

Examining the influence of extrinsic factors on herbivore assemblage composition in a southern African savanna

By

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Declaration

I, CYANNE YOUNG (213419238), hereby declare that the dissertation for *Magister Scientae* in the Faculty of Science is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.



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Abstract

Globally, herbivore populations have become threatened by the effects of a growing human population. This has resulted in over-hunting, habitat encroachment, fragmentation and degradation and competition leading to the replacement of wild herbivore populations with livestock. African herbivores, in particular, have experienced a severe decline in abundance and distribution, and vast conservation management efforts are underway to preserve herbivore populations and promote their growth. However, conservation management efforts sometimes have unintended consequences on the abundance and distribution of herbivores as a result of the complex interactions they have with their ecosystem. The aim of this study was to: 1) examine the drivers of herbivore distribution at the Satara section of Kruger National Park (hereafter 'KNP') at a landscape scale, to determine assemblage composition under the constraints of different environmental attributes; and 2) examine feeding selection by grazing herbivores of different morpho-physiological characteristics at a patch scale of differing environmental attributes. To achieve this, thirty-six experimental plots were established at three distances from water at Satara, and manipulated by mowing, mowing and fertilising or fertilising only over the course of a year, to account for seasonal effects. Each plot was fitted with a camera trap which ran for five weeks in each sampling season, and the data collected focussed on eleven herbivore species of differing body size, digestive strategy and feeding preference. These species were selected due to their abundance at Satara, and their representation of a variety of morpho-physiological characteristics. To achieve both aims, generalised linear models were used to determine the probability of occurrence of a functional type (for aim 1- Chapter 3), and individual species (for aim 2- Chapter 4).

To construct the generalised linear models for Chapter 3, hypotheses about species' relative distribution and abundance were developed through a literature review of forage and water availability constraints on feeding preference and body size of herbivore biomass at a landscape scale. I expected strong seasonal relationships between vegetation biomass and quality, and biomass of water-dependent herbivores with increasing distance to water. My analyses of herbivore distribution across the region confirmed broad-scale descriptions of

interactions between forage requirements and water availability, across a set of species which differ in functional traits, at a landscape scale.

In Chapter 4, trends in probability of occurrence by seven grazing herbivore species were determined using camera trap data at a patch scale. My results showed that season was a major determinant of species distribution, especially those which are not obligate grazers or feed exclusively in the 0.5 km to 2 km zone from water. I found that most selective feeding occurred in the late wet season when water would be more evenly distributed across the landscape and forage resources close to water would have had the chance to recover from depletion as a result of dry season use.

The collective efforts of this study show that distance from water was a critical determinant of herbivore distribution across the landscape, and that forage utilisation by small mixed-feeders and large grazers in particular, altered significantly across seasons. This has important implications for the provision of artificial water, given that foraging pressure is increased closer to water. Landscape heterogeneity needs to be maintained through efficient water provision, to allow areas of forage reserve to be maintained in the dry season, where species are constrained by water availability and forage quality and quantity.

Publication and presentations related to this research

Details of publications that form part of the research presented in this dissertation.

Papers to be submitted for publication

Chapter 3: Young, C., Fritz, H., Smithwick, E., Venter, J.A. The landscape scale drivers of herbivore assemblage distribution in the basalt grassland plains of Kruger National Park. Paper in preparation for submission to the *Journal of Tropical Ecology*.

Chapter 4: Young, C., Fritz, H., Smithwick, E., Venter, J.A. Patch-scale selection patterns in grazing herbivores at the Satara section of Kruger National Park. Paper in preparation for submission to the *Journal of Tropical Ecology*.

Presentations

The Savanna Science Network Meeting. Mdluli Conference Centre, Skukuza, 4-8 March 2018. Poster presentation: “*The effect of herbivore species on soil available nutrient levels in Kruger National Park.*” by Young C, Smithwick E, Fritz H and Venter JA.

South African Wildlife Management Association, 9-13 September 2018. Oral presentation: “*An evaluation of the drivers of herbivore community composition in the Satara section of Kruger National Park*” by Young C, Fritz H, Smithwick E, and Venter JA.

Authors contributions:

JV and CY conceptualized the research and developed the experimental design. CY collected data, processed and analysed the data, and designed and wrote the manuscripts. HF assisted with data analysis. JV, HF and ES provided valuable comments on the manuscripts.

Dissertation layout

This study sought to improve knowledge on the interactions between extrinsic and intrinsic factors on the composition of herbivore assemblages at different distances from water by testing their observable biomass against environmental variables at the Satara section of Kruger National Park in South Africa. By gaining such insights we add to an existing base of understanding of herbivore distribution across landscapes, which aids in the conservation management of herbivores and their surrounding environment. The dissertation is structured as follows:

Chapter 1 provides a general introduction to the extrinsic and intrinsic drivers of herbivores and the resultant impacts on their distribution across the landscape. It unpacks the interactions between these drivers and provides context for the importance of understanding the relationships between drivers and herbivore distribution. From the literature discussed, the rationale for this study is contextualised.

Chapter 2 gives descriptive details of the study area, details the study design and eleven study species which are the focus of Chapters 3 and 4.

Chapter 3 describes the influence of extrinsic and intrinsic drivers on herbivore assemblage composition at a landscape scale.

Chapter 4 describes the influence of extrinsic and intrinsic factors on forage and habitat selection in herbivores at a patch scale.

Chapter 5 synthesises the findings from the previous chapters.

Chapters 3 and 4 were written as independent papers for a journal, dictating some replication and non-uniform formatting. Each chapter nonetheless contributes to the central theme of the dissertation.

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Chapter 1: General Introduction

Introduction

In this chapter the role of herbivores in the ecosystem, herbivore forage constraints, their interactions with water availability and fire, the effects of predation on their behaviour, and their management historically in Kruger National Park is discussed. This is to improve the understanding of how extrinsic and intrinsic drivers in the ecosystem interact with herbivore distribution and abundance to make up assemblages across the landscape. Lastly, the rationale, aims and objectives of this study are stated.

The role of large herbivores in ecosystems

Globally, we are experiencing an increased decline in populations of herbivores (Hempson, *et al.*, 2015; Ripple *et al.*, 2015; Vié *et al.*, 2009). African herbivores, in particular, have experienced a dramatic, continent-wide decline in the abundance over the last three decades (Chase *et al.*, 2016; Craigie *et al.*, 2010). This decline can be attributed to the increasing demand for resources by the growing human population (Ripple *et al.*, 2015; Vié *et al.*, 2009), and the consequent effects of habitat transformation and over-hunting (Craigie *et al.*, 2010). These consequences, such as habitat fragmentation and the edge effect decrease biodiversity (Fahrig, 2003), and are sometimes relatively more negative for herbivores than predators (Bender & Grouven, 1998). In order to mitigate the negative impacts of biodiversity loss and the subsequent ecosystem functions, it is important to continually develop the understanding of the role and function of herbivores in natural ecosystems.

Herbivores form an essential component of natural ecosystems by acting as ecosystem engineers (Bond, 1994; Hempson *et al.*, 2017; Skarpe *et al.*, 2004; Waldram *et al.*, 2008; Wilby *et al.*, 2001), enabling plant succession and promoting grassland diversity (Olf & Ritchie, 1998). Furthermore, herbivores develop and maintain key resource areas (McNaughton, 1984), create opportunities for grazing through facilitation for other grazers (Prins, 1998) and act as an important food source for carnivores (Ripple *et al.*, 2011). Herbivores also influence soil nitrogen (N) availability through the uptake of nutrients within plant growth material, and through the provision of ephemeral N pulses through processes of defecation and soil leaching (Frost & Hunter, 2007; le Roux *et al.*, 2018). As the turnover rates of soil organic matter in systems vary, N can often end up immobile in the soil (Knops *et al.*, 2002). However, through the stimulation of primary production by herbivory (Frank & McNaughton, 1993)

herbivores enhance nutrient cycling. Alternatively, herbivores can slow nutrient cycling through the reduction in abundance of plants with N-rich tissue, or plants which fix N (Ritchie & Raina, 2016).

Herbivore effects on soil available N are affected by body size of the species. Body size of herbivores is a critical parameter influencing the behaviour, metabolic rate and digestive capacity (Brown *et al.*, 1999) and foraging parameters (Peters & Wassenberg, 1983) of a species. This affects defecation, and in turn, soil available N. Large herbivores deposit large amounts of dung in patches, whereas smaller herbivores may produce small pellets which are more widely distributed across their habitat (Bakker *et al.*, 2004). These processes further interact with predator avoidance by herbivores, and mesoherbivore dung may accumulate more in open habitats than thickets. Megaherbivores, such as the African elephant (*Loxodonta africana*), offset the unequal distribution of nutrients across the landscape by defecating widely across the landscape, particularly in thicket areas, allowing consistent distribution of dung across both open woodland and thicket habitats (Le Roux *et al.*, 2018).

Large deposits of dung may have a slower decomposition rates than small, widely dispersed dung pellets, and as such may not inherently result in the immediate increase of N available for soil mineralisation (Bakker *et al.*, 2004). Furthermore, decomposition and N mineralisation interact with season, and these processes speed up with increased air and soil temperature (Bakker *et al.*, 2004). Nutrient enriched patches, such as grazing lawns, are attractive to herbivores when their resources are freely available (Hempson *et al.*, 2015) (i.e. after rain when nutrients are available in forage), and there is a clear feedback between herbivore presence, nutrient deposition and site enrichment. We wanted to understand the beginning of this feedback loop- what dictates herbivore presence, and what factors affect their selection of forage at both a patch scale and landscape scale. Herbivores drive spatial heterogeneity through these described roles in the environment, and this heterogeneity at different scales is what provides structure and function to the environment (Wu, 2004).

Herbivore assemblage composition is dictated over spatial and temporal scales (Bailey *et al.*, 1996) and this is dependent on the requirements of the species within the assemblage. Herbivores are constrained by extrinsic and intrinsic factors, which interact with the anatomy and metabolic requirements of the species.

Herbivore forage constraints

i. Intrinsic constraints

A large proportion of African herbivores are ruminant bovids, with few non-ruminant equids (Grange *et al.*, 2004). These species make up the broad feeding types of grazers, mixed feeders preferring grass, mixed feeders preferring browse, and browsers (McNaughton & Georgiadis, 1986). This classification can be further separated into obligate grazers (Gagnon & Chew, 2000) which consume > 95% monocotyledonous graminoid matter annually (Codron *et al.*, 2005); variable grazers which consume a small amount of woody and non-woody dicotyledon matter in addition to their mainly monocotyledon diet; browser-grazer intermediaries (i.e. mixed feeders) which consume equal parts monocotyledon and dicotyledon matter and a small proportion of fruit; generalists which typically consume more dicotyledon than monocotyledon matter; browsers which consume > 95% dicotyledon matter in their diet; and frugivores.

Ruminants have further been classified into concentrate selectors, intermediate feeders and roughage eaters (Hoffman, 1989), and nonruminants as non-selective roughage eaters (Bell, 1971). Ruminants are limited by their low intake rate and capacity to process low-quality forage and thus select for high protein plant matter to effectively extract energy (Duncan *et al.*, 1990), whereas nonruminants are more tolerant of low quality forage but must maintain a high level of intake (Clauss *et al.*, 2003; Duncan *et al.*, 1990).

Body size of a species interacts with metabolic requirements of herbivores, in that large bodied species require more total energy than small bodied species, but smaller bodied species have higher energy requirements relative to their body weight than the former (Demment & Soest, 1985). Thus, smaller herbivores are more selective for high quality forage than larger herbivores, which are more tolerant of poor-quality forage (Bell, 1971; Codron *et al.*, 2007; Demment *et al.*, 1985; Redfern *et al.*, 2006). Due to the interactions between an array of factors, which includes body size, digestive type and feeding preference, species can thus be grouped together to describe herbivore functional types. These are as follows: small, non-social browsers, medium-sized social mixed feeders, large browsers, water-dependent grazers and nonruminants (Hempson *et al.*, 2015).

Mouth morphology acts as the link between fulfilling dietary requirements and obtaining the physical forage material. Mouth architecture is linked to body mass and feeding strategy (Gordon and Illius, 1996; Wilmschurst *et al.*, 2000) and muzzle width and incisor arcades are structured to maximise bite intake by each herbivore species in order to meet nutritional requirements (Pretorius, 2009). Grazers typically have wider muzzles and larger incisor arcades than browsers of the same size (Arsenault & Owen-Smith, 2008), and this combination dictates an overall lower selectivity exercised over their preferred forage (Gordon & Illius, 1988). Browsers typically have a narrower incisor arcade and softer mouth parts than grazers, which allows them to feed selectively between branches (Clauss *et al.*, 2008). Mixed feeders have the advantage of adapting forage intake to maximise nutritional intake, and their morphology allows them to select for browse resources when grass quality is low in the dry season (Du Toit, 2003). Furthermore, the selectivity of some browsers and mixed feeders is enabled through the enlarged soft mouth parts (e.g. giraffe and elephant), allowing an increased leaf mass within each bite volume (Pretorius, 2009).

ii. Extrinsic constraints

Herbivore abundance and distribution is driven by complex interactions between extrinsic and intrinsic factors (Venter *et al.*, 2015), at a variety of scales. Extrinsic factors within this study include water availability, forage quantity and quality, risk of predation, fire and landscape homogeneity. Typically, extrinsic factors affect the spatial and temporal distribution of herbivores at a landscape scale, and intrinsic factors at a patch scale. For example, transient grazing species are only tolerant of new grass growth (Murray & Brown, 1993), driven by extrinsic processes of fire and rainfall, which is reflected in landscape changes in their distribution and abundance across seasons (Archibald & Bond, 2004). Less transient species, such as small browsers, are highly constrained by dietary tolerance and habitat specificity (Du Toit, 2003), and as such their spatial and temporal distribution is driven at a patch scale by intrinsic physiognomic requirements.

Extrinsic factors have also been described as top-down (predation) and bottom-up (primary production) processes (Hopcraft *et al.*, 2012). Predation interacts with the body size, and the regulating effects are therefore dependent on the relative body size of both the predator and prey (Hopcraft *et al.*, 2010). Bottom-up processes are described by the plant community structure and architecture, which is as a result of underlying abiotic variables- geology,

topography, soil type and quality, water availability and climate (Hopcraft *et al.*, 2010). These abiotic variables determine the quality and quantity of plant community structure, and as such the herbivore abundance and distribution is constrained through their physiognomic requirements for forage quality and quantity (Fryxell, 1991; Hopcraft *et al.*, 2010). Bottom-up processes have stronger influences on smaller herbivores than large herbivores, but contributes across body size scales to the division of niche space of herbivores (Hopcraft *et al.*, 2010).

Similar niches are inherently occupied when species within the same guild are of similar body sizes, because they have the same dietary requirements (i.e. small herbivores require high quality forage and large herbivores tolerate low quality forage) (Gordon & Illius, 1996; Prins & Olf, 1998), increasing the likelihood of competition (Wilmhurst *et al.*, 2000). Competition for high quality forage may also come in the form of large herbivores which cannot tolerate low quality, and as such, species with differing body size and digestive strategies could end up in direct competition (Illius & Gordon, 1996). Direct competition between herbivores could result in the local extinction of the weaker competitor (Prins & Olf, 1998; Olf *et al.*, 2002), decreasing its competitive influence and potentially resulting in the ecological release of other species (Moreno *et al.*, 2006).

The ecological release of species has impacts on the immediate species diversity of the herbivore guild, with the foraging behaviour of the released herbivore species affecting the foraging behaviour of the lower trophic levels – resulting in trophic cascades (Ripple *et al.*, 2001; Legendijk *et al.*, 2012). Species diversity in herbivore guilds is inherently high in African ecosystems due to high landscape heterogeneity (Pimm, 1984; Prins & Olf, 1998), and a relationship exists between the species present within the guild and the total herbivore biomass of an area (Prins & Olf, 1998; Cromsigt & Olf, 2006). Hutchinson's weight ratio theory predicts that displacement among sympatric species creates a sequence in which species packing (i.e. grouping) will result in each species in the sequence being twice the mass of the next (Hutchinson, 1959); and with high species diversity species packing is closer, i.e. a smaller difference between body mass amongst species (Prins & Olf; Olf *et al.*, 2002; Venter *et al.*, 2014). Smaller grazers are facilitated for by large grazing herbivores (McNaughton, 1976) through increased grazing, which increases quality of forage (Drescher *et al.*, 2006) – thus developing the relationship between species packing and total grazer biomass.

The combination of these intrinsic and extrinsic factors drives complex interactions and constrains the distribution and abundance of herbivores (Bailey *et al.*, 1996; Venter *et al.*, 2015). This causes species of different functional types to overlap in their habitat selection (Illius & Gordon, 1992), and they thus congregate to form an assemblage. Defining assemblages is necessary given their effect on the ecosystem (Hempson *et al.*, 2017). It is important to clarify that this study evaluates assemblage composition by habitat-overlap, and not by their associations or competitive processes (for example Arsenault & Owen-Smith (2002); Redfern *et al.* (2006)).

Scale in herbivore ecology

Foraging choices by herbivores occur over different temporal and spatial scales, and affect large-scale heterogeneity and processes (Shiple, 2007). However, herbivores make foraging choices in response to a variety of factors at multiple scales. Abiotic factors, such as temperature, water availability and topography alter the quality and quantity of forage, and as such are the primary determinant of distribution of herbivores across these scales (Bailey *et al.* 1996; Bailey & Provenza, 2008). Scales are defined by the boundaries between vegetation units, herbivore behaviour, foraging and ecosystem processes (Senft *et al.*, 1987), and as such six scales have been described by Bailey *et al.* (1996). These are the bite scale, affected by plant size, nutrients and secondary compounds; feeding station and patch scales are both affected by forage quality and quantity, and social interactions (the latter is also affected by topography); feeding sites, affected by distance from water, forage abundance and predation; camps, affected by water availability, cover, competition, forage abundance; and home ranges which are affected by water availability, forage abundance, competition and thermoregulation (Bailey *et al.*, 1996). Mechanisms which regulate the forage intake by herbivores at different scales interact with body size and digestive strategy, and as such smaller herbivores can spend more time extending search effort for high quality forage at a fine-scale to meet nutritional requirements, whereas larger herbivores must select for high quantities of forage at a coarser-scale (Bailey *et al.*, 1996), and once there may employ more selective feeding behaviours.

Predation

Herbivores are not only regulated by bottom-up processes of primary production, but also by top-down processes in the form of predation (Hopcraft *et al.*, 2010). Predation directly lowers

herbivore numbers, but also constrains the abundance of species at lower trophic levels by changing the use of resources under the risk of predation (i.e. fear) (Gallagher *et al.*, 2017; van Ginkel, Kuijper *et al.*, 2018). Risk of predation alters the use of the environment by herbivores, through the 'landscape of fear', which can have significant impacts on the structure and function of the environment (Gallagher *et al.*, 2017; Laundre *et al.*, 2010; Ripple & Beschta, 2012). At a landscape scale, predator distribution and activity patterns complement foraging requirements and water availability to determine herbivore distribution (van Ginkel *et al.*, 2018). At a patch scale the perceived risk of predation alters herbivore behaviour by individuals practising increased vigilance in areas of lower visibility (Riginos, 2015; van Ginkel *et al.*, 2018).

Because herbivores must meet their metabolic requirements under both forage and predation constraints, body size and gregariousness play an important role in how they face the trade-off (Gallagher *et al.*, 2017). Herbivores display different anti-predator behaviour when faced under direct or indirect threat. All species practise vigilance, especially in areas to which they are not adapted to minimise risk of predation (Bailey *et al.*, 1996), such as waterholes (Valeix *et al.*, 2009). Smaller, less social herbivores are unable to actively defend themselves and typically cannot flee with enough speed to escape direct threat of predation, and thus they rely on crypsis and the utilisation of densely vegetated habitats (Jarman, 1974). Medium-bodied herbivores employ anti-predator strategies of large grouping, practising vigilance and fleeing from direct threat of predation (Estes, 1991; Pays *et al.*, 2012). Typically, large and gregarious herbivores may choose to meet forage requirements and ignore the risk of predation (Prins, 1996), but are also capable of defending themselves against direct threat of predation (Prins, 1989). In KNP, the common herbivores of Satara comprise an important food source for charismatic large carnivores, the lion (*Panthera leo*), leopard (*Panthera pardus*) spotted hyena (*Crocuta crocuta*), cheetah (*Acinonyx jubatus*) and wild dog (*Lycaon pictus*). Smaller herbivores are typically not selected for by larger carnivores (Hayward & Kerley, 2005), but experience a higher risk as they are vulnerable to predation by both large and small predators (caracal (*Caracal caracal*) and serval (*Leptailurus serval*)) (Hopcraft *et al.*, 2010). Although a lower risk of predation for medium-large and large herbivores would be expected on this basis, these species experience increased risk, as they are the preferred prey species of the predators of the area (Hayward *et al.*, 2005; Hayward *et al.*, 2006; Hayward &

Kerley, 2008). The effects of predation on herbivore behaviour are expected to be stronger in African savanna systems due to the hunting methods of dominant predators, which choose to stalk and sit-and-wait, in addition to the increased diversity of predators, when compared to predators-prey dynamics (e.g. wolves (*Canis lupus*) and elk (*Cervus canadensis*) or pumas (*Puma concolor*) and deer (*Odocoileus hemionus*)) in the Americas (Riginos, 2015).

Herbivores and water availability

The driving forces of herbivore movement have complex relationships with seasonal water availability. Water is a principal determinant of primary production, limiting uptake of soil available N (Knops *et al.*, 2002; Scholes *et al.*, 2003), and dictating the movement (Cain *et al.*, 2012; Chamaillé-Jammes *et al.*, 2007; Gaylard *et al.*, 2003; Valeix, 2011) and seasonal population fluctuations of herbivore species (Owen-Smith & Ogotu, 2003). Seasonal rainfall has a strong influence on the distribution and abundance of herbivore species independent of surface water availability (Gaylard *et al.*, 2003) because of its constraining effects on forage quality (Valeix, 2011). In addition, herbivores require surface water to complement foraging in semi-arid environments, and thus their abundance further from water is strongly constrained (Chamaillé-Jammes *et al.*, 2007; Gaylard *et al.*, 2003). In KNP, plain's zebra (*Equus burchellii*), South African giraffe (*Giraffa camelopardalis giraffa*) and blue wildebeest (*Connochaetes taurinus*) populations peaked in recurrent low rainfall years, whereas southern savanna buffalo (*Syncerus caffer*), greater kudu (*Tragelaphus strepsiceros*), roan antelope (*Hippotragus equinus*), waterbuck (*Kobus ellipsiprymnus ellipsiprymnus*), common eland (*Taurotragus oryx*) and tsessebe (*Damaliscus lunatus*), populations peaked during recurrent high rainfall years (Owen-Smith *et al.*, 2003). Dry season rainfall allows for the retention of moisture in forage, affecting grazing species in particular (Owen-Smith *et al.*, 2003), reducing the necessity to utilise artificial water sources (Valeix *et al.*, 2008). Rainfall interacts with forage quality and quantity, and predation in constraining herbivore populations (Owen-Smith *et al.*, 2003). As such, in recurrent years of low rainfall, predator abundance increases due to weakened prey (as a result of malnutrition) and the increased use of artificial surface water (Owen-Smith *et al.*, 2003).

Across the spectrum of savanna ungulates, species have varying dependence on surface water and face trade-offs between forage selection and water dependence (Cain *et al.*, 2012). Foraging requirements influence water dependency, with grazers becoming increasingly

dependent on water as the dry season progresses, and moisture content of forage decreases (Cain *et al.*, 2012). Browsers typically favour nutritional requirements over surface water availability when faced with the trade-off (Gaylard *et al.*, 2003), which is enabled by the water content of browse remaining higher than that of grass in the dry season (Western, 1975).

The influence of water can be manipulated at a local scale through management interventions, through the provision of water. This is a major intervention into natural animal movement, and the consequences thereof are comparable to that of fire management and culling (Owen-Smith, 1996). Because herbivore drinking needs vary across species, with preference for water sources and temporal patterns of drinking varying across seasons and between species, artificial water sources alter the typical patterns observed at a large scale between herbivore populations and water availability (Gaylard *et al.*, 2003). In KNP, grazers have been associated with artificial water holes, whereas browsers and mixed feeders were associated with rivers (Smit *et al.*, 2007), emphasising the large scale alteration of habitat use patterns across functional types of species.

KNP began water provision in 1933, and eventually created more than 300 artificial, constant sources of water (Gaylard *et al.*, 2003). This manipulation of surface water availability influenced the distribution of water-dependent species such as zebra and wildebeest, and concurrently the distribution of large predators, at the expense of less common herbivores such as roan antelope (*Hippotragus equinus*), tsessebe (*Damascalis lunatus*) and reedbuck (*Redunca arundinum*) (Owen-Smith, 1996). Water distribution also impacted the spatial distribution of nutrients, and in the case of KNP was the cause of a homogenised woody vegetation structure across the landscape (Gaylard *et al.*, 2003), and the depletion of woody resources as far as 2.8 km from water holes (Brits *et al.*, 2002). Due to the negative impacts of surface water provision, a large proportion of the waterholes across the landscape have subsequently been closed (Carruthers, 2017; Gaylard *et al.*, 2003). Large scale alterations in habitat usage following the closing of these waterholes is expected, particularly in elephants, which will traverse areas further from water when artificial water is not available, having implications for habitat use intensity (Purdon & van Aarde, 2017).

Fire and herbivory

Fire and herbivory are unequivocally linked and globally, savanna and grassland systems are shaped by interactions between the two (Burkepile *et al.*, 2016) due to their role in nutrient cycling (Anderson *et al.*, 2006; Venter *et al.*, 2014), changes in plant diversity (Archibald *et al.*, 2005) and alteration of the woody to grass plant ratio (Burkepile *et al.*, 2016). Whilst fires affect the foraging resource available to herbivores (Archibald *et al.*, 2004; Burkepile *et al.*, 2016), herbivory alters the fuel load by changing quantity, type and areas of fuel burned (Archibald *et al.*, 2005; Hopcraft *et al.*, 2012). Increased herbivory may result in grasses dominating the plant structure, resulting in increased fire frequency, intensity and return (Hopcraft *et al.*, 2010), which suppresses the tree layer from establishing (Bond & Keeley, 2005). Fire frequency interacts with rainfall, and in areas of rainfall > 800 mm per annum grass biomass may increase beyond what herbivores can remove between fire intervals (Archibald, 2008; Venter *et al.*, 2014), in turn increasing fire frequency. Fire thus acts as a top-down controlling factor of herbivore distribution, by attracting grazing herbivores to nutritious post-fire regrowth (Archibald *et al.*, 2004) and by altering the landscape of fear by changing the tree-grass ratio (Burkepile *et al.*, 2016).

Grazer body size and digestive strategy interact with preference for burned areas (Tomor & Owen-Smith, 2002; Klop *et al.*, 2007; Sensenig *et al.*, 2010). A negative body size relationship for preference of burned areas would be expected, as a result of increased metabolic requirements in species of a smaller body size (Wilsey, 1996). However, crude protein in burned areas is overall higher than unburned areas (Sensenig *et al.*, 2010), and thus nutritional requirements (as a product of body size and digestive strategy) likely determine preference for burned areas (Tomor & Owen-Smith, 2002). Body size further interacts with digestive strategy to determine preference for burned areas at varying patch scales. Smaller burn areas maintain higher quality grass due to increased close cropping (Sensenig *et al.*, 2010), as a result of re-grazing on burned patches (Archibald *et al.*, 2004). This increases preference by smaller-bodied grazers and mixed feeders (Eby *et al.*, 2014; Klop *et al.*, 2007), whereas larger burned areas are preferred by larger-bodied species (Eby *et al.*, 2014; Sensenig *et al.*, 2010). Grazing pressure of unburned areas decreases following fires, and at a landscape scale the intensity of grazing pressure is reduced as forage quality is more uniform across the

landscape after burning, and low quantity results in a wide dispersal of individuals across the burned area (Archibald *et al.*, 2004).

KNP management policies affecting herbivore abundance and distribution

International and local socio-political climates have significantly altered the management and scientific research of KNP (Carruthers, 2017). Prior to the conception of KNP, the formal protection of game was undertaken with the explicit purpose of creating a game sanctuary to be used as hunting grounds by Colonial sportsmen (Mabunda *et al.*, 2003). Following concern of the first warden, James Stevenson-Hamilton, regarding the lack of adequate protection by provincial ordinances to protect the game reserve from increasing commercial farming and mining pressure, lobbying was undertaken to declare the reserve a national park, under the recently passed National Parks Act (1926) (Carruthers, 1995; Mabunda *et al.*, 2003). At this time, surface water was restricted to the main rivers and in times of drought, herbivores experienced severe pressure. Herbivore condition declined, along with vegetation condition, due to the intense grazing pressure concentrated in places with remaining surface water. This also attracted herbivores to water sources outside of the park's unfenced boundaries, where they became susceptible to poaching (Carruthers, 2017). Following the declaration of the park, there was a marked change in degree of management intervention into the ecosystem, beginning the implementation of policies for experimental fire management (1926) (van Wilgen *et al.*, 2003), species reintroductions (1930), culling (1966) artificial water provision (1933) (Gaylard *et al.*, 2003) and fencing (1959) (Mabunda *et al.*, 2003).

Experimental burning policies began with the intention of providing a green flush of grazing for grazing species (van Wilgen *et al.*, 2003). However, with change in the wardenship fire suppression was undertaken in order to mitigate the perceived negative effects of fire (van Wilgen *et al.*, 2003). This policy was reviewed in 1956, and until 1981 prescribed burns were undertaken at fixed intervals. This resulted in overgrazing and the dominance of unpalatable species (van Wilgen *et al.*, 2003), the decline of large trees (Eckhardt *et al.*, 2000) and the increase of homogeneity across the landscape (van Wilgen *et al.*, 2003). When coupled with the effects of artificial water provision, overgrazing, soil erosion, piospheres and landscape homogenisation were becoming evident (Gaylard *et al.*, 2003; van Wilgen *et al.*, 2003). Artificial water provision was additionally meant to bolster species within the park in times of drought, in particular, rare antelope species. However, the water provision resulted in the

increase of predators, disease and common water-dependent species, causing population declines (Harrington *et al.*, 1999). The increase of common water-dependent species compounded grazing pressure on the available resources, and water sources were distributed in close proximity to one another across the landscape (less than 20% of the park was more than 5 kilometres from water in periods of extreme drought) (Gaylard *et al.*, 2003). As a result, there were no areas of forage reserve and in droughts KNP incurred losses of 20 – 30 percent declines in sensitive herbivore species (Gaylard *et al.*, 2003). Subsequently, artificial water provision policies were revised in 1997 and a large proportion of waterholes have been closed (Carruthers, 2017; Gaylard *et al.*, 2003). Although several research projects are investigating the effect of these more recent management interventions, much of the consequences are still unknown. Recent studies have shown that buffalo mortalities in KNP during the drought period of 2014-2016 were almost half of previous mortalities resulting from drought. This has been attributed to the closing of waterholes, which allowed areas of reserve forage to develop, and forced buffalo to migrate from the southern parts of the park to use these reserves (Swemmer, 2018).

Rationale

The influence of anthropogenic effects in our global environment are becoming increasingly prevalent, as we begin to understand the indirect effects of our actions. By continually trying to sustain the needs of the ever-growing human population, we are changing the functionality of our ecosystems (Ripple *et al.*, 2015). Through water abstraction, bushmeat poaching, habitat destruction and conversion, fencing and competition for resources we have seen a global halving of our herbivore populations (Ripple *et al.*, 2015; Hopcraft *et al.*, 2010). Furthermore, conservation management efforts to protect species from these effects, such as fencing and artificial water provision, affect the abundance and distribution of herbivores across the landscape.

The composition of herbivore assemblages has implications for the functionality of an ecosystem (Pretorius, 2009). KNP is not immune to human-impacts, and their history of management interventions has had significant long-term effects on herbivore abundance and distribution throughout the park. This promotes the study of the ecological patterns and processes which influence large herbivores in KNP. Furthermore, by contributing to the existing body of understanding regarding drivers of herbivore assemblage composition, we

can better predict the outcomes of management interventions which may be necessary in the future. For example, understanding habitat selection by herbivores of different functional characteristics, or the effects of distance from water on the composition of herbivore assemblages, can allow management to better predict the response of herbivore assemblages to their interventions. This study was undertaken in the Satara section of KNP, which is characterised by the nutrient-rich basaltic soils, where the effects of surface water availability, both artificial and natural, have stronger effects on shaping herbivore distributions than on granitic soils (Smit *et al.*, 2007).

The overall aim of this study was to evaluate the mechanisms behind what drives forage selection, at both a landscape- and a patch-scale, in the common herbivore species of the Satara section of Kruger National Park, South Africa. In order to achieve this, the following objectives were identified:

- i. To determine the primary drivers behind foraging and habitat selection at a landscape-scale in herbivores which vary in body size, feeding preference and digestive type.
- ii. To unpack the mechanisms, both extrinsic and intrinsic, behind the strength of the primary drivers for landscape scale selection by species of differing functional type, to determine how these constraints influence assemblage composition.
- iii. To evaluate foraging preference under a variety of constraints in common grazing herbivores of Satara, through experimental landscape manipulation.
- iv. To examine the mechanisms behind patch-scale selection, with relation to both extrinsic and intrinsic influences.

Literature Cited

- Anderson, R. H., Fuhlendorf, S. D., & Engle, D. M. 2006. Soil Nitrogen Availability in Tallgrass Prairie Under the Fire–Grazing Interaction. *Rangeland Ecology & Management*, 59(6), 625-631.
- Archibald, S. 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *The journal of wildlife management*, 72(2), 492-501.
- Archibald, S., & Bond, W. J. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13(3), 377-385.
- Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. 2005. Shaping the Landscape: Fire-Grazer Interactions in an African Savanna. *Ecological Applications*, 15(1), 96-109.
- Arsenault, R., & Owen-Smith, N. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos*, 97(3), 313-318.
- Arsenault, R., & Owen-Smith, N. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, 117(11), 1711-1717.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386-400.
- Bailey, D.W. & Provenza F.P. 2008. Mechanisms determining large-herbivore distribution. Pp 7-28 in Prins, H.H.T. & F. van Langevelde (Eds.), *Resource Ecology*. Springer, New York.
- Bakker, E., Olff, H., Boekhoff, M., Gleichman, J., & Berendse, F. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia*, 138(1), 91-101.
- Bell, R. H. V. 1971. A grazing ecosystem in the Serengeti. *Scientific American*, 225(1), 86-93.
- Bender, R., & Grouven, U. 1998. Using Binary Logistic Regression Models for Ordinal Data with Non-proportional Odds. *Journal of clinical epidemiology*, 51(10), 809-816.
- Bond, W.J. 1994. Keystone species. In *Biodiversity and ecosystem function* (pp. 237-253). Springer, Berlin, Heidelberg.
- Bond, W.J. & Keeley, J.E. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in ecology & evolution*, 20(7), pp.387-394.

- Brits, J., Rooyen, M. W. V., & Rooyen, N. V. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*, 40(1), 53-60.
- Brown, J. S., Laundré, J. W., & Gurung, M. 1999. The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *Journal of Mammalogy*, 80(2), 385-399.
- Burkepile, D. E., Thompson, D. I., Fynn, R. W., Koerner, S. E., Eby, S., Govender, N., Hagenah, N., Lemoine, N. P., Macthett, K. J., Wilcox, K. R. & Collins, S. L. 2016. Fire frequency drives habitat selection by a diverse herbivore guild impacting top-down control of plant communities in an African savanna. *Oikos*, 125(11), 1636-1646.
- Cain, J., Owen-Smith, N., & Macandza, V. 2012. The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology*, 286(1), 58-67.
- Carruthers, J. 1995. *The Kruger National Park: a social and political history*. University of Natal Press, Pietermaritzburg.
- Carruthers, J. 2017. The Kruger National Park. Pp 368-410 in *National Park Science: A Century of Research in South Africa*. Cornwall, Cambridge University Press, United Kingdom.
- Chamaillé-Jammes, S., Fritz, H., & Murindagomo, F. 2007. Climate-driven fluctuations in surface-water availability and the buffering role of artificial pumping in an African savanna: Potential implication for herbivore dynamics. *Austral Ecology*, 32(7), 740-748.
- Chamaillé-Jammes, S., Valeix, M., & Fritz, H. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, 44(3), 625-633.
- Chase, M. J., Schlossberg, S., Griffin, C. R., Bouché, P. J. C., Djene, S. W., Elkan, P. W., Ferreira, S., Grossman, F., Kohi, E. M., Landen, K., Omondi, P., Peltier, A., Selier, S. A. J., & Sutcliffe, R. 2016. Continent-wide survey reveals massive decline in African savannah elephants. *PeerJ*, 4, e2354.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., & Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, 136(1), 14-27.

- Clauss, M., Kaiser, T., & Hummel, J. 2008. The morphophysiological adaptations of browsing and grazing mammals. Pp 47-88 in I. J. Gordon & H. H. T. Prins (Eds.), *The ecology of browsing and grazing*. Springer, Heidelberg.
- Codron, D., Codron, J., Sponheimer, M., Lee-Thorp, J., Robinson, T., Grant, C. C., & De Ruiter, D. 2005. Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces. *Koedoe*, 48(1), 115-124.
- Codron, D., Lee-Thorp, J. A., Sponheimer, M., Codron, J., de Ruiter, D., & Brink, J. S. 2007. Significance of diet type and diet quality for ecological diversity of African ungulates. *Journal of Animal Ecology*, 76(3), 526-537.
- Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221-2228.
- Demment, M. W., & Soest, P. J. V. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125(5), 641-672.
- Du Toit, J. T. 2003. Large herbivores and savanna heterogeneity. Pp 292-310 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G., & Lloyd, M. 1990. Comparative Nutrient Extraction from Forages by Grazing Bovids and Equids: A Test of the Nutritional Model of Equid/Bovid Competition and Coexistence. *Oecologia*, 84(3), 411-418.
- Eby, S. L., Anderson, T. M., Mayemba, E. P., & Ritchie, M. E. 2014. The effect of fire on habitat selection of mammalian herbivores: the role of body size and vegetation characteristics. *Journal of Animal Ecology*, 83(5), 1196-1205.
- Eckhardt, H., Wilgen, B., & Biggs, H. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, 38(2), 108-115.
- Estes, R., 1991. Hartebeests, Topi, Blesbok and Wildebeests: Tribe Alcelaphini. Pp 133-167 in Estes, R., (Ed.), *The behavior guide to African mammals* (Vol. 64). University of California Press, Berkeley.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual review of ecology, evolution, and systematics*, 34(1), 487-515.

- Frank, D. A., & McNaughton, S. J. 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia*, 96(2), 157-161.
- Frost, C. J., & Hunter, M. D. 2007. Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia*, 151(1), 42-53.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist*, 138(2), 478.
- Gagnon, M., & Chew, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, 81(2), 490-511.
- Gallagher, A. J., Creel, S., Wilson, R. P., & Cooke, S. J. 2017. Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, 32(2), 88-96.
- Gaylard, A., Owen-Smith, N., & Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pp 171-189 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Gordon, I. J., & Illius, A. W. 1988. Incisor arcade structure and diet selection in ruminants. *Functional Ecology*, 2(1), 15-22.
- Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R., & Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, 90(1), 69-78.
- 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(2), 298-313.
- Hayward, M. W., & Kerley, G. I. 2008. Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research*, 38(2), 93-108.
- Hayward, M. W., & Kerley, G. I. H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, 267(3), 309-322.
- 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(6264), 1056-1061.
- Hempson, G. P., Archibald, S., & Bond, W. J. 2017. The consequences of replacing wildlife with livestock in Africa. *Scientific reports*, 7(1), 17196.

- Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J., & Vickers, K. J. 2015. Ecology of grazing lawns in Africa. *Biological Reviews*, 90(3), 979-994.
- Hopcraft, J.G.C., Anderson, T.M., Pérez-Vila, S., Mayemba, E. & Olff, H. 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, 81(1), 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 & Evolution*, 25(2), 119-128.
- Illius, A. W., & Gordon, I. J. 1992. Modeling the nutritional ecology of ungulate herbivores: Evolution of body size and competitive interactions. *Oecologia*, 89(3), 426-434.
- Jarman, P. J. 1974. The Social Organisation of Antelope in Relation To Their Ecology. *Behavior*, 48(1), 215-267.
- Klop, E., van Goethem, J., & de longh, H. H. 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research*, 34(2), 77-83.
- Knops, J., Bradley, K., & Wedin, D. 2002. Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*, 5(3), 454-466.
- 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.
- Le Roux, E., Kerley, G. I., & Cromsigt, J. P. 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, 28(15), 2493-2499.
- Mabunda, D., Pienaar, D. J., & Verhoef, J. 2003. The Kruger National Park: a century of management and research. Pp 3-21 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- McNaughton, S. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist*, 124(6), 863-886.
- Murray, M. G., & Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti: An experimental test. *Journal of Animal Ecology*, 62(2), 10.

- Olf, H., & Ritchie, M. E. 1998. Effects of herbivores on grassland plant diversity. *Trends in ecology & evolution*, 13(7), 261-265.
- Owen-Smith, N., & Ogutu, J. 2003. Rainfall influences on ungulate population dynamics. Pp 310-332 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, 169(2), 419-430.
- Peters, R. H., & Wassenberg, K. 1983. The effect of body size on animal abundance. *Oecologia*, 60(1), 89-96.
- Pretorius, Y. 2009. *Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores*. Unpublished MSc Thesis, Wageningen University, Netherlands.
- Prins, H. H. T. 1989. Buffalo herd structure and its repercussions for condition of individual African buffalo cows. *Ethology*, 81, 47-71.
- Prins, H. 1996. *Ecology and behaviour of the African buffalo: social inequality and decision making* (Vol. 1). Springer Science & Business Media.
- Prins, H.H.T. & Olf, H., 1998. Species-richness of african grazer assemblages: towards a functional explanation. Pp 449-490 in H. H. T. Prins & N. D. Brown (Eds.), *Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society*. Cambridge University Press, United Kingdom.
- Purdon, A. & van Aarde, R.J., 2017. Water provisioning in Kruger National Park alters elephant spatial utilisation patterns. *Journal of Arid Environments*, 141, 45-51.
- Redfern, J. V., Ryan, S. J., & Getz, W. M. 2006. Defining herbivore assemblages in the Kruger National Park: a correlative coherence approach. *Oecologia*, 146, 9.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124-133.
- Ripple, W. J., & Beschta, R. L. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation*, 145(1), 205-213.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P. & Schmitz, O.J. 2014. Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 1241484.

- 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(4), e1400103.
- Ritchie, M. E., & Raina, R. 2016. Effects of herbivores on nitrogen fixation by grass endophytes, legume symbionts and free-living soil surface bacteria in the Serengeti. *Pedobiologia*, 59(5), 233-241.
- Scholes, M. C., Scholes, R. J., Otter, L. B., & Woghiren, A. J. 2003. Biogeochemistry: the cycling of elements. Pp 292-309 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, & D. M. Swift. 1987. Large Herbivore Foraging and Ecological Hierarchies. *BioScience*, 37 (11), 789-799.
- 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(10), 2898-2907.
- Skarpe, C., Aarrestad, P. A., Andreassen, H. P., Dhillion, S. S., Dimakatso, T., Du Toit, J. T., Halley, D., J, Hytteborn, H., Makhabu, S., & Mari, M. 2004. The return of the giants: ecological effects of an increasing elephant population. *AMBIO: A Journal of the Human Environment*, 33(6), 276-282.
- Smit, I. P. J., Grant, C. C., & Devereux, B. J. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136(1), 85-99.
- Swemmer, A. M., Bond, W. J., Donaldson, J., Hempson, G. P., Malherbe, J., & Smit, I. P. 2018. The ecology of drought-a workshop report. *South African Journal of Science*, 114(9), 1-3.
- Tomor, B. M., & Owen-Smith, N. 2002. Comparative use of grass regrowth following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology*, 40(2), 201-204.
- Valeix, M. 2011. Temporal dynamics of dry-season water-hole use by large African herbivores in two years of contrasting rainfall in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology*, 27(2), 163-170.

- Valeix, M., Fritz, H., Loveridge, A., Davidson, Z., Hunt, J., Murindagomo, F., & Macdonald, D. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology*, 63(10), 1483-1494.
- 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(3), 402-410.
- van Ginkel, H. A. L., Kuijper, D. P. J., Schotanus, J., & Smit, C. 2018. Wolves and Tree Logs: Landscape-Scale and Fine-Scale Risk Factors Interactively Influence Tree Regeneration. *Ecosystems*, 1-11.
- van Wilgen, B. W., Trollope, W. S., Biggs, H. C., Potgieter, A. L., & Brockett, B. H. 2003. Fire as a driver of ecosystem variability. Pp 149-170 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Venter, J. A., Nabe-Nielsen, J., Prins, H. T., & Slotow, R. 2014. Forage patch use by grazing herbivores in a South African grazing ecosystem. *Acta Theriologica*, 59(3), 457-466.
- Venter, J. A., Prins, H. H. T., Mashanova, A., de Boer, W. F., & Slotow, R. 2015. Intrinsic and extrinsic factors influencing large African herbivore movements. *Ecological Informatics*, 30, 257-262.
- Vie, J.-C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2009). State of the world's species. Pp 15-43 in *Wildlife in a changing world: An analysis of the 2008 IUCN Red List of Threatened Species*. Gland, Switzerland, IUCN.
- Waldram, M. S., Bond, W. J., & Stock, W. D. 2008. Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna. *Ecosystems*, 11, 101-112.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, 13(3-4), 265-286.
- Wilby, A., Shachak, M., & Boeken, B. 2001. Integration of ecosystem engineering and trophic effects of herbivores. *Oikos*, 92(3), 436-444.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.
- Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape ecology*, 19(2), 125-138.

Chapter 2: Study area, focus species and study design

Introduction

This chapter provides a detailed description of the Satara section of Kruger National Park (KNP), specifically in terms of location, climate, geology and vegetation. I also provide a detailed description of the study species: steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus melampus*), blue wildebeest (*Connochaetes taurinus taurinus*), greater kudu (*Tragelaphus strepsiceros*), waterbuck (*Kobus ellipsiprymnus ellipsiprymnus*), plain's zebra (*Equus quagga burchellii*), southern savanna buffalo (*Syncerus caffer caffer*), South African giraffe (*Giraffa camelopardalis giraffa*), white rhinoceros (*Ceratotherium simum simum*) and African elephant (*Loxodonta africana*). Finally, the overall experimental design of the study is included to provide the methodological context for how the main questions of Chapter 3 and Chapter 4 were tested.

Study Area

The formal protection of the Kruger National Park, began in 1902 with the end of the Anglo-Boer War, with the intent of preserving a game sanctuary that could be used as exclusive hunting grounds by sportsmen (Carruthers, 1995). In 1903, the area between the Sabie and Olifants rivers were added, and the Sabi Game Reserve was proclaimed (Mabunda *et al.*, 2003). The focus from 1903 to 1926 was the protection and rebuilding of game populations, which had become decimated by excessive hunting and the rinderpest epidemic (Mabunda *et al.*, 2003). Then, in 1926, the Sabi and Shingwitsi reserves were amalgamated and the Kruger National Park was officially declared. The start of more permanent management interventions began in 1933, with the sinking of six boreholes to distribute game more evenly and counter the perceived degradation of the Lowveld (Mabunda *et al.*, 2003). Fence establishment began in 1959, and marked the beginning of intensive water provision for game unable to migrate to water, and other negative ecological consequences (Gaylard, Owen-Smith *et al.*, 2003). However, across this period a stronger focus on research was developing, with population studies beginning in 1963, aerial wildlife censuses in 1978 and vegetation types being delineated in 1983 (Mabunda *et al.*, 2003). Today, the park is world-renowned for the reestablishment of game species which had become locally extinct, the vast tourism-industry which operates within the park, and the scientifically-based management which aims to adapt and respond to ever-increasing environmental changes (Mabunda *et al.*, 2003).

Location

KNP is situated at the north-eastern corner of the South Africa (24.01°S, 31.49 °E), and borders Mozambique and Zimbabwe to the east and north respectively (Cromsigt & te Beest, 2014). The park is 350 km in length and approximately 60 km wide (Cromsigt *et al.*, 2014). It is situated in the low-lying area between the Mozambican coastal plains and the foothills of the Drakensberg (Venter *et al.*, 2003), forming part of the greater Lowveld. The Lowveld lies on average 300m above sea level and consists largely of plains, constituting a large part of the Eastern Plateau Slope (Venter *et al.*, 2003).

Climate

KNP falls within two climate zones, the Lowveld-bushveld zone (rainfall of 500-700 mm per annum) in the central and southern parts; and the northern arid bushveld zone (300-500 mm per annum) in the north. Both areas receive rainfall in the summer, with most being concentrated between October and April. KNP experiences high mean temperatures in summer and mild frost-free winters. The climate of KNP is slightly different to that of the rest of southern Africa, as its climate is determined by a different predominant weather system. The temperature is generally warm due to the low-lying location, and humidity is high – especially in the summer. Historically, KNP has experienced hot, wet summers and dry, mild winters with predictable rainfall patterns, however this is expected to change with human-induced climate change. The climate is expected to become significantly warmer (+2-6°C) during the twenty-first century, but due to the effects of climate change the predictions for future rainfall patterns are made with uncertainty. Future rainfall trends could be up to 20% higher or lower. The area where my study took place is in the Satara region, which receives 537 mm of rain per annum (Venter *et al.*, 2003); and experiences mean minimum temperatures of 10°C and 20°C and mean maximum temperatures of 26.3°C and 32.6°C in July and December respectively (Parr, 2008).

Geology

There is a diverse assemblage of igneous, sedimentary and metamorphic rocks, and unconsolidated sediments in Kruger. The majority of Kruger is underlain by north-south lying lithology, resulting in successional changes in underlying geology and soils running from west to east. The predominant rock forms are granite in the west and basalt in the east. The sample sites are within the Karoo basic lava- Sabie river olivine-poor basalt geological formation

(Satara), which features a small island of Karoo basic lava- Letaba olivine-rich basalt (Mavumbye) (Venter *et al.*, 2003). Despite the differing underlying geology, the Satara land type persists across the region of the sample site. The landform is predominantly flat, and the sample sites fall within both the Mavumbye and Satara habitat types; which are characterised by deep to shallow red and brown, structured soils and paraduplex clay (Brits *et al.*, 2002). The A-horizon soil of this land type typically has a 42,4% sand: 24% silt: 25,2% clay ratio (Gertenbach, 1983).

Vegetation

Kruger falls with the Savanna Biome (Rutherford *et al.*, 2006), which is defined as having a dominant herbaceous layer of C₄ grasses, with a discontinuous over-story of woody plants. Savannas cover 60% of sub-Saharan Africa, however the highest species richness within this biome is observed in the Southern Hemisphere (Venter *et al.*, 2003). Within Kruger itself, there are seven distinctive vegetation types (Low & Rebelo, 2007), giving rise to 1 998 indigenous plant taxa within the park (Zambatis, 2002). There are high levels of heterogeneity within each of these land type types, and as such they are described by grouping the most dominant soil and vegetation patterns. Vegetation of the Satara land type is described as *Sclerocarya birrea* – *Acacia nigrescens* (now *Senegalia nigrescens*) tree savanna, one of the largest landscapes of Kruger (Gertenbach, 1983). The Mavumbye habitat type is characterised by dense to open *S. nigrescens* bush savanna, and the Satara habitat type by *S. nigrescens*/*Sclerocayra birrea* tree savanna with a high presence of the shrub, *Dichrostachys cinerea*.

Dominant trees within both habitat types include *Sclerocarya birrea*, *S. nigrescens*, and *Combretum imberbe*. The shrub layer is moderately-dense to sparse and is characterised by *Dichrostachys cinerea* subsp. *africana*, *Vachellia gerrardii*, *V. tortilis*, *Grewia bicolor*, *Combretum hereroense*, and *Maerua parvifolia* at the sites. The grass layer is dense and dominated by *Themeda triandra*, *Bothriachloa radicans*, *Urochloa mosambicensis*, *Aristida congesta* subsp. *barbicollis* and *Eragrostis superba*. Other species present include *Enneapogon cenchroides*, *Setaria sphacelata*, *Panicum maximum*, *Heteropogon contortus* and *Sporobolus fimbriatus* (Gertenbach, 1983). Forbs are generally scarce. This area is attractive to high densities of grazing herbivores, as the basalt rock forms in the east gives rise to soils which are high in calcium carbonate (CaCO₃), resulting in extensive, palatable grassy plains (Venter, 1986).

The environment within Kruger has been subject to intervention by management, with experimental practises being subject to knowledge at the time and pragmatism. In savanna vegetation, climate, soils, herbivory and fire interact to shape the environment (van Wilgen *et al.*, 2003). Water provision, fire and culling policies are the main interventions that managers can use to alter this environment (Owen-Smith, 1996). KNP has adopted changing policies on all three of these major interventions throughout the course of its history, with each policy reflecting the evolution of understanding of these drivers in this system.

Fire

Between 1926 and 1947 fire management was limited and practised to induce a green flush for grazers, but by 1948 all prescribed burning was stopped, and firebreaks were established to control wildfires which were perceived as negative (van Wilgen *et al.*, 2003). However, over the course of the next sixty years experimentation with block burning, ring burning and fixed burning intervals brought an understanding of the effects of fire on the vegetation. Furthermore, the development of non-equilibrium theories by Mentis and Bailey (1990) assisted the change from fixed condition burning to burning under diverse conditions (van Wilgen *et al.*, 2003). The current mean fire return intervals in KNP vary between 5.6 and 7.3 years, but are predominantly driven by annual rainfall rather than management interventions. After implementing the principles of the non-equilibrium paradigm, the majority of fire incidences shifted from the wet -season to the dry-season (Van Wilgen *et al.*, 2004). The average size of an area burned is approximately 2500 hectares (ha) (Van Wilgen *et al.*, 2000), and herbivore densities in recently burned areas typically increase for a period following the fire (Biggs, 2003) as grazing herbivores are attracted to the post-fire green flush (Archibald *et al.*, 2005). Fires further alter landscape heterogeneity, and patches which are grazed on post-fire may often be returned to for re-grazing, and may create patches of shorter, more palatable grass interspersed with long, less palatable grasses (Archibald & Bond, 2004).

Water

Similar experimental approaches were taken with water provision throughout KNP. As mentioned, waterholes were first established in the 1930's to stabilise perceived landscape degradation, support rare, water-dependent species and to improve tourism, as animals were drawn close to water points near the roads (Pienaar, 1997). However, the anticipated effects

of support for rare species, such as roan antelope (*Hippotragus equinus*) and tsessebe (*Damaliscus lunatus*), were not realised and instead the distribution of common water-dependent species, such as zebra and wildebeest, and predators increased (Gaylard *et al.*, 2003; Owen-Smith, 1996). Consequently, a large proportion of the waterholes across the landscape have been closed to reverse these effects. There are five perennial rivers which flow across KNP, and many ephemeral rivers, of which larger ones may maintain pools throughout the dry season. Furthermore, the perennial rivers and some of the larger ephemeral rivers have weirs constructed along their watercourses, as a result of the historic water-provision policy, which may also hold water longer in to the dry season (Gaylard *et al.*, 2003). These factors interact to maintain a high level of heterogeneity across the landscape, the primary determinant of the diversity of herbivore species which is supported.

Focus Species

Steenbok

The steenbok (*Raphicerus campestris*, Thunberg 1811) is a small-bodied grazer, relatively common browser that is solitary or occurring in pairs, occasionally with young offspring (Jarman, 1974). The body mass range of the steenbok is 9 – 13 kilograms (kg) (Gagnon & Chew, 2000), and it is classified as a small, non-social, water independent, ruminant browser-grazer intermediate (Hempson *et al.*, 2015). The species occurs widely across East Africa and southern African grasslands, shrublands and savannas. Population dynamics are described as stable and threats faced by habitat conversion is, at present, is not enough to threaten the listing of Least Concern on the IUCN Global Mammal Red List (Palmer *et al.*, 2016). The steenbok is one of the smallest ruminant browsers and as such experiences high metabolic requirements (Demment & Soest, 1985). To overcome their nutritional constraints, steenbok will feed on a variety of high quality forage, including geophytes, berries, forbs, browse and seed pods (Du Toit, 2016), consuming a ratio of 61% dicot forage to 34% monocot and 5% fruit forage (Gagnon & Chew, 2000). Steenbok experience high risk of predation due to their small body size, putting them at risk to both small and large carnivores (Hopcraft, Olff *et al.*, 2010). Because they are a solitary species and cannot rely on aggression or speed to escape predation, they employ methods of crypsis in dense vegetation to avoid predation (Jarman, 1974).

Common Duiker

The common duiker (*Sylvicapra grimmia*, Linnaeus 1758) is a small-bodied, elusive browser that typically occurs singly or in pairs, occasionally accompanied by young offspring (Jarman, 1974). The body mass of the common- duiker is 11 - 25 kg (Gagnon & Chew, 2000; Wilson & Kerley, 2003), and it is classified as a small, non-social, water independent, ruminant obligate browser (Hempson *et al.*, 2015). Common duikers are highly adaptable and unlike other duiker species occur in savanna rather than forest (Birss *et al.*, 2016). This species occurs extensively across southern Africa, and is widespread in all southern African countries excepting Lesotho (Skinner & Chimimba, 2005). Their population dynamics are described as stable and they have no major threats and are thus listed as least concern on the IUCN Global Mammal Red List (Birss *et al.*, 2016). Due to their body size and muzzle width, common duiker are limited to small bites either by means of front bites to obtain single leaves or clusters with the incisors, or cheek bites to remove terminal sections of stems with the molars (Wilson *et al.*, 2003). These smaller bites may have a higher nutritional content due to lower crude fiber, but the common duiker will have to exert increased search effort to obtain higher quality browse (Bailey *et al.*, 1996). Common duiker typically select for a diet of 83% dicot forage, 12% monocot forage and 5% fruit forage (Gagnon & Chew, 2000). Common duiker experience high risk of predation due to their small body size, and the high diversity of predators and predator body size in KNP – they are thus at risk of predation by both small and large carnivores (Hopcraft *et al.*, 2010). Because they are a solitary species and cannot rely on aggression or speed to escape predation, they employ methods of crypsis in dense vegetation to avoid predation (Jarman, 1974).

Impala

The common impala (*Aepyceros melampus melampus*, Lichtenstein 1812), hereafter 'impala', is a small-medium bodied mixed feeder that occurs in groups of 30-150 individuals (Hempson *et al.*, 2015). The body mass of the impala ranges between 30-80 kg (Gagnon & Chew, 2000) and it is classified as a social, water dependent, ruminant browser-grazer intermediate (Hempson *et al.*, 2015). The impala occurs widely across East and southern Africa savannas, and has been introduced to numerous privately-owned game ranches and nature reserves as an extra-limital species in the Northern, Western and Eastern Cape provinces of South Africa. The population is described as stable at present, and the species is thus listed as Least Concern

on the IUCN Global Mammal Red List. The impala is a highly adaptive generalist (Selier *et al.*, 2016), which selects for the highest quality forage available. Impala typically feed on grass heights intermediate between those selected for by wildebeest and zebra (11-20 cm) (Arsenault & Owen-Smith, 2008), as their narrow and small muzzle allows them to pluck green leaves from taller grass swards (Owen-Smith *et al.*, 2017). In the dry season, when grass resources become too high in fiber and low in protein to meet metabolic requirements of impala (McNaughton & Georgiadis, 1986), they are able to effectively switch across to browse resources to meet their nutritional requirements (Du Toit, 2003). Faecal samples collected by Codron *et al.* (2005) showed that impala diet consists of equal parts grass and browse on average. This can be further disseminated into a typical diet selection of 45% monocot forage, 45% dicot forage and 10% fruit forage determined by Gagnon & Chew (2000). Impala experience a high risk of predation due to their smaller body size and the large suite of predators to which they are prey. Due to the gregarious nature of the species, the primary anti-predator strategy is large grouping and employing vigilance (Pays *et al.*, 2012), but under the threat of predation will flee at high speed, making jumps up to 3 metres (m) high and 11 m in length (Estes, 1991a).

Blue wildebeest

The blue wildebeest (*Connochaetes taurinus taurinus*, Burchell 1823), hereafter 'wildebeest', is medium bodied variable grazer that occurs in groups of > 500 individuals (Hempson *et al.*, 2015). The body mass of the wildebeest ranges between 118-290 kg (Gagnon & Chew, 2000) and is classified as a medium-large, social, water dependent, ruminant grazer (Hempson *et al.*, 2015). The wildebeest is typically distributed across southern Kenya, eastern Namibia, Botswana along the Orange River in South Africa and Mozambique, but has also been introduced to parts of Zimbabwe, Namibia and private game farms outside of their range in South Africa. Although the wildebeest population is severely fragmented, the current trend is that it is increasing, and thus the species is listed as Least Concern on the IUCN Global Mammal Red List (Tambling *et al.*, 2016). Wildebeest alter their local distributions by following rainfall in search of high quality forage and typically occur in savanna woodland, as shade and water availability are critical habitat requirements (Skinner *et al.*, 2005). Wildebeest have a wide muzzle, allowing them to maximise nutritional intake through the selection for short grass and recently burned patches (Archibald *et al.*, 2005; Arsenault *et al.*,

2008). Wildebeest will make use of grazing lawns during the wet and early dry season selecting for grass < 10 centimetres (cm), and towards the peak of the late dry season will start distributing more evenly across the landscape and utilising remaining resources of 10-25 cm high (Arsenault *et al.*, 2008; Hempson *et al.*, 2015). Although they have been described as variable grazers, Codron *et al.* (2005) found that on average 95% of wildebeest diet comprised C₄ (monocot) matter. These results are slightly higher than Gagnon & Chew (2000), who described wildebeest as selecting for 87.5% monocot forage, 12% dicot forage and 0.5% fruit forage, suggesting that diet selection may become more varied when foraging resources are more limited. Wildebeest experience a high risk of predation and are the preferred prey of large predators. Their utilisation of grazing lawns and short grass areas aids them in vigilance, the primary means to their anti-predatory strategies (Tambling *et al.*, 2016). Wildebeest will flee at speed from attacking predators, but typically move slowly away from predators prior to attack or form a solid front and walk after predators, preventing them from being able to attack individuals within the herd (Jarman, 1974).

Greater kudu

The greater kudu (*Tragelaphus strepsiceros*, Pallas 1776), hereafter 'kudu', is a medium bodied, ruminant generalist that typically occurs in family groups of 5-15 individuals (Parrini & Child, 2016). The body mass of the kudu ranges between 120-315 kg (Gagnon & Chew, 2000) and is classified as a large, social, water dependent browser (Hempson *et al.*, 2015). The kudu occurs widely across eastern and southern Africa. Although some of the historical range has become restricted in the north of Africa, it generally persists in a large part of its former range due to their ability to survive in areas of sufficient cover. The species is not restricted by livestock fencing and therefore does not experience severe fragmentation, as such the current population trend is increasing, and the species is listed as Least Concern on the IUCN Global Mammal Red List (Parrini & Child, 2016). Kudu preferred habitat is mixed scrub woodland, typically selecting for browse between 1.5 and 2 m high (O'Kane *et al.*, 2011). This species has a narrow muzzle, allowing improved selection of leaves in between browse stems (Pretorius, 2009). Kudu will consume a small amount of monocots (15%), but their diet mostly comprises fruit and dicot forage (30% and 55% respectively) (Gagnon & Chew, 2000). Codron *et al.* (2005) found the consumption of C₄ matter to be very slightly lower, with isotopic analysis indicating C₃ matter comprising 90% of the kudu's diet. Kudu utilise both

cover and crypsis to avoid predation (Bailey *et al.*, 1996), and will become increasingly vigilant in open areas. Furthermore, they will make costly trade-offs to avoid waterholes in open areas, and spend less time browsing to practice high quality vigilance under any threat of predation (Van Der Meer *et al.*, 2012).

Waterbuck

The waterbuck (*Kobus ellipsiprymnus ellipsiprymnus*, Ogilby 1833), is a medium-large bodied, ruminant variable grazer that typically occurs in family groups of 5-15 individuals (Parrini & Relton, 2016). The body mass of the waterbuck ranges between 150-300 kg (Gagnon & Chew, 2000), and it is classified as a medium-large, social, water dependent grazer (Hempson *et al.*, 2015). Waterbuck historically occurred across most of sub-Saharan Africa, however overexploitation and habitat alteration restricted the range of the waterbuck. In South Africa, waterbuck were typically restricted to the north-eastern parts of the country, however introductions outside of their natural range have resulted in some free-roaming populations in the north-western parts of the country. The current population trend of waterbuck is stable, and the species is classified as Least Concern on the IUCN Global Mammal Red List (Parrini & Relton, 2016). Waterbuck are able to efficiently digest fiber and are thus classified as roughage eaters (Parrini & Relton, 2016), typically favouring tall grass swards (Arsenault & Owen-Smith, 2002; Traill, 2004). This species consumes predominantly monocot forage (84%) but will supplement their diet with dicot and fruit (15% and 1% respectively) (Gagnon & Chew, 2000), particularly in the dry season. Waterbuck have also been known to eat aquatic vegetation, and will wade into water to find hydrophytic plant matter (Tomlinson, 1980). Waterbuck prefer dense savanna woodlands in areas of high water density (Parrini & Relton, 2016), and will utilise crypsis, freezing and hiding within or behind dense vegetation to avoid predation (Jarman, 1974), as they experience high risk of predation by large predators such as lions (*Panthera leo*) and leopards (*Panthera pardus*) (Parrini & Relton, 2016).

Plain's Zebra

Plains zebra (*Equus quagga burchellii* Boddeart 1785), hereafter 'zebra', is a medium-large, non-ruminant, obligate grazer that typically occurs in groups of 5-15 individuals (Hempson *et al.*, 2015). However, in KNP where migratory subpopulations exist (Stears *et al.*, 2016), groups of > 50 are not uncommon. The body weight of zebra ranges between 136 and 410 kg (Clauss *et al.*, 2003) and it is classified as a large, water-dependent non-ruminant (Hempson *et al.*,

2015). This zebra sub-species occurs north of the Vaal and Orange rivers of South Africa, extending north into Botswana and south-east into Kwa-Zulu Natal and Swaziland. The zebra is a common, widespread mammal within its distribution range, and the populations on protected areas and private wildlife ranches is increasing, thus the species is classified as Least Concern on the IUCN Global Mammal Red List (Stears *et al.*, 2016). Zebras are so widespread because they are able to utilise a variety of habitats in both temperate and subtropical Africa, typically occurring in open grasslands and savanna woodlands (Skinner *et al.*, 2005). As a hindgut fermenter, zebras are limited in their digestive efficiency (Demment *et al.*, 1985) and must therefore select for large quantities of forage to maintain digestive fill (Redfern *et al.*, 2006). Furthermore, they have a low relative muzzle width to body size and thus they select for grasses > 10 cm to increase intake (Arsenault *et al.*, 2008), and typically consume 90% C₄ (monocot) matter (Codron *et al.*, 2005). Zebras experience high predation and, as a result, modify their behaviour to avoid areas where lions are present, utilising woodland areas rather than open grasslands at night, despite their overall preference for open grasslands (Fischhoff *et al.*, 2007). When under attack from predators, zebras will flee if possible, or stallions will attempt to chase down predators and females will group together and encircle young (Estes, 1991b).

Buffalo

The southern savanna Buffalo (*Syncerus caffer caffer* Sparrman 1779), hereafter 'buffalo', is a large, ruminant variable grazer that typically occurs in groups of > 500 individuals (Hempson *et al.*, 2015). The body mass of the buffalo ranges between 265-850 kg (Gagnon & Chew, 2000), and it is classified as a medium-large, social, water-dependent grazer (Hempson *et al.*, 2015). Buffaloes are widely distributed across Africa, with the southern savanna buffalo occurring in the eastern and southern portions of Uganda, Kenya, Tanzania, Botswana, Zimbabwe and South Africa (Smitz *et al.*, 2013). Buffalo distribution is limited by fences, and their populations are largely restricted to national parks and private game ranches. However, these resident populations are increasing and the species is thus classified as Least Concern by the IUCN Global Mammal Red List (Tambling *et al.*, 2016). Buffaloes are able to inhabit a wide variety of habitats, for which they select based on forage availability, proximity to water, cover against predators and mobility of the herd (Funston *et al.*, 1994). They select for tall grass swards as they have to meet their metabolic requirements in large numbers (Pretorius,

2009), and their digestive system is suited for bulk and roughage intake, although they will sometimes ingest browse to meet nutritional requirements (Venter & Watson, 2008). Their selection for browse however, does not include any fruit material, and their typical diet consists of a ratio of 77.5% monocot matter to 22.5% dicot matter (Gagnon & Chew, 2000). Buffalo are an important food source for lions (Hayward & Kerley, 2005), but are not as vigilant of predators than smaller herbivores. They are easily detected by lions due to their noise and smell, and although they are a risky species to hunt, the reward is so great that some lions will prey upon buffalo exclusively (Hayward *et al.*, 2005). Buffalo will go out of their way to chase lions, and are capable of successfully defending themselves against these predators (Prins & Iason, 1989).

South African giraffe

South African Giraffe (*Giraffa camelopardalis giraffa* Schreber 1784), hereafter 'giraffe', is a browsing ruminant megaherbivore that typically occurs in groups of 30-150 individuals (Hempson *et al.*, 2015). The body mass of giraffes ranges between 680-1400 kg (Clauss *et al.*, 2003), and it is classified as a large, social, water-dependent browser (Hempson *et al.*, 2015). Giraffe formerly occurred in arid and dry-savanna in sub-Saharan Africa, and in South Africa they have been reintroduced in many regions, and now occur in the Mpumalanga Lowveld, north of the Limpopo province, west into the Northern Cape and North West. It has also been introduced into all other South African provinces as an extra-limital species (Deacon & Parker, 2016). Giraffe populations experience severe fragmentation, and although the trend for regional populations in South Africa is increasing, the species has been classified as 'Vulnerable to extinction' on the IUCN Global Mammal Red List (Deacon *et al.*, 2016). Giraffe typically feed in *Vachellia* savanna woodlands, preferring habitat between 0.5 km and 1 km from water (Gaylard *et al.*, 2003). They have a nutritional advantage, as they obtain more biomass per bite in the canopy (>2 m), by avoiding competition with smaller browsers (Cameron & Du Toit, 2007), and typically do not consume any C₄ matter (Codron *et al.*, 2005). Giraffe are one of the preferred prey species of lions, but actively defend themselves and their young under attack of predation (Deacon *et al.*, 2016). Giraffe experience a high risk of predation due to their height, which increases detection capability for predators, and between 50% and 75% of giraffe calves are preyed upon in their first few months (Hayward

et al., 2005). Furthermore, lions prefer to prey upon larger species, as the return for their efforts is greater.

White rhinoceros

The white rhinoceros (*Ceratotherium simum simum* Burchell 1817), hereafter 'rhino', is a non-ruminant obligate megagrazer, usually occurring in groups of 5-15 individuals (Hempson *et al.*, 2015). The body mass of this rhino ranges between 1400-2300 kg (Clauss *et al.*, 2003), and it is classified as a large, water-dependent non-ruminant (Hempson *et al.*, 2015). Rhino historically ranged from Morocco south to South Africa (Skinner *et al.*, 2005), however the species reached the brink of extinction in 1895 as a result of colonial overhunting and habitat loss to agriculture (Emslie & Adcock, 2016). The species was saved by a population of 20-50 individuals which remained in the Umfolozi area of Kwa-Zulu Natal, South Africa. Extensive reintroductions have occurred across Africa to restore the species, and in South Africa more white rhino are protected than anywhere else in the continent. This species experiences severe fragmentation and most subpopulations occur in small, fenced reserves and wildlife ranches, and this species is classified as Near Threatened on the IUCN Global Mammal Red List (Emslie *et al.*, 2016). White rhino prefer open grassland and bushveld savanna, particularly sweetveld (areas that remain highly productive, i.e. nutritious and palatable enough across seasons to prevent weight loss in grazing animals (Masama, 2016)), and require short grass availability, close proximity to water, bush cover and relatively flat terrain (Emslie *et al.*, 2016; Skinner *et al.*, 2005). Rhino have a high muzzle width to body size ratio, and the broad muzzle and wide incisor arcade allows them to select grass < 5 cm to maximise nutrition intake (Arsenault *et al.*, 2008). Rhino are regarded a keystone species due to their role in the creation and facilitation of grazing lawns (Archibald, 2008). They utilise these lawns into the beginning of the dry season, and in the late dry season will select for a mean grass height of 24 cm (Owen-Smith & Goodall, 2014). Rhino are typically an avoided prey species for large predators, however they will opportunistically hunt their young against which rhino will actively defend themselves (Hayward *et al.*, 2005).

African elephant

The African elephant (*Loxodonta africana* Blumenbach 1797), hereafter 'elephant', is a non-ruminant, browser-grazer intermediate that typically occurs in groups of 30-150 individuals (Hempson *et al.*, 2015). The body mass of the elephant ranges between 1700-6100 kg (Clauss

et al., 2003) and it is classified as a large, water dependent, non-ruminant (Hempson *et al.*, 2015). Elephant are distributed across 37 countries in sub-Saharan Africa but have become regionally extinct in five countries since 1913. In South Africa, they occur in all provinces except the Northern Cape and Free State. However, the populations in South Africa are severely fragmented and translocation and intensive management has become necessary to mitigate environmental damage by high-density elephant populations in small reserves. Despite localised population increases in protected areas, elephant are classified as 'Vulnerable to extinction' on the IUCN Global Mammal Red List (Selier *et al.*, 2016). Elephant occur in most habitat types, showing preference for riverine habitats and areas where surface water is available (Chamaillé-Jammes *et al.*, 2007; Gaylard *et al.*, 2003). They typically select forage between 1-1.5 m above ground and have a maximum reach of 6 metres (Stokke & Du Toit, 2000). The enlarged soft mouth parts of the elephant, i.e. the trunk, increases the bite volume and bite mass taken by elephants, but also allows them to select soft plant parts which typically have lower fiber (Pretorius *et al.*, 2015). Elephant are not typically prey species for large predators, however lion will opportunistically try hunting young elephant, against which the herd can successfully defend themselves (Hayward *et al.*, 2005).

Study design

To test the effects of extrinsic and intrinsic constraints on herbivore distribution, I set up 36 experimental plots at three different distances from water at Satara. Suitable sites were identified by mapping distance to water as buffers of 0.5 kilometres (km), 2.5 km and 5 km from all surface water (rivers and artificial waterholes), overlaid across the soil and habitat type layers using ArcGIS v10.5 (ESRI, 2012). Each site consisted of six plots, and each site was replicated once at a location > 2 km from the other (Table 1). Thus, 12 experimental plots were established at each distance of the three distances from water. The 0.5 km sites were located north of the N'wanetsi river, and those 2.5 km and 5 km from water were south of the N'wanetsi (Fig. 1). Five of the six sites fell within the Satara land type in KNP, dominated by *Senegalia nigrescens*/*Sclerocarya birrea* tree savanna, but due to constraints of site suitability (accessibility and distance from water) one of the six sites fell within the Mavumbye habitat type, characterised as *Senegalia nigrescens* bush savanna (Gertenbach, 1983).

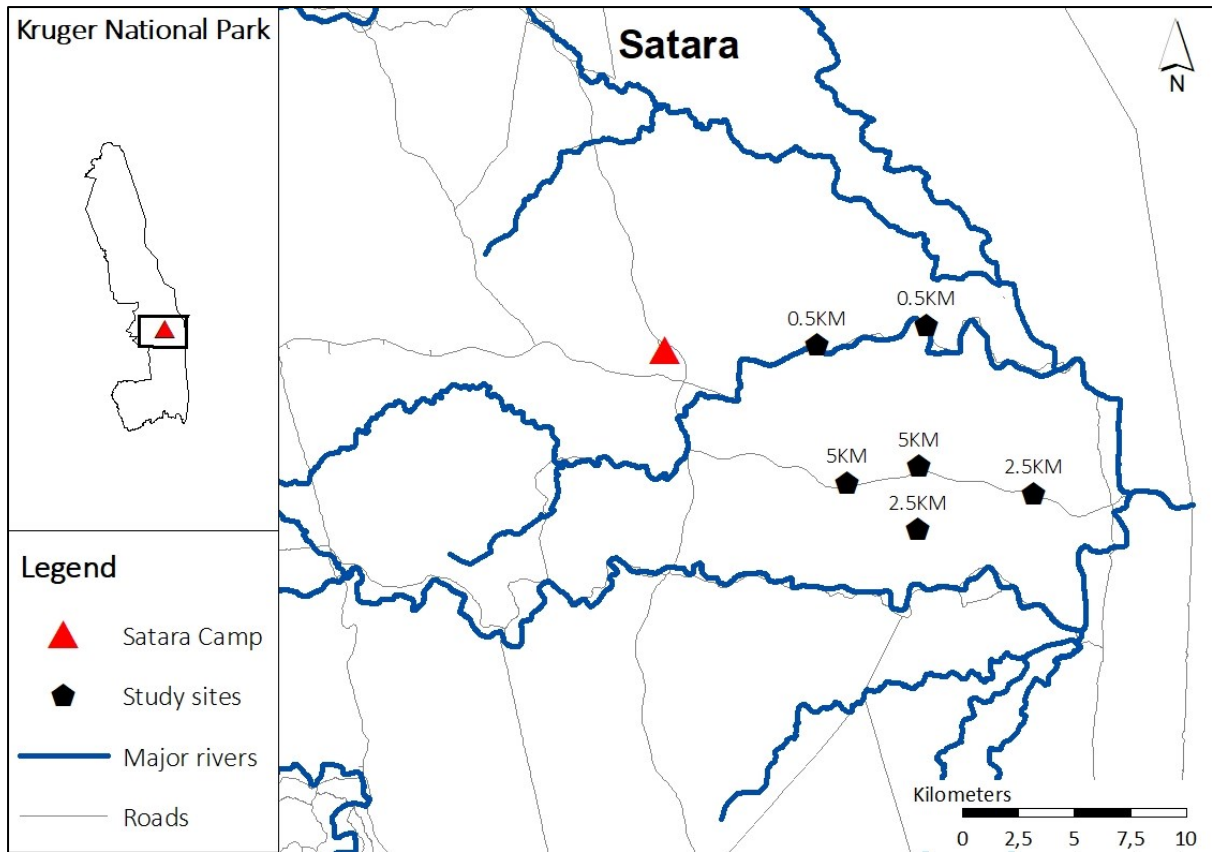


Figure 1: A visual representation of the location of the experimental sites at Satara, KNP in relation to the rest camp, main rivers and road infrastructure.

Table 1: Treatment and location details of experimental sites at the Satara section of KNP.

Replicate 1	Site Code	Treatment	Latitude	Longitude
500m	500-1A	Mown	-24.3826083	031.8927722
500m	500-1B	Mown and Fertilised	-24.3833472	031.8932444
500m	500-1C	Fertilised	-24.3831472	031.8941167
500m	500-1A/C	Control	-24.3832000	031.8926389
500m	500-1B/C	Control	-24.3836556	031.8928861
500m	500-1C/C	Control	-24.3837889	031.8936667
2.5km	2.5-1A	Mown	-24.4639361	031.8900722
2.5km	2.5-1B	Mown and Fertilised	-24.4640306	031.8891611
2.5km	2.5-1C	Fertilised	-24.4636500	031.8881111
2.5km	2.5-1A/C	Control	-24.4648222	031.8899278
2.5km	2.5-1B/C	Control	-24.4647472	031.8892833
2.5km	2.5-1C/C	Control	-24.4643917	031.8879111
5km	5-1A	Mown	-24.4473389	031.8571167
5km	5-1B	Mown and Fertilised	-24.4469917	031.8579417
5km	5-1C	Fertilised	-24.4466500	031.8588583
5km	5-1A/C	Control	-24.4466556	031.8570139
5km	5-1B/C	Control	-24.4461667	031.8573944
5km	5-1C/C	Control	-24.4457944	031.8592472
Replicate 2				
500m	500-2A	Mown	-24.3906861	031.8450306
500m	500-2B	Mown and Fertilised	-24.3908139	031.8459111
500m	500-2C	Fertilised	-24.3910250	031.8465083
500m	500-2A/C	Control	-24.3912361	031.8445917
500m	500-2B/C	Control	-24.3912528	031.8452917
500m	500-2C/C	Control	-24.3918083	031.8460500
2.5km	2.52A	Mown	-24.4508250	031.9392472
2.5km	2.5-2B	Mown and Fertilised	-24.4512417	031.9398917
2.5km	2.5-2C	Fertilised	-24.4515472	031.9405861
2.5km	2.5-2A/C	Control	-24.4513722	031.9392306
2.5km	2.5-2B/C	Control	-24.4515806	031.9397083
2.5km	2.5-2C/C	Control	-24.4519278	031.9402361
5km	5-2A	Mown	-24.4401333	031.8887778
5km	5-2B	Mown and Fertilised	-24.4402806	031.8895167
5km	5-2C	Fertilised	-24.4401750	031.8903000
5km	5-2A/C	Control	-24.4393889	031.8889917
5km	5-2B/C	Control	-24.4393778	031.8894528
5km	5-2C/C	Control	-24.4396139	031.8901250

At each site, six experimental plots were established at the patch scale (Bailey *et al.*, 1996), an ecological neighbourhood where an herbivore undertakes some form of interaction for 1-30 minutes, takes breaks in foraging and would be affected by forage abundance and quality, plant species and social interactions (Addicott *et al.*, 1987; Bailey *et al.*, 1996). Three of the six plots at each site were controls and three underwent the following treatments respectively: removal of the above-ground biomass layer through brushcutting; removal of the above-ground biomass layer through brushcutting and application of fertiliser; and application of fertiliser only (Fig. 2; Fig. 3). Each plot was 400 m² and plots were approximately 100 m apart at each site (Fig. 3). Ritchie and Ollf (1999) hypothesis that large herbivores select resources at a coarse scale, however Crowsigt *et al.*, 2006 found that species across an array of body sizes (warthog, impala, zebra and white rhino) were not affected by the fine-scale plot size (8x8 m). We thus chose an intermediate plot size to optimise data collection across the array of species. At mown plots, small woody shrubs above 1 m were not removed, and plots with little woody biomass were selected for. At fertilised plots, 4 kilograms of 28% LAN/KAN N fertiliser and 3.2 kg of 14% Carbon-enriched, slow-release N fertiliser was applied evenly (Woolley, unpublished data). Sites were evaluated two weeks before each data collection period to determine whether retreatment was necessary, as regrowth in the dry season was low.



Figure 2: A typical representation of treated plots in the wet season (February 2018), with uncut regrowth in the background and the clear removal of above-ground biomass in the foreground.

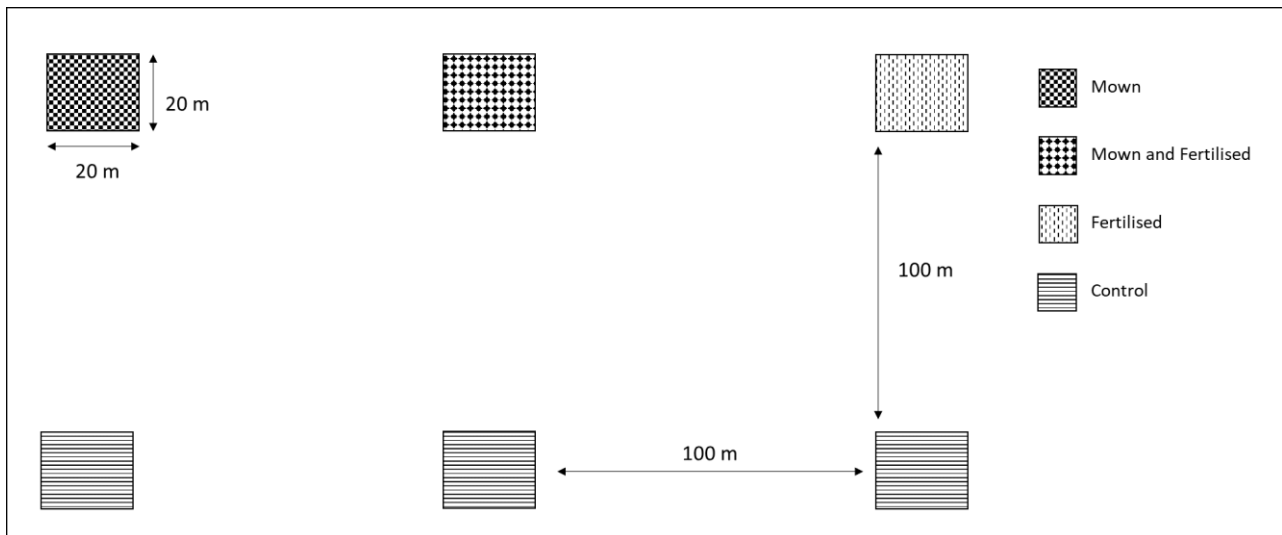


Figure 3: A graphic representation of the plot layout and treatments at each site. This layout was replicated twice at each distance to water, totalling six sites of 36 plots.

Plots were fitted with a Cuddeback Attack Interchangeable Flash (Blue Series, Model 1255) camera trap (Fig. 4). Camera trapping is an effective, non-intrusive and replicable means of surveying mammals over a wide range of environmental and temporal scales (Carbone *et al.*, 2001), allowing a novel means to overcome observational error of dung counts or animal observation counts.



Figure 4: A typical example of camera traps fitting at the sites. Cameras were fitted to trees or tree stumps along the edge of the plot where possible, at 0.5 m to 1 m above ground to have the best view of the plot. The treatment edge is also visible along the back and sides of the camera, with uncut regrowth in the background.

Camera traps were fitted to each plot to have the best visual of the 400 m² plot area and were placed between 0.5 m and 1 m from the ground. They were angled away from the sun where possible, and set to a wide view angle, Fresnel cover lowered and aspect wide. The camera traps were set to take photographs at 10-minute intervals when activity was sensed. Finally, they were serviced (batteries replaced, and data retrieved) every three months, but batteries lasted on average five weeks, resulting in five weeks of data per season.

This experimental design allowed me to test for the effects of environmental attributes on the composition of herbivore assemblages through the combined effort of the camera traps at each site in Chapter 3, and the effect of plot treatment on grazing herbivores in Chapter 4.

Literature Cited

- Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S., & Soluk, D. A. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos*, 340-346.
- Archibald, S. 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *The journal of wildlife management*, 72(2), 492-501.
- Archibald, S., & Bond, W. J. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13(3), 377-385.
- Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. 2005. Shaping the Landscape: Fire-Grazer Interactions in an African Savanna. *Ecological Applications*, 15(1), 96-109.
- Arsenault, R., & Owen-Smith, N. 2002. Facilitation versus competition in grazing herbivore assemblages. *Oikos*, 97(3), 313-318.
- Arsenault, R., & Owen-Smith, N. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, 117(11), 1711-1717.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386-400.
- Biggs, H.C., J. T. Du Toit, Rodgers, K.H. (Eds.) 2003. *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Birss C, Relton, C, Selier, J. 2016. A conservation assessment of *Sylvicapra grimmia*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT (Eds.). *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Bonnet, O., Fritz, H., Gignoux, J., & Meuret, M. 2010. Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. *Journal of Ecology*, 98(4), 908-916.
- Brits, J., Rooyen, M. W. V., & Rooyen, N. V. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*, 40(1), 53-60.
- Cameron, E. Z., & Du Toit, Johan T. 2007. Winning by a Neck: Tall Giraffes Avoid Competing with Shorter Browsers. *The American Naturalist*, 169(1), 130-135.

- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., & Kinnaird, M. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4(1), 75-79.
- Carruthers, J. 1995. *The Kruger National Park: a social and political history*. University of Natal Press, Pietermaritzburg.
- Chamaillé-Jammes, S., Valeix, M., & Fritz, H. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal of Applied Ecology*, 44(3), 625-633.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., & Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, 136(1), 14-27.
- Codron, D., Codron, J., Sponheimer, M., Lee-Thorp, J., Robinson, T., Grant, C. C., & De Ruiter, D. 2005. Assessing diet in savanna herbivores using stable carbon isotope ratios of faeces. *Koedoe*, 48(1), 115-124.
- Codron, D., Lee-Thorp, J. A., Sponheimer, M., Codron, J., de Ruiter, D., & Brink, J. S. 2007. Significance of diet type and diet quality for ecological diversity of African ungulates. *Journal of Animal Ecology*, 76(3), 526-537.
- Creel, S., Winnie, J., Jr., Maxwell, B., Hamlin, K., & Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86(12), 3387-3397.
- Cromsigt, J. P., Prins, H. H., & Olf, H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions*, 15(3), 513-522.
- Cromsigt, J. P. G. M., & Olf, H. 2006. Resource Partitioning among Savanna Grazers Mediated by Local Heterogeneity: An Experimental Approach. *Ecology*, 87(6), 1532-1541.
- Cromsigt, J.P. & Te Beest, M., 2014. Restoration of a megaherbivore: landscape-level impacts of white rhinoceros in Kruger National Park, South Africa. *Journal of Ecology*, 102(3), 566-575.

- De Knegt, H. J., Van Langevelde, F., Skidmore, A. K., Delsink, A., Slotow, R., Henley, S., Bucini, G., De Boer, W. F., Coughenour, M. B., Grant, C. C., Heitkönig, I. M. A., Henley, M., Knox, N. M., Kohi, E. M., Mwakiwa, E., Page, B. R., Peel, M., Pretorius, Y., Van Wieren, S. E., & Prins, H. H. T. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, 80(1), 270-281.
- Deacon F, Parker D. 2016. A conservation assessment of *Giraffa camelopardalis giraffa*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Demment, M. W., & Soest, P. J. V. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125(5), 641-672.
- Du Toit, J. T. 2003. Large herbivores and savanna heterogeneity. Pp 292-309 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Du Toit, J. T. 2016. *Raphicerus campestris* Steenbok (*Steinbuck, Steinbok*). Pages 311-314 in: Kingdon, J. & Hoffmann, M. (eds.) Mammals of Africa, vol. VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids.) Bloomsbury, London, UK.
- Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G., & Lloyd, M. 1990. Comparative Nutrient Extraction from Forages by Grazing Bovids and Equids: A Test of the Nutritional Model of Equid/Bovid Competition and Coexistence. *Oecologia*, 84(3), 411-418.
- Emslie R, Adcock K. 2016. A conservation assessment of *Ceratotherium simum simum*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa
- ESRI. 2012. ArcGIS (Version 9.3). Redlands, CA.
- Estes, R., 1991a. Hartebeests, Topi, Blesbok and Wildebeests: Tribe Alcelaphini. Pp 133-167 in Estes, R., (Ed.). *The behavior guide to African mammals* (Vol. 64) University of California Press, Berkeley.
- Estes, R., 1991b. Zebras, Asses, and Horses: Family Equidae. Pp 235-249 in Estes, R., (Ed.). *The behavior guide to African mammals* (Vol. 64) University of California Press, Berkeley.

- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5), 1155-1164.
- Fischhoff, I. R., Sundaesan, S. R., & Cordingley, J., D.I. 2007. Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology*, 18, 725-729.
- Fleurance, G., Duncan, P., Fritz, H., Gordon, I.J. & Grenier-Loustalot, M.F. 2010. Influence of sward structure on daily intake and foraging behaviour by horses. *Animal: an international journal of animal bioscience*, 4(3), 480-485.
- Funston, P. J., Skinner, J. D., & Dott, H. M. 1994. Seasonal variation in movement patterns, home range and habitat selection of buffaloes in a semi-arid habitat. *African Journal of Ecology*, 32(2), 100-114.
- Gagnon, M., & Chew, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, 81(2), 490-511.
- Gaylard, A., Owen-Smith, N., & Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pp 171-189 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Gertenbach, W. D. 1983. Landscapes of the Kruger National Park. *Koedoe*, 26(1), 9-121.
- Gordon, I. J., & Illius, A. W. 1996. The nutritional ecology of African ruminants: A reinterpretation. *Journal of Animal Ecology*, 65(1), 18-28.
- Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R., & Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, 90(1), 69-78.
- Hassan, S. N., Rusch, G. M., Hytteborn, H., Skarpe, C., & Kikula, I. 2007. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *African Journal of Ecology*, 46(2), 174-185.
- Hayward, M. W., & Kerley, G. I. H. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, 267(3), 309-322.
- 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(6264), 1056-1061.

- Holland, E. A., & Detling, J. K. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology*, 71(3), 1040-1049.
- Hopcraft, J. G. C., Olf, H., & Sinclair, A. R. E. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2), 119-128.
- Jarman, P. J. 1974. The Social Organisation of Antelope in Relation To Their Ecology. *Behavior*, 48(1), 215-267.
- Kay, R. 1997. Responses of African livestock and wild herbivores to drought. *Journal of Arid Environments*, 37(4), 683-694.
- Klop, E., van Goethem, J., & de longh, H. H. 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research*, 34(2), 77-83.
- Le Roux, E., Kerley, G.I. & Cromsigt, J.P. 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, 28(15), 2493-2499.
- Low, A., Rebelo, A. (Eds.), 2007. *The Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs, Pretoria.
- Ludwig, F., De Kroon, H., Berendse, F., & Prins, H. H. 2004. The influence of savanna trees on nutrient, water and light availability and the understory vegetation. *Plant Ecology*, 170(1), 93-105.
- Mabunda, D., Pienaar, D. J., & Verhoef, J. 2003. The Kruger National Park: a century of management and research. Pp 3-22 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Masama, E. 2016. Research note: Impact of climate change on livestock production in Zimbabwe. *International Open and Distance Learning Journal*, 2(1).
- McNaughton, S. J., & Georgiadis, N. J. 1986. Ecology of African Grazing and Browsing Mammals. *Annual Review of Ecology and Systematics*, 17, 39-65.
- Mentis, M., & Bailey, A. 1990. Changing perceptions of fire management in savanna parks. *Journal of the Grassland Society of Southern Africa*, 7(2), 81-85.
- Murray, M. G., & Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti: An experimental test. *Journal of Animal Ecology*, 62(2), 10.

- O'Connor, T. G., & Pickett, G. A. 1992. The Influence of Grazing on Seed Production and Seed Banks of Some African Savanna Grasslands. *Journal of Applied Ecology*, 29(1), 247-260.
- O'Kane, C. A., Duffy, K. J., Page, B. R., & Macdonald, D. W. 2011. Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, 27(3), 249-258.
- O'Kane, C. A., & Macdonald, D. W. 2018. Seasonal influences on ungulate movement within a fenced South African reserve. *Journal of Tropical Ecology*, 34(3) 200-203.
- Owen-Smith, N. 1985. Niche separation among African ungulates. *Species and Speciation. Transvaal Museum Monograph*, 4, 167-171.
- Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, 26(4), 107-112.
- Owen-Smith, N., Cromsigt, J. P., & Arsenault, R. 2017. Megaherbivores, Competition and Coexistence within the Large Herbivore Guild. Pp 111-135 In Cromsigt J. P. M., Archibald, S. & Owen-Smith, N. (Eds.) *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. Cambridge University Press, Cornwall.
- 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(3), 181-191.
- Owen-Smith, N., & Novellie, P. 1982. What Should a Clever Ungulate Eat? *The American Naturalist*, 119(2), 151-178.
- Palmer G, Birss C, Du Toit JT. 2016. A conservation assessment of *Raphicerus campestris*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. *Journal of Animal Ecology*, 77(6), 1191-1198.
- Parrini F, Child MF. 2016. A conservation assessment of *Tragelaphus strepsiceros*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

- Parrini F, Relton C. 2016. A conservation assessment of *Kobus ellipsiprymnus ellipsiprymnus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT,(Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, 169(2), 419-430.
- Pérez-Barbería, F. J., Gordon, I. J., & Nores, C. 2001. Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research*, 3(2), 221-230.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D. W., & Loveridge, A. J. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, 23(5), 970-976.
- Pienaar, D., H. Biggs, A. Deacon, W. Gertenbach, S. Joubert, F. Nel, L. van Rooyen, & F. Venter. 1997. A revised water-distribution policy for biodiversity maintenance in the KNP. *Kruger Park Management Plan, Vol. 8, South African National Parks, Skukuza, South Africa*.
- Pretorius, Y. 2009. *Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores*. Unpublished MSc Thesis, Wageningen University, Netherlands.
- Pretorius, Y., de Boer, W.F., Kortekaas, K., van Wijngaarden, M., Grant, R.C., Kohi, E.M., Mwakiwa, E., Slotow, R. & Prins, H.H. 2016. Why elephant have trunks and giraffe long tongues: how plants shape large herbivore mouth morphology. *Acta Zoologica*, 97(2), pp.246-254.
- Prins, H. H. T., & Iason, G. R. 1989. Dangerous Lions and Nonchalant Buffalo. *Behaviour*, 108(3), 262-296.
- Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8), pp.2092-2107.
- Redfern, J. V., Ryan, S. J., & Getz, W. M. 2006. Defining herbivore assemblages in the Kruger National Park: a correlative coherence approach. *Oecologia*, 146(4), 632-640.

- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124-133.
- Riginos, C., & Grace, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, 89(8), 2228-2238.
- 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(4), e1400103.
- Rutherford, M. C., Mucina, L., Lotter, M. C., Smit, J. H. L., Bredenkamp, G. J., Scott-Shaw, C. R., Hoare, D. B., Goodman, P. S., Bezuidenhout, H., Scott, L., Ellis, F., Powrie, L. W., Siebert, S. J., Matthews, W. S., Burrows, J. E., Dobson, L., van Rooyen, N., Schmidt, E., Winter, P. J. D., du Preez, P. J., Ward, R. A., Williamson, S., & Hurter, P. J. H. 2006. Savanna Biome. In L. Mucina & M. C. Rutherford (Eds.), *The vegetation of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.
- Selier SAJ, Henley M, Pretorius Y, Garai M., 2016. A conservation assessment of *Loxodonta africana*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Selier SAJ, Hoffman L, Castley G. 2016. A conservation assessment of *Aepyceros melampus melampus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa
- Shackleton, C. M. 1992. Area and species selection by wild ungulates in coastal sour grasslands of Mkambati Game Reserve, Transkei, southern Africa. *African Journal of Ecology*, 30, 189-202.
- Shipley, L.A., 1999. Grazers and browsers: how digestive morphology affects diet selection. *Grazing behavior of livestock and wildlife*, 70, pp.20-27.
- Shrader, A. M., Bell, C., Bertolli, L., & Ward, D. 2012. Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica*, 42(0), 3-10.
- Sinclair, A., Mduma, S., & Brashares, J. S. 2003. Patterns of predation in a diverse predator–prey system. *Nature*, 425(6955), 288.

- Sinclair, A.R.E. & Norton-Griffiths, M. (Eds.) 1995. Chapter One. Pp 1-28 in *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Skinner, J. D., & Chimimba, C. T. 2005. *The Mammals of the Southern African Subregion* (Third edition). Cambridge University Press, New York.
- Smit, I. P. J., Grant, C. C., & Devereux, B. J. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136(1), 85-99.
- Smitz, N., Berthouly, C., Cornelis, D., Heller, R., Van Hooft, P., Chardonnet, P., Caron, A., Prins, H., Van Vuuren, B. J., & De longh, H. 2013. Pan-African genetic structure in the African buffalo (*Syncerus caffer*): investigating intraspecific divergence. *PLoS One*, 8(2), e56235.
- Stears K, Shrader A, Castley G. 2016. A conservation assessment of *Equus quagga*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT,(Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Stokke, S., & Du Toit, J. T. 2000. Sex and size related differences in the dry season feeding patterns of elephants in Chobe National Park, Botswana. *Ecography*, 23(1), 70-80.
- Tambling C, Venter J, Du Toit J, Child M. 2016. A conservation assessment of *Syncerus caffer caffer*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Tambling C, Viljoen P, Kotze A. 2016. A conservation assessment of *Connochaetes taurinus taurinus*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, (Eds.). The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.
- Tomlinson, D. 1980. Seasonal food selection by water buck *Kobus ellipsiprymnus* in a Rhodesian Game Park. *South African Journal of Wildlife Research*, 10(1), 22-28.
- Tomor, B. M., & Owen-Smith, N. 2002. Comparative use of grass regrowth following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology*, 40(2), 201-204.

- Trails, L. W. 2004. Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. *South African Journal of Wildlife Research*, 34(1), 13-24.
- Trollope, W., & Potgieter, A. 1986. Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa*, 3(4), 148-152.
- Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23-30.
- Van Der Meer, E., Pays, O., & Fritz, H. 2012. The Effect of Simulated African Wild Dog Presence on Anti-predator Behaviour of Kudu and Impala. *Ethology*, 118(10), 1018-1027.
- van Ginkel, H. A. L., Kuijper, D. P. J., Schotanus, J., & Smit, C. 2018. Wolves and Tree Logs: Landscape-Scale and Fine-Scale Risk Factors Interactively Influence Tree Regeneration. *Ecosystems*, 1-11.
- van Wilgen, B.W., Biggs, H.C., O'Regan, S.P. & Marè, N. 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science*, 96(4), pp.167-178.
- Van Wilgen, B., Govender, N., Biggs, H., Ntsala, D., & Funda, X. 2004. Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, 18(6), 1533-1540.
- van Wilgen, B. W., Trollope, W. S., Biggs, H. C., Potgieter, A. L., & Brockett, B. H. 2003. Fire as a driver of ecosystem variability. Pp 149-170 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Venter, F. 1986. Soil patterns associated with the major geological units of the Kruger National Park. *Koedoe*, 29(1), 125-138.
- Venter, F., Scholes, R. J., & Eckhardt, C. 2003. The abiotic template and its associated vegetation pattern. Pp 83-130 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Venter, J. A., Prins, H. H. T., Mashanova, A., de Boer, W. F., & Slotow, R. 2015. Intrinsic and extrinsic factors influencing large African herbivore movements. *Ecological Informatics*, 30, 257-262.

- 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(1), 42-51.
- Vie, J.-C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2009). State of the world's species. Pp 15-43 in *Wildlife in a changing world: An analysis of the 2008 IUCN Red List of Threatened Species*. Gland, Switzerland, IUCN.
- Waldram, M. S., Bond, W. J., & Stock, W. D. 2008. Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna. *Ecosystems*, 11(1), 101-112.
- Walker, S. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research*, 6(1), 1-32.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, 13(3-4), 265-286.
- Westhoff, V. & Van Der Maarel, E. 1978. The braun-blanquet approach. Pp 287-399 in R. H. Whittaker (Ed.), *Classification of plant communities*. Springer, Dordrecht.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.
- Wilson, S. L., & Kerley, G. I. 2003. Bite diameter selection by thicket browsers: the effect of body size and plant morphology on forage intake and quality. *Forest Ecology and Management*, 181(1-2), 51-65.
- Woolley, L. A. Ecosystem level N and P effects on carbon assimilation and growth by savanna shrubs. Unpublished data.
- Zambatis, N. 2002. *Checklist of species of the Kruger National Park, Skukuza Herbarium*. Scientific Services, Kruger National Park Skukuza, South Africa. Skukuza.

Chapter 3: The landscape scale drivers of herbivore assemblage distribution in the basalt grassland plains of Kruger National Park

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Abstract

The distribution and abundance of herbivores in African savannas are constrained by interactions between abiotic and biotic factors. At the species-level, herbivores face trade-offs among foraging requirements, vegetation structure, and the availability of surface water that change over spatial and temporal scales. Characterising herbivore requirements is necessary for the management of the environment in which they occur, as conservation management interventions such as fencing and artificial water provision consequently have effects on how herbivores address these trade-offs. We tested the effects of environmental attributes on the probability of presence of herbivore functional types at different distances to water in the Satara section of Kruger National Park over the period of a year. Hypotheses about species' relative distribution and abundance were developed through a literature review of forage and water availability constraints on feeding preference and body size of herbivore biomass. We expected strong seasonal relationships between vegetation biomass and quality, and biomass of water-dependent herbivores with increasing distance to water. Our analyses of herbivore distribution across the region confirmed broad-scale descriptions of interactions between forage requirements and water availability across a set of species which differ in functional traits.

Introduction

Large mammalian herbivores form an essential component of the natural environment in which they occur due to the impact that they have on the structure and functioning of ecosystems (Hempson *et al.*, 2015). Their preference for certain habitat types is determined by complex interactions between external factors including forage availability and quality, water availability, soil type, topography, season and predation (Bailey *et al.*, 1996; O'Kane & Macdonald, 2018). Furthermore, intrinsic factors such as feeding type and morphology interact with resource competition, habitat requirements and facilitation, affecting species-richness and the structure of herbivore assemblages (Cromsigt *et al.*, 2009; Gordon & Illius, 1996). Due to the impacts that herbivores have on their surrounding environment, understanding the interactions which govern the selection for certain habitats by herbivores is important for their conservation management.

Herbivores select the habitat in which they feed over several temporal and spatial scales. At broader spatial extents, dispersal or migration may be necessary due to constraints of water availability, forage abundance, competition and thermoregulation, whereas at smaller extents these constraints include topography, distance from water, forage quality and quantity, and predation (Bailey *et al.*, 1996). Along the body size spectrum, the quality of forage becomes less important than quantity of forage due to the digestive constraints of smaller herbivores (Demment & Soest, 1985). As a result, smaller herbivores exert larger search efforts compared to larger herbivores to find higher quality forage (Bailey *et al.*, 1996). Thus, in times where forage quality is limited, smaller herbivores are expected to search for areas where they can improve diet quality. However, larger herbivores are expected to feed in areas where they can maximise forage intake (Demment *et al.*, 1985). Forage quality is affected by soil nutrient content (Holland & Detling, 1990), season and regrowth as a response to herbivory and/or fire (Wilsey, 1996). Finally, the feeding type of herbivores is also closely related to their water dependency, with grazers and mixed feeders experiencing higher levels of water dependency than browsers (Hempson *et al.*, 2015).

Habitat attributes selected for by herbivores also include predator avoidance. In areas of diverse herbivore and predator body sizes, smaller herbivores are exposed to a greater risk of predation than larger herbivores, as both small and large predators can consume small-bodied

prey (Hopcraft *et al.*, 2010). Gregariousness of the species and body size affects predator-avoidance strategies, and herbivores may select more open or dense habitats dependent on the anti-predator strategies they employ (Creel *et al.*, 2005; Riginos & Grace, 2008). Herbivores are therefore regulated by top-down (predation) or bottom-up (forage quality and availability) processes (Hopcraft *et al.*, 2010). These processes however may not be mutually exclusive. The underlying environmental gradients at the larger scale: soil, climate and water availability and their subsequent effect on forage quality and quantity is therefore the primary constraint on herbivore distribution across the landscape (Bailey *et al.*, 1996; Hopcraft *et al.*, 2010).

The complexity of interactions between these processes underpins the importance of understanding savanna ecology to management. Substantial contributions to this understanding have been made by the rich history of monitoring and research which has emerged over the last century from Kruger National Park (hereafter 'KNP') (Biggs, 2003). KNP has a vastly heterogeneous landscape with diverse herbivore assemblages, which facilitates the study of the trade-offs herbivores face across multiple spatial and temporal scales. One of the primary environmental gradients which determines herbivore distribution, water availability, has been contentious in the context of KNP due to extensive water provision policies (Pienaar, 1997; Smit *et al.*, 2007). In 2003, KNP had less than 8% surface area further than 5 kilometres (km) from water (Gaylard *et al.*, 2003). This resulted in an observable decrease in grasses and woody cover closer to artificial water points, the decline of rare herbivores due to an increase in predators, and fluctuations in common herbivore population numbers (Brits *et al.*, 2002; Gaylard *et al.*, 2003; Harrington *et al.*, 1999). Due to these effects, KNP management revised their water provision policy and began to close waterholes across the landscape (Pienaar, 1997).

Considering the increasing decline in global herbivore populations (Ripple, Newsome *et al.*, 2015; Vie, Hilton-Taylor *et al.*, 2009); it is critical that a comprehensive understanding of the drivers of herbivore distribution across landscapes be developed. study aimed to test whether herbivores follow previously described trends across the Satara landscape, and to test effective means of measuring the determinants of herbivore biomass within certain habitats across a set of species which differ in functional traits. Herbivore studies typically classify

species into groups of similar traits (Hempson *et al.*, 2015; Shipley, 1999), and this provides a baseline against which to evaluate broad-level trends across different feeding types and body sizes of herbivores. Using these trends, we tested the effect of habitat attributes on eleven herbivore species at the Satara section of KNP. We tested a number of hypotheses related to the body size and feeding type of these herbivores against habitat attributes: a) we expected risk of predation to be a stronger predictor of space use by small-bodied herbivores than larger herbivores; b) we expected feeding type to be a strong predictor of increased daily herbivore presence in relation to distance from water because grazers tend to be more water-dependent; c) we expected the daily presence of certain body sizes and feeding types of herbivores to be strongly predicted by forage quality and quantity, with medium-bodied grazers and small mixed-feeders increasing at higher quality forage, and large grazers increasing at higher quantity forage; and d) we expected a strong effect of season on the biomass of grazing and mixed-feeder herbivore distribution across the landscape, with biomass and distribution decreasing further from water in the dry season and the reverse for the wet season.

Methods

Study area

This study was conducted in the Satara section of KNP, which is situated at the north-eastern corner of South Africa (24.01°S, 31.49°E). Satara receives a mean annual rainfall of 547 mm (February *et al.*, 2013). The region experiences mean minimum temperatures of 10°C and 20°C and mean maximum temperatures of 26.3°C and 32.6°C in July and December respectively (Parr, 2008). The vegetation is characterised by *Senegalia nigrescens/Sclerocarya birrea* tree savanna (Gertenbach, 1983). Habitats of this area are attractive to herbivores as two ephemeral rivers, the N'wanetsi and Sweni rivers, typically flow once or twice in the wet season and have a number of pools which may persist in the dry season. Furthermore, surface water may take longer to evaporate on the clayey basaltic soils of the region, resulting in water being more locally available across the landscape in the wet season in the form of pans (Gaylard *et al.*, 2003). The Letaba basalt soil type contributes to study area suitability, as it has higher calcium carbonate (CaCO₃) concentrations, which gives rise to extensive grassy plains (Venter, 1986) that are dominated by highly palatable grass species such as *Urochloa*

mosambicensis and *Digitaria eriantha* (O'Connor & Pickett, 1992). The area is also exposed to occasional wild-fires and prescribed burns (Van Wilgen *et al.*, 2004).

Site design

Suitable sites were identified by mapping distance to water, soil type and vegetation type as buffers of 0.5 km, 2.5 km and 5 km from all surface water (rivers and artificial waterholes), overlaid across the soil and habitat type layers using ArcGIS v10.5 (ESRI, 2012). Site suitability was characterised by relative distance to water, soil type, habitat type, accessibility and the absence of previous experimental manipulation. Six sites were placed at three different distances to water, with sites 0.5 km from water situated north of the N'wanetsi river and those 2.5 km and 5 km from water south of the N'wanetsi river (Fig. 1). Five of the six sites fell within the Satara land type in KNP, dominated by *Senegalia nigrescens*/*Sclerocarya birrea* tree savanna, but due to constraints of site suitability one of the six sites fell within the Mavumbye habitat type, a similar land type characterised as *Senegalia nigrescens* bush savanna (Gertenbach, 1983). Sites were sampled in June 2017, October 2017, February 2018 and June 2018, resulting in three sets of seasonal data, namely 'late dry', 'early wet' and 'late wet' seasons. Wildfires occurred throughout the sampling period, resulting in one site at 2.5 km burning in June 2017, and both 5 km sites burning in November 2017.

Each site consisted of six 20x20 m plots, 100 m apart, each fitted with a Cuddeback Attack Interchangeable Flash (Blue Series, Model 1255) camera trap. Plots were set up as part of a study on patch scale selection by herbivores. Camera trap data was thus the combined trapping effort of six cameras per site, each totalling an approximate area of 3.12 ha. We are confident that the plot treatments have not affected our evaluation of these landscape scale patterns, as the scale at which this paper is focused is inherently inclusive of patch scale selection in some species (Cromsigt & Olf, 2006; Pretorius, 2009). Camera trapping is an effective, non-intrusive and replicable means of surveying mammals over a wide range of environmental and temporal scales (Carbone *et al.*, 2001), allowing a novel means to overcome observational error of dung counts or animal observation counts.

Camera traps were fitted to each plot to have the best visual of the 400 m² plot area and were placed between 0.5 m and 1 m from the ground. They were angled away from the sun where possible, and set to a wide view angle, Fresnel cover lowered and at a wide aspect. The camera traps were set to take photographs at 10-minute intervals when activity was sensed. Finally,

they were serviced (batteries replaced, and data retrieved) every three months, but batteries lasted on average five weeks, resulting in five weeks of data per season.

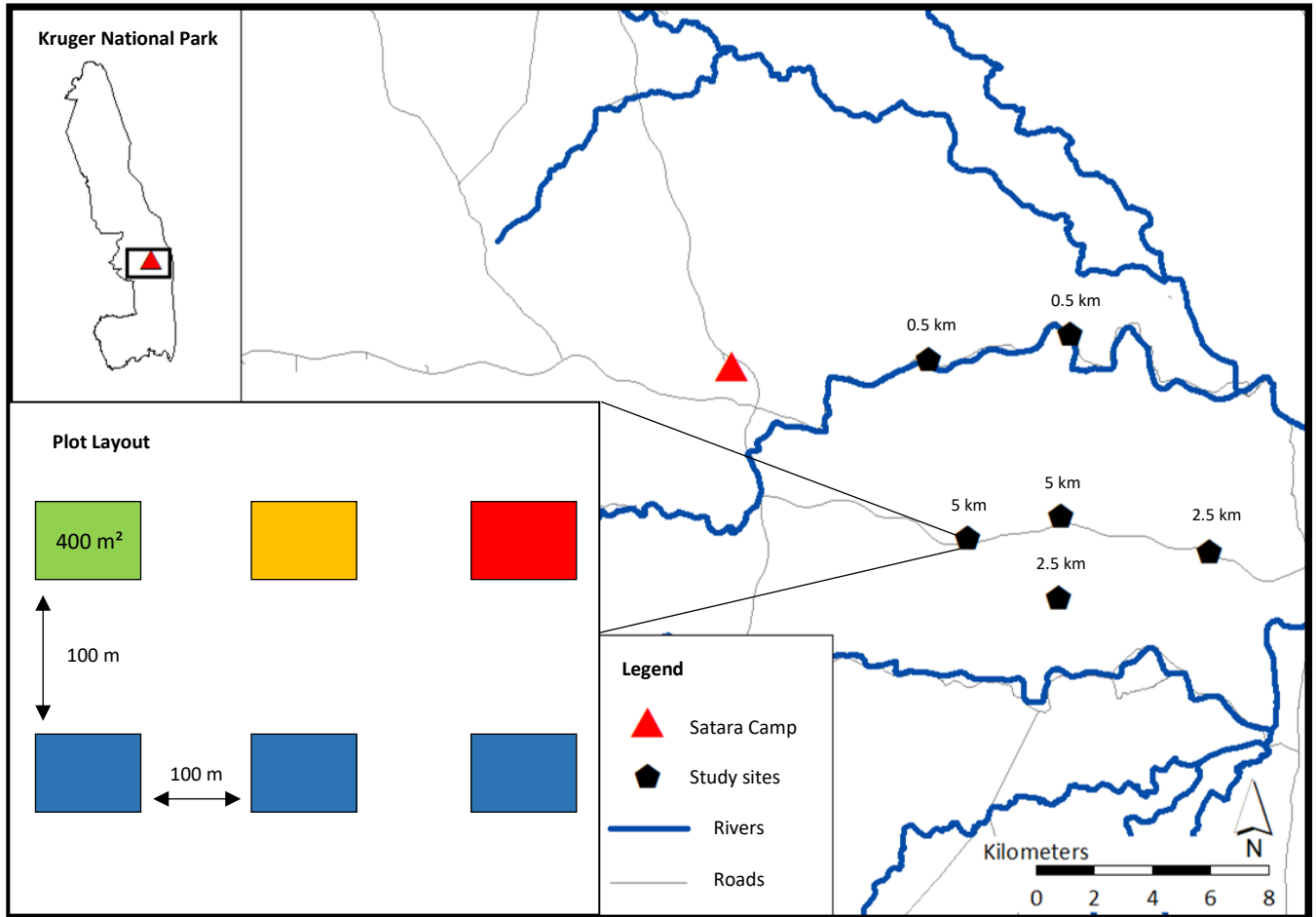


Figure 1: Map of the Satara section where the study was conducted, relative to the Satara Rest Camp. The site layout reads as follows: green plot= mown; yellow= mown and fertilised; red=fertilised only; blue=control. Plots were placed approximately 100 m apart and were 400 m² in size.

Herbivore biomass

The broad spatial and seasonal trends assessed in this study focused on water availability, forage constraints and habitat requirements of the herbivore species which commonly occur in the Satara region of KNP. These herbivore species were selected due to their representation of a suite of feeding preferences and body sizes, and the quantity of data collected by camera traps. The herbivore species were thus: five grazers (blue wildebeest *Connocheates taurinus*, Burchell's zebra *Equus quagga burchelli*, buffalo *Syncerus caffer*, waterbuck *Kobus ellipsiprymnus*, white rhinoceros *Ceratotherium simum*); four browsers (common duiker

Sylvicapra grimmia, giraffe *Giraffa camelopardalis giraffa*, greater kudu *Tragelaphus strepsiceros*, steenbok *Raphicerus campestris*); and two mixed feeders (elephant *Loxodonta africana* and impala *Aepyceros melampus*). Attributes were assigned to camera trap data as follows: date; species within the photo; number of individuals; time of day; functional characteristics (body size, feeding preference and digestive type), hereafter 'functional types'. Feeding preference followed the three generalist functional classifications of ungulate herbivores: namely grazer, browser and mixed feeder (Gordon *et al.*, 1996; McNaughton & Georgiadis, 1986; Owen-Smith & Novellie, 1982). Count data from captures were converted to the midpoint of the body weight range per species as described by Clauss *et al.* (2003). As biomass values for size classes 'small' and 'large' were low due to low detection by camera traps, these size classes were merged with 'small-medium' and 'medium-large' respectively. Biomass duplications for species which remained at the site for the period of more than one hour were removed from data prior to analysis.

Environmental covariates

Distance to water (km) was the primary determinant of site placement as it typically dictates herbivore movement (Gaylard *et al.*, 2003) and seasonal population fluctuations of herbivore species in savanna systems. The distance from the N'wanetsi and Sweni rivers, and the associated waterholes of the area, was used to determine suitable sites of the three distances from water. Predation was measured through camera trap data, allowing covariates of predator species, incidences of multiple predators and days since predator presence to be measured. Lion (*Panthera leo*) photo captures were also recorded as an individual variable due to the strong influence they have on foraging and vigilance behaviour of a range of herbivore body sizes (Périquet *et al.*, 2012; Valeix *et al.*, 2009). Camera trap data were also used to determine grass height (using a marked pole in front of each camera), and plot burn data (burnt/unburnt and days since fire).

The average distance to the nearest visual obstruction was measured as a proxy for landscape of fear, given that distance to the nearest obstruction changes risk of ambush by a predator and anti-predator strategies employed by herbivore species. This value was the mean of measurements to the nearest obstruction (trees or shrubs) on each plot, using a range finder at a height of 1.5 m every 15 degrees, totalling 24 measurements (Riginos, 2015). The inverse of these measures was used to determine the distance between trees.

The following environmental variables were taken on each plot at each data collection period to measure forage quantity and quality: grass biomass using a disc pasture meter (Trollope & Potgieter, 1986), for which the measurement value was used as a representation for biomass; grass quality using the Walker 8-point scale (Walker, 1976); and grass species were identified and a percentage cover within the plot estimated using Braun-Blanquet measure (Westhoff & Van Der Maarel, 1978). The percentage of vigorous grass cover was determined using the mean of 'vigorous' values determined using the Walker 8-point scale (Walker, 1976). Percentage available browse was assigned using height classes and tree counts (Riginos, 2015). The coefficient of variation (CV) for grass biomass values was used as a measure of biomass heterogeneity, and the CV of distance to the nearest obstruction as landscape heterogeneity.

Data analysis

Camera trap data in our study had a high proportion of zeros, even when aggregated into night and day periods. We thus decided to first work on presence/absence data to determine which environmental variables have the strongest effect on the species composition of the herbivore community. We estimated the probability of presence of a given species or functional group using generalised linear model for binomial data. We then investigated the drivers of biomass structure of the community by testing the variables associated with the relative biomass of the various functional groups, using presence data. We used a generalised linear model to analyse the determinants of daily observed biomass values per species and functional group biomass values for species with sufficient occurrence data for models to produce robust results. Biomass data were log-transformed to reduce the large variance generated through high heterogeneity in body size, allowing data to conform to parametric analyses. All analyses were performed using R packages v3.4.1 (R-Development-Core-Team, 2011).

The 'dredge' function in package 'MuMIn' (Bartoń, 2014) was applied to the most complex models for both binomial and biomass data to generate subsets of the fixed effects of the global model. Models with AICc values that differed by < 2 were then averaged using the model.avg function (Appendix A, Appendix B). Some variables retained in the average model gave estimates that had very large standard errors including 0; they were subsequently removed to simplify the final model.

Predation data were insufficient to determine an effect of predation on daily biomass. Data were initially split according to five time periods; namely ‘pre-sunrise’ (00h00 to 05h59), ‘morning’ (06h00 to 09h59), ‘midday’ (10h00 to 13h59), ‘afternoon’ (14h00 to 17h59) and ‘night’ (18h00 to 23h59). In the process of determining whether predator incidence was sufficient to have an effect on herbivore presence and biomass for 24 hours thereafter (Valeix *et al.*, 2009), presence/absence and biomass values for night and day were created by merging the relevant time of day classes together. There was no significant effect of predator occurrence on any of the functional types, and we thus do not present analysis with predator incidence in the result section, but we will briefly comment on this observation in the discussion.

Table 1: A summary of the expected outcomes and results produced by GLMs for binomial data for each functional type, indicating the probability of presence by a functional type at certain habitat attributes. Species traits and expectations were based off the following literature: Gagnon & Chew, 2000; Clauss *et al.*, 2003; Arsenault *et al.*, 2008; Hempson, Archibald *et al.*, 2015.

Functional Type	Expected outcome	Predictor variable	Result
Grazer	Occur close to water; select for quality forage	Grass biomass	Select for quality close to water; select for quantity further from water. Preference for burned areas
Mixed Feeder	Select for browse in dry season and grass in wet season	Grass biomass	Low presence further from water and in increased grass height
Browser	Occur further from water; select dense habitat	CV distance to nearest obstruction	As expected
Small-Medium herbivore	Occur closer to water; select forage for quality	Grass height	Occur at higher grass height and further from water
Medium herbivore	Occur closer to water; select forage for quality	CV distance to nearest obstruction	As expected
Medium-large herbivore	Occur closer to water; select for quantity	Grass height	Higher probability of presence further from water at increased grass height in dry season; higher probability of presence closer to water at decreased grass height in wet season.
Megaherbivore	Occur closer to water; select for quantity	Grass height	Occur further from water; select for short grass height

Results

Probability of occurrence

Feeding types

Overall, binomial data models produced results (Table 1, Appendix C) that followed expected trends from literature. Probability of grazer presence decreased with increasing distance from water, with the effect increasing in the dry season (Fig. 2A). For grazers, distance additionally interacted with grass biomass, and grazer probability of presence increased with higher grass biomass further from water (Fig. 2A). We expected an increased biomass of grazers on burned sites than unburned sites however, burn effects were not selected within the 'dredge' process and thus did not have an effect on the overall grazer functional type.

For mixed feeders, distance did not have effects on probability of presence unless in interaction with grass biomass. Mixed feeder probability of presence was lower at higher grass biomass and at greater distance from water (Fig. 2B).

Browser probability of presence increased with increasing distance from water and this effect remained consistent across seasons (Fig. 2C, Fig 6D). Across all distances from water, probability of browser presence was lower on burnt sites (Fig. 2C). Overall, probability of browser presence was lower in the late wet season when compared with late dry and early wet seasons (Fig. C, Fig. 2D).

Body size

For all body sizes, except medium-large herbivores, probability of presence was lower with increasing distance from water (Fig. 3, Fig. 4). For small-medium herbivores, probability of presence increased at higher grass heights (Fig. 3A).

Medium herbivore probability of presence decreased with increasing CV (distance to nearest visual obstruction), i.e. landscape heterogeneity (Fig. 3C, Fig. 3D). Additionally, CV and distance from water interacted, with medium herbivore probability of presence increasing at higher CV further from water. Probability of medium herbivore presence was higher on burned than unburned sites, decreasing with distance from water (Fig. 3C).

Probability of medium-large herbivore presence was highest on areas of burned, short grass height, particularly in the early wet season (Fig. 4A), decreasing with increased distance from water. The inverse was true for unburned areas, with medium-large herbivore presence being

highest further from water (Fig.4B). Probability of presence increased with increasing distance from water in the late-dry and late-wet seasons (Fig. A, Fig. B).

For megaherbivores, probability of presence was highest further from water and at decreased grass height (Fig. 4C).

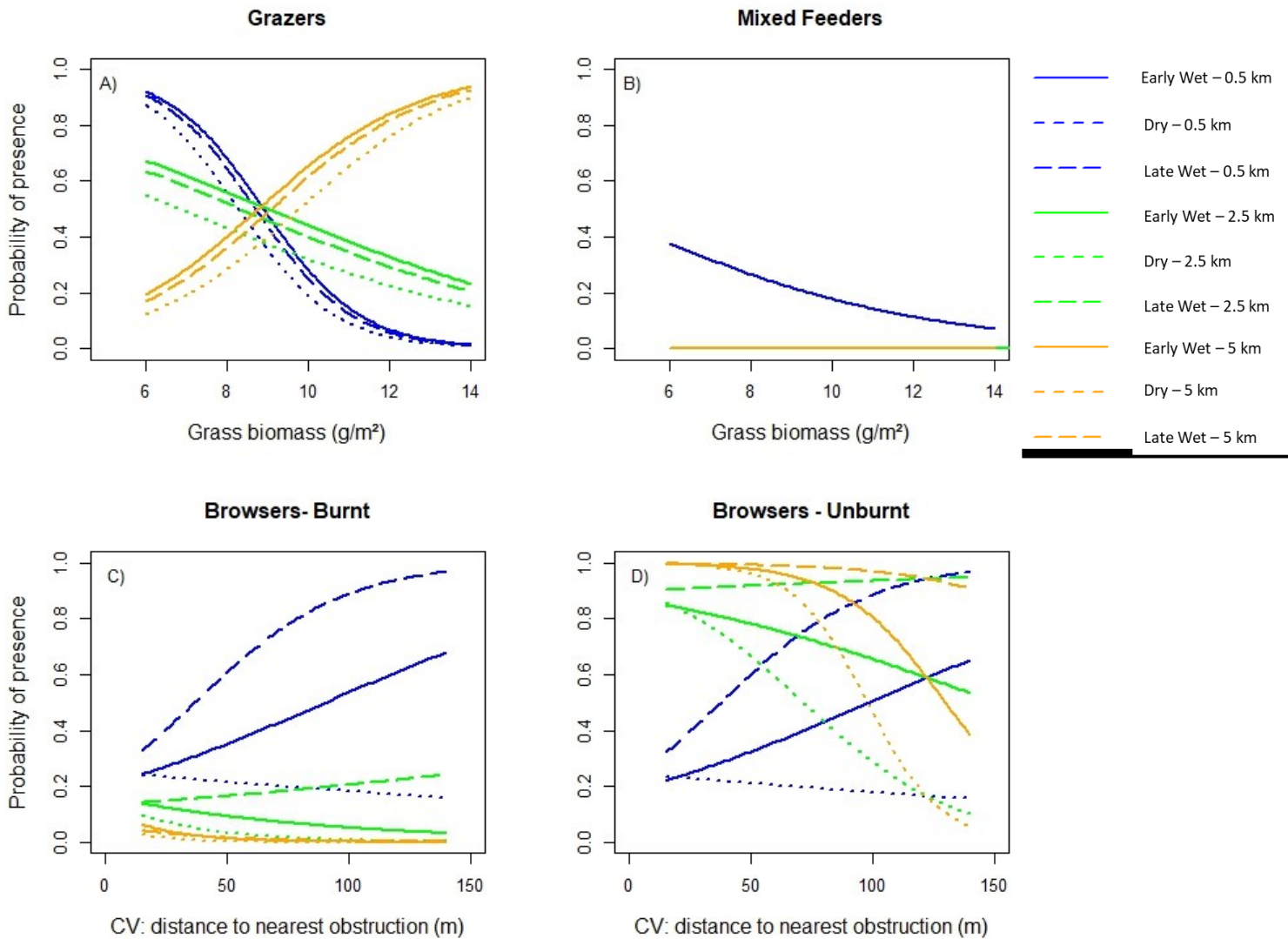


Figure 2: Model simulation over the relevant gradients for the results of each feeding type's estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; feeding types). Values represented indicate the probability of occurrence by each feeding type predicted by the relevant environmental variables. For mixed feeders, season was not a valid descriptor of biomass; thus, values were lumped to only have 3 curves representing distance from water. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

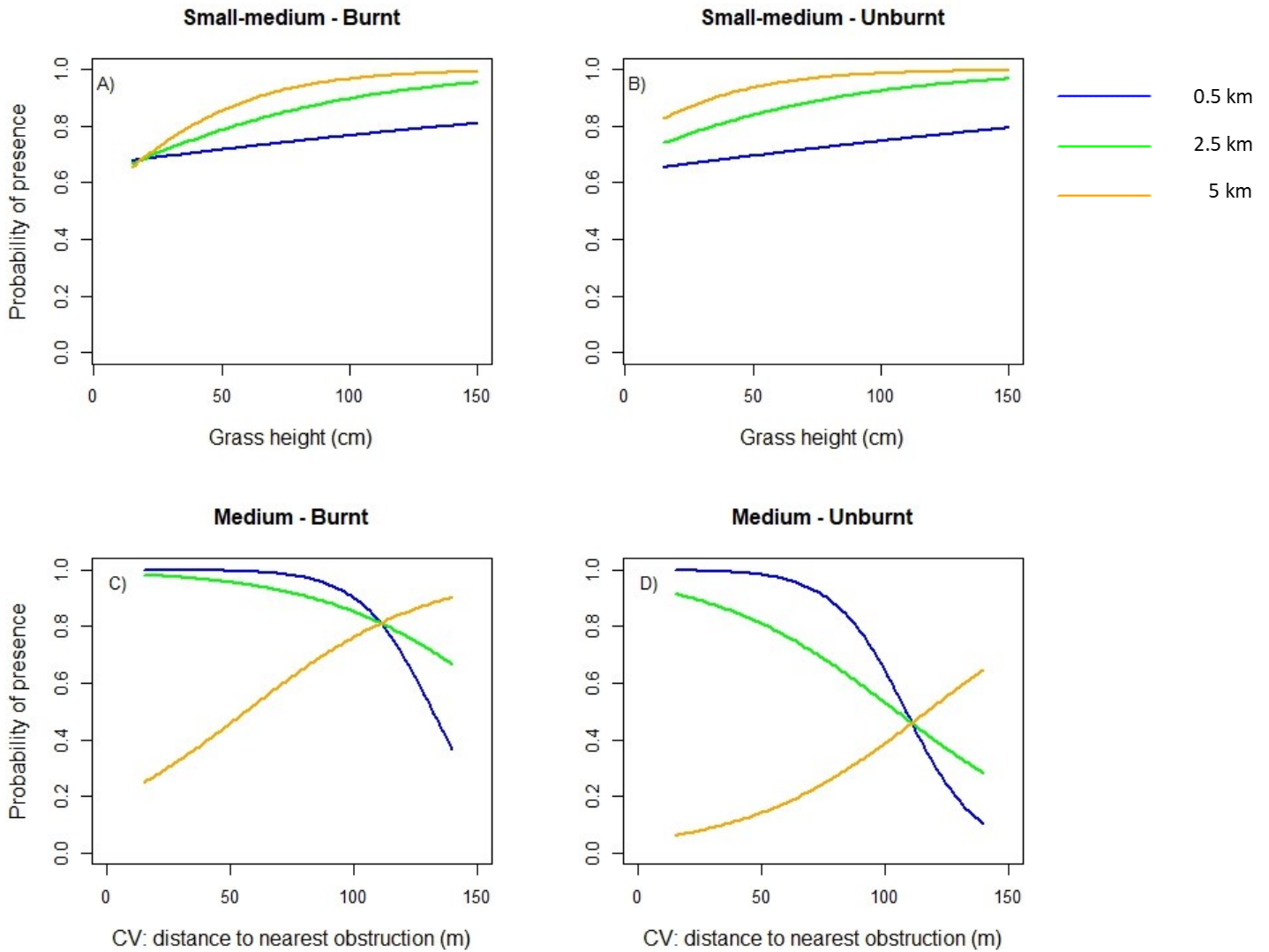


Figure 3: Model simulation over the relevant gradients for the results of each body size’s estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; body size classes). Values represented indicate the probability of occurrence by small medium and medium sized herbivores predicted by the relevant environmental variables. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

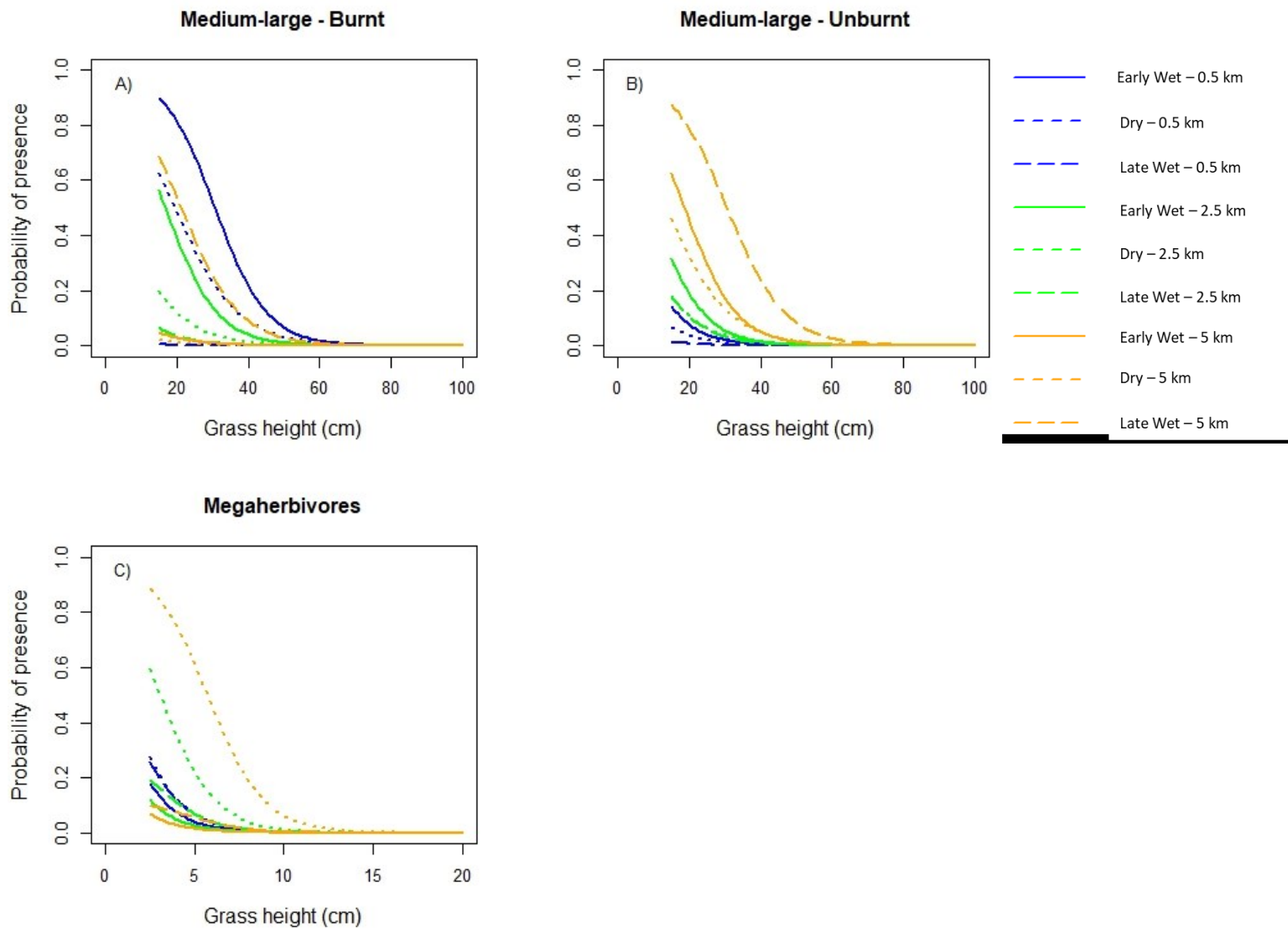


Figure 4: Model simulation over the relevant gradients for the results of each body size's estimated coefficients in the Generalised Linear Model (Appendix A – Binomial values; body size classes). Values represented indicate the probability of occurrence by medium-large sized and megaherbivores predicted by the relevant environmental variables. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

Daily biomass results

Feeding types

Daily biomass models revealed that grazer biomass decreased closer to water when grass biomass was lower and increased further from water when grass biomass was higher (Fig. 5A, Appendix D). Mixed feeder biomass was highest at unburnt sites (Fig. 5B). Browser biomass was overall higher further from water and increased with higher CV (distance to the nearest visual obstruction) in the early-wet and late-wet seasons (Fig. 5C, Fig. 5D).

Body size

Small medium-herbivore biomass was lower in the dry season than early- and late-wet seasons, was highest closer to water and increased with increasing CV (Fig. 6A). Medium herbivore biomass was highest in the early wet season and highest further from water (Fig. 6B). Furthermore, medium herbivore biomass increased with increasing CV at 2.5 km and 5 km from water but remained the same across all CV values at 0.5 km from water (Fig. 6B).

Medium-large herbivore biomass was higher in the early- and late-wet seasons and closer to water on both burned and unburned sites (Fig. 6C, Fig. 6D). Medium-large herbivore biomass decreased with increasing distance between trees at 2.5 km and 5 km from water on both burned and unburned sites, remained consistent at all distances between trees at 0.5 km on burned sites, and decreased again slightly on unburned sites at 0.5 km (Fig. 6C, Fig. 6D).

Megaherbivore biomass was higher in the late-wet season than late-dry and early-wet seasons (Fig. 6E).

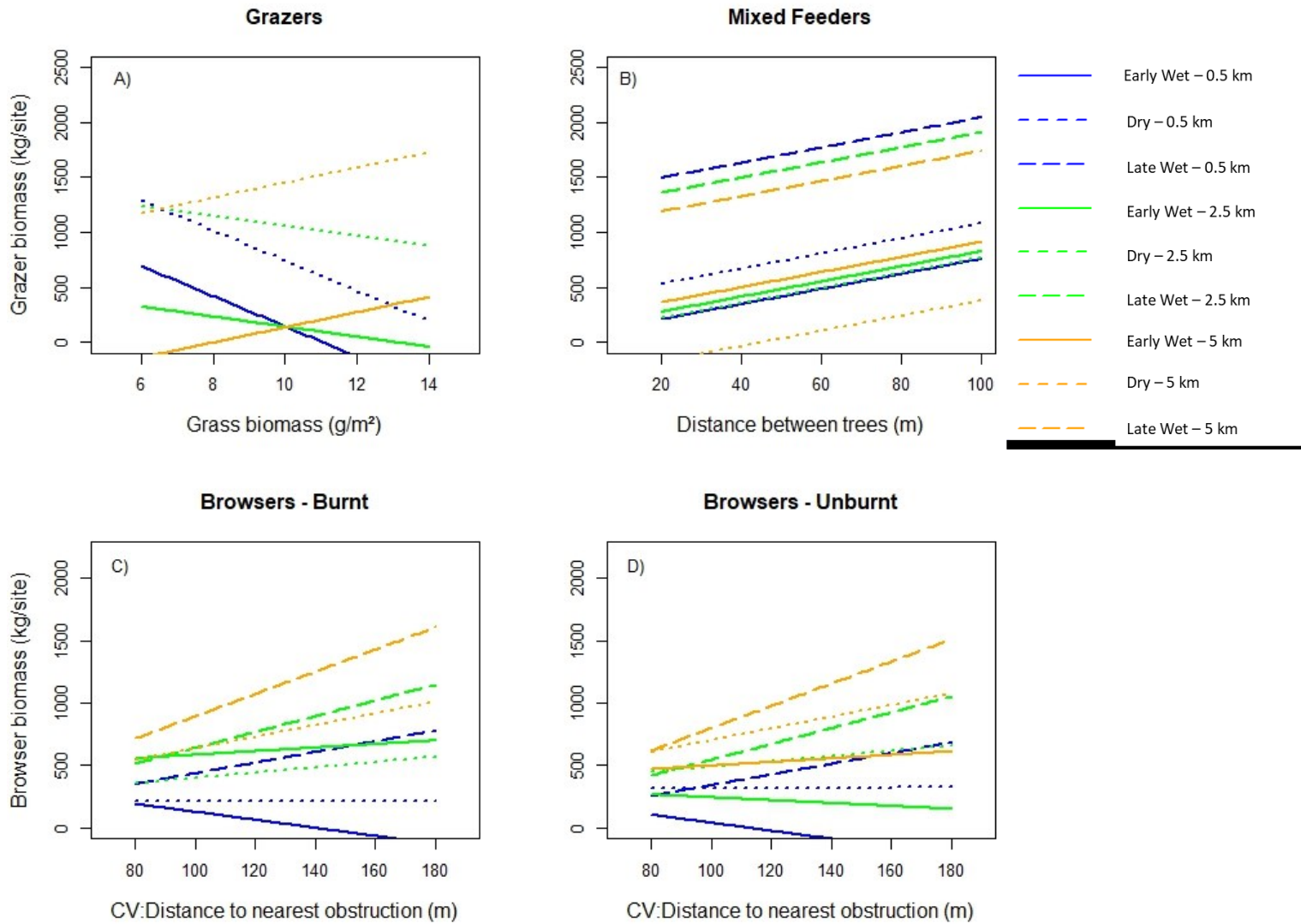


Figure 5: Model simulation over the relevant gradients for the results of each feeding types estimated coefficients in the Generalised Linear Model (Appendix B – Biomass values; feeding types). Values represented indicate the biomass by each feeding type in relation to the functional type’s relevant describing environmental variable. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

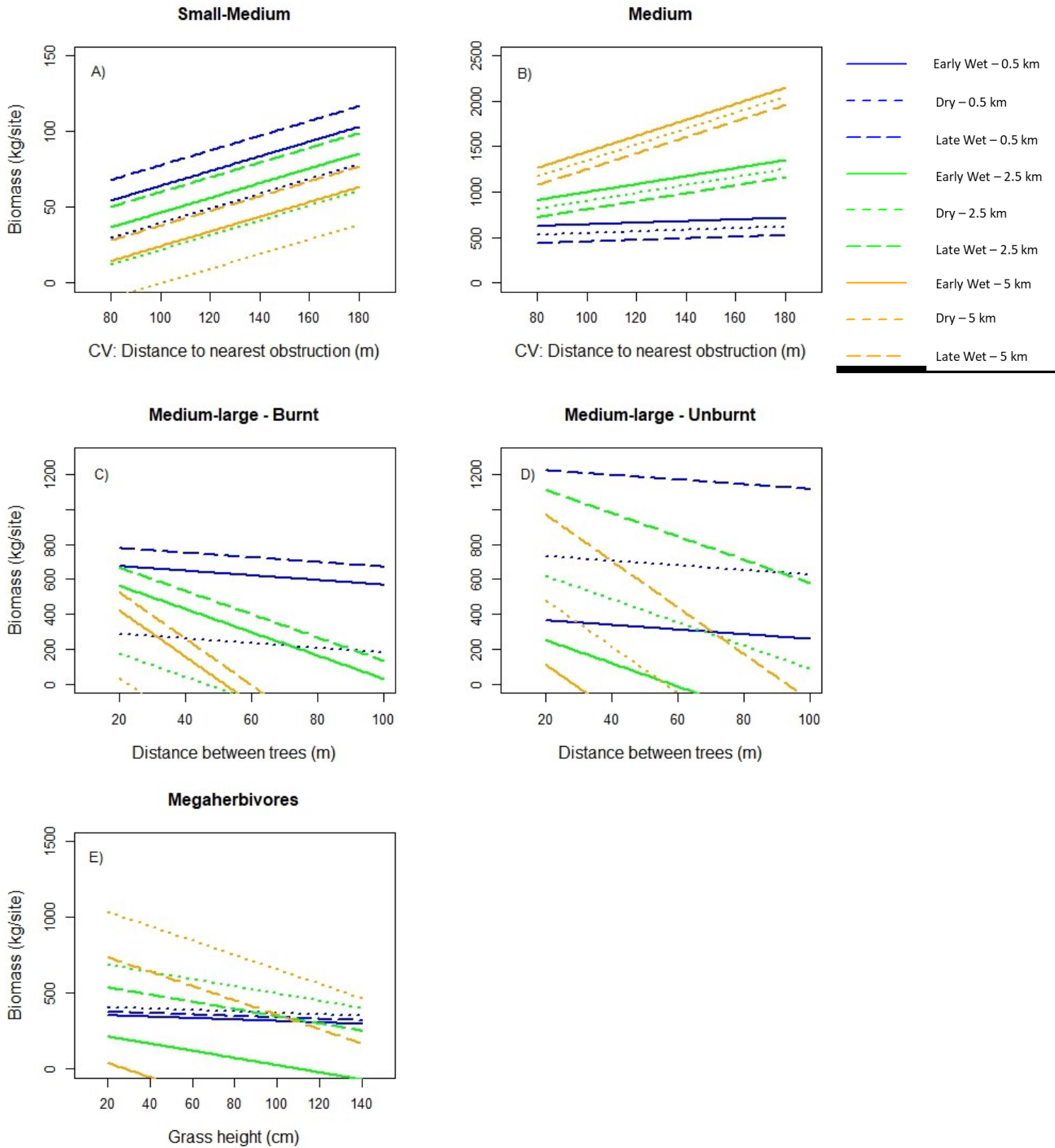


Figure 6: Model simulation over the relevant gradients for the results of each body size's estimated coefficients in the Generalised Linear Model (Appendix B – Biomass values; body size classes). Values represented indicate the biomass by each body size group in relation to the functional type's relevant describing environmental variable. Blue curves represent 0.5 km from water; green represents 2.5 km from water and orange represents 5 km from water.

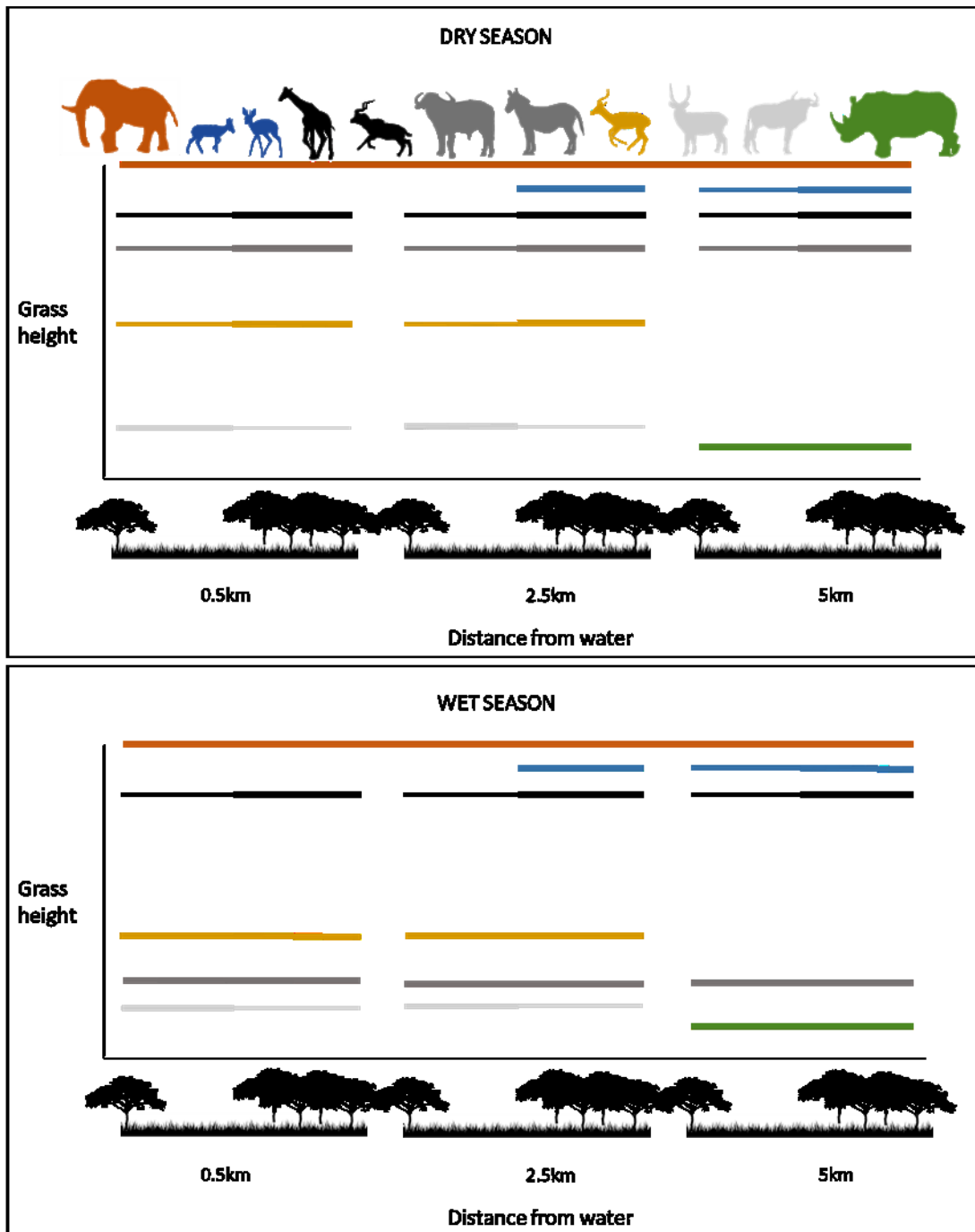


Figure 7: A visual representation of the assemblage composition across the three distances from water for the wet and dry season, and under two types of habitat density. Single trees on the left of each distance represent open habitat and multiple trees on the right represent dense habitat. Thickness of the line represents strength of the probability of presence by the functional types described by species of the same colour. Orange lines = megaherbivore, mixed feeder; Dark blue = large browser; light blue= small browser; black= megagazer; medium grey=large grazer; light grey= small-medium grazer.

In terms of assemblage composition, determined by habitat overlap, large changes in abundance and distribution of small mixed feeders and large grazers (Fig. 7) were observed as a result of resource availability.

Discussion

Grazers

Medium and medium-large grazing herbivores are commonly described as water-dependent, typically being found in the 0.5 km to 2 km zone from water (Gaylard *et al.*, 2003). They are comparatively more dependent on surface water than browsing species, as the moisture content of grass generally falls below 10% in the dry season (Kay, 1997). Although the home range of grazing herbivores is typically closer to water during periods of drought, buffalo, waterbuck and zebra (medium-large body size class) generally occur further than 2.5 km from water (Gaylard *et al.*, 2003). Grazing large herbivores alter their distribution to occur further from water to mitigate poor forage conditions (i.e. forage constraints are more important than that of being close to water) (Gaylard *et al.*, 2003; Venter *et al.*, 2015). Our results show that grazers are attracted to short grass resources closer to water, whereas further from water species are attracted to high grass biomass resources which have not yet been depleted. This indicates that distance from water is a critical determinant of foraging selection patterns by species of different feeding preferences. Additionally, grass growth stage is a critical parameter of preference for a site (Murray & Brown, 1993). Accordingly, grazers will return to sites at previously-grazed areas which are green with palatable regrowth (Archibald, 2008). Our results supported this, with grazer biomass being higher at lower grass biomass at 0.5 km and 2.5 km. Furthermore, grazer biomass was highest at 2.5 km in the early wet season, following the typical magnet effect post-fire regrowth has on the distribution of grazing herbivores (Archibald *et al.*, 2005). Forage constraints remained the primary determinant of herbivore biomass across the landscape in the wet season— with clear preference of burnt and shorter grass areas. Finally, distance from water and grass regrowth may be a good reflection of the relationships between grazers and grass biomass, given that body size interacts with whether grazers select forage for quality or quantity, and areas of forage reserve are typically maintained further from water.

Browsers

Our models did not produce conclusive results regarding the relationship between browser biomass and the availability of browse across the landscape, and at a local scale, the relationship between browsing species and the height of browse availability described by Owen-Smith (1985). However, our results supported evidence that browsers are typically less water-dependent and feed > 3 km from water (Gaylard *et al.*, 2003). It is worth noting that the browser functional type spanned across three body size classes: namely small (common duiker and steenbok), medium (kudu) and megaherbivore (giraffe); but the effect of distance from water remained consistent with browsers typically occurring further away from water. This may be true for common duiker, steenbok and kudu, as giraffe typically feed within 0.5 km and 1 km from water (Gaylard *et al.*, 2003) despite being a less water-dependent species. These effects, however, may not be clear in our results due to the confounding nature of the body size classes within this functional type. Browsers occupy habitat further away from water due to higher moisture content of browse compared to grass (Western, 1975). The relationship between browser habitat occupancy and distance to water may also be as a product of the nature of the landscape. Shrub density typically increases with distance from watering points at Satara, with woody vegetation resources having been largely depleted by large herbivores as far as 2.8 km from water (Brits *et al.*, 2002). Giraffe and steenbok occupy mixed-habitat, and kudu and common duiker occupy closed habitat for most of the year (Pérez-Barbería *et al.*, 2001). However, larger species are able to use a higher diversity of habitat types and are less constrained by dietary tolerance and habitat specificity than smaller species (Du Toit, 2003). Our environmental covariates did not define habitats as closed-, mixed- or open-habitats, however the positive relationship between browser biomass and the distance to the nearest visual obstruction indicates that browsers we focused on prefer denser areas.

Mixed feeders

Mixed feeders are able to effectively change the utilisation of grazing versus browsing resources across seasons, grazing predominantly in the wet season and browsing in the dry season. In KNP mixed feeders are observed to 'switch' from a preference of predominantly graze to browse when the 2-month concurrent mean annual rainfall has dropped below ~30 mm (Du Toit, 2003). Although it is expected that there would be a clear trend between

distance to water and mixed feeder biomass, as both species are water-dependent (Redfern, Grant *et al.*, 2003), our model results did not show any clear trends, possibly due to high variation across the sample size. This could potentially be because the body size classes in this functional type spanned from small-medium (impala) to megaherbivore (elephant). Impala show preference to feeding within 1-2 km of water (Gaylard *et al.*, 2003) with a preference for green grass when rainfall is not limiting (Sinclair & Norton-Griffiths, 1995). Impala will revert to browsing in the dry season when green grass is not available (Du Toit, 2003), as browse maintains a higher protein content for longer into the dry season than grass (McNaughton *et al.*, 1986). This was supported by our results in that probability of mixed feeders was higher at shorter grass heights in the wet season when regrowth would be green. This result is likely not representative of elephant biomass, as they experience a weak relationship with forage quality, but a stronger relationship with forage quantity (Redfern *et al.*, 2003). Impala will take 2-3 day intervals between drinking although this interval can become twice as frequent in the dry season. Although elephant have shorter drinking intervals (1-2 days in the dry season) than impala, and typically feed in the riparian zone (Gaylard *et al.*, 2003), their feeding preference range extends as far as 3 km from water (Smit *et al.*, 2007). Overall biomass trends indicate that there is an increase in mixed feeder biomass in the wet season, likely caused by higher elephant biomass in the region in the late wet season especially when elephants display increased movement across the landscape, as the constraints of forage and water availability are not as severe as in the dry season (De Knegt *et al.*, 2011).

Body size classes

Smaller herbivores have higher metabolic constraints than large herbivores due to increased energy demands (McNaughton *et al.*, 1986) and their body size furthermore governs the rate and extent of energy which can be extracted from their diet. This is as a result of the retention time of food causing digestion efficiency to be lower in smaller animals than larger animals given the same food source (Demment *et al.*, 1985), and thus smaller bodied species must shift to the higher protein diet provided by browse (McNaughton *et al.*, 1986). Our results supported evidence that forage is the primary determinant of small-medium herbivore biomass. However, our results also indicated that smaller bodied herbivores prefer areas of increased grass height. This is in contradiction of theory that smaller herbivores, which are more susceptible to predation (Sinclair, Mduma *et al.*, 2003), would choose more open

habitats to improve predator visibility (Riginos *et al.*, 2008). Small herbivores are usually solitary or in pairs (Hempson *et al.*, 2015), and are not able to use aggression or speed to prevent predation and thus rely on crypsis in more dense vegetation as an anti-predator strategy (Jarman, 1974). Our models could not test the effects of predation, and we therefore cannot speculate as to whether risk of predation would be a stronger driver of small herbivore biomass, rather than forage preference. In terms of preference for increased grass height, it is also likely that this pattern is more representative of small bodied browsers (steenbok and common duiker) (Pérez-Barbería *et al.*, 2001), rather than the small-medium bodied impala in the wet season. This pattern will be representative of all three species in the dry season, however impala feeding preference will shift to short, green grass in the wet season as previously discussed.

For medium herbivores, the strongest predictor of biomass at a site was whether it had burnt or not, and also the homogeneity of the landscape. The medium body size class comprises wildebeest and kudu, and thus some results may be confounding. The preference for burnt areas is likely representative of wildebeest biomass, which is well documented throughout the literature (Hassan *et al.*, 2007; Shackleton, 1992; Tomor & Owen-Smith, 2002; Wilsey, 1996). In times when burnt regrowth is not available, water availability may be a stronger determinant of wildebeest biomass at a site, as they typically feed in 0.5-1 km zone, despite having longer intervals of 2-3 days between drinking. The burnt areas were at 2.5 km and 5 km from water, indicating that forage quality may be a stronger driver of wildebeest biomass than distance from water. Kudu are water-independent and typically feed > 3 km from water (Gaylard *et al.*, 2003), and thus the relationship between decreasing medium herbivore biomass and distance from water is also more likely representative of wildebeest than kudu. Results which are not confounding however, are the relationship between distance to water and coefficient of variation on the distance to the nearest obstruction (Fig. 4). Kudu are likely more representative of the 2.5 km and 5 km trend, occurring at higher biomass in more dense areas (which had a higher coefficient of variation), as they are classified as species which prefer closed habitat (Pérez-Barbería *et al.*, 2001). The function remains relatively flat for the 0.5 km zone, suggesting that homogeneity of the landscape, both in structure and composition, is not as important a driver of wildebeest biomass as forage quality and water availability.

Our results support findings that preference for burnt areas does not decrease with body size (Klop *et al.*, 2007; Tomor *et al.*, 2002), contrary to Wilsey (1996). Preference for burnt areas was evident in small-medium, medium and medium-large body size classes. In addition to preference of burnt areas, medium-large herbivores had a clear preference for areas of short grass (Fig. 4). This is especially clear at the burnt 2.5 km zone in the early wet season, when medium-large biomass is at its highest. This further indicates that forage quality and quantity is a stronger driving factor for where medium-large biomass occurs, rather than water availability, as all the three species in this body size class (buffalo, zebra and waterbuck) typically feed in the 0.5 km-2 km zone from water (Gaylard *et al.*, 2003). Medium-large herbivore biomass is highest in the late wet season, suggesting that there are population-level movements across the park when water is less easily accessible. This is likely explained by buffalo distribution in the park across seasons, as buffalo typically move further away from water sources in the dry season to meet forage requirements of quantity rather than quality (Redfern *et al.*, 2003). This could also explain the relationship between grass height and biomass at the 5 km zone (Fig. 3), although our model for binomial data does not then adequately explain the effects of season, as this trend would only make sense in the dry season. Finally, medium-large herbivores were at higher biomass with decreased distance between trees, where they might have been compelled to feed in areas of higher forage quality (le Roux *et al.*, 2018). Forage quality is likely higher because grass layer growth may be facilitated by increased nutrient availability as a result of increased tree density (Ludwig *et al.*, 2004).

Results for megaherbivores could not be clearly interpreted as the functional type comprises all three feeding preferences, namely giraffe (browser), white rhinoceros (grazer) and elephant (mixed feeder). Furthermore, elephant and white rhinoceros are classified as water-dependent species, whilst giraffe are water independent (Gaylard *et al.*, 2003; Hempson *et al.*, 2015), creating complex interactions with forage requirements and habitat type preference. Our model results indicated that the strongest predictor of megaherbivore biomass was the presence of short grass at 2.5 km and 5 km. This pattern could be explained by forage utilisation by white rhinoceros, as they prefer feeding on short grass areas (McNaughton *et al.*, 1986; Pretorius, 2009; Waldram *et al.*, 2008). The relationship between grass height and distance from water at 0.5 km indicates that grass height was not a valid

predictor of megaherbivore biomass close to water, where giraffe are most likely to feed (Gaylard *et al.*, 2003).

Finally, assemblage composition differed across season as a result of altered forage use by the small-mixed feeder and large grazer functional types. In the wet season when resource quality is improved and water is more uniformly distributed across the landscape (Gaylard *et al.*, 2003), the abundance of grazers and mixed feeders increases. Furthermore, the change in resource quality causes small mixed feeders and large grazers to alter their resource use from browse and tall grass swards respectively, to short grass swards which contain less fiber and increased crude protein (Arsenault & Owen-Smith, 2008; Du Toit, 2003; Kutilek, 1979). In the wet season, assemblages close to water comprise largely grazers across the body size spectrum, particularly in more open, short grass habitats, mixed feeders across the body size spectrum, with few large browsers. Further from water, assemblages comprise less grazers and more browsers across the body size spectrum, particularly in denser habitat of increased grass height. In the dry season, assemblages close to water comprise largely of medium grazers, which occupy open habitat of short grass height, and mega- mixed feeders. As the distance from water increases, assemblage composition includes more small mixed feeders, browsers and large grazers, particularly in denser habitat of increased grass height. Furthest from water, assemblages comprise largely of large grazers and browsers, particularly in denser habitat of increased grass height, megagrazers at short grass height, and mega- mixed feeders.

Conclusion

Our results supported trends across body size classes and feeding types which have previously been described. However, herbivore studies have typically looked at aspects of the effects of environmental attributes on herbivores, whereas our study has tested a combination of aspects across scales and seasons, on an herbivore assemblage which differs in functional traits. The results of this study showed that water availability and forage quality and quantity largely alter the composition of the assemblage, particularly in the grazer and mixed feeder guild. The means utilised to test predation effects were insufficient to explore the relationship across functional types, indicating that broad-scale camera trap surveys, in our case, may not have been an effective tool in this regard.

The use of distance from water and grass regrowth measurements to reflect grazer biomass warrants more investigation at a finer scale, especially in areas further from water and which experience less grazing pressure. Finally, the models developed in this study are a comprehensive analysis of a wide spectrum of body sizes and feeding types across a broad environmental gradient. The detection and confirmation of previously described trends indicates that the use of environmental attributes in GLMs may be a useful means to predict herbivore presence across seasons at a landscape scale.

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Literature Cited

- Archibald, S. 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *The journal of wildlife management*, 72(2), 492-501.
- Archibald, S., Bond, W. J., Stock, W. D., & Fairbanks, D. H. K. 2005. Shaping the Landscape: Fire-Grazer Interactions in an African Savanna. *Ecological Applications*, 15(1), 96-109.
- Arsenault, R., & Owen-Smith, N. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, 117(11), 1711-1717.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386-400.
- Biggs, H.C., J. T. Du Toit, Rodgers, K.H. (Eds.) 2003. *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Brits, J., Rooyen, M. W. V., & Rooyen, N. V. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*, 40(1), 53-60.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., & Kinnaird, M. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4(1), 75-79.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., & Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, 136(1), 14-27.
- Creel, S., Winnie, J., Jr., Maxwell, B., Hamlin, K., & Creel, M. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86(12), 3387-3397.
- Cromsigt, J. P., Prins, H. H., & Olf, H. 2009. Habitat heterogeneity as a driver of ungulate diversity and distribution patterns: interaction of body mass and digestive strategy. *Diversity and Distributions*, 15(3), 513-522.
- Cromsigt, J. P. G. M., & Olf, H. 2006. Resource Partitioning among Savanna Grazers Mediated by Local Heterogeneity: An Experimental Approach. *Ecology*, 87(6), 1532-1541.

- De Knegt, H. J., Van Langevelde, F., Skidmore, A. K., Delsink, A., Slotow, R., Henley, S., Bucini, G., De Boer, W. F., Coughenour, M. B., Grant, C. C., Heitkönig, I. M. A., Henley, M., Knox, N. M., Kohi, E. M., Mwakiwa, E., Page, B. R., Peel, M., Pretorius, Y., Van Wieren, S. E., & Prins, H. H. T. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, 80(1), 270-281.
- Demment, M. W., & Soest, P. J. V. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125(5), 641-672.
- Du Toit, J. T., 2003. Large herbivores and savanna heterogeneity. Pp 292-309 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- ESRI. 2012. ArcGIS (Version 9.3). Redlands, CA.
- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5), 1155-1164.
- Gaylard, A., Owen-Smith, N., & Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pp 171-189 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Gertenbach, W. D. 1983. Landscapes of the Kruger National Park. *Koedoe*, 26(1), 9-121.
- Gordon, I. J., & Illius, A. W. 1996. The nutritional ecology of African ruminants: A reinterpretation. *Journal of Animal Ecology*, 65(1), 18-28.
- Harrington, R., Owen-Smith, N., Viljoen, P. C., Biggs, H. C., Mason, D. R., & Funston, P. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation*, 90(1), 69-78.
- Hassan, S. N., Rusch, G. M., Hytteborn, H., Skarpe, C., & Kikula, I. 2007. Effects of fire on sward structure and grazing in western Serengeti, Tanzania. *African Journal of Ecology*, 46(2), 174-185.
- 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(6264), 1056-1061.
- Hempson, G. P., Archibald, S., & Bond, W. J. 2017. The consequences of replacing wildlife with livestock in Africa. *Scientific reports*, 7(1), 17196.

- Holland, E. A., & Detling, J. K. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology*, 71(3), 1040-1049.
- Hopcraft, J.G.C., Olf, H., & Sinclair, A.R.E. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2), 119-128.
- Jarman, P. J. 1974. The Social Organisation of Antelope in Relation To Their Ecology. *Behavior*, 48(1), 215-267.
- Kay, R. 1997. Responses of African livestock and wild herbivores to drought. *Journal of Arid Environments*, 37(4), 683-694.
- Klop, E., van Goethem, J., & de longh, H. H. 2007. Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildlife Research*, 34(2), 77-83.
- Kutilek, M. J. 1979. Forage-habitat relations of nonmigratory African ungulates in response to seasonal rainfall. *The journal of wildlife management*, 34(4), 899-908.
- Le Roux, E., Kerley, G. I., & Cromsigt, J. P. 2018. Megaherbivores modify trophic cascades triggered by fear of predation in an African savanna ecosystem. *Current Biology*, 28(15), 2493-2499.
- Ludwig, F., De Kroon, H., Berendse, F., & Prins, H. H. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. *Plant Ecology*, 170(1), 93-105.
- McNaughton, S. J., & Georgiadis, N. J. 1986. Ecology of African Grazing and Browsing Mammals. *Annual Review of Ecology and Systematics*, 17, 39-65.
- Murray, M. G., & Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti: An experimental test. *Journal of Animal Ecology*, 62(2), 10.
- O'Connor, T. G., & Pickett, G. A. 1992. The Influence of Grazing on Seed Production and Seed Banks of Some African Savanna Grasslands. *Journal of Applied Ecology*, 29(1), 247-260.
- O'Kane, C. A., & Macdonald, D. W. 2018. Seasonal influences on ungulate movement within a fenced South African reserve. *Journal of Tropical Ecology*, 34(3) 200-203.
- Owen-Smith, N. 1985. Niche separation among African ungulates. *Species and Speciation. Transvaal Museum Monograph*, 4, 167-171.
- Owen-Smith, N., & Novellie, P. 1982. What Should a Clever Ungulate Eat? *The American Naturalist*, 119(2), 151-178.

- Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. *Journal of Animal Ecology*, 77(6), 1191-1198.
- Pérez-Barbería, F. J., Gordon, I. J., & Nores, C. 2001. Evolutionary transitions among feeding styles and habitats in ungulates. *Evolutionary Ecology Research*, 3(2), 221-230.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D. W., & Loveridge, A. J. 2012. Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, 23(5), 970-976.
- Pienaar, D., H. Biggs, A. Deacon, W. Gertenbach, S. Joubert, F. Nel, L. van Rooyen, & F. Venter. 1997. A revised water-distribution policy for biodiversity maintenance in the KNP. *Kruger Park Management Plan, Vol. 8, South African National Parks, Skukuza, South Africa*.
- Pretorius, Y. 2009. *Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores*. Unpublished MSc Thesis, Wageningen University, Netherlands.
- Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8), pp.2092-2107.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124-133.
- Riginos, C., & Grace, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, 89(8), 2228-2238.
- 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(4), e1400103.
- Shackleton, C. M. 1992. Area and species selection by wild ungulates in coastal sour grasslands of Mkambati Game Reserve, Transkei, southern Africa. *African Journal of Ecology*, 30, 189-202.
- Shipley, L.A. 1999. Grazers and browsers: how digestive morphology affects diet selection. *Grazing behavior of livestock and wildlife*, 70, pp.20-27.
- Sinclair, A., Mduma, S., & Brashares, J. S. 2003. Patterns of predation in a diverse predator–prey system. *Nature*, 425(6955), 288.

- Sinclair, A.R.E. & Norton-Griffiths, M. (Eds.) 1995. Chapter One. Pp 1-28 in *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago.
- Smit, I. P. J., Grant, C. C., & Devereux, B. J. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136(1), 85-99.
- Tomor, B. M., & Owen-Smith, N. 2002. Comparative use of grass regrowth following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology*, 40(2), 201-204.
- Trollope, W., & Potgieter, A. 1986. Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa*, 3(4), 148-152.
- Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23-30.
- Van Wilgen, B., Govender, N., Biggs, H., Ntsala, D., & Funda, X. 2004. Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, 18(6), 1533-1540.
- Venter, J. A., Prins, H. H. T., Mashanova, A., de Boer, W. F., & Slotow, R. 2015. Intrinsic and extrinsic factors influencing large African herbivore movements. *Ecological Informatics*, 30, 257-262.
- Vie, J.-C., Hilton-Taylor, C., & Stuart, S. N. (Eds.). 2009. State of the world's species. Pp 15-43 in *Wildlife in a changing world: An analysis of the 2008 IUCN Red List of Threatened Species*. Gland, Switzerland, IUCN.
- Waldram, M. S., Bond, W. J., & Stock, W. D. 2008. Ecological Engineering by a Mega-Grazer: White Rhino Impacts on a South African Savanna. *Ecosystems*, 11(1), 101-112.
- Walker, S. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research*, 6(1), 1-32.
- Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, 13(3-4), 265-286.

- Westhoff, V. & Van Der Maarel, E. 1978. The braun-blanquet approach. Pp 287-399 in R. H. Whittaker (Ed.), *Classification of plant communities*. Springer, Dordrecht.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.

APPENDICES

Appendix A: AICc value comparisons for global and final generalised linear models by functional types by binomial data. Final models are the product of the global model with the lowest AICc value, following the removal of variables which had large standard errors including 0.

	Component models:	AICc	Term Codes:
Grazers – Global Model	1/2/3/4/5/6/7/8/10	808.00	Burnt: 1; Dist:2; disttrees:3; grassbiomass:4; season 5; burnt:Dist:6; burnt:season:7; Dist;disttrees:8; Dist;grassbiomass:9; Dist:season:10
	1/2/3/4/5/6/7/8/9/10	809.79	
	1/2/3/4/5/7/8/10	809.82	
Grazers – Final Model	5/2/1/4	907.14	
Browsers-Global Model	1/2/3/4/6/7/9/10/11/14/15	1037.90	Access:1; Burnt:2; coefvarObst:3; Dist:4; disttrees:5; Pred:6; season:7; access:Dist:8; burnt:Dist:9; coefvarObst:Dist:10; coefvarObst:season:11; Dist:disttrees:12; Dist:Pred:13; Dist:season:14; Pred:season:15
	1/2/3/4/6/7/10/11/14/15	1039.13	
	1/2/3/4/6/7/9/10/11/13/14/15	1039.31	
Browsers- Final Model	4/7/9/10/11	1047.11	
Mixed Feeders – Global Model	2/3/5/6/7/8/9/10/11/12/14/15	981.72	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassbiomass:5; grassheight:6; season:7; coefvargrassb:Dist:8; coefvargrassb:season:9; Dist:grassbiomass:10; Dist:grassheight:11; Dist:season:12; grassbiomass:season:13; grassheight:season:14; Dist:grassheight:season:15
	2/3/5/6/7/8/9/12/13/14	982.11	
	2/3/5/6/7/8/9/10/12/13/14	982.18	
Mixed Feeders – Final Model	1/3/10	1031.24	
Small-Medium – Global Model	1/2/3/4/5/6/7/8/9/10/11/13/14	1033.50	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvargrassb:season:10; Dist:disttrees:11; Dist:Pred:12; Dist:season:13; grassheight:season:14
	3/4/5/6/7/11/14	1034.20	
	1/2/3/4/5/6/7/8/9/10/11	1034.44	
Small-Medium – Final Model	5/3/1	1085.68	
Medium – Global Model	1/2/3/4/6/7/8/9/10/11/12/14	917.08	Burnt:1; coefvargrassb:2; coefvarObst:3; Dist:4; grassbiomass:5; grassheight:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvarObst:Dist:10; Dist:grassheight:11; Dist:season:12; grassbiomass:season:13; grassheight:season:14
	1/2/3/4/5/6/7/10/11/12/13/14	918.00	
	1/2/3/4/6/7/8/9/10/12/14	918.23	
Medium – Final Model	4/8/10	943.43	
Medium Large – Global Model	1/2/3/4/5/7/8/9/10/12/14/15	893.31	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; burnt:season:9; coefvargrassb:Dist:10; coefvargrassb:season:11; Dist:disttrees:12; Dist:grassheight:13; Dist:season:14; grassheight:season:15
	1/2/3/4/5/7/8/9/10/11/12/14/15	893.33	
	1/2/3/4/5/6/7/8/9/10/11/12/13/14/15	893.72	
Medium Large – Final Model	14/12/8/9/15	911.83	
Megaherbivores – Global Model	3/5/6/9/10/12	980.87	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; burnt:Dist:7; burnt:season:8; Dist:grassheight:9; Dist:season:10; disttrees:season:11; grassheight:season:12
	1/3/5/6/9/10/12	981.52	
	1/3/5/6/8/9/10/12	981.80	
Megaherbivores – Final Model	10/9	986.35	

Appendix B: AICc value comparisons for global and final generalised linear models by functional types for biomass data. Final models are the product of the global model with the lowest AICc value, following the removal of variables which had large standard errors including 0.

	Component models:	AICc	Term Codes:
Grazers – Global Model	2/3/4/5/8	13352.37	Burnt: 1; Dist:2; disttrees:3; grassbiomass:4; season 5; Dist:disttrees:6; Dist:grassbiomass:7; Dist:season:8; grassbiomass:season:9
	2/3/4/5/7/8	13353.53	
	2/3/4/5/6/8	13353.53	
Grazers – Final Model	8/7	13361.28	
Browsers-Global Model	2/3/4/5/8	11293.77	Access:1; coefvarObst:2; Dist:3; disttrees:4; season:5; coefvarObst:Dist:6; Dist:disttrees:7; disttrees:season:8; Dist:season:9; Dist:burnt:10; coefvarObst:season:11
	1/3/4/5/8	11294.27	
	3/4/5/7/8	11294.31	
Browsers- Final Model	9/10/6/11	11301.33	
Mixed Feeders – Global Model	4/7	14600.95	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassbiomass:5; grassheight:6; season:7; Dist:grassbiomass:8; Dist:season:9; grassbiomass:season:10; Dist:burnt:11
	1/3/4/5/7/8/9/10	14601.37	
	1/4/7	14601.46	
Mixed Feeders – Final Model	11/9/4	14605.09	
Small-Medium – Global Model	3/4/5/9/10	10194.59	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; coefvargrassb:Dist:7; coefvargrassb:season:8; Dist:disttrees:9; Dist:grassheight:10; Dist:season:11; grassheight:season:12; coefvarObst:12
	3/4/5/6/9/10	10195.41	
	3/4/5/6/10/11/12	10195.43	
Small-Medium – Final Model	3/6/12/4	10205.92	
Medium – Global Model	2/3/4/6/7/8/9/10/13/14	10747.97	Burnt:1; coefvargrassb:2; coefvarObst:3; Dist:4; grassbiomass:5; grassheight:6; season:7; coefvargrassb:Dist:8; coefvargrassb:season:9; coefvarObst:Dist:10; Dist:grassbiomass:11; Dist:grassheight:12; Dist:season:13; grassheight:season:14; Dist:burnt:15
	2/3/4/5/6/7/8/10/13/14	10748.14	
	2/3/4/6/7/8/10/13/14	10748.35	
Medium – Final Model	15/13/10	10785.06	
Medium Large – Global Model	2/3/4/6/7/9/10/11/12	12502.33	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; Pred:6; season:7; burnt:Dist:8; coefvargrassb:Dist:9; coefvargrassb:season:10; Dist:disttrees:11; Dist:Pred:12; Dist:season:13; season:burnt:14; season:grassheight:15
	2/3/4/7/9/10/11	12502.57	
	2/3/4/6/7/9/10/11	12503.86	
Medium Large – Final Model	13/11/8/14/15	12512.63	
Megaherbivores – Global Model	4/6/7	14600.62	Burnt:1; coefvargrassb:2; Dist:3; disttrees:4; grassheight:5; season:6; burnt:Dist:7; burnt:season:8; Dist:grassheight:9; Dist:season:10; disttrees:season:11; grassheight:season:12; Dist:grassheight:13
	3/4/6/7	14601.03	
	4/5/6/7	14601.56	
Megaherbivores – Final Model	10/13	986.35	

Appendix C: Results from the final generalised linear model selected for each functional type – binomial data.

	Covariate	Estimate	Std Error	Relative weight of variable Pr(> z)
Grazers	(Intercept)	8.06121	1.01368	1.83e-15
	seasonLateDry	2.18050	0.54457	6.23e-05
	seasonLateWet	-0.76469	0.54968	0.164183
	Dist	-1.57261	0.47910	0.001029
	burntYes	-3.11859	0.64414	1.29e-06
	grassbiomass	-0.85347	0.09602	< 2e-16
	seasonLateDry:Dist	-0.51808	0.15377	0.000754
	seasonLateWet:Dist	-0.16511	0.28504	0.562415
	Dist:burntYes	0.87671	0.20861	2.64e-05
	Dist:grassbiomass	0.17457	0.04529	0.000116
Browsers	(Intercept)	-2.343568	1.025437	0.022287
	Dist	1.702312	0.437024	9.81e-05
	seasonLateDry	-1.485998	0.911010	0.102858
	seasonLateWet	-5.600421	0.986508	1.37e-08
	burntYes	-0.657523	0.533007	0.217348
	coefvarObst	0.022113	0.009035	0.014380
	Dist:seasonLateDry	0.355492	0.118960	0.002805
	Dist:seasonLateWet	0.223108	0.122794	0.069228
	Dist:burntYes	-0.033271	0.160600	0.835878
	Dist:coefvarObst	-0.013921	0.003747	0.000203
	seasonLateDry:coefvarObst	0.002804	0.007381	0.704058
	seasonLateWet:coefvarObst	0.040099	0.007657	1.63e-07
	Mixed Feeders	(Intercept)	1.19192	0.49032
Dist		0.25259	0.19742	0.2007
burntYes		-0.18670	0.47048	0.6915
grassbiomass		-0.04631	0.05296	0.3819
Dist:burntYes		-0.14768	0.15772	0.3491
Dist:grassbiomass		-0.04274	0.01945	0.0280
Small-Medium	(Intercept)	0.963478	0.174865	3.59e-08
	grassheight	-0.011321	0.002358	1.58e-06
	Dist	-0.193426	0.045895	2.50e-05
	burntYes	-0.011258	0.169794	0.947
Medium	(Intercept)	8.704021	1.013352	< 2e-16
	Dist	-2.368525	0.470886	4.91e-07
	burntYes	2.109025	0.457945	4.12e-06
	coefvarObst	-0.079908	0.009137	< 2e-16
	Dist:burntYes	-0.478874	0.120134	6.71e-05
	Dist:coefvarObst	0.021340	0.004080	1.69e-07
Medium-Large	(Intercept)	0.178340	1.056084	0.865899
	Dist	0.513731	0.260964	0.049000
	seasonLateDry	-1.610237	1.209978	0.183255
	seasonLateWet	-3.507476	1.053140	0.000867
	disttrees	0.064524	0.008886	3.84e-13
	burntYes	4.190783	0.734861	1.18e-08
	grassheight	-0.137933	0.038144	0.000299
	Dist:seasonLateDry	0.055031	0.173905	0.751668
	Dist:seasonLateWet	1.382180	0.212612	7.98e-11
	Dist:disttrees	-0.020052	0.005303	0.000156
	Dist:burntYes	-0.959827	0.194811	8.35e-07
	seasonLateDry:burntYes	-2.446295	0.695641	0.000437
	seasonLateWet:burntYes	-4.386148	0.601337	3.01e-13
	seasonLateDry:grassheight	0.113081	0.041539	0.006483
	seasonLateWet:grassheight	0.123812	0.038246	0.001207

Megaherbivore	(Intercept)	-0.234219	0.265602	0.377862
	Dist	-0.246827	0.084227	0.003384
	seasonLateDry	0.357250	0.354378	0.313405
	seasonLatewet	0.658354	0.385639	0.087789
	grassheight	-0.004750	0.005431	0.381736
	Dist:seasonLateDry	-0.660151	0.185675	0.000377
	Dist:seasonLatewet	-0.046825	0.123068	0.703588
	Dist:grassheight	0.004614	0.001838	0.012067

Appendix D: Results from the final generalised linear mixed model for each functional type – Biomass data.

	Covariate	Estimate	Std Error	Relative weight of variable Pr(> z)
Grazers	(Intercept)	1706.64	249.33	1.53e-11
	seasonLateDry	510.29	157.85	0.00128
	seasonLateWet	16.84	167.57	0.91995
	Dist	-441.79	138.35	0.00146
	grassbiomass	-155.68	25.06	8.40e-10
	seasonLateDry:Dist	-156.94	56.16	0.00532
	seasonLateWet:Dist	61.96	89.86	0.49072
	Dist:grassbiomass	43.83	13.76	0.00151
Browsers	(Intercept)	666.0602	128.7896	2.94e-07
	Dist	-153.3911	52.7525	0.003742
	seasonLateDry	-187.6341	116.2476	0.106906
	seasonLateWet	-563.0795	116.7134	1.68e-06
	burntYes	-95.4571	69.3591	0.169125
	coefvarObst	-3.7183	1.1237	0.000978
	Dist:seasonLateDry	17.4005	14.6738	0.236048
	Dist:seasonLateWet	31.5720	15.3211	0.039658
	Dist:burntYes	8.1865	20.9675	0.696318
	Dist:coefvarObst	1.0284	0.4521	0.023192
	seasonLateDry:coefvarObst	0.4521	0.9528	0.635319
seasonLateWet:coefvarObst	3.7515	0.9416	7.40e-05	
Mixed Feeders	(Intercept)	1227.61	482.74	0.0112
	Dist	164.98	191.65	0.3896
	burntYes	-926.44	469.27	0.0487
	grassbiomass	-37.82	52.93	0.4751
	Dist:burntYes	142.17	153.69	0.3552
	Dist:grassbiomass	-29.43	18.97	0.1213
Small-Medium	(Intercept)	-29.3164	46.1202	0.52519
	Dist	-8.8791	2.9971	0.00314
	seasonLateDry	-24.5793	12.8962	0.05702
	seasonLateWet	13.5843	11.0867	0.22083
	coefvarObst	0.4864	0.2588	0.06058
	disttrees	0.9034	0.3971	0.02316
Medium	(Intercept)	874.7946	81.6184	< 2e-16
	Dist	-225.3505	37.9651	4.37e-09
	burntYes	99.3904	44.5435	0.025939
	seasonLateDry	-113.1886	30.5328	0.000224
	seasonLateWet	-14.7870	29.7457	0.619247
	coefvarObst	-6.1636	0.7162	< 2e-16
	Dist:burntYes	-36.1809	14.5862	0.013326
	Dist:seasonLateDry	21.0764	10.5029	0.045117
	Dist:seasonLateWet	17.3643	11.0814	0.117517
	Dist:coefvarObst	1.7599	0.3250	8.11e-08
Medium-Large	(Intercept)	-381.2352	257.5771	0.13925
	Dist	108.0031	67.5041	0.11001
	seasonLateDry	507.4630	264.7298	0.05561
	seasonLateWet	114.8351	228.5649	0.61551
	disttrees	11.4233	1.9852	1.25e-08
	burntYes	378.0833	154.8004	0.01481
	grassheight	-0.5836	7.2558	0.93592
	Dist:seasonLateDry	-61.8614	42.2265	0.14332
	Dist:seasonLateWet	39.4113	48.2637	0.41441

	Dist:disttrees	-2.6626	1.3844	0.05480
	Dist:burntYes	-67.3345	45.0104	0.13506
	seasonLateDry:burntYes	-452.7706	174.1962	0.00952
	seasonLatewet:burntYes	-390.2106	133.6622	0.00361
	seasonLateDry:grassheight	-5.2432	7.8782	0.50590
	seasonLatewet:grassheight	0.6163	7.2578	0.93235
Megaherbivore	(Intercept)	438.8717	267.7629	0.10160
	Dist	-50.4891	79.5282	0.52570
	seasonLateDry	315.2018	340.6921	0.35515
	seasonLatewet	1250.1835	396.3888	0.00167
	grassheight	-0.8535	5.6007	0.87892
	Dist:seasonLateDry	-159.1821	122.5622	0.19439
	Dist:seasonLatewet	-99.0315	120.2232	0.41034
	Dist:grassheight	0.9517	1.8200	0.60119

Chapter 4: Patch-scale selection patterns in grazing herbivores at the Satara section of Kruger National Park

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Abstract

Large herbivores form an essential component in the ecosystem, due to the impact that they have on their surrounding habitat. In this study, we aimed to evaluate some of the mechanisms behind how herbivores select forage at a patch scale. Thirty-six experimental plots were established and fitted with camera traps in the Kruger National Park to test forage selectivity by grazers. Plots were manipulated through clearing with a brush cutter, and the application of fertiliser. We used generalised linear models to detect trends in probability of occurrence by seven grazing herbivore species using camera trap data. Our results showed that season was a major determinant of species distribution, especially those that are not obligate grazers or feed exclusively in the 0.5 km to 2 km zone from water. We found that most selective feeding occurred in the late wet season when water would be more evenly distributed across the landscape and forage resources close to water would have had the chance to recover from depletion as a result of dry season use. These changes in feeding behaviour have implications for the distribution of artificial water points across the landscape, as areas of reserve forage must be maintained to alleviate grazing pressure close to water.

Introduction

Large mammalian herbivores form an essential component of the ecosystem in which they occur, due to the impact that they have on its structure and function (Hempson *et al.*, 2015). Grazing herbivores, in particular, engineer their surrounding ecosystem through enabling plant succession and promoting grassland diversity (Ollf & Ritchie, 1998). Furthermore, they develop and maintain key resource areas (McNaughton, 1984), facilitate for other selective grazers (Prins & Ollf, 1998) and provide ephemeral nitrogen pulses to vegetation through processes of dunging and soil leaching (Frost & Hunter, 2007). Because of the effects that herbivores have on the ecosystem, understanding habitat selection and patch scale foraging processes is becoming increasingly important. Grazing habitats in Africa are under threat as C₄ grasses (which are dominant across savannas) decrease with increasing CO₂ levels (Bond, 2008), and the patch scale foraging patterns of herbivores significantly affect landscape scale processes (Shiple, 2007). Herbivores select for the habitat in which they feed over several temporal and spatial scales (Bailey *et al.*, 1996), under the constraints of their morphology – body size (Clauss *et al.*, 2003), mouth morphology (Pretorius *et al.*, 2016), dietary preference (Gordon & Illius, 1996; Hempson *et al.*, 2015), digestive strategy (Gagnon & Chew, 2000) and water-dependency (Hempson *et al.*, 2015).

Body size constrains digestive requirements in that larger species require more total energy than smaller species, but smaller species require more energy relative to their body weight than larger species (Demment *et al.*, 1985). Thus, smaller grazers experience greater digestive constraints than larger grazers (Codron *et al.*, 2007) and must extend a larger search effort in order to obtain high quality forage (Bailey *et al.*, 1996). Larger grazers are able to maximise their forage consumption through high intake of low quality forage, particularly in the dry season when high quality forage is limited (Demment *et al.*, 1985; Owen-Smith *et al.*, 2017). Digestive strategy further alters the efficiency with which herbivores meet metabolic requirements, as non-ruminants experience an increased turnover rate in digestion which allows them to tolerate higher fibre and lower nutrition content than ruminants (Clauss *et al.*, 2003; Duncan *et al.*, 1990). In order to meet nutritional requirements within the constraints of morphology, herbivores have adapted mouth structures which optimise rate of forage intake (Shiple, 2007). For this reason, grazers tend to have wider muzzles and incisor arcades than browsers (Gordon & Illius, 1988), allowing higher bite rates (Pretorius, 2009). Within the

grazer guild, variation in muzzle width occurs to allow maximum nutrient intake based on digestive strategy and metabolic requirements, and as such the scaling between muzzle width and body size governs grass height selection (Arsenault & Owen-Smith, 2008). Thus, even though large herbivores may be better able to extract nutrients from high-fiber grasses of lower quality (Demment *et al.*, 1985), the relationship between body size and tolerance for low quality forage is not strictly linear and is better explained by constraints in forage quantity and quality (Owen-Smith *et al.*, 2017).

Within the constraints of physiognomic requirements, herbivores must use their daily activity budgets to select habitat which provides optimal forage and facilitate the evasion of predators (Owen-Smith & Goodall, 2014). As such, herbivore populations are regulated by top-down processes (predation) in which case they need to minimize mobile activity; or bottom-up processes (forage quality and availability) for which they need to maximize foraging time (Hopcraft *et al.*, 2010; Owen-Smith *et al.*, 2014). Body size interacts with risk of predation, and in areas of diverse herbivore and predator body size, smaller herbivores experience a greater risk of predation than larger herbivores, as both small and large predators can consume small-bodied prey (Hopcraft *et al.*, 2010). Furthermore, behaviour of species (e.g. gregariousness) affects predator-avoidance strategies and determines whether herbivores may select more open or dense habitats (Riginos & Grace, 2008). The underlying environmental gradients: soil, climate, water availability and their subsequent effect on forage quality and quantity, provides structure to the landscape. This determines herbivore abundance and distribution across the landscape within the constraints of bottom-up and top-down processes (Bailey *et al.*, 1996; Hopcraft *et al.*, 2010). Forage quality is additionally affected by nutrient content of the soil, (Holland & Detling, 1990), season, regrowth as a response to herbivory and/or fire, and water availability (Wilsey, 1996). Water availability strongly constrains the distribution and abundance of grazers through its effects on forage quality and quantity, and high water dependency experienced by grazers (Hempson *et al.*, 2015).

There is complexity and a high degree of interaction between these processes, which operate differently under a variety of scales. At a landscape scale, water availability, foraging requirements and predator distribution and activity patterns determine abundance and

distribution of herbivores (van Ginkel *et al.*, 2018). At a patch scale, perceived risk of predation and selective foraging alters herbivore behaviour (Riginos *et al.*, 2008; van Ginkel *et al.*, 2018); and ultimately these patch processes determine landscape heterogeneity. The complexity and degree of interactions between these processes highlights the importance of understanding savanna ecology to management. Conservation management interventions, such as artificial water provision, without full comprehension of these interactions can have unintended consequences.

Kruger National Park, hereafter 'KNP', has throughout its history altered its management approaches, and has contributed substantially to the understanding of savanna ecology through the monitoring and research of their management efforts (Biggs, 2003). The study of patch scale selection processes in KNP is facilitated by the heterogenous landscape, which supports diverse herbivore assemblages. Patch scale foraging processes have significant impacts on large scale distribution patterns of herbivores (Shiple, 2007). Due to the associated effects that herbivore presence has on the environment, understanding patch scale selection is important to the prediction of their presence, and thus for the purpose of their management (Pretorius, 2009). This study aims to evaluate the mechanisms behind patch scale habitat selection by a variety of grazing species across a spectrum of body sizes and differing digestive strategies. We used descriptions of feeding preference, digestive strategy, body size, mouth morphology and water-dependency to make informed predictions against which to test patch selection in seven grazer species at the Satara section of KNP (Table 1). We tested habitat attributes against species probability of presence at a patch-scale by manipulating plots to test the following predictions; a) season would have a strong effect on grazer presence at certain distances to water, with grazers concentrating close to water in the dry season, and distributing more uniformly across the landscape in the wet season; b) feeding selectivity of herbivores would determine what type of treatment they responded to, with more selective feeders responding to low grass biomass and high nutrient plots, and less selective feeders responding to high biomass and high nutrient plots; c) selectivity by species would change across seasons, with species such as zebra and buffalo selecting high biomass plots in the dry season, and low grass biomass and high nutrient plots in the wet season; d) risk of predation would influence probability of small grazer presence more than large grazer presence.

Methods

Study area

This study was conducted in the Satara section of KNP, which is situated at the north-eastern corner of South Africa (24.01°S, 31.49°E). Satara receives a mean annual rainfall of 547 mm (February *et al.*, 2013). The region experiences mean minimum temperatures of 10°C and 20°C, and mean maximum temperatures of 26.3°C and 32.6°C in July and December respectively (Parr, 2008). The vegetation is characterised by *Senegalia nigrescens/Sclerocarya birrea* tree savanna (Gertenbach, 1983). Habitats of this area are attractive to grazers as the N'wanetsi and Sweni rivers typically flow once or twice in the wet season and have a number of pools which may persist in the dry season (Gaylard *et al.*, 2003). Furthermore, surface water takes longer to evaporate on the clayey basaltic soils of the region, resulting in water being more locally available across the landscape in the wet season in the form of pans (Gaylard *et al.*, 2003). The Letaba basalt soil type contributes to study area suitability, as it has higher calcium carbonate (CaCO₃) concentrations, which gives rise to extensive grassy plains (Venter, 1986) that are dominated by highly palatable grass species such as *Urochloa mosambicensis* and *Digitaria eriantha* (O'Connor & Pickett, 1992). The area is also exposed to occasional wild-fires and prescribed burns (Van Wilgen *et al.*, 2004).

Site design

Suitable sites were identified by mapping distance to water as buffers of 0.5 km, 2.5 km and 5 km from all surface water (rivers and artificial waterholes), overlaid across the soil and habitat type layers using ArcGIS v10.5 (ESRI, 2012). Site suitability was characterised by relative distance to water (km), soil type, habitat type, accessibility and the absence of previous experimental manipulation. Sites were replicated at a location > 2 km away from each other, hence six sites were studied in total (Fig. 1). Sites were located at three different distances to water, with sites 0.5 km from water situated north of the N'wanetsi river and those 2.5 km and 5 km from water south of the N'wanetsi river. Five of the six sites fell within the Satara land type in KNP, dominated by *Senegalia nigrescens/Sclerocarya birrea* tree savanna (Gertenbach, 1983), but due to constraints of site suitability one of the six sites fell within the Mavumbye habitat type, characterised as *Senegalia nigrescens* bush savanna (Gertenbach, 1983). Sites were sampled in June 2017, October 2017, February 2018 and June 2018, resulting in three sets of seasonal data, namely 'late dry', 'early wet' and 'late wet'

seasons. Wildfires occurred throughout the sampling period, resulting in one site at 2.5 km burning in June 2017, and both 5 km sites burning in November 2017.

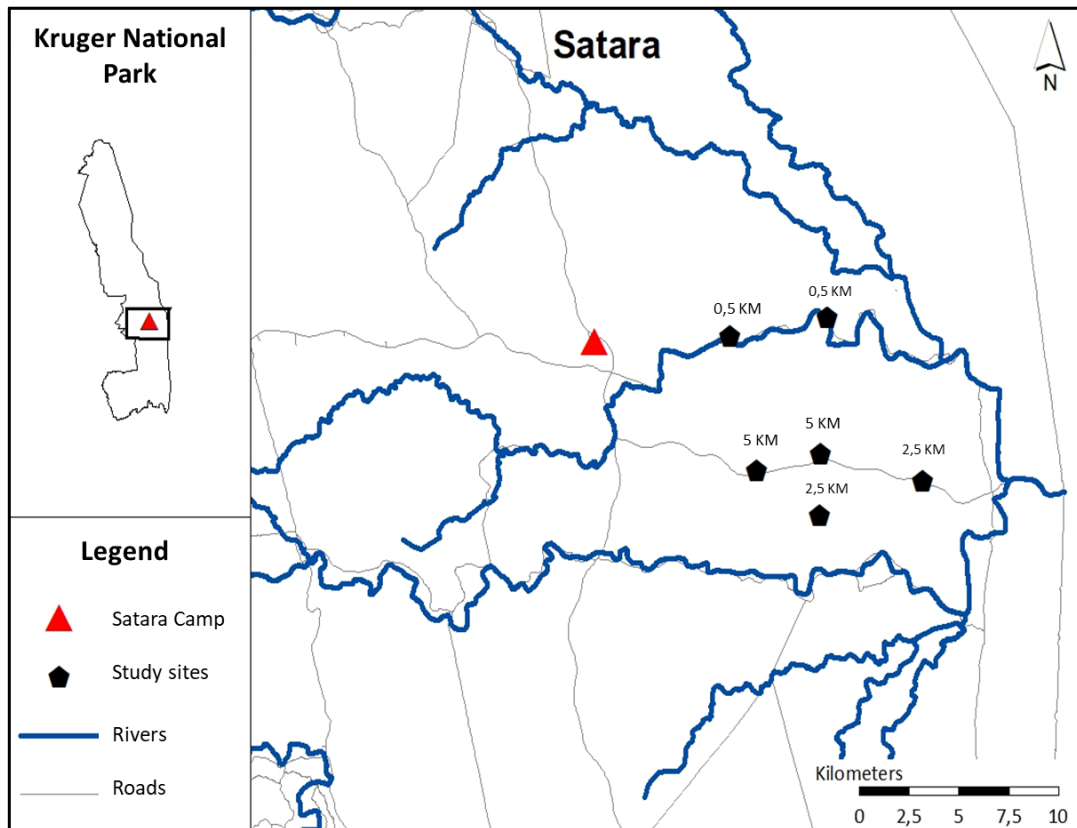


Figure 1: Map of the Satara section where the study was conducted, relative to the Satara Rest Camp.

At each site, six experimental plots were established at a patch level scale (Fig. 2)- an area that an herbivore interacts for 1-30 min, takes breaks in foraging and would be affected by forage abundance and quality, plant species and social interactions (Bailey *et al.*, 1996). For this study, patch level scale refers to the 400 m² plot. Ritchie and Ollf (1999) hypothesis that large herbivores select resources at a coarse scale, however Cromsigt *et al.*, 2006 found that species across an array of body sizes (warthog, impala, zebra and white rhino) were not affected by the fine-scale plot size (8x8 m). We thus chose an intermediate plot size to optimise data collection across the array of species. Three of the six plots at each site were controls and three underwent the following treatments respectively: removal of the above-ground biomass layer through brushcutting; removal of the above-ground biomass layer through brushcutting and application of fertiliser; and application of fertiliser. Each plot was

400 m² and plots were approximately 100 m apart at each site. At mown plots, small woody shrubs above 1 m were not removed, and plots with little woody biomass were selected for. At fertilised plots, 4 kilograms (kg) of 28% LAN/KAN N fertiliser and 3.2 kg of 14% Carbon-enriched, slow-release N fertiliser was applied evenly (Woolley, unpublished data). Sites were evaluated two weeks before each data collection period to determine whether retreatment was necessary. Lack of rainfall in the dry season resulted in a limited increase of grass height regrowth of the treated plots, and thus the sites were not mown in October 2017, however fertiliser was reapplied. The full treatment was conducted again in February 2018. Overall, monthly rainfall was below average for all months except October 2017 across the duration of the study, which would likely have affected absorption of fertiliser applied in June 2017 and February 2018.

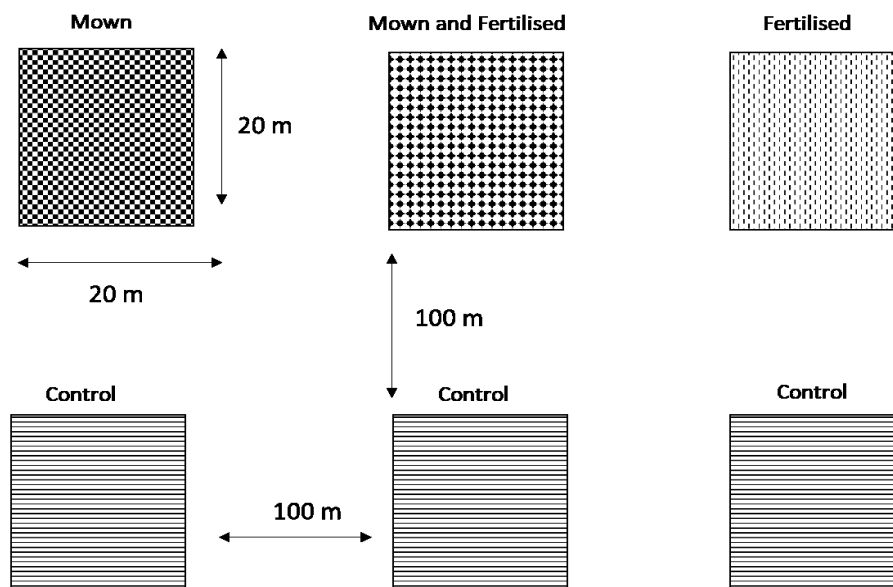


Figure 2: A visual representation of the plot layout at each of the six sites. Plots were 20 m x 20m (400m²) and were set up approximately 100 m apart.

Plots were fitted with a Cuddeback Attack Interchangeable Flash (Blue Series, Model 1255) camera trap. Camera trapping is an effective, non-intrusive and replicable means of surveying mammals over a wide range of environmental and temporal scales (Carbone *et al.*, 2001), allowing a novel means to overcome observational error of dung counts or animal observation counts. Camera traps were fitted to each plot to have the best visual of the 400m² plot area and were placed between 0.5 m and 1 m from the ground. They were angled away from the sun where possible, and set to a wide view angle, Fresnel cover lowered and aspect

wide. The Camera traps were set to take photographs at 10-minute intervals when activity was sensed. Finally, they were serviced (batteries replaced, and data retrieved) every three months, but batteries lasted on average five weeks, resulting in five weeks of data per season.

Herbivore species

This study assesses the patch scale selection processes which grazers and mixed feeders undertake when foraging within the constraints of water availability, forage quality and quantity and habitat requirements using camera trap captures. We thus focused on nine commonly occurring grazer and mixed feeder species in the Satara region of KNP. These species were selected due to their representation of a suite of digestive strategies, feeding preferences and body sizes. The selected species were: five grazers (plain's zebra *Equus quagga*, waterbuck *Kobus ellipsiprymnus*, blue wildebeest *Connocheates taurinus*, buffalo *Syncerus caffer*, white rhinoceros *Ceratotherium simum*); and two mixed feeders (elephant *Loxodonta africana* and impala *Aepyceros melampus*). Attributes assigned to camera trap data were as follows: date; species within the photo; time of day; functional characteristics (body size, feeding preference and digestive type), hereafter 'functional types', and number of individuals. Feeding preference followed the generalist functional classifications of grazing and mixed feeding ungulate herbivores described by Owen-Smith (1982).

Environmental covariates

Distance to water was the primary determinant of site placement as it typically dictates herbivore movement (Gaylard *et al.*, 2003) and seasonal population fluctuations of herbivore species. The distance from the N'wanetsi and Sweni rivers, and the associated waterholes of the area, were used to determine suitable sites of the three distances from water. Predation was measured through camera trap data, allowing covariates of predator species, incidences of multiple predators and days since predator presence to be measured. Lions (*Panthera leo*) were also recorded as an individual variable due to the strong influence they have across the spectrum of herbivore body sizes (Valeix *et al.*, 2009). Camera trap data additionally used to determine grass height (using a marked pole in front of each camera), and plot burn data (burnt/unburnt and days since fire).

The average distance to the nearest visual obstruction was measured as a proxy for landscape of fear, given that distance to the nearest obstruction changes ambush risk by a predator and anti-predator strategies by herbivores (Riginos, 2015). This value was the mean of

measurements to the nearest obstruction (trees or shrubs) on each plot, using a range finder at a height of 1.5 m every 15 degrees, totalling 24 measurements (Riginos, 2015). The inverse of these measures was used to determine the distance between trees.

The following environmental variables were taken on each plot at each data collection period to measure forage quantity and quality: grass biomass using a disc pasture meter (Trollope & Potgieter, 1986), for which the measurement value was used as a proxy for biomass; grass quality using the Walker 8-point scale (Walker, 1976); and grass species were identified and a percentage cover within the plot estimated using Braun-Blanquet measure (Westhoff & Van Der Maarel, 1978). Grass quality and percentage cover were estimated in a 1 m² grid which was dropped at 10 random points in the plot. The percentage of vigorous grass cover was determined using the mean of 'vigorous' values determined using the Walker 8-point scale (Walker, 1976). The coefficient of variation (CV) for grass biomass values was used as a measure of biomass heterogeneity, and the CV of distance to the nearest obstruction as landscape heterogeneity.

Data analysis

Data were split into five time classes, namely: 'pre-sunrise' (00h00 to 05h59), 'morning' (06h00 to 09h59), 'midday' (10h00 to 13h59), 'afternoon' (14h00 to 17h59) and 'night' (18h00 to 23h59). Camera trap captures for each treated plot were recorded individually, however control plot data for the respective site was grouped together. Each capture was recorded as detection/non-detection irrespective of number of individuals in the capture, to determine probability of a species occurring at a site. To determine which environmental variables had the strongest effect on plot selection by species, daily time of day binomial values were tested against environmental covariates using a generalised linear model in R v3.4.1 (R-Development-Core-Team, 2011). We used the Akaike Information Criterion (AICc) (library AICcmodavg in R) to inform which model most suitably described the probability of a species selecting a plot to forage. Using literature, we developed predictions (Table 1) of what environmental variables would result in the lowest AICc value for each species and wrote a model to test these predictions. Thirty-four plausible models were then constructed, and each species was tested against the prediction model for each species; and the AICc values of the prediction model compared to the plausible model results. For species that had low capture rates over the data collection period, models were restricted to additive models rather than

interactive models, as we had a set of variables against which to test species detection, and interactions between these variables could not be tested due to small sample size. The temporal resolution of the data did not allow us to test the effects of predation against time of day, and as such predation was not included as a variable in the models.

Table 1: Study species characters and the predictions of expected model outcomes based on the effect of environmental variables on these characteristics. Species traits were based off the following literature: Gagnon & Chew, 2000; Clauss *et al.*, 2003; Hopcraft *et al.*, 2010; Hempson, Archibald *et al.*, 2015.

Species	Characteristics	Prediction
Impala	Small-medium mixed feeder (browser-grazer intermediate), ruminant, selective feeder, water dependent	Alters distribution in response to water availability across seasons by moving closer to water in the dry season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Wildebeest	Medium grazer, ruminant, selective feeder (variable grazer), water dependent	Alters distribution in response to water availability across seasons by moving closer to water in the dry season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Waterbuck	Medium-large grazer, ruminant, selective feeder (variable grazer), water dependent	Remains closer to perennial water sources throughout in the dry and wet season, responds to mown, mown and fertilised treatments, responds to risk of predation.
Zebra	Medium-large grazer, non-ruminant, non-selective feeder (obligate grazer), water dependent	Alters distribution in response to water availability but will trade-off feeding close to water to obtain a higher quantity of forage. Responds to fertilised treatments in the dry season and mown and fertilised treatments in the wet season. Less responsive to risk of predation.
Buffalo	Large grazer, ruminant, non-selective feeder (variable grazer), water dependent	Alters distribution in response to water and forage availability. Trade-off being close to water to obtain high quantity forage, responds to fertilised treatments in both the dry and wet season. Less responsive to risk of predation.
Elephant	Megaherbivore mixed feeder (browser-grazer intermediate), non-ruminant, non-selective feeder, water dependent	Alters distribution in response to water and forage availability, will occur further from water to obtain high quantity forage. Unlikely to respond to treatments, will not respond to risk of predation.
White Rhinoceros	Megaherbivore selective feeder (obligate grazer), non-ruminant, water dependent	Remains closer to perennial water across seasons, responds to mown, mown and fertilised treatments across seasons, will not respond to risk of predation.

Results

For most species, the predictive models had higher AICc values than the plausible models against which they were tested (Appendix A). This is likely because the predictive models that were written had few variables and were thus not explanatory enough of species patterns. Species with low detection data typically experienced more specialised feeding requirements, and as such trends at all treatments and/or all distances from water cannot be represented in the figures.

Impala

In the late dry season, preference was shown for mown sites closer to water (0.5 km and 2.5 km), and for mown and fertilised sites furthest from water (5 km) (Table 2, Fig. 3., Fig.4, Fig. 5). In the early wet season, preference was shown for mown plots at all three distances to water, and at the mown and fertilised plot at 0.5 km from water. In the late wet season, preference was shown for mown and fertilised plots at all distances from water. No preference was shown for fertilised treatments across all three seasons.

Wildebeest

In the late dry season, preference was shown for mown plots further from water (2.5 km and 5 km), and fertilised plots closer to water) (Table 3, Fig. 3., Fig.4, Fig. 5). In the early wet season, preference was shown for mown plots furthest from water. In the late wet season, preference was shown for mown and fertilised plots closer to water (0.5 km and 2.5 km), and fertilised plots furthest from water.

Waterbuck

Across all three seasons, preference was shown for mown plots at 0.5 km and 2.5 km from water (Table 2, Fig. 3). Waterbuck did not respond to any other treatments and were not detected 5 km from water.

Zebra

In the late dry season, zebra responded to fertilised plots at all three distances from water (Table 3, Fig. Fig. 3, Fig.4, Fig. 5). In the early wet season, they did not show a response to any treatment at any distance from water. In the late wet season, zebra showed preference for mown and fertilised plots further from water (2.5 km and 5 km).

Buffalo

No trends for buffalo were detected at 0.5 km from water (Table 2). In the late dry season, preference was shown for mown plots 2.5 km from water and mown and fertilised plots at 2.5 km and 5 km from water. In the early wet season, preference was shown for mown plots at 2.5 km and 5 km from water. Preference was shown for fertilised plots at 2.5 km and 5 km from water.

No discernible trends for white rhino or elephant could be detected due to their capture frequency (Table 2). Broad models were not robust enough to determine trends.

Table 2: The results of model outcomes with the lowest AICc value for each species across the seasons (late dry, early wet and late wet), and three distances to water (0.5 km, 2.5 km and 5 km). For treatment, 'M' refers to mown plots, 'MF' refers to mown and fertilised plots and 'F' refers to fertilised plots. A '+' represents a preference for the treated plot, and a '-' represents a preference for the control plots. 'X' represents effects that could not be detected, either because results between treated and control plots did not differ significantly, or because the effect could not be tested due to small sample size.

Species	Season	Treatment	Response			Species	Season	Treatment	Response		
			0.5	2.5	5				0.5	2.5	5
<i>Impala</i>	Late dry	M	+	+	-	<i>Buffalo</i>	Late dry	M	x	+	-
		MF	-	-	+			MF	x	+	+
		F	-	-	-			F	x	-	-
	Early wet	M	+	+	+		Early wet	M	x	+	+
		MF	+	-	-			MF	x	-	-
		F	-	-	-			F	x	-	-
	Late wet	M	-	-	-		Late wet	M	x	-	-
		MF	+	+	+			MF	x	x	-
		F	-	-	-			F	x	+	+
<i>Wildebeest</i>	Late dry	M	-	+	+	<i>White rhinoceros</i>	Late dry	M	x	x	x
		MF	-	-	-			MF	x	x	x
		F	+	-	-			F	x	x	x
	Early wet	M	-	-	+		Early wet	M	x	x	x
		MF	-	-	-			MF	x	x	x
		F	-	-	-			F	x	x	x
	Late wet	M	-	-	-		Late wet	M	x	x	x
		MF	+	+	-			MF	x	x	x
		F	-	-	+			F	x	x	x
<i>Waterbuck</i>	Late dry	M	+	+	x	<i>Elephant</i>	Late dry	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
	Early wet	M	+	+	x		Early wet	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
	Late wet	M	+	+	x		Late wet	M	x	x	x
		MF	-	-	x			MF	x	x	x
		F	-	-	x			F	x	x	x
<i>Zebra</i>	Late dry	M	-	-	-						
		MF	-	-	-						
		F	+	+	+						
	Early wet	M	-	-	-						
		MF	-	-	-						
		F	-	-	-						
	Late wet	M	-	-	-						
		MF	-	+	+						
		F	-	-	-						

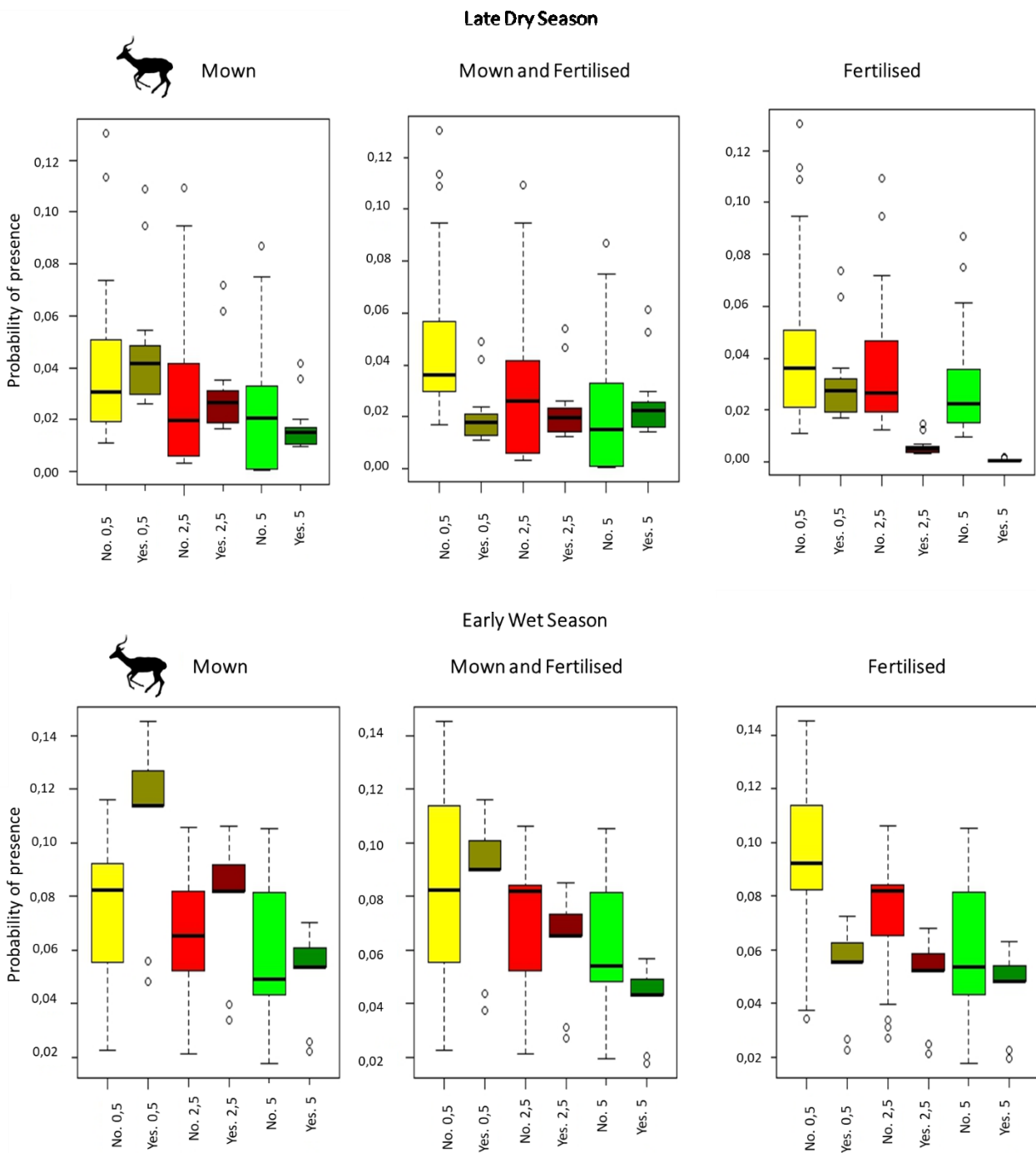


Figure 3: Results from lowest AICc value models for impala across distance from water throughout the 3 sampling seasons. 'No.0.5' represents probability of presence for the species at untreated sites at 0.5 km from water, and 'Yes.0.5' represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

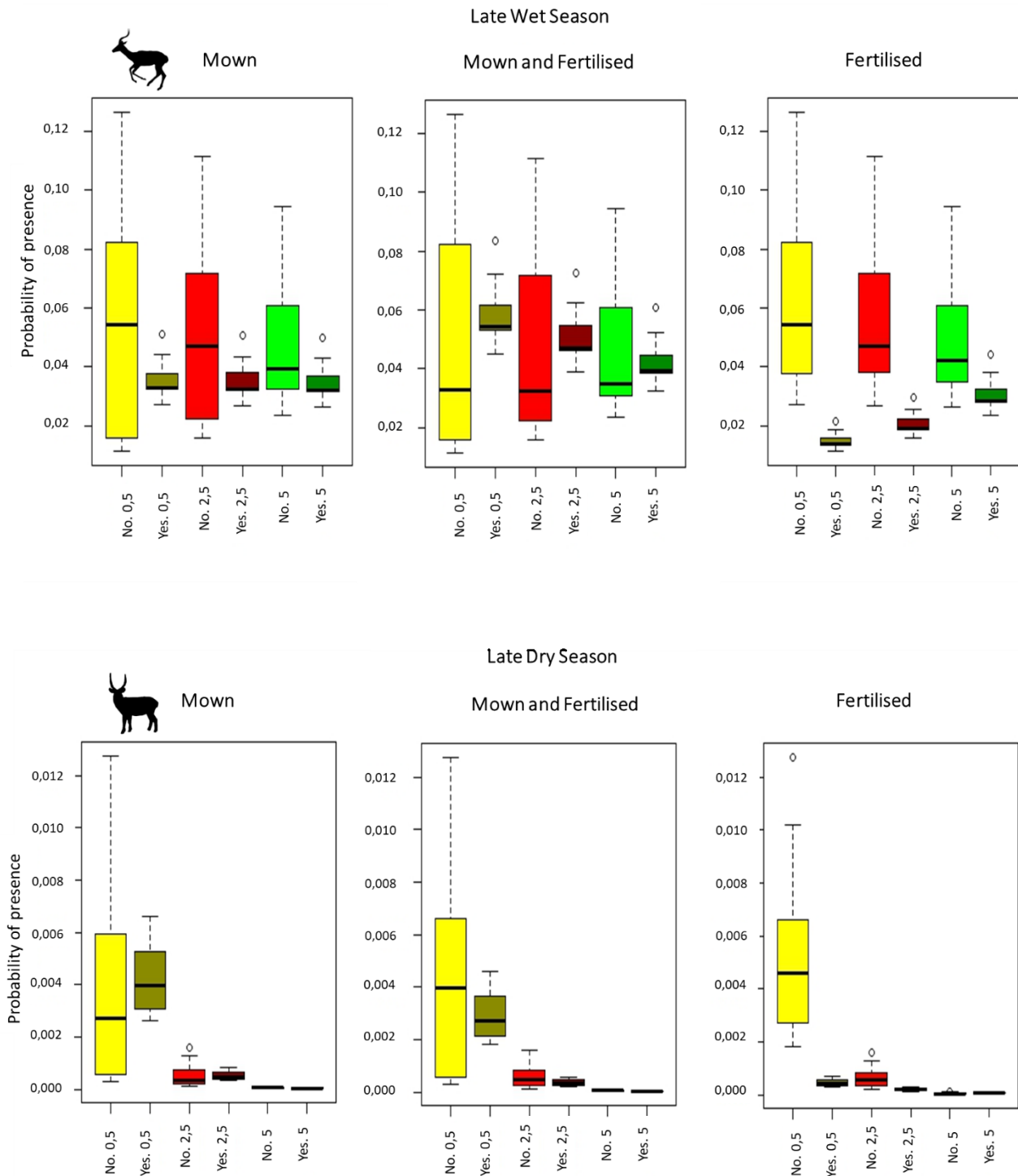


Figure 4: Results from lowest AICc value models for impala and waterbuck across distance from water throughout the 3 sampling seasons. 'No.0.5' represents probability of presence for the species at untreated sites at 0.5 km from water, and 'Yes.0.5' represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

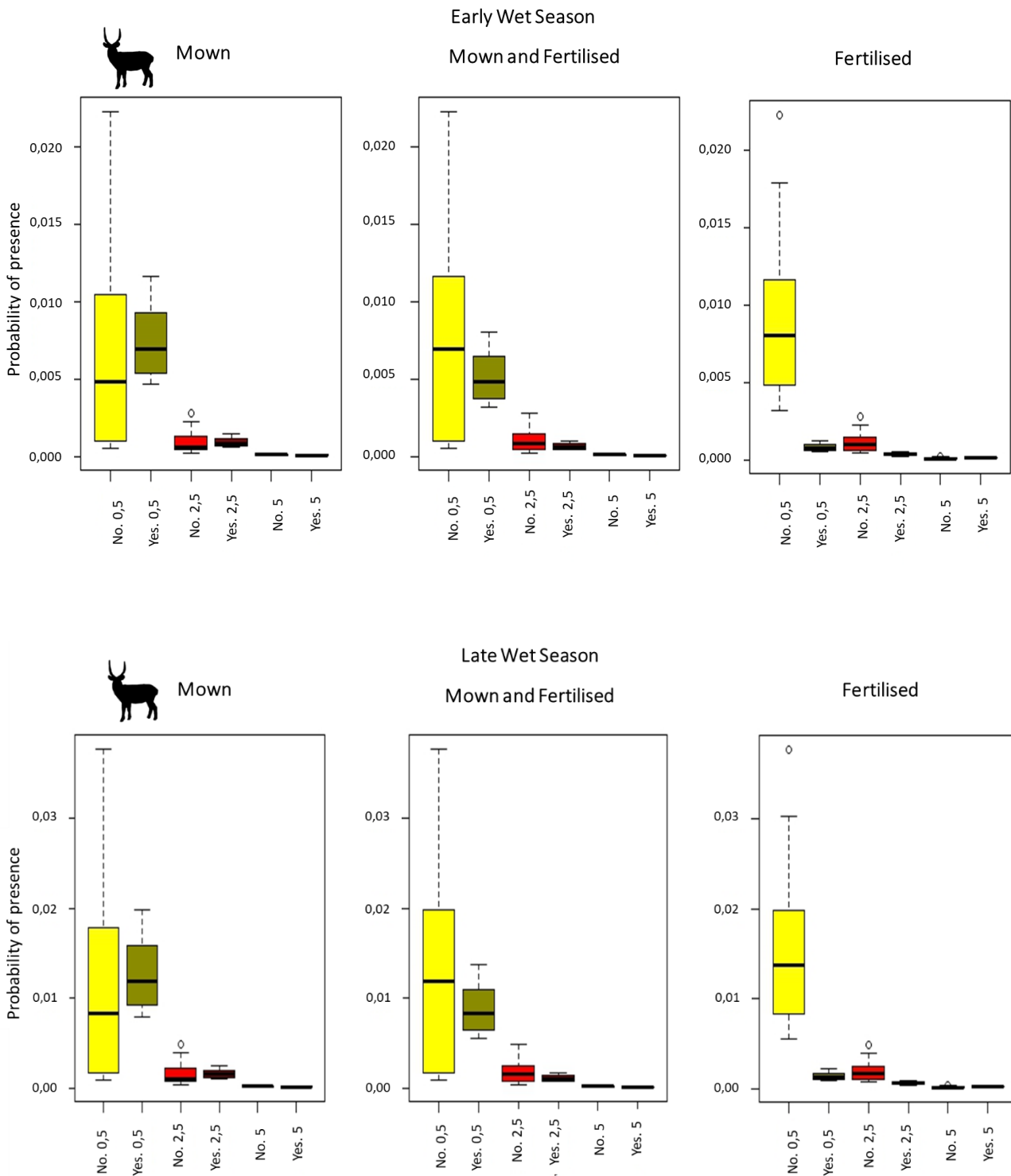


Figure 5: Results from lowest AICc value models for waterbuck across distance from water throughout the 3 sampling seasons. 'No.0.5' represents probability of presence for the species at untreated sites at 0.5 km from water, and 'Yes.0.5' represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

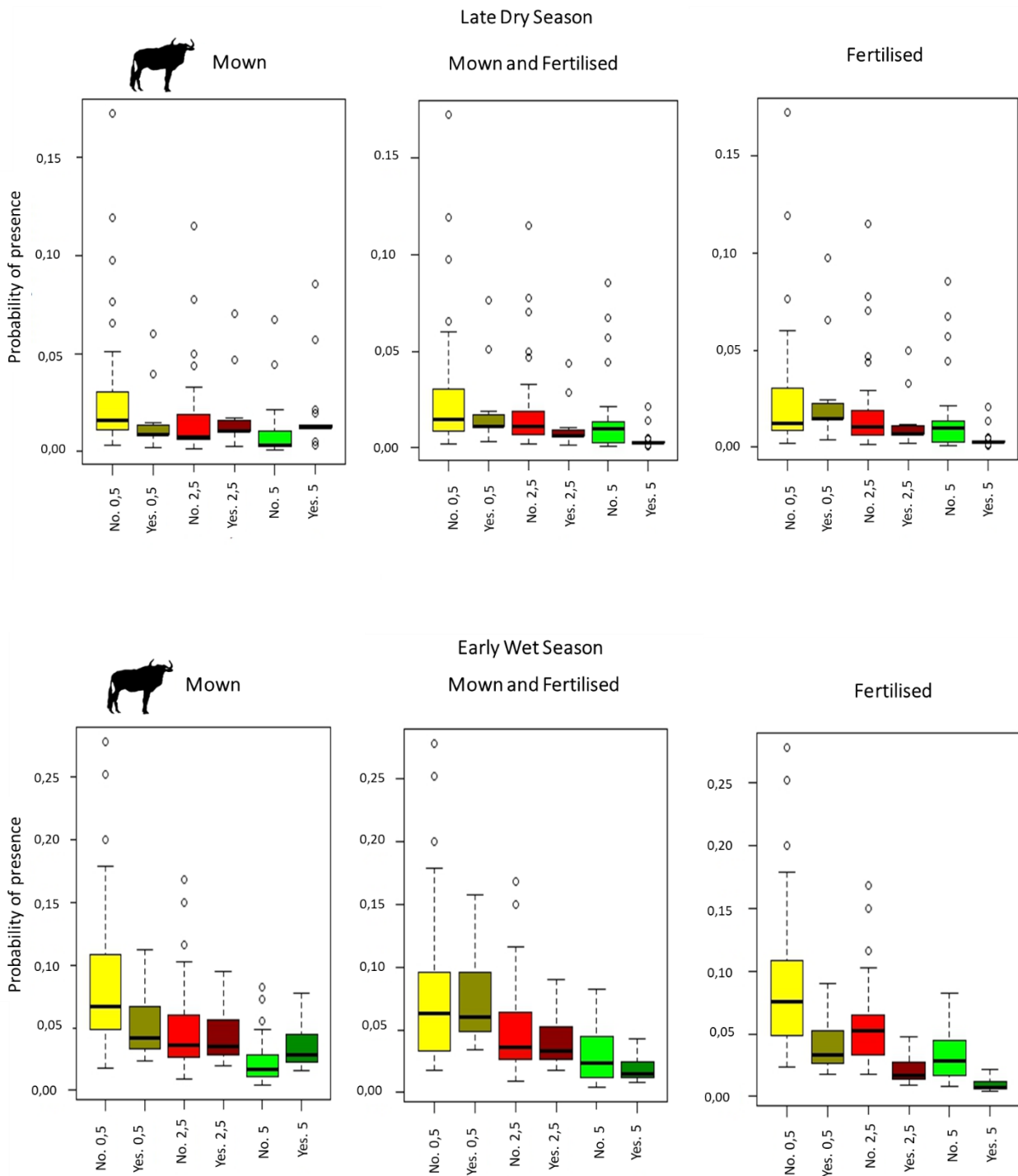


Figure 6: Results from for lowest AICc value models for wildebeest across distance from water throughout the 3 sampling seasons. 'No.0.5' represents probability of presence for the species at untreated sites at 0.5 km from water, and 'Yes.0.5' represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

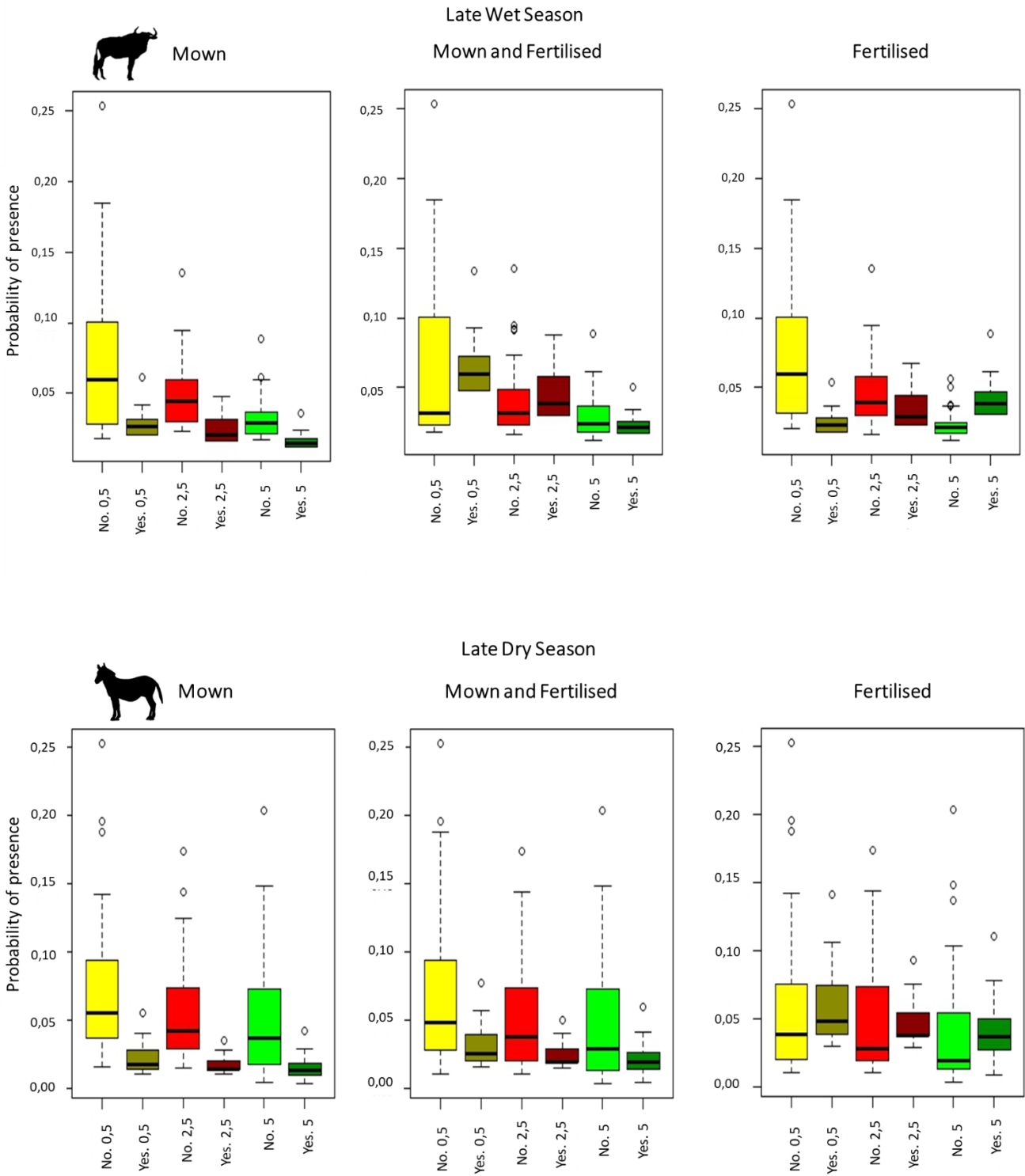


Figure 7: Results from lowest AICc value models for wildebeest and zebra across distance from water throughout the 3 sampling seasons. ‘No.0.5’ represents probability of presence for the species at untreated sites at 0.5 km from water, and ‘Yes.0.5’ represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

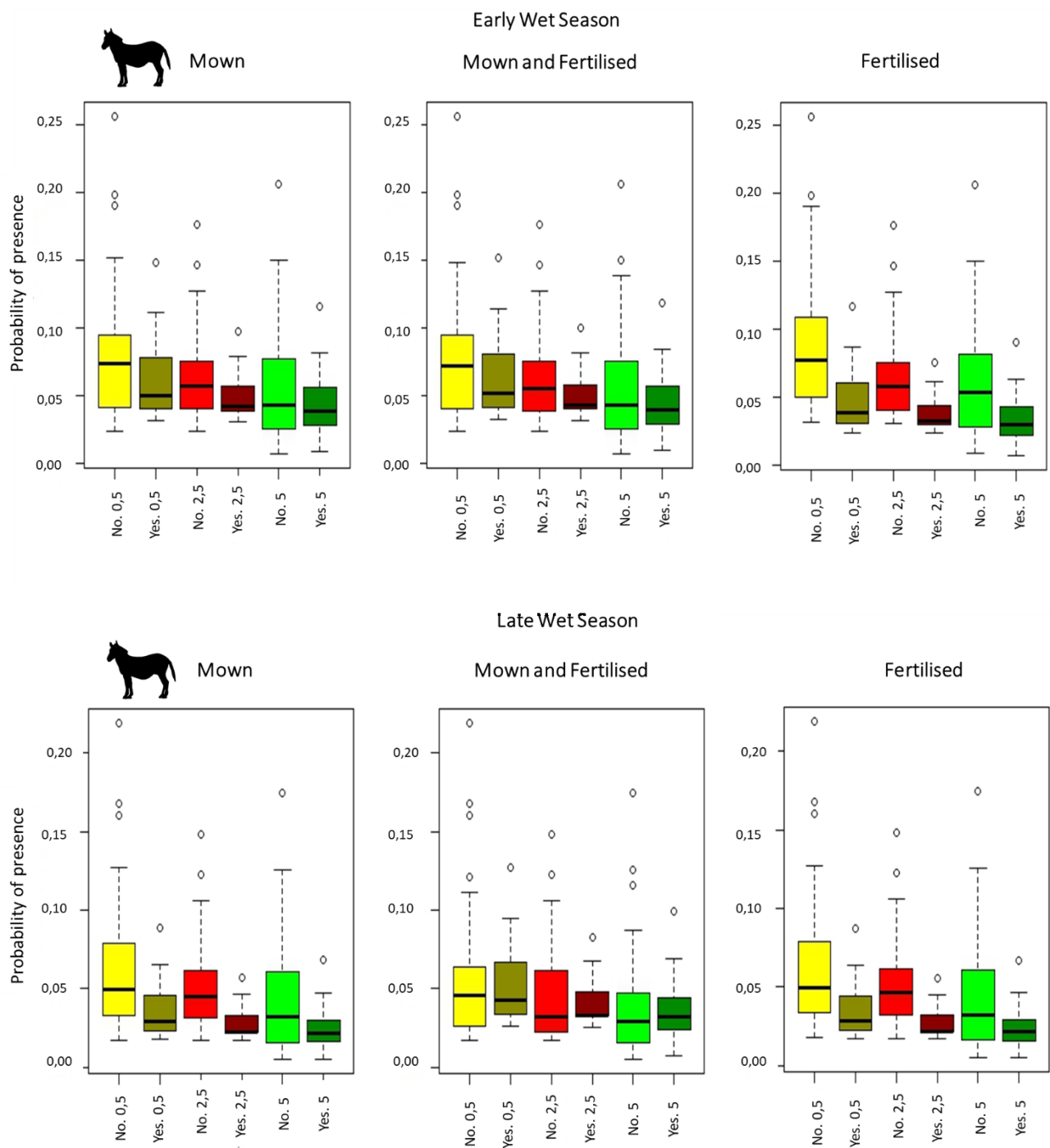


Figure 8: Model results for lowest AICc value models for zebra across distance from water throughout the 3 sampling seasons. 'No.0.5' represents probability of presence for the species at untreated sites at 0.5 km from water, and 'Yes.0.5' represents the respective treatment at 0.5 km from water. The three distance values are 0.5 km from water, 2.5 km from water and 5 km from water. The graphics have been rescaled to be clearly interpreted, and thus probability values are not shown on a full axis (i.e. 0-0.1 probability of presence).

Discussion

Trade-offs and complex interactions alter how herbivores select for forage at a patch-scale, which consequently affects larger distribution patterns of grazing species. As such, when forage quality and quantity decreases, so does intake rate, resulting in an increase in movement rate (Bailey *et al.*, 1996). Herbivores are able to improve foraging efficiency through spatial memory, allowing them to select more nutritious patches, avoid areas that have little food and remember which resources have recently been depleted (Bailey *et al.*, 1996). These patterns were evident in the utilisation of resources by grazing herbivores in KNP. Each species in this analysis can be considered a representative of functional types, however to avoid over-representing species-specific traits within functional types, these results are discussed by species.

For impala, results indicated that in the dry season they will utilise mown plots closer to water and mown and fertilised plots further from water. The utilisation of resources further from water is likely because in the dry season they will be browsing rather than grazing (Du Toit, 2003), as browse maintains a higher protein content longer into the dry season than grass (McNaughton & Georgiadis, 1986). Although impala are highly water dependent and typically feed 1-2 km from water (Gaylard *et al.*, 2003), they face trade-offs between browse availability and being close to water in the dry season. Shrub density typically increases with distance from watering points at Satara, with woody vegetation resources having been largely depleted by large herbivores as far as 2.8 km from water (Brits *et al.*, 2002). To overcome this trade-off, they will utilise mown plots in the dry season where they would be able to graze the most nutritious leaves from grass due to their relatively narrow muzzles (Owen-Smith *et al.*, 2017). Impala showed preference for mown and mown and fertilised plots in both the early wet and late wet season, similar to results observed in Hluhluwe-iMfolozi Park, where impala utilise grazing lawns in the wet season and reduce their use going into the dry season (Owen-Smith *et al.*, 2017).

Similarly, wildebeest also use unmown plots closer to water and mown plots further from water, also likely as a result of the trade-offs faced between water dependency and metabolic requirements. Due to their water dependency, wildebeest typically feed 0.5 km to 2 km from water (Gaylard *et al.*, 2003), but unlike mixed feeders they cannot extend this reach in the dry season by utilising browse resources. This could explain their selection for fertilised plots,

which would have had higher biomass and higher N content than other mown plots close to water in the dry season. However, in the wet season when water becomes more locally available across the landscape (Gaylard *et al.*, 2003) and grass regrowth is more nutritious after rain (Archibald, 2008), wildebeest show preference for mown and fertilised plots closer to water. Typically, wildebeest are able to exploit short grass resources as a result of their broad muzzle (Arsenault *et al.*, 2008), and will select for these resources of lower structural fiber content (Stock *et al.*, 2010). Overall wildebeest showed low preference for fertilised plots, for which grass heights closer to water remained > 30 cm; and their use of grasses > 21 cm is proportionally much lower than those < 20 cm (Arsenault *et al.*, 2008). The selection of short, low fiber grass in impala and wildebeest improve their digestive rates, allowing them to increase their forage intake (Wirtz & Oldekop, 1991).

In contrast to impala and wildebeest, waterbuck indicated a clear preference for mown plots close to water across all three seasons. Although ruminants, waterbuck are variable grazers (Hempson *et al.*, 2015) and will thus select for grass and other roughage which has the highest available crude protein (Tomlinson, 1980). Grasses typically decrease in crude protein and increase in crude fiber in the dry season (Kutilek, 1979), and waterbuck will alter the forage they select for. This selection is exclusively in the 0.5 km to 2 km zone from water, and our results supported this strong probability of presence only in the 0.5 km zone. Waterbuck are likely competitively displaced by short-grass grazers such as wildebeest and white rhino in the dry season (Cromsigt *et al.*, 2017) when short-grass resources are scarce, and in the wet season on mown and fertilised plots when high densities of impala, wildebeest and zebra select for these resources.

Although zebra are water dependent and typically feed in the 0.5 km to 2 km zone from water (Gaylard *et al.*, 2003), they trade off being close to water to obtain higher quantity of forage in the dry season and periods of drought (Gaylard *et al.*, 2003; Venter *et al.*, 2015). Zebra thus responded to fertilised treatments at all distances from water in the dry season, where grass swards maintained a height of > 50 cm, which zebra typically select for at this time (Arsenault *et al.*, 2008; Sinclair, 1985). Zebra are constrained by metabolic requirements in the dry season and must select for higher quantity forage in order to maintain digestive fill, as hindgut fermenters experience a faster rate of digestive passage (Clauss *et al.*, 2003). In the wet season they typically experience a habitat use overlap with smaller and more selective grazers

(Owen-Smith *et al.*, 2017; Sinclair, 1985) which our results did not indicate at a plot level in the early wet season. However, we did find a preference for mown and fertilised plots further from water in the late wet season. Typically, equids select for heterogenous grazing areas, allowing them to maximise their optimal forage intake by consuming short grass offering high quality and tall grass offering high instantaneous intake rates (Fleurance *et al.*, 2010). This likely explains why we did not detect an overall selection for treated plots, results also found by Owen-Smith *et al.* (2017).

Buffalo trends were difficult to detect and accurately interpret as they may be abundant in biomass but moved through the study area infrequently. Buffalo overlap in their grass utilisation with zebra and white rhino in the dry season (Owen-Smith *et al.*, 2017), unselectively feeding on bulk resources (Sinclair, 1977). Buffalo have large distribution changes across the KNP landscape throughout seasonal changes, likely because they need to meet metabolic requirements in large numbers. They therefore change their habitat and grass selection to optimize nutrition (Venter & Watson, 2008), because of high intraspecific competition between herd members (Pretorius, 2009) and as such, they select for high nutrition at a small local scale but prefer larger patches. Although the scale at which we tested was small enough, there was not a consistent enough capture rate from which to make clear assumptions about selectivity.

White rhinoceros are strictly grazers, and their broad muzzles enable them to obtain adequate forage from grasses which would otherwise be too short to meet their nutritional requirements (Owen-Smith *et al.*, 2017). Their ability to mow down large grass swards to repeatedly cropped short grass patches promotes the growth of low-growing species which then form grazing lawns (Hempson *et al.*, 2015; McNaughton, 1984). These grazing lawns comprise less structural fiber and have higher sodium concentrations (Hempson *et al.*, 2015; Stock *et al.*, 2010) necessary for hindgut fermenters, who experience greater sodium losses due to increased digestive passage rates (Clauss *et al.*, 2003). However, these lawns cannot be maintained indefinitely, as grazing species respond to primary production as a result of rainfall, and as such the resource availability is unpredictable (Bonnet *et al.*, 2010). Thus, in the dry season white rhino will select for the most nutritious bunch grasses which can be found in the areas of reserve forage (Owen-Smith *et al.*, 2017), and overall rhino select for high nutrient grass swards at a landscape scale. Our data was not sufficient to detect these

trends across seasons, as the capture rate of white rhinoceros was much lower than other species.

No clear seasonal or distance trends could be detected for elephant at the scale at which we tested. Pretorius (2009) found that species with an extreme mouth to body mass ratio, such as elephant, select nutrient-rich areas at large scales. Elephants select foraging areas with large-scale characteristics, such as high forage availability and distance from water across seasons (De Knegt *et al.*, 2011; Shrader, Bell *et al.*, 2012), and thus our experiment was not at a scale at which this foraging selectivity by this species could be detected.

Conclusion

Herbivores form an essential component in the environment in which they occur, due to the impact that they have on their ecosystem. In this paper we aimed to unpack some of the mechanisms behind what affects how herbivores select forage at a patch scale. Results from this study showed that season was a major determinant of species distribution across the landscape, especially those which are not obligate grazers or feed exclusively in the 0.5 km to 2 km zone from water. We found that when freed from the constraints of decreased forage quality and quantity, and limited water availability in the dry season, the probability of presence by species at their preferred forage resource increased. This highlights the trade-off species face under the constraints of the dry season, and species-specific traits which they have adapted to meet metabolic requirements when resources are not readily available. Overall, selectivity in larger-bodied species was harder to unravel either due to low camera detection across the sampling period, or their selectivity being at scales greater than what we tested.

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Literature Cited

- Archibald, S. 2008. African grazing lawns—how fire, rainfall, and grazer numbers interact to affect grass community states. *The journal of wildlife management*, 72(2), 492-501.
- Arsenault, R., & Owen-Smith, N. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, 117(11), 1711-1717.
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. 1996. Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386-400.
- Biggs, H.C., J. T. Du Toit, Rodgers, K.H. (Eds.) 2003. *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Bonnet, O., Fritz, H., Gignoux, J., & Meuret, M. 2010. Challenges of foraging on a high-quality but unpredictable food source: the dynamics of grass production and consumption in savanna grazing lawns. *Journal of Ecology*, 98(4), 908-916.
- Brits, J., Rooyen, M. W. V., & Rooyen, N. V. 2002. Ecological impact of large herbivores on the woody vegetation at selected watering points on the eastern basaltic soils in the Kruger National Park. *African Journal of Ecology*, 40(1), 53-60.
- Carbone, C., Christie, S., Conforti, K., Coulson, T., Franklin, N., Ginsberg, J., Griffiths, M., Holden, J., Kawanishi, K., & Kinnaird, M. 2001. The use of photographic rates to estimate densities of tigers and other cryptic mammals. *Animal Conservation*, 4(1), 75-79.
- Claus, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., & Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, 136(1), 14-27.
- Codron, D., Lee-Thorp, J. A., Sponheimer, M., Codron, J., de Ruiter, D., & Brink, J. S. 2007. Significance of diet type and diet quality for ecological diversity of African ungulates. *Journal of Animal Ecology*, 76(3), 526-537.
- Cromsigt, J. P., Veldhuis, M. P., Stock, W. D., le Roux, E., Gosling, C. M., & Archibald, S. 2017. The Functional Ecology of Grazing Lawns: how grazers, termites, people and fire shape HiP's Savanna Grassland Mosaic. Pp 135 -161 In Cromsigt J. P. M., Archibald, S. & Owen-Smith, N. (Eds.) *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. Cambridge University Press, Cornwall.

- De Knegt, H. J., Van Langevelde, F., Skidmore, A. K., Delsink, A., Slotow, R., Henley, S., Bucini, G., De Boer, W. F., Coughenour, M. B., Grant, C. C., Heitkönig, I. M. A., Henley, M., Knox, N. M., Kohi, E. M., Mwakiwa, E., Page, B. R., Peel, M., Pretorius, Y., Van Wieren, S. E., & Prins, H. H. T. 2011. The spatial scaling of habitat selection by African elephants. *Journal of Animal Ecology*, 80(1), 270-281.
- Demment, M. W., & Soest, P. J. V. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125(5), 641-672.
- Du Toit, J. T. 2003. Large herbivores and savanna heterogeneity. Pp 292-310 in J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Duncan, P., Foose, T. J., Gordon, I. J., Gakahu, C. G., & Lloyd, M. 1990. Comparative Nutrient Extraction from Forages by Grazing Bovids and Equids: A Test of the Nutritional Model of Equid/Bovid Competition and Coexistence. *Oecologia*, 84(3), 411-418.
- ESRI. (2012). ArcGIS (Version 9.3). Redlands, CA.
- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. 2013. Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5), 1155-1164.
- Fleurance, G., Duncan, P., Fritz, H., Gordon, I.J. & Grenier-Loustalot, M.F., 2010. Influence of sward structure on daily intake and foraging behaviour by horses. *Animal: an international journal of animal bioscience*, 4(3), 480-485.
- Frost, C. J., & Hunter, M. D. 2007. Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia*, 151(1), 42-53.
- Gagnon, M., & Chew, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, 81(2), 490-511.
- Gaylard, A., Owen-Smith, N., & Redfern, J. 2003. Surface water availability: implications for heterogeneity and ecosystem processes. Pp 171-189 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Gertenbach, W. D. 1983. Landscapes of the Kruger National Park. *Koedoe*, 26(1), 9-121.
- Gordon, I. J., & Illius, A. W. 1988. Incisor arcade structure and diet selection in ruminants. *Functional Ecology*, 2(1), 15-22.

- Gordon, I. J., & Illius, A. W. 1996. The nutritional ecology of African ruminants: A reinterpretation. *Journal of Animal Ecology*, 65(1), 18-28.
- 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(6264), 1056-1061.
- Holland, E. A., & Detling, J. K. 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology*, 71(3), 1040-1049.
- Hopcraft, J.G.C., Olf, H., & Sinclair, A.R.E., 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(12), 681-689.
- Kutilek, M. J. 1979. Forage-habitat relations of nonmigratory African ungulates in response to seasonal rainfall. *The journal of wildlife management*, 899-908.
- McNaughton, S. 1984. Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalist*, 124(6), 863-886.
- McNaughton, S. J., & Georgiadis, N. J. 1986. Ecology of African Grazing and Browsing Mammals. *Annual Review of Ecology and Systematics*, 17, 39-65.
- O'Connor, T. G., & Pickett, G. A. 1992. The Influence of Grazing on Seed Production and Seed Banks of Some African Savanna Grasslands. *Journal of Applied Ecology*, 29(1), 247-260.
- Olf, H., & Ritchie, M. E. 1998. Effects of herbivores on grassland plant diversity. *Trends in ecology & evolution*, 13(7), 261-265.
- Owen-Smith, N., Cromsigt, J. P., & Arsenault, R. 2017. Megaherbivores, Competition and Coexistence within the Large Herbivore Guild. Pp 111-135 In Cromsigt J. P. M., Archibald, S. & Owen-Smith, N. (Eds.) *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. Cambridge University Press, Cornwall.
- 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(3), 181-191.
- Owen-Smith, N., & Novellie, P. 1982. What Should a Clever Ungulate Eat? *The American Naturalist*, 119(2), 151-178.
- Parr, C. L. 2008. Dominant ants can control assemblage species richness in a South African savanna. *Journal of Animal Ecology*, 77(6), 1191-1198.

- Pretorius, Y. 2009. *Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores*. Unpublished MSc Thesis, Wageningen University, Netherlands.
- Pretorius, Y., de Boer, W.F., Kortekaas, K., van Wijngaarden, M., Grant, R.C., Kohi, E.M., Mwakiwa, E., Slotow, R. & Prins, H.H., 2016. Why elephant have trunks and giraffe long tongues: how plants shape large herbivore mouth morphology. *Acta Zoologica*, 97(2), 246-254.
- Prins, H.H.T. & Olff, H., 1998. Species-richness of african grazer assemblages: towards a functional explanation. Pp 449-490 in H. H. T. Prins & N. D. Brown (Eds.), *Dynamics of Tropical Communities: 37th Symposium of the British Ecological Society*. Cambridge University Press, United Kingdom.
- Riginos, C. 2015. Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84(1), 124-133.
- Riginos, C., & Grace, J. B. 2008. Savanna tree density, herbivores, and the herbaceous community: bottom-up vs. top-down effects. *Ecology*, 89(8), 2228-2238.
- Shipley, L. A. 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, 116(12), 1964-1974.
- Shrader, A. M., Bell, C., Bertolli, L., & Ward, D. 2012. Forest or the trees: At what scale do elephants make foraging decisions? *Acta Oecologica*, 42(0), 3-10.
- Sinclair, A. R. E. 1977. *The African buffalo: a study of resource limitation of populations*. University Press, Chicago.
- Sinclair, A. R. 1985. Does interspecific competition or predation shape the African ungulate community? *The Journal of Animal Ecology*, 899-918.
- Stock, W. D., Bond, W. J., & Van De Vijver, C. A. 2010. Herbivore and nutrient control of lawn and bunch grass distributions in a southern African savanna. *Plant Ecology*, 206(1), 15-27.
- Tomlinson, D. 1980. Seasonal food selection by water buck *Kobus ellipsiprymnus* in a Rhodesian Game Park. *South African Journal of Wildlife Research*, 10(1), 22-28.
- Trollope, W., & Potgieter, A. 1986. Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa*, 3(4), 148-152.

- Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23-30.
- van Ginkel, H. A. L., Kuijper, D. P. J., Schotanus, J., & Smit, C. 2018. Wolves and Tree Logs: Landscape-Scale and Fine-Scale Risk Factors Interactively Influence Tree Regeneration. *Ecosystems*, 1-11.
- Van Wilgen, B., Govender, N., Biggs, H., Ntsala, D., & Funda, X. 2004. Response of savanna fire regimes to changing fire-management policies in a large African national park. *Conservation Biology*, 18(6), 1533-1540.
- Venter, F. 1986. Soil patterns associated with the major geological units of the Kruger National Park. *Koedoe*, 29(1), 125-138.
- Venter, J. A., Prins, H. H. T., Mashanova, A., de Boer, W. F., & Slotow, R. 2015. Intrinsic and extrinsic factors influencing large African herbivore movements. *Ecological Informatics*, 30, 257-262.
- 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(1), 42-
- Walker, S. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research*, 6(1), 1-32.
- Westhoff, V. & Van Der Maarel, E. 1978. The braun-blanquet approach. Pp 287-399 in R. H. Whittaker (Ed.), *Classification of plant communities*. Springer, Dordrecht.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.
- Wirtz, P., & Oldekop, G. 1991. Time budgets of waterbuck (*Kobus ellipsiprymnus*) of different age, sex and social status. *International Journal of Mammal Biology*, 56, 48-58.

APPENDICES

Appendix A: AICc model results for each species probability of presence; 1, 2 and 3 represent the 3 best predictive models with lowest AICc values, and ‘Pred’ represents the predictive model against which general models were tested. Shortened variable names are as follow: ‘Dist’ = distance from water; ‘Fert’ = fertilised; ‘MownFert’= mown and fertilised; ‘Pred’=predator incidence (yes or no).

	Models	AICc	ΔAICc
1	<i>Impala</i> Season*TimeOfDay + Dist*season*Mown + Dist*season*Fert + Dist*season*MownFert +	6036.38	0.00
2	Pred	6057.21	20.83
3	TimeOfDay*Season + Mown + MownFert + Fert + Dist + Pred	6062.17	25.79
Predicted	TimeOfDay + season*Dist*Mown + season*Dist*MownFert + season*Dist*Fert + Pred Season*Dist + TimeOfDay*Mown + TimeOfDay*MownFert + Pred	6158.4	122.02
1	<i>Wildebeest</i> Season*TimeOfDay + Dist*season*Mown + Dist*season*Fert + Dist*season*MownFert +	4887.83	0.00
2	Pred	4896.47	8.64
3	Dist*TimeOfDay + season*Mown + season*MownFert + season*Fert + Pred	4906.21	18.38
Predicted	Season*TimeOfDay + Mown + MownFert + Fert + Pred + Dist Season*Dist + TimeOfDay + Dist*Mown + Dist*MownFert + Pred	5019.52	131.17
1	<i>Waterbuck</i> Season + TimeOfDay + Mown + MownFert + Fert + Dist + Pred	587.92	0.97
2	Season*TimeOfDay + Mown + MownFert + Fert + Pred + Dist	591.02	4.07
3	Pred*Dist + season + TimeOfDay*Mown + TimeOfDay*MownFert + TimeOfDay*Fert	591.51	4.56
Predicted	Season + TimeOfDay + Mown + MownFert + Dist*Fert	586.95	0.00
1	<i>Zebra</i> Dist*TimeOfDay + season*Mown + season*MownFert + season*Fert + Pred	6250.51	0.00
2	Season*TimeOfDay + Dist*season*Mown + Dist*season*MownFert + Dist*season*Fert +	6252.3	1.79
3	Pred	6259.04	8.53
Predicted	Pred*season + Dist*TimeOfDay*Mown + Dist*season*MownFert + Dist*season*Fert Dist*season + Dist*Fert + TimeOfDay + Pred	6473.63	223.12
1	<i>Buffalo</i> Dist*season + TimeOfDay*Mown + TimeOfDay*MownFert + TimeOfDay*Fert + Pred	781.49	2.70
2	Season + TimeOfDay + Mown + MownFert + Fert + Dist + Pred	796.24	17.45
3	Dist + TimeOfDay + season*Mown + season*MownFert + season*Fert + Pred	797.33	18.54
Predicted	Dist*season + Dist*Fert + TimeOfDay + Pred	778.79	00.00
1	<i>Elephant</i> Dist*season + TimeOfDay*Mown + TimeOfDay*MownFert + TimeOfDay*Fert + Pred	2817.66	0.00
2	Season + TimeOfDay + Mown + MownFert + Fert + Dist + Pred	2839.48	21.82
3	TimeOfDay+ season + Dist*Mown + Dist*MownFert + Dist*Fert + Pred	2839.56	21.90
Predicted	Season*Dist + TimeOfDay+ Fert	2833.67	16.01
1	<i>White Rhino</i> TimeOfDay + season + Dist*Mown + Dist*MownFert + Dist*Fert + Pred	384.45	0.00
2	Season + TimeOfDay + Mown + MownFert + Fert + Dist + Pred	384.95	0.50
3	Pred*TimeOfDay + Dist*Mown + Dist*MownFert + Dist*Fert + season	387.70	3.25
Predicted	Season*Dist + Dist*Fert + TimeOfDay	385.39	0.94

Chapter 5: Synthesis

Introduction

In this chapter I highlight the main findings and how these addressed the aims and objectives of my research. I also provide recommendations relating to the management of herbivores across differing landscape scales and conclude with potential future research possibilities.

The effective management and preservation of protected areas is becoming increasingly important at a global scale. Globally herbivore populations are threatened by the combined impacts of habitat fragmentation and degradation, over-hunting and the encroachment of humans and their livestock (Ripple *et al.*, 2015). The scale of these threats has rapidly increased, and globally we are experiencing a severe decline in herbivore populations (Hempson *et al.*, 2015; Ripple *et al.*, 2015; Vie *et al.*, 2009). In Africa, there has been a dramatic decline in the abundance of herbivores over the last three decades despite the scale and number of protected areas throughout Africa, (Craigie *et al.*, 2010). Herbivores undeniably have ecological roles within ecosystems (Hempson *et al.*, 2017), but we cannot expect to effectively preserve these roles if we do not understand what is driving herbivore assemblages to occupy the spaces that they do. Furthermore, herbivores are susceptible to the effects of conservation management interventions such as artificial water provision (Owen-Smith, 1996; Smit *et al.*, 2007), fencing (Boone & Hobbs, 2004; Freitag-Ronaldson & Foxcroft, 2003) and effects of the removal or re-introduction of species (Lagendijk *et al.*, 2012; Ripple *et al.*, 2001).

Given the rate at which threats to herbivore distribution and abundance are escalating, it is critical to find tools which allow us to understand and predict herbivore habitat selection and distribution over a landscape scale. Herbivore distribution is furthermore driven by fine-scale foraging decisions (Pretorius, 2009; Shipley, 2007), which are governed by extrinsic (water availability, forage quantity and quality, risk of predation) and intrinsic factors (mouth morphology, body size, feeding preference, digestive type) (Kramer, 2001; Venter, 2015) (Table 1). Furthermore, the relative strength of extrinsic versus intrinsic factors determine assemblage composition and as a result, the interspecific processes and diversity thereof. Thus, we must focus at a patch scale to strengthen our understanding of the mechanisms that influence broader, landscape scale, temporal and spatial distribution of herbivores.

Table 1: The intrinsic and extrinsic factors evaluated across functional types, the expected outcomes predicted against these factors, and the effects observed in the dry and wet seasons. Species traits were based off of the: Gagnon & Chew, 2000; Clauss *et al.*, 2003; Hopcraft *et al.*, 2010; Hempson, Archibald *et al.*, 2015.

Functional types	Intrinsic constraints	Extrinsic constraints	Effect – Dry season	Effect – wet season
Medium grazer	selective grazer; ruminants; water dependent	Water availability; forage quality; high risk of predation	Occurs close to water in lower density; select open habitats; select short grass resources where possible	Occurs further from water, select short grass resources, occur at higher density in open habitats
Large grazer	Bulk grazer; non-ruminants and ruminants; Water dependent	Water availability; forage quantity; intermediate risk of predation	Occurs further from water in dry season; select high quantity resources and mixed (more dense) habitats	Occurs closer to water; select a mixture of high quality (short) and quantity (tall) grass resources to maintain fill; select both open and more closed habitats
Megagrazer	Bulk grazer; non-ruminant; water dependent	Water availability; low risk of predation	Low data; but occurs at short grass resources further from water	Low data; but occurs at short grass resources further from water
Small browser	Selective browser; ruminants; Less water-dependent	Forage quality; high risk of predation; water availability	Occurs far from water in dense habitats	Occurs far from water in dense habitats
Large browser (includes giraffe)	Selective browser; ruminants; intermediate water dependent	Forage quality; intermediate risk of predation; water availability.	Occurs far from water in dense habitats	Occurs closer to water, still selecting for dense habitats
Small mixed-feeder	Selective mixed-feeder; ruminant; water dependent	Water-availability; forage quality; high risk of predation	Occurs further from water, selects for browse resources in dense habitats	Occurs more evenly across the landscape, selects for short-intermediate grass resources in more open habitat
Mega mixed-feeder	Bulk mixed-feeder; non-ruminant; water dependent	Water- availability; forage quantity; low risk of predation	Occurs across all distances from water, selects dense habitats with high quantity of browse resources	Occurs across all distances from water, selects dense habitats with high quantity of browse and graze resources

In this context, my study has addressed these concepts by 1) assessing the drivers of herbivore assemblage composition across seasons, at a landscape scale, and across a set of herbivores which differ in functional traits; and 2) by assessing the patch foraging choices that grazing herbivores make. Addressing the combined effects of extrinsic and intrinsic factors at varying scales is critical to the effective management and preservation of herbivore biodiversity.

Furthermore, by addressing these impacts at different scales we allow the implementation of management policies at the correct scales (Delsink *et al.*, 2013; Venter, 2014).

Thus far, studies have evaluated how forage quality and quantity (Augustine *et al.*, 2003; Grant & Scholes, 2006; Owen-Smith *et al.*, 2010), distance from water (Hopcraft *et al.*, 2012; Smit *et al.*, 2007), fire (Archibald & Bond, 2004; Wilsey, 1996), human-induced risk (Venter *et al.*, 2014), fencing restrictions (Boone *et al.*, 2004; Venter, 2014) and predation risk (Hopcraft *et al.*, 2012; Valeix *et al.*, 2009) affect herbivore distribution across spatial and temporal scales. In this study I present a novel analysis of the combination of some of these effects on a single ecosystem, and across a wide range of herbivore species.

Key research findings

My first research objective was to determine the relative strength of a variety of environmental drivers on the distribution of a differing set of herbivores across seasons at a landscape scale in the Kruger National Park. This was achieved through determining the probability of an herbivore's presence at sites of certain environmental characteristics within its morphological constraints; and evaluating the daily biomass of these herbivores at these sites using generalised linear models (GLM). The results supported findings that forage quality and quantity had strong relationships with body size, mouth morphology and digestive type (Owen-Smith *et al.*, 2017; Pretorius, 2009), and that water-dependency was a critical determinant of herbivore distribution across the landscape (Redfern *et al.*, 2003). Furthermore, I found distance from water to be a stronger driver on herbivore distribution at shorter distances than expected. Although water-dependent species typically select habitats at shorter distances (0.5 km to 2 km) from water (Redfern *et al.*, 2003), I expected a presence of them between 2.5 km and 5 km from water. My results showed that there were stark differences in species' biomass and probability of presence across the different distances from water, especially between the 0.5 km and 2.5 km distances from water. I found the trade-offs between forage quantity and water-availability in larger grazing species to be more apparent despite their differing digestive strategies, with these species selecting quantity resources further from water, probably to maintain digestive fill (Clauss *et al.*, 2003). Overall, the relationship between grazer presence and grass biomass was closely linked with distance from water, in that the probability of grazer presence was highest at low grass biomass close to water, and at high grass biomass furthest from water, likely because grass biomass close

to water was depleted and reserve forage was further from water in the dry season. Finally, season considerably altered these relationships, and with the increase in quality of forage resources and water availability across the landscape in the wet seasons, herbivores distributed more evenly across the landscape and made increased use of burned, short-grass resources.

My second research objective was to evaluate patch scale foraging selection in grazing herbivores of differing morphological traits, at sites of differing environmental characteristics. To achieve this, I used GLMs to determine the probability of presence of a set of focus species at experimental plots of three treatments – mown, mown and fertilised, and fertilised (each with an untreated control). I found that digestive type and body size of species was a stronger determinant of patch scale foraging patterns than mouth morphology and water dependency, as expected. For example, zebra, which must select for high quantity of forage due its increased rate of digestive passage (Clauss *et al.*, 2003), selected for fertilised plots in the late dry season, although in theory mown and fertilised plots would have the highest quality forage. Buffalo, however, selected for mown and fertilised plots in the same season, despite usually needing to obtain high quantity of forage due to their nutritional needs (Venter & Watson, 2008) and increased herd size (Pretorius, 2009), however they are ruminants, whereas zebra are hindgut fermenters and as such need to maintain digestive fill by utilising a high quantity resource (Clauss *et al.*, 2003). Additionally, season was a major determinant of herbivore distribution across all sites, due to its effects on water distribution across the landscape, and forage quality. Selective feeding (i.e. the selection for treated plots) was highest in the wet season, when water was more uniformly available across the landscape. The coupled effects of water availability and the increased quality of forage resources is likely what explains this strategy, in other words, species of differing intrinsic constraints all maximise their nutritional intake in the wet season when freed from extrinsic constraints of forage quality and limited water availability.

Finally, I found that the use of GLMs in predicting the probability of presence and biomass of herbivores across a range of characteristics was an effective method, through the confirmation of previously described trends in species at both landscape and patch scales. Investigating the drivers of herbivore distribution and probability of presence at multiple scales is beneficial to the understanding of herbivore ecology because of the interaction

among drivers at different scales. At a patch scale, an herbivore is driven, for example, by its risk of predation and foraging preference, but at a landscape scale an herbivore is driven by distance from water, landscape heterogeneity (i.e. structure and composition of the vegetation) and changes in these factors throughout the year. The composition of herbivore assemblages at different scales affects spatial heterogeneity of the landscape and is thus what maintains the structure and function of the landscape (Fig. 1). Hence, defining the drivers of herbivore assemblage composition, through evaluating the mechanisms behind habitat and forage selection by herbivores, contributes to informed conservation management efforts.

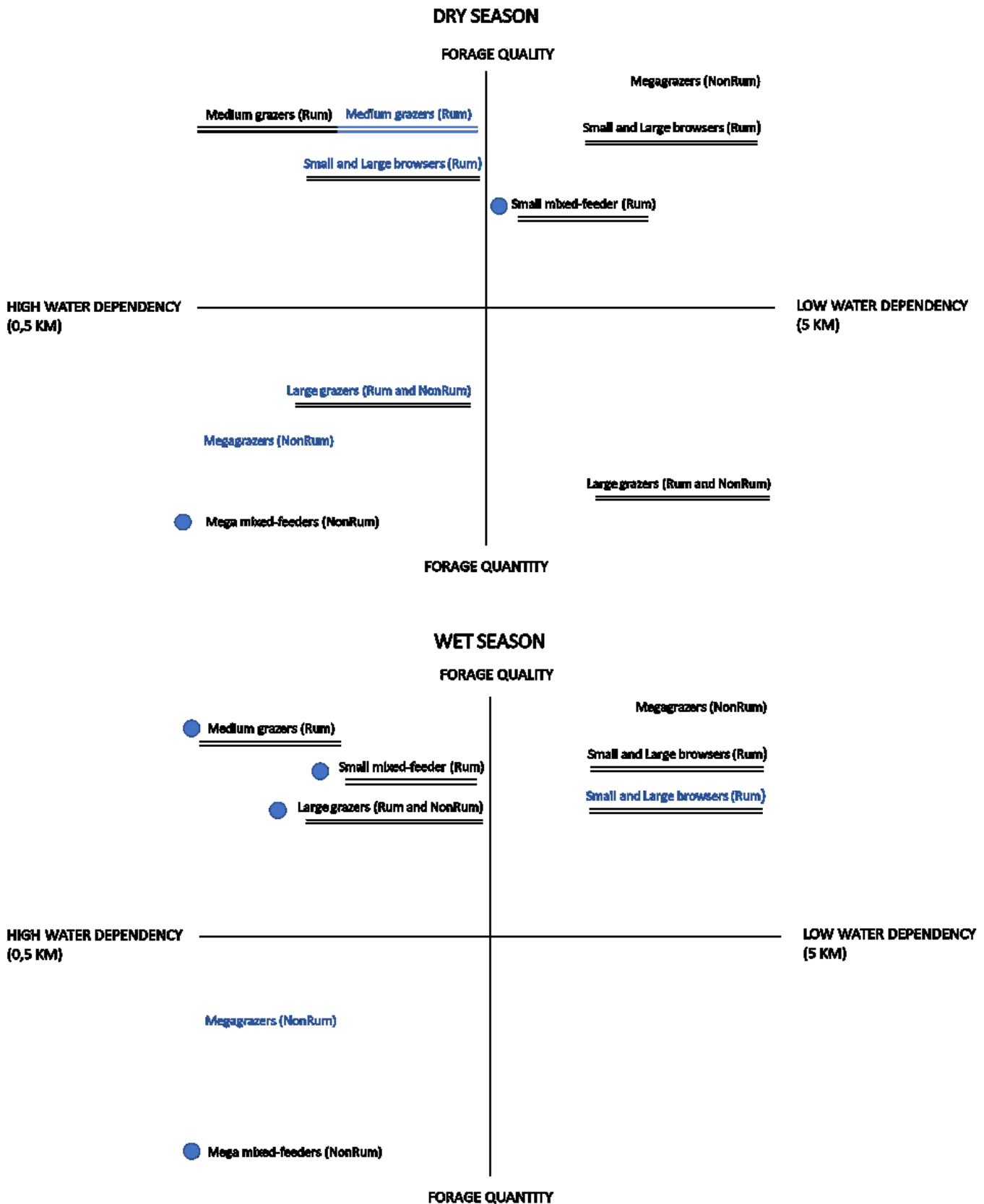


Figure 1: A representation of the expected versus actual drivers of functional types across the wet and dry seasons. Underlining of each functional type represents degree of risk of predation (2= high, 1= lower); Rum=ruminant and NonRum= Non-ruminant. Blue text indicates the predicted response and black the results. Blue dots next to a functional type indicate the results are as theory predicts.

Management implications

Based on the findings and insights determined through the course of this study, I propose the following management recommendations.

1. In properties which have existing artificial water provision, consideration should be given to whether all waterholes should remain open, and whether sufficient buffers are being maintained between water holes to promote landscape heterogeneity (vegetation structure and diversity) and biodiversity. Chapter 3 showed that herbivore distribution changed as close as 2.5 km from water, and in both Chapter 3 and Chapter 4 I showed that species such as zebra and buffalo altered their resource use across seasons. The increased pressure of foraging close to artificial water sources could result in the depletion of bulk grass resources necessary to support these species throughout the dry season (Swemmer, 2018). I found that these species foraged at higher densities at 5 km from that, and thus recommend that buffers which exceed 5 km be maintained to maintain bulk resources for bulk-feeding and rare species, such as roan antelope.
2. In properties which are considering the placement of new artificial water holes, careful consideration needs to be given to the vegetation type in which the water source will be placed, and what type of structure will be used to provide the water. Species differ in their preference for water sources (Gaylard *et al.*, 2003), and in situations where multiple forms of water provision are being considered, management should aim to place different types of water sources across the landscape in an attempt to distribute the increased foraging pressure at artificial water sources in order to maintain landscape heterogeneity.
3. In systems with artificial water provision I would recommend seasonal vegetation monitoring at the site of water and a comparable site without water provision are undertaken to inform management decisions that would ensure the continuation of vegetation biodiversity, given the species level impacts on grass, forb and browse diversity (McNaughton, 1985).
4. I would recommend mapping fire scars and maintaining records of fire frequency, and where possible, intensity. Chapter 3 showed that post-fire grazing pressure is highest

close to water in the late wet season (fires were at the start of the early wet season). Management needs to consider the timing of fire and the post-fire magnet effect on herbivores, to determine whether sites of burning will promote heterogeneity and vegetation biodiversity at the site, or whether fire returns are too frequent and are suppressing the aforementioned factors when coupled with herbivory pressure.

5. Post-fire grazing and foraging preference at certain distances from water are responses which occur at a species-level. Understanding herbivore distribution across the landscape through means of monitoring and annual censuses are critical to ensuring that water provision and fire policies are informed by the distribution of species which occur in that specific system.

Animal distribution, and to a certain degree density, can be manipulated at a management level through water provision and fire policies. It is important to note that these processes are system-specific, and the degree of intervention effect is intensified in smaller reserves.

Knowledge gaps and future research opportunities

Whilst this study found effective means to predict herbivore biomass across a variety of environmental attributes and scales, it does have shortcomings and raises further questions.

- This study did not adequately address the risk of predation on the distribution of herbivores due to experimental constraints. Risk of predation must be taken into consideration when applying predictive modelling to herbivore distribution due to its strong effect on herbivore foraging behaviour (Pays *et al.*, 2012) and habitat choice or spatial distribution (Valeix *et al.*, 2009). Due to difficulty in measuring predator occurrence and distribution without doing intensive field work, I recommend incorporating landscape features such as landscape curvature, woody cover, distance to drainage beds and water sources (Hopcraft *et al.*, 2012) to create an index of risk of predation as a proxy for actual predator incidence.
- Additionally, I believe the outputs of this model could be greatly improved by including the following factors: distance to the nearest fence, distance to the nearest road, plot fire history and poaching risk due to their respective effects on herbivore distribution at a landscape scale.

- In Chapter 3, we found a strong explanatory relationship between grazer presence and grass biomass across a distance from water gradient. This relationship warrants investigation at a finer scale, especially in areas which experience less grazing pressure and have increased distances from water.
- The role of herbivores has been clearly defined in Chapter 1 of this study, in particular how herbivores alter nutrient distribution across the landscape. Quantifying species-level nutrient inputs into the soil would further improve the understanding of how herbivore assemblages alter their surrounding environment and create feedbacks of selecting for high-nutrient patches, and enriching patches through defecation and soil leaching processes.
- Capture frequencies of certain species greatly affected whether GLMs were robust enough to effectively determine the main drivers of herbivore movement. Due to time constraints, this study was not able to obtain sufficient data on the following species: waterbuck (*Kobus ellipsiprymnus ellipsiprymnus*), buffalo (*Syncerus caffer caffer*) and white rhinoceros (*Ceratotherium simum simum*). Further research over a greater time period, and perhaps with an increased number of camera traps at a large-scale, would be necessary to improve the strength of GLMs to predict these species use of habitat.
- GLMs could further be improved by focusing on more refined functional types, with the inclusion of more species within the type, to eliminate the confounding factors such as varying body size (e.g. mixed feeders) or feeding type (e.g. megaherbivores).
- The effects of these variables on functional types should also be tested in small fenced reserves and open natural systems to determine whether these drivers maintain their relative strength across different systems.
- Finally, the scales at which the study was designed to test the strength of extrinsic and intrinsic characteristics on herbivore distribution were fixed so as to allow the measurement of environmental attributes whilst detecting broad changes in herbivore distribution. These scales may not necessarily have been relevant for large bodied species which select at coarser scales than the habitat scale, and small bodied species which select a finer scales.

Concluding remarks

In this study, the complexity of interactions between extrinsic and intrinsic drivers of herbivore assemblage composition (Table 1), at sites of different environmental attributes at the Satara section of KNP, have been interpreted to improve understanding of the main drivers of herbivore distribution across the landscape at both landscape- and patch- scales. It was established that at a landscape-scale, water distribution, forage quality and quantity and post-fire regrowth were strong determinants of grazer distribution, whereas forage availability and habitat density were stronger determinants of browser distribution. Season affected resource utilisation across all functional types and considerably increased the strength of driving effects on functional types. At a patch scale, it was found that digestive type, mouth morphology and social structure primarily affect grazer resource utilisation across seasons and distance from water. These results further illustrated how water dependency shapes herbivore distribution and forage selectivity across the landscape, highlighting the importance of well-informed water provision policies.

Given the increasing global threats to herbivore populations, and inescapable anthropogenic effects on the environment, characterising the drivers of herbivore distribution and clearly understanding their roles in the environment is becoming increasingly important to the preservation of protected areas and their encompassed ecosystems.

Literature Cited

- Archibald, S., & Bond, W. J. 2004. Grazer movements: spatial and temporal responses to burning in a tall-grass African savanna. *International Journal of Wildland Fire*, 13(3), 377-385.
- Augustine, D. J., McNaughton, S. J., & Frank, D. A. 2003. Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. *Ecological Applications*, 13(5), 13.
- Boone, R. B., & Hobbs, N. T. 2004. Lines around fragments: effects of fencing on large herbivores. *African Journal of Range & Forage Science*, 21(3), 147-158.
- Clauss, M., Frey, R., Kiefer, B., Lechner-Doll, M., Loehlein, W., Polster, C., Rössner, G., & Streich, W. J. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. *Oecologia*, 136(1), 14-27.
- Craigie, I. D., Baillie, J. E. M., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221-2228.
- Delsink, A., Vanak, A. T., Ferreira, S., & Slotow, R. 2013. Biologically relevant scales in large mammal management policies. *Biological Conservation*, 167(0), 116-126.
- Freitag-Ronaldson, S., & Foxcroft, L. C. 2003. Anthropogenic influences at the ecosystem level. *The Kruger experience: Ecology and management of savanna heterogeneity*, 391-421.
- Gagnon, M., & Chew, A. E. 2000. Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, 81(2), 490-511.
- Gaylard, A., Owen-Smith, N., & Redfern, J. 2003. *Surface water availability: implications for heterogeneity and ecosystem processes*. Pp 171-189 In J. T. Du Toit, K. H. Rodgers & H. C. Biggs (Eds.), *The Kruger experience: Ecology and management of savanna heterogeneity*. Island Press, Washington.
- Grant, C. C., & Scholes, M. C. 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, 130(3), 426-437.
- 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(6264), 1056-1061.
- Hempson, G. P., Archibald, S., & Bond, W. J. 2017. The consequences of replacing wildlife with livestock in Africa. *Scientific reports*, 7(1), 17196.

- Hopcraft, J.G.C., Anderson, T.M., Pérez-Vila, S., Mayemba, E. & Olf, H., 2012. Body size and the division of niche space: food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, 81(1), pp.201-213.
- Kramer, D. L. 2001. Foraging behavior. Pp 232-246 in Fox, C. W., Roff, D. A., & Fairbairn, D., J, (Eds.) *Evolutionary ecology: concepts and case studies*. Oxford University Press, New York.
- Legendijk, G., Page, B. R., & Slotow, R. 2012. Short-term Effects of Single Species Browsing Release by Different-sized Herbivores on Sand Forest Vegetation Community, South Africa. *Biotropica*, 44(1), 63-72.
- McNaughton, S. J. 1985. Ecology of a Grazing Ecosystem: The Serengeti. *Ecological Monographs*, 55(3), 260-294.
- Owen-Smith, N. 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Journal of Wildlife Research*, 26(4), 107-112.
- Owen-Smith, N., Cromsigt, J. P., & Arsenault, R. 2017. *Megaherbivores, Competition and Coexistence within the Large Herbivore Guild*. Pp 111-135 In Cromsigt J. P. M., Archibald, S. & Owen-Smith, N. (eds.) *Conserving Africa's Mega-Diversity in the Anthropocene: The Hluhluwe-iMfolozi Park Story*. Cambridge University Press, Cornwall.
- Owen-Smith, N., Fryxell, J. M., & Merrill, E. H. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society* 365(365), 2267-2278.
- Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. 2012. Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, 169(2), 419-430.
- Pretorius, Y. 2009. *Satisfying giant appetites: mechanisms of small scale foraging by large African herbivores*. Unpublished MSc Thesis, Wageningen University, Netherlands.
- Redfern, J.V., Grant, R., Biggs, H. & Getz, W.M. 2003. Surface-water constraints on herbivore foraging in the Kruger National Park, South Africa. *Ecology*, 84(8), pp.2092-2107.
- Ripple, W. J., Larsen, E. J., Renkin, R. A., & Smith, D. W. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, 102(3), 227-234.

- 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(4), e1400103.
- Shiple, L. A. 2007. The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*, 116(12), 1964-1974.
- Smit, I. P. J., Grant, C. C., & Devereux, B. J. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation*, 136(1), 85-99.
- Swemmer, A. M., Bond, W. J., Donaldson, J., Hempson, G. P., Malherbe, J., & Smit, I. P. 2018. The ecology of drought-a workshop report. *South African Journal of Science*, 114(9), 1-3.
- Valeix, M., Loveridge, A., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & Macdonald, D. 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, 90(1), 23-30.
- Venter, J. A., Nabe-Nielsen, J., Prins, H. T., & Slotow, R. 2014. Forage patch use by grazing herbivores in a South African grazing ecosystem. *Acta Theriologica*, 59(3), 457-466.
- 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(1), 42-51.
- Vie, J.-C., Hilton-Taylor, C., & Stuart, S. N. (Eds.) 2009. State of the world's species. Pp 15-43 in *Wildlife in a changing world: An analysis of the 2008 IUCN Red List of Threatened Species*. Gland, Switzerland, IUCN.
- Wilsey, B. J. 1996. Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, 34(1), 32-38.