Caravaggi et al. 2017). Moreover, advances in statistical modelling approaches have improved the accuracy of species distribution and occupancy estimates obtained from camera trap detection data(Rowcliffe et al. 2008).

Traditional statistical modelling approaches focused predominantly on quantifying the distribution and occupancy patterns of uniquely identifiable, single focal species (Connell et al. 2006, Pacifici et al. 2016, Devarajan et al. 2020), disregarding the impact of rare and elusive species on overall community dynamics (Doser et al. 2022). A solution to account for underrepresented estimates of individual species resulting from insufficient sample replicates involves grouping species according to intrinsic functional traits, such as feeding guild (Rich et al. 2016, Drouilly et al. 2018). In this regard, a higher number of replicate samples are produced, thereby discounting the issue of imperfect detection and leading to an asymptotically unbiased estimator of feeding guild occupancy (Guillera-Arroita 2011).

A problem with this approach, however, is that certain species may display seasonal dietary shifts and move between feeding guilds as a consequence. For example, herbivores in the KNP significantly varied (> 10%) their proportions of graze (C_4-plants) intake seasonally (Codron et al. 2007a). Further, possible shifts among feeding guilds drives season- and habitat-specific variations in spatial occupancy (Burton-Roberts et al. 2022). For example, mixed feeder impala feed predominantly on high-quality graze in the wet season and shift to browse in the dry season when the nutritional quality of grass decreases (Botha & Stock 2005, Codron et al. 2005). Consequently, impala tend to occupy open habitats with high grass cover in the wet season, and shift occupancy to closed-woodland habitats with high browse cover in the dry season (Staver & Hempson 2020). Therefore, to account for seasonal variations in diet that may consequently result in shifts among feeding guilds, herbivore dietary assessments need to be quantified on a seasonal basis.

Stable carbon isotope ecology provides a reliable technique for studying spatiotemporal variations in the dietary intake of herbivore species (Post 2002). In African savanna ecosystems, stable carbon isotope proxies for diet, obtained from herbivore faeces, reliably reflect proportions of consumed browse (C_3-photosynthesizing plants) to graze (C_3-plants) (Cerling & Harris 1999, Codron et al. 2007b, Ben-David & Flaherty 2012). The use of stable carbon isotope ratios are preferred owing to their accuracy at detecting slight seasonal shifts in the dietary intake of herbivores (Codron et al. 2005).

Numerous studies have evaluated seasonal variations in diet (Sponheimer et al. 2003, Codron et al. 2005, 2007c) and assessed spatiotemporal variations in herbivore occupancy separately (Anderson et al. 2016, Dlamini et al. 2020, Young et al. 2020).However, few have sought to evaluate seasonal dietary shifts of herbivores using stable carbon isotope proxies and incorporated these findings into broad scale assessments of spatiotemporal variability in the occupancy patterns of herbivore communities (Miranda et al. 2014). Thus, making this study one of the first of its kind to do so.

In this chapter, I aim to (1) classify species into feeding guilds based on seasonal variations of their dietary intake; and (2) assess spatiotemporal variations in the occupancy patterns of these feeding guilds between seasons and habitats. Given these aims, I predict that (1) grazers will feed predominantly on graze forage (C_4-plants) and browsers, predominantly on browse forage (C_3-plants) irrespective of season, (2) mixed feeders will increase their dietary intake of graze in the wet season owing to increased nutritional quality of grass during the same period (Botha & Stock 2005, Codron et al. 2005), and increase their dietary intake of browse in the dry season when the quality of grass declines; (3) across all feeding guilds, herbivore occupancy will decrease in the dry season owing to reductions in forage and water availability; (4) across all feeding guilds and in both seasons, herbivore occupancy will decrease in habitats with reduced forage and water availability, and increased predation and anthropogenic risks.

The findings of this chapter will provide context for subsequent analyses on the roles that bottom-up and top-down factors play in driving the occupancy patterns of individual herbivore species in the Pafuri, KNP.

MATERIALS AND METHODS

Study site

Details of the study site are described in Chapter 2.

Camera trap survey

To assess the spatial occupancy and activity patterns of herbivores, camera traps were deployed in a portion of the Pafuri, KNP during the dry (n = 2 surveys) and wet (n = 2) seasons between 2019 and 2021. A 2 x 2 km² grid was overlayed onto a vegetation map to stratify camera trap sites according to vegetation types (Bland et al. 2015; Figure 3.1). Forty-three Cuddeback Attack cameras (Non-Typical, Inc., Green Bay, WI, USA) were attached to tree trunks or metal dropper poles as close to the centre of each grid cell as possible. When the centre of a grid cell was topographically inaccessible (i.e., locations atop rocky outcrops or within rivers), cameras were erected at reselected sites within the same grid cell and vegetation type. Each camera was secured at ~50 cm above ground level to ensure both medium and large sized (±70 cm - ±180 cm) mammals were captured (Anderson et al. 2016).

Where necessary, vegetation was cleared within a 5 m semi-circular radius in front of each camera to prevent false triggering.

Camera trap surveys are typically conducted over short periods (30 – 90 days) to ensure demographic closure (no immigration or emigration) of the animals being photographed (Karranth & Nichols 1998, Comley et al. 2020). Therefore, I originally aimed to deploy the cameras for 60 consecutive nights at a time. Inaccessibility to the study site due to the COVID-19 pandemic, however, resulted in the cameras being deployed for variable periods during the first wet and dry season surveys of 2019/2020 (Table 3.1). High levels of theft and vandalism were also recorded during the seasonal surveys in 2019/2020, requiring a revision of the approach used for the subsequent surveys. Camera site selection and security of cameras at each selected site were investigated according to the findings by Meek *et al.* (2019) who recommended shorter camera deployment times, avoidance of areas with high human traffic and the use of security chains, locks and steel boxes as possible deterrents. Taking these into consideration, cameras were deployed during the 2020/2021 sampling period away from areas of high illegal human incursions, for 30 consecutive days, and secured to trees using chains, locks, and steel boxes. Nevertheless, the revised camera site selection approach was still able to account for the same proportions of each vegetation type sampled in the first two surveys.

Each camera was programmed to take a single high quality (5MP) image per trigger, with the strobe flash range set to 3.3 m to avoid the risk of capturing overexposed photographs. Cameras were active for 24 hours per day with a 15 second interval between consecutive photographs. Cameras were checked every two days.

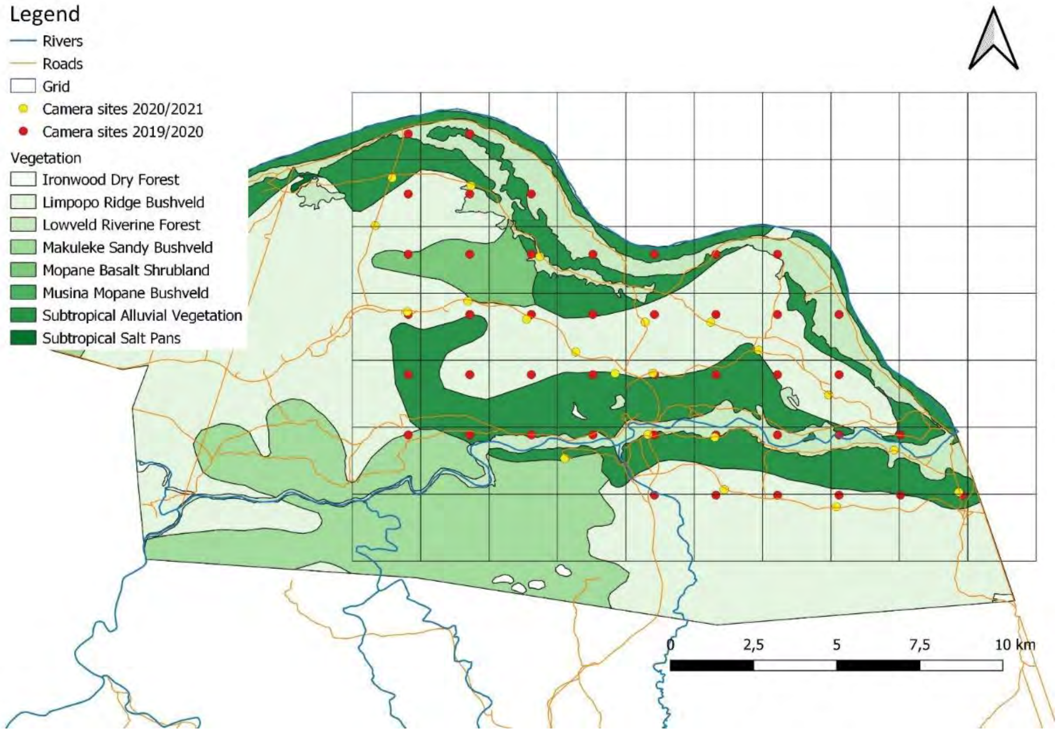


Figure 3.1: Camera sites selected using a 2 x 2 km^2 grid and stratified according to vegetation type in the Pafuri, Kruger National Park. Sites for both the 2019/2020 (red) and 2020/2021 (yellow) sampling periods are depicted.

Table 3.1: Summary of each sampling period during the wet/dry seasons of 2019/2020 and 2020/2021, showing the number of cameras that successfully recorded images as well as the number of days these remained deployed.

Sampling period	Season	No. of cameras that recorded images	No. of days deployed	No. of images recorded
1 2019/2020	Wet	27	128	4902
2 2019/2020	Dry	25	126	5931
3 2020/2021	Wet	16	30	2020
4 2020/2021	Dry	14	30	1509

Vegetation and faecal sample collection

Plants and herbivore faeces were collected seasonally in 2021. At each camera site, grass (C_4-plants), shrub (C_3-plants) and tree (C_3-plants) species within a 50m^2 quadrat were identified and their percentage cover estimated (Eberhardt & Thomas 1991). Samples from grass, shrub, and tree species accounting for the highest estimated percentage cover were collected for stable carbon isotope analysis. In total, 21 grass and 64 shrub/tree (hereafter collectively referred to as browse) samples were collected in the wet season, and 37 grass and 84 browse samples were collected in the dry season.

Herbivore faeces were collected at each camera site and opportunistically between sites. To obtain accurate estimates of dietary variations among species within each feeding guild, only fresh faecal specimens were collected to ensure that samples represented the appropriate season, and were not contaminated by fungi, soil and/or insects (Wrench et al. 1996, Codron et al. 2005). A total of 59 faecal samples representative of 11 herbivore species were collected in the wet season, and 56 faecal samples representative of 13 herbivore species were collected in the dry season. However, to facilitate seasonal comparisons of dietary intake, species from which faecal samples were only collected in a single season (i.e., steenbok (*Raphicerus campestris*) and waterbuck (*Kobus ellipsoprymnus*)) were removed from analyses. Given that the effects of bottom-up (Chapter 4) and top-down (Chapter 5) factors on herbivore occupancy are evaluated in the following two chapters, species that were undetected on camera trap images in either season (i.e., blue wildebeest (*Connochaetes taurinus*), eland and giraffe (*Giraffa camelopardalis*)) were also removed from the analyses. In total, 52 and 47 faecal samples from eight herbivore species in the wet and dry season respectively were retained for analyses. Both plant and faeces were stored in sealed medical polystyrene containers and placed in cool, dry environments prior to laboratory analysis.

Laboratory analysis

Faecal and plant samples were homogenized using an IKA MF 10 basic mill with a 1 mm sieve. After grinding, the samples were further sieved using a 0.5 mm sieve before being stored in Eppendorf tubes prior to weighing for isotope analysis. The mill was cleaned with 70% ethanol between samples to prevent contamination. Aliquots of both faecal and plant samples of ~ 1.0 mg were weighed into pre-cleaned tin capsules. Samples for isotopic analysis were combusted at 1020°C using an elemental analyser (Flash EA 1112 Series) coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany; Ben-David & Flaherty 2012), housed at the Stable Isotope Laboratory at the University of Pretoria.

Two laboratory running standards (Merck Gel: $\delta^{13}C$ = -20.26‰, $\delta^{15}N$= 7.89‰, C%= 41.28, N%= 15.29 and DL-Valine: $\delta^{13}C$ = -10.57‰, $\delta^{15}N$= -6.15‰, C%= 55.50, N%= 11.86) and a blank sample were run after every 11 unknown samples to identify analytical errors associated with the isotope ratio mass spectrometry (Ben-David & Flaherty 2012).

All results are referenced to Vienna Pee-Dee Belemnite (VPDB) for carbon isotope values, and to air for nitrogen isotope values (Coplen 2011). Results are expressed in delta notation using a per mille scale, expressed with the following standard equation:

$$\delta X(‰) = \frac{R_{Sample} - R_{Standard}}{R_{Standard} - 1}$$

where X= ^{15}N or ^{13}C and R represents $^{15}N/^{14}N$ or $^{13}C/^{12}C$ respectively.

Stable carbon isotopic data analyses

All statistical analyses were performed using the R programming language (version 3.4.2, R Development Core Team, 2017). To classify herbivores according to feeding guild, the %C_4

intake per species was estimated from faeces using a seasonal dual-endpoint mixing model (Codron et al. 2007b, 2007a). Previous studies have utilized global plant mean %$\delta^{13}C$ estimates (i.e., -27.0 and -12.5% for graze (C_4) and browse (C_3) forage respectively; Codron et al. 2007a). However, I made use of season- and habitat-specific endpoint values calculated from %$\delta^{13}C$ estimates of graze and browse forage in Pafuri to improve the accuracy of %C_4 estimates of herbivore dietary intake. Estimated %C_4 intake per herbivore species, per season were compared to pre-existing estimates of the same species (see Codron et al. 2005, 2007a). Herbivores were classified as grazers (dietary composition range: 84 – 100% C_4-plants), browsers (0 – 15% C_4-plants) and mixed feeders (4 – 76% C_4-plants). To test if each feeding guild displayed seasonal dietary shifts, a two-way ANOVA was used to determine whether mean %$\delta^{13}C$ differed across all feeding guilds seasonally. Tukey's HSD *post hoc* test was then used to test for differences in mean %$\delta^{13}C$ for each feeding guild in the wet and dry season. To determine similarities in the dietary niches of herbivore species, %$\delta^{13}C$ estimates from all plant and herbivore species were aggregated and grouped using the *k*-means clustering methodology in the R package *factoextra* (Kassambara & Mundt 2017). This approach utilizes the clustering error criterion in which the squared distance of each point is calculated from the predetermined cluster centroids and grouped based on the shortest Euclidean distance (Likas et al. 2003). The discriminant number of clusters was determined through the manual identification of elbow points along a visualisation curve (Appendix 3.1; Shi et al. 2021).

The influence of season and habitat feeding guild occupancy

The detection and occupancy probability of each herbivore feeding guild was modelled as a function of habitat and season. Following Drouilly *et al*. (2018), detection and non-detection data for all herbivore species were extracted from camera trap images per season and grouped according to feeding guild based on results from stable carbon isotopic analysis of faeces. Habitat types were classified per camera site (Appendix Table 3.1; Mucina & Rutherford 2006) and season was classified as either wet or dry.

Occupancy modelling framework

To model detection and occupancy of herbivore feeding guilds, I used single-species occupancy models (Mackenzie et al. 2017) implemented within a Bayesian framework using the R package *ubms* version 1.1.0 in R (Kellner et al. 2022). A single occupancy model per feeding guild was fitted to evaluate season- and habitat-specific variations in occupancy.

Season and habitat were factorised to represent discrete events. Default vague priors for each model per feeding guild were used (mean = 0 and SD = 10). I ran four parallel Markov chains with 10 000 iterations; the first 5 000 of which were discarded as burn-in samples. Model convergence was based on the Gelman-Rubin statistic (i.e., Rhat statistic), with model convergence being achieved when the Rhat statistic equalled one (Gelman et al. 1992). Furthermore, model convergence was evaluated through the visual examination of model traceplots (Nguyen et al. 2022). To determine the significance of season- and habitat-specific effects, 95% and 75% Bayesian Credible Intervals (BCI) of the posterior distribution were generated. Coefficients of which the 95% and 75% BCI did not overlap 0 were regarded as having significant and moderate effects on feeding guild occupancy, respectively.

RESULTS

Faecal isotopic ratios and herbivore feeding guild classification

The average (± 95% CI) %δ^{13}C endpoint estimates for graze (C_4-plants) and browse (C_3-plants) forage decreased between the wet (graze: -12.60 ± 1.30; browse: -26.80 ± 1.40) and dry (graze: -11.90 ± 0.70; browse: -26.60 ± 1.70) seasons. Similarly, the average %C_4 intake for herbivores decreased from 58.38 ± 25.36% in the wet season, to 43.50 ± 34.94% in the dry season, with all herbivores, except common duiker and elephant, decreasing their %C_4 intake between the wet and dry seasons (Table 3.2).

The %C_4 intake of common duiker fell within the predefined %C_4 range of browsers (0 – 15% C_4-plants) in both seasons (Figure 3.2), as predicted. In contrast, kudu displayed seasonal dietary shifts from a mixed feeder (predefined range: 4 – 76% C_4-plants) diet (30% C_4-plants) in the wet season to a predominantly browse-based diet in the dry season (2% C_4-plants) – contrary to predictions. As predicted, the diet of all grazers – buffalo, warthog, and zebra – comprised predominantly of C_4-plants and fell within the predefined %C_4 range of grazers (84 – 100% C_4-plants) in both seasons. Impala and nyala (*Tragelaphus angasii*) decreased their %C_4 intake between the wet (impala: 58%; nyala: 64%) and dry (impala: 43%; nyala: 12%) seasons, as predicted. However, based on the predefined %C_4 range, impala were classified as mixed feeders in both seasons, whereas nyala shifted from a mixed feeder diet in the wet season, to a predominantly browse-based diet in the dry season. Contrary to predictions, elephant displayed seasonal dietary shifts from a predominantly browse-based diet in the wet season (14% C_4-plants) to a mixed feeder diet with a high browse component in the dry season (19% C_4-plants). Overall, based on seasonal %C_4 estimates, two browsers, three grazers and three mixed feeders were identified in the wet season whereas three browsers, three grazers and two mixed feeders were identified in the dry season.

There was a significant difference in estimated %δ^{13}C among the feeding guilds ($F_{(5,92)} = 27.5$, $p < 0.001$). Specifically, comparisons of %δ^{13}C estimates among feeding guilds indicated that grazers consumed a significantly greater proportion of grass than both browsers and mixed feeders in the wet (browsers: $p < 0.001$, 95% CI: 7.98, 16.52; mixed feeders: $p < 0.001$, 95% CI: -10.35, -3.54) and dry (browsers: $p < 0.001$, 95% CI: 6.83, 16.56; mixed feeders: $p < 0.001$, 95% CI: -12.20, -5.24) seasons. Moreover, mixed feeders consumed significantly greater proportions of grass than browsers in the wet season, with the reverse holding for the dry season (Figure 3.3).

Camera trapping

Three camera traps failed in the wet season and six failed in the dry season resulting in a total of 510 and 420 camera trap-nights per season respectively. A total of 2633 independent images of eight herbivore species were captured in both seasons.

Table 3.2 Mean seasonal %δ^{13}C and %C_4 intake estimated from the faeces of eight herbivores collected in the Pafuri, KNP. Species are classified according to feeding guild based on individual %C_4 dietary intake (i.e., 0 – 15%: browser; 4 – 76%: mixed feeder; 84 – 100%: grazer) per season. Differences (Δ) in %C_4 between seasons are illustrated.

	Faecal %δ^{13}C						**%C_4 in diet**				
Species	**n**		**x̄**		**SD**		**% C_4**				**Δ%C_4**
	Wet	**Dry**	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**	**Guild**	**Dry**	**Guild**	**Wet**
Buffalo	7	5	-13.7	-15.2	1.2	1.0	98	Grazer	84	Grazer	15
Common duiker	1	1	-27.1	-25.5	0	0	4	Browser	13	Browser	-9
Elephant	9	9	-25.7	-24.7	1.6	2.0	14	Browser	19	Mixed feeder	-5
Impala	19	17	-19.4	-21.1	4.8	2.4	58	Mixed feeder	43	Mixed feeder	15
Kudu	9	3	-23.5	-27.2	6.0	0.4	30	Mixed feeder	2	Browser	28
Nyala	2	2	-18.6	-25.8	5.1	1.3	64	Mixed feeder	12	Browser	52
Warthog	1	2	-13.3	-14.5	0	1.8	100	Grazer	88	Grazer	22
Zebra	4	8	-13.5	-14.5	0.2	0.7	99	Grazer	88	Grazer	11

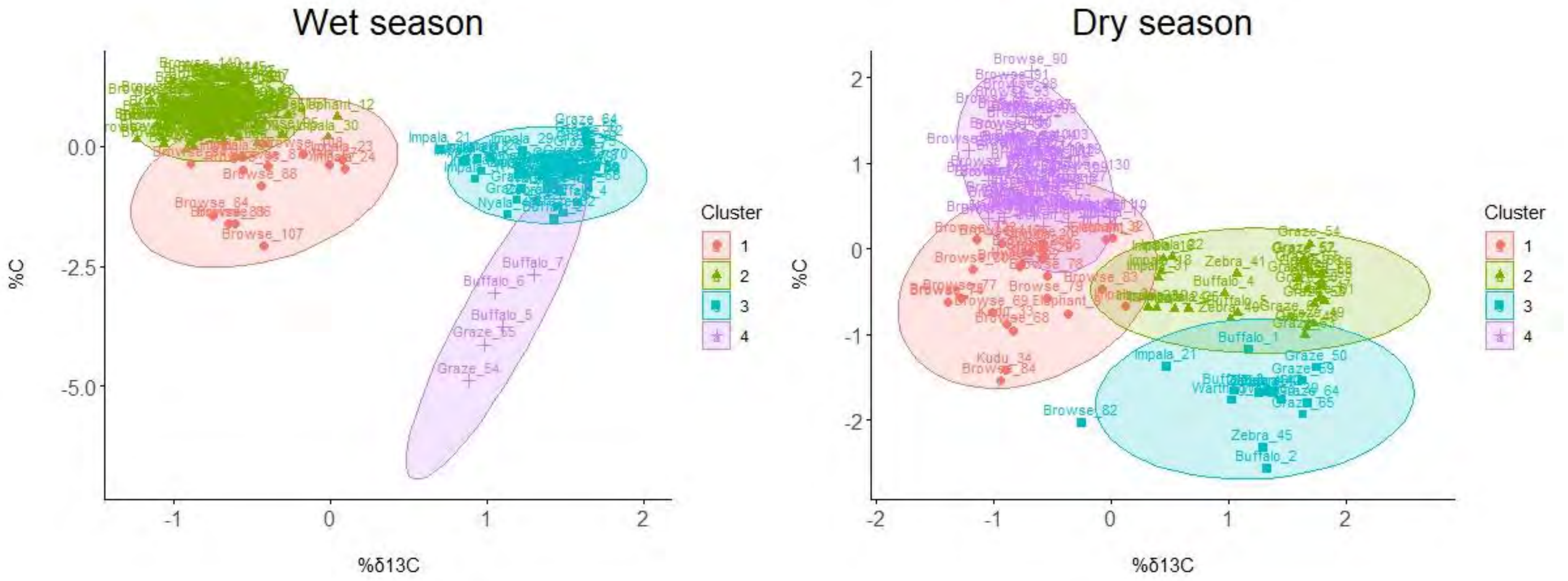


Figure 3.2: Cluster analysis illustrating similarities in the mean %δ^{13}C and %C estimates for herbivore species, and graze (C$_4$-plants) and browse (C$_3$-plants) forage seasonally. **Wet season:** Clusters 1 and 2 depict similarities in %δ^{13}C and %C estimates of browse forage (C$_3$-plants), and browser and mixed feeder herbivore diets; Clusters 3 and 4 depict similarities in %δ^{13}C and %C estimates of graze forage (C$_4$-plants), and grazer and mixed feeder herbivore diets. **Dry season:** Clusters 1, 3 and 4 depict similarities in %δ^{13}C and %C estimates of browse forage, and browser and mixed feeder herbivore diets, whereas Cluster 2 depicts similarities in %δ^{13}C and %C estimates of graze forage, and grazer and mixed feeder diets.

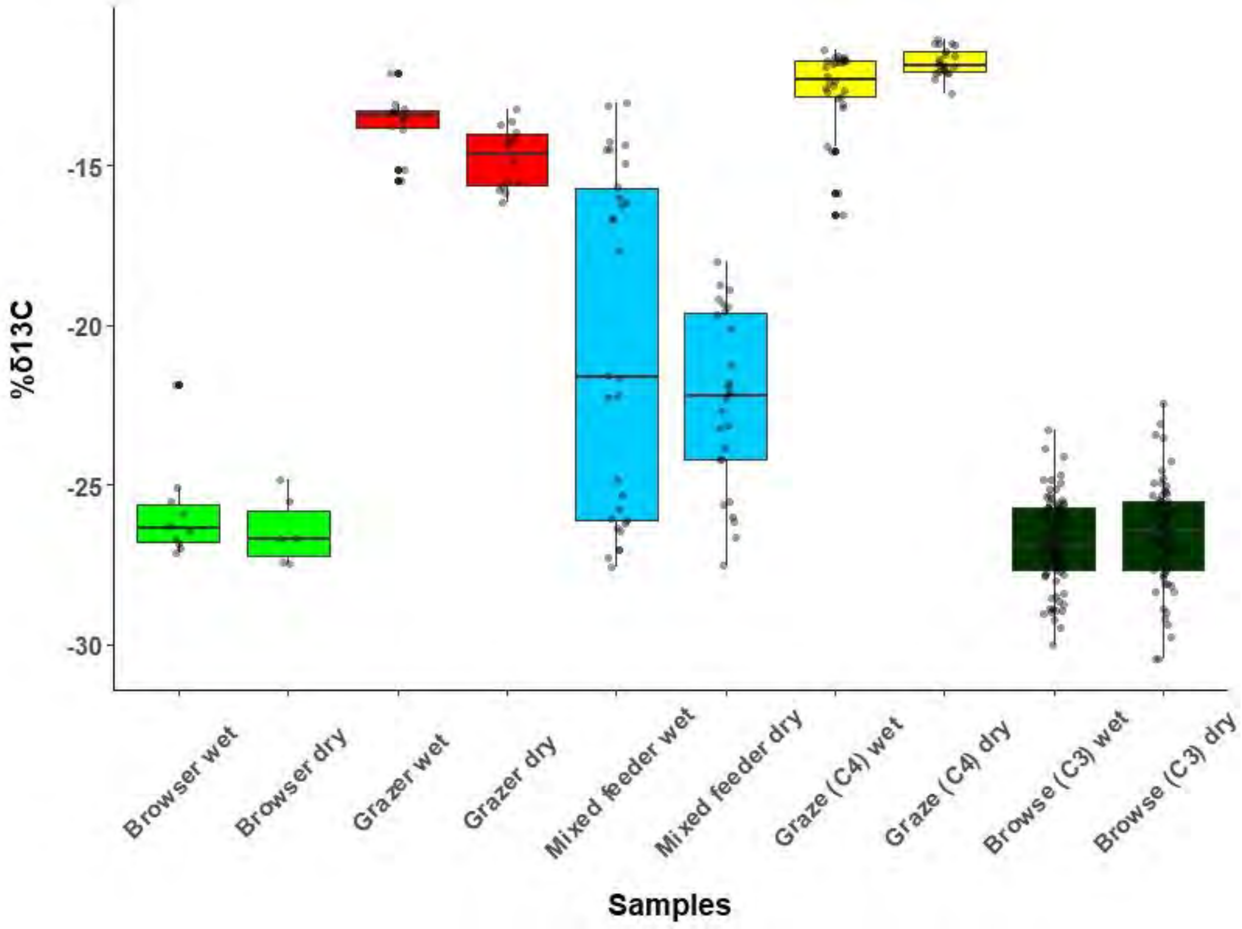


Figure 3.3: Seasonal estimates of %δ^{13}C obtained from herbivore faeces, and from grass, shrub, and tree samples. Herbivores are grouped according to feeding guild and plants are grouped into graze (C_4-plants) and browse (C_3-plants) forage per season. Horizontal lines = median; boxes = Interquartile Range (IQR); vertical lines = maximum and minimum estimates respectively.

Season- and habitat-specific effects on herbivore occupancy

There was no detected change in the average occupancy (Ψ_i) of herbivores between the wet (Ψ_i = 0.89, 95% CI: ± 0.03) and dry (Ψ_i = 0.88 ± 0.08) season. As predicted, the occupancy of browsers decreased between the wet (Ψ_i = 0.88 ± 0.01) and dry (Ψ_i = 0.79 ± 0.06) season, with the reverse holding for grazers (wet: Ψ_i = 0.92 ± 0.01; dry: Ψ_i = 0.95 ± 0.01) and mixed feeders (wet: Ψ_i = 0.86 ± 0.02; dry: Ψ_i = 0.89 ± 0.02), contrary to predictions. Across habitats, browser occupancy was highest in Lowveld Riverine Forest (LRF) (Ψ_i = 0.91 ± 0.01) and lowest in Subtropical Alluvial Vegetation (SAV) (Ψ_i = 0.74 ± 0.11). In contrast, grazer and mixed feeder occupancies were highest in SAV (Grazer: Ψ_i = 0.95 ± 0.01; Mixed feeder: Ψ_i = 0.93 ± 0.01) and lowest in Limpopo Ridge Bushveld (LRB) (Grazer: Ψ_i = 0.93 ± 0.01; Mixed feeder: Ψ_i = 0.84 ± 0.01).

Browser occupancy appeared to increase marginally in LRB during the dry season, with the reverse holding for LRF and SAV (Figure 3.4). Irrespective of the contrasting season- and habitat-specific variations in browser occupancy, however, only the effects of season and habitat in SAV during the dry season were moderately significant ($\beta 1$ = -1.65, 75% BCI: -3.13 – -0.23). Although grazers and mixed feeders appeared to increase occupancy in LRB and decrease occupancy in LRF between the wet and dry seasons, the effects of season and habitat were not significant (Figure 3.5).

Figure 3.4: Seasonal variations in herbivore feeding guild occupancy across habitats sampled in the Pafuri, KNP. LRB: Limpopo Ridge Bushveld; LRF: Lowveld Riverine Forest; SAV: Subtropical Alluvial Vegetation.

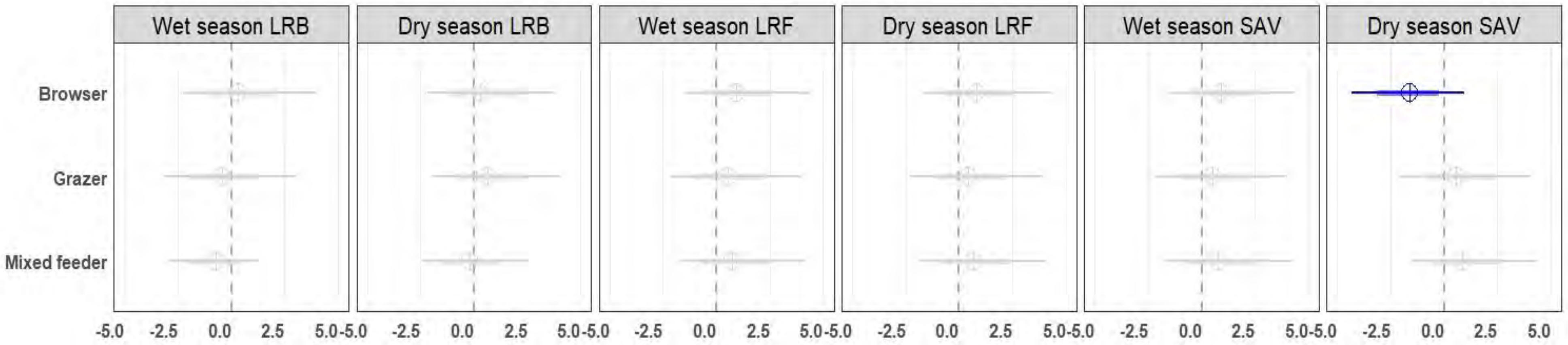


Figure 3.5: Standardized beta (β) coefficients representative of season- and habitat-specific covariate effects on the occupancy of herbivore feeding guilds. Grey bars indicate no significant covariate effects (95% BCI overlap 0), and blue bars illustrates moderate covariate effects (75% BCI does not overlap 0).

DISCUSSION

Across the savanna biome in Africa and specifically in the KNP, bottom-up factors such as forage cover, quality, and water availability exert a stronger driving force on the occupancy and space-use of herbivores than top-down factors such as predation risks (Owen-Smith & Mills 2006, Hopcraft et al. 2010). However, herbivore responses to season- and habitat-specific variation in bottom-up factors differ according to individual functional traits such as feeding guild (Seydack et al. 2012). Thus, given that the diets of feeding guild members vary between seasons owing to interspecific nutritional requirements, and differences in the availability and quality of forage (Sponheimer et al. 2003, Codron et al. 2007c), robust dietary assessments that account for the possibility that herbivores may shift between feeding guilds seasonally are required (Staver & Hempson 2020). Moreover, to better understand the factors influencing herbivore occupancy and space-use, seasonal dietary shifts need to be quantified first. Despite the importance of accounting for interguild shifts, no studies have quantified seasonal dietary variations of herbivores in Pafuri, making my study novel. Moreover, by accounting for potential interguild shifts by herbivores owing to seasonal variations in dietary intake, biased estimates of season- and habitat-specific effects on the occupancy patterns of herbivores are subsequently reduced leading to more accurate measures of species space-use. In this Chapter, I evaluated the seasonal dietary intakes of herbivores and classified species according to feeding guild. Contrary to predictions, three herbivores (i.e., elephant, kudu and nyala) displayed broader dietary ranges than previously documented (see Codron et al. 2007a). Specifically, elephants increased their graze intake in the dry season, but consumed higher proportions of browse in the wet season. In contrast, kudu and nyala shifted from a more mixed feeder-based diet in the wet season, to a diet dominated by browse in the dry season.. Using this feeding guild classification, I then evaluated variation in season- and habitat-specific occupancy of herbivores. With the exception of browsers in SAV in the dry season, there was a ubiquitous lack of seasonal- and habitat effects on herbivore occupancy – contrary to predictions. The general lack of season- and habitat-specific effects could potentially be an artefact of cameras being in close proximity to other habitats, confounding the occupancy analysis. In this instance, minimal variation in herbivore occupancy could be a consequence of the spatial scale at which the study was conducted, suggesting that detection probability (*p*) rather than occupancy may have been a better metric to use to quantify herbivore space-use between seasons and across habitats (Mackenzie et al. 2018).

Herbivore feeding guild classification

Importantly, seasonal %δ^{13}C endpoint estimates of graze (C_4-plants) and browse (C_3-plants) forage differed from global %δ^{13}C endpoints (see Sponheimer et al. 2003) and from site-specific %δ^{13}C endpoints estimated by Codron *et al*. (2007a) in the neighbouring Punda Maria Section, KNP. Dissimilar seasonal %δ^{13}C endpoint estimates of forage in the Pafuri highlights the importance of using site-specific isotope analyses when classifying herbivores into feeding guilds, as global isotopic endpoints will lead to inaccurate estimates of herbivore dietary intake resulting in erroneous feeding guild classifications (Codron et al. 2007a). This is particularly true for mixed feeders which may increase/decrease grass intake depending on seasonal quality/availability (Codron et al. 2007a, Abraham et al. 2019, Staver & Hempson 2020). The use of site-specific endpoints allowed me to identify broader dietary ranges than previously documented for three species (see Botha & Stock 2005, Codron et al. 2006, 2007a). Although most herbivores displayed some seasonal shifts in graze/browse consumption, all their diets – with the exception of elephants, kudu and nyala – fell within the predefined isotopic dietary ranges for grazers, browsers, and mixed feeders. Contrary to predictions, elephants (predefined mixed feeder; Codron et al. 2006) shifted from being browsers in the wet season to mixed feeders in the dry season, with kudu (predefined browser; Codron et al. 2007a) and nyala (predefined mixed feeder; Codron et al. 2007a) switching from mixed feeders in the wet season to browsers in the dry season. The recorded dietary flexibilities of elephant, kudu and nyala reflects a plausible resiliency by each species to changes in plant community structure and compositions (Staver & Hempson 2020).

a. Browsers

Although common duiker were classified as browsers as predicted, they increased their grass intake during the dry season. Across their range in Africa, common duiker are concentrate selective feeders (Furstenburg 2008), with their diets ranging from a pure browse-based diet (Cerling et al. 2003, Sponheimer et al. 2003) to including some (< 15%) graze (Gagnon & Chew 2000), as was the case in Pafuri. However, no studies have linked increased graze consumption to seasons (Codron et al. 2007a, Djagoun et al. 2013). The seasonal increase in graze consumption in the dry season is surprising, given the relatively lower quality of grasses in the dry season (Seydack et al. 2014). This suggests that this dietary shift in common duiker may be driven by interspecific competition. Common duiker may employ shifts along the dietary niche axis, rather than the spatial niche axis, during periods of increased interspecific competition for relatively higher quality browse in the dry season, to reduce competition (Sinclair 1985, Prins et al. 2006). Alternatively, common duiker may be occupying less optimal habitats with reduced foraging opportunities in the dry season to reduce predation and/or anthropogenic risks (Abu Baker & Brown 2014, Mills & Harris 2020), as reflected in the reduced occupancy in SAV during the dry season. For example, common duiker in the Indian Ocean Coastal Belt, South Africa, varied space-use in response to predation and anthropogenic risks, occupying lower quality habitats to reduce predation risks from mesocarnivores (e.g., black-backed jackal (*Canis mesomelas*)), and reduce anthropogenic impacts associated with agriculture and urban expansion (Ehlers Smith et al. 2019).

The higher graze intake by kudu in the wet season could be attributed to increases in the quality and availability of grasses during the same period, illustrating a plausible bottom-up effect (Barbehenn et al. 2004, Mbatha & Ward 2010). For example, kudu in KNP increased their graze intake in recently burned areas with green flushes of high quality grass (Owen-Smith & Cooper 1985). Irrespective, seasonal dietary shifts suggests that kudu are not exclusively non-selective browsers; contrary to literature (Owen-Smith 1994, Furstenburg 2005, Gray et al. 2007). The higher proportion of graze intake by kudu in the wet season suggests a broader dietary flexibility by the species than what has previously been reported (Gagnon & Chew 2000, Codron et al. 2007a). Similarly, Spitzer *et al*. (2020) found that the diets of roe deer (*Capreolus capreolus*) contained more than 25% grasses owing to land-use and climatic changes in Europe, despite the species being a presumed browser. The dietary flexibility for kudu documented here suggests that they may be more resilient to changes in plant community structure owing to, amongst others, bush encroachment and climate change (Abraham et al. 2019, Staver & Hempson 2020), than previously thought. However, this hypothesis requires long-term dietary analyses (see Raynor et al. 2017) including estimates of changes in body condition and vital rates to asses if these dietary shifts are affecting population survival rates.

b. Grazers

Despite significant decreases in graze intake during the dry season, the diets of buffalo and zebra fell within the predefined dietary range for grazers (i.e., 84 - 100% grass; Codron et al. 2007a), as predicted. High proportions of graze intake by buffalo in the wet season correspond with Cerling *et al*. (2003) who reported diets of ~100% grass in East African

Buffalo. Moreover, reduced graze intake by buffalo in the dry season corresponds with Sponheimer *et al*. (2003) and Codron *et al*. (2007a) who reported greater than 10% browse in the diets of buffalo in KNP. In contrast, significant reductions in graze intake by zebra in the dry season contradicts Codron *et al*. (2005; 2007a) who reported less than 10% browse in the diets of zebra in KNP. It is possible that significant seasonal variations in grass intake by both buffalo and zebra may be attributed to differences in the carbon isotopic composition of graze forage that follow different C_4-sub-pathways, rather than actual increases in proportions of browse consumed in the dry season (Hattersley & Roksandic 1983, Cerling et al. 2003). Alternatively, and more likely, significant decreases in grass availability/quality in the dry seasons may be driving buffalo and zebra to increase browse intake to maintain nutritional requirements (e.g., Venter & Watson 2008, Havarua et al. 2014). Thus, highlighting a bottom-up, resource regulated effect responsible for seasonal dietary variations in grazers. For example, buffalo (Landman & Kerley 2001) and zebra (Potgieter & Kerley 2022) in the Eastern Cape, South Africa, increased their intake of browse during periods of reduced grass cover.

As predicted, warthogs were predominantly grazers in both seasons, although significantly reducing grass intake from ~100% in the wet season to ~88% in the dry season. The significant seasonal decreases in %C_4-plant intake by warthog in the Pafuri contradicts findings by Codron *et al*. (2007a) in the neighbouring Punda Maria, KNP, and Botha & Stock (2005) in Hluhluwe-iMfolozi Park, who reported small proportions of browse (i.e., < 10% C_3-plants) present in the diets of warthogs. Warthog are selective grazers that depend on high-quality food to maintain nutritional requirements (Field 1970, Treydte et al. 2006). Consequently, warthog feed predominantly on annual grasses in the wet season when the quality of graze is high, and shift to a diet comprised of fruits, forbs, legumes and roots in the dry season when the quality and quantity of graze decreases (White 2010, Adeola et al. 2019, Edossa et al.

2021). It has been documented that fruits, forbs, legumes and roots are 0.5– 2% enriched in ^{13}C compared with C_3-foliage in KNP and elsewhere (Cerling et al. 2004, Codron et al. 2007a, Yang et al. 2015). Thus, it is plausible that the ^{13}C-enriched portion of warthog diets in Pafuri may reflect utilization of fruits, forbs, legumes, and roots – particularly in the dry season.

c. Mixed feeders

As predicted, impala fell within the predefined dietary range of mixed feeders (4 – 76% grass) in both seasons, feeding on a higher proportion of graze in the wet season, and a higher proportion of browse in the dry season. Shifts from a higher proportion of graze in the wet season, to a higher proportion of browse in the dry season highlights the seasonal dietary flexibility of impala (Van Rooyen 1992, Sponheimer et al. 2003, Botha & Stock 2005). Specifically, impala are intermediate mixed feeders that feed predominantly on C_4-plants in the wet season when the quality of graze increases, shifting to a more C_3-based diet in the dry season owing to the higher protein content of browse relative to graze during the same period (Kos et al. 2012, Staver & Hempson 2020, Young et al. 2020).

Although feeding on higher proportions of graze in the wet season and switching to a predominantly browse based diet in the dry season; contrary to predictions, nyala were not classified as mixed feeders across all seasons. Moreover, similarly high proportions of graze in the diets of nyala in the wet season have not been documented (see Gagnon & Chew 2000, Sponheimer et al. 2003, Codron et al. 2007a). Nyala are classified as intermediate mixed feeders that preferably occupy closed, woodland habitats (Furstenburg 2016). Consequently, previous dietary estimates have recorded higher proportions of browse in the diets of both Southern (Codron et al. 2007b, 2007a) and East African (Gagnon & Chew 2000, Sponheimer et al. 2003) conspecifics. Like kudu, the documented dietary flexibility of nyala reported in this study suggests that the species could be resilient to variations in plant community structure attributed to bush encroachment and climate change. Irrespective, significant seasonal variations in dietary intake suggests that nyala display a higher dietary flexibility than previously documented (Van Rooyen 1992, Sponheimer et al. 2003, Codron et al. 2007a).

Contrary to predictions, elephant displayed a predominantly browse-based diet in the wet season, and a mixed feeder diet with a high proportion of browse in the dry season. Irrespective, this seasonal shift in diet was not significant (< 10% graze). Despite being classified as intermediate mixed feeders (Hansen et al. 1985, Cerling et al. 2006), seasonal increases in the proportion of graze consumed by elephants in the Pafuri contradicts Codron *et al*. (2006) who reported inverse seasonal decreases in %C_4-plant intake by elephant in northern KNP between the wet and dry seasons. Moreover, Codron *et al*. (2006) reported significantly higher proportions of graze present in the diets of elephant during the wet season in contrast to this study. Although individual plant taxa were not assessed, it is plausible that the unexpectedly high proportions of browse intake by elephants in both seasons could correlate with the higher abundance and quality of evergreen mopane shrub in the Pafuri (Deacon 2007) which are prevalent in the diets of elephants in similar regions across Africa (Kos et al. 2012).

Season- and habitat-specific effects on patterns of herbivore occupancy

Browser occupancy decreased moderately in SAV in the dry season, as predicted. Decreased occupancy may be due to reductions in the availability and quality of browse (i.e., bottom-up regulation) driving species to occupy alternative habitats with improved foraging opportunities in the dry season (Turkington 2009, Gandiwa 2013a). For example, reduced quality of browse during winter in Norway drove moose to occupy habitats with more abundant but lower-quality browse species (Van Beest et al. 2011). However, to understand if bottom-up factors are primarily responsible for impacting these seasonal shifts in browser occupancy, the potential role of top-down factors (i.e., predation and/or anthropogenic risks) needs to investigated (Riginos 2015, Vinks et al. 2020). For example, browsers in Hwange National Park shifted occupancy to open habitats with fewer browsing opportunities in response to increased predation risks from lions in closed, woodland habitats (Valeix et al. 2009a). Similarly, herbivore occupancy decreased along the boundaries in Kafue National Park where bushmeat poaching was concentrated (Matandiko 2016). Like predation, risks associated with humans evoke similar "antipredator" responses in herbivores which reflect in their patterns of spatial occupancy (Everatt et al. 2015, Smith et al. 2021). Unlike browsers and contrary to predictions, season and habitat type did not influence the occupancy of grazers or mixed feeders. The lack of habitat-specific and seasonal shifts in occupancy for grazers and mixed feeders, as well as limited shifts in occupancy for browsers, may reflect a real pattern owing to similar habitat quality (i.e., forage quantity and quality, water availability, and predation and anthropogenic risks) across habitats and seasons. However, this is unlikely given that habitat quality varies in response to changes in elevation, slope, landform type and annual precipitation (Chen et al. 2021). Alternatively, and more likely by evaluating the broad-scale impacts of habitat and season driving the occupancy of entire feeding guilds, species-specific behavioural differences could be obscuring each species' response to individual bottom-up and top-down factors. Intrinsic functional traits such as diet and body size interact with resource competition, habitat requirements and facilitative interactions among species, affecting individual herbivore responses to specific bottom-up and top-down factors (Cromsigt & Olff 2006, Young et al. 2020). For example, Anderson *et al*. (2016) suggested that the occupancy of smaller-bodied herbivores in Serengeti National Park were regulated by predation risks (i.e., top-down effect), whereas the occupancy of larger-bodied (≥ 150kg) herbivores were predominantly regulated by forage availability (i.e., bottom-up effect).

CONCLUSION

Overall, disparities between seasonal endpoint estimates of C_4- (graze) and C_3- (browse) forage in Pafuri, and global (see Sponheimer et al. 2003) and local endpoints estimated in other regions of KNP (see Codron et al. 2007a) highlights the importance of using site-specific endpoints when undertaking seasonal dietary analyses of herbivores. By using site-specific endpoints, I was able to identify broader dietary ranges in three herbivore species (i.e., elephants, kudu and nyala) than what has previously been reported, which would not have been detected if I had used global endpoints. Generalist species capable of exhibiting seasonal dietary shifts are likely more adaptable to variations in plant community structure attributed to, for example, bush encroachment and climate change (Abraham et al. 2019, Staver & Hempson 2020) in contrast to specialist species incapable of exhibiting seasonal dietary shifts. It is recommended that future studies undertake long-term dietary analyses (see Raynor et al. 2017), including estimates on the changes in herbivore body conditions and vital rates in response to landscape-level changes in habitat quality (i.e., forage quantity and quality, water availability, and predation and anthropogenic risks) over multiple seasons, to delineate drivers of herbivore dietary flexibility and the consequences thereof for population survival rates. Although surprising, the limited shifts in occupancy by browsers, and the ubiquitous lack of habitat-specific and seasonal shifts in occupancy by grazers and mixed feeders suggests that, at the guild level, fine-scale, species-specific responses to individual bottom-up (i.e., forage quantity and quality, and water availability) and top-down (i.e., predation and anthropogenic risks) factors are likely being masked. Further, it is possible that the overall lack of season- and habitat-specific effects driving herbivores could be a consequence of the non-independence of cameras among habitats, confounding occupancy estimates. As such, the findings of this chapter will form the basis for Chapters 4 and 5 wherein the effects of bottom-up and top-down factors driving the space-use and occupancy of herbivores in Pafuri will be assessed.

Chapter 4: The influence of bottom-up drivers in shaping occupancy and space-use of a savanna herbivore community.

INTRODUCTION

African savanna ecosystems support the highest diversity of terrestrial herbivore species in the world (Owen-Smith 2013, Hempson et al. 2015, Ripple et al. 2015). However, threats attributed to the expansion of the human population that include: (1) landcover change and transformation, (2) human-induced changes to fire, browsing and grazing regimes, (3) increased poaching, and (4) climatic shifts in rainfall and temperature impacting forage and water availability (Osborne et al. 2018, Owen-Smith et al. 2020) have induced substantial population declines in approximately 59% of Africa's herbivore species (Ripple et al. 2015). Population declines may be particularly detrimental to ecosystem structure and function (Pringle et al. 2011, Balfour et al. 2021), given the fundamental role of herbivores in regulating predator populations at higher trophic levels and plant community structure and abundance at lower trophic levels (Gordon et al. 2004, Estes et al. 2011, Vinks et al. 2020). However, herbivore impacts within ecosystems vary with their space-use and occupancy which is driven by complex interactions between various bottom-up and top-down factors (Bailey et al. 1996, Hopcraft et al. 2010, O'Kane & Macdonald 2018). Considering the increasing decline in herbivore populations (Ripple et al. 2015, Smith et al. 2022), it is therefore critical that a comprehensive understanding of drivers regulating herbivore space-use and occupancy be developed to facilitate management interventions (Young et al. 2020).

Optimal foraging (MacArthur & Pianka 1966) and habitat selection (Rosenzweig 1981) theories dictate that herbivores face constant trade-offs between acquiring resources (i.e., bottom-up control) and avoiding risks attributed to predators and humans (i.e., top-down control) to maximise energetic gains (Mitchell & Powell 2012). Apart from top-down factors which impact the survival of herbivores through direct and indirect predation and anthropogenic risks (Gandiwa 2013a, Gaynor 2019), bottom-up factors – including forage quantity and quality, and water availability – regulate herbivores through resource restrictions from lower trophic levels (Turkington 2009). In addition, bottom-up factors may be more important in regulating herbivore populations than predation and anthropogenic top-down risks (e.g., Slobodkin 1960, Owen-Smith & Mills 2006, Riginos & Grace 2008, Gandiwa 2013b, Wenda et al. 2023). For example, seasonal decreases in the availability and quality of forage drove reductions in pregnancy, parturition, and adult survival rates of moose in North America, inducing substantial population declines (Oates et al. 2021). Moreover, significant decreases in forage and water availability attributed to frequent and prolonged periods of drought drove substantial declines in the population of blue wildebeest in Kenya and Tanzania (Sitati et al. 2014).

African savannas are distinctive owing to spatiotemporal fluctuations in rainfall – impacting forage growth and water availability (Owen-Smith et al. 2020) – which regulate herbivore space-use and occupancy (Redfern et al. 2005, le Roex et al. 2019). However, variations in intrinsic functional traits (e.g., foraging strategy, body size and metabolic rates) influence herbivore responses to spatiotemporal variations in forage and water availability which reflect in their patterns of space-use and occupancy (Cromsigt & Olff 2006, Young et al. 2020, Davies et al. 2021). For example, grazers (e.g., zebra) and browsers (e.g., giraffe) occupy habitats with higher grass and shrub/tree availability to facilitate foraging opportunities and maximise energetic gains, irrespective of season (O'Kane & Macdonald 2018, Davies et al. 2021). In contrast, mixed feeders (e.g., impala) exhibit seasonal dietary shifts from graze in the wet season to browse in the dry season when the quality of grasses decrease (Chapter 3). Consequently, mixed feeders tend to shift occupancy from habitats with higher graze availability in the wet season, to habitats with higher browse availability in the dry season (Botha & Stock 2005, Codron et al. 2007a, Janecke & Smit 2015). Moreover, herbivore foraging strategies are closely related to water dependency, with grazers and mixed feeders exhibiting higher levels of water dependency in contrast to browsers who acquire most of their water from the leaves of shrubs and trees (Chirima et al. 2012, Chinomona et al. 2018, Young et al. 2020). Therefore, the interplay between water availability and foraging strategy can influence herbivore space-use by either: (1) driving water dependent species to expend more energy travelling larger distances to facilitate water acquisition – particularly during the dry season – reducing forage and resting times (le Roex et al. 2019); (2) constraining water dependent species to occupy habitats in closer proximity to water sources, leading to increased levels of inter- and intraspecific competition and predation risks (Cain et al. 2012). Along the body size spectrum, smaller selective feeders are more reliant on forage quality than quantity owing to their highly selective diets (Grange & Duncan 2006, Anderson et al. 2016, O'Kane & Macdonald 2018) which reflect in their patterns of space-use and occupancy. For example, large-bodied, bulk grazers and browsers such as buffalo and black rhinoceros (*Diceros bicornis*) occupy habitats with higher forage availability whereas medium-bodied, selective grazers and browsers such as warthogs and common duiker occupy habitats with high quality forage (Bailey et al. 1996, Abu Baker & Brown 2014, Young et al. 2020).

Although various studies have quantified the impacts of season- and habitat-specific bottom-up factors regulating herbivore space-use and occupancy (Owen-Smith & Mills 2006, Riginos & Grace 2008, Gandiwa 2013b), few have assessed the effects of bottom-up factors driving the occupancy and space-use of entire herbivore communities (Rich et al. 2016, Staver &

Hempson 2020, Young et al. 2020). Moreover, no studies have analysed the impacts of bottom-up factors on the herbivore community in Pafuri, KNP. Although herbivores are regulated by a myriad of bottom-up and top-down drivers, the effects of which may not be mutually exclusive (Jedrzejewska & Jedrzejewski 2005, Gandiwa 2013a, Burkepile et al. 2013, Panebianco et al. 2022), in this Chapter, I aim to quantify the effects of bottom-up factors influencing herbivore occupancy.

Here, I hypothesise that habitat-specific and seasonal variations in bottom-up factors including forage availability, quality and proximity to water sources will impact herbivore occupancy. Furthermore, I hypothesise that herbivore responses, measured as variation in occupancy, to bottom-up factors will differ according to feeding guild and body size. Specifically, I predict that: (1) the occupancy of larger, bulk grazers (e.g., buffalo) and browsers (e.g., kudu) will increase in the wet season when the availability of forage (i.e., grass and browse) increases, and in habitats with higher forage availability; (2) the occupancy of medium-sized, selective grazers (e.g., warthog) will increase in the wet season and in habitats with higher grass quality; (3) the occupancy of medium-sized, selective browsers (e.g., common duiker) will increase in habitats with higher browse quality; (4) mixed feeders, irrespective of body size (e.g., impala), will occupy habitats with higher grass quality in the wet season, and habitats with higher browse availability in the dry season; and (5) water dependent, mixed feeders' and grazers' occupancy will decrease further from water whereas browsers will remain unaffected owing to their ability to acquire moisture from the leaves of shrubs and trees.

MATERIALS AND METHODS

Study site

Details of the study site are described extensively in Chapter 2.

Camera trap analysis

Camera trap survey methods and analyses of camera trap data are described in Chapter 3. Medium- to large-sized herbivore species (> 0.5kg; Clements et al. 2014) were identified from camera trap images and classified according to feeding guild based on stable carbon isotopic faecal analysis (Chapter 3). I focussed on medium- to large-sized herbivores because of their functional importance in maintaining ecosystem processes by (i) acting as a food source for carnivores, (ii) promoting soil nutrient cycling through faecal deposits, and (iii) controlling plant populations by preventing single species dominance (Balfour et al. 2021). To avoid pseudo-replication, only images of independent capture events of the same species (> 30 minutes between consecutive photos; Linkie & Ridout 2011) were used in the data analysis. The number of individual species per capture event was recorded. I pooled independent detections of each species across seasons and only focussed on the species for which isotopic faecal analyses had been performed (i.e., buffalo, common duiker, elephant, impala, kudu, nyala, warthog and zebra).

Species occupancy

Detection and occupancy probability was modelled as a function of habitat and season, to account for spatial and temporal variability in resource availability, which affects mammal activity patterns, abundance and subsequently detection probabilities (Sarmento et al. 2010, Zanón-Martínez et al. 2016, Suárez-Tangil & Rodríguez 2021). Habitat type (i.e., Lowveld Riverine Forest (LRF), Limpopo Ridge Bushveld (LRB), and Subtropical Alluvial Vegetation (SAV)) was determined at each camera trap site according to the vegetation classification by Mucina & Rutherford (2006). Seasons were classified as wet (March/April) or dry (August/September) based on recorded rainfall (Chapter 2). Both habitat and season were modelled as categorical variables.

I estimated the detection and occupancy probability of eight herbivore species as a function of seven covariates, including: percentage grass- (C_4), shrub- (C_3), and tree (C_3) cover, grass-, shrub-, and tree quality (%$\delta^{15}N$), and distance to nearest rivers (m). Seasonal forage availability was determined by visually estimating the percentage cover of plant growth forms – grasses, shrubs, and trees – within a 50m^2 quadrat centred on each camera trap site (Collins & Smith 2006, Burkepile et al. 2013). The dominant plant species (> 50% cover) of each growth form in each quadrat were collected and processed using stable carbon isotope analysis to determine forage quality (Chapter 3). Nitrogen contents (expressed as %$\delta^{15}N$), measured from each collected sample, were used as a proxy for forage quality (Craine et al. 2015). Although forage quality is often expressed in terms of plant crude protein (Burkepile et al. 2013), a positive correlation between the protein content of herbivore faeces and the nitrogen content of its feed exists (Holecheck et al. 1982, Botha & Stock 2005). Thus, plant nitrogen can be used as a proxy for forage quality (Ramoelo et al. 2013).

Spatial data on all available water sources were not available for the Pafuri and thus I used perennial rivers as a proxy for available water. The proximity of each camera site to the nearest perennial river (i.e., nearest straight-line distance) was calculated using the *nearest hub* function in QGIS (version 3.16.3, QGIS Development Team, 2009).

Autocorrelation between covariates was assessed using a Spearman rank correlation in R programming language (version 3.4.2, R Development Core Team, 2017). Shrub quality was correlated with both grass and tree quality ($|r|>0.7$; Appendix Figure 4.1) and was therefore removed from the analysis.

Occupancy modelling framework

To model species detection and occupancy, I used single-species occupancy models (Mackenzie et al. 2017) implemented within a Bayesian framework using the R package *ubms* version 1.1.0 (Kellner et al. 2022). I fitted three occupancy models per herbivore species: a fixed effects model (Model 1), a model which accounted for season-specific variability of covariate estimates (Model 2), and a model which accounted for habitat-specific variability of covariate estimates (Model 3; Table 4.1). Model structures were identical for each herbivore species to facilitate interspecific comparisons.

Covariates were scaled to have a mean of 0 and a standard deviation (SD) of 1. Default vague priors for all models were used (mean = 0 and SD = 10). I ran four parallel Markov chains with 10 000 iterations; the first 5 000 of which were discarded as burn-in iterations. Model convergence was evaluated based on the Gelman-Rubin statistic (i.e., Rhat statistic), with model convergence being achieved when the Rhat statistic equalled one (Gelman et al. 1992). Additionally, model convergence was evaluated through the visual examination of individual model traceplots (Nguyen et al. 2022). To determine the significance of the covariate effects, 95% and 75% Bayesian credible intervals (BCI) of the posterior distribution were generated. Coefficients of which the 95% and 75% BCI did not overlap 0 were regarded as having significant and moderate effects on herbivore occupancy, respectively.

The predictive accuracy of each model per species was evaluated by using the expected log pointwise predictive density (elpd). Models were ranked and compared based on the elpd estimates. Elpd was calculated using leave-one-out (LOO) cross-validation for pairwise model comparisons (Vehtari et al. 2017). Model support was assessed by calculating the pairwise differences in elpd (Δelpd) for each model relative to the top performing model with the standard errors included therein (SE[Δelpd]). A model was considered to have less support than the top ranking model when the absolute difference in elpd was greater than the standard error of that difference (i.e., $|\Delta\text{elpd}| > \text{SE}[\Delta\text{elpd}]$; Nguyen et al. 2022, Kellner et al. 2022). Herbivore occupancy was predicted based on the outputs of the top performing model, per species. Instances in which multiple models exhibited equal predictive accuracy (i.e., $|\Delta\text{elpd}| < \text{SE}[\Delta\text{elpd}]$) were averaged to obtain a single predicted occupancy estimate (Kaplan & Lee 2018).

RESULTS

Camera trapping

Three camera traps failed in the wet season and six failed in the dry season resulting in a total of 510 and 420 camera trap-nights per season respectively (Chapter 3). A total of 2633 independent detections of eight herbivore species were captured in the wet and dry seasons of 2021. Using the body size classification of Clements *et al*. (2014) and results from the isotopic faecal analysis performed in Chapter 3, I identified one medium-sized grazer (warthog) and two large-sized grazers (buffalo and zebra), one medium-sized browser (common duiker) and one medium-sized mixed feeder (impala) in both seasons. Nyala and kudu were classified as medium- and large-sized mixed feeders respectively in the wet season owing to high proportions of grasses in their diets (Table 3.2; Chapter 3). However, nyala and kudu significantly increased their intakes of browse in the dry season and were consequently classified as browsers (Chapter 3). Elephants displayed seasonal dietary shifts from a predominantly browse based diet in the wet season, to a mixed feeder diet with high proportions of browse intake in the dry season. Thus, elephants were classified as large-sized browsers in the wet season, and as mixed feeders in the dry season. Although isotopic faecal analysis was performed on five other herbivore species (Chapter 3), too few independent detections (< 5 detections; Kays et al. 2020) were obtained after the camera trapping. I therefore excluded these species (i.e., eland, giraffe, steenbok, waterbuck, and blue wildebeest) from my analysis.

Estimated forage cover, quality, and proximity to rivers

Estimated grass- (C_4), shrub- and tree (both C_3) cover were highest in the wet season (Figure 4.1). Grass cover was highest in LRB ($\bar{x}$ = 72 ± 12%) and lowest in LRF ($\bar{x}$ = 44 ± 23%), shrub cover was lowest in LRB and highest in LRF (Figure 4.1), and tree cover was lowest in LRF ($\bar{x}$ = 44 ± 6%). There was minimal variation (< 1%) in tree cover between LRB and SAV.

Grass quality was higher in the wet ($\bar{x}$ = 5.16 ± 1.77 %δ^{15}N) than the dry season ($\bar{x}$ = 3.78 ± 1.51 %δ^{15}N), with no difference in tree (hereafter referred to as browse) quality seasonally. Grass and browse quality were highest in SAV ($\bar{x}$ = 6.57 ± 2.48; $\bar{x}$ = 6.55 ± 2.76 %δ^{15}N) and lowest in LRB ($\bar{x}$ = 3.06 ± 1.43; $\bar{x}$ = 3.77 ± 1.34 %δ^{15}N).

There was no seasonal variation in the mean distance from habitats to rivers (Figure 4.1). However, on average, cameras located within LRB occurred further from perennial rivers ($\bar{x}$ = 2692.44 ± 488.02m) and cameras located in SAV occurred closer to rivers ($\bar{x}$ = 1183.31 ± 410.24m).

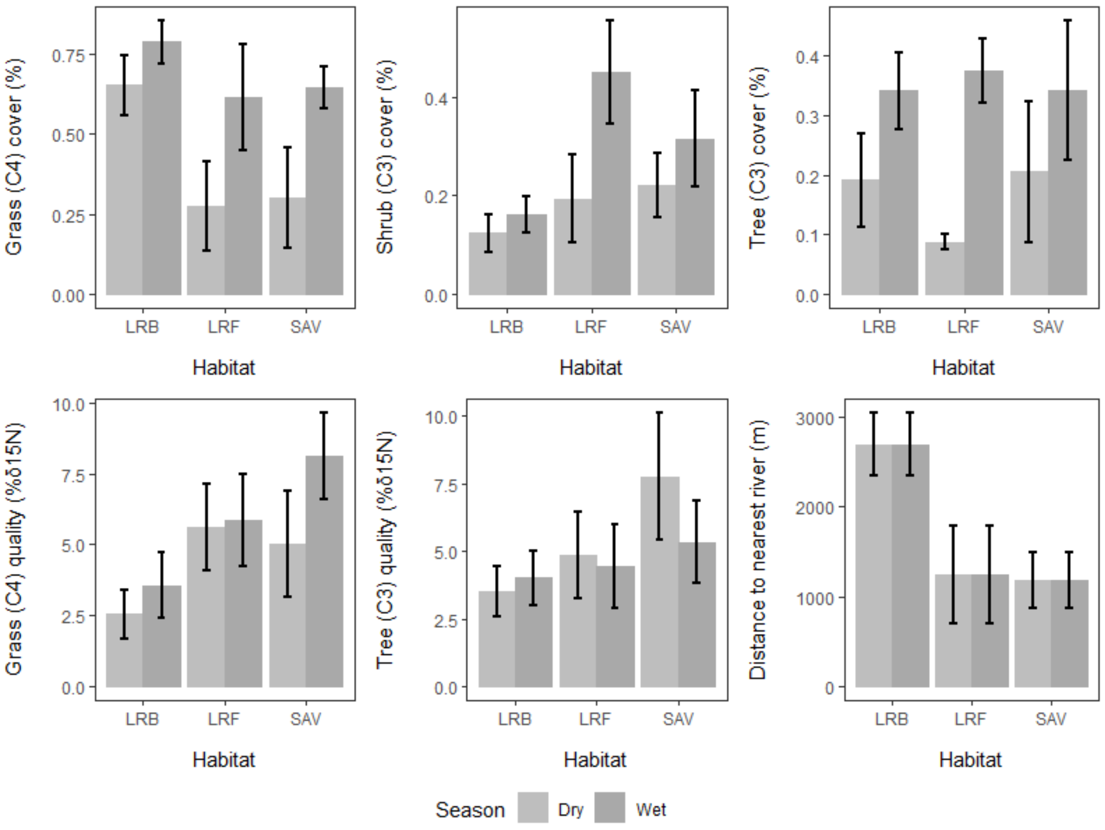


Figure 4.1: Season- and habitat-specific variation in bottom-up drivers of the herbivore community in Pafuri, KNP. Including, mean (± 95% CI) forage availability (% cover) and quality (%δ^{15}N), and distance to nearest perennial rivers (m). LRB: Limpopo Ridge Bushveld; LRF: Lowveld Riverine Forest; SAV: Subtropical Alluvial Vegetation.

Bottom-up spatial drivers of herbivore occupancy

a. Browsers

The season and habitat models explained the most variation in common duiker occupancy (Table 4.1), with averaged β-coefficients indicating that only seasonal variation in shrub cover and habitat-specific browse quality affected occupancy (Figure 4.3). The effect of shrub cover on common duiker occupancy was directly proportional to shrub cover in the wet season and inversely proportional in the dry season, with only the latter being moderately significant (β1 = -1.83, 75% BCI: -3.72 – -0.07). In addition, common duiker occupancy decreased with increasing browse quality in both LRB and SAV, contrary to predictions, with the reverse holding for LRF, as predicted (Figure 4.2). However, the effect of browse quality was non-significant in LRF and LRB (95% BCI overlapped 0) and moderately significant in SAV (β1 = -1.83, 75% BCI: -3.72 – -0.07). The fixed effects and season models explained the most variation in kudu occupancy, with averaged β-coefficients indicating that distance to rivers, grass quality and seasonal variability in shrub cover affected kudu occupancy. As predicted, kudu occupancy increased further from rivers in both the wet and dry seasons, with only the former being moderately significant (β1 = 1.99, 75% BCI: 0.28 – 3.88). However, contrary to predictions, kudu decreased occupancy in habitats with higher shrub (β1 = -1.01, 75% BCI: -1.84 – -0.22) cover but increased occupancy in habitats with higher grass quality (β1 = 1.75, 75% BCI: 0.44 – 3.09) in both seasons.

b. Grazers

The season model explained the most variation in buffalo occupancy, with averaged β-coefficients indicating that only seasonal variation in tree cover affected occupancy. Buffalo occupancy was inversely proportional to tree cover in both the wet and dry seasons, with only the former being moderately significant (β1 = -2.25, 75% BCI: -4.15 – -0.42). Although buffalo increased occupancy in habitats with higher grass cover in the wet and dry season (Figure 4.2), as predicted, seasonal effects of grass cover on buffalo occupancy were non- significant in both seasons. Moreover, contrasting seasonal effects of distance to rivers were observed, with buffalo decreasing occupancy further from rivers in the wet season, as predicted, but increasing occupancy further from rivers in the dry season, contrary to predictions. However, seasonal effects of distance to rivers were neither significant in the wet nor the dry season.

The fixed effects and habitat models explained the most variation in warthog occupancy, with averaged β-coefficients indicating that grass cover and tree cover impacted occupancy across all habitat types. Further, averaged β-coefficients from the habitat model indicated that warthogs decreased occupancy across all habitat types with higher grass (β1 = -1.35, 75% BCI: -2.63 – -0.11) and tree cover (β1 = -1.73, 75% BCI: -2.95 – -0.57). Moreover, the effects of habitat-specific variation in shrub cover on warthog occupancy were inversely proportional in SAV, and directly proportional in LRF and LRB, with only the effects in SAV (β1 = -1.73, 75% BCI: -2.95 – -0.57) being moderately significant. Although warthogs decreased occupancy further from rivers and increased occupancy with increasing grass quality in LRF and SAV, as predicted, the habitat-specific effects of distance to rivers and grass quality were non-significant.

The habitat model explained the most variation in zebra occupancy, with averaged β-coefficients indicating that all bottom-up factors excluding habitat-specific variations in shrub cover and grass quality affected occupancy. As predicted, zebra occupancy decreased further from rivers in SAV with the reverse holding for LRB and LRF, contrary to predictions. However, the effects of distance to rivers were only moderately significant in SAV (β1 = -1.78, 75% BCI: -3.84 – -0.15). Zebra increased occupancy in LRB with higher grass cover and lower tree cover, as predicted, but antithetically increased occupancy in LRF and SAV with lower grass cover and higher tree cover, contrary to predictions. Irrespective of the contrasting patterns of zebra occupancy across habitat types, the effects of grass (β1 = 2.45, 75% BCI: 0.66 – 4.33) and tree cover (β1 = -1.98, 75% BCI: -3.52 – -0.52) were only moderately significant in LRB. Moreover, browse quality had an inversely proportional effect on zebra occupancy in SAV, with the reverse holding for LRB and LRF. However, habitat-specific effects of browse quality were only moderately significant in SAV (β1 = -1.26, 75% BCI: -2.57 – -0.02).

c. Mixed feeders

The habitat and fixed effects models explained the most variation in elephant occupancy, with averaged β-coefficients indicating that only habitat-specific variation in tree cover affected occupancy. The effects of tree cover on elephant occupancy were inversely proportional in LRB and LRF, contrary to predictions, and directly proportional in SAV, as predicted, with only the effect of tree cover in LRB being moderately significant (β1 = -1.63, 75% BCI: -3.25 – -0.01). Although elephants increased occupancy in habitats with higher grass quality in the wet season, as predicted, the season model explained minimal variation in elephant occupancy with averaged β-coefficients illustrating that seasonal effects of grass quality were non-significant. Moreover, elephant decreased occupancy further from rivers across all three habitat types, as predicted. However, habitat-specific effects of distance to rivers were non-significant.

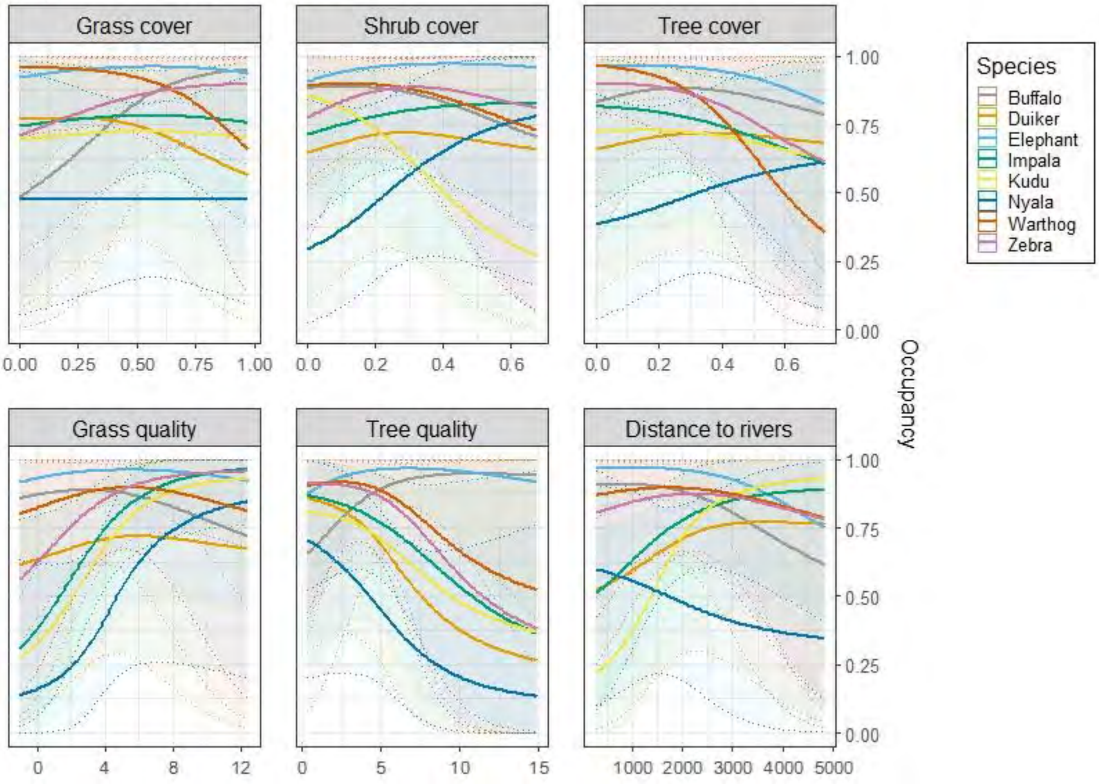
All three models explained equal variation in impala occupancy, with averaged β-coefficients indicating that seasonal variation in grass quality and shrub cover, and habitat-specific variation in distance to rivers and browse quality affected occupancy. Grass quality significantly affected impala occupancy (β1 = 1.65, 95% BCI: 0.08 – 3.75), particularly in the wet season, resulting in increased occupancy with increasing grass quality, as predicted. Unexpectedly, contrasting seasonal effects of shrub cover on impala occupancy were observed. Specifically, impala occupancy was directly proportional to shrub cover in the wet season (β1 = 1.98, 95% BCI: 0.20 – 4.29), and inversely proportional in the dry season (β1 = -2.15, 75% BCI: -3.79 – -0.68), contrary to predictions. Impala occupancy increased further from rivers across all habitat types, with only the effect of distance to rivers in LRB being moderately significant (β1 = 1.51, 75% BCI: 0.07 – 3.11), contrary to predictions. Further, impala occupancy decreased in SAV but increased in LRB and LRF with increasing browse quality. However, only the effect of browse quality on impala occupancy in SAV was moderately significant (β1 = 1.51, 75% BCI: 0.07 – 3.11).

The habitat and fixed effects models explained the most variation in nyala occupancy. Averaged β-coefficients indicated that grass and browse quality had the highest impact on nyala occupancy across all habitat types. Further, averaged β-coefficients indicated that habitat-specific variation in grass and shrub cover affected nyala occupancy. Nyala occupancy was directly proportional to grass quality (β1 = 1.96, 75% BCI: 0.27 – 3.94), as predicted, and inversely proportional to browse quality (β1 = -1.16, 75% BCI: -2.28 – -0.12) with both effects being moderately significant. Further, nyala occupancy was directly proportional to grass cover in SAV and LRB, and inversely proportional to grass cover in LRF. However, only the effect of grass cover in SAV was moderately significant (β1 = 1.30, 75% BCI: 0.05 – 2.28). In addition, nyala occupancy increased with increasing shrub cover in LRB and LRF, as predicted, and decreased with increasing shrub cover in SAV, contrary to predictions. However, only the effect of shrub cover on nyala occupancy in LRF was significant (β1 = 1.93, 75% BCI: 0.40 – 3.54).

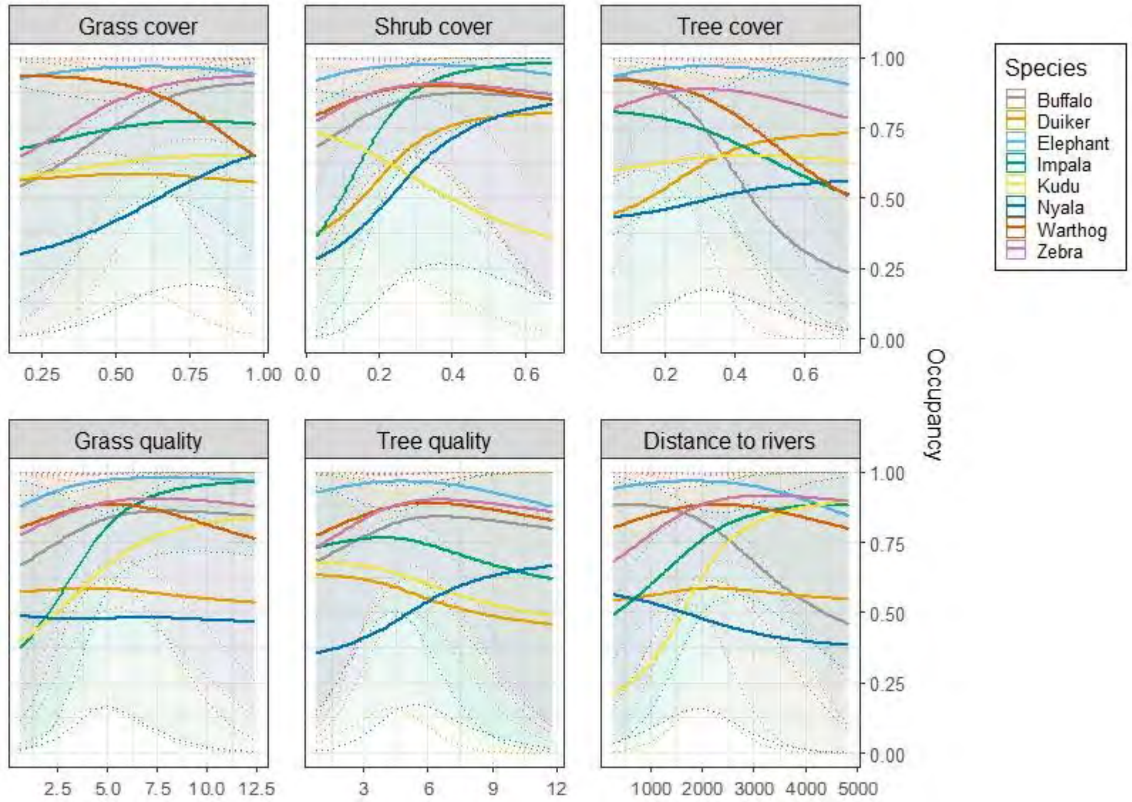
Table 4.1: Single-species occupancy models for eight focal herbivores in Pafuri, KNP. Models are ranked according to model performance (i.e., elpd which is the expected log pointwise predictive density). Δelpd indicates the pairwise differences in elpd relative to the top performing model (model rank). SE (Δelpd) is the standard error of Δelpd. $\hat{p}\_loo$ is the effective number of model parameters. Model formulation: Model 1 (Fixed effects): p (~season + habitat). ψ (~grass cover + shrub cover + tree cover + grass quality + tree quality + proximity to rivers); Model 2 (Season) = p (~season + habitat). ψ (~season: grass cover + season: shrub cover + season: tree cover + season: grass quality + season: tree quality + season: proximity to rivers); Model 3 (Habitat): p (~season + habitat). ψ (~habitat: grass cover + habitat: shrub cover + habitat: tree cover + habitat: grass quality + habitat: tree quality + habitat: proximity to rivers).

Guild	**Species**	**Model**	**elpd**	**Δelpd**	**SE(Δelpd)**	$\hat{p}\_loo$
Browser	Common duiker	Model 2	-61.49	0.00	0.00	8.36
		Model 3	-61.56	-0.07	2.53	8.67
		Model 1	-63.76	-2.27	1.21	9.08
	Kudu	Model 1	-146.74	0.00	0.00	13.27
		Model 2	-148.37	-1.62	1.83	15.61
		Model 3	-151.75	-5.01	2.89	19.46
Grazer	Buffalo	Model 2	-113.55	0.00	0.00	8.45
		Model 1	-116.66	-3.10	2.08	8.08
		Model 3	-117.02	-3.47	2.09	9.73
	Warthog	Model 3	-117.21	0.00	0.00	7.19
		Model 1	-118.79	-1.57	1.66	6.98
		Model 2	-120.74	-3.52	2.50	9.07
	Zebra	Model 3	-263.07	0.00	0.00	32.93
		Model 1	-266.16	-3.10	2.57	31.25
		Model 2	-266.99	-3.92	2.95	32.63
Mixed feeder	Elephant	Model 3	-245.26	0.00	0.00	12.59
		Model 1	-245.97	-0.70	1.02	11.84
		Model 2	-247.93	-2.67	1.32	13.87
	Impala	Model 2	-393.38	0.00	0.00	46.43
		Model 1	-395.58	-2.21	4.18	44.19
		Model 3	-398.20	-4.82	4.94	49.80
	Nyala	Model 3	-216.91	0.00	0.00	40.51
		Model 1	-219.81	-2.89	4.33	39.39
		Model 2	-223.71	-6.80	4.02	44.97

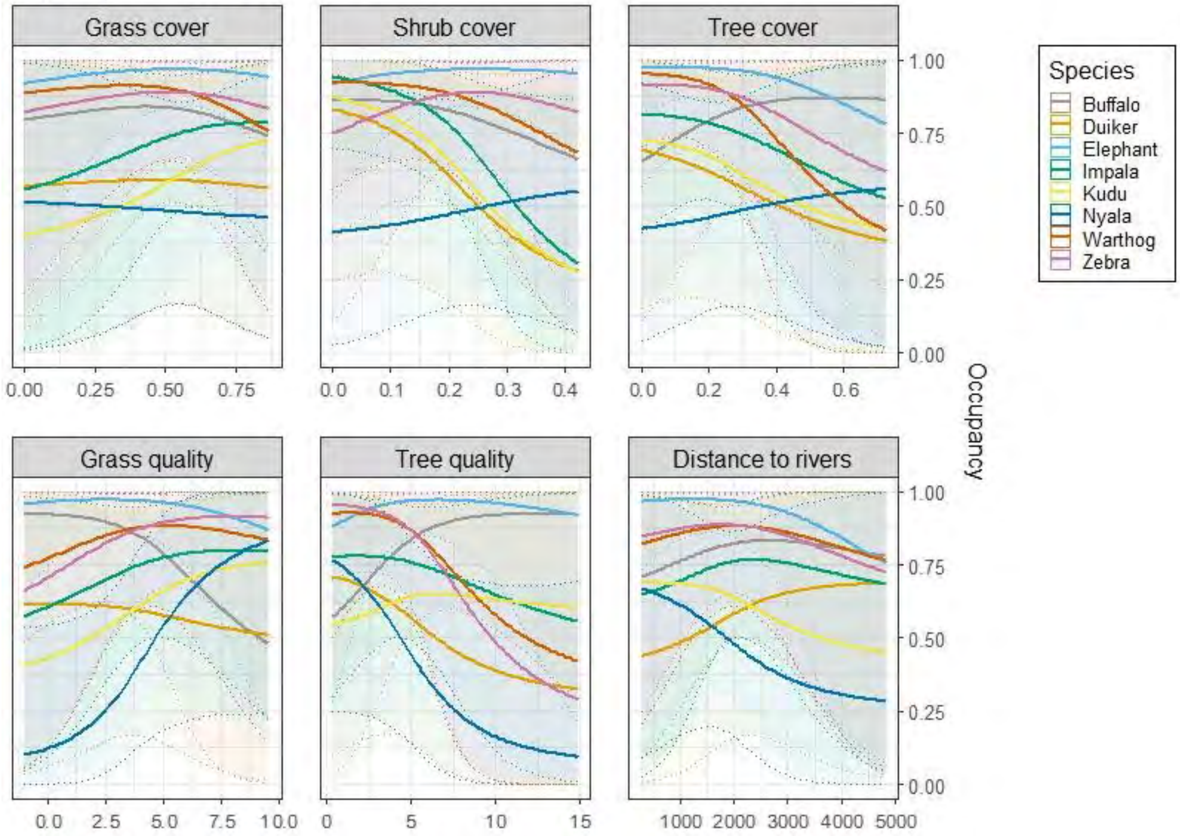
(a) Fixed effects model 1



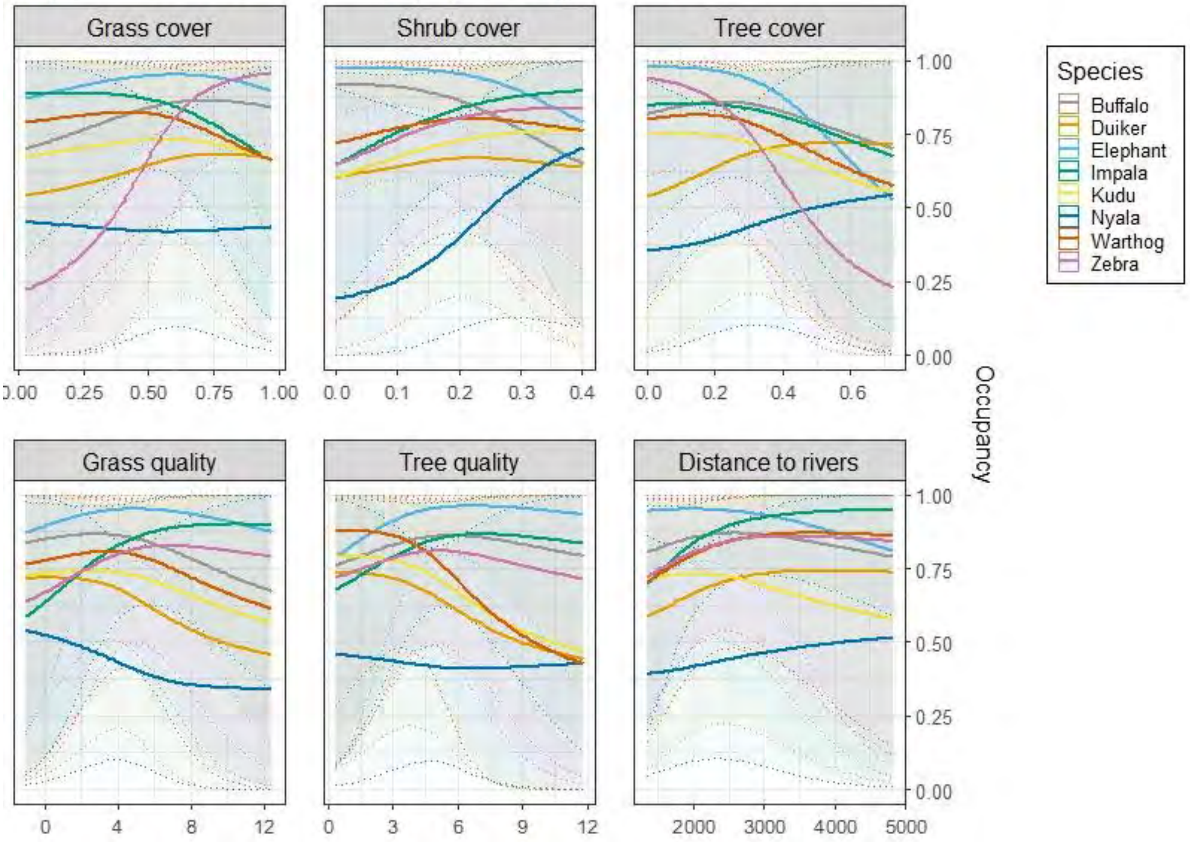
(b) Wet season model 2



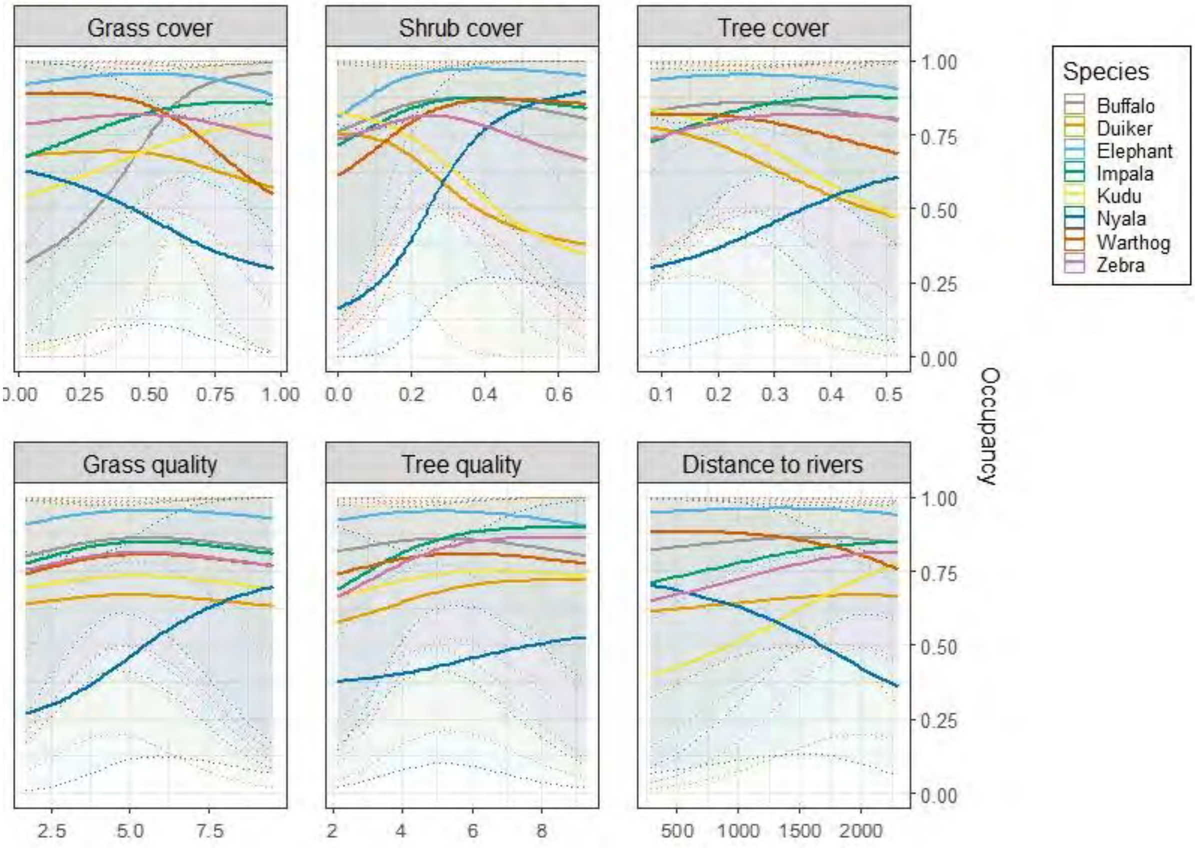
(c) Dry season model 2



(d) Habitat model 3 - Limpopo Ridge Bushveld



(e) Habitat model 3 - Lowveld Riverine Forest



(f) Habitat model 3 - Subtropical Alluvial Vegetation

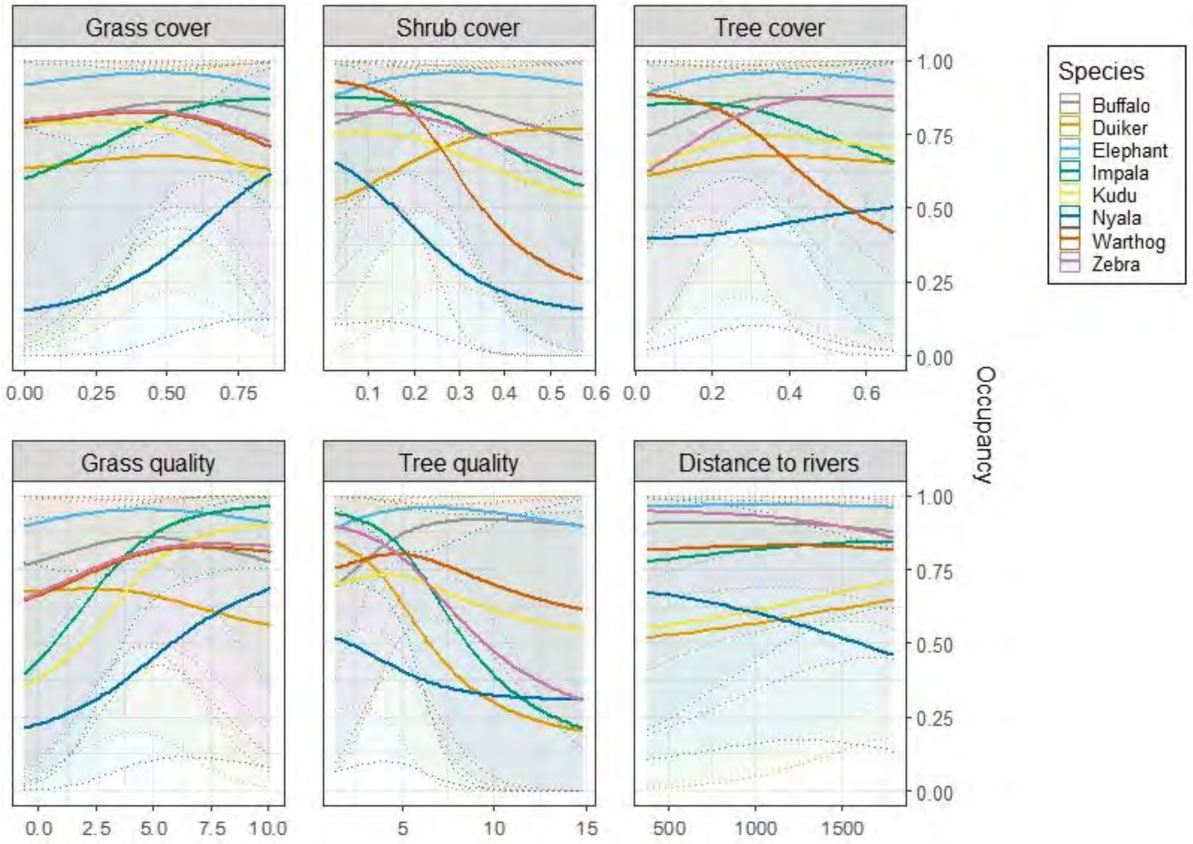
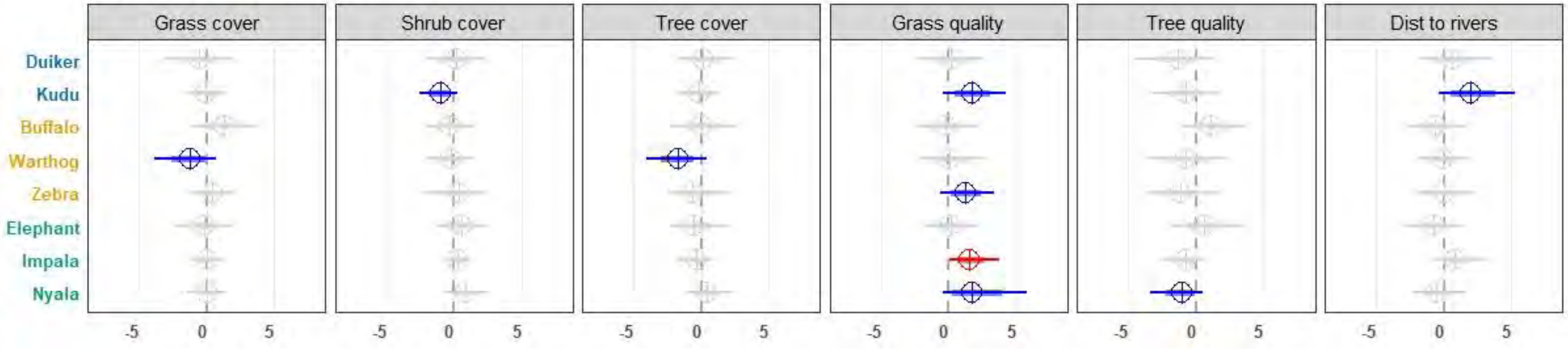
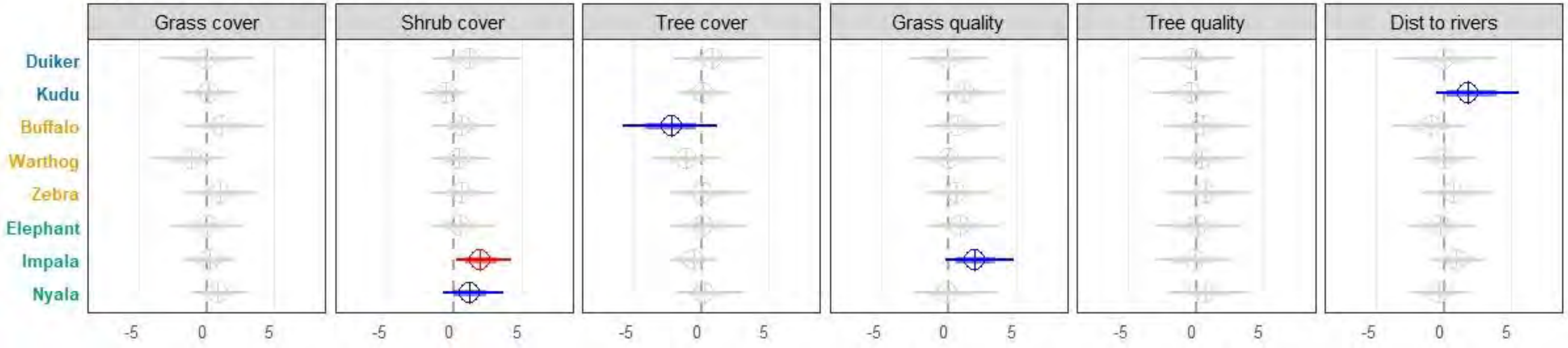


Figure 4.2: Herbivore occupancy relative to season- and habitat-specific variability in bottom-up covariates. Bold lines represent the posterior mean estimates and ribbons represent the 95% Bayesian Credible Interval (BCI). Results are presented according to three model outputs: fixed effects (a); season (b & C); and habitat (d, e & f) per species

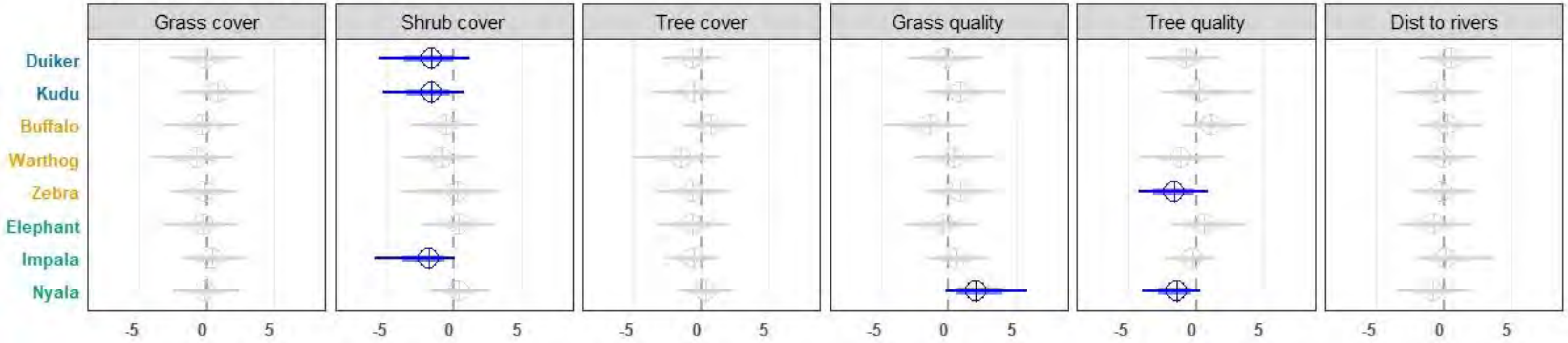
(a) Fixed effects model 1



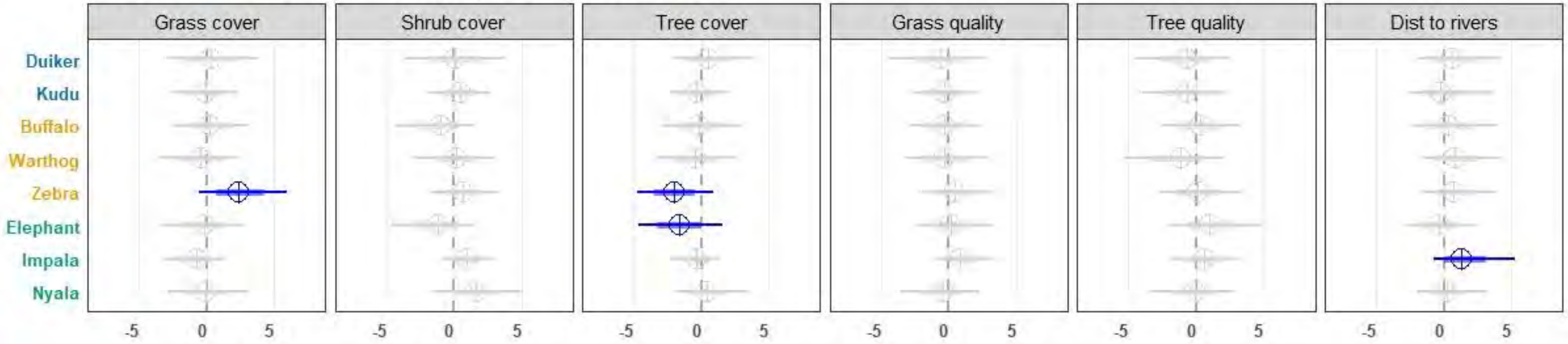
(b) Wet season model 2



(c) Dry season model 2



(d) Habitat model 3 - Limpopo Ridge Bushveld



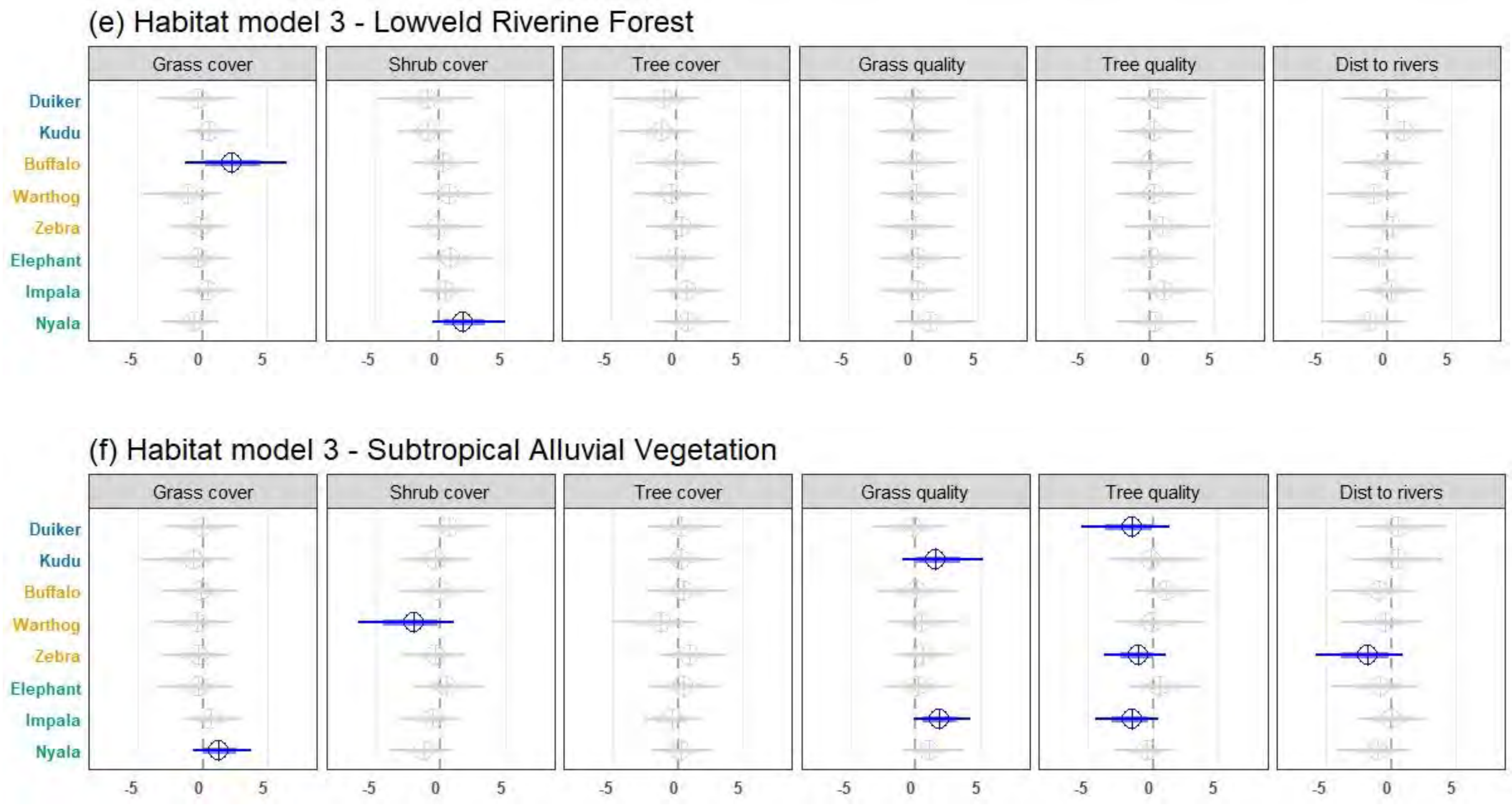


Figure 4.3: Standardized β coefficients of covariate effects on herbivore occupancy obtained from a fixed effects model (a), and models accounting for season- (b & c) and habitat-specific (d, e & f) variability. Grey bars indicate no significant covariate effects (95% BCI overlap 0), and red (95% BCI does not overlap 0) and blue (75% BCI does not overlap 0) bars illustrate significant and moderate covariates respectively. Species are coloured and categorised according to feeding guild (i.e., blue: browsers; yellow: grazers; green: mixed feeders).

DISCUSSION

Habitat use and selection (i.e., occupancy) of mammalian herbivores is generally influenced by a complex interplay between bottom-up (variation in climatic conditions, forage production and shifting habitat conditions) and top-down (spatiotemporal variation in predation and anthropogenic risks) factors (Jedrzejewska & Jedrzejewski 2005, Gandiwa 2013b, Burkepile et al. 2013, Panebianco et al. 2022). According to optimal foraging (MacArthur & Pianka 1966) and habitat selection (Rosenzweig 1981) theories, herbivores occupy habitats that maximise foraging opportunities whilst minimising predation and anthropogenic risks. However, in savanna systems, bottom-up factors such as forage availability and quality, and water availability may be more important in regulating herbivore space-use and occupancy than top-down predation and anthropogenic factors (Owen-Smith & Mills 2006). Additionally, interspecific variation in herbivore responses to bottom-up and top-down factors are related to intrinsic functional traits (e.g., foraging strategy and body size; Seydack et al. 2012). This was the case for the herbivore community in Pafuri, KNP, as herbivore responses to season- and habitat-specific variation in bottom-up factors (i.e., forage cover, quality, and water availability) varied within and among feeding guilds and across various body sizes.

a. Browsers

Occupancy of common duiker appeared to be driven by shrub cover and browse quality. Common duiker exhibited seasonal shifts in habitat use, occupying closed habitats with higher shrub and tree cover in the wet season, and open habitats in the dry season. This seasonal shift in habitat use coincided with slight seasonal shifts in diet, with common duiker increasing their graze intake in the dry season (Chapter 3). Contrary to literature (see Abu Baker & Brown 2014), this suggests that common duiker are not closed-habitat specialists. Further, common duiker decreased occupancy in habitat patches with higher browse quality – particularly in

SAV – contrary to predictions. The inversely proportional effects of browse quality are surprising given that common duiker are highly selective feeders that require a constant intake of high-quality browse to maintain their metabolic requirements (Codron et al. 2007a, Furstenburg 2008). It is possible that interspecific competition could be regulating season- and habitat-specific changes in occupancy, driving common duiker to occupy open habitats with lower browse quality to limit competition for resources with other herbivores (e.g., Prins 2016). However, given the unreliability of quantifying competitive interactions between species using camera trap data alone (Caravaggi et al. 2017), further investigations are required to determine the impacts of interspecific competition on common duiker occupancy. Unexpectedly, kudu occupancy increased in habitats with increasing grass quality, with seasonal variations in grass quality having no impact. Further, kudu appeared to occupy habitats with lower shrub and tree cover in both seasons, but only the effect of shrub cover in the dry season was significant. This shift towards more open habitats with increased grass quality explains the seasonal dietary shifts of kudu from a diet dominated by browse in the dry season, to a mixed feeder with a high grass component in the wet season (Chapter 3). These results are surprising given that kudu are considered non-selective bulk browsers that feed on the leaves, shoots, pods or fruits from a wide range of shrubs, trees, broad leaved forbs and succulents, irrespective of season (Owen-Smith 1994, Furstenburg 2005, Gray et al. 2007). Increased occupancy in habitats with higher quality graze and corresponding decreased occupancy in habitats with higher browse cover, in conjunction with seasonal dietary shifts (Chapter 3), highlights a broader dietary flexibility displayed by kudu than previously documented (Botha & Stock 2005, Gray et al. 2007, Codron et al. 2007a). For example, diets of roe deer (*Capreolus capreolus*), a presumed browser, frequently contained > 25% grass in Europe owing to dietary shifts induced by land-use and climatic changes (Spitzer et al. 2020).

It is possible that recurring natural hazards such as drought, linked to climate change, may be driving seasonal dietary shifts of kudu, causing the species to occupy habitats with higher grass quality and lower shrub cover. However, testing this hypothesis requires long term dietary assessments and multi-season occupancy analyses (See Raynor et al. 2017) that were unfortunately beyond the scope of my study.

b. Grazers

Surprisingly, only seasonal variation in tree cover, and not grass cover, affected buffalo occupancy. In the wet season, buffalo occupied open habitats with higher grass cover and lower tree cover, as predicted. In contrast, buffalo increased occupancy in closed habitats in the dry season, contrary to predictions. However, irrespective of the contrasting seasonal effects of grass and tree cover, only the effects of tree cover in the wet season were moderately significant. Although predominantly an open habitat specialist (Sensenig et al. 2010, Mandinyenya et al. 2020), buffalo regularly increase occupancy in habitats with higher tree cover which are interspersed with patches of palatable green grass in the dry season when grasses in open habitats lignifies and becomes unpalatable (Ryan et al. 2006). This increased occupancy in closed habitats during the dry season was also associated with increased browse intake (Chapter 3; e.g., Vesey-Fitzgerald 1974, Stark 1986). Although largely unaffected by grass cover, buffalo utilized open habitats in the wet season, probably to facilitate foraging opportunities owing to increased graze availability (Figure 4.1), and occupied closed habitats in the dry season when the availability and quality of graze decreased in open habitats (Ryan et al. 2006). Contrary to predictions, buffalo were largely unaffected by spatial variations in distance to rivers, despite their high water dependency (Ogutu et al. 2014, Young et al. 2020). However, perennial rivers were used as proxy for water availability due to a lack of spatial data on all available water sources in Pafuri. Therefore, it is possible that the impacts of water availability on buffalo occupancy may be underestimated, requiring further investigations.

The occupancy of zebra appeared to be driven by habitat-specific variability in distance to rivers, grass cover, tree cover and browse quality. Zebra occupancy decreased further from rivers – particularly in SAV – as predicted. Occupancy of habitat patches near rivers in SAV is expected as zebra are highly water dependent, typically occurring with 2km of available water to facilitate regular drinking events (Western 1975, Young et al. 2020). Zebra occupied open habitat patches with higher grass cover and lower tree cover in LRB, supporting the hypothesis that bulk grazers (i.e., zebra) increase occupancy in open habitats with higher grass cover to facilitate bulk foraging opportunities needed to maintain nutritional requirements (Codron et al. 2007a, Gandiwa 2013a, Mandlate & Rodrigues 2020). Zebra are unselective bulk grazers that mitigate poor foraging conditions by spending 60 – 80% of their time feeding on nutrient poor, coarse grass species to maintain a healthy body condition (Okello et al. 2002, de Vos et al. 2020). The inversely proportional effects of browse quality on zebra occupancy in SAV cannot be interpreted in isolation, given that browse constitutes a very small proportion (i.e., < 10%) of a zebra's dietary composition (Chapter 3; Sponheimer et al. 2003, Codron et al. 2007). Moreover, zebra appeared to occupy grassland habitat patches with reduced shrub cover near rivers in SAV, which corresponds with their preferences for open areas with improved grazing opportunities and high water availability (Ogutu et al. 2014, Young et al. 2020), as predicted.

Warthog occupancy decreased with increasing grass and tree cover across all habitat types. Moreover, warthogs were driven by habitat-specific variability in shrub cover, decreasing occupancy in habitat patches in SAV with increasing shrub cover. Combined, the inversely proportional effects of grass, tree and habitat-specific shrub cover are unsurprising given that warthogs preferably occupy open habitats with short grass layers and higher proportions of nutritional forage (Field 1970, Treydte et al. 2006), owing to their highly selective diets (Edossa et al. 2021). Although forage quality did not appear to significantly affect warthog occupancy, contrary to predictions, grass quality was only measured from the most abundant C_4-plant species at each camera trap site using above ground biomass, whereas a large proportion of a warthog's diet includes roots, rhizomes, bulbs and forbs (Sponheimer et al. 2003, Codron et al. 2005) which were not analysed here. Regardless, open habitats were not synonymous with higher forage quality, with only a weak negative correlation ($|r| < -0.40$; Appendix Figure 4.1) between forage cover and quality. Thus, it is implausible that warthog occupy open habitats with lower grass, shrub and tree cover specifically to acquire higher quality forage (e.g., Field 1970, Treydte et al. 2006). Alternatively, I hypothesise that warthogs occupy open habitats to facilitate predator detection and consequently limit predation risks (Davies et al. 2021). For example, the probability of occurrence for warthog in Karongwe Game Reserve decreased in closed riverine and woodland habitats, which were associated with higher predation risks (Thaker et al. 2011). Despite their high water dependency (Hayward & Hayward 2012, Kihwele et al. 2020), warthogs were largely unaffected by distance to rivers, contrary to predictions. Like buffalo, the effects of water availability driving warthog occupancy may be underestimated owing to a lack of spatial data on all water sources in Pafuri. Thus, requiring further investigation.

c. Mixed feeders

Elephants decreased occupancy in closed, woodland habitat patches with higher shrub and tree cover, and increased occupancy in open habitat patches with higher grass quality in LRB. Although browse (> 84%; Chapter 3) rather than graze constitutes the highest proportion of elephant diets, habitat patches in LRB are dominated by grasses (60 – 80%; Figure 4.1) with shrubs (0 – 20%) and trees (20 – 40%) occurring at lower densities. Thus, it is plausible that the lower availability of browse in LRB is driving elephants to occupy open habitats with higher quality graze to facilitate foraging opportunities required to mitigate high energetic demands (Munyati & Sinthumule 2016, Young et al. 2020).

Impala space-use was regulated by seasonal changes in grass quality and shrub cover, and by habitat-specific variations in browse quality and distance to rivers. As predicted, seasonal increases in the nutritional quality of graze during the wet season (Figure 4.1; Botha & Stock 2005, Codron et al. 2007) drove impala to increase occupancy in habitats with higher quality graze. Moreover, increased occupancy in habitats with higher grass quality corresponds with the higher intake of graze by impala in the wet season (Chapter 3). In contrast and contrary to predictions, impala decreased occupancy in habitats with higher shrub cover in the dry season when graze quality decreased (Kos et al. 2012, Staver & Hempson 2020), despite results from isotopic faecal analysis indicating higher proportions of browse intake by impala during the same period. Although the habitat-specific effects of shrub cover were not significant (Figure 4.3), impala increased occupancy in habitat patches with higher shrub cover in LRB and LRF, with the reverse holding for SAV (Figure 4.2). Moreover, impala increased occupancy in open habitat patches with higher quality graze and lower tree cover and browse quality in SAV. It is possible that impala displayed seasonal shifts in space-use, increasing occupancy in open habitat patches with higher quality graze (particularly in SAV) during the wet season, and increasing occupancy in closed, woodland habitat patches with higher shrub cover in LRB and LRF during the dry season; corresponding with seasonal dietary shifts. Thus, highlighting a plausible bottom-up regulated effect. Alternatively, impala could be occupying more open habitat patches in SAV to facilitate predator detection and avoidance (e.g., van Deventer & Shrader 2021); highlighting a plausible top-down regulated effect. Irrespective, contrasting season- and habitat-specific effects that do not correspond with seasonal dietary estimates suggests that the seasonal effects of forage cover and quality could potentially be masking fine-scale, spatial responses by impala to habitat-specific variations in forage cover and quality between seasons. Moreover, given that the effects of spatial (i.e., habitat-specific) and temporal (i.e., seasonal) variations in resources are not necessarily mutually exclusive (see le Roex et al. 2019, Owen-Smith et al. 2020), it is recommended that the season- and habitat-specific effects of resources regulating herbivore space-use and occupancy be quantified in tandem to limit potential bias that may arise from evaluating these effects separately. Contrary to predictions, impala increased occupancy further from rivers across all habitat types with only the habitat-specific effects of distance to rivers in LRB being moderately significant. Impala are water dependent and tend to occupy habitats in close proximity to water (Kihwele et al. 2020, Young et al. 2020, Janecke 2021). Given their high-water dependency, it is possible that the use of perennial rivers as a proxy for water availability could be masking the effects of all available water sources driving impala occupancy in Pafuri, particularly during the wet season when the availability of surface water increases. Thus, requiring further investigation.

Nyala occupancy was regulated by grass and browse quality, and by habitat-specific variations in grass and shrub cover. Nyala occupancy increased with increasing grass quality in the wet season and in LRF and SAV. Moreover, nyala occupancy increased with increasing shrub cover in the dry season and in LRB and LRF. These seasonal and habitat-specific shifts in occupancy coincided with dietary shifts including a higher proportion of graze in the wet season and higher proportion of browse in the dry season (Chapter 3), supporting the prediction that nyala increase occupancy in habitats with higher grass quality in the wet season and increase occupancy in habitats with higher shrub cover in the dry season when the quality of graze decreases (Van Rooyen 1992). Seasonal dietary shifts enable nyala to maintain nutritional status by selecting shrubs or trees in the dry season due to the higher crude protein levels of browse compared to graze (Van Rooyen 1992, Botha & Stock 2005). Further, nyala decreased occupancy in habitats with higher browse quality, particularly in the dry season. It is possible that nyala decrease occupancy in habitats with high quality browse to limit interspecific competition (Sinclair 1985). For example, nyala decreased occupancy in habitats preferably utilized by kudu in the dry season to limit competitive interactions (O'Kane et al. 2013). Alternatively, and as shown by (Van Rooyen 1992), nyala may be increasing occupancy in habitats with higher shrub cover of a lower quality to facilitate nutritional demands. Moreover, nyala occupied open habitat patches with higher grass cover but lower shrub and tree cover in SAV. Contrary to the literature (see Van Rooyen 1992, Furstenburg 2016), this finding suggests that nyala are not closed habitat specialists, at least not across all habitat types. It is possible that nyala are occupying open habitat patches, particularly in SAV, to facilitate predator and/or human detection, subsequently limiting predation and/or anthropogenic risks (e.g., Canter 2008). Thus, highlighting the importance of top-down drivers in regulating nyala space use.

CONCLUSION

The importance of bottom-up factors (i.e., forage cover, quality, and distance to rivers) in shaping occupancy of the herbivore community in Pafuri varied among feeding guilds and between species within feeding guilds based on body size. Contrary to predictions, occupancy of medium-sized, selective grazers (i.e., warthogs) and browsers (i.e., common duiker) was not regulated by forage quality, suggesting that competition (e.g., Prins 2016) and/or top-down (i.e., predation and anthropogenic risks) factors (e.g., Abu Baker & Brown 2014, Davies et al. 2021) could be regulating the occupancy of both species in Pafuri. Similarly, with the exception of zebra, large-size bulk grazers (i.e., buffalo) and browsers (i.e., kudu) did not occupy habitats with higher forage cover, but rather displayed habitat-specific and seasonal shifts in occupancy that potentially reflects top-down regulation (e.g., Du Toit 1995, Valeix et al. 2008, Becker et al. 2013) and/or competition (e.g., du Toit 1995, Perrin & Brereton-Stiles 1999). Contrary to predictions, with the exception of nyala, the occupancy of mixed feeders (i.e., elephants and impala) did not correspond with their seasonal dietary shifts (Chapter 3) suggesting that top-down factors could be regulating habitat-specific and seasonal shifts in occupancy (e.g., Matandiko 2016, Vinks et al. 2020, Valenta et al. 2021). Despite kudu occupying habitat patches further from rivers owing to their low water dependencies (Furstenburg et al. 2000), and zebra decreasing occupancy further from rivers owing to their high water dependencies (Western 1975) – as predicted – the occupancy of grazers and mixed feeders were largely unaffected by distance to rivers suggesting that space-use could be regulated by seasonal variations in water availability, driving grazers and mixed feeders to occupy habitat patches near non-perennial water sources such as pans and dams (e.g., le Roex et al. 2019). Expansion of the human population has driven landcover changes and transformations, and caused climatic shifts in precipitation and temperature, inducing landscape-level changes in resource availability that impact the space-use and occupancy of herbivore populations (Ripple et al. 2015, Osborne et al. 2018, Kihwele et al. 2020). Given the functional importance that herbivores have in maintaining ecosystem structure and functionality (Pringle et al. 2011, Balfour et al. 2021) and the ever increasing impacts of humans on ecosystems (McGill et al. 2015), this study contributes to a better understanding of the affects that spatiotemporal variations in forage and water (i.e., bottom-up factors) play in regulating the space-use and occupancy of an herbivore community in an African savanna ecosystem.

Chapter 5: The influence of top-down drivers in shaping the activity patterns, occupancy, and space-use of a savanna herbivore community.

INTRODUCTION

Approximately 60% of large terrestrial herbivores are listed as threatened, with 58% experiencing population declines (Ripple et al. 2015, 2017). Population declines undoubtedly have ecosystem-level impacts, as herbivores are fundamental to maintaining ecosystem structure and function (Pringle et al. 2011, Balfour et al. 2021). However, their impacts in ecosystems vary with their spatial occupancy which is influenced by interacting bottom-up (e.g., resources such as forage- and water distribution and availability) and top-down (e.g., predation risk, fear of predation, and anthropogenic pressures) factors (Bailey et al. 1996, Hopcraft et al. 2010, O'Kane & Macdonald 2018). Moreover, intrinsic functional traits such as body size and foraging strategy interact with species-specific habitat requirements and inter- and intraspecific competition, affecting individual herbivore responses to bottom-up (Chapter 4) and top-down factors (Cromsigt & Olff 2006, Young et al. 2020). As a result, herbivore occupancy likely reflects inter-specific variability in herbivore responses to bottom-up and top-down factors. For example, the spatial distribution of an entire herbivore community, irrespective of body size, in Białowieża Forest, Poland was influenced by species-specific responses to both bottom-up and top-down factors in combination with human-induced effects (Bubnicki et al. 2019). In contrast, Anderson *et al*. (2016) showed that the occupancy of smaller-bodied species in Tanzania were predominantly regulated by predation risks (i.e., top-down effect), whereas the occupancy of larger-bodied species (≥ 150kg) were predominantly regulated by forage availability (i.e., bottom-up effect).

Apart from bottom-up regulation, which regulates herbivore populations through resource restrictions from lower trophic levels (see Chapter 4; Dorresteijn et al. 2015), top-down processes affect the survival and behaviour of herbivores through risks associated with predators and humans at higher trophic levels (Gandiwa 2013a, Gaynor et al. 2019). Predators can alter the demography (Van Buskirk & Yurewicz 1998), population density (Sheriff et al. 2020), space-use (Zalewska et al. 2021), habitat selection (Creel & Christianson 2008) and activity patterns (Lima & Bednekoff 1999) of prey through direct predation (i.e., consumption) and perceived predation risks (i.e., landscape of fear; Brown et al. 1999, Laundré et al. 2001, Gaynor et al. 2019). Accordingly, herbivores need to balance forage acquisition with avoiding areas and times of high predation risk (Riginos 2015, Davies et al. 2016b). Perceived predation risks can have stronger effects on herbivore population dynamics than the effects of direct predation itself (Winnie & Creel 2017, Gaynor et al. 2019), influencing species' behaviour, habitat selection, diet and physiology (Lima & Dill 1990, Creel & Christianson 2008, Hopcraft et al. 2010, Creel et al. 2017). Moreover, antipredator responses (e.g., vigilance) can limit foraging success and consequently impact species survival, population growth and reproduction (Creel & Christianson 2008, Gaynor et al. 2019). For example, the reintroduction of wolves in Yellowstone National Park resulted in increased vigilance and decreased foraging efforts in elk and bison, ultimately leading to reduced reproductive successes and juvenile survival (Laundré et al. 2001). Similarly, impala and Grant's gazelle (*Nanger granti*) increased vigilance in the presence of lions and spotted hyaena in the South Rift Valley, resulting in reduced foraging efficiency (Creel *et al*. 2014).

The relative strength of top-down predation risks on herbivore populations vary according to functional traits such as body size and foraging strategy (Hopcraft et al. 2012), and on the relative density of predators and prey (Anders Nilsson 2001). According to optimal foraging theory (Pyke et al. 1977), predators should select prey that maximises energetic benefits in terms of size while simultaneously minimising energetic costs and risks incurred during prey capture. Consequently, energetic costs and risks associated with hunting and subduing prey increases with increasing body size, resulting in larger herbivores being less prone to predation risks than smaller-bodied herbivore species (Owen-Smith & Mills 2008, Hopcraft et al. 2010, Clements et al. 2016, Annear et al. 2023). Thus, larger-bodied herbivores may be predominantly regulated by bottom-up, resource-driven processes (Hopcraft et al. 2010) whereas smaller herbivores may be predominantly regulated by top-down, predation-driven processes (Sinclair et al. 2003, Hopcraft et al. 2012). Further, the influence of predation risk on herbivores could vary according to foraging strategy and consequent habitat selection (Davies et al. 2021). For example, browsers in Hwange National Park were more responsive to predation risk by lions than grazers because they were able to move away from high-risk woodland areas and increase occupancy in relatively less risky open habitats (Valeix et al. 2009a).

Like natural predators, humans also exert top-down pressure on herbivore populations and, in some instances, these effects may be stronger than those associated with natural predators (Everatt et al. 2019b, Smith et al. 2021). Humans are keystone species that affect herbivore populations by acting as generalist “super predators” able to select any species, regardless of body size (Gandiwa 2013b). Like predators, humans influence herbivores directly and indirectly. Specifically, direct, or lethal anthropogenic effects include wildlife persecution (often illegal), which, in some cases, has resulted in extensive population declines and local extirpation (Dorresteijn et al. 2015, Suraci et al. 2019, Mills & Harris 2020). For example, excessive poaching of black rhinoceros between 1970 and 1980 in Kafue National Park resulted in the species becoming locally extinct (Chomba & Matandiko 2011). Similarly, illegal poaching of African elephants throughout Africa contributed to substantial, unsustainable population declines (Wittemyer et al. 2014). In contrast to direct anthropogenic effects, indirect or non-lethal anthropogenic effects are associated with activities that include infrastructure development and expansion, unregulated ecotourism and human encroachment of nature reserve boundaries (Schuette et al. 2016, Mills & Harris 2020, Smith et al. 2021). Increased anthropogenic activities have contributed to herbivore range contractions resulting in increased levels of inter- and intra-specific competition among herbivores (Ogutu et al. 2011, Matandiko 2016). For example, impala avoided reserve boundaries close to human settlements in Kafue National Park, which were correlated with high levels of wire snare poaching (Matandiko 2016). As a result, impala density increased further from park boundaries resulting in higher levels of inter- and intraspecific competition among herbivores species; consequently, reducing the foraging efficiency of impala (Matandiko 2016). Similarly, warthogs in Kafue National Park avoided roads during the wet season and occupied habitats with lower forage quality, owing to the increased utilization of roads by poachers (Matandiko 2016). Thus, non-lethal anthropogenic effects, like perceived predation risks, can be stronger than direct, lethal effects, limiting herbivore foraging success and consequently impacting species survival, population growth and reproduction (Lindsey et al. 2013, Suraci et al. 2019, Mills & Harris 2020). Understanding the influence of predation risk, amongst other factors (e.g., bottom-up drivers, Chapter 4; competition) broadens our understanding of drivers responsible for regulating herbivore communities.

Although numerous studies have analysed the effects of predation (e.g., Burkepile et al. 2013, Zalewska et al. 2021) and anthropogenic (e.g., Vinks et al. 2020, Stabach et al. 2022) top-down factors on herbivore density and occupancy separately, few studies have evaluated these effects simultaneously (cf. Dorresteijn et al. 2015, Everatt et al. 2015, Schuette et al. 2016).

Furthermore, no studies have assessed the impacts of predation and anthropogenic risks driving the occupancy and space-use of herbivores in South Africa. My study took place in the northern Pafuri region of the Kruger National Park, which includes high levels of biodiversity and intact predator and herbivore guilds (Deacon 2007, Ferreira & Funston 2020). Additionally, Pafuri is bordered to the East by Mozambique, and Zimbabwe to the North, with high levels of illegal wildlife offtake being attributed to the high density of human settlements occurring adjacent to the park's boundaries (SANParks unpublished data*,* 2022).

Herbivores are driven by the interaction between bottom-up (Chapter 4) and top-down factors, with the relative strength of each varying between systems and species (Grange & Duncan 2006, Gandiwa 2013a). Here, I focus on the top-down drivers of herbivore communities in Pafuri and hypothesise that prey species with body sizes less than 1600kg (i.e., accessible prey; Clements et al. 2014) will adjust space-use and activity patters to avoid predation threats (e.g., Valeix et al. 2009b, Everatt et al. 2015, Tambling et al. 2015), whereas inaccessible prey species (i.e., body size > 1600kg) will not. In contrast, I hypothesise that all herbivores, irrespective of body size, will adjust space use in response to anthropogenic factors. Specifically, I predict that, in response to spatial and temporal variations in predation risks, accessible herbivores should: (1) shift activity periods to avoid peak predator activity, (2) shift spatial occupancy to avoid areas occupied by predators, or (3) a combination of the two responses. In contrast, I predict that (4) inaccessible prey species, like elephants, will neither show temporal shifts in activity patterns nor shifts in occupancy (Clements et al. 2014, Riginos 2015, Valenta et al. 2021). Finally, I predict that (5) both accessible and inaccessible prey species should shift occupancy away from areas of increased human activity.

MATERIALS AND METHODS

Study site

Details of the study site are extensively covered in Chapter 2.

Camera trap analysis

Camera trap survey methods and analysis of camera trap data are described in Chapter 3. In addition to herbivores (Chapter 4), all large carnivore species capable of preying upon accessible medium- to large-sized herbivores (see Gittleman 1985, Clements et al. 2014) were identified from camera trap images. For each herbivore and predator detection, the corresponding date and time per image were recorded.

Temporal overlap in predator and prey activity

To estimate temporal overlap of predator and prey activity patterns, I calculated the number of detections for each herbivore and predator species seasonally. However, I combined large predators (i.e., spotted hyaena and leopard (*Panthera pardus*); see results) to account for the limited sample size of predators detected seasonally. Limited sample sizes decrease the precision of temporal activity estimates which can be avoided by grouping species with similar functional traits such as diet and body size (Lashley et al. 2018, Allen et al. 2021).

Most studies (e.g., Vilella et al. 2020, Rossa et al. 2021, Searle et al. 2021) apply time-to-independence data filters in camera trap-based estimates of species activity patterns to avoid pseudoreplication. However, Peral *et al*. (2022) discourage the use of time-to-independence data filters which can bias estimates of activity patterns. Therefore, all detections for each herbivore species and predators were used to represent daily activity patterns (Zanni et al. 2021). Firstly, I converted the time for each capture event into radians (2π radians = 24 hours) to account for the circular distribution of the time of day (Ridout & Linkie 2009, Meredith & Ridout 2021). I estimated seasonal activity patterns for herbivores and predators by fitting a circular kernel density distribution to radian time-of-day data using the *overlap* package (version 0.3.4; Meredith & Ridout 2021) in R version 4.2.1 (R Core Development Team 2021). To determine activity overlaps, I calculated pairwise overlap (Δ) between herbivore species and predators seasonally using the *overlapEst* function in R (Meredith & Ridout 2021). The Δ coefficient measures the area shared between two kernel density curves (Zanni et al. 2021) and ranges from 0 (no overlap) to 1 (complete overlap; Ridout & Linkie 2009). I used the Δ_1 overlap estimator which is recommended for pairwise comparisons between species with less than 75 detections (Meredith & Ridout 2021). I calculated 95% confidence intervals (CI) for each overlap index by bootstrapping 10 000 estimates using the *bootEst* and *bootCI* functions in R (Meredith & Ridout 2021).

To test whether the activity patterns of herbivores and predators differed significantly, I created a null distribution of 10 000 random overlap indices from bootstrapped samples taken indiscriminately from the density distributions of herbivore species and predators (Vilella et al. 2020). The Δ_1 coefficient was compared to the null distribution to assess the probability that it had arisen by chance (p). I considered the activity patterns of herbivores and predators to differ significantly when $p < 0.05$.

Species occupancy

Herbivore occupancy in each habitat and season was modelled in relation to two top-down drivers including predation risk and anthropogenic factors. I identified two covariates of predation risk hypothesized to influence herbivore occupancy. These included: (1) predator occupancy probability, and (2) vegetation density. Predator occupancy represents a proxy of predation risk whereas vegetation density represents a metric of perceived predation risk (i.e., landscape of fear; Brown et al. 1999, Laundré et al. 2001, Laundre et al. 2010, Iranzo et al. 2018). I estimated predator occupancy probability using a single-species occupancy modelling approach (Mackenzie et al. 2017) implemented within a Bayesian framework using the package *ubms* version 1.1.0 in R (Kellner et al. 2022). A binary matrix of detection/non-detection capture histories for all medium- to large-sized predators was created per camera trap site (Mackenzie et al. 2017). To account for spatiotemporal variability, I modelled predator occupancy as a function of habitat and season. Habitat type was determined at each camera trap site according to the vegetation classification by Mucina & Rutherford (2006). Seasons were classified as wet (March/April) or dry (August/September) based on rainfall (Chapter 2). Several studies (e.g., Davis et al. 2021, 2022) have used predator relative abundance indices (RAI) rather than occupancy probability when analysing the spatial distribution patterns of predators and prey. However, I opted to estimate predator occupancy probability to account for high levels of camera trap failure (Chapter 3) and imperfect predator detection, which can limit the reliability of RAI estimates (Chen et al. 2019). I estimated seasonal vegetation density with a 2.5m vegetation profile board at a distance of 15m in each cardinal direction per camera trap site (Nudds 2006). Density was measured as the proportion of vegetation covering the profile board. Vegetation density estimates were taken relative to the mean shoulder height of medium- to large-sized herbivores (~100cm; Clements et al. 2014) to represent species' line of site (Nudds 2006). To account for spatio-temporal variability, mean vegetation density was calculated per season and habitat.

I identified three covariates of anthropogenic pressure, hypothesized to influence herbivore occupancy, including proximity of camera traps to (1) roads, (2) administrative park boundaries (hereafter boundaries), and (3) human habitation (i.e., camps, lookout points, picnic sites and access gates). I calculated the proximity (i.e., nearest straight-line distance) of each camera trap to the nearest road, boundary and human habitation location using the *nearest hub* plugin in QGIS (version 3.16.3, QGIS Development Team, 2009).

To test for spatial autocorrelation of predation and anthropogenic variables, a Spearman rank correlation was performed in R (version 3.4.2; R Core Development Team 2021). No covariates were correlated ($|r| < 0.6$; Appendix Figure 5.1).

Herbivore occupancy modelling framework

Herbivore detection and occupancy was modelled using a single-species occupancy modelling approach implemented within a Bayesian framework (Mackenzie et al. 2017, Kellner et al. 2022). I fitted three occupancy models for each herbivore species: a fixed effects model that included predation and anthropogenic covariates without accounting for habitat- and season-specific variability (Model 1), a model which accounted for season-specific (Model 2) and habitat-specific (Model 3) variability of predation and anthropogenic covariates (Table 5.1). Model structures were identical for each herbivore species to facilitate interspecific occupancy comparisons.

The occupancy modelling framework used here was identical to the framework used to model bottom-up drivers in Chapter 4. Model performance per herbivore species was evaluated using the expected log pointwise predictive density (elpd). Models were ranked and compared based on the elpd estimates. Herbivore occupancy was predicted based on the outputs of the top performing model, per species. The estimated occupancy for models that exhibited equal predictive accuracy were averaged (Kaplan & Lee 2018).

RESULTS

Camera trapping

Details on camera trapping effort are covered in Chapters 3 and 4. A total of 2633 detections of eight herbivore species were recorded during the study (Chapter 3; Table 3.1). Given that only two carnivore species (i.e., spotted hyaena and leopard) were recorded, detections from both species were pooled resulting in a total of 48 predator detections (wet season: 27; dry season: 21).

Season- and habitat-specific estimates of top-down factors

Predator occupancy decreased slightly from 0.66 (95% CI: 0.25 – 0.95) in the wet season to 0.58 (95% CI: 0.19 – 0.94) in the dry season. However, the seasonal decrease in predator occupancy was not significant (Figure 5.1). Similarly, despite there being slight variations in predator occupancies between habitat types, these were not significant. Further, large confidence intervals associated with estimated predator occupancies between seasons and habitats suggest that these estimates should be treated with caution. Mean (± 95% CI) vegetation density decreased from 0.53 ± 0.25% in the wet season to 0.24 ± 0.22% in the dry season. Vegetation density ($\bar{x}$ = 0.62 ± 0.28) was highest in LRF during the wet season and lowest in LRB during the dry season. The proximity of camera traps to boundaries exceeded 3000m across all three habitat types (Figure 5.1), with LRF occurring closer to boundaries than LRB and SAV. Camera traps in LRB occurred closer to roads ($\bar{x}$ = 38.37 ± 3.16m) but further away from human habitation ($\bar{x}$ = 2 972.98 ± 219.99m). In contrast, camera traps in SAV occurred further from roads ($\bar{x}$ = 88.65 ± 44.49m) but closer to human habitation ($\bar{x}$ = 1 757.98 ± 430.42m).

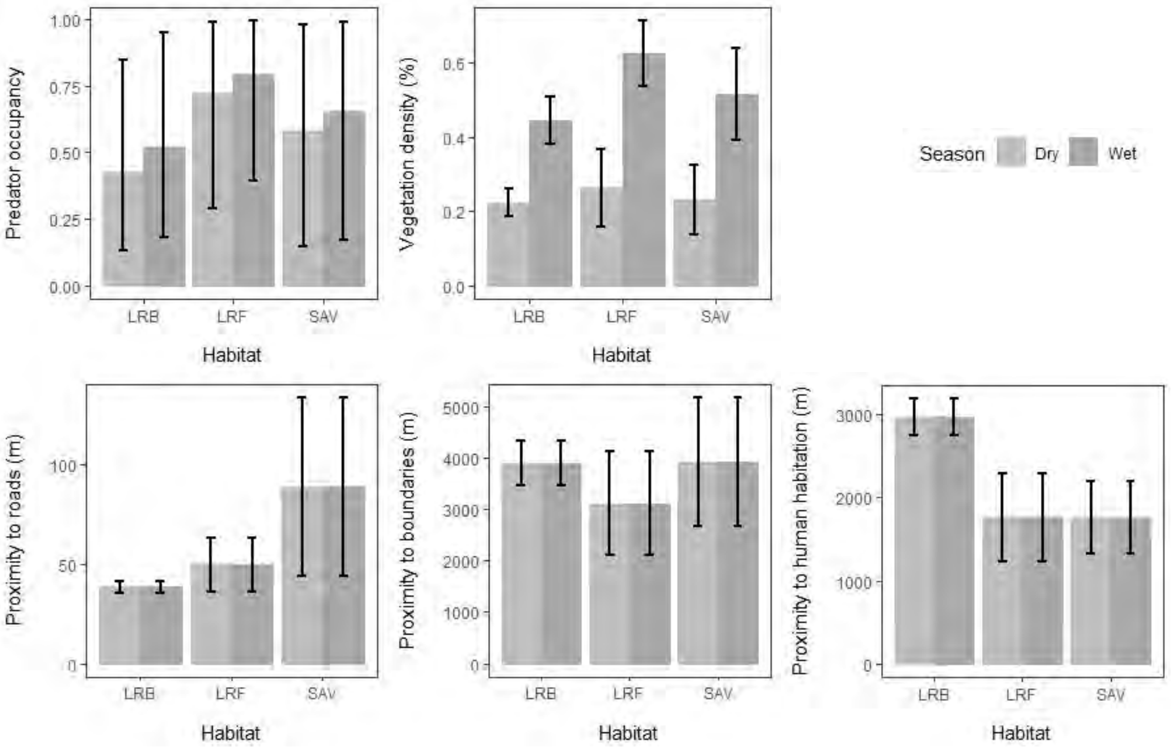


Figure 5.1: Season- and habitat-specific variation in hypothesised top-down drivers of the herbivore community in Pafuri, KNP. Including, mean (± 95% CI) predator occupancy, vegetation density (%), and proximity to roads, boundaries, and human habitation (m). LRB: Limpopo Ridge Bushveld; LRF: Lowveld Riverine Forest; SAV: Subtropical Alluvial Vegetation.

Temporal overlap in predator and prey activity patterns

Predators

Although there was no difference in the activity patterns of predators between seasons (*p* = 0.29), slight variation in peak activity occurred between seasons (Δ_1 = 0.68, 95% CI: 0.56 – 0.87). Predators were nocturnal during both the wet and dry season, with peak activity occurring before sunrise and sunset in the dry season and increased diurnal activity occurring during the wet season (Figure 5.2).

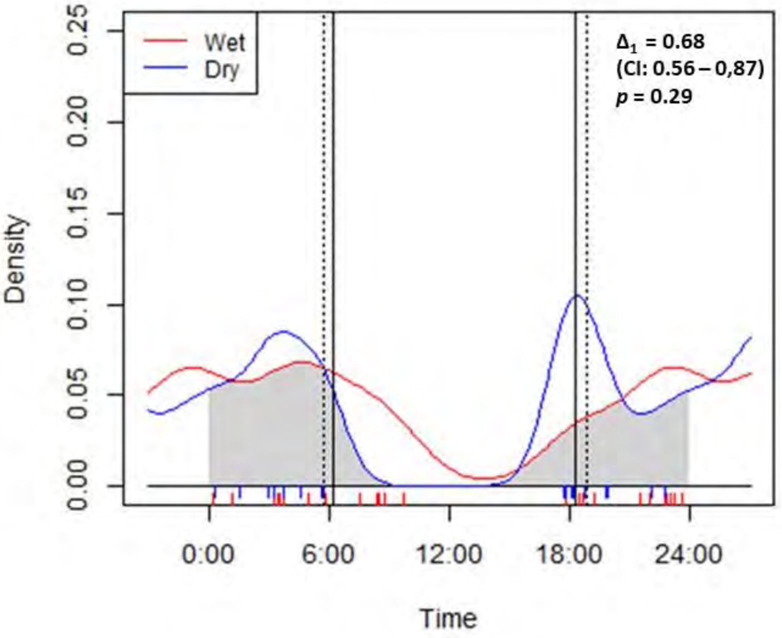


Figure 5.2: Seasonal overlap in predator activity patterns, illustrating the coefficient of overlap (Δ_1), 95% confidence intervals and *p*-value. Sunrise and sunset times are represented by dashed (wet season) and solid (dry season) vertical lines respectively. The rug indicates predator detections in the wet (n = 27) and dry (n = 21) seasons.

Inaccessible herbivores

a. Mixed feeders

Elephant activity patterns were cathemeral in both seasons with peak periods of activity occurring around midday in the dry season, and after sunset in the wet season. However, contrary to predictions for inaccessible prey (i.e., > 1600kg), there was a significant difference ($p < 0.05$) in overlap in the activity patterns of elephant and predators in both the dry (Δ_1 = 0.54, 95% CI: 0.35 – 0.63) and wet (Δ_1 = 0.59, 95% CI: 0.43 – 0.72) seasons.

Accessible herbivores

a. Browsers

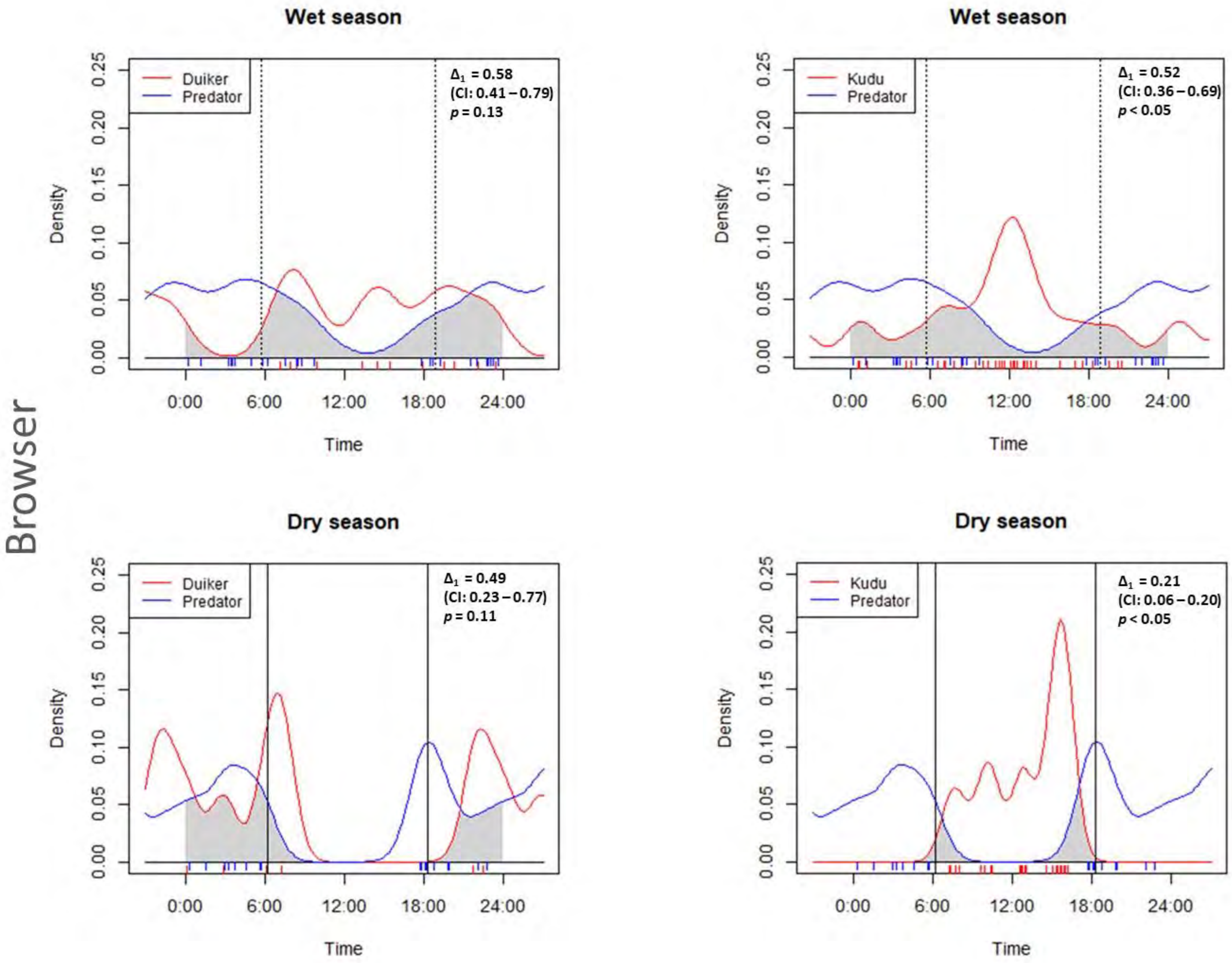
Common duiker shifted from a more cathemeral activity pattern in the wet season – peak activity just after sunrise – to a bimodal activity pattern in the dry season – peak activity just after sunrise and before midnight (Figure 5.3). Although the activity patterns of common duiker and predators did not differ (*p* > 0.05), contrary to predictions, there was relatively low overlap in peak activity periods (wet: Δ_1 = 0.58; dry: Δ_1 = 0.49). In contrast, kudu were diurnal during both seasons with peak activity around midday in the wet season, and before sunset in the dry season. Unlike common duiker, kudu activity differed significantly (*p* < 0.05) from predators in both the wet and dry seasons, as predicted.

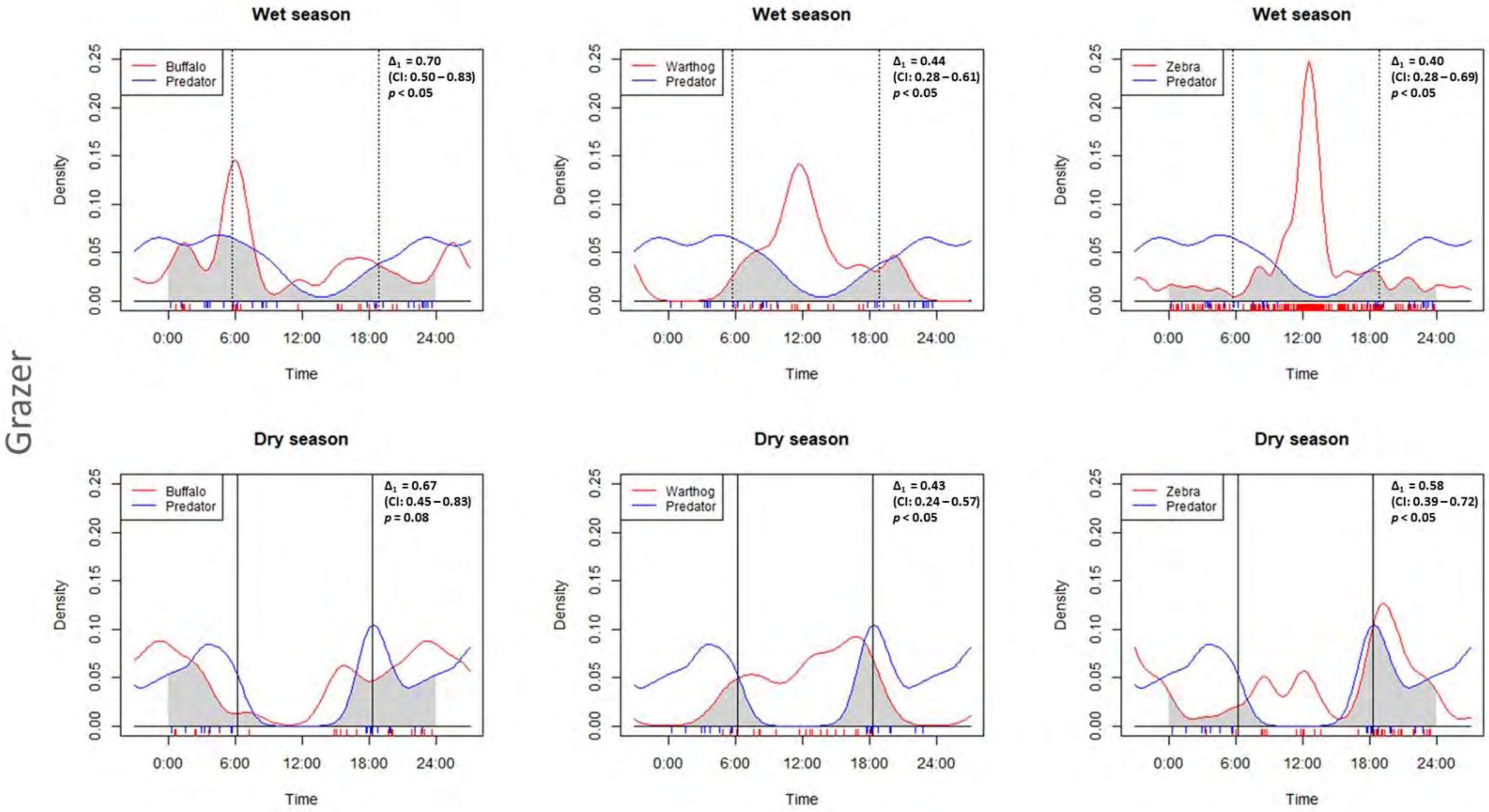
b. Grazers

Buffalo shifted from a crepuscular activity pattern in the wet season – peak activity just before sunrise – to a bimodal activity pattern in the dry season – peak activity before midnight and before sunset. Buffalo and predator activity displayed high overlap in both the wet (Δ_1 = 0.70, 95% CI: 0.50 – 0.83) and dry (Δ_1 = 0.67, 95% CI: 0.45 – 0.83) seasons. However, buffalo use of the diel cycle differed significantly (*p* < 0.05) from predators in the wet season only, as predicted, owing to peak activity before sunrise. Warthogs were diurnal during both seasons with peak activity occurring before sunset in the dry season and around midday in the wet season. In contrast, zebra shifted from a crepuscular activity pattern in the dry season – peak activity just after sunset – to a more diurnal activity pattern in the wet season – peak activity around midday. Irrespective of the differences in their activity patterns, warthog and zebra activity displayed relatively low overlap with predator activity which differed significantly (*p* < 0.05) in both the dry (warthog: Δ_1 = 0.43; zebra: Δ_1 = 0.58) and wet (warthog: Δ_1 = 0.44; zebra: Δ_1 = 0.40) seasons, as predicted.

c. Mixed feeders

Impala and nyala exhibited diurnal activity patterns during both seasons with peak impala activity occurring between 9:00 and 11:00, and peak nyala activity occurring after sunrise and before sunset during the dry season. In contrast, activity patterns of both impala and nyala peaked around midday during the wet season. Impala and nyala activity displayed relatively low overlap with predators in the dry season (impala: $\Delta_1 = 0.25$; nyala: $\Delta_1 = 0.32$). However, overlap in the activity patterns of impala and predators increased in the wet season ($\Delta_1 = 0.63$, 95% CI: 0.51 – 0.76), whereas a slight decrease in activity overlap between nyala and predators occurred in the wet season ($\Delta_1 = 0.31$, 95% CI: 0.19 – 0.41). Irrespective of the shifts in activity, seasonal activity patterns of both impala and nyala differed significantly from those of predators in both seasons, as predicted.


Browser
Wet season
Duiker
Predator
Δ₁ = 0.58
(CI: 0.41 – 0.79)
p = 0.13
Wet season
Kudu
Predator
Δ₁ = 0.52
(CI: 0.36 – 0.69)
p < 0.05
Dry season
Duiker
Predator
Δ₁ = 0.49
(CI: 0.23 – 0.77)
p = 0.11
Dry season
Kudu
Predator
Δ₁ = 0.21
(CI: 0.06 – 0.20)
p < 0.05
Density
0.00
0.05
0.10
0.15
0.20
0.25
Time
0:00
6:00
12:00
18:00
24:00


Grazer
Wet season
Buffalo
Predator
$\Delta_1 = 0.70$
(CI: 0.50 – 0.83)
$p < 0.05$
Wet season
Warthog
Predator
$\Delta_1 = 0.44$
(CI: 0.28 – 0.61)
$p < 0.05$
Wet season
Zebra
Predator
$\Delta_1 = 0.40$
(CI: 0.28 – 0.69)
$p < 0.05$
Dry season
Buffalo
Predator
$\Delta_1 = 0.67$
(CI: 0.45 – 0.83)
$p = 0.08$
Dry season
Warthog
Predator
$\Delta_1 = 0.43$
(CI: 0.24 – 0.57)
$p < 0.05$
Dry season
Zebra
Predator
$\Delta_1 = 0.58$
(CI: 0.39 – 0.72)
$p < 0.05$
Density
0.00
0.05
0.10
0.15
0.20
0.25
Time
0:00
6:00
12:00
18:00
24:00

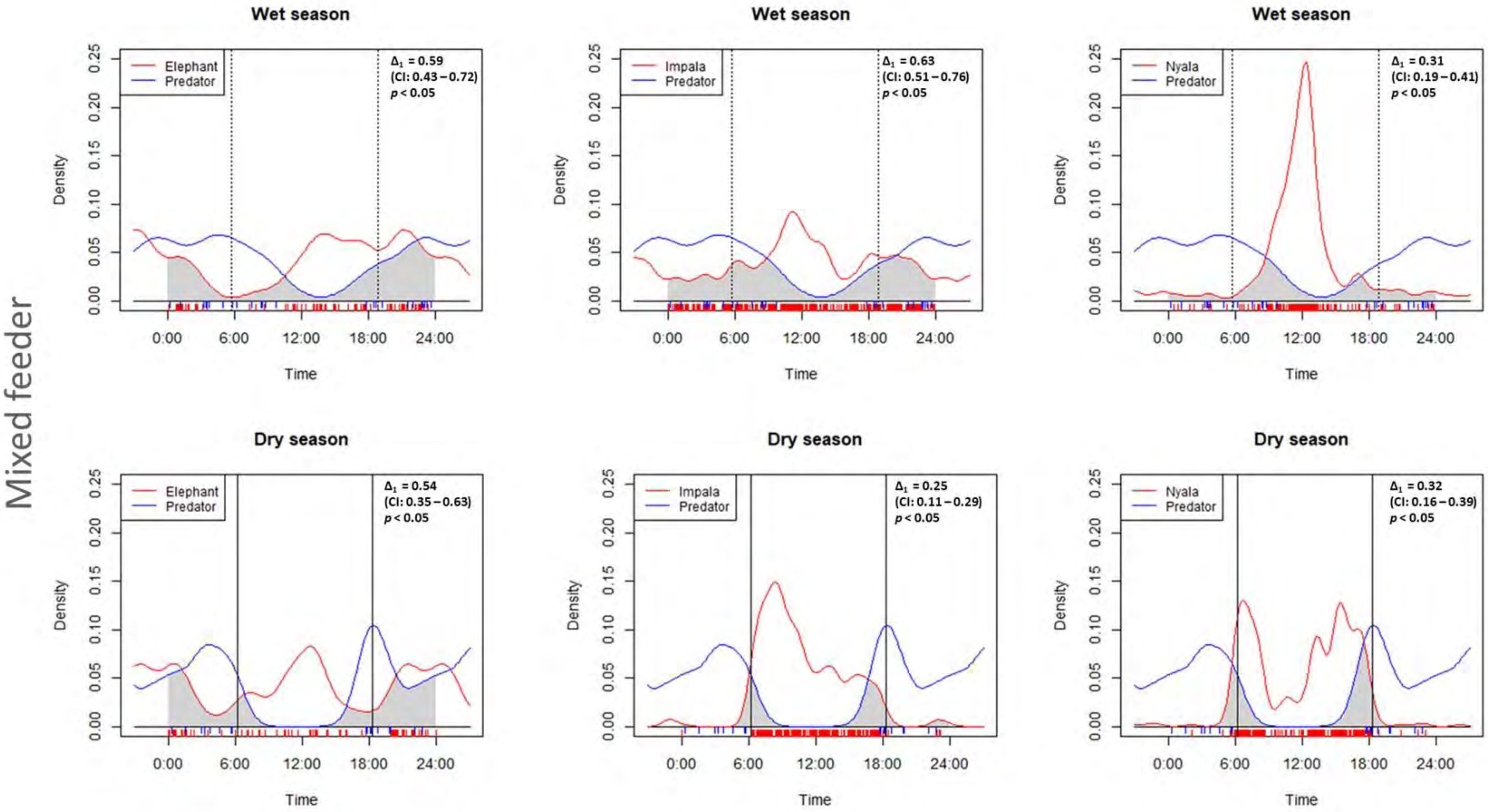

Mixed feeder
Wet season
Elephant
Predator
$\Delta_1 = 0.59$
(CI: 0.43 – 0.72)
$p < 0.05$
Wet season
Impala
Predator
$\Delta_1 = 0.63$
(CI: 0.51 – 0.76)
$p < 0.05$
Wet season
Nyala
Predator
$\Delta_1 = 0.31$
(CI: 0.19 – 0.41)
$p < 0.05$
Dry season
Elephant
Predator
$\Delta_1 = 0.54$
(CI: 0.35 – 0.63)
$p < 0.05$
Dry season
Impala
Predator
$\Delta_1 = 0.25$
(CI: 0.11 – 0.29)
$p < 0.05$
Dry season
Nyala
Predator
$\Delta_1 = 0.32$
(CI: 0.16 – 0.39)
$p < 0.05$
Density
0.00
0.05
0.10
0.15
0.20
0.25
Time
0:00
6:00
12:00
18:00
24:00

Figure 5.3: Seasonal overlap in predator and prey activity patterns. Herbivore species are grouped according to feeding guild. The coefficient of overlap (Δ_1), 95% confidence intervals and *p*-value associated with the overlap index, are illustrated. Sunrise and sunset times are represented by dashed (wet season) and solid (dry season) vertical lines respectively. The rug indicates herbivore and predator detections.

Top-down spatial drivers of herbivore occupancy

Inaccessible herbivores

a. Mixed feeders

The fixed effects and habitat models explained the most variation in elephant occupancy, with averaged β-coefficients indicating that only habitat-specific variability in proximity to areas of human habitation affected elephant occupancy. Contrary to predictions, elephant increased occupancy closer to habitation across all habitat types in the Pafuri, with the effects of habitation proximity on elephant occupancy being moderately significant (β1 = -1.25, 75% BCI: -2.55 – -0.01).

Accessible herbivores

a. Browsers

The habitat model explained the most variation in common duiker occupancy (Table 5.1), with averaged β-coefficients indicating that only habitat-specific variability in proximity to roads affected occupancy (Figure 5.5). As predicted, common duiker increased occupancy further from roads in SAV, LRB and LRF (Figure 5.4) with only the effect of proximity to roads in SAV being significant (β1 = 1.81, 95% BCI: 0.10 – 4.56). All three models explained equal variation in kudu occupancy, with averaged β-coefficients indicating that season- and habitat-specific variability in proximity to roads, season-specific variability in predator occupancy, and habitat-specific variability in proximity to boundaries and vegetation density affected occupancy. Kudu increased occupancy further from roads irrespective of habitat type (β1 = 2.08, 95% BCI: 0.04 – 5.04) in both the wet and dry seasons, as predicted. Contrasting seasonal effects of predator occupancy were observed. Despite there being a non-significant difference in predator occupancy between seasons (Figure 5.1), kudu decreased occupancy in habitats with higher predator occupancy in the wet season, as predicted, and increased occupancy in habitats with higher predator occupancy in the dry season, contrary to predictions. However, only the effects of predator occupancy in the wet season were moderately significant. Contrary to predictions, kudu occupancy appeared to be directly proportional to vegetation density in LRB and SAV, albeit non-significant. However, in LRF, kudu occupancy showed a moderately significant (β1 = -1.82, 75% BCI: -3.16 – -0.57) decrease at higher vegetation density, as predicted. As predicted, kudu appeared to increase occupancy further from boundaries in SAV and LRF with the reverse holding for LRB. Irrespective of the contrasting effects of boundaries, only the effects of proximity to boundaries in SAV were moderately significant (β1 = 1.51, 75% BCI: 0.12 – 2.96).

b. Grazers

The habitat and fixed effects models explained the most variation in buffalo occupancy, with averaged β-coefficients indicating that top-down factors, including predation (i.e., predator occupancy and vegetation density) and anthropogenic factors (i.e., proximity to roads, boundaries, and habitation) did not affect occupancy, contrary to predictions. The habitat model explained the most variation in warthog occupancy, with averaged β-coefficients indicating that habitat-specific predator occupancy and proximity to boundaries affected occupancy. Contrary to predictions, warthog occupancy appeared to be directly proportional to predator occupancy in LRF (β1 = 2.05, 75% BCI: 0.42 – 3.78), with the reverse holding for LRB and SAV; albeit non-significant. As predicted, warthog occupancy increased further from boundaries in LRB and SAV, but not in LRF, contrary to predictions. Irrespective of the contrasting habitat-specific effects of boundaries, only the effect of proximity to boundaries on warthog occupancy in SAV was significant (β1 = 2.40, 95% BCI: 0.002 – 5.88). The fixed effects and habitat models explained the most variation in zebra occupancy, with averaged β-coefficients indicating that all predation and anthropogenic top-down factors affected occupancy. Across all habitat types, zebra occupancy increased moderately significantly (β1 = 1.60, 75% BCI: 0.35 – 3.01) with increasing predator occupancy – contrary to predictions – but decreased moderately significantly (β1 = -0.90, 75% BCI: -1.78 – -0.06) with increasing vegetation density – as predicted. As predicted, zebra occupancy increased further from roads (β1 = 1.46, 75% BCI: 0.18 – 2.90) and boundaries (β1 = 1.11, 75% BCI: 0.18 – 2.07) across all habitat types in the Pafuri, Similarly, zebra occupancy appeared to increase further from habitation in LRB and SAV as predicted, albeit non-significant. However, in LRF, zebra occupancy increased moderately (β1 = -2.08, 75% BCI: -4.09 – -0.21) closer to habitation, contrary to predictions.

c. Mixed feeders

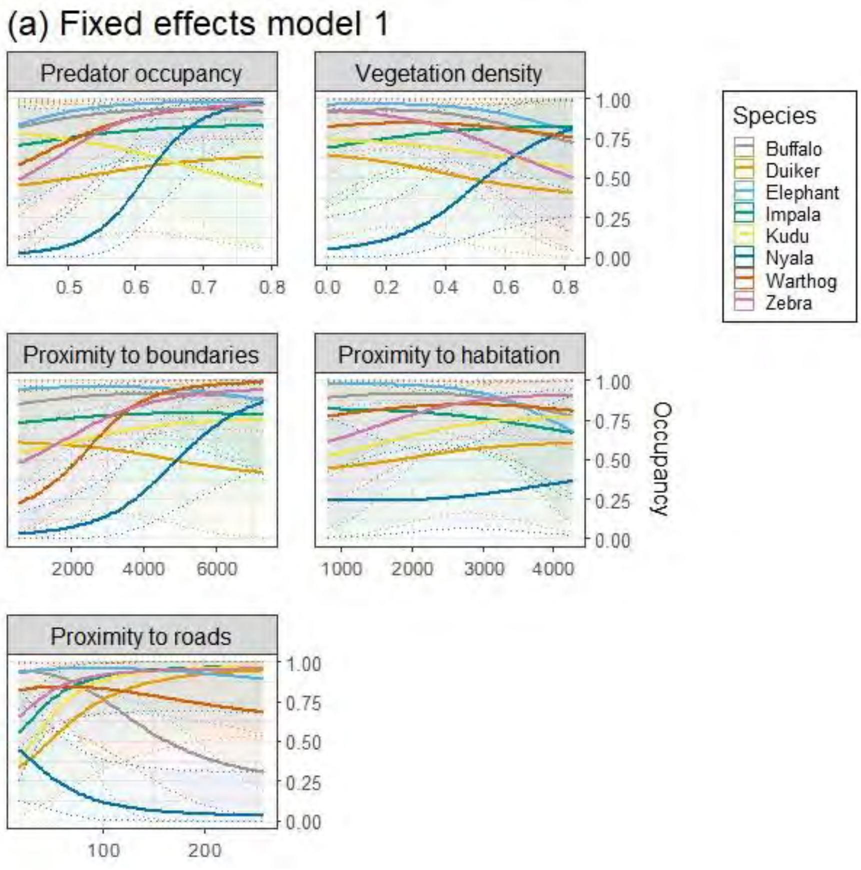
All three models explained equal variation in impala occupancy. Contrary to predictions, impala occupancy appeared to be directly proportional to predator occupancy in the wet season, with the reverse holding for the dry season, as predicted. However, only the seasonal effects of predator occupancy in the wet season were moderately significant (β1 = 1.51, 75% BCI: 0.26 – 2.82). Contrary to predictions, impala moderately increased occupancy closer to habitation, albeit only in LRF (β1 = -1.67, 75% BCI: -3.45 – -0.001). However, impala decreased occupancy further from boundaries, but only in SAV (β1 = 1.56, 75% BCI: 0.30 – 2.88), and increased occupancy further from roads across all habitat types (β1 = 1.62, 75% BCI: 0.46 –u 2.85), as predicted. The fixed effects model explained the most variation in nyala occupancy, with averaged β-coefficients indicating that predator occupancy, vegetation density, proximity to roads and proximity to boundaries affected occupancy. Contrary to predictions, nyala occupancy was directly proportional to both predator occupancy (β1 = 3.24, 95% BCI: 1.31 – 5.77) and vegetation density (β1 = 1.71, 95% BCI: 0.22 – 3.54). As predicted, nyala significantly increased occupancy further from boundaries (β1 = 1.93, 95% BCI: 0.54 – 3.66) but moderately decreased occupancy further from roads across all habitat types in Pafuri (β1 = -1.36, 75% BCI: -2.29 – -0.50), contrary to predictions.

Table 5.1: Single-species occupancy models for eight focal herbivores in Pafuri, KNP. Models are ranked according to model performance (i.e., elpd which is the expected log pointwise predictive density). Δelpd indicates the pairwise differences in elpd relative to the top performing model (model rank). SE (Δelpd) is the standard error of Δelpd. $\hat{p}\_loo$ is the effective number of model parameters.

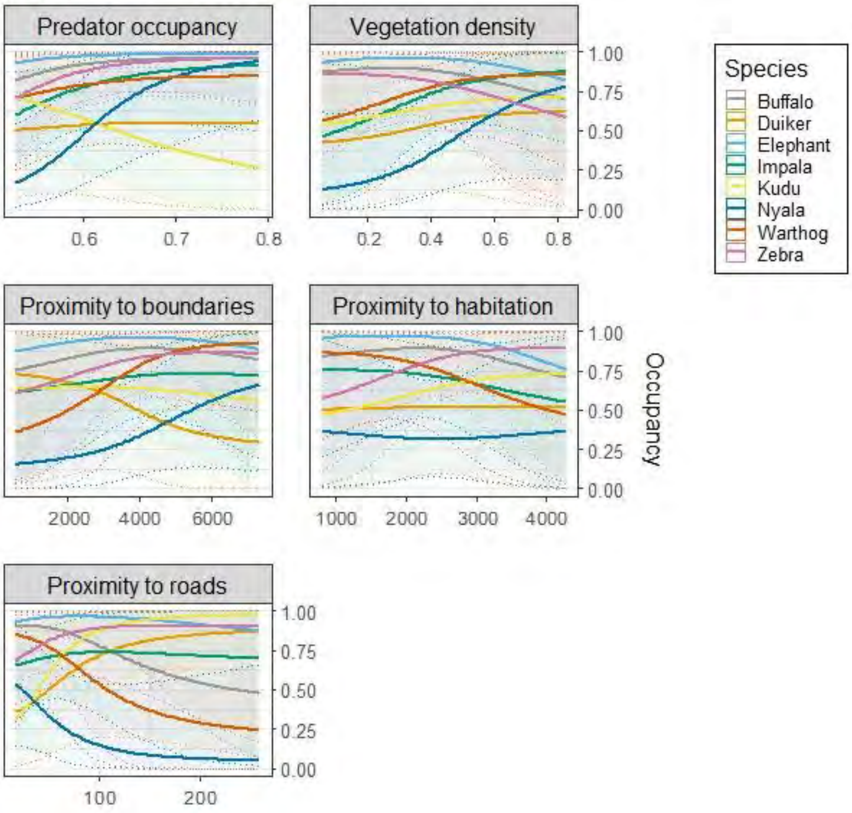
Guild	Species	Model*	elpd	Δelpd	SE(Δelpd)	$\hat{p}\_loo$
Browser	Common duiker	Model 3	-59.88	0.00	0.00	7.61
		Model 2	-62.75	-2.88	1.56	8.70
		Model 1	-63.41	-3.53	2.29	8.78
	Kudu	Model 3	-146.29	0.00	0.00	15.59
		Model 1	-146.49	-0.20	2.65	12.78
		Model 2	-147.75	-1.47	2.34	15.74
Grazer	Buffalo	Model 3	-115.65	0.00	0.00	8.48
		Model 1	-115.82	-0.16	1.19	6.82
		Model 2	-117.20	-1.55	1.27	8.83
	Warthog	Model 3	-117.43	0.00	0.00	6.78
		Model 2	-119.61	-2.18	1.81	7.98
		Model 1	-120.31	-2.88	1.50	7.47
	Zebra	Model 1	-259.12	0.00	0.00	25.90
		Model 3	-260.55	-1.42	1.65	28.49
		Model 2	-262.73	-3.61	1.44	30.02
Mixed feeder	Elephant	Model 1	-244.80	0.00	0.00	11.10
		Model 3	-245.21	-0.40	0.76	11.89
		Model 2	-246.02	-1.22	0.63	12.20
	Impala	Model 1	-392.61	0.00	0.00	40.13
		Model 3	-392.62	-0.02	3.10	43.99
		Model 2	-395.09	-2.48	2.81	45.61

	Nyala	Model 1	-206.90	0.00	0.00	34.12
		Model 2	-210.01	-3.11	1.64	36.17
		Model 3	-211.08	-4.18	1.98	36.76

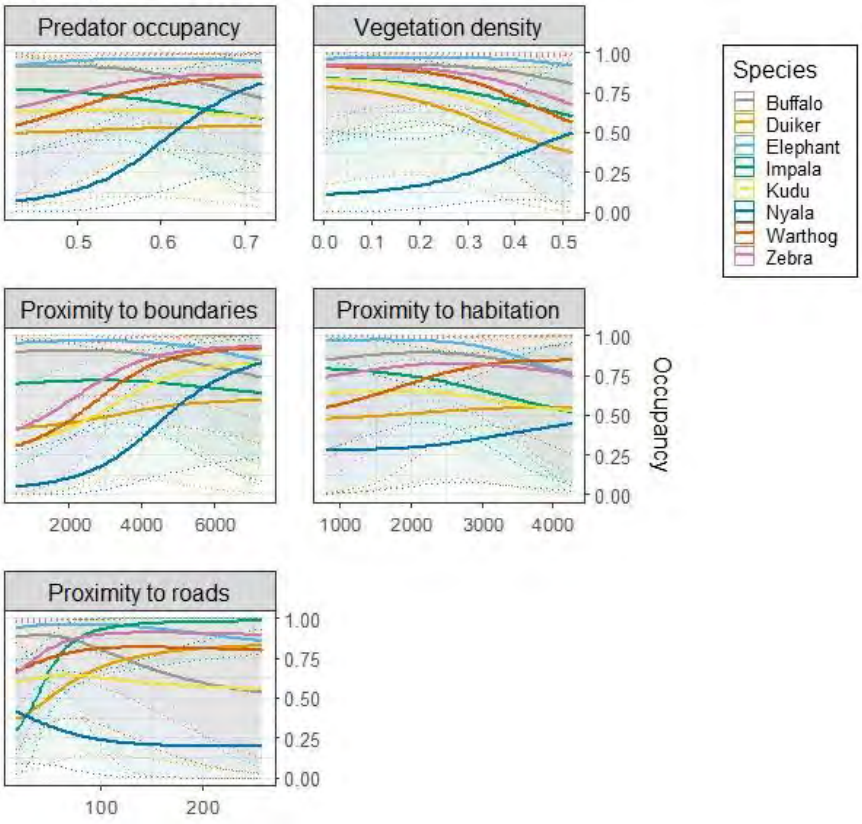
*Model formulation: Model 1 (Fixed effects) = p (~season + habitat). ψ (~predator occupancy + vegetation density + proximity to roads + proximity to boundaries + proximity to habitation); Model 2 (Season) = p (~season + habitat). ψ (~season: predator occupancy + season: vegetation density + season: proximity to roads + season: proximity to boundaries + season: proximity to habitation); Model 3 (Habitat) = p (~season + habitat). ψ (~habitat: predator occupancy + habitat: vegetation density + habitat: proximity to roads + habitat: proximity to boundaries + habitat: proximity to habitation)



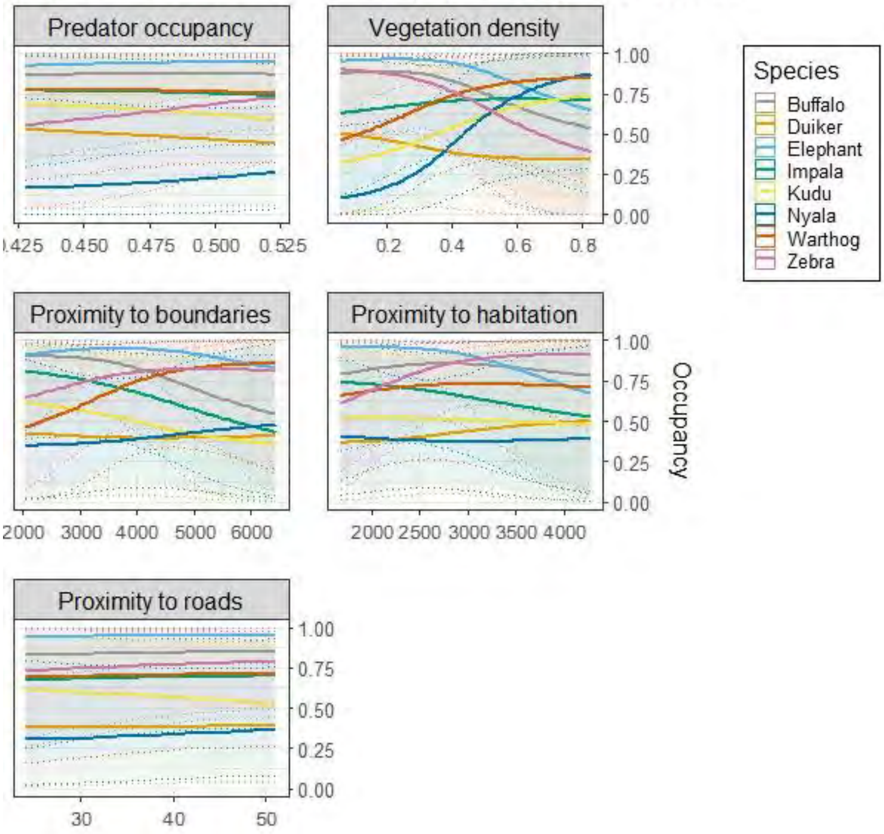
(b) Wet season model 2



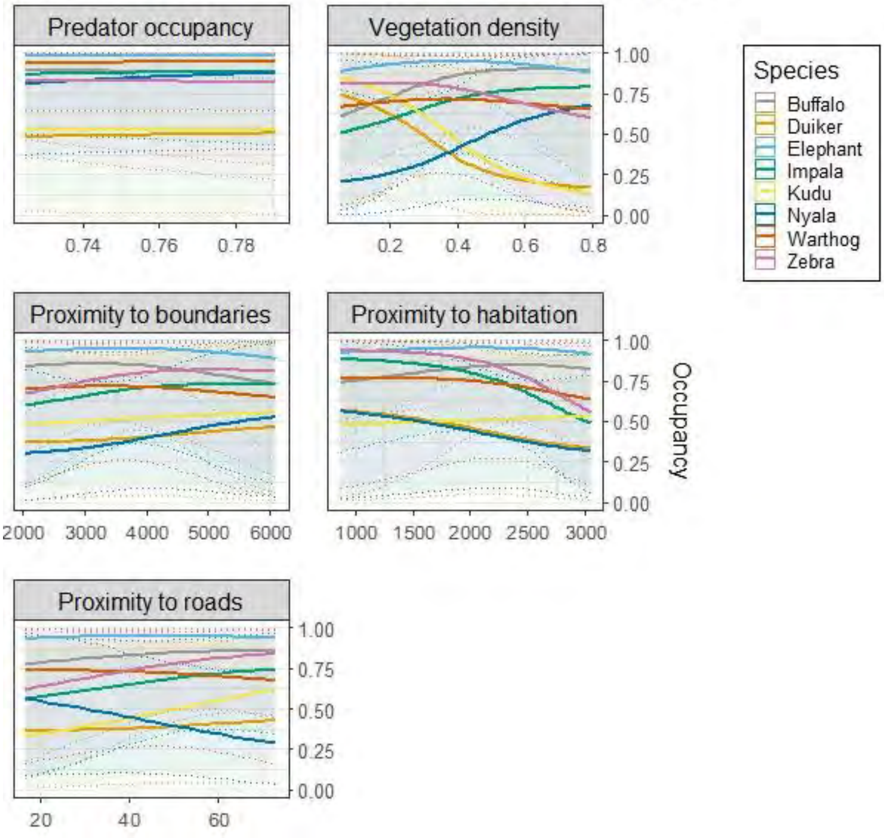
(c) Dry season model 2



(d) Habitat model 3 - Limpopo Ridge Bushveld



(e) Habitat model 3 - Lowveld Riverine Forest



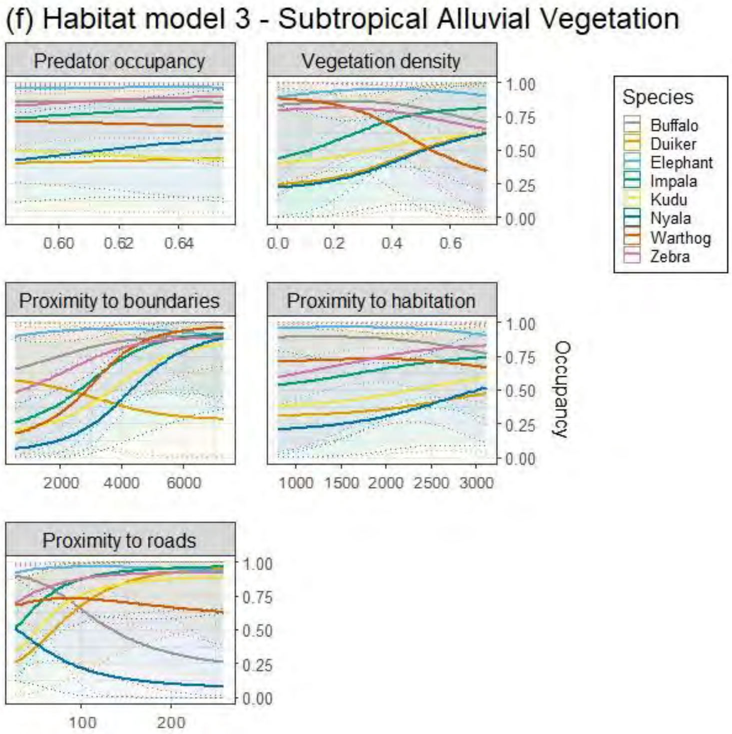
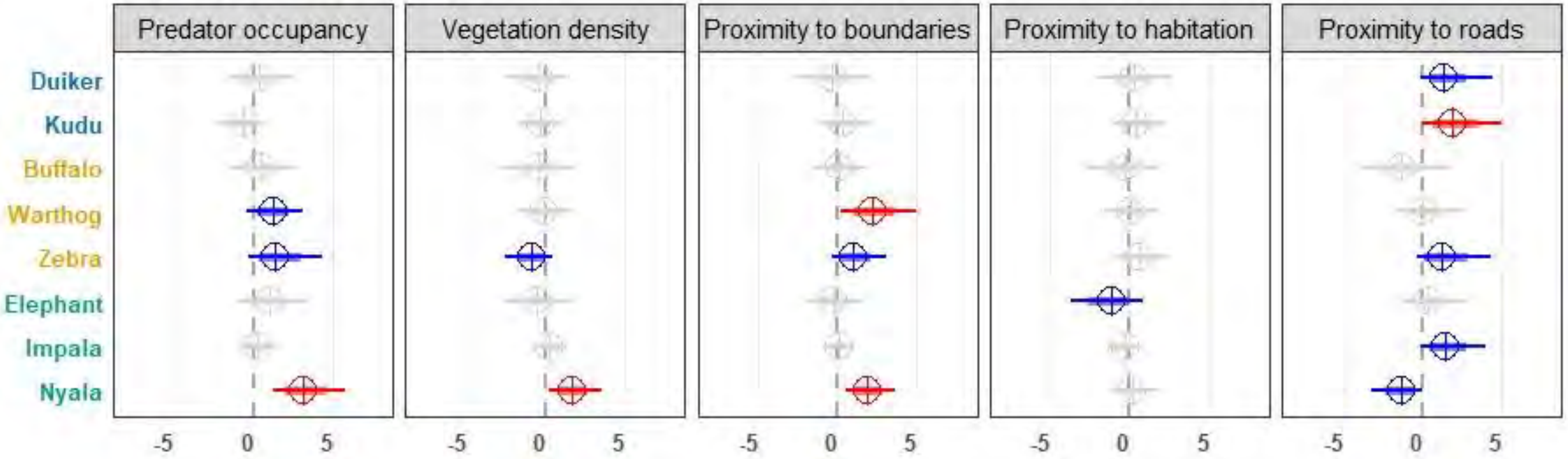
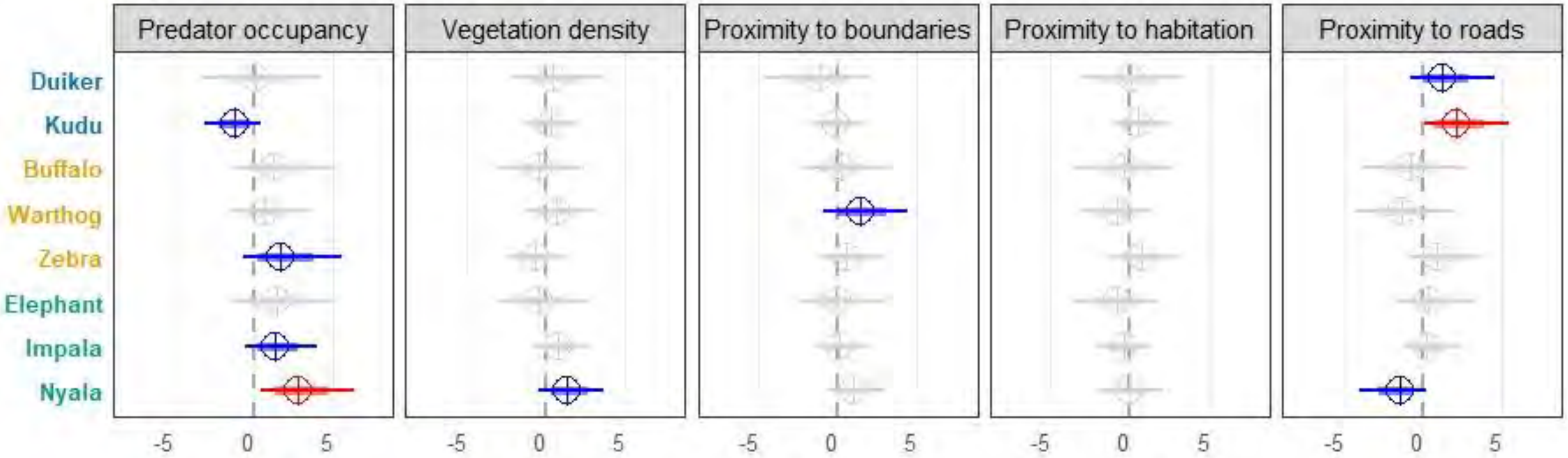


Figure 5.4: Response curves illustrating herbivore occupancy probability relative to season- and habitat-specific variability in predation and anthropogenic top-down effects. Bold lines represent the posterior mean estimates and ribbons, the 95% Bayesian Credible Interval (BCI). Results are presented according to three model outputs: fixed effects (a); season (b & C); and habitat (d, e & f) per species.

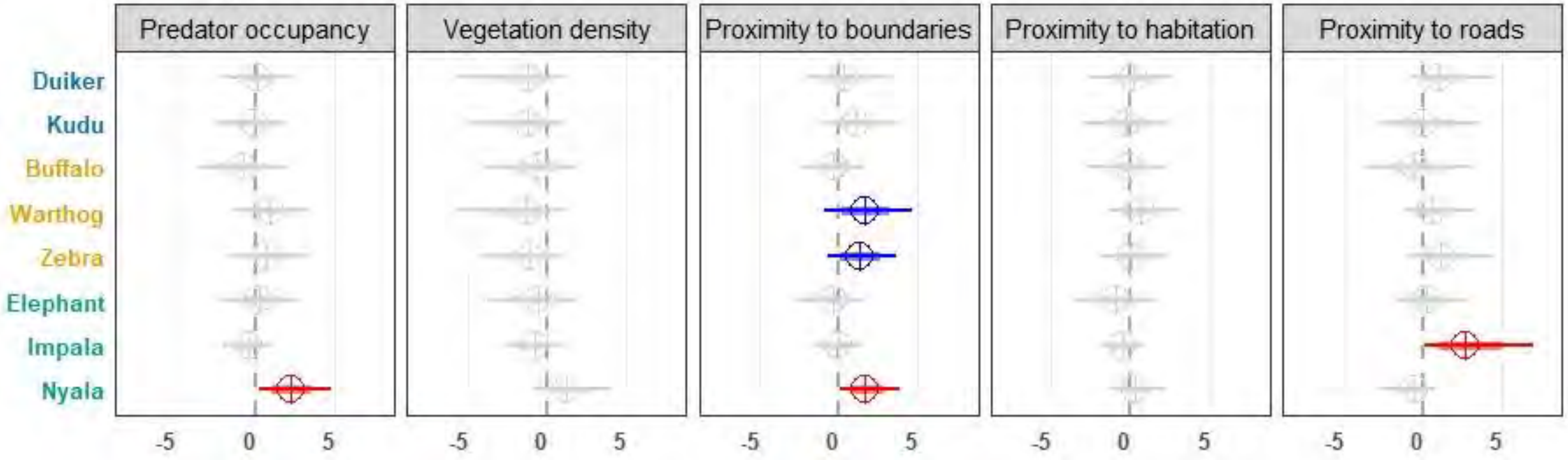
(a) Fixed effects model 1



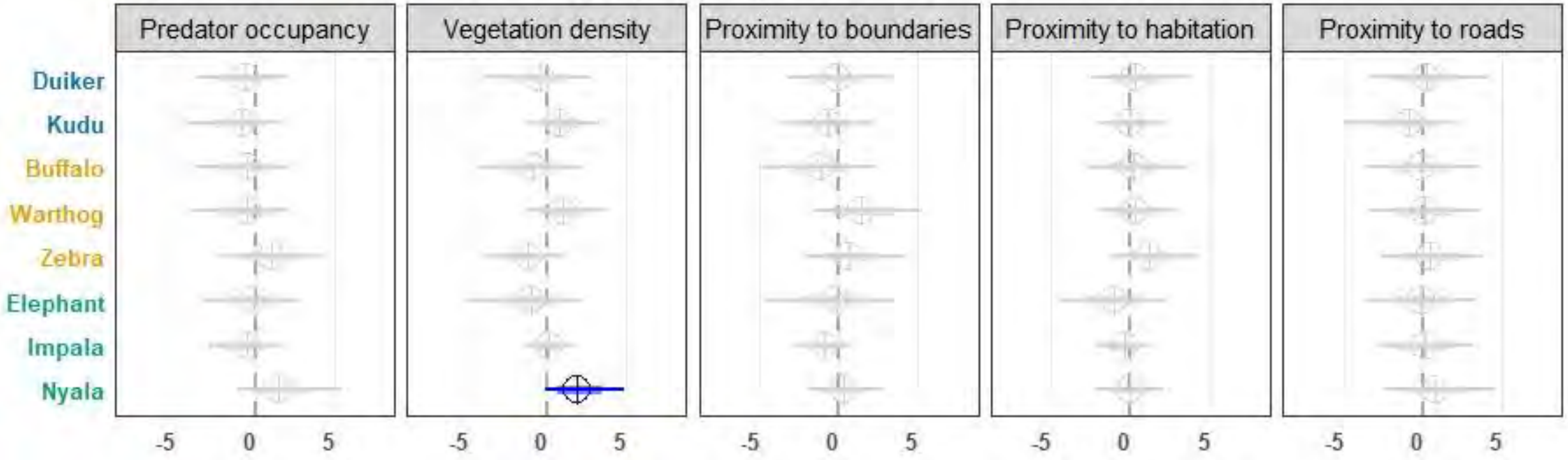
(b) Wet season model 2



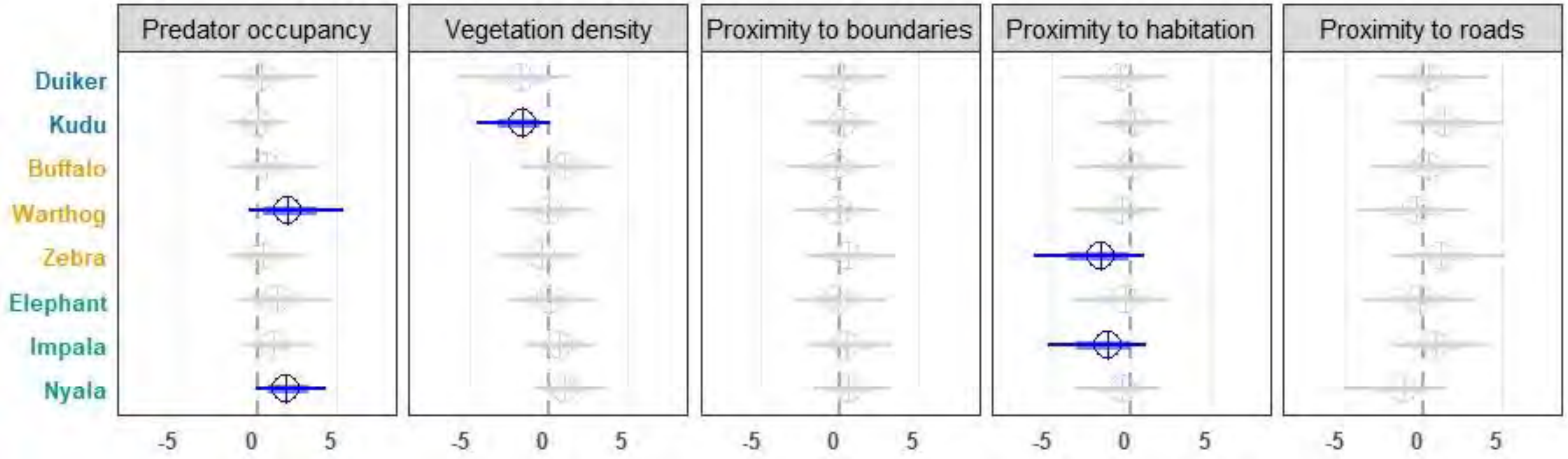
(c) Dry season model 2



(d) Habitat model 3 - Limpopo Ridge Bushveld



(e) Habitat model 3 - Lowveld Riverine Forest



(f) Habitat model 3 - Subtropical Alluvial Vegetation

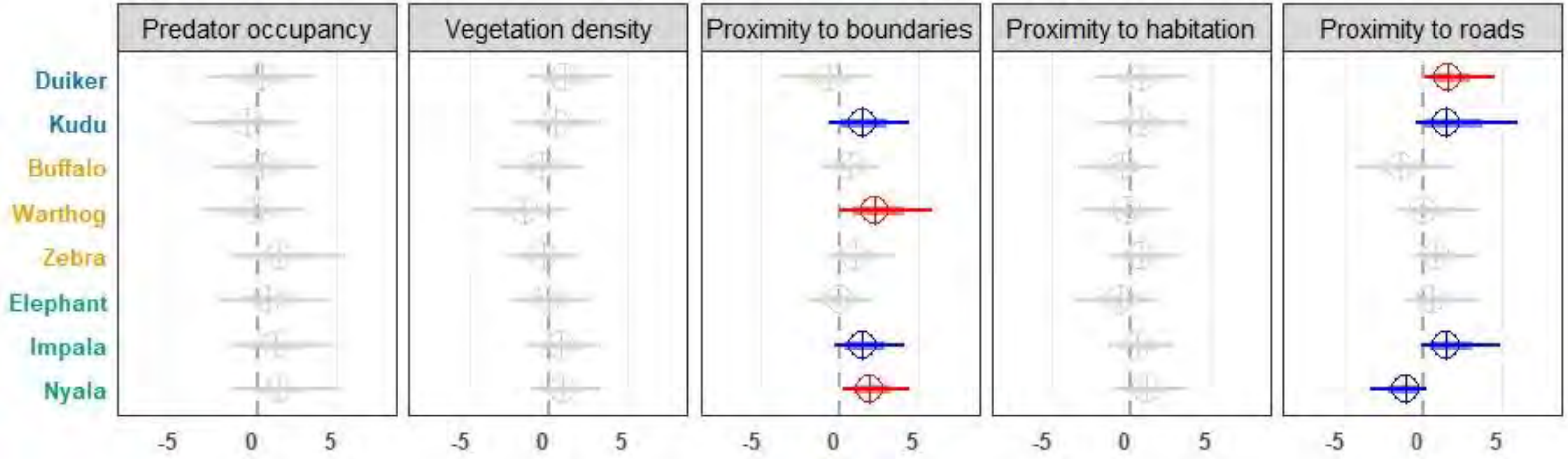


Figure 5.5: Standardized β-coefficients representative of covariate effects on herbivore occupancy obtained from a fixed effects model (a), and models accounting for season- (b & c) and habitat-specific (d, e & f) variability. Grey bars indicate no significant covariate effects (95% BCI overlap 0), and red (95% BCI does not overlap 0) and blue (75% BCI does not overlap 0) bars illustrate significant and moderate covariates respectively. Species are coloured and grouped according to feeding guild (i.e., blue: browsers; yellow: grazers; green: mixed feeders).

DISCUSSION

The occurrence and space-use of mammalian herbivore populations are influenced by complex interactions between bottom-up (i.e., season- and habitat-specific variations in forage availability and quality, and water availability) and top-down (spatiotemporal variations in predation and anthropogenic risks) factors (Jedrzejewska & Jedrzejewski 2005, Burkepile et al. 2013, Panebianco et al. 2022). In multi-predator/prey systems, exposed to high levels of human activity, herbivores face trade-offs between resource acquisition and reducing risks associated with predators and humans (Schuette et al. 2016, Balfour et al. 2021, Davies et al. 2021). Similar to the effects of bottom-up factors (Chapter 4), herbivore responses to spatial and temporal variations in top-down factors were species-specific, even for members of the same guild, which reflected in their activity, occupancy, and space-use.

Inaccessible prey species

a. Mixed feeders

As predicted for large inaccessible prey (i.e., > 1600kg; Clements et al. 2014), elephants displayed no spatial responses to predator occupancy and perceived predation risks but avoided periods of peak predator activity in both seasons, contrary to predictions. Given that elephants are largely free from predation in South Africa (Bastille-Rousseau et al. 2020, Valenta et al. 2021), it is unlikely that elephant activity reflects temporal predator avoidance behaviour. Rather, given their large body size, elephants struggle to thermoregulate in an energy efficient manner during periods of increased ambient temperatures (Veldhuis et al. 2019, du Plessis et al. 2021). In response, elephants tend to limit activity during the hotter periods of the day, opting to forage more after sunset when the temperatures are lower (Williams et al. 2018, Thaker et al. 2019), as was the case in the wet season. In contrast, elephants tend to concentrate around water sources during hotter diurnal periods in the dry season (Chapter 4; Hayward & Hayward 2012), thus, explaining peak elephant activity around midday in the dry season. Similar seasonal shifts in activity patterns were also documented by du Plessis *et al*. (2021), Mole *et al*. (2016) and Mramba *et al*. (2019). Contrary to predictions, elephants increased occupancy closer to areas of high tourist activity (i.e., tourist camps, access gates, lookout points and picnic spots) across all habitat types. It is possible that elephants are attracted to habitation as these have been shown to offer refuge from poaching (see Rimaze et al. 2020). For example, herbivore densities increased near traditional fishing camps in the Greater Kafue Ecosystem owing to increased human presence, providing some level of refuge from poachers (Vinks et al. 2020). Alternatively, elephants could be attracted to human habitation, as these are coincidentally located in habitats that offer improved foraging and access to permanent water (Chapter 4; e.g., Rimaze et al. 2020). Although not specific to elephants, Matandiko (2016) attributed increased herbivore densities near habitation (specifically tourist camps) in Kafue National Park to the location of camps that concentrated in habitats that offered optimum foraging opportunities. Thus, the lack of spatial responses to predation risk coupled with spatial attraction to areas of human habitation suggests that elephants in Pafuri are likely bottom-up, resource regulated (see Chapter 6 for comparative evaluation between bottom-up and top-down drivers).

Accessible prey species

a. Browsers

Common duiker did not display temporal or spatial avoidance of predator occupancy and perceived predation threats, contrary to predictions. This, despite being highly susceptible to predation, particularly from leopards (Hayward et al. 2006, Abu Baker & Brown 2014). It is possible that the lack of a spatial and temporal response by common duiker could be attributed to low predator densities (e.g., Chamaillé-Jammes et al. 2019). Specifically, the limited number of predator detections, resulting in estimated predator occupancies with high confidence intervals that do not differ significantly spatially nor temporally, could be masking the effects of predation driving herbivore activity and space-use. Thus, requiring further investigation. Contrary to predation, anthropogenic top-down drivers impacted common duiker space-use, as occupancy increased further from roads, as predicted. It is likely that common duiker are avoiding roads owing to (1) increased probability of vehicular mortality (Hill et al. 2019), (2) habitat destruction and poaching synonymous with high levels of human activity (Coffin 2007), and/or (3) barrier-effects created by roads restricting mammal movements (Goosem 2000). Thus, given the lack of spatial and temporal responses to predation risks, it is possible that common duiker in Pafuri are bottom-up regulated (Chapter 6) with responses to these drivers augmented by anthropogenic risks (e.g., Ehlers Smith et al. 2019). Alternatively, I hypothesise that common duiker activity and occupancy may be influenced by competitive interactions with other herbivores, resulting in spatial and temporal niche partitioning (Sinclair 1985, Prins et al. 2006, Ehlers Smith et al. 2019). For example, common duiker, suni (*Neotragus moschatus*) and red duiker (*Cephalophus natalensis*) adjusted habitat use to reduce interspecific competition in Mozambique (Prins et al. 2006). However, quantifying competitive interactions using camera trap data alone can lead to unreliable estimates (Chapter 4; Caravaggi et al. 2017). Thus, further analyses that focus on interspecific competition along the spatial, temporal, and dietary niche axes of common duiker populations are required to quantify the influence that competition plays in regulating common duiker activity and space-use.

As predicted, kudu avoided direct and perceived predation risks and anthropogenic threats via a combination of spatial and temporal responses. However, these responses varied seasonally. Kudu were more active outside peak periods of predator activity, increasing diurnal activity (e.g., Tambling et al. 2015) in the wet season and decreasing occupancy in closed habitats with increased vegetation density and cover (Chapter 4; e.g., Du Toit 1995) irrespective of season, to avoid predators and the threat of predation. Thus, reflecting a landscape of fear (Laundré et al. 2001). Kudu exhibited similar responses to anthropogenic factors, occupying habitat patches further from roads, irrespective of season, and boundaries – specifically in SAV. Contrary to Malherbe *et al*. (2021), kudu in Pafuri appear to be avoiding roads, likely owing to roads (1) acting as a boundary impeding movements (Newmark et al. 1996), (2) reducing habitat quality (Rytwinski & Fahrig 2015), and (3) causing mortality attributed to fatal collisions with vehicles (Ramp et al. 2006). Like roads, decreased kudu occupancy closer to boundaries can be attributed to high levels of bushmeat poaching concentrated on the boundaries of Pafuri (SANParks unpublished data 2022; Appendix Figure 5.2). Similar to antipredator responses, kudu may have developed learned responses to decrease occupancy in habitats closer to boundaries to reduce the risks associated with poaching (Lindsey et al. 2013), reflecting a human-induced landscape of fear (Laundré et al. 2001, Lodberg-Holm et al. 2019). Alternatively, the direct predatory effects of poaching may have caused an edge effect resulting in reduced population densities, and thus occupancy, in habitats close to the reserve boundary (Matandiko 2016).

b. Grazers

Contrary to predictions, buffalo did not exhibit any spatial or temporal responses to predator occupancy and perceived predation risks, except for reducing activity during peak periods of predator activity in the wet season. In the wet season, buffalo were predominantly crepuscular with predators being more diurnal. The temporal shifts in buffalo activity between seasons – peak activity at sunrise in the wet season and at sunset and midnight in the dry season – suggests that they may be avoiding peak predator activity in the wet season (e.g., Tambling et al. 2015). Alternatively, it is possible that buffalo increase activity during cooler periods (i.e., before sunrise) in the wet season to limit thermal stresses related to foraging during periods of high ambient diurnal temperature (Chapter 2; Owen-Smith & Goodall 2014). Thus, temporal activity shifts by buffalo between seasons highlights the existence of a potential ecological trade-off between predation and thermal tolerance. Given their limited risks of predation from spotted hyaena (Hayward 2006) and leopard (Hayward et al. 2006), and their high susceptibility to thermal stress owing to their large body size (Porter & Kearney 2009, Veldhuis et al. 2019), I hypothesise that buffalo will shift their activity and space-use more strongly to minimise the effects of high temperatures in contrast to predation risks. Trade-offs between predator avoidance and thermal tolerance should be investigated by assessing how herbivores vary activity and space-use in response to increased temperatures in both the presence and absence of predators, and contrasting these responses between seasons (Veldhuis et al. 2019). In addition to predation and perceived predation risks, buffalo occupancy was neither affected by season- nor habitat-specific anthropogenic risks, contrary to predictions, despite numerous studies reporting that buffalo avoid areas of increased human activity (e.g., Metzger et al. 2010, Ogutu et al. 2014, Gaynor 2019). Thus, buffalo in

Pafuri are likely bottom-up regulated with temporal responses to these drivers augmented by seasonal variations in temperature.

Warthogs avoided predators temporally but not spatially (cf. Thaker et al. 2011). The predominantly diurnal activity patterns in both seasons could reflect antipredator behaviour (e.g., Tambling et al. 2015), but likely reflects an evolved diel pattern to facilitate thermoregulation (i.e., avoiding lower nocturnal temperatures; Skinner & Chimimba 2005). The lack of spatial responses by warthogs to season- and habitat-specific predation and perceived predation risks (cf. Thaker et al. 2011) were surprising given their high susceptibility to predation (see Hayward 2006, Hayward et al. 2006) and inability to employ temporal responses owing to thermoregulatory constraints. Contrary to predation and predation risks, warthog increased occupancy further from boundaries, likely to reduce anthropogenic threats associated with bushmeat poaching, as predicted. Thus, anthropogenic top-down factors and temporal variations in predation risk/temperatures are likely modulating the effects of bottom-up drivers impacting warthog activity and space-use in Pafuri.

Zebra displayed temporal and spatial responses to predation threats by avoiding peak periods of predator activity and decreasing occupancy in habitats with higher vegetation density, as predicted. Although spotted hyaena (Hayward 2006) and leopard (Hayward et al. 2006) tend to avoid zebra, it is plausible that zebra are displaying spatial and temporal avoidance of habitats and periods they perceive as risky in both seasons (e.g., Fischhoff et al. 2007, Reta & Solomon 2014, Creel et al. 2014), reflecting a landscape of fear (Laundré et al. 2001). Zebra space-use was also regulated by top-down, anthropogenic factors with the species increasing occupancy further from boundaries and roads across all habitat types, as predicted. Contrary to Malherbe *et al*. (2021), zebra appear to avoid roads in Pafuri, likely owing to perceived risks attributed to vehicles and human activity (Leblond et al. 2013), and reductions in habitat quality and connectivity (Teixeira et al. 2020). Similarly, zebra appear to avoid boundaries likely owing to increased bushmeat poaching (SANParks unpublished data 2022). In contrast, zebra increased occupancy closer to habitation (specifically in LRF), suggesting that the species are habituated to high levels of anthropogenic activity synonymous with areas of human habitation and may not perceive these as risky (Mason 1990, Jackson et al. 2017, Malherbe et al. 2021), contrary to predictions. Like elephant, it is possible that zebra are attracted to areas of human habitation as these offer increased protection from poaching, enhanced by the presence of guests and security (Beier & Loe 1992). Alternatively, zebra could be attracted to habitation as these offer improved foraging opportunities and access to water irrespective of season (Rimaze et al. 2020). Overall, zebra could be shifting activity and space-use to avoid periods and habitats of increased perceived predation risks with responses to these drivers being further augmented by top-down anthropogenic drivers.

c. Mixed feeders

Impala avoided peak periods of predator activity – as predicted – but increased occupancy in habitats with higher predator occupancy and perceived predation risks in the wet season, contrary to predictions. Thus, impala appear to favour temporal responses over spatial responses to limit predation risks in the wet season. Mixed feeders (including impala) should be able to avoid predators spatially in the wet season owing to increased foraging opportunities (Chapter 4) relative to the dry season (e.g., Thaker et al. 2011, Gaynor 2019, Davies et al. 2021). Irrespective, impala occupancy in the wet season is likely bottom-up regulated. In contrast, impala exhibited temporal and spatial responses by avoiding peak periods of predator activity and decreasing occupancy in habitats with higher predation and perceived predation risks in the dry season. Contrary to the wet season, significant reductions in forage availability during the dry season (Chapter 4) forces herbivores to regularly exhibit riskier behaviour by increasing occupancy in habitats with increased foraging opportunities with higher predation risks (Owen-Smith 2015, Riginos 2015, Davies et al. 2021). However, my results contradict this with impala decreasing occupancy in habitats with higher predator occupancy and vegetation density in the dry season. Thus, impala are likely predominantly top-down regulated by predation and perceived predation risks in the dry season, reflecting a landscape of fear (Laundré et al. 2001). Moreover, impala space-use was also affected by top-down, anthropogenic factors with the species increasing occupancy further from boundaries – specifically in SAV – and from roads across all habitat types, as predicted. Impala appear to avoid boundaries owing to increased bushmeat poaching (e.g., Matandiko 2016). Contrary to Jackson *et al*. (2017), impala appear to avoid roads in Pafuri, owing to direct threats (see Leblond et al. 2013) and indirect threats (see Teixeira et al. 2020) that were highlighted previously. However, further fine-scale behavioural analyses are required to disentangle the effects of roads on impala space-use (see Mulero-Pázmány et al. 2016, Jackson et al. 2017). Finally, impala space-use was further driven by habitat-specific proximity to habitation, with the species increasing occupancy closer to areas of human habitation – specifically in LRF – contrary to predictions. Increased occupancy closer to habitation implies spatial attraction that may suggest that impala are habituated to areas of human habitation (see Mason 1990, Jackson et al. 2017, Malherbe et al. 2021). Alternatively, like elephants and zebra, impala may be attracted to habitats that offer improved foraging opportunities that coincidentally centre around areas of human habitation (e.g., Matandiko 2016). Overall, impala are likely bottom-up regulated in the wet season, and top-down regulated by predator occupancy and vegetation density in the dry season with responses to these drivers augmented by habitat-specific anthropogenic, top-down pressures.

As predicted, nyala avoided peak periods of predator activity in both seasons. However, nyala occupied habitats with increased predator occupancy and perceived predation risks, contrary to predictions. Thus, nyala appear to favour temporal responses over spatial responses to reduce the threat of predation. The ubiquitous lack of spatial avoidance by nyala to predation risks in addition to species-specific preferences for closed, woodland habitats (Chapter 4; Furstenburg 2016) and seasonal dietary shifts (Chapter 3; Van Rooyen 1992) suggests that nyala are likely tolerating increased predation threats in exchange for improved foraging opportunities. For example, nyala in Hluhluwe-iMfolozi Park occurred more frequently in habitats with higher lion encounter risk where forage was abundant, suggesting that the species prioritized forage acquisition over predator avoidance (Davies et al. 2021). Further, anthropogenic factors influenced nyala space-use with occupancy increasing further from boundaries – as predicted – but decreasing further from roads across all habitat types, contrary to predictions. Decreased occupancy closer to boundaries implies spatial avoidance behaviour likely owing to increased poaching risks (e.g., Matandiko 2016). Alternatively, nyala occupied habitats with higher grass quality and shrub cover (Chapter 4) that occurred adjacent to perennial rivers located further from the park boundaries (Chapter 2). Thus, it is possible that the effects of boundaries are being somewhat masked by nyala habitat preferences which are likely responsible for regulating the observed occupancy patterns of the species. Contrary to boundaries, increased occupancy near roads implies spatial attraction behaviour suggestive of habituation by nyala to increased anthropogenic activity attributed to roads (e.g., Atickem et al. 2014). However, given that nyala are highly sensitive to increased human activity (Furstenburg 2016, Worku et al. 2021), an alternative explanation could be that nyala are tolerating greater human disturbances for improved foraging opportunities in optimum habitats that are coincidentally centred around roads (e.g., Matandiko 2016). Thus, to delineate the effects of roads on the occupancy patterns of nyala, behavioural responses to varying levels of anthropogenic activity linked to roads (see Mulero-Pázmány et al. 2016, Jackson et al. 2017) are required.

CONCLUSION

The findings of this Chapter follow on from the two preceding chapters wherein seasonal dietary analyses (Chapter 3), and the effects of bottom-up factors (i.e., forage quantity, quality, and water availability) on herbivore occupancy (Chapter 4), were evaluated. As in Chapter 4, herbivore responses to season- and habitat-specific predation risks (i.e., predator activity patterns, predator occupancy and vegetation density) and anthropogenic (i.e., proximity to roads, boundaries, and human habitation) top-down factors were species-specific, even amongst members of the same feeding guild. All herbivore species except common duiker (in both seasons) and buffalo (in the dry season) significantly avoided peak periods of predator activity in both seasons. Thus, both accessible (< 1600kg; Clements et al. 2014) and inaccessible (i.e., elephants) herbivores displayed temporal avoidance of predators, contrary to predictions. This may suggest a ubiquitous temporal response of all herbivores to predators or alternatively other factors may be driving shifts in activity pattens between seasons. Although significant differences in herbivore and predator activity may reflect temporal predator avoidance behaviour (Ridout & Linkie 2009, Laundre et al. 2010, Kuijper et al. 2014), larger herbivores (i.e., buffalo and elephant) which are least at risk of predation from spotted hyaena (Hayward 2006) and leopard (Hayward et al. 2006) are likely altering activity patterns seasonally to reduce thermal stress attributed to foraging during periods of increased diurnal ambient temperatures (Owen-Smith & Goodall 2014).. Except for impala in the dry season, kudu in wet season and in LRF, and zebra across all habitat-types, space-use by accessible herbivores was largely unaffected by season- and habitat-specific predation and perceived predation risks, contrary to predictions. However, the limited number of predator detections, resulting in estimated predator occupancies with high confidence intervals that did not differ significantly spatially and temporally, could be masking the effects of predation risk driving herbivore space-use and activity patterns. Thus, it is possible that there may be a degree of uncertainty surrounding the influence of predation driving herbivores in Pafuri, requiring further investigation. Unlike predator occupancy and predation risk, both accessible and inaccessible herbivores spatially avoided anthropogenic pressures (i.e., proximity to roads, boundaries, and human habitation). Like antipredator responses, the direct and indirect effects attributed to increased anthropogenic activity have driven herbivores to develop learned behavioural responses to reduce risks associated with humans (Everatt et al. 2015, Vinks et al. 2020). As predicted, accessible (except buffalo and nyala) and inaccessible herbivores occupied habitats further from roads. All herbivores (except elephant and buffalo) avoided boundaries, presumably due to increased poaching risks which were concentrated along the boundaries of the park (SANParks unpublished data 2022). Alternatively, the direct predatory impacts of poaching may have caused an edge effect resulting in population declines for accessible herbivores in habitats along the reserve boundaries (Matandiko 2016). Finally, elephant, impala, and zebra increased occupancy near areas of human habitation implying spatial attraction behaviour (Malherbe et al. 2021), contrary to predictions. It is possible that herbivores are attracted to human habitation as these offer refuge from poaching (see Vinks et al. 2020). Alternatively, herbivores could be occupying optimum habitats that offer improved foraging opportunities that are coincidentally centred around areas of human habitation (e.g., Matandiko 2016). Overall, herbivores exhibited temporal partitioning to avoid peak periods of predator activity (e.g., common duiker, kudu, warthog, impala and nyala) or limit thermal stress (e.g., elephant, buffalo, and zebra) with predation and perceived predation risks eliciting minimal spatial responses from both accessible and inaccessible herbivore species. In contrast, spatial occupancy of accessible and inaccessible herbivores is likely bottom-up, resource regulated (Chapter 4) with responses to these drivers augmented predominantly by top-down anthropogenic factors and, to a lesser extent, predation risks.

Chapter 6: Synthesis

Modelling the drivers of herbivore communities is not a trivial task given the myriad of potential bottom-up and top-down drivers, and the interactions between the two, as well as the species-specific variations in intrinsic functional traits (e.g., feeding strategy, body size, metabolic rate, thermoregulation, osmoregulation, etc.) which interact with competition and habitat requirements, influencing herbivore responses (e.g., social structure, space-use, activity patterns, antipredator responses, etc.) to these drivers (Bailey et al. 1996, Cromsigt & Olff 2006, Hopcraft et al. 2010, O'Kane & Macdonald 2018, Young et al. 2020). Consequently, few studies have attempted to model both bottom-up and top-down drivers in structuring herbivore communities, particularly in an African context with predator-prey guilds including multiple species, exposed to high-levels of human activity (Gandiwa 2013a, Dorresteijn et al. 2015, Matandiko 2016). Therefore, I attempted to disentangle both bottom-up and top-down effects on herbivores by analysing them separately via the use of a subset of drivers. In this Chapter, I will discuss the relative importance and possible interactions between bottom-up and top-down factors regulating the herbivore community in Pafuri, KNP, using a conceptual, graphical model (Figures 6.1 , 6.2, and 6.3).

First, I focussed on delineating herbivore feeding guilds using a stable carbon isotope approach (Chapter 3). Although most species within the herbivore community fell within the predefined feeding guilds (e.g., Gagnon & Chew 2000, Sponheimer et al. 2003, Codron et al. 2007) across both the wet and dry seasons, kudu, nyala and elephants displayed previously undocumented seasonal shifts between feeding guilds. Kudu (predefined browser) and nyala (predefined mixed feeder) significantly increased their grass intake in the wet season and were thus classified as mixed feeders in the wet season and as browsers in the dry season. Elephants shifted from browsers in the wet season to mixed feeders that fed on high proportions of browse forage in the dry season. These seasonal shifts in resource use indicates that species may display previously undocumented levels of dietary flexibility and select forage outside of their documented feeding preferences. Such seasonal dietary flexibility may reflect either behavioural plasticity to changes in forage quality and availability owing to, amongst others, climate change (Abraham et al. 2019, Carla Staver & Hempson 2020) or an "emergency response" to periods of limited preferred forage availability (Abraham et al. 2019, Rosenblatt 2021). Alternatively, competition for resources (Sinclair 1985), as well as variations in threats posed by predators (Owen-Smith 2019) and humans (Maibeche et al. 2015) across multiple spatiotemporal scales may be causative factors driving seasonal dietary shifts of herbivore populations. Irrespective of the mechanism, species with broader diets, capable of exhibiting seasonal shifts in diet (i.e., generalists) can potentially achieve higher population abundances than specialist species incapable of displaying dietary shifts, particularly in variable savanna environments (Armstrong & Mcgehee 1980, Abrams 2006) where climate change has the potential to impact the quantity and reliability of forage production, quality of forage, and the availability of water (Giridhar & Samireddypalle 2015, Kupika et al. 2018).

Thereafter, I showed that neither season nor habitat significantly influenced the spatial occupancy of each guild. It is possible that the ubiquitous lack of habitat-specific and seasonal shifts in guild occupancy may reflect an actual response, but this is not the case, as I documented several species-specific bottom-up (Chapter 4) and top-down (Chapter 5) factors regulating herbivore space-use and activity patterns. The contrasting responses at the guild- and species-level highlights that using a guild-level approach to delineate bottom-up and top-down structuring of herbivore communities masks fine-scale, species-specific responses to individual bottom-up and top-down factors. This is not surprising, given the tremendous variations in body size, metabolism, species-specific densities and feeding strategies among species within these feeding guilds (Thompson 1988, Davies et al. 2016a, Rhoades et al. 2018).

DRIVERS OF HERBIVORE ACTIVITY PATTERNS AND SPACE-USE

Herbivores vary their activity patterns and space-use to facilitate resource acquisition and maximise energetic gains, while simultaneously limiting predation and anthropogenic risks (i.e., optimal foraging and habitat selection theories; MacArthur & Pianka 1966, Rosenzweig 1981). The spatiotemporal responses of the herbivore community in Pafuri to bottom-up and top-down factors varied interspecifically. Contrary to literature (e.g., Owen-Smith & Mills 2006), I found little evidence to support the hypothesis that herbivores, irrespective of body size and feeding strategy, explicitly occupy habitats to facilitate resource acquisition (i.e., bottom-up regulated control; Figures 6.1, 6.2, and 6.3). Instead, predation and/or anthropogenic top-down factors are modulating the impacts of bottom-up factors driving the activity patterns and space-use of herbivores (varying in body size) in Pafuri.

a. Browsers

Seasonal shifts in occupancy by common duiker from closed, woodland habitats with higher shrub and tree cover in the wet season, to open habitats with higher grass cover in the dry season (Chapter 4) correspond with slight seasonal increases in graze intake (13% grass) in the dry season (Chapter 3). Further, despite being highly selective feeders requiring high-quality browse (Codron et al. 2007a, Furstenburg 2008), common duiker decreased occupancy in habitat patches (particularly in SAV) with higher quality browse in the dry season. It is likely that seasonal decreases in the availability and quality of browse across habitat types in the dry season (Chapter 4) is driving increased levels of interspecific competition among herbivores varying in body size (Kleynhans et al. 2011), with larger-, bulk feeders (i.e., kudu) competitively displacing medium-, selective feeders (i.e., common duiker) from habitats that offer optimum foraging opportunities in terms of availability and quality of forage (Prins et al. 2006, De Iongh et al. 2011, Prins 2016). Moreover, seasonal shifts in space-use (Chapter 4) that correspond with slight seasonal dietary shifts (Chapter 3) suggests that common duiker may exhibit spatial and dietary niche partitioning in the dry season to limit competition for resources with larger herbivores. However, given the unreliability of quantifying competitive interactions among species using camera trap data alone (Caravaggi et al. 2017), future studies should evaluate interspecific patterns of dietary, temporal, and spatial niche overlap and partitioning to delineate competitive interactions for resources among herbivore species (Dohn et al. 2013, Terborgh 2015, Prins 2016). Despite their high susceptibility to predation (Hayward et al. 2006, Abu Baker & Brown 2014), common duiker displayed no temporal or spatial responses to predation and perceived predation risks (Chapter 5). Although surprising, it is important to note that few predators (i.e., n = 47) were detected during the study. The low number of predator detections resulted in estimated predator occupancies with large confidence intervals that did not significantly differ spatially or temporally. Consequently, there is a level of uncertainty surrounding the effects of predators driving herbivore space-use and should thus be treated with caution. Interestingly, common duiker occupied habitats further from roads implying spatial avoidance. It is possible that common duiker are avoiding roads owing to direct and perceived threats attributed to vehicles (Leblond et al. 2013), and reductions in habitat quality and connectivity (Teixeira et al. 2020), reflecting a human induced landscape of fear (Everatt et al. 2015, Vinks et al. 2020). However, fine-scale behavioural responses (i.e., vigilance, tolerance, flight responses, etc.) (Mulero-Pázmány et al. 2016, Jackson et al. 2017) need to be quantified to determine the effects of road proximity on herbivore space-use. Thus, although the effects of competition regulating space-use remain to be quantified, seasonal shifts in space-use suggest a bottom-up regulated effect by browse availability in the wet season, and a possible competition-regulated effect in the dry season with responses to these drivers augmented by the anthropogenic, top-down effects of roads (Figure 6.1).

The relative importance of top-down and bottom-up drivers for accessible browsers (i.e., kudu) varied between seasons. Kudu avoided predators through spatial and temporal shifts in the wet season (Chapter 5). Specifically, they shifted to more open habitat patches (particularly in LRF, Chapter 5), with lower shrub cover and increased grass quality (Chapter 4) in the wet season, coinciding with increased graze consumption leading to a mixed feeder dietary strategy (30% grass; Chapter 3) (Gagnon & Chew 2000, Codron et al. 2007a). However, in the dry season when grass availability and quality is less than browse availability and quality, kudu were predominantly browsers (Chapter 3), although they included a small proportion (2%) of grass in their diet (Chapter 3 and 4). This, despite kudu increasing occupancy in more open patches with higher quality graze (Chapter 4). In these open habitat patches, kudu do not avoid predators spatially, but shifted their activity patterns to avoid peak periods of predator activity temporally, reflecting a landscape of fear (Laundré et al. 2001). Unexpectedly and previously undocumented, this suggests that access to high quality graze in both seasons is likely constraining kudu's ability to avoid predators temporally and spatially. For example, bison herbivory were largely driven by a search for high quality forage and, to a lesser extent, the spatial distribution of wolves (Harvey & Fortin 2013). Further, kudu space-use was regulated by anthropogenic, top-down factors, occupying habitats further from roads, owing to the direct and perceived threats (Leblond et al. 2013, Teixeira et al. 2020) and habitat patches (particularly in SAV; Chapter 5) further from reserve boundaries. High levels of bushmeat poaching were recorded adjacent to the reserve boundaries (SANParks unpublished data 2022) owing to limited cross border control protocols prohibiting illegal incursions by people from Mozambique and Zimbabwe (Chapter 2). Consequently, perceived risks associated with boundaries have likely driven evolved behavioural adaptations resulting in herbivores avoiding reserve boundaries to reduce the direct predatory effects of poaching (Kimanzi et al. 2015, Matandiko 2016, Loveridge et al. 2020). Alternatively, the direct predatory impacts of poaching could have caused an edge effect driving herbivore population declines along the boundaries of the reserve (Chapter 5; Matandiko 2016). Overall, spatiotemporal variations in predation (i.e., predator occurrence) and perceived predation (i.e., vegetation density and predator activity) risks in conjunction with anthropogenic risks attributed to roads and boundaries, are modulating the effects of bottom-up factors (i.e., graze quality) regulating kudu activity patterns and occupancy in Pafuri (Figure 6.1).

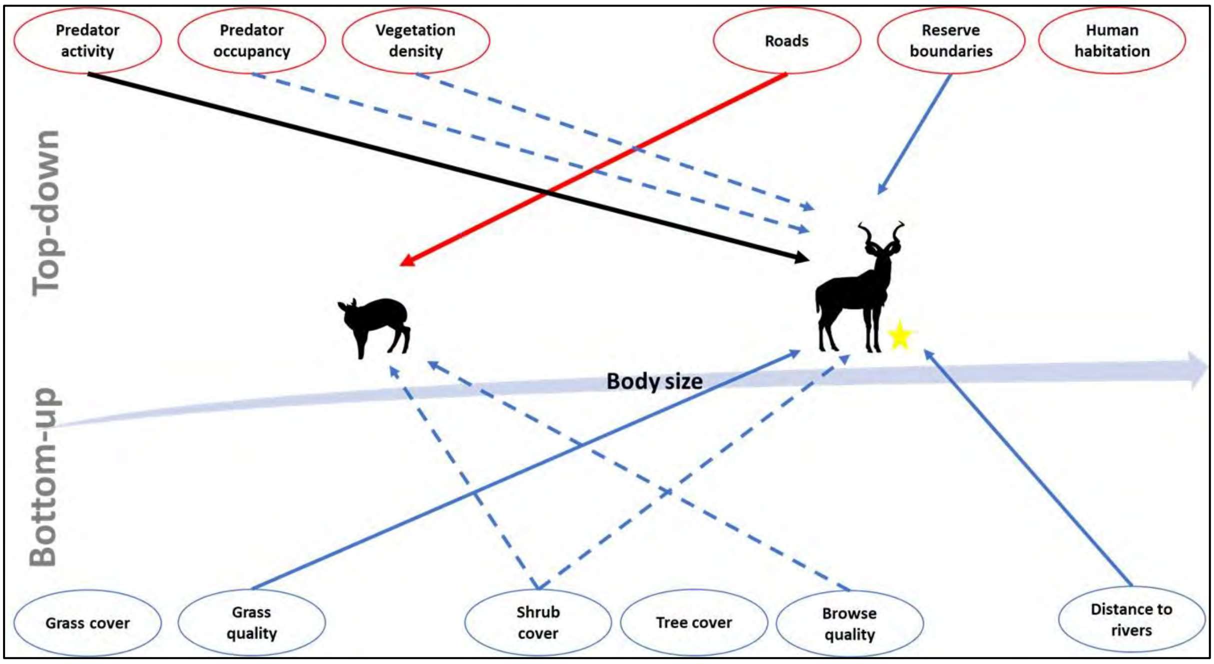


Figure 6.1: Bottom-up and top-down drivers regulating activity and space-use patterns of browser herbivores in Pafuri, KNP. Solid black lines represent temporal avoidance of peak predator activity. Solid and dashed lines represent directly and inversely proportional effects of drivers shaping herbivore space-use respectively, with blue lines depicting moderate

effects, and red lines, significant effects. Stars represent species that displayed seasonal feeding guild shifts.

b. Grazers

I could not identify any specific drivers for buffalo in the dry season, as none of the bottom-up (Chapter 4) nor top-down (Chapter 5) drivers significantly influenced buffalo occupancy and activity patterns. It is possible that declines in the quality and availability of graze attributed to grass senescence in the dry season (Owen-smith & Novellie 1982, Duru & Ducrocq 2000) could potentially be driving buffalo to migrate and occupy habitats with improved foraging opportunities beyond my study area. For example, buffalo travelled further and occupied habitats with higher graze availability and quality in the dry season, and conversely reduced their movements in the wet season, increasing occupancy near water sources (Ryan et al. 2006). However, I found that buffalo space-use in Pafuri was largely unaffected by the availability of water in both seasons (Chapter 4), despite their high water dependency (Ogutu et al. 2014, Young et al. 2020). However, perennial rivers were used as a proxy for water availability owing to a lack of spatial data on all available water sources in Pafuri. Consequently, it is likely that the effects of water driving herbivore space-use have been somewhat underestimated given that herbivores regularly drink from seasonal pans, dams, and non-perennial rivers (Young et al. 2020, Janecke 2021). Contrary to the dry season, buffalo occupied habitat patches with reduced tree cover (Chapter 4) and increased activity at sunrise (Chapter 5) in the wet season. This suggests that thermoregulatory constraints (see Veldhuis et al. 2019) may be an important driver for buffalo in the hot, wet season (Chapter 2). Here, they occupied open patches with reduced tree cover (and concomitant increased grass cover) – corresponding with their high graze intake (98% grasses; Chapter 3) – but predominantly utilized these habitat patches during the cooler times of the day (i.e., sunrise). Given their large body size which limits their predation risk but increases their susceptibility to thermal stress (Porter & Kearney 2009, Veldhuis et al. 2019), the activity patterns and space-use of buffalo in Pafuri is likely driven by a combination of spatiotemporal variations in graze availability and quality, water availability, and by thermal constraints (Figure 6.2).

Despite their highly selective grazer diets (Chapter 3; Edossa et al. 2021), space-use by warthogs was largely unaffected by graze quality and availability in both seasons (Chapter 4). However, graze quality was determined using above ground biomass (Chapter 4) whereas warthogs maximise energetic gains by regularly foraging on nutritious roots, rhizomes, bulbs and forbs (Sponheimer et al. 2003, Codron et al. 2007a) which were not analysed in this study. Thus, it is plausible that the effects of forage quality regulating warthog space-use could be underestimated, requiring further investigation. Warthogs avoided predators temporally by displaying predominantly diurnal activity in both seasons, but exhibited no spatial responses to predators (Chapter 5), despite their high susceptibility to predation from spotted hyaena (Hayward 2006) and leopard (Hayward et al. 2006). Diurnal activity could reflect antipredator behaviour (e.g., Tambling et al. 2015), or more likely an evolved behavioural adaptation to facilitate thermoregulation by avoiding lower nocturnal temperatures (Chapter 2; Skinner & Chimimba 2005). Thus, ecological trade-offs between thermal and predator tolerance needed to be quantified by evaluating the activity patterns of herbivores (varying in body size) to temperature variations in both the presence and absence of predators (Veldhuis et al. 2019). The lack of spatial responses by warthogs to predators was contrasted by the anthropogenic impacts of reserve boundaries (Chapter 5), driving warthogs to decrease occupancy near boundaries plausibly owing to increased mortality risks associated with high levels of bushmeat poaching (SANParks unpublished data 2022; Appendix Figure 5.2) (e.g., Kimanzi et al. 2015). Thus, the anthropogenic effects of reserve boundaries and lower nocturnal temperatures impacting thermoregulation are likely modulating bottom-up effects driving warthog activity patterns and space-use in Pafuri (Figure 6.2).

Zebra occupied open habitat patches (Chapter 5) with higher grass cover near rivers (Chapter 4). Increased occupancy in habitat patches with higher grass cover corresponds with high intakes of graze by zebra in both seasons (Chapter 3) which is required to maintain the high metabolic demands of bulk foragers such as zebra (Okello et al. 2002, de Vos et al. 2020). Moreover, the high water dependency of zebra (Western 1975, Young et al. 2020) supports increased occupancy by the species in habitat patches (particularly SAV) near rivers. Despite their reduced predation susceptibility (Hayward 2006, Hayward et al. 2006), zebra responded temporally but not spatially to predators (Chapter 5) by avoiding peak periods of predator activity in both seasons, reflecting a landscape of fear (Laundré et al. 2001). Contrary to the spatial effects of predators, zebra occupied habitats further from reserve boundaries and roads, owing to the likely risks that were previously highlighted (e.g., common duiker, kudu, and warthogs), but increased occupancy near areas of human habitation synonymous with high human activity (Chapter 5), implying spatial attraction. It is possible that zebra are attracted to areas of human habitation as these offer protection from poachers enhanced by the presence of guests and security (Beier & Loe 1992) and/or improved foraging opportunities and access to water irrespective of season (Rimaze et al. 2020). Thus, zebra appear to favour temporal responses to avoid predators which reflect in their activity patterns, whereas space-use is predominantly regulated by graze and water availability with responses to these drivers augmented by anthropogenic risks synonymous with roads and boundaries, and by the possible refuge and/or improved access to resources synonymous with areas of human habitation (Figure 6.2).

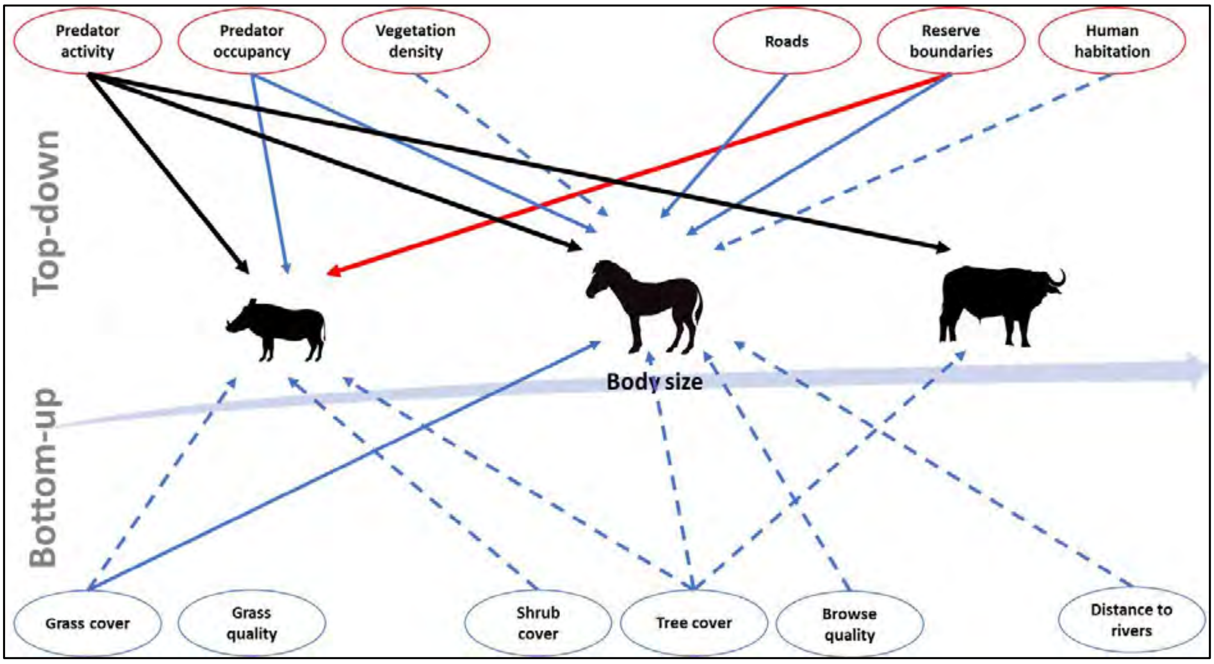


Figure 6.2: Bottom-up and top-down drivers regulating activity and space-use patterns of grazer herbivores in Pafuri, KNP. Solid black lines represent temporal avoidance of peak predator activity. Solid and dashed lines represent directly and inversely proportional effects of drivers shaping herbivore space-use respectively, with blue lines depicting moderate effects, and red lines, significant effects.

c. Mixed feeders

I could not discern any season specific bottom-up or top-down drivers of elephant space-use. However, across habitat types, elephants occupied open patches with limited shrub and tree cover and higher graze quality (specifically in LRB; Chapter 4) near areas of human habitation (Chapter 5). Although decreased occupancy in open habitat patches with reduced browse cover does not correspond with high proportions of browse intake by elephants in both seasons (Chapter 3), grasses occur at lower densities than shrubs and trees in LRB (Chapter 4) which could explain the slightly higher graze intake (19% grasses) by elephants (specifically in the dry season), leading to their mixed feeder classification (see Codron et al. 2007a) during the same period. Like zebra, increased occupancy by elephants in habitat patches near habitation implies spatial attraction, likely owing to the perceived safety from poaching attributed to high levels of human activity synonymous with areas of human habitation (e.g., Vinks et al. 2020) and/or the locations of habitation that may coincidentally occur in optimum habitats offering high quality forage and permanent water (e.g., Rimaze et al. 2020). Elephants were cathemeral in both seasons, but increased activity after sunset in the wet season, and around midday in the dry season (Chapter 5). Although elephants significantly avoided peak periods of predator activity in both seasons, elephants are largely free from predation in southern Africa (Valeix et al. 2008, Valenta et al. 2021), particularly in Pafuri as no lions were detected (Chapter 5). Thus, the activity patterns of elephant are likely driven by behavioural adaptations to limit thermal stress resulting in a perceived landscape of heat (Sears et al. 2016, Veldhuis et al. 2019), rather than a landscape of fear (Laundré et al. 2001). Overall, habitat-specific forage availability and quality is likely driving elephant space-use in the Pafuri with activity patterns being regulated by seasonal variations in temperature impacting the ability of elephant to thermoregulate (Figure 6.3).

Impala were regulated by both bottom-up and top-down drivers; the effects of which varied spatiotemporally. In the wet season, impala avoided predators temporally but not spatially, avoiding peak periods of predator activity, but increasing occupancy in habitats with higher predation risks (Chapter 5). Further, impala increased occupancy in habitats with higher quality graze (Chapter 4) and increased their intake of grasses in the wet season (Chapter 3). In contrast, impala responded temporally and spatially to predators in the dry season by avoiding periods and habitats with higher predation and perceived predation risks (Chapter 5) and increasing occupancy in open habitats with lower shrub cover (Chapter 4). This, despite including a higher proportion of browse in their diet in the dry season (Chapter 3). However, at the habitat-specific scale, impala increased occupancy in habitat patches with higher shrub (specifically in LRB and LRF; Chapter 4), which likely corresponds with the higher proportions of browse intake (57%) by impala in the dry season. Irrespective, it appears as if impala's ability to acquire forage is constrained by their ability to avoid predators spatially and temporally in the dry season. Further, impala occupied habitat patches further from reserve boundaries (specifically in SAV; e.g., Matandiko 2016) and roads (e.g., Mulero-Pázmány et al. 2016), near areas of human habitation (specifically in LRF; e.g., Matandiko 2016, Vinks et al. 2020) (Chapter 5). Thus, impala are likely bottom-up regulated in the wet season, with spatial responses to grass quality augmented by top-down anthropogenic pressures (i.e., boundaries, roads, and habitation), and temporal variations in predator activity. In contrast, the effects of spatial and temporal variations in predation and anthropogenic risks are likely modulating the impacts of shrub cover driving impala activity patterns and space-use in the dry season (Figure 6.3).

Nyala responded temporally but not spatially to predators by avoiding peak predator activity in both seasons (Chapter 5). Contrary to the lack of spatial responses to predators, nyala occupied habitat patches (specifically in LRF and SAV) with higher quality graze in the wet season (Chapter 4) – corresponding with increased grass intake (Chapter 3) – and increased occupancy in habitat patches (specifically in LRB and LRF) with higher shrub cover in the dry season – corresponding with high proportions of browse intake. In line with optimal foraging (MacArthur & Pianka 1966) and habitat selection (Rosenzweig 1981) theories, nyala are likely trading spatial avoidance of predators for improved foraging opportunities in habitats with higher quality graze in the wet season, and higher browse availability in the dry season – corresponding with seasonal dietary shifts (e.g., Davies et al. 2021). Moreover, anthropogenic factors regulated nyala space-use, driving the species to occupy habitats near roads and further from reserve boundaries (Chapter 5). Although it is possible that high poaching risks could be driving spatial avoidance by nyala to boundaries (e.g., Matandiko 2016), nyala occupied habitats with higher graze quality and shrub cover (Chapter 4) near rivers located further from the reserve boundaries (Chapter 2), suggesting that the effects of boundaries on nyala space-use could be masked by species-specific habitat preferences (e.g., Furstenburg 2016). Further, it is likely that nyala are not attracted to roads per se but rather to habitats that offer improved foraging opportunities that coincidentally occur near roads (Chapter 5; e.g., Matandiko 2016). Thus, similar to boundaries, it is possible that species-specific habitat preferences are likely masking fine-scale behavioural responses (see Mulero-Pázmány et al. 2016, Jackson et al. 2017) by nyala to anthropogenic pressures synonymous with roads. Irrespective, nyala are likely bottom-up regulated by graze quality in the wet season, and by browse cover in the dry season, with responses to these drivers augmented by temporal variations in predator activity seasonally (Figure 6.3).

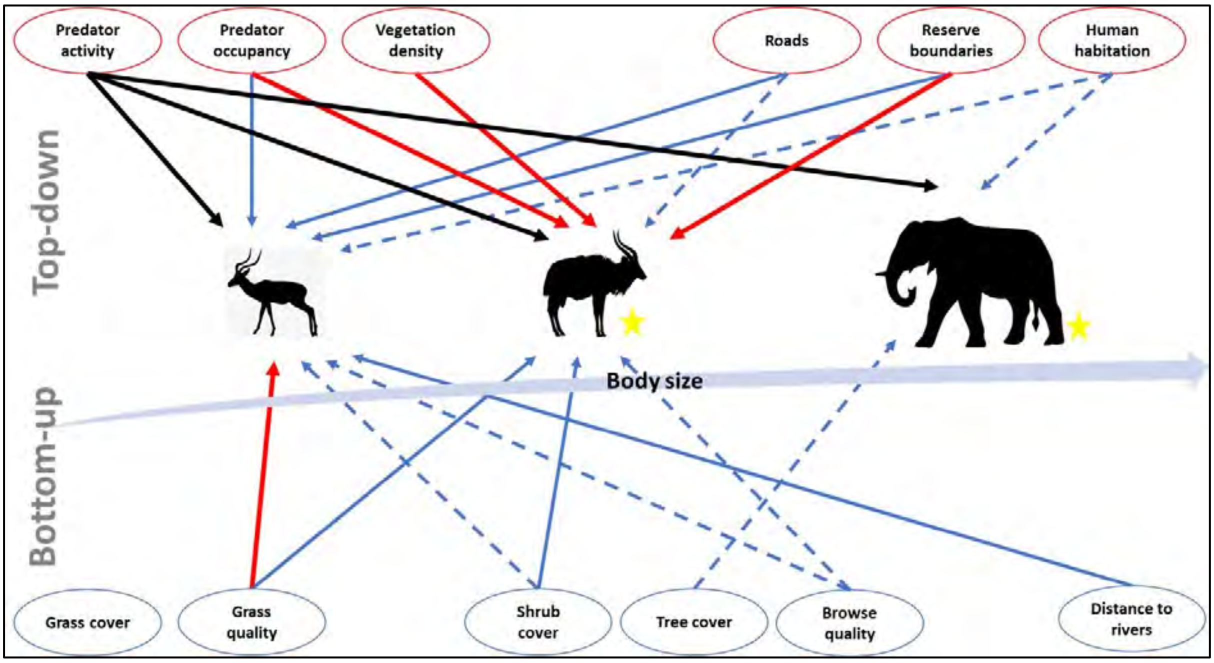


Figure 6.3: Bottom-up and top-down drivers regulating activity and space-use patterns of mixed feeder herbivores in Pafuri, KNP. Solid black lines represent temporal avoidance of peak predator activity. Solid and dashed lines represent directly and inversely proportional effects of drivers shaping herbivore space-use respectively, with blue lines depicting moderate effects, and red lines, significant effects. Stars represent species that displayed seasonal feeding guild shifts.

CONCLUSION

Climate change and habitat fragmentation attributed to the expansion of the human population poses a potentially devastating threat to biodiversity (Hetem et al. 2014, Osborne et al. 2018, Balfour et al. 2021). Current estimates predict that by 2050, Africa will be among the continents with the largest habitat and biodiversity losses (Visconti et al. 2011, Comley 2019). In this instance, conserving the high levels of biodiversity synonymous with South African protected areas is crucial for stemming the wide-spread and potentially irreversible impacts of human-mediated biodiversity losses. Protecting herbivore populations is vital for preserving ecosystem structure and function (Pringle et al. 2011, Balfour et al. 2021). However, the impacts of herbivores vary according to their space-use which is regulated by complex interactions between a myriad of bottom-up (i.e., forage and water) and top-down (i.e., predators and humans) drivers; the effects of which vary spatiotemporally (Bailey et al. 1996, Hopcraft et al. 2010, O’Kane & Macdonald 2018). As highlighted in my study, drivers of herbivore space-use varied interspecifically with varying body size and feeding strategies. Importantly, using Pafuri as a model system, I found that in savanna systems with high spatiotemporal variations in resources, relatively low densities of natural predators, and relatively high levels of human activity, pressures exerted by humans can surpass the effects of resources and natural predation risks, driving herbivores to occupy a resultant human induced landscape of fear. Therefore, while single species assessments remain important, quantifying the drivers of entire communities is vital to facilitate the proactive management of biodiversity in protected areas exposed to high levels of human activity throughout southern Africa.

REFERENCES

ABRAHAM, J. O., HEMPSON, G. P. & STAVER, A. C. 2019. Drought-response strategies of savanna herbivores. *Ecology and Evolution* 9:7047–7056.

ABRAMS, P. A. 2006. The Prerequisites for and Likelihood of Generalist-Specialist Coexistence. *The American Naturalist* 167:329.

ABU BAKER, M. A. & BROWN, J. S. 2014. Foraging and habitat use of common duikers, Sylvicapra grimmia, in a heterogeneous environment within the Soutpansberg, South Africa. *African Journal of Ecology* 52:318–327.

ADEOLA, A., ADEYEMO, A. & EJIDIKE, B. 2019. Population status and habitat preferences of common warthog (Phacochoerus africanus) in Kainji Lake National Park, Niger State Nigeria. *Journal of Research in Forestry, Wildlife and Environment* 11:64–69.

AGHA, M., BATTER, T., BOLAS, E. C., COLLINS, A. C., GOMES DA ROCHA, D., MONTEZA-MORENO, C. M., PRECKLER-QUISQUATER, S. & SOLLMANN, R. 2018. A review of wildlife camera trapping trends across Africa. *African Journal of Ecology* 56:694–701.

ALLEN, M. L., SIBARANI, M. C. & KROFEL, M. 2021. Predicting preferred prey of Sumatran tigers Panthera tigris sumatrae via spatio-temporal overlap. *Oryx* 55:197–203.

ANDERS NILSSON, P. 2001. Predator Behaviour and Prey Density: Evaluating Density-Dependent Intraspecific Interactions on Predator Functional Responses. *Journal of Animal Ecology* 70:14–19.

ANDERSON, T. M., WHITE, S., DAVIS, B., ERHARDT, R., PALMER, M., SWANSON, A., KOSMALA, M. & PACKER, C. 2016. The spatial distribution of African savannah herbivores: species associations and habitat occupancy in a landscape context. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150314.

ANNEAR, E., MINNIE, L., ANDREW, K. & KERLEY, G. I. H. 2023. Can smaller predators expand their prey base through killing juveniles? The influence of prey demography and season on prey selection for cheetahs and lions. *Oecologia* 201:649–660.

ARMSTRONG, R. A. & MCGEHEE, R. 1980. Competitive Exclusion. *The American Naturalist* 115:151–170.

ATICKEM, A., LOE, L. E. & STENSETH, N. C. 2014. Individual heterogeneity in use of human shields by mountain nyala. *Ethology* 120:715–725.

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* 49:386–400.

BALFOUR, N. J., DURRANT, R., ELY, A. & SANDOM, C. J. 2021. People, nature and large herbivores in a shared landscape: A mixed-method study of the ecological and social outcomes from agriculture and conservation. *People and Nature* 3:418–430.

BARBEHENN, R. V., CHEN, Z., KAROWE, D. N. & SPICKARD, A. 2004. C3 grasses have higher nutritional quality than C4 grasses under ambient and elevated atmospheric CO2. *Global Change Biology* 10:1565–1575.

BASTILLE-ROUSSEAU, G., WALL, J., DOUGLAS-HAMILTON, I., LESOWAPIR, B., LOLOJU, B., MWANGI, N. & WITTEMYER, G. 2020. Landscape-scale habitat response of African elephants shows strong selection for foraging opportunities in a human dominated ecosystem. *Ecography* 43:149–160.

BECKER, M., MCROBB, R., WATSON, F., DROGE, E., KANYEMBO, B., MURDOCH, J. & KAKUMBI, C. 2013. Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation* 158:26–36.

VAN BEEST, F. M., RIVRUD, I. M., LOE, L. E., MILNER, J. M. & MYSTERUD, A. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology* 80:771–785.

BEIER, P. & LOE, S. 1992. In my experience: A checklist for evaluating impacts to wildlife movement corridors. *Wildlife Society Bulletin* 20:434–440.

BEN-DAVID, M. & FLAHERTY, E. A. 2012. Stable isotopes in mammalian research: A beginner's guide. *Journal of Mammalogy* 93:312–328.

BEZUIDENHOUT, H. 2009. The classification, mapping and description of the vegetation of the Rooipoort Nature Reserve, Northern Cape, South Africa. *Koedoe* 51:1–12.

BHOLA, N., OGUTU, J. O., SAID, M. Y., PIEPHO, H. P. & OLFF, H. 2012. The distribution of large herbivore hotspots in relation to environmental and anthropogenic correlates in the Mara region of Kenya. *Journal of Animal Ecology* 81:1268–1287.

BLAND, L. ., KEITH, D. ., MURRAY, N. . & RODRIGUEZ, J. . 2015. Guidelines for the application of IUCN red list of ecosystem categories and criteria. Gland, Switzerland. 104 pp.

BORON, V., DEERE, N. J., XOFIS, P., LINK, A., QUIÑONES-GUERRERO, A., PAYAN, E. & TZANOPOULOS, J. 2019. Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological Conservation* 232:108–116.

BOTHA, M. S. & STOCK, W. D. 2005. Stable isotope composition of faeces as an indicator of seasonal diet selection in wild herbivores in southern Africa. *South African Journal of Science* 101:371–374.

BROWN, J. S., LAUNDRÉ, J. W. & GURUNG, M. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385–399.

BUBNICKI, J. W., CHURSKI, M., SCHMIDT, K., DISERENS, T. A. & KUIJPER, D. P. J. 2019. Linking spatial patterns of terrestrial herbivore community structure to trophic interactions.

eLife 8:e44937.

BURKEPILE, D. E., BURNS, C. E., TAMBLING, C. J., AMENDOLA, E., BUIS, G. M., GOVENDER, N., NELSON, V., THOMPSON, D. I., ZINN, A. D. & SMITH, M. D. 2013. Habitat selection by large herbivores in a southern African savanna: The relative roles of bottom-up and top-down forces. *Ecosphere* 4:1–19.

BURTON-ROBERTS, R., CORDES, L. S., SLOTOW, R., VANAK, A. T., THAKER, M., GOVENDER, N. & SHANNON, G. 2022. Seasonal range fidelity of a megaherbivore in response to environmental change. *Scientific Reports* 12:1–12.

VAN BUSKIRK, J. & YUREWICZ, K. L. 1998. Effects of predators on prey growth rate: relative contribution of thinning and reduced activity. *Oikos* 82:20–28.

CAIN, J. W., OWEN-SMITH, N., MACANDZA, V. A., OWEN-SMITH, N. & MACANDZA, V. A. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology* 286:58–67.

CANTER, K. 2008. Habitat use by ungulate in Thanda Private Game Reserve, KwaZulu-Natal. University of KwaZulu-Natal. 89 pp.

CARAVAGGI, A., BANKS, P. B., BURTON, A. C., FINLAY, C. M. V., HASWELL, P. M., HAYWARD, M. W., ROWCLIFFE, M. J. & WOOD, M. D. 2017. A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation* 3:109–122.

CERLING, T. E. & HARRIS, J. M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347–363.

CERLING, T. E., HARRIS, J. M. & PASSEY, B. H. 2003. Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* 84:456–470.

CERLING, T. E., HART, J. A. & HART, T. B. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138:5–12.

CERLING, T. E., WITTEMYER, G., RASMUSSEN, H. B., VOLLRATH, F., CERLING, C. E., ROBINSON, T. J. & DOUGLAS-HAMILTON, I. 2006. Stable isotopes in elephant hair document migration patterns and diet changes. *Proceedings of the National Academy of Sciences of the United States of America* 103:371–373.

CHAMAILLÉ-JAMMES, S., VALEIX, M. & CROMSIGT, J. 2019. Predator Effects on Herbivore Dynamics and Behavior. Pp. 279–308 *Savanna Woody Plants and Large Herbivores*. Wiley.

CHEN, L., XIAO, W. & XIAO, Z. 2019. Limitations of relative abundance indices calculated from camera-trapping data. *Biodiversity Science* 27:243–248.

CHEN, M., BAI, Z., WANG, Q. & SHI, Z. 2021. Habitat quality effect and driving mechanism of land use transitions: A case study of henan water source area of the middle route of the south-to-north water transfer project. *Land* 10:796.

CHINOMONA, R. R., GANDIWA, E., MUPOSHI, V. K., MUBOKO, N. & MOYO, M. S. 2018. Forage preference of the greater kudu (Tragelaphus strepsiceros) in a miombo woodland adjacent to Umfurudzi Park, Zimbabwe. *Cogent Environmental Science* 4:1–8.

CHIRIMA, G. J., OWEN-SMITH, N. & ERASMUS, B. F. N. 2012. Changing distributions of larger ungulates in the Kruger National Park from ecological aerial survey data. *Koedoe* 54:1–11.

CHIUTSI, S. & SAARINEN, J. 2017. Local participation in transfrontier tourism: Case of Sengwe community in Great Limpopo Transfrontier Conservation Area, Zimbabwe. *Development Southern Africa* 34:260–275.

CHOMBA, C. & MATANDIKO, W. 2011. Population status of black and white rhinos in

Zambia. *Pachyderm* 50:50–55.

CLEMENTS, H. S., TAMBLING, C. J., HAYWARD, M. W. & KERLEY, G. I. H. 2014. An objective approach to determining the weight ranges of prey preferred by and accessible to the five large African carnivores. *PLoS ONE* 9:e0101054.

CLEMENTS, H. S., TAMBLING, C. J. & KERLEY, G. I. H. 2016. Prey morphology and predator sociality drive predator prey preferences. *Journal of Mammalogy* 97:919–927.

CODRON, D., CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R. & FOURIE, N. 2007a. Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology* 273:21–29.

CODRON, D., CODRON, J., SPONHEIMER, M., LEE-THORP, J. A., ROBINSON, T., GRANT, C. C. & DE RUITER, D. 2005. Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces. *Koedoe* 48:115–124.

CODRON, D., LEE-THORP, J. A., SPONHEIMER, M. & CODRON, J. 2007b. Stable carbon isotope reconstruction of ungulate diet changes through the. *South African Journal of Wildlife Research* 37:117–125.

CODRON, D., LEE-THORP, J. A., SPONHEIMER, M. & CODRON, J. 2007c. Nutritional content of savanna plant foods: Implications for browser/grazer models of ungulate diversification. *European Journal of Wildlife Research* 53:100–111.

CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., CODRON, D., GRANT, R. C. & DE RUITER, D. J. 2006. Elephant (Loxodonta Africana) diets in Kruger National Park, South Africa: Spatial and landscape differences. *Journal of Mammalogy* 87:27–34.

COE, M. J., CUMMING, D. H. & PHILLIPSON, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22:341–354.

COFFIN, A. W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography* 15:396–406.

COLLINS, S. L. & SMITH, M. D. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87:2058–2067.

COMLEY, J. 2019. CARNIVORE INTRA-GUILD COMPETITION IN SELATI GAME RESERVE , LIMPOPO PROVINCE , SOUTH AFRICA by. Rhodes University. 222 pp.

COMLEY, J., JOUBERT, C. J., MGQATSA, N. & PARKER, D. M. 2020. Lions do not change rivers: Complex African savannas preclude top-down forcing by large carnivores. *Journal for Nature Conservation* 56:125844.

CONNELL, A. F. O., TALANCY, N. W., BAILEY, L. L., SAUER, J. R., GILBERT, A. T. & CAROLINA, N. 2006. Estimating Site Occupancy and Detection Probability Parameters for Meso- And Large Mammals in a Coastal Ecosystem. *The Journal of Wildlife Management* 70:1625–1633.

COPLEN, T. B. 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid Communications in Mass Spectrometry* 25:2538–2560.

CRAINE, J. M., BROOKSHIRE, E. N. J., CRAMER, M. D., HASSELQUIST, N. J., KOBA, K., MARIN-SPIOTTA, E. & WANG, L. 2015. Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant and Soil* 396:1–26.

CREEL, S. & CHRISTIANSON, D. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23:194–201.

CREEL, S., DRÖGE, E., M’SOKA, J., SMIT, D., BECKER, M., CHRISTIANSON, D. & SCHUETTE, P. 2017. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. *Ecology* 98:2081–2092.

CREEL, S., SCHUETTE, P. & CHRISTIANSON, D. 2014. Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology* 25:773–784.

CROMSIGT, J. P. G. M. & OLFF, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology* 87:1532–1541.

DANGAL, S. R. S., TIAN, H., LU, C., REN, W., PAN, S., YANG, J., DI COSMO, N. & HESSL, A. 2017. Integrating Herbivore Population Dynamics Into a Global Land Biosphere Model: Plugging Animals Into the Earth System. *Journal of Advances in Modeling Earth Systems* 9:2920–2945.

DAVIES, A. B., CROMSIGT, J. P. G. M., TAMBLING, C. J., LE ROUX, E., VAUGHN, N., DRUCE, D. J., MARNEWECK, D. G. & ASNER, G. P. 2021. Environmental controls on African herbivore responses to landscapes of fear. *Oikos* 130:171–186.

DAVIES, A. B., VAN RENSBURG, B. J., ROBERTSON, M. P., LEVICK, S. R., ASNER, G. P. & PARR, C. L. 2016a. Seasonal variation in the relative dominance of herbivore guilds in an African savanna. *Ecology* 97:1618–1624.

DAVIES, A. B., TAMBLING, C. J., KERLEY, G. I. H. & ASNER, G. P. 2016b. Limited spatial response to direct predation risk by African herbivores following predator reintroduction. *Ecology and Evolution* 6:5728–5748.

DAVIS, R. S., GENTLE, L. K., MGOOLA, W. O., STONE, E. L., UZAL, A. & YARNELL, R. W. 2022. Habitat structure and the presence of large carnivores shapes the site use of an understudied small carnivore: caracal ecology in a miombo woodland. *Mammal Research*. Springer Berlin Heidelberg.

DAVIS, R. S., YARNELL, R. W., GENTLE, L. K., UZAL, A., MGOOLA, W. O. & STONE, E. L. 2021. Prey availability and intraguild competition regulate the spatiotemporal dynamics of a modified large carnivore guild. *Ecology and Evolution* 11:7890–7904.

DEACON, A. 2007. RIS for Makuleke Wetlands. *Information Sheet on Ramsar Wetlands* 7:1–8.

DEVARAJAN, K., MORELLI, T. L. & TENAN, S. 2020. Multi-species occupancy models: review, roadmap, and recommendations. *Ecography* 43:1612–1624.

VAN DEVENTER, A. & SHRADER, A. M. 2021. Predation risk and herd position influence the proportional use of antipredator and social vigilance by impala. *Animal Behaviour* 172:9–16.

DJAGOUN, C. A. M. S., CODRON, D., SEALY, J., MENSAH, G. A. & SINSIN, B. 2013. Stable carbon isotope analysis of the diets of West African bovids in Pendjari Biosphere Reserve, Northern Benin. *African Journal of Wildlife Research* 43:33–43.

DLAMINI, T. B., REILLY, B. K., THOMPSON, D. I., BURKEPILE, D. E., BOTHA, J. M. & REBELO, A. G. 2020. Differential herbivore occupancy of fire-manipulated savannas in the satara region of the Kruger National Park, South Africa. *Koedoe* 62:1–8.

DOHN, J., DEMBÉLÉ, F., KAREMBÉ, M., MOUSTAKAS, A., AMÉVOR, K. A. & HANAN, N. P. 2013. Tree effects on grass growth in savannas: Competition, facilitation and the stress-gradient hypothesis. *Journal of Ecology* 101:202–209.

DORRESTEIJN, I., SCHULTNER, J., NIMMO, D. G., FISCHER, J., HANSPACH, J., KUEMMERLE, T., KEHOE, L. & RITCHIE, E. G. 2015. Incorporating anthropogenic effects into trophic ecology: Predator - Prey interactions in a human-dominated landscape. *Proceedings of the Royal Society B: Biological Sciences* 282:20151602.

DOSER, J. W., LEUENBERGER, W., SILLETT, T. S., HALLWORTH, M. T. & ZIPKIN, E. F. 2022. Integrated community occupancy models: A framework to assess occurrence and biodiversity dynamics using multiple data sources. *Methods in Ecology and Evolution* 13:919–932.

DROUILLY, M., CLARK, A. & O'RIAIN, M. J. 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally. *Biological Conservation* 224:16–25.

DURU, M. & DUCROCQ, H. 2000. Growth and senescence of the successive grass leaves on a tiller. Ontogenic development and effect of temperature. *Annals of Botany* 85:635–643.

EBERHARDT, L. L. & THOMAS, J. M. 1991. Designing Environmental Field Studies. *Ecological Monographs* 61:53–73.

EDOSSA, A., BEKELE, A. & DEBELLA, H. J. 2021. Diet preferences of common warthogs (Phacochoerus africanus) in Gassi and Haro Aba Diko controlled hunting areas, Western Ethiopia. *Global Ecology and Conservation* 29:e01722.

EDOSSA, A., BEKELE, A. & DEBELLA, H. J. 2022. Population density and distribution of common warthog (Phacochoerus africanus Gmelin, 1788) in Dabena Valley Forest, Western Ethiopia. *African Journal of Ecology* 60:386–397.

EHLERS SMITH, Y. C., EHLERS SMITH, D. A., RAMESH, T. & DOWNS, C. T. 2019. Novel predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species. *Behavioural Processes* 159:9–22.

ESTES, J. A., TERBORGH, J., BRASHARES, J. S., POWER, M. E., BERGER, J., BOND, W. J., CARPENTER, S. R., ESSINGTON, T. E., HOLT, R. D., JACKSON, J. B. C., MARQUIS, R. J., OKSANEN, L., OKSANEN, T., PAINE, R. T., PIKITCH, E. K., RIPPLE, W. J., SANDIN, S. A., SCHEFFER, M., SCHOENER, T. W., SHURIN, J. B., SINCLAIR, A. R. E., SOULÉ, M. E., VIRTANEN, R. & WARDLE, D. A. 2011. Trophic downgrading of planet earth. *Science* 333:301–306.

EVERATT, K. T., ANDRESEN, L. & SOMERS, M. J. 2015. The influence of prey, pastoralism and poaching on the hierarchical use of habitat by an apex predator. *African Journal of Wildlife Research* 45:187–196.

EVERATT, K. T., KOKES, R. & LOPEZ PEREIRA, C. 2019a. Evidence of a further emerging threat to lion conservation; targeted poaching for body parts. *Biodiversity and Conservation* 28:4099–4114.

EVERATT, K. T., MOORE, J. F. & KERLEY, G. I. H. 2019b. Africa's apex predator, the lion, is limited by interference and exploitative competition with humans. *Global Ecology and Conservation* 20:e00758.

FERREIRA, S. M. & FUNSTON, P. 2020. African lion and spotted hyaena changes in Kruger National Park, South Africa. *African Studies Quarterly* 19:37–50.

FERREIRA, S. M. & VILJOEN, P. 2022. African large carnivore population. *African Journal of Wildlife Research* 52:1–11.

FIELD, C. R. 1970. Observations on the Food Habits of Tame Warthog and Antelope in Uganda. *African Journal of Ecology* 8:1–17.

FISCHHOFF, I. R., SUNDARESAN, S. R., CORDINGLEY, J. & RUBENSTEIN, D. I. 2007. Habitat use and movements of plains zebra (Equus burchelli) in response to predation danger from lions. *Behavioral Ecology* 18:725–729.

FRYXELL, J. M., MDUMA, S., MASOY, J., SINCLAIR, A. R. E., HOPCRAFT, G. J. C. & PACKER, C. 2022. Stabilizing effects of group formation by Serengeti herbivores on predator-prey dynamics. *Frontiers in Ecology and Evolution* 10:1–9.

FURSTENBURG, D. 2005. The Greater Kudu (Tragelaphus strepsiceros). Pp. 147–168 in Martini, L. (ed.). *Intensive wildlife procution in southern Africa* (1st edition). Van Schaik Publishers, Pretoria.

FURSTENBURG, D. 2008. Focus on the common/grey duiker (Sylvicapra grimmia). *SA Hunter*

11022:38–41.

FURSTENBURG, D. 2016. Tragelaphus angasii – Nyala. Pp. 1–14 *The new game rancher* (1st edition). Briza Publications, Pretoria.

FURSTENBURG, D., KLEYNHANS, M. & BARNARD, H. J. 2000. Integrated kudu, duiker, bushbuck and boer goat production systems in Valley Bushveld: ecological interactions, processes & constraints. *Pelea* 19:134–141.

GAGNON, M. & CHEW, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy* 81:490–511.

GANDIWA, E. 2013a. Top-down and bottom-up control of large herbivore populations: A review of natural and human-induced influences. *Tropical Conservation Science* 6:493–505.

GANDIWA, E. 2013b. Vegetation factors influencing density and distribution of wild large herbivores in a southern African savannah. *African Journal of Ecology* 52:274–283.

GAYNOR, K. M. 2019. Spatial and temporal responses of animals to landscape heterogeneity, predation risk, and human activity. University of California, Berkeley. 1–173 pp.

GAYNOR, K. M., BROWN, J. S., MIDDLETON, A. D., POWER, M. E. & BRASHARES, J. S. 2019. Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends in Ecology and Evolution* 34:355–368.

GELMAN, A., RUBIN, D. B., GELMAN, A. & RUBIN, D. B. 1992. Inference from Iterative Simulation Using Multiple Sequences Linked references are available on JSTOR for this article : Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science* 7:457–472.

GEORGIADIS, N., HACK, M. & TURPIN, K. 2003. The influence of rainfall on zebra population dynamics: implications for management. *Journal of Applied Ecology* 40:125–136.

GIRIDHAR, K. & SAMIREDDYPALLE, A. 2015. Impact of Climate Change on Forage Availability for Livestock. Pp. 97–112 *Climate Change Impact on Livestock: Adaptation and Mitigation*. Springer India, New Delhi.

GITTLEMAN, J. L. 1985. Carnivore body size: Ecological and taxonomic correlates. *Oecologia* 67:540–554.

GOOSEM, M. 2000. Effects of tropical rainforest roads on small mammals: edge changes in community composition. *Wildlife Research* 27:151.

GORDON, I. J., HESTER, A. J. & FESTA-BIANCHET, M. 2004. The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology* 41:1021–1031.

GRANGE, S. & DUNCAN, P. 2006. Bottom-up and top-down processes in African ungulate communities: Resources and predation acting on the relative abundance of zebra and grazing bovids. *Ecography* 29:899–907.

GRAY, S. S., SIMPSON, T. R., BACCUS, J. T., MANNING, R. W. & SCHWERTNER, T. W. 2007. Seasonal diet and foraging preference of greater kudu Tragelaphus strepsiceros in the Llano Uplift of Texas. *Wildlife Biology* 13:75–83.

GRIPENBERG, S. & ROSLIN, T. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos* 116:181–188.

GUILLERA-ARROITA, G. 2011. Impact of sampling with replacement in occupancy studies with spatial replication. *Methods in Ecology and Evolution* 2:401–406.

HANSEN, R. M., MUGAMBI, M. . & BAUNI, S. M. 1985. Diets and Trophic Ranking of Ungulates of the Northern Serengeti. *The Journal of Wildlife Management* 49:823–829.

HARVEY, L. & FORTIN, D. 2013. Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in wolf country. *PloS one* 8:1–8.

HATTERSLEY, P. & ROKSANDIC, Z. 1983. δ13C values of C3 and C4 species of Australian Neurachne and its allies (Poaceae). *Australian Journal of Botany* 31:317–321.

HAVARUA, Z., TURNER, W. C. & MFUNE, J. K. E. 2014. Seasonal variation in foraging behaviour of plains zebra (Equus quagga) may alter contact with the anthrax bacterium (Bacillus anthracis). *Canadian Journal of Zoology* 92:331–337.

HAYWARD, M. W. 2006. Prey preferences of the spotted hyaena (Crocuta crocuta) and degree of dietary overlap with the lion (Panthera leo). *Journal of Zoology* 270:606–614.

HAYWARD, M. W. & HAYWARD, M. D. 2012. Waterhole use by African fauna. *African Journal of Wildlife Research* 42:117–127.

HAYWARD, M. W., HENSCHEL, P., O'BRIEN, J., HOFMEYR, M., BALME, G. & KERLEY, G. I. H. 2006. Prey preferences of the leopard (Panthera pardus). *Journal of Zoology* 270:298–313.

HEBBLEWHITE, M. & MERRILL, E. H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454.

HEMPSON, G. P., ARCHIBALD, S. & BOND, W. J. 2015. A continent-wide assessment of the form and intensity of large mammal herbivory in Africa. *Science* 350:1056–1061.

HETEM, R. S., FULLER, A., MALONEY, S. K. & MITCHELL, D. 2014. Responses of large mammals to climate change. *Temperature* 1:115–127.

HILL, J. E., DEVAULT, T. L. & BELANT, J. L. 2019. Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography* 28:680–689.

HOLECHECK, J. L., VAVRA, M. & PIEPER, R. D. 1982. Methods for Determining the Nutritive Quality of Range Ruminant Diets: a Review. *Journal of Animal Science* 54:363–376.

HOOGENDOORN, G., KELSO, C. & SINTHUMULE, I. 2019. Tourism in the Great Limpopo Transfrontier Park: A review. *African Journal of Hospitality, Tourism and Leisure* 8.

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* 81:201–213.

HOPCRAFT, J. G. C., OLFF, H. & SINCLAIR, A. R. E. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25:119–128.

ILLIUS, A. W. & GORDON, I. J. 1992. Modelling the nutritional ecology of ungulate herbivores: evolution of body size and competitive interactions. *Oecologia* 89:428–434.

DE IONGH, H. H., DE JONG, C. B., VAN GOETHEM, J., KLOP, E., BRUNSTING, A. M. H., LOTH, P. E. & PRINS, H. H. T. 2011. Resource partitioning among African savanna herbivores in North Cameroon: The importance of diet composition, food quality and body mass. *Journal of Tropical Ecology* 27:503–513.

IRANZO, E. C., WITTMER, H. U., TRABA, J., ACEBES, P., MATA, C. & MALO, J. E. 2018. Predator occurrence and perceived predation risk determine grouping behavior in guanaco (Lama guanicoe). *Ethology* 124:281–289.

JACHMANN, H. 2002. Comparison of aerial counts with ground counts for large African herbivores. *Journal of Applied Ecology* 39:841–852.

JACKSON, C. R., FOSSØY, F., RØSKAFT, E. & MAY, R. 2017. Do impala really avoid tourist roads? A response to Mulero-Pázmány, D’Amico & González-Suárez (2016). *Journal of Zoology* 302:219–223.

JANECKE, B. B. 2021. Mammal species richness at a catena and nearby waterholes during a drought, kruger national park, South Africa. *Diversity* 13:387.

JANECKE, B. B. & SMIT, G. N. 2015. Faecal nitrogen of browser and mixed feeder game species during different seasons. *African Journal of Range and Forage Science* 32:203–212.

JEDRZEJEWSKA, B. & JEDRZEJEWSKI, W. 2005. Large carnivores and ungulates in European temperate forest ecosystems: bottom-up and top-down control. Pp. 230–246 in Ray, J., Redford, K., Steneck, R. & Berger, J. (eds.). *Large carnivores and the conservation of biodiversity*. Island Press, Washington DC.

JOUBERT, S. 2007. *The Kruger National Park: A History, Volume 3* (3rd edition). High Branching. 224–226 pp.

KAPLAN, D. & LEE, C. 2018. Optimizing Prediction Using Bayesian Model Averaging: Examples Using Large-Scale Educational Assessments. *Evaluation Review* 42:423–457.

KARRANTH, K. & NICHOLS, J. 1998. Estimation of tiger densities in India using photographis captures and recaptures. *Ecology1* 79:2852–2862.

KASSAMBARA, A. & MUNDT, F. 2017. Factoextra: extract and visualize the results of multivariate data analyses. *R package version* 1:337–354.

KAWAMURA, K., YAMAURA, Y., SENZAKI, M., UETA, M. & NAKAMURA, F. 2019. Seasonality in spatial distribution: Climate and land use have contrasting effects on the species richness of breeding and wintering birds. *Ecology and Evolution* 9:7549–7561.

KAYS, R., ARBOGAST, B. S., BAKER-WHATTON, M., BEIRNE, C., BOONE, H. M., BOWLER, M., BURNEO, S. F., COVE, M. V., DING, P., ESPINOSA, S., GONÇALVES, A. L. S., HANSEN, C. P., JANSEN, P. A., KOLOWSKI, J. M., KNOWLES, T. W., LIMA, M. G. M., MILLSPAUGH, J., MCSHEA, W. J., PACIFICI, K., PARSONS, A. W., PEASE, B. S., ROVERO, F., SANTOS, F., SCHUTTLER, S. G., SHEIL, D., SI, X., SNIDER, M. & SPIRONELLO, W. R. 2020. An empirical evaluation of camera trap study design: How many, how long and when? *Methods in*

Ecology and Evolution 11:700–713.

KELLNER, K. F., FOWLER, N. L., PETROELJE, T. R., KAUTZ, T. M., BEYER, D. E. & BELANT, J. L. 2022. ubms: An R package for fitting hierarchical occupancy and N-mixture abundance models in a Bayesian framework. *Methods in Ecology and Evolution* 13:577–584.

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* 90:1–11.

KIMANZI, J. K., SANDERSON, R. A., RUSHTON, S. P. & MUGO, M. J. 2015. Spatial distribution of snares in Ruma National Park, Kenya, with implications for management of the roan antelope Hippotragus equinus langheldi and other wildlife. *Oryx* 49:295–302.

KLEYNHANS, E. J., JOLLES, A. E., BOS, M. R. E., OLFF, H., KLEYNHANS, E. J., JOLLES, A. E., BOS, M. R. E., OLFF, H., KLEYNHANS, E. J., JOLLES, A. E., BOS, M. R. E., OLFF, H., ECOLOGICAL, C. & STUDIES, E. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers Published by : Wiley on behalf of Nordic Society Oikos Stable URL : https://www.jstor.org/stable/29783548 Linked references are available on JSTOR for this 120:591–600.

KOS, M., HOETMER, A. J., PRETORIUS, Y., DE BOER, W. F., DE KNEGT, H., GRANT, C. C., KOHI, E., PAGE, B., PEEL, M., SLOTOW, R., VAN DER WAAL, C., VAN WIEREN, S. E., PRINS, H. H. T. & VAN LANGEVELDE, F. 2012. Seasonal diet changes in elephant and impala in mopane woodland. *European Journal of Wildlife Research* 58:279–287.

KOTTEK, M., GRIESER, J., BECK, C., RUDOLF, B. & RUBEL, F. 2006. World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15:259–263.

KUCERA, T. E. & BARRETT, R. 2011. A History of Camera Trapping. Pp. 9–26 in O’Connell, A.

F., Nichols, J. D. & Karanth, K. U. (eds.). *Camera Traps in Animal Ecology: Methods and Analyses* (1st edition). Springer Japan, Tokyo.

KUIJPER, D. P. J., VERWIJMEREN, M., CHURSKI, M., ZBYRYT, A., SCHMIDT, K., JEDRZEJEWSKA, B. & SMIT, C. 2014. What cues do ungulates use to assess predation risk in dense temperate forests? *PLoS ONE* 9:1–12.

KUPIKA, O. L., GANDIWA, E., KATIVU, S. & NHAMO, G. 2018. Impacts of Climate Change and Climate Variability on Wildlife Resources in Southern Africa: Experience from Selected Protected Areas in Zimbabwe. P. *Selected Studies in Biodiversity*. InTech.

LANDMAN, M. & KERLEY, G. I. H. 2001. Dietary shifts: do grazers become browsers in the Thicket Biome? *Koedoe* 44:31–36.

LASHLEY, M. A., COVE, M. V., CHITWOOD, M. C., PENIDO, G., GARDNER, B., DEPERNO, C. S. & MOORMAN, C. E. 2018. Estimating wildlife activity curves: Comparison of methods and sample size. *Scientific Reports* 8:1–11. Springer US.

LAUNDRÉ, J. W., HERNÁNDEZ, L. & ALTENDORF, K. B. 2001. Wolves, elk, and bison: reestablishing the ‘landscape of fear’ in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* 79:1401–1409.

LAUNDRE, J. W., HERNANDEZ, L. & RIPPLE, W. J. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal* 3:1–7.

LEBLOND, M., DUSSAULT, C. & OUELLET, J. P. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. *Journal of Zoology* 289:32–40.

LIKAS, A., VLASSIS, N. & J. VERBEEK, J. 2003. The global k-means clustering algorithm. *Pattern Recognition* 36:451–461.

LIMA, S. L. & BEDNEKOFF, P. A. 1999. Temporal Variation in Danger Drives Antipredator Behavior: The Predation Risk Allocation Hypothesis. *The American Naturalist* 153:649–

659.

LIMA, S. L. & DILL, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.

LINDSEY, P. A., BALME, G., BECKER, M., BEGG, C., BENTO, C., BOCCHINO, C., DICKMAN, A., DIGGLE, R. W., EVES, H., HENSCHEL, P., LEWIS, D., MARNEWICK, K., MATTHEUS, J., WELDON MCNUTT, J., MCROBB, R., MIDLANE, N., MILANZI, J., MORLEY, R., MURPHREE, M., OPYENE, V., PHADIMA, J., PURCHASE, G., RENTSCH, D., ROCHE, C., SHAW, J., WESTHUIZEN, H. VAN DER, VLIET, N. VAN & ZISADZA-GANDIWA, P. 2013. The bushmeat trade in African savannas: Impacts, drivers, and possible solutions. *Biological Conservation* 160:80–96.

LINKIE, M. & RIDOUT, M. S. 2011. Assessing tiger–prey interactions in Sumatran rainforests. *Journal of Zoology* 284:224–229.

LODBERG-HOLM, H. K., GELINK, H. W., HERTEL, A. G., SWENSON, J. E., DOMEVSCIK, M. & STEYAERT, S. M. J. G. 2019. A human-induced landscape of fear influences foraging behavior of brown bears. *Basic and Applied Ecology* 35:18–27.

LOVERIDGE, A. J., SOUSA, L. L., SEYMOUR-SMITH, J., HUNT, J., COALS, P., O'DONNELL, H., LINDSEY, P. A., MANDISODZA-CHIKEREMA, R. & MACDONALD, D. W. 2020. Evaluating the spatial intensity and demographic impacts of wire-snare bush-meat poaching on large carnivores. *Biological Conservation* 244:108504.

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* 34:113–121.

MACARTHUR, R. H. & PIANKA, E. R. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist* 100:603–609.

MACKENZIE, D. I., NICHOLS, J. D., ROYLE, J. A., POLLOCK, K. H., BAILEY, L. L. & HINES, J. E. 2017. Single-species, single-season occupancy models. Pp. 115–214 *Occupancy estimation and modelling: Inferring patterns and dynamics of species occurrence* (2nd edition). Elsevier.

MACKENZIE, D. I., NICHOLS, J. D., ROYLE, J. A., POLLOCK, K. H., BAILEY, L. L. & HINES, J. E. 2018. Basic Presence/Absence Situation. Pp. 115–215 *Occupancy Estimation and Modeling (Second edition)*. Elsevier.

MAIBECHE, Y., MOALI, A., YAHI, N. & MENARD, N. 2015. Is diet flexibility an adaptive life trait for relictual and peri-urban populations of the endangered primate Macaca sylvanus? *PLoS ONE* 10:1–22.

MALHERBE, M., MCINTYRE, T., HATTINGH, T. V., LERESCHE, P. M. & HAUSSMANN, N. S. 2021. Mammal road-type associations in Kruger National Park, South Africa: Common mammals do not avoid tar roads more than dirt roads. *Ecology and Evolution* 11:15622–15629.

MANDINYENYA, B., MONKS, N., MUNDY, P. J., SEBATA, A. & CHIRIMA, A. 2020. Habitat choices of African buffalo (Syncerus caffer) and plains zebra (Equus quagga) in a heterogeneous protected area. *Wildlife Research* 47:137–145.

MANDLATE, L. J. C. & RODRIGUES, F. H. G. 2020. Post-Release Monitoring Diet Quality and Nutritional Status of Reintroduced Burchell's Zebra and Blue Wildebeest in Maputo Special Reserve, Mozambique. *Tropical Conservation Science* 13.

MASON, D. R. 1990. Monitoring of sex and age ratios in ungulate populations of the Kruger National Park by ground survey. *Koedoe* 33:19–28.

MATANDIKO, W. 2016. Factors affecting the size and distribution of large herbivores in Kafue National Park, Zambia. Montana State University. 99 pp.

MBATHA, K. R. & WARD, D. 2010. The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. *Journal of Arid Environments* 74:1294–1301.

MCGILL, B. J., DORNELAS, M., GOTELLI, N. J. & MAGURRAN, A. E. 2015. Fifteen forms of biodiversity trend in the anthropocene. *Trends in Ecology and Evolution* 30:104–113.

MEEK, P. D., BALLARD, G. A., SPARKES, J., ROBINSON, M., NESBITT, B. & FLEMING, P. J. S. 2019. Camera trap theft and vandalism: occurrence, cost, prevention and implications for wildlife research and management. *Remote Sensing in Ecology and Conservation* 5:160–168.

MEREDITH, M. & RIDOUT, M. 2021. Overlap. R Core Development Team. *R project*:1–9.

METZGER, K. L., SINCLAIR, A. R. E., HILBORN, R., HOPCRAFT, J. G. C. & MDUMA, S. A. R. 2010. Evaluating the protection of wildlife in parks: The case of African buffalo in Serengeti. *Biodiversity and Conservation* 19:3431–3444.

MILLS, K. & HARRIS, N. 2020. Humans induce differential access to prey for large African carnivores. *eLife* 9:e60690.

MIRANDA, M., DALERUM, F. & PARRINI, F. 2014. Interaction patterns within a multi-herbivore assemblage derived from stable isotopes. *Ecological Complexity* 20:51–60.

MITCHELL, M. S. & POWELL, R. A. 2012. Foraging optimally for home ranges. *Journal of Mammalogy* 93:917–928.

MOLE, M. A., DÁRAUJO, S. R., VAN AARDE, R. J., MITCHELL, D. & FULLER, A. 2016. Coping with heat: Behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology* 4:1–11.

MRAMBA, R. P., ANDREASSEN, H. P., MLINGI, V. & SKARPE, C. 2019. Activity patterns of African elephants in nutrient-rich and nutrient-poor savannas. *Mammalian Biology*

94:18–24. Elsevier GmbH.

MUCINA, L. & RUTHERFORD, M. C. 2006. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia 19*:1–30.

MULERO-PÁZMÁNY, M., D'AMICO, M. & GONZÁLEZ-SUÁREZ, M. 2016. Ungulate behavioral responses to the heterogeneous road-network of a touristic protected area in Africa. *Journal of Zoology* 298:233–240.

MUNYATI, C. & SINTHUMULE, N. I. 2016. Change in woody cover at representative sites in the Kruger National Park, South Africa, based on historical imagery. *SpringerPlus* 5:1–23.

NEWMARK, W. D., BOSHE, J. I., SARIKO, H. I. & MAKUMBULE, G. K. 1996. Effects of a highway on large mammals in Mikumi National Park, Tanzania. *African Journal of Ecology* 34:15–31.

NGUYEN, T. V., WILTING, A., NIEDBALLA, J., NGUYEN, A., RAWSON, B. M., NGUYEN, A. Q. H., CAO, T. T., WEARN, O. R., DAO, A. C. & TILKER, A. 2022. Getting the big picture: Landscape-scale occupancy patterns of two Annamite endemics among multiple protected areas. *Conservation Science and Practice* 4:1–15.

NICHOLSON, K. L., MILLERET, C., MÅNSSON, J. & SAND, H. 2014. Testing the risk of predation hypothesis: The influence of recolonizing wolves on habitat use by moose. *Oecologia* 176:69–80.

NORTJÉ, G. P. 2018. Soils and soil form characteristics of the Makuleke Contractual Park, KNP. Pretoria. 1–9 pp.

NORTJÉ, G. P., VAN HOVEN, W. & LAKER, M. C. 2012. Factors affecting the impact of off-road driving on soils in an area in the Kruger National Park, South Africa. *Environmental Management* 50:1164–1176.

NUDDS, T. D. 2006. Quantifying the Vegetative Structure of Wildlife Cover. *Wildlife Society Bulletin* 5:113–117.

O'CONNELL, A. F., NICHOLS, J. D. & KARANTH, K. U. 2011. *Camera traps in animal ecology: Methods and analyses*. P. *Camera Traps in Animal Ecology: Methods and Analyses*. . 1–271 pp.

O'CONNOR, T. G. 1991. Influence of rainfall and grazing on the compositional change of the herbaceous layer of a sandveld savanna. *Journal of the Grassland Society of Southern Africa* 8:103–109.

O'KANE, C. A. J., DUFFY, K. J., PAGE, B. R. & MACDONALD, D. W. 2013. Effects of resource limitation on habitat usage by the browser guild in Hluhluwe-iMfolozi Park, South Africa. *Journal of Tropical Ecology* 29:39–47.

O'KANE, C. A. J. & MACDONALD, D. W. 2018. Seasonal influences on ungulate movement within a fenced South African reserve. *Journal of Tropical Ecology* 34:200–203.

OATES, B. A., MONTEITH, K. L., GOHEEN, J. R., MERKLE, J. A., FRALICK, G. L. & KAUFFMAN, M. J. 2021. Detecting Resource Limitation in a Large Herbivore Population Is Enhanced With Measures of Nutritional Condition. *Frontiers in Ecology and Evolution* 8:1–15.

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* 285:99–109.

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* 23:573–596.

OKELLO, M. M., WISHITEMI, R. E. L. & MUHORO, F. 2002. Forage intake rates and foraging efficiency of free-ranging zebra and impala. *African Journal of Wildlife Research* 32:93–100.

OLFF, H., RITCHIE, M. E. & PRINS, H. H. T. 2002. Global environmental controls of diversity in large herbivores. *Nature* 415:901–904.

OSBORNE, C. P., CHARLES-DOMINIQUE, T., STEVENS, N., BOND, W. J., MIDGLEY, G. & LEHMANN, C. E. R. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist* 220:10–24.

OWEN-SMITH, N. 1994. Foraging responses of kudus to seasonal changes in food resources: Elasticity in constraints. *Ecology* 75:1050–1062.

OWEN-SMITH, N. 2013. Contrasts in the large herbivore faunas of the southern continents in the late Pleistocene and the ecological implications for human origins. *Journal of Biogeography* 40:1215–1224.

OWEN-SMITH, N. 2015. Mechanisms of coexistence in diverse herbivore-carnivore assemblages: Demographic, temporal and spatial heterogeneities affecting prey vulnerability. *Oikos* 124:1417–1426.

OWEN-SMITH, N. 2019. Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological Conservation* 232:51–58. Elsevier.

OWEN-SMITH, N., HOPCRAFT, G., MORRISON, T., CHAMAILLÉ-JAMMES, S., HETEM, R., BENNITT, E. & VAN LANGEVELDE, F. 2020. Movement ecology of large herbivores in African savannas: current knowledge and gaps. *Mammal Review* 50:252–266.

OWEN-SMITH, N. & MILLS, M. G. L. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* 76:73–92.

OWEN-SMITH, N. & MILLS, M. G. L. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* 77:173–183.

OWEN-SMITH, N. & NOVELLIE, P. 1982. What Should a Clever Ungulate Eat ? *The American Naturalist* 119:151–178.

OWEN-SMITH, N. & COOPER, S. M. 1985. Comparative consumption of vegetation components by kudus, impalas and goats in relation to their commercial potential as browsers in savanna regions. *South African Journal of Science* 81:72–76.

OWEN-SMITH, N. & GOODALL, V. 2014. Coping with savanna seasonality: comparative daily activity patterns of African ungulates as revealed by GPS telemetry. *Journal of Zoology* 293:181–191.

PACIFICI, K., REICH, B. J., DORAZIO, R. M. & CONROY, M. J. 2016. Occupancy estimation for rare species using a spatially-adaptive sampling design. *Methods in Ecology and Evolution* 7:285–293.

PALMER, M. S. 2018. Survival in a landscape of fear: prey behavioral responses to predation risk across a gradient of time and space. University of Minnesota. 1–114 pp.

PALMER, M. S., SWANSON, A., KOSMALA, M., ARNOLD, T. & PACKER, C. 2018. Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology* 56:791–803.

PANEBIANCO, A., GREGORIO, P. F., SCHROEDER, N. M., MAROZZI, A., OVEJERO, R., HEIDEL, L., PEÑA, F., LEGGIERI, L. R., TARABORELLI, P. A. & CARMANCHAHI, P. D. 2022. Where are the males? The influence of bottom-up and top-down factors and sociability on the spatial distribution of a territorial ungulate. *Behavioral Ecology and Sociobiology* 76. Springer Berlin Heidelberg.

PERAL, C., LANDMAN, M. & KERLEY, G. I. H. 2022. The inappropriate use of time- - independence biases estimates of activity patterns of free- - ranging mammals derived from camera traps. *Ecology and*:1–10.

PERRIN, M. . & BRERETON-STILES, R. 1999. Habitat use and feeding behaviour of the buffalo and the white rhinoceros in the Hluhluwe-Umfolozi Game Reserve. *South African Journal of Wildlife Research* 29:72–80.

DU PLESSIS, K., GANSWINDT, S. B., BERTSCHINGER, H., CROSSEY, B., HENLEY, M. D., RAMAHLO, M. & GANSWINDT, A. 2021. Social and Seasonal Factors Contribute to Shifts in Male African Elephant (Loxodonta africana) Foraging and Activity Patterns in Kruger National Park, South Africa. *Animals* 11:3070.

PORTER, W. P. & KEARNEY, M. 2009. Size, shape, and the thermal niche of endotherms. *Proceedings of the National Academy of Sciences of the United States of America* 106:19666–19672.

POST, D. M. 2002. Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology* 83:703.

POTGIETER, T. & KERLEY, G. I. H. 2022. The zebra as a grazer: Selectivity for grass consumption differs as grass availability varies. *African Journal of Ecology* 60:818–823.

PRINGLE, R. M., PALMER, T. M., GOHEEN, J. R., MCCAULEY, D. J. & KEESING, F. 2011. Ecological Importance of Large Herbivores in the Ewaso Ecosystem. *Smithsonian Contributions to Zoology*:43–53.

PRINS, H. H. T. 2016. Interspecific Resource Competition in Antelopes: Search for Evidence. Pp. 51–77 in Bro-Jørgensen, J. & Mallon, D. P. (eds.). *Antelope Conservation: From Diagnosis to Action*. John Wiley and Sons.

PRINS, H. H. T., DE BOER, W. F., VAN OEVEREN, H., CORREIA, A., MAFUCA, J. & OLFF, H. 2006. Co-existence and niche segregation of three small bovid species in southern Mozambique. *African Journal of Ecology* 44:186–198.

PYKE, G. ., PULLIAM, H. . & CHARNOV, E. . 1977. Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology* 52:137–154.

R CORE DEVELOPMENT TEAM. 2021. R: A language and environment for statistical computing.

RAMOELO, A., SKIDMORE, A. K., SCHLERF, M., HEITKÖNIG, I. M. A., MATHIEU, R. & CHO, M. A. 2013. Savanna grass nitrogen to phosphorous ratio estimation using field spectroscopy and the potential for estimation with imaging spectroscopy. *International Journal of Applied Earth Observation and Geoinformation* 23:334–343.

RAMP, D., WILSON, V. K. & CROFT, D. B. 2006. Assessing the impacts of roads in peri-urban reserves: Road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. *Biological Conservation* 129:348–359.

RAYNOR, E. J., BEYER, H. L., BRIGGS, J. M. & JOERN, A. 2017. Complex variation in habitat selection strategies among individuals driven by extrinsic factors. *Ecology and Evolution* 7:1802–1822.

REDFERN, J. V., GRANT, C. C., GAYLARD, A. & GETZ, W. M. 2005. Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments* 63:406–424.

REID, H. 2018. Contractual National Parks and the Makuleke Community Author (s): Hannah Reid Published by : Springer Stable URL : http://www.jstor.org/stable/4603391 Contractual National Parks and the Makuleke Community 29:135–155.

RETA, R. & SOLOMON, Y. 2014. Diurnal activity patterns of Burchells zebra (Equus quagga, Gray 1824) in Yabello Wildlife Sanctuary, Southern Ethiopia. *International Journal of Biodiversity and Conservation* 6:616–623.

RHOADES, O. K., BEST, R. J. & STACHOWICZ, J. J. 2018. Assessing Feeding Preferences of a

Consumer Guild: Partitioning Variation Among versus Within Species. *The American Naturalist* 192:287–300.

RICH, L. N., MILLER, D. A. W. W., ROBINSON, H. S., MCNUTT, J. W. & KELLY, M. J. 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. *Journal of Applied Ecology* 53:1225–1235.

RIDOUT, M. S. & LINKIE, M. 2009. Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14:322–337.

RIGINOS, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* 84:124–133. Blackwell Publishing Ltd.

RIGINOS, C. & GRACE, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology* 89:2228–2238.

RIMAZE, D., MACHUMU, A., MREMI, R. & EUSTACE, A. 2020. Diversity and abundance of wild mammals between different accommodation facilities in the Kwakuchinja Wildlife Corridor, Tanzania. *Scientific African* 9:e00480.

RIPPLE, W. J., CHAPRON, G., LÓPEZ-BAO, J. V., DURANT, S. M., MACDONALD, D. W., LINDSEY, P. A., BENNETT, E. L., BESCHTA, R. L., BRUSKOTTER, J. T., CAMPOS-ARCEIZ, A., CORLETT, R. T., DARIMONT, C. T., DICKMAN, A. J., DIRZO, R., DUBLIN, H. T., ESTES, J. A., EVERATT, K. T., GALETTI, M., GOSWAMI, V. R., HAYWARD, M. W., HEDGES, S., HOFFMANN, M., HUNTER, L. T. B., KERLEY, G. I. H., LETNIC, M., LEVI, T., MAISELS, F., MORRISON, J. C., NELSON, M. P., NEWSOME, T. M., PAINTER, L., PRINGLE, R. M., SANDOM, C. J., TERBORGH, J., TREVES, A., VAN VALKENBURGH, B., VUCETICH, J. A., WIRSING, A. J., WALLACH, A. D., WOLF, C., WOODROFFE, R., YOUNG, H. & ZHANG, L. 2017. Conserving the world’s megafauna and biodiversity: The fierce urgency of now. *BioScience* 67:197–200.

RIPPLE, W. J., NEWSOME, T. M., WOLF, C., DIRZO, R., EVERATT, K. T., GALETTI, M., HAYWARD, M. W., KERLEY, G. I. H., LEVI, T., LINDSEY, P. A., MACDONALD, D. W., MALHI, Y., PAINTER, L. E., SANDOM, C. J., TERBORGH, J. & VAN VALKENBURGH, B. 2015. Collapse of the world's largest herbivores. *Science Advances* 1:e1400103.

ROBINS, S. & WAAL, K. VAN DER. 2008. 'Model Tribes' and Iconic Conservationists? The Makuleke Restitution Case in Kruger National Park. *Development and Change* 39:53–72.

LE ROEX, N., DREYER, C., VILJOEN, P., HOFMEYR, M. & FERREIRA, S. M. 2019. Seasonal space-use and resource limitation in free-ranging black rhino. *Mammalian Biology* 99:81–87.

VAN ROOYEN, A. F. 1992. Diets of impala and nyala in two game reserves in Natal, South Africa. *South African Journal of Wildlife Research* 22:98–101.

ROSENBLATT, A. E. 2021. Drought rewires an old field food web through shifts in plant nutrient content and herbivore feeding behaviors. *Climate Change Ecology* 2:100019.

ROSENZWEIG, M. L. 1981. A Theory of Habitat Selection. *Ecology* 62:327–335.

ROSSA, M., LOVARI, S. & FERRETTI, F. 2021. Spatiotemporal patterns of wolf, mesocarnivores and prey in a Mediterranean area. *Behavioral Ecology and Sociobiology* 75. Behavioral Ecology and Sociobiology.

ROWCLIFFE, J. M., FIELD, J., TURVEY, S. T. & CARBONE, C. 2008. Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45:1228–1236.

RUBLE, D. B., VERSCHUEREN, S., CRISTESCU, B. & MARKER, L. L. 2022. Rewilding Apex Predators Has Effects on Lower Trophic Levels: Cheetahs and Ungulates in a Woodland Savanna. *Animals* 12:1–10.

RUNGE, C. A., WITHEY, J. C., NAUGLE, D. E., FARGIONE, J. E., HELMSTEDT, K. J., LARSEN, A. E., MARTINUZZI, S. & TACK, J. D. 2019. Single species conservation as an umbrella for management of landscape threats. *PLoS ONE* 14:1–17.

RYAN, S. J., KNECHEL, C. . & GETZ, W. 2006. Range and Habitat Selection of African Buffalo in South Africa. *Journal of Wildlife Management* 70:764–776.

RYTWINSKI, T. & FAHRIG, L. 2015. The impacts of roads and traffic on terrestrial animal populations. Pp. 237–246 in van der Ree, R., Smith, D. & Grilo, C. (eds.). *Handbook of Road Ecology*. John Wiley and Sons.

SARMENTO, P. B., CRUZ, J. P., EIRA, C. I. & FONSECA, C. 2010. Habitat selection and abundance of common genets Genetta genetta using camera capture-mark-recapture data. *European Journal of Wildlife Research* 56:59–66.

SCHMITZ, O. J. 2008. Herbivory from Individuals to Ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 39:133–152.

SCHUETTE, P., CREEL, S. & CHRISTIANSON, D. 2016. Ungulate distributions in a rangeland with competitors, predators and pastoralists. *Journal of Applied Ecology* 53:1066–1077.

SCHULZE, R. E. & MCGEE, O. S. 1978. Climatic indices and classifications in relation to the biogeography of southern Africa. Pp. 19–52.

SEARLE, C. E., SMIT, J. B., CUSACK, J. J., STRAMPELLI, P., GRAU, A., MKUBURO, L., MACDONALD, D. W., LOVERIDGE, A. J. & DICKMAN, A. J. 2021. Temporal partitioning and spatiotemporal avoidance among large carnivores in a human-impacted African landscape. *PLoS ONE* 16:1–20.

SEARS, M. W., ANGILLETTA, M. J., SCHULER, M. S., BORCHERT, J., DILLIPLANE, K. F., STEGMAN, M., RUSCH, T. W. & MITCHELL, W. A. 2016. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences* 113:10595–10600.

SENSENIG, R. L., DEMMENT, M. W. & LACA, E. A. 2010. Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology* 91:2898–2907.

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* 54:1–20.

SEYDACK, A. H. W., VERMEULEN, W. J., KNOX, N., GOVENDER, N., SMIT, I. P. J., GRANT, R. C. & MACFADYEN, S. 2014. Forage Quality for Grazing Herbivores in a Semi- Arid Savanna System As Affected By Fire and Rainfall (Kruger National Park). 1–96 pp.

SHERIFF, M. J., PEACOR, S. D., HAWLENA, D. & THAKER, M. 2020. Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology* 89:1302–1316.

SHI, C., WEI, B., WEI, S., WANG, W., LIU, H. & LIU, J. 2021. A quantitative discriminant method of elbow point for the optimal number of clusters in clustering algorithm. *Eurasip Journal on Wireless Communications and Networking* 2021. Springer International Publishing.

SIEBERT, F., BREDENKAMP, G. J. & SIEBERT, S. J. 2003. A comparison of Mopaneveld vegetation in South Africa, Namibia and Zimbabwe. *Bothalia* 33:121–134.

SINCLAIR, A. R. E. 1985. Does Interspecific Competition or Predation Shape the African Ungulate Community? P. *Source: Journal of Animal Ecology*. . 899–918 pp.

SINCLAIR, A. R. E., MDUMA, S. & BRASHARES, J. S. 2003. Patterns of predation in a diverse predator–prey system. *Nature* 425:288–290.

SITATI, N., LEKISHON, K., BAKARI, S., WARINWA, F., MWIU, S. N., GICHOHI, N., BITOK, E., MWITA, M., IJA, H. K. & MUKEKA, J. 2014. Wildebeest (Connochaetes taurinus)

Population Densities and Distribution in Dry and Wet Season in the Kilimanjaro Landscape. *Natural Resources* 05:810–821.

SKARPE, C. 1992. Dynamics of savanna ecosystems. *Journal of Vegetation Science* 3:293–300.

SKINNER, J. D. & CHIMIMBA, C. T. 2005. *The Mammals of the Southern African Sub-region*. Cambridge University Press.

SLOBODKIN, L. B. 1960. Ecological Energy Relationships at the Population Level. *The American Naturalist* 94:213–236.

SMITH, F. A., ELLIOTT SMITH, E. A., VILLASEÑOR, A., TOMÉ, C. P., LYONS, S. K. & NEWSOME, S. D. 2022. Late Pleistocene megafauna extinction leads to missing pieces of ecological space in a North American mammal community. *Proceedings of the National Academy of Sciences of the United States of America* 119:1–11.

SMITH, J. A., GAYNOR, K. M. & SURACI, J. P. 2021. Mismatch Between Risk and Response May Amplify Lethal and Non-lethal Effects of Humans on Wild Animal Populations. *Frontiers in Ecology and Evolution* 9:1–13.

SPENCELEY, A. 2006. Tourism in the Great Limpopo Transfrontier Park. *Development Southern Africa* 23:649–667.

SPITZER, R., FELTON, A., LANDMAN, M., SINGH, N. J., WIDEMO, F. & CROMSIGT, J. P. G. M. 2020. Fifty years of European ungulate dietary studies: a synthesis. *Oikos* 129:1668–1680.

SPONHEIMER, M., LEE-THORP, J. A., DERUITER, D. J., SMITH, J. M., VAN DER MERWE, N. J., REED, K., GRANT, C. C., AYLIFFE, L. K., ROBINSON, T. F., HEIDELBERGER, C. & MARCUS, W. 2003. Diets of southern African Bovidae: Stable isotope evidence. *Journal of Mammalogy* 84:471–479.

STABACH, J. A., HUGHEY, L. F., CREGO, R. D., FLEMING, C. H., HOPCRAFT, J. G. C., LEIMGRUBER, P., MORRISON, T. A., OGUTU, J. O., REID, R. S., WORDEN, J. S. & BOONE, R. B. 2022. Increasing Anthropogenic Disturbance Restricts Wildebeest Movement Across East African Grazing Systems. *Frontiers in Ecology and Evolution* 10.

STARK, M. A. 1986. Daily movement, grazing activity and diet of savanna buffalo, Syncerus caffer brachyceros, in Benoue National Park, Cameroon. *African Journal of Ecology* 24:255–262.

STAVER, A. C. & HEMPSON, G. P. 2020. Seasonal dietary changes increase the abundances of savanna herbivore species. *Science Advances* 6:eabd2848.

STEENKAMP, P. J., HEERDEN, H. VAN & SCHALKWYK, O. L. VAN. 2013. Ecological Suitability Modelling for Anthrax in the Kruger National Park, South Africa. *PLoS One*:110.

STEINBEISER, C. M., KIOKO, J., MARESI, A., KAITILIA, R. & KIFFNER, C. 2019. Relative abundance and activity patterns explain method-related differences in mammalian species richness estimates. *Journal of Mammalogy* 100:192–201.

STYLES, C. V. & SKINNER, J. D. 2000. The influence of large mammalian herbivores on growth form and utilization of mopane trees, Colophospermum mopane , in Botswana’s Northern Tuli Game Reserve. *African Journal of Ecology* 38:95–101.

SUÁREZ-TANGIL, B. D. & RODRÍGUEZ, A. 2021. Uniform performance of mammal detection methods under contrasting environmental conditions in Mediterranean landscapes. *Ecosphere* 12:e03349.

SURACI, J. P., CLINCHY, M., ZANETTE, L. Y. & WILMERS, C. C. 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* 22:1578–1586.

TAMBLING, C. J., MINNIE, L., MEYER, J., FREEMAN, E. W., SANTYMIRE, R. M., ADENDORFF, J.

& KERLEY, G. I. H. 2015. Temporal shifts in activity of prey following large predator reintroductions. *Behavioral Ecology and Sociobiology* 69:1153–1161.

TEIXEIRA, F. Z., RYTWINSKI, T. & FAHRIG, L. 2020. Inference in road ecology research: what we know versus what we think we know. *Biology Letters* 16.

TERBORGH, J. W. 2015. Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences of the United States of America* 112:11415–11422.

THAKER, M., GUPTE, P. R., PRINS, H. H. T., SLOTOW, R. & VANAK, A. T. 2019. Fine-scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water. *Frontiers in Ecology and Evolution* 7:1–12.

THAKER, M., VANAK, A. T., OWEN, C. R., OGDEN, M. B. 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* 92:398–407.

THOMPSON, J. N. 1988. Variation in Interspecific Interactions. *Annual Review of Ecology and Systematics* 19:65–87.

TINLEY, K. 1981. The Northern Kruger National Park-an Ecological Inventory. *African Wildlife-Special* 35:6–23.

DU TOIT, J. T. 1995. Sexual segregation in kudu: sex differences in competitive ability, predation risk or nutritional needs? *South African Journal of Science* 25:127–132.

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* 87:889–898.

TROLLIET, F., HUYNEN, M. C., VERMEULEN, C. & HAMBUCKERS, A. 2014. Use of camera traps for wildlife studies. A review. *Biotechnologie, Agronomie, Société et Environnement* 18:446–454.

TURKINGTON, R. 2009. Top-down and bottom-up forces in mammalian herbivore - vegetation systems: An essay review. *Botany* 87:723–739.

UHR, J. & STEENKAMP, C. 2000. THE MAKULEKE LAND CLAIM : POWER RELATIONS AND COMMUNITY-BASED NATURAL RESOURCE MANAGEMENT Conrad Steenkamp. *Iied*:28.

VALEIX, A. M., LOVERIDGE, A. J., DAVIDSON, Z., MURINDAGOMO, F., MACDONALD, D. W., ECOLOGY, S., JAN, N., CHAMAILL, S., LYON, U. DE & MENDEL, B. G. 2009a. Behavioral Adjustments of African Herbivores to Predation Risk by Lions : Spatiotemporal Variations Influence Habitat Use Published by : Ecological Society of America Linked references are available on JSTOR for this article : You may need to log in to JS. *Ecology* 90:23–30.

VALEIX, M., FRITZ, H., MATSIKA, R., MATSVIMBO, F. & MADZIKANDA, H. 2008. The role of water abundance, thermoregulation, perceived predation risk and interference competition in water access by African herbivores. *African Journal of Ecology* 46:402–410.

VALEIX, M., LOVERIDGE, A. J., CHAMAILLÉ-JAMMES, S., DAVIDSON, Z., MURINDAGOMO, F., FRITZ, H. & MACDONALD, D. W. 2009b. Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology* 90:23–30.

VALENTA, K., SCHMITT, M. H., AYASSE, M. & NEVO, O. 2021. The sensory ecology of fear: African elephants show aversion to olfactory predator signals. *Conservation Science and Practice* 3:1–9.

VEHTARI, A., GELMAN, A. & GABRY, J. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432.

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* 22:1536–1546.

VENTER, F. J. 1986. Soil Patterns Associated with the Major Geological Units of the Kruger National Park.

VENTER, F. J. 1990. A Classification of Land for Management Planning in the Kruger National Park. University of South Africa.

VENTER, J. A. & WATSON, L. H. 2008. Feeding and habitat use of buffalo (Syncerus caffer caffer) in the Nama-Karoo, South Africa. *South African Journal of Wildlife Research* 38:42–51.

VESEY-FITZGERALD, D. F. 1974. Utilization of the grazing resources by buffaloes in the Arusha National Park, Tanzania. *African Journal of Ecology* 12:107–134.

VILELLA, M., FERRANDIZ-ROVIRA, M. & SAYOL, F. 2020. Coexistence of predators in time: Effects of season and prey availability on species activity within a Mediterranean carnivore guild. *Ecology and Evolution* 10:11408–11422.

VINKS, M. A., CREEL, S., SCHUETTE, P., ROSENBLATT, E., MATANDIKO, W., SANGUINETTI, C., BANDA, K., GOODHEART, B., BECKER, M., CHIFUNTE, C. & SIMUKONDA, C. 2020. Testing the effects of anthropogenic pressures on a diverse African herbivore community. *Ecosphere* 11.

VISCONTI, P., PRESSEY, R. L., GIORGINI, D., MAIORANO, L., BAKKENES, M., BOITANI, L., ALKEMADE, R., FALCUCCI, A., CHIOZZA, F. & RONDININI, C. 2011. Future hotspots of terrestrial mammal loss. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:2693–2702.

DE VOS, C., LESLIE, A. J. & RANSOM, J. I. 2020. Plains zebra (Equus quagga) behaviour in a restored population reveals seasonal resource limitations. *Applied Animal Behaviour*

Science 224.

WEARN, O. R. & GLOVER-KAPFER, P. 2019. Snap happy: Camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science* 6.

WELTI, E. A. R., PRATHER, R. M., SANDERS, N. J., DE BEURS, K. M. & KASPARI, M. 2020. Bottom-up when it is not top-down: Predators and plants control biomass of grassland arthropods. *Journal of Animal Ecology* 89:1286–1294.

WENDA, C., NAKAMURA, A. & ASHTON, L. A. 2023. Season and herbivore defence trait mediate tri-trophic interactions in tropical rainforest. *Journal of Animal Ecology* 92:466–476.

WESTERN, D. 1975. Water availability and its influence on the structure and dynamics of. *East African Wildlife Journal* 13:265–286.

WETERINGS, M. J. A., MOONEN, S., PRINS, H. H. T., VAN WIEREN, S. E. & VAN LANGEVELDE, F. 2018. Food quality and quantity are more important in explaining foraging of an intermediate-sized mammalian herbivore than predation risk or competition. *International Journal of Business Innovation and Research* 17:8419–8432.

WHITE, A. M. 2010. A pigheaded compromise: Do competition and predation explain variation in warthog group size? *Behavioral Ecology* 21:485–492.

WILLIAMS, H. F., BARTHOLOMEW, D. C., AMAKOBE, B. & GITHIRU, M. 2018. Environmental factors affecting the distribution of African elephants in the Kasigau wildlife corridor, SE Kenya. *African Journal of Ecology* 56:244–253.

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* 267:345–349.

WINNIE, J. & CREEL, S. 2017. The many effects of carnivores on their prey and their implications for trophic cascades, and ecosystem structure and function. *Food Webs* 12:88–94.

WITTEMYER, G., NORTHRUP, J. M., BLANC, J., DOUGLAS-HAMILTON, I., OMONDI, P. & BURNHAM, K. P. 2014. Illegal killing for ivory drives global decline in African elephants. *Proceedings of the National Academy of Sciences of the United States of America* 111:13117–13121.

WOLMER, W. 2003. Transboundary conservation: The politics of ecological integrity in the Great Limpopo transfrontier park. *Journal of Southern African Studies* 29:261–278.

WORKU, E. A., ATICKEM, A., BRO-JØRGENSEN, J., BEKELE, A., EVANGELISTA, P. & STENSETH, N. C. 2021. Human activities increase vigilance, movement and home range size of the endangered mountain nyala (Tragelaphus buxtoni) at the cost of foraging and resting. *Global Ecology and Conservation* 32.

WRENCH, J. M., MEISSNER, H. H., GRANT, C. C. & CASEY, N. H. 1996. Environmental factors that affect the concentration of P and N in faecal samples collected for the determination of nutritional status.

YANG, Y., SIEGWOLF, R. T. W. & KÓRNER, C. 2015. Species specific and environment induced variation of δ13C and δ15N in alpine plants. *Frontiers in Plant Science* 6:1–14.

YOUNG, C., FRITZ, H., SMITHWICK, E. A. H. & VENTER, J. A. 2020. The landscape-scale drivers of herbivore assemblage distribution on the central basalt plains of Kruger National Park. *Journal of Tropical Ecology* 36:13–28.

ZALEWSKA, K., WAGGERSHAUSER, C. N., KORTLAND, K. & LAMBIN, X. 2021. The best defence is not being there: avoidance of larger carnivores is not driven by risk intensity. *Journal of Zoology* 315:110–122.

ZANNI, M., BRIVIO, F., GRIGNOLIO, S. & APOLLONIO, M. 2021. Estimation of spatial and temporal overlap in three ungulate species in a Mediterranean environment. *Mammal Research* 66:149–162. Mammal Research.

ZANÓN-MARTÍNEZ, J. I., KELLY, M. J., MESA-CRUZ, J. B., SARASOLA, J. H., DEHART, C. & TRAVAINI, A. 2016. Density and activity patterns of pumas in hunted and non-hunted areas in central Argentina. *Wildlife Research* 43:449.

APPENDIX

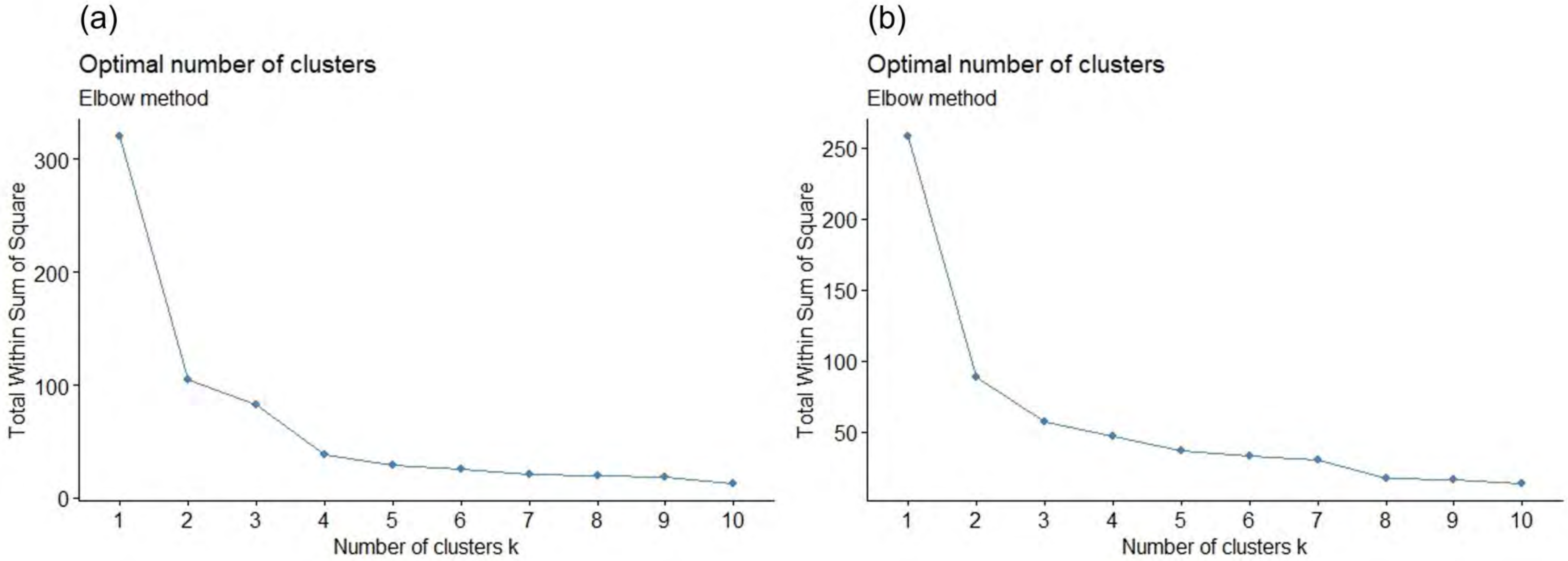
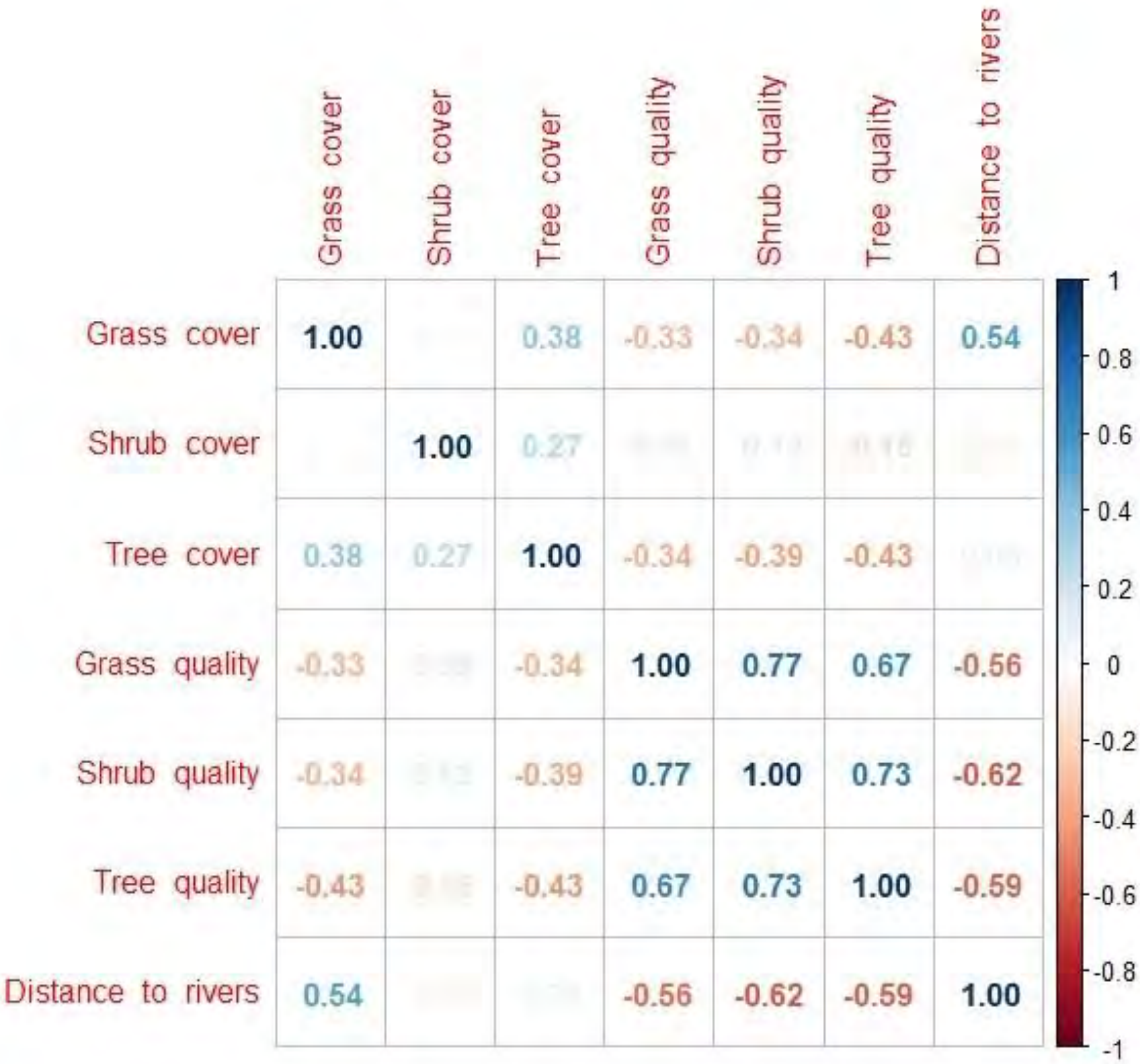


Figure 3.1: Elbow plot depicting the optimal number of clusters used to illustrate similarities in the mean %δ^{13}C and %C estimates for herbivore species, and graze (C_4-plants) and browse (C_3-plants) forage in the wet (a) and dry (season).

Table 3.1 Camera trap ID and corresponding season and habitats in which each camera trap was deployed.

Camera trap ID	Season	Habitat
37W	Wet	Lowveld Riverine Forest
3W	Wet	Subtropical Alluvial Vegetation
4W	Wet	Lowveld Riverine Forest
6W	Wet	Limpopo Ridge Bushveld
8W	Wet	Lowveld Riverine Forest
13W	Wet	Limpopo Ridge Bushveld
14W	Wet	Limpopo Ridge Bushveld
16W	Wet	Limpopo Ridge Bushveld
17W	Wet	Limpopo Ridge Bushveld
18W	Wet	Limpopo Ridge Bushveld
24W	Wet	Subtropical Alluvial Vegetation
25W	Wet	Limpopo Ridge Bushveld
26W	Wet	Limpopo Ridge Bushveld
35W	Wet	Subtropical Alluvial Vegetation
36W	Wet	Lowveld Riverine Forest
38W	Wet	Limpopo Ridge Bushveld
39W	Wet	Limpopo Ridge Bushveld
41W	Wet	Limpopo Ridge Bushveld
43W	Wet	Subtropical Alluvial Vegetation
44W	Wet	Subtropical Alluvial Vegetation
24D	Dry	Subtropical Alluvial Vegetation
25D	Dry	Limpopo Ridge Bushveld
26D	Dry	Limpopo Ridge Bushveld
35D	Dry	Subtropical Alluvial Vegetation
36D	Dry	Lowveld Riverine Forest
37D	Dry	Lowveld Riverine Forest
38D	Dry	Limpopo Ridge Bushveld
39D	Dry	Limpopo Ridge Bushveld
41D	Dry	Limpopo Ridge Bushveld
43D	Dry	Subtropical Alluvial Vegetation
44D	Dry	Subtropical Alluvial Vegetation
3D	Dry	Subtropical Alluvial Vegetation
4D	Dry	Lowveld Riverine Forest
6D	Dry	Limpopo Ridge Bushveld
8D	Dry	Lowveld Riverine Forest
13D	Dry	Limpopo Ridge Bushveld
14D	Dry	Limpopo Ridge Bushveld
16D	Dry	Limpopo Ridge Bushveld
17D	Dry	Limpopo Ridge Bushveld
18D	Dry	Limpopo Ridge Bushveld



	Grass cover	Shrub cover	Tree cover	Grass quality	Shrub quality	Tree quality	Distance to rivers
Grass cover	1.00	[illegible]	0.38	-0.33	-0.34	-0.43	0.54
Shrub cover	[illegible]	1.00	0.27	[illegible]	[illegible]	[illegible]	[illegible]
Tree cover	0.38	0.27	1.00	-0.34	-0.39	-0.43	[illegible]
Grass quality	-0.33	[illegible]	-0.34	1.00	0.77	0.67	-0.56
Shrub quality	-0.34	[illegible]	-0.39	0.77	1.00	0.73	-0.62
Tree quality	-0.43	[illegible]	-0.43	0.67	0.73	1.00	-0.59
Distance to rivers	0.54	[illegible]	[illegible]	-0.56	-0.62	-0.59	1.00

Figure 4.1: Correlation matrix of bottom-up drivers influencing the space-use of the herbivore community in Pafuri, KNP.

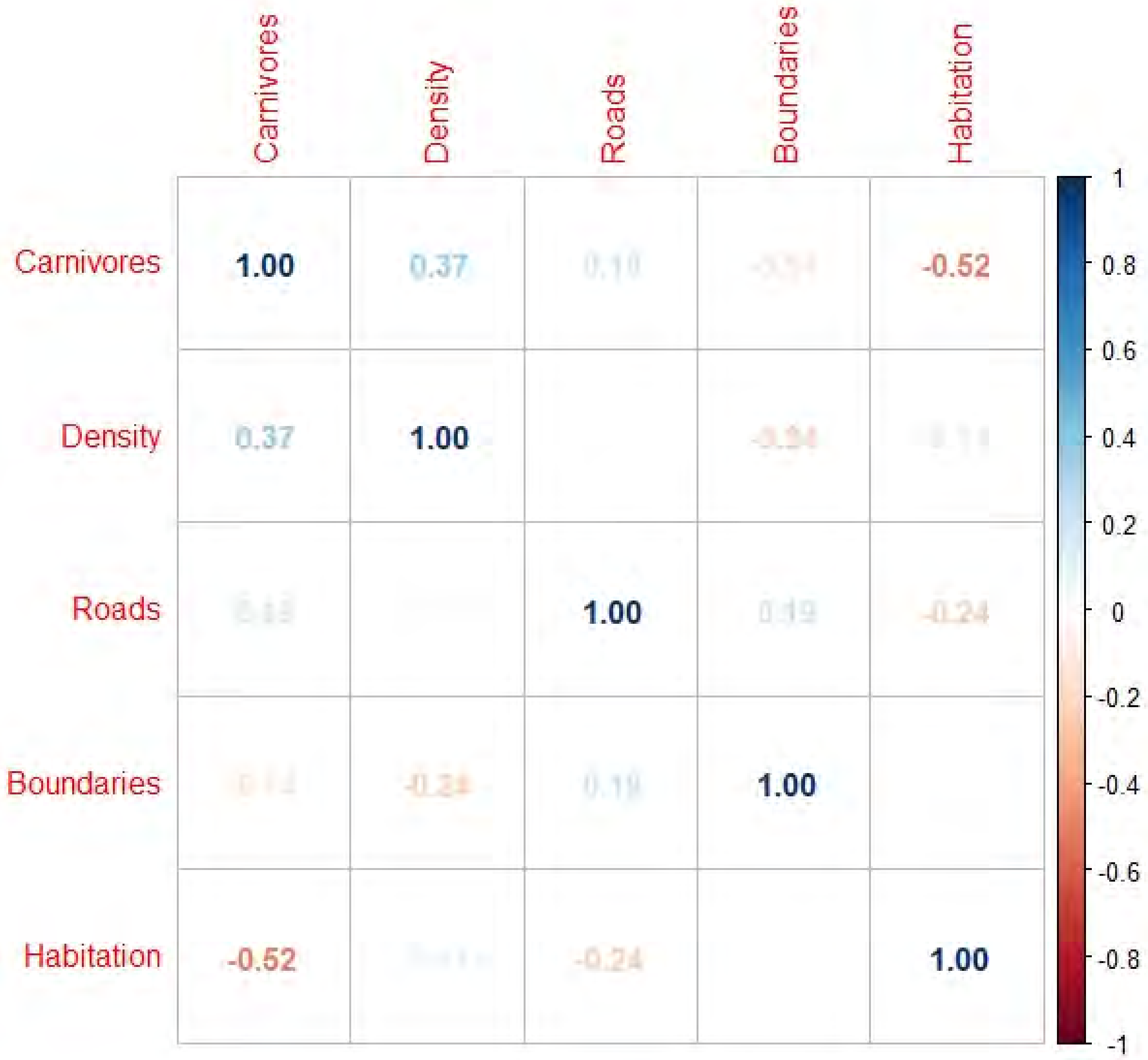


Figure 5.1: Correlation matrix of predation and anthropogenic drivers influencing the space-use of the herbivore community in Pafuri, KNP.

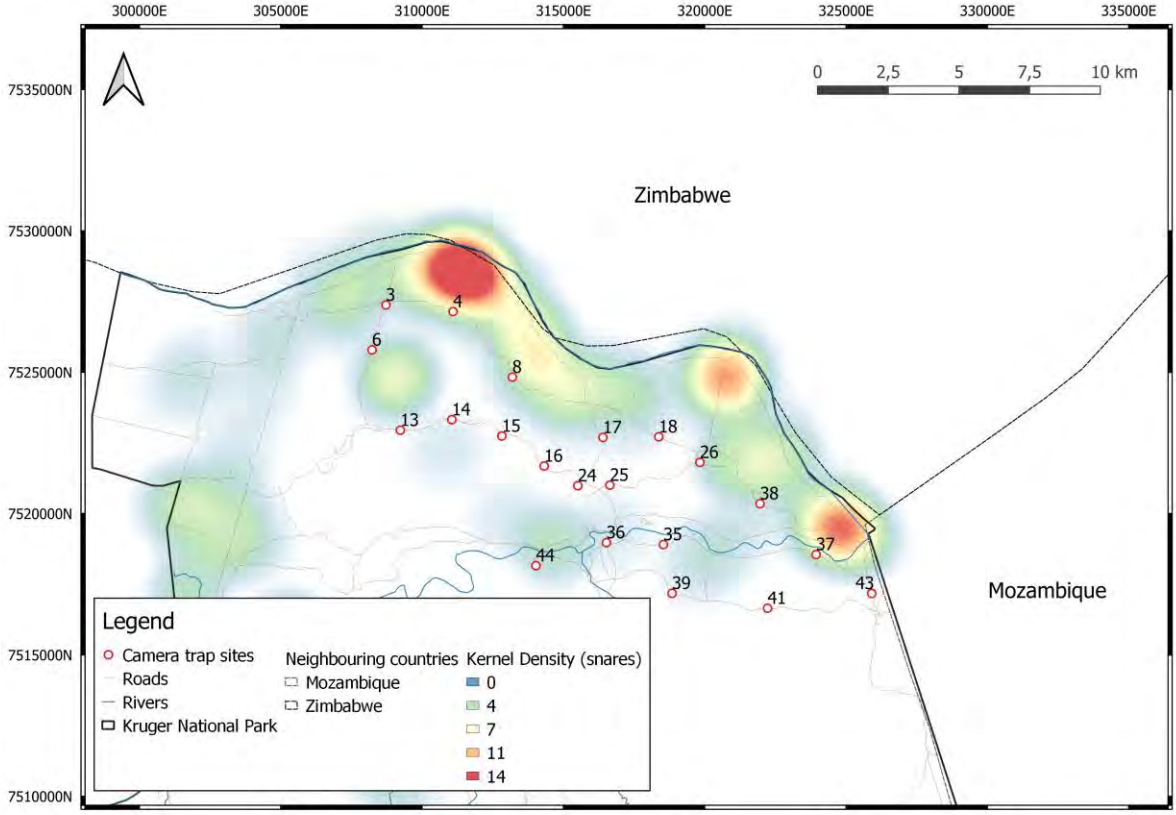


Figure 5.2: Kernel density plot depicting snares located in Pafuri, KNP.