Impacts of African elephant feeding on white rhinoceros foraging opportunities

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In accordance with Rule G5.6.3, I hereby declare that this dissertation is my own work and that it has not previously been submitted for assessment to another University or for another qualification.

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CONTENTS

SUMMARY

In this study, I investigated the interaction between two megaherbivores, the African elephant and white rhinoceros, that has the potential to impact grazing lawns of which white rhino are the creators and maintainers and elephants are potentially the modifiers. I hypothesized that as elephants browse, they discard a variety of coarse woody debris onto the ground; should this woody debris (of varying amounts and sizes) fall onto grazing lawns, white rhino either move them, consume grass around the woody debris or abandon the lawn entirely. If high levels of woody debris are deposited here, grazing by white rhino is likely to be prevented, at which time I predicted that mesoherbivores would have a competitive advantage in accessing forage that white rhino cannot.

I examined the mechanistic links between different levels of elephant-deposited woody debris and grass response at a point scale and feeding patch spatial scale of grazing lawns in an African savanna. In addition, I assessed the response of mesoherbivores in terms of vigilance behaviour with increasing levels of predation risk posed by increasing levels of woody debris.

I present the first evidence of an indirect effect of elephant on white rhino foraging behaviour. I demonstrate how increasing levels of woody debris lead to a decreasing probability of foraging by white rhino. I also demonstrate how the probability of foraging by mesoherbivores increases as the amount of forage increases. However, since this study took place during a severe drought where resources are extremely limited, I was unable to properly separate the effects of elephant-deposited woody debris from the severe lack of rainfall on grass response and subsequently herbivore foraging behaviour. Due possibly to the drought, mesoherbivores responded less or not at all to risk factors such as woody debris therefore woody debris was not a predictor of vigilance behaviour in my study.

This study contributes to our understanding of how the impacts of elephants, as ecosystem engineers, have cascading effects on savanna ecosystems. My study showed that elephant impact mediates the foraging behaviour of white rhino during a drought. However, under average rainfall periods, my original hypothesized effect of the indirect impacts of elephants on white rhino foraging and grazing lawn dynamics could still hold. This key hypothesis that I was unable to test under ‘normal’ conditions due to the drought is still valid and functionally important for understanding the ecosystem processes driving grazing lawn formation, persistence and composition in African savannas where elephants and white rhinos coexist.

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CHAPTER 1: GENERAL INTRODUCTION

> “*On the following morning we were up before the sun, and, travelling in a northerly direction, soon became aware that we were in a district frequented by elephants, for wherever we looked, trees were broken down, large branches snapped off, and bark and leaves strewn about in all directions, whilst the impress of their huge feet was to be seen in every piece of sandy ground.”*
>
> *F C Selous (1881, 48), north of Gweru, Zimbabwe, in 1872*

In African savannas, among the most conspicuous animals are the megaherbivores, specifically the hippopotamus *Hippopotamus amphibius*, giraffe *Giraffa camelopardalis*, black rhinoceros *Diceros bicornis*, white rhinoceros *Ceratotherium simum* and African elephant *Loxodonta africana* (Owen-Smith 1988). Megaherbivores (body mass > 1,000 kg) play a major role as landscape sculptors and ecosystem engineers (Jones *et al*. 1994; Jones *et al*. 1997; Butler 1995; Haynes 2012) through their feeding strategies or physical alterations on vegetation (Naiman 1988). The reverberations of these alterations are transmitted to all trophic levels (predator, herbivore and plant), thereby affecting community structure (Naiman 1988). Megaherbivores are generally considered as invulnerable to (non-human) predation and tend to have a disproportionately larger impact on vegetation in comparison to predator-limited mesoherbivores owing to their size, longevity, food and habitat requirements (Naiman 1988; Owen-Smith 1988; Zavada and Mentis 1992). They make up the greater share in biomass of many herbivore communities due to their ability to utilise a large share of available resources and their tolerance of forage with low and varied nutritional quality (Owen-Smith 1987, 1988; Illius and Gordon 1992; Stuart-Hill 1992, Fritz *et al*. 2002). Here I investigate the novel concept that foraging interactions occur between functionally different species of megaherbivores coexisting in the savanna ecosystem, and that these interactions have cascading effects on vegetation dynamics and coexisting herbivores’ foraging behaviour.

Functional Diversity of Megaherbivores

It is widely accepted that mammalian herbivores are functionally diverse and can be divided into separate guilds based on their diet selection: grazers that consume primarily graminoids; browsers that consume primarily dicotyledons; and mixed feeders that consume both (Hoffman and Stewart 1972). The dependence of herbivore dietary tolerance on body size translates into important size-related differences between savanna ungulate species in terms of habitat specificity, geographical range, and the share of community resources exploited (Du Toit and Cumming 1999). Smaller-bodied ungulate species (mesoherbivores) have narrower dietary tolerances than the larger species (megaherbivores) and tend to specialize on vegetation types that provide high quality forage throughout the year (Du Toit and Owen-

Smith 1989). Megaherbivores, with their wider feeding tolerances, can feed in a wider range of vegetation types and are thus more evenly spread through the ecosystem (Owen-Smith 1988; Du Toit and Cumming 1999). For example, in African savannas, the white rhinoceros and hippopotamus are megagrazers, responsible for converting medium-tall grasslands to short grass lawns (Owen-Smith 1987; 1988). Megabrowsers include the black rhinoceros, which concentrates on forbs and low-growing woody scrub, and the giraffe, feeding primarily on the leaves and stems of woody plants and dicotyledonous herbs (Owen-Smith 1988). The African elephant, is a mega-mixed feeder, incorporating varying proportions of grass and browse into their diets, the ratio of which varies seasonally and depends on forage availability (Kerley *et al*. 2008). Savanna ungulate communities, with species distributed across body size classes and feeding guilds (grazer/browser), have strong regulatory influences on savanna ecosystem structure and function (Du Toit and Cumming 1999). Most studies examine the impact on ecosystem structure and function by a single megaherbivore species, the African elephant (e.g.: Parker 1983; Owen-Smith 1987, 1988; Illius and Gordon 1992; Herremans 1995; Cumming *et al*. 1997; Fritz *et al*. 2002; Pringle 2008; Kerley *et al*. 2008; Landman *et al*. 2013; Tambling *et al*. 2013). Few studies have considered interactions between megaherbivores (e.g. Slotow and van Dyk 2001; Landman *et al*. 2013; Landman and Kerley 2014) and the impact of these interactions on the surrounding plant and animal communities. My study looks at an indirect interaction between elephants and white rhinos in an African savanna.

White Rhinos as Ecosystem Engineers

The white rhino is a megaherbivore whose impact on savanna grasslands may be as large as that of the elephant on tree communities (Waldram *et al.* 2008). White rhinos are specialised grass feeders with low-slung heads, wide mouths and broad, sensitive upper lips suitable for plucking grass (Owen-Smith 1988; Pienaar 1994; Shrader *et al.* 2006). Repeated grazing by white rhino and other grazers leads to the establishment and maintenance of a type of short grassland called a grazing lawn (Owen-Smith 1988; Cromsigt *et al.* 2017). Grazing lawns are dominated by a specific community of short grass species that are prostrate-growing and grazing-tolerant with high foliar nutrient levels and leaf-shoot ratios (McNaughton 1984; Vesey-Fitzgerald 1965). According to Hempson *et al.* (2014), there are four compositionally distinct grazing lawn grass types where the grass species (1) are prostrate with lateral spread by stolons or rhizomes (e.g. couch grass *Cynodon dactylon*); (2) are prostrate with lateral spread by long looping stolons (e.g. LM grass *Dactyloctenium australe*); (3) switch from upright to lateral spreading (e.g. bushveld signal grass *Urochloa mosambicensis*); and (4) are either upright with prostrate leaves (with regular grazing) or short caespitose plants (without grazing; e.g. curly-leaved dropseed grass *Sporobolus nitens*). Grazing lawns also have a dicotyledonous forb component (henceforth referred to as “forbs”), which refers to erect, perennial, herbaceous flowering plants other than grass (excluding tree saplings; e.g. porcupine root *Tallinum caffrum*). Forbs typically constitute a minor part of a grazing lawn (McNaughton 1983) but may "erupt" in response to rainfall, particularly after long dry periods, due to underlying seed banks (O'Connor 1991; 1995). Grazing lawns can occur as large grasslands comprising short *Sporobolus* grass species in the south east of Serengeti National Park in northern Tanzania (McNaughton 1985) or as relatively small patches (from a few square metres to a few hectares) surrounded by taller, less productive bunch grasses, such as in Hluhluwe-iMfolozi Park (HiP) in South Africa (Bonnet *et al.* 2010). Grazing lawns play an important functional role in savannas (Cromsigt et al. 2017). These lawns in HiP may support a high abundance and diversity of grazer species (> 40 individuals km^2 of six species; Cromsigt and Olff 2008). These lawns may be of importance during late-stage pregnancy and lactation of ungulate grazers, as well as for their young, owing to the mineral-enriched grass tufts (McNaughton et al. 1997).

In HiP, white rhinos play an important role in the creation and maintenance of grazing lawns (Waldram *et al.* 2008). White rhino will utilise different grassland types during the seasonal cycle, with rainfall as the major driver behind this pattern (Owen-Smith 1988; Shrader and Perrin 2006). Owen-Smith (1988) found that white rhino utilised grazing lawns during the wet season, but when the short grasses began to senesce at the start of the dry season, the white rhino changed to utilizing shade-loving grasses, such as *Panicum maximum*, in woodland grasslands before moving on to accessible *Themeda* grasslands later in the dry season. When these grasslands were depleted at the end of the dry season, white rhino utilised *Themeda* grasslands on hillslopes until the rains began, allowing the rhino to return to short grasslands (Fig. 1.1a; Owen-Smith 1998). For an above-average rainfall year, Shrader and Perrin (2006) found that white rhino used short grasslands consistently throughout the cycle and did not utilise the remote *Themeda* grasslands on hillslopes (Fig. 1.1b). Should white rhino (or other) herbivores be prevented from maintaining these lawns, grass height will increase, tall-grass species will invade and the lawn is likely to change its state from a short grassland to a taller bunch grass community (Waldram *et al.* 2008; Hempson *et al.* 2014). White rhinos are therefore important regulators of ecosystem processes in grazing ecosystems (Frank *et al.* 1998) and can be considered ecosystem engineers (Owen-Smith 1988; Waldram *et al.* 2008).

<u>*Elephants as Ecosystem Engineers*</u>

Elephants utilize a wide range of browse, graze and herb species – the ratio of which depends on the availability of each food type and the season (Kerley *et al*. 2008). Elephants can be very destructive in their feeding habits to access the young, fresh foliage – pushing over trees and breaking and discarding branches (Kerley *et al*. 2008). Elephants are considered "keystone modifiers" due to these activities, which may greatly affect habitat features but may not necessarily have direct trophic effects on other species (Paine 1969; Mills *et al*. 1993). Therefore, elephant foraging may act as a potential disturbance

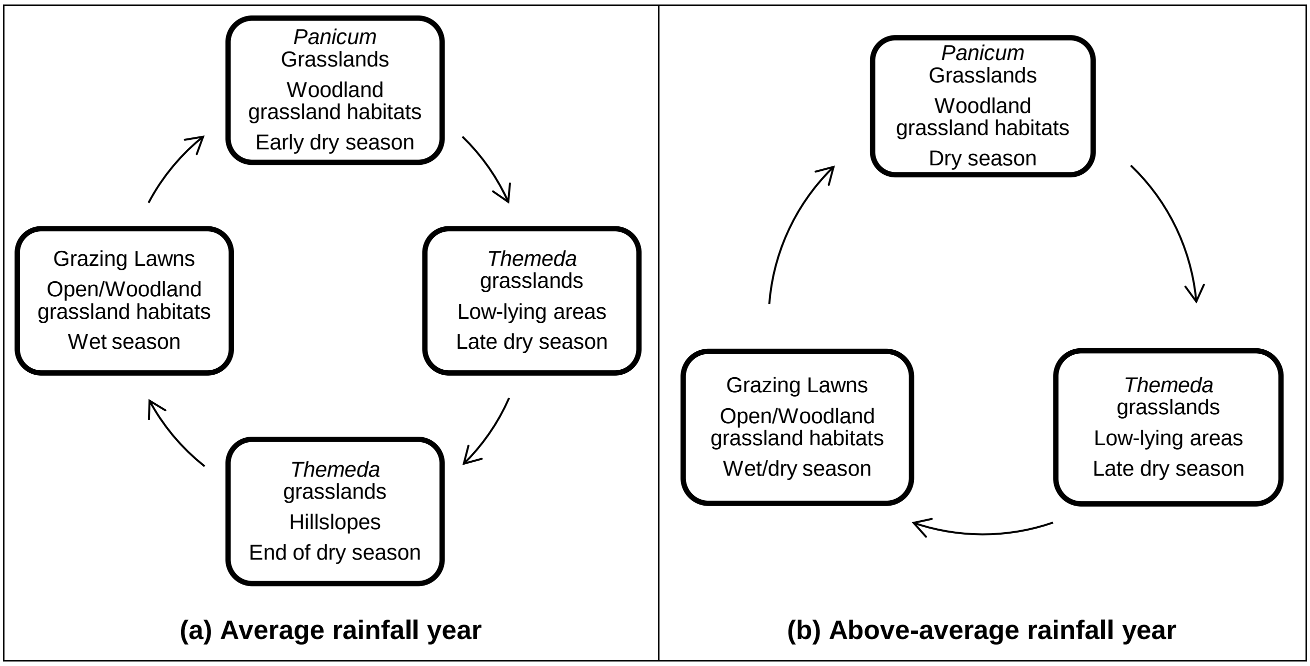

Figure 1.1. Grazing lawns are key foraging habitats during the wet season and into the early dry season for white rhino as seen in the seasonal grassland utilisation cycle in HiP (a) as described by Owen-Smith (1988) and (b) Shrader and Perrin (2006).

that can promote or impede species richness in many habitats (e.g. Herremans 1995), and indeed has threatened the existence of entire habitats (e.g. Thompson 1975; Cumming *et al*. 1997). As early as 1881, elephant disturbance was observed and recorded by F. C. Selous (1881, page 48), a British explorer and big-game hunter, who noted that “trees were broken down, large branches snapped off, and bark and leaves strewn about in all directions”. This disturbance is particularly strong on habitats surrounding permanent water sources (Thrash and Derry 1999), in areas where their seasonal and long-term dispersal is constrained by fences, and when their populations exceed their food supply (Landman *et al*. 2013).

Elephants are the major agents of ecosystem disturbance, which help create coarse woody debris (Spies and Cline 1988; Stokland 2001). Coarse woody debris refers to fallen trees, large branches, large stems and large pieces of bark that are not consumed entirely by the disturbances that create them (Spies and Cline 1988). Stokland (2001) formulated the Coarse Woody Debris Profile, which is broadly defined as the composition of coarse woody debris with respect to dimensions (trees and branches) and decay classes (i.e. recent to very decayed). There is much literature on the structure, composition and ecological value of coarse woody debris in boreal forests in the Northern hemisphere (e.g.: Spies and Cline 1988; Stokland 2001) yet little is known about the coarse woody debris profile in African systems (Mgqatsa 2017). One study has explicitly focused on the role of elephants in shaping the full structure of coarse woody debris, i.e.: Mgqatsa (2017) showed that elephants play an important role in the production of coarse woody debris through tree toppling and consequently provided insight into the Coarse Woody

Debris Profile in the Karoo Thicket Mosaic vegetation type. However, there is gap in the literature regarding the top down effects of elephant-deposited woody debris and its accumulation on not only underlying vegetation in African savannas, but coexisting species as well. I believe elephant-deposited woody debris may have similar effects to fire-produced woody debris on ungulate survival by influencing forage availability and perceived predation risk (Ripple and Beschta 2004). In this manner, elephants modify vegetation, regulate resources and influence predation risk, thereby limiting the abundance of other herbivores (Fritz *et al.* 2002).

The Megaherbivore-Megaherbivore Interaction

There exists a megaherbivore-megaherbivore interaction wherein I hypothesize that elephant foraging indirectly influences foraging by white rhinoceros (hereafter white rhino) at a grazing lawn patch scale in a savanna ecosystem. The interaction between these two megaherbivores has the potential to impact grazing lawns of which white rhino are the creators and maintainers and elephants are potentially the modifiers – as elephants browse, they discard a variety of coarse woody debris onto the ground (Owen-Smith 1988); should this woody debris (of varying amounts and sizes) fall onto grazing lawns (Fig. 1.2), white rhino either move them, consume grass around the woody debris or abandon the lawn entirely. If high levels of woody debris are deposited here, grazing by white rhino is likely to be prevented if there is no longer adequate space between pieces of debris for their muzzles.

Figure 1.2. Grasses differ in height underneath, adjacent to and away from branches deposited by elephants onto a grazing lawn in Hluhluwe-iMfolozi Park, KwaZulu Natal, South Africa.

However, the presence of cropped grasses among pieces of woody debris indicates that grazing still occurs (J.P.G.M. Cromsigt, *personal observations*). This forms the basis of my alternative hypothesis, which suggests that mesoherbivores (weighing between 50 and 500 kg) may have a competitive advantage over white rhino in areas with medium to high levels of woody debris due to their smaller-sized muzzles. Grazing lawns are not only maintained by white rhino but also by mesoherbivores (Cromsigt and Olff 2008), therefore mesoherbivores should be able to access tufts in-between woody debris that white rhino cannot. However, as per the risk allocation hypothesis as developed by Lima and Bednekoff (1999), these mesoherbivores may have to weigh the risk of predation posed by increasing levels of woody debris against resource acquisition, i.e.: vigilance behaviour versus feeding behaviour. By accessing grass (that white rhino cannot) in grazing lawns with high levels of woody debris, mesoherbivores expose themselves to a potentially higher risk of predation and therefore should allocate more vigilance behaviour than feeding behaviour (e.g.: Lima and Bednekoff 1999). The spatial variation in the level of predation risk, also known as a landscape of fear (Laundre *et al*. 2010), may be a direct result of different levels of woody debris. This has been studied in the predator-prey relationship where down wood impedes elk in their attempt to avoid predation by wolves in Yellowstone National Park, USA (Halofsky and Ripple 2008). Halofsky and Ripple (2008) found that the variable "distance to wood" significantly predicted elk vigilance where vigilance behaviour increased with decreasing distance to woody debris. However, they implied that elk could also be responding to a cluster of woody debris rather than just to the distance of the nearest single impediment. This suggests that different levels of woody debris may affect perceived predation risk by herbivore prey. I propose that the creators of this woody debris, such as elephants in African savannas, would indirectly affect sympatric herbivore foraging and vigilance behaviour.

Ecologists are still in the early stages of understanding the cascading effects of elephants (Kerley *et al.* 2008) therefore in this thesis, I explore the novel concept regarding the impact of elephant-deposited woody debris on the foraging behaviour of white rhino and the resulting cascading effects on the white rhinos' impact on grazing lawns in an African savanna. I look at how this indirect interaction has the potential to influence not only grazing lawn structure but ungulate foraging and vigilance behaviour as well. Should woody debris discarded by elephant fall onto grazing lawns, white rhino may either move them, consume grass around the woody debris or abandon the lawn entirely. If a large amount of woody debris is deposited, grazing by white rhino is likely to be prevented as they may not be able to manoeuvre around these branches.

I want to address the following overarching questions: How does woody debris discarded by elephant onto grazing lawns influence visitation by and foraging behaviour of white rhino? White rhinos are particularly influential in maintaining grazing lawns in their short grass state (Owen-Smith 1979). Should white rhino neglect grazing lawns highly impacted by elephant, do mesoherbivores assume this role in maintaining grazing lawns, as indicated by Cromsigt and Olff (2006)? Does this woody debris affect the visitation, foraging behaviour and vigilance behaviour of mesoherbivores? What are the consequences of elephant-deposited woody debris on grazing lawn foraging opportunities in terms of lawn structure and composition, specifically grass height underneath and adjacent to branches as well as the frequency of lawn-forming grasses, tussock-forming grasses, forbs and bare soil?

Aims, Objectives and Hypotheses

In the two chapters outlined below, I develop and test the main hypothesis that elephants indirectly mediate the foraging behaviour of white rhino and mesoherbivores, with cascading effects on grazing lawn dynamics and role of white rhino in shaping HiP's savanna grasslands.

In Chapter 2, I aim to investigate whether the visitation and foraging behaviour of white rhino and mesoherbivores is influenced by the amount of woody debris deposited by elephant onto grazing lawns. I specifically address the following questions:

2.1. Does elephant-deposited woody debris influence visitation and foraging behaviour of white rhino?
2.2. Does elephant-deposited woody debris influence visitation and foraging behaviour of mesoherbivore to grazing lawns?
2.3. Does elephant-deposited woody debris influence mesoherbivore vigilance behaviour?

I hypothesize that increasing amounts of woody debris leads to (1) decreasing visitation by white rhino; (2) less foraging by white rhino and (3) more foraging by mesoherbivores until an intermediate amount of woody debris is reached after which mesoherbivores will visit less and a switch from foraging to vigilance as the dominant behaviour owing to a perceived higher risk of predation.

In Chapter 3, I aim to investigate the consequences of this predicted reduction in white rhino foraging due to the impact of woody debris on grazing lawn structure by addressing the following questions:

3.1. What are the dimensions of woody debris deposited by elephant onto grazing lawns?
3.2. How much woody debris is deposited onto grazing lawns?
3.3. Does woody debris affect the growth of grasses in these lawns?
3.4. Does woody debris influence lawn composition between lawn-forming and tussock-forming grasses?

I predict that increasing amounts of woody debris onto grazing lawn patches leads to increased average grass height as white rhino can no longer access a large portion of the available forage and, as such, can no longer maintain the lawn. I also hypothesize that there will be a shift from lawn-forming grasses to tussock-forming grasses at high levels of elephant-deposited woody debris.

Hluhluwe-iMfolozi Park (HiP) in northern Kwazulu Natal, South Africa, provided the unique opportunity to investigate the impact of the indirect interaction between two extant megaherbivore species in a natural system containing actively maintained grazing lawns. These megaherbivores are the African elephant, which exist in high densities and thus greatly impact vegetation (Druce *et al.* 2017) and the white rhino – HiP's flagship species – which has a unique and unbroken history of habitation at HiP.

This thesis follows a style where both chapters have been written as journal-style articles. Thus, there is some degree of repetition between the chapters. Data collected in chapter 3 were used to formulate the treatment levels for the experiment described in chapter 2. Results from chapter 2 were used to substantiate the results in chapter 3.

CHAPTER 2: EVALUATING THE IMPACT OF AFRICAN ELEPHANT FEEDING ON THE FORAGING BEHAVIOUR OF OTHER HERBIVORES

INTRODUCTION

Megaherbivores are hypothesized to have a disproportionately larger impact on vegetation than predator-limited mesoherbivore populations owing to their size (> 1,000 kg) and longevity as well as their food and habitat requirements (Naiman 1988; Owen-Smith 1988; Zavada and Mentis 1992). They make up the greater share in biomass than many ungulate communities in Africa due to their ability to utilise a large share of available resources, particularly forage with low and varied nutritional quality (Owen-Smith 1987, 1988; Illius and Gordon 1992; Stuart-Hill 1992; Fritz *et al.* 2002). Megaherbivores may also facilitate smaller and more selective species (such as mesoherbivores weighing between 4 kg and 450 kg) in accessing forage through induced regrowth of new shoots of higher quality because of trampling and feeding (Owen-Smith 1988). The presence or absence of high densities of megaherbivores has the potential to influence trophic guild structure in ungulate communities as well as forage availability, quality and quantity (Fritz *et al.* 2002). In this manner, megaherbivores may transform entire savanna landscapes, especially where their movements are confined (Cumming *et al.* 1997; Trollope *et al.* 1998).

Most studies examine the impact on the surrounding plant and animal communities by a single megaherbivore species – the African elephant *Loxodonta africana* – that dominates megaherbivore assemblages and occurs in high densities in most savanna sites (e.g.: Parker 1983; Owen-Smith 1987; 1988; Illius and Gordon 1992; Herremans 1995; Cumming *et al.* 1997; Fritz *et al*. 2002; Pringle 2008; Kerley *et al.* 2008; Landman *et al.* 2013). Other studies on megaherbivore impacts look at the impact on plant communities by white rhinoceros (e.g.: Owen-Smith 1988; Pienaar 1994; Waldram *et al*. 2008; Shrader *et al.* 2006), black rhinoceros (e.g.: Owen-Smith 1988; Landman *et al.* 2008) and hippopotamus (e.g.: Lock *et al.* 1972; Owen-Smith 1988). Few studies have considered interactions between megaherbivores and the impact of these interactions on the foraging behaviour and forage selection, e.g.: the Asian elephant *Elephas maximus* and the greater/Indian one-horned rhinoceros *Rhinoceros unicornis* (Sukumar 1990; Steinheim *et al*. 2005) and the African elephant and the black rhino (Landman *et al*. 2013; Landman and Kerley 2014). In this study, I look at the interaction between a megagrazer and a megamixed-feeder and hypothesize that elephant foraging indirectly influences the foraging behaviour of white rhinoceros (hereafter white rhino) and mesoherbivores at a grazing lawn patch-scale in a savanna ecosystem.

Grazing lawns are subjected to the activities of many mammals in a savanna ecosystem, including sympatric megaherbivores, such as elephants and white rhino. As elephants browse, they discard a variety of coarse woody debris onto the ground (Kerley *et al.* 2008). Woody debris is produced through debarking stems, breaking branches, or toppling, pollarding or uprooting whole trees (O'Connor *et al.* 2007; Kerley *et al.* 2008; Mgqatsa 2017). Here, I suggest that if woody debris falls onto grazing lawns, this will influence the foraging behaviour of white rhino. They could either move the wood, consume grass around the wood or abandon the lawn entirely in search of more readily accessible forage. Harvesting methods that involve laborious, time-consuming actions may considerably lower the rate of food intake even if large amounts are rapidly chewed and swallowed (Clegg and O'Connor 2016). Therefore, I predict that white rhino should show higher preferences for forage that can be located and harvested quickly rather than that obstructed by elephant-deposited woody debris. If a high amount of woody debris is deposited, grazing by white rhino is likely to be prevented as their large-sized muzzles can no longer access grass growing in between the pieces of woody debris. Grazing lawns are not only maintained by white rhino but also by mesograzers such as impala *Aepyceros melampus*, warthog *Phacochoerus africanus* and blue wildebeest *Connochaetes taurinus* (Cromsigt and Olff 2008). I predict that mesoherbivores may have an advantage over megaherbivores in accessing grass on grazing lawns in the presence of woody debris due to their small-sized muzzles. In this manner, white rhino and mesoherbivore foraging behaviour may be influenced indirectly by the impact of elephant feeding behaviour.

However, a grazing lawn covered in woody debris may affect the risk of predation thereby influencing the "landscape of fear" and herbivore prey, in their attempt to avoid predation, will distribute themselves accordingly (Laundre *et al*. 2010). As the body size of a herbivore decreases, its vulnerability to predation is expected to increase because smaller species have potentially more predators (Hayward and Kerley 2005). This means that megaherbivores are practically impervious to non-human predation (Owen-Smith 1988), whilst mesoherbivores are considered as prey. Elephants may indirectly influence the perceived risk of predation as well as the quality of the foraging resource. I predict that mesoherbivores will switch between foraging behaviour and vigilance behaviour depending on the amount of woody debris covering the grazing lawn. In areas with low levels of woody debris, predation-risk may be lower but competition with white rhino for access to forage will increase. In areas with medium to high levels of woody debris, mesoherbivores can access grass that white rhino cannot but will increase their vigilance behaviour. This is because coarse woody debris may act as escape impediments (Lima and Bednekoff 1999; Halofsky and Ripple 2008). This is in line with the "predation risk allocation hypothesis" where herbivores may have to allocate more antipredator effort to high-risk situations and more feeding to low-risk situations (Lima and Bednekoff 1999; Le Roux 2016).

I developed a field study where my objective was to provide empirical evidence on the effects of elephant-deposited woody debris on the visitation, foraging behaviour and vigilance behaviour of white rhinos and mesoherbivores in a natural savanna grassland in the Hluhluwe section of Hluhluwe-iMfolozi Park, South Africa (HiP). I tested the hypothesis that the visitation and behaviour of white rhino and mesoherbivores is influenced by the amount of woody debris deposited from the browsing activities of elephants. This led to the following predictions: at a foraging patch scale, an increasing gradient of impact by elephants, which equates to increasing amounts of woody debris: (1) leads to decreasing visitation and decreasing foraging probability by white rhino; (2) leads to increasing visitation and increasing foraging probability by mesoherbivores at an intermediate level of woody debris, thereafter visitation and foraging probability will decline; and (3) vigilance probability will increase due to increasing perceived predation risk with increasing levels of woody debris.

METHODS

Study Site

The study was conducted in the Hluhluwe section of the Hluhluwe iMfolozi Park (HiP; 28º00 - 28º26, 31º43 - 32º09), a protected area of 96 000 ha situated in the southern African savanna biome in central Zululand, KwaZulu Natal, South Africa. The climate is characterised by a rainy season from September to March and a dry season from April to August (Shrader *et al*. 2006). The mean annual rainfall ranges from 650 mm to 1000 mm, dependent on altitude, which ranges from 40 m to 750 m above sea level (Balfour and Howison 2002). This variation in altitude and rainfall has led to a large diversity of vegetation types, ranging from forests to grasslands to open and closed woodlands (Whateley and Porter 1983). The park is characterized by a high heterogeneity in grassland types and these include grasslands dominated by tall, bunch grass (tussock forming) communities of *Sporobolus pyramidalis*, *Eragrostis curvula* and *Themeda triandra* and grasslands dominated by short, prostrate growing stoloniferous grass species, known as grazing lawns (Cromsigt *et al.* 2006). Grazing lawns cover < 10% of the total area of HiP and occur as small patches (mostly < 8 ha) in a taller bunch-grass matrix (Archibald *et al.* 2005). The species central to this study were the white rhino and other indigenous grazing lawn users (mesoherbivores hereafter) including nyala *Tragelaphus angasii* and zebra *Equus quagga*.

The study was conducted at four sites in the Hluhluwe section with these selected based on the following criteria: (1) the presence of frequently utilized grazing lawns based on the presence of cropped lawn grass; and (2) the presence of woodlands adjacent to grazing lawns where there was potential for wood to be deposited. The selected sites satisfied the criteria as they comprised active grazing lawns in *Acacia burkeii* and *Spirostachys africana* closed woodland vegetation types that commonly occur in riverine terraces and valley bottoms in the Hluhluwe section of HiP (Fig. 2.1) (Whateley and Porter 1983).

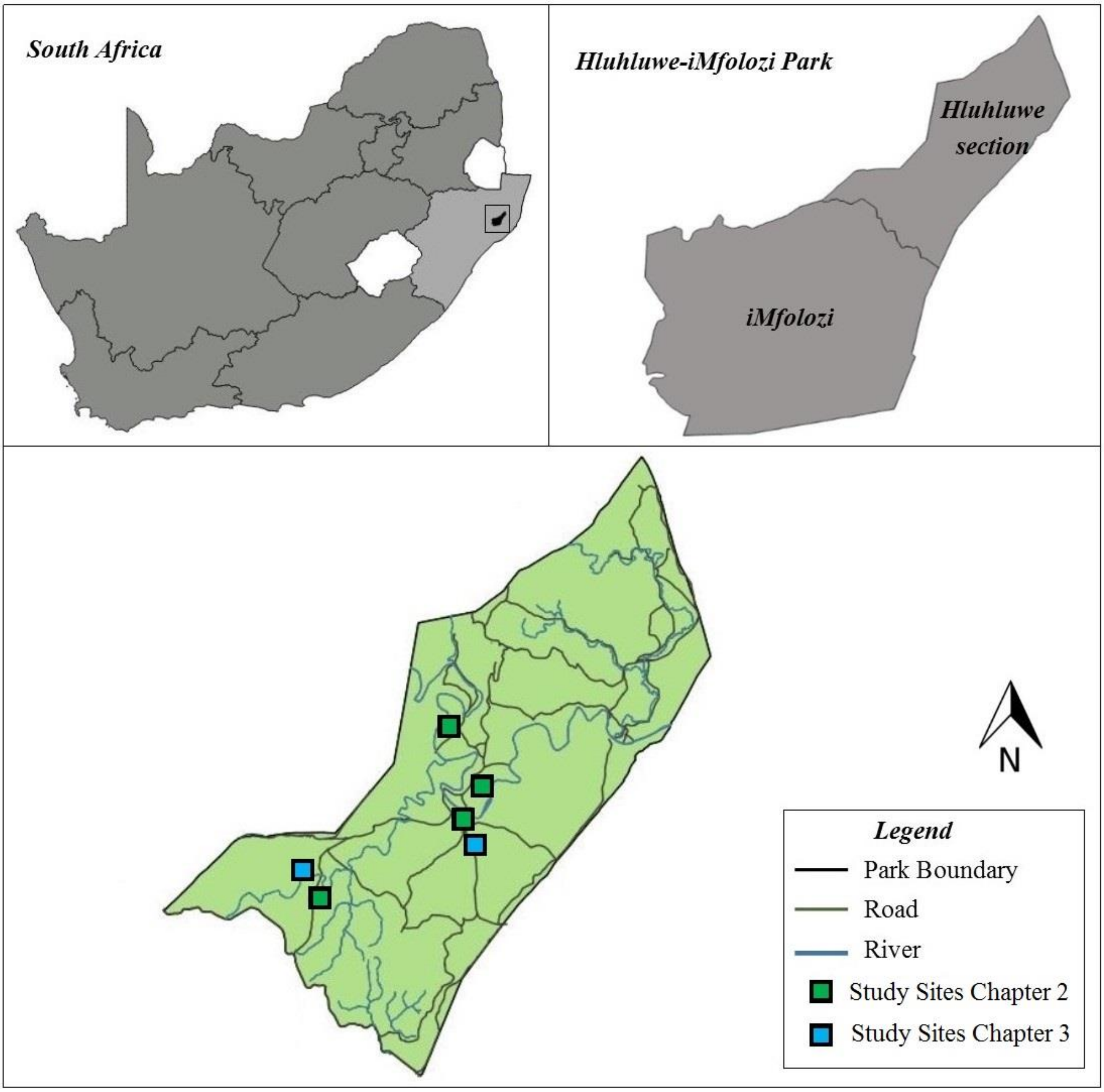

Figure 2.1. Map showing the location of the four study sites sampled in Chapter 2 and the two study sites sampled in Chapter 3 in the Hluhluwe section of Hluhluwe-iMfolozi Park, KwaZulu Natal, South Africa. The map highlights the park boundary, major rivers and road network within the reserve.

<u>*Experimental Design and Sampling*</u>

Levels of Impact

I used data collected in chapter 3, where I quantified actual elephant impact in terms of the extent of woody debris cover, type of woody debris deposited and woody debris size to determine the treatments for this chapter. The most frequently deposited woody debris type were branches of no more than 2 m in length and maximum 25% of a plot was covered with woody debris (Fig. 2.2). From this, I determined the following four treatment levels of impact: 0%, 5%, 10% and 20% of a plot covered by woody debris.

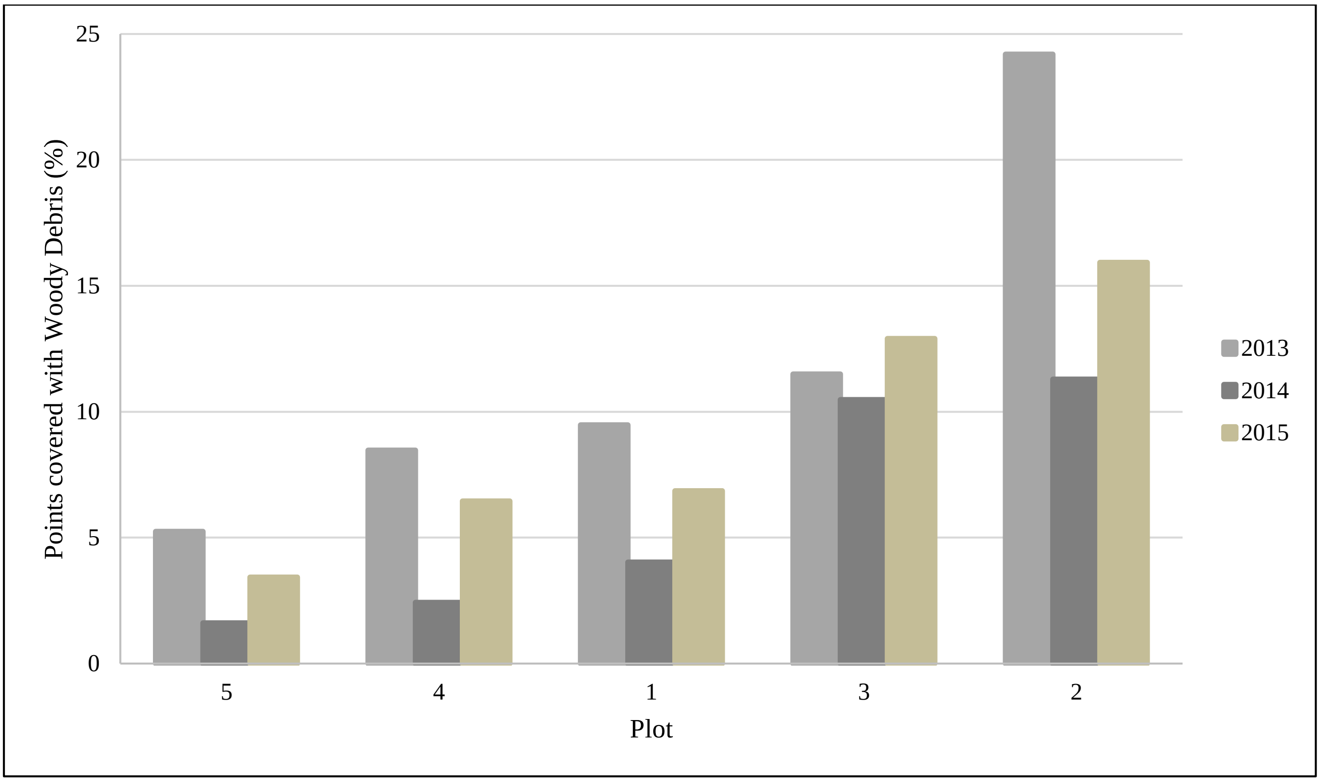

Figure 2.2. The percentage of points covered with woody debris observed in the high elephant impact site in chapter 3 in Hluhluwe-iMfolozi Park, South Africa. The area had five plots (x-axis) that were sampled each year for three consecutive years (2013, 2014, 2015). The number of points covered in woody debris was counted and overall, no more than 25 % of the plot was covered in woody debris.

Experiment

To mimic the impact of elephant browsing activities in the form of the deposit of branches, I selected four sites and within each site, a total of four 5 m x 5 m grazing lawn plots were marked. Each plot formed a grid of points where points were spaced 25 cm apart (441 points in total per plot) and formed coordinates comprising the intersections between 21 east-west transects and 21 north-south transects. This grid resolution of 25 cm x 25 cm is finer than that used in chapter 3 and was selected to obtain precise results regarding the detection of grazing by white rhino as their bite width was taken to be 20 cm (Owen-Smith 1988). Each of the four plots within each site was randomly assigned a treatment level. Plot 1 received no woody debris and acted as a control (Fig. 2.3a); plot 2 received the 5% treatment level and not more than 22 points were covered with woody debris (Fig. 2.3b); plot 3 received the 10% treatment level and not more than 44 points were covered with woody debris (Fig. 2.3c) and plot 4 received the 20% treatment level and not more than 88 points were covered with woody debris (Fig. 2.3d).

Branches measuring no more than 2 m in length were collected from the surrounding vegetation. Each branch was allocated a random set of starting coordinates in the grid at which the tip of the branch was placed. The branch would fall in the direction of the second set of randomly drawn coordinates until all points allocated for that treatment level were covered with branches. On average, plots within a site were spaced at least 3 m apart to be considered independent and sites were spaced at least 6 km apart. This latter distance was chosen to maximize the chance that we were sampling different rhino individuals, since the size of white rhino core home ranges varies between 3 to 6 km^2 in optimum foraging conditions (Shrader 2003). There were no branches added or removed by animals during this study as the coordinates of each branch was monitored at each trapping period.

Prior to depositing the branches, the vegetation was sampled by counting the number of points in each plot covered with grass and forbs. The plots were sampled again three times after the deposit of woody debris which resulted in four periods (TP1, TP2, TP3 and TP4), with each trapping period being 2 weeks long. This also coincided with the downloading of photographs and maintenance of the camera traps.

Camera Trapping

Camera traps were deployed at each plot (16 plots in total) between January and April 2016. A single camera trap was placed in each plot, with cameras located on grazing lawns and near roads to facilitate maintenance. Cameras were set at approximately 0.5 – 1.0 m above ground level, enabling the capture of images of a wide range of small and large mammals, set on low sensitivity and programmed to take three consecutive pictures every second after being triggered. Cameras were rotated between plots across all sites during the study to reduce camera bias (Welch and Parker 2016).

Two analyses were conducted using the camera trap photographs: a visitation analysis and a foraging behaviour analysis. For the visitation analysis, camera trap photographs were sorted per species with a time to independence between images of 30 minutes (Tambling *et al*. 2015; Welch and Parker 2016). As per Rovero *et al.* (2005), this 30-minute time to independence assumes that multiple photographs of an individual or herd taken at a single plot within a short period of time represent a single capture event and thus a single independent record. Photographs separated by the 30-minute time to independence were assumed to be a representative random sample of the large animal population at each site (Tambling *et al.* 2013). For the behaviour analysis, all camera trap photographs were used to estimate the proportion of activity types for each animal at each camera during each time period. The main activity types were foraging and vigilance and all other activities were combined to reflect either not foraging or not vigilant.

Figure 2.3. Photographs displaying: A - 0% of a plot covered with branches; B - 5% of a plot covered with branches; C - 10% of a plot covered with branches; D - 20% of a plot covered with branches; and E - an example of a branch deposited at a plot in the grazing lawns plots used in my study in Hluhluwe-iMfolozi Park, South Africa.

Data Analyses

Effect of Woody Debris on Visitation

A candidate set of generalized linear mixed effects models (GLMMs) using the *lme4* package (Bates *et al.* 2015) in R software version 3.3.0; R Core Team 2016 was constructed for each species (white rhino, impala and nyala) with visitation as the response variable. Visitation was calculated as the number of independent capture events regardless of group size. Fixed effects included woody debris level and the amount of forage, which was calculated as the sum of all points covered with grass and/or forbs. The distribution family was specified as Poisson, which is appropriate for count data (Crawley 2007). In the models, I specified that the fixed effects were continuous and that site (S1 to S4) was nested within trapping period (TP1 to TP4) and included as a random effect to account for repeated measures of sites (Zuur *et al*. 2009). To correct for varying number of camera trap days, visitation was offset by the log of the number of active days that the camera trap was running for. Variables were scaled as their numeric values were on different orders of magnitude (Crawley 2007). Collinearity among main effects was investigated using variance inflation factors (VIFs) in the *car* package (Fox and Weisberg 2011). Model selection was performed on the candidate models using a modified version of Akaike information criteria (AICc) which approximates AIC at large sample sizes if the sample size is small (n/k < 40; Simonds and Moussalli 2010) using the R package *AICcmodavg* (Mazerolle 2016). The model with the lowest AICc value was selected, but model averaging using the *MuMln* package (Barton 2016) was performed if the delta AICc value of models differed by less than 2 (Burnham and Anderson 2002). Robust inferences cannot be made from any of the models if their Akaike weights are less than 0.90 (Burnham and Anderson 2002).

Effect of CWD on Behaviour

A candidate set of generalized linear mixed effects models (GLMMs) using the *lme4* package (Bates *et al.* 2015) in R software version 3.3.0; R Core Team 2016 was constructed for each species (white rhino, impala and nyala) with behaviour as the response variable. Two behavioural activities were considered: (1) foraging behaviour was calculated as the number of independent behaviour events of foraging and not foraging for white rhino, impala and nyala and (2) vigilance behaviour was calculated as the number of independent behaviour events of vigilant and not vigilant for impala and nyala. Vigilance was defined as an alert position where the animal is erect with its head above shoulder height and is looking around (Underwood 1982). This behaviour was not observed for white rhino. Fixed effects included woody debris level and the amount of forage, which was calculated as the sum of all points covered with grass and/or forbs. The distribution family was specified as binomial with the logit link function and the random effects fulfilled the role of assigning repeated measures (Zuur *et al*. 2007; 2009). In the models, I specified that the fixed effects were continuous and that site (S1 to S4) was nested within trapping period (TP1 to TP4) which I considered as random effects. Variables were scaled as their numeric values were on different orders of magnitude (Crawley 2007). Collinearity among main effects was investigated using variance inflation factors (VIFs) in the *car* package (Fox and Weisberg 2011). Model selection was performed on the candidate models using a modified version of Akaike information criteria (AICc) which approximates AIC at large sample sizes if the sample size is small (n/k < 40; Simonds and Moussalli 2010) using the R package *AICcmodavg* (Mazerolle 2016). The model with the lowest AICc value was selected, but model averaging using the *MuMln* package (Barton 2016) was performed if the delta AICc value of models differed by less than 2 (Burnham and Anderson 2002). Robust inferences cannot be made from any of the models if their Akaike weights are less than 0.90 (Burnham and Anderson 2002). Results were plotted where the response was the probability of each behaviour occurring in relation to the presence of increasing levels of woody debris.

RESULTS

Over the four trapping periods, cameras were active for 915 camera trap days. Sampling lengths and the number of active days are shown in Table 2.1. Nyala had the most photographs and the highest number of group visits out of the seven species recorded. Nyala, white rhino and zebra were selected for analysis as they were represented in 3 or more sites.

Table 2.1. Table showing the number of photographs and the number of group visits per species.

	Number of Photographs				Number of Group Visits			
	Site 1	*Site 2*	*Site 3*	*Site 4*	*Site 1*	*Site 2*	*Site 3*	*Site 4*
Camera Trap Days	227	228	222	238	227	228	222	238
Active Days (mean±SE)	56.75±6.91	57±3.7	55.5±6.4	59.5±3.6	56.75±6.91	57±3.7	55.5±6.4	59.5±3.6
Species								
Buffalo	966	0	234	0	45	0	28	0
Impala	5442	87	0	0	63	15	0	0
Nyala	392	1528	399	2597	33	166	65	263
Warthog	115	4	5	0	18	1	4	0
White Rhino	289	36	230	27	12	3	24	2
Wildebeest	0	0	0	15	0	0	0	5
Zebra	83	30	53	0	9	5	5	0

Effect of Woody Debris

As the amount of woody debris increased, the amount of forage increased (Fig. 2.4; $\beta = 0.46$, SE = 0.04, z-value = 12.17, $p < 0.05$).

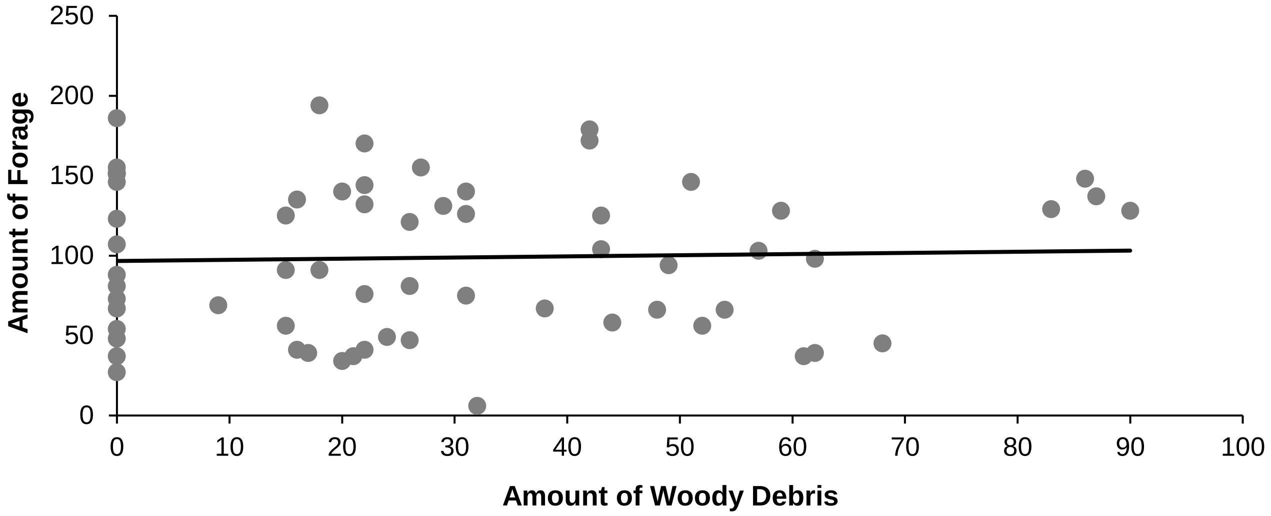

Figure 2.4. The amount of forage (number of points covered with forage) increased significantly with increasing levels of woody debris (β = 0.46, SE = 0.04, z-value = 12.17, p < 0.05) during this experiment in Hluhluwe-iMfolozi Park, South Africa.

Effect of Woody Debris on Visitation

For white rhino visitation, the intercept model, the model with the amount of woody debris and the model with the amount of forage had the lowest AICc values that differed by less than 2 and therefore, model averaging was performed (Table 2.2). White rhino visitation was not significantly influenced by the amount of woody debris (VIF < 2; β = -0.04, SE = 0.11, z-value = 0.38, *p* = 0.705) nor by the amount of forage (VIF < 2; β = -0.04, SE = 0.18, z-value = 0.21, *p* = 0.833).

For nyala, the model with the interaction between the amount of woody debris and the amount of forage had the lowest AICc value (Table 2.2) and nyala visitation was significantly affected by this interaction (VIF < 2; β = - 0.21, SE = 0.06, z-value = -3.4, *p* < 0.05). As the amount of forage increased, nyala visitation increased and this relationship was similar in each plot (Fig. 2.5).

For zebra visitation, the intercept model, the model with the amount of woody debris, the model with the amount of forage and the model with both the amount of woody debris and forage had the lowest AICc values that differed by less than 2 and therefore, model averaging was performed (Table 2.2). The amount of woody debris (VIF < 2; β = -0.08, SE = 0.2, z-value = 0.41, *p* = 0.681) and the amount of forage (VIF < 2; β = 0.39, SE = 0.46, z-value = 0.85, *p* = 0.681) did not significantly affect zebra visitation.

Table 2.2. Results of model comparison using AICc (a) and model averaging (b) where the response variable is visitation by (1) white rhino, (2) nyala and (3) zebra. Selected models are shaded in grey.

1. Effect of Woody Debris on White Rhino Visitation

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 1: H_0	3	137.29	0	0.44	0.44	-65.44
Model 2: WD	4	138.64	1.35	0.23	0.67	-64.98
Model 3: Forage	4	139.29	2	0.16	0.83	-65.3
Model 5: WD * Forage	6	140.45	3.16	0.09	0.92	-63.49
Model 4: WD + Forage	5	140.76	3.47	0.08	1	-64.86

(b) Component Models	***df***	***logLik***	***AICc***	***ΔAICc***	***Weight***
H_0	3	-65.44	137.29	0	0.53
H_0; Forage	4	-64.98	138.64	1.35	0.27
H_0; WD	4	-65.3	139.29	2	0.2

2. Effect of Woody Debris on Nyala Visitation

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 5: WD * Forage	6	490.2	0	0.97	0.97	-238.36
Model 2: WD	4	498.02	7.82	0.02	0.99	-244.67
Model 4: WD + Forage	5	498.94	8.74	0.01	1	-243.95
Model 1: H_0	3	523.35	33.15	0	1	-258.48
Model 3: Forage	4	525.57	35.37	0	1	-258.45

3. Effect of Woody Debris on Zebra Visitation

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 3: Forage	4	83.74	0	0.37	0.37	-37.53
Model 1: H_0	3	84.46	0.71	0.26	0.63	-39.03
Model 4: WD + Forage	5	85.4	1.65	0.16	0.79	-37.18
Model 2: WD	4	85.64	1.9	0.14	0.93	-38.48
Model 5: WD * Forage	6	87.1	3.35	0.07	1	-36.81

(b) Component Models	***df***	***logLik***	***AICc***	***ΔAICc***	***Weight***
H_0; WD	4	-37.53	83.74	0	0.4
H_0	3	-39.03	84.46	0.71	0.28
H_0; Forage	5	-37.18	85.4	1.65	0.17
H_0; WD; Forage	4	-38.48	85.64	1.9	0.15

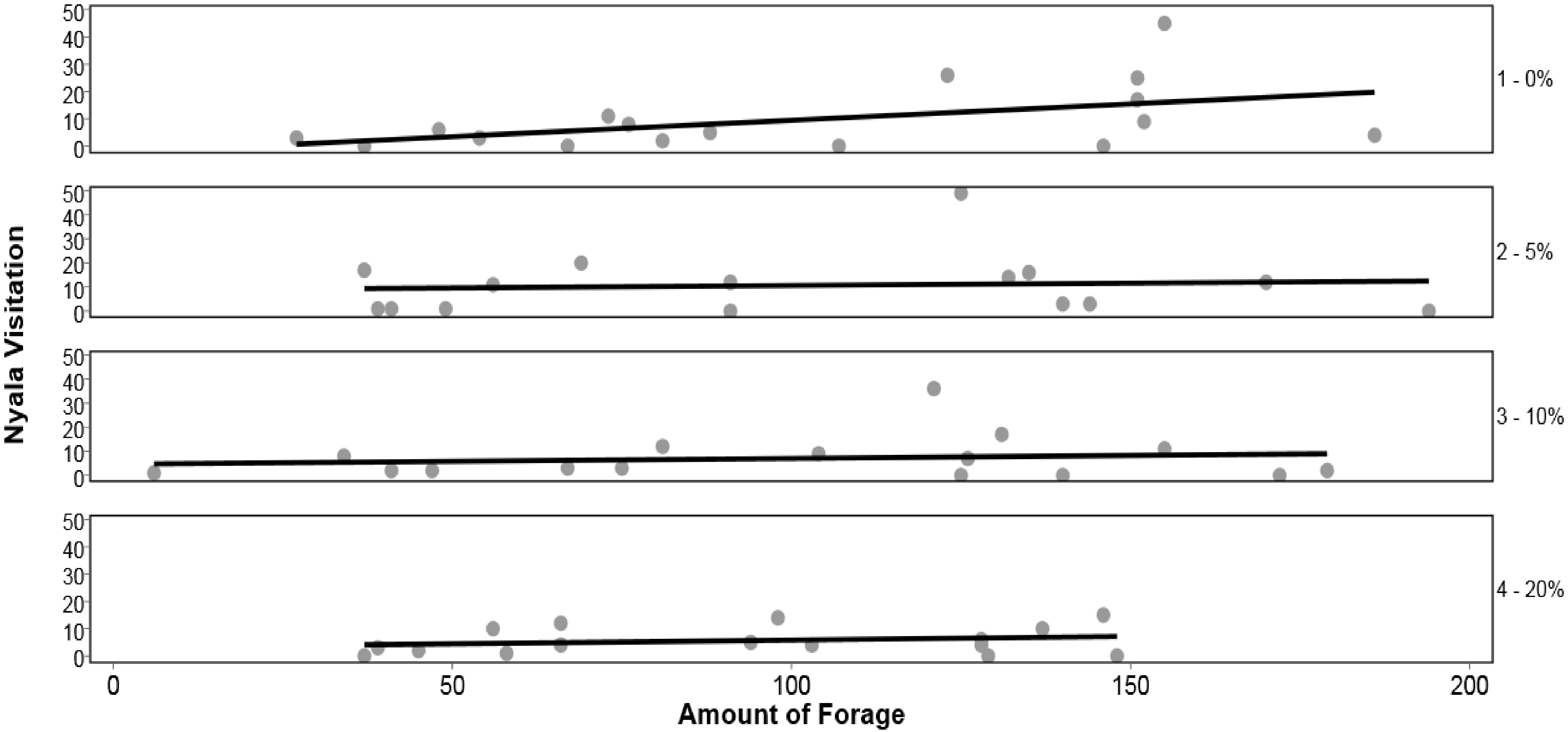

Figure 2.5. The interaction between the amount of woody debris and the amount of forage significantly influenced nyala visitation. Nyala visitation increased as the amount of forage increased in all four woody debris levels during this study in Hluhluwe-iMfolozi Park, South Africa.

Effect of Woody Debris on Foraging Behaviour

For white rhino foraging behaviour, the model with the amount of woody debris alone had the lowest AICc value (Table 2.3). An increase in the amount of woody debris led to a significant decrease in the probability of white rhino foraging (Fig. 2.6a and 2.6b; VIF < 2; $\beta = -0.66$, SE = 0.29, z-value = -2.29, $p < 0.05$).

Figure 2.6a. A camera trap photograph showing a white rhino foraging on the edge of a plot with a high level of woody debris during the last trapping period in Hluhluwe-iMfolozi Park, South Africa.

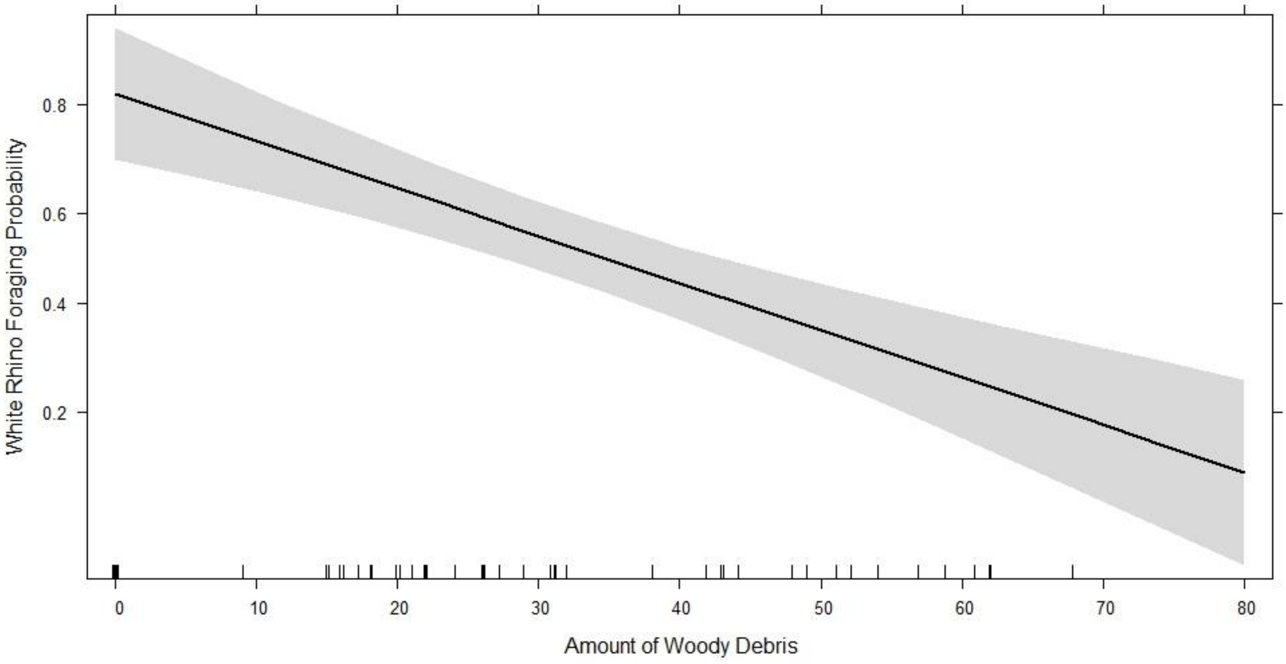

Figure 2.6b. As the amount of woody debris increased, the probability of white rhino foraging decreased significantly ($\beta = -0.66$, SE = 0.29, z-value = -2.29, $p < 0.05$) during this study in Hluhluwe-iMfolozi Park, South Africa.

For nyala foraging behaviour, the model with the interaction between the amount of woody debris and the amount of forage had the lowest AICc value (Table 2.3). However, the interaction did not significantly affect the probability of nyala foraging (VIF < 2; $\beta = 0.81$, SE = 0.85, z-value = -0.96, $p = 0.337$). The probability of foraging increased significantly as the amount of woody debris alone increased (Fig. 2.7a and 2.7b; VIF < 2; $\beta = 0.53$, SE = 0.07, z-value = 7.9, $p < 0.05$) and as the amount of forage alone increased (VIF < 2; $\beta = 0.64$, SE = 0.16, z-value = 3.97, $p < 0.05$). The amount of woody debris did not significantly affect the probability of nyala vigilance (Table 2.3; VIF < 2; $\beta = -0.06$, SE = 0.1, z-value = 0.61, $p = 0.542$).

Figure 2.7a. A camera trap photograph showing an nyala foraging at a plot with a high level of woody debris during the last trapping period in Hluhluwe-iMfolozi Park, South Africa.

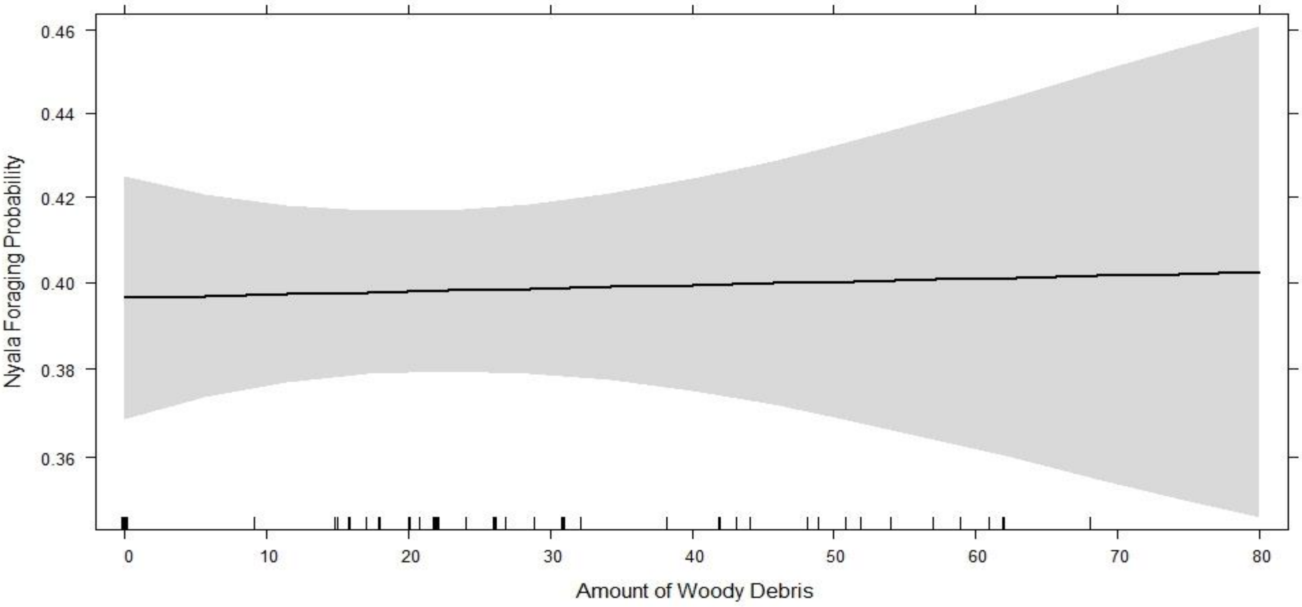

Figure 2.7b. As the amount of woody debris increased, the probability of nyala foraging increased gradually ($\beta = 0.53$, SE = 0.07, z-value = 7.9, $p < 0.05$) during this study in Hluhluwe-iMfolozi Park, South Africa.

For zebra foraging behaviour, the model with the interaction between the amount of forage and the amount of woody debris as well as the model with both the amount of woody debris and the amount of forage had the lowest AICc values that differed by less than 2 and therefore, model averaging was performed (Table 2.3). This interaction did not significantly affect the probability of zebra foraging (VIF < 2; $\beta = 0.25$, z-value = 0.42, $p = 0.68$), The amount of woody debris did not significantly affect the probability of zebra being vigilant (Table 2.3; Fig. 2.8b; VIF < 2; $\beta = 0.4312$, SE = 0.41, z-value = 1.04, $p = 0.3$).

Figure 2.8a. A camera trap photograph showing a zebra grazing at a plot without woody debris during the last trapping period in Hluhluwe-iMfolozi Park, South Africa.

Table 2.3. Results of model comparison using AICc (a) and model averaging (b) where the response variable is behaviour by (1) white rhino, (2) impala and (3) nyala. Selected models are shaded in grey.

1. Effect of Woody Debris on White Rhino Foraging Behaviour

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 2: WD	4	83.28	0	0.56	0.56	-37.3
Model 4: WD + Forage	5	85.48	2.2	0.19	0.74	-37.22
Model 1: H_0	3	86.14	2.85	0.13	0.88	-39.87
Model 5: WD * Forage	6	87.31	4.03	0.07	0.95	-36.92
Model 3: Forage	4	88.23	4.95	0.05	1	-39.78

2. Effect of Woody Debris on Nyala Foraging Behaviour

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 5: WD * Forage	6	694.31	0	1	1	-340.42
Model 4: WD + Forage	5	706.58	12.27	0	1	-347.77
Model 2: WD	4	749.11	54.8	0	1	-370.22
Model 3: Forage	4	776.17	81.85	0	1	-383.74
Model 1: H_0	3	787.5	93.19	0	1	-390.5

2. Effect of Woody Debris on Nyala Vigilance Behaviour

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 1: H_0	3	23.52	0	0.74	0.74	-8.56
Model 2: WD	4	25.58	2.06	0.26	1	-8.45

3. Effect of Woody Debris on Zebra Foraging Behaviour

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 4: WD + Forage	5	89.2	0	0.45	0.45	-39.08
Model 5: WD * Forage	6	90.77	1.57	0.21	0.66	-38.65
Model 2: WD	4	91.72	2.52	0.13	0.79	-41.52
Model 1: H_0	3	91.91	2.71	0.12	0.9	-42.76
Model 3: Forage	4	92.28	3.08	0.1	1	-41.8

(b) Component Models	***df***	***logLik***	***AICc***	***ΔAICc***	***Weight***
Forage; WD	5	-39.08	89.2	0	0.69
Forage; WD; WD * Forage	6	-38.65	90.77	1.57	0.31

3. Effect of Woody Debris on Zebra Vigilance Behaviour

(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 1: H_0	3	497.43	0	0.57	0.57	-245.52
Model 2: WD	4	497.95	0.52	0.43	1	-244.64

(b) Component Models	***df***	***logLik***	***AICc***	***ΔAICc***	***Weight***
H_0	3	-245.52	497.43	0	0.57
H_0; WD	4	-244.64	497.95	0.52	0.43

DISCUSSION

My results partly support the hypotheses described in my introduction regarding the indirect interactions between elephant and white rhino. The amount of woody debris did not significantly affect white rhino, nyala or zebra visitation to the grazing lawns, yet visitation by nyala was significantly affected by the interaction between the amount of forage and amount of woody debris. As predicted, as the amount of elephant-deposited woody debris increased, the probability of white rhino foraging decreased. The probability of foraging by nyala increased as the amount of woody debris increased and as the amount of forage increased. The amount of woody debris did not significantly influence vigilance behaviour by nyala and zebra.

Forage Selection

Crucial to understanding these results is the decision-making process that these herbivores use when choosing places to forage (Bailey *et al*. 1996). Foraging patterns may result from decisions made by animals at different spatial and temporal scales (Bailey *et al*. 1996). In the event of woody debris deposited by elephant onto areas with foraging potential, this is likely to affect the animal's foraging velocity and intake rate. Over and above the hindrance of the woody debris, this study took place during a drought and it is therefore likely that palatable forage that was usually abundant in average to high rainfall years, was now scarce. And both these factors likely resulted in the foraging patterns observed in this study.

Forage Availability

The amount of food available was unseasonably low. Yet, I found that the amount of forage increased with increasing levels of woody debris. This is likely due to an interaction between the woody debris, herbivory and the surrounding plants, which is modulated by the potential influence of woody debris traits on surface moisture availability (Haughian and Frego 2017) as well as the creation of associational refuges, whereby focal plant individuals grow near neighbours or structures that physically impede herbivore access thereby reducing herbivory damage (Milchunas and Noy-Meir 2002). Therefore, the presence of woody debris may have prevented herbivory and reduced the foraging availability at the study sites during the drought.

Predation Risk

In African savannas, there are top-down (predation risk) or bottom-up (forage quality/quantity) forces that impact population regulation and habitat selection of herbivores particularly if risk of predation varies among habitats with different levels of complexity (Thaker *et al*. 2011; Burkepile *et al*. 2013). According to Valeix *et al*. (2007), water abundance, perceived predation risk and interference competition are factors known to affect resource acquisition by herbivores. Even though large herd sizes are considered an advantage for anti-predator behaviour (Lima, 1995), aggregation of animals induces depletion of resources and may result in interference competition (Wilson and Richards 2000). During drier periods, foraging patches of acceptable quality are fewer, as are drinking sites such as waterholes. This means that herbivores are likely to take greater risk as the probability of acquiring resources is low. I predicted that increasing levels of woody debris may act as escape impediments to mesoherbivores thereby increasing perceived predation risk leading to an increased level of vigilance. If valuable foraging areas, such as the grazing lawn plots in this study during this drought, and areas of high predation risk often overlap, such as the plots with high levels of woody debris, ungulates must balance obtaining the resources they need to survive while avoiding predation. This was partly supported by my results showing that as the amount of forage increased, nyala and zebra were observed to forage more despite the increasing risk posed by the increasing levels of woody debris. However, the amount of woody debris in my study did not significantly predict the probability of vigilance behaviour by these mesoherbivores. This contradiction may have been because of the drought, where mesoherbivores may have responded less or not at all to risk factors such as woody debris (Sinclair 1985). This is predicted to occur in situations where resources are limited as described by the predation risk hypothesis (Lima and Bednekoff 1999), however this requires further investigation. I recommend that future studies focus on not just visitation and behaviour events alone but also time allocation patterns as determined by the duration of each behaviour in response to increasing levels of woody debris. Crucial to this would be to classify plots into feeding patches versus feeding stations, which could then result in a refined approach to classifying vigilance as opposed to simply reorientation of a new feeding location (Bailey *et al*. 1996). This would contribute to the growing body of research on the trade-off between time spent foraging versus time spent vigilant by mesoherbivores (e.g.: Valeix *et al*. 2007). And both kinds of data collected would contribute to a better understanding on how the behaviour of mesoherbivores utilising grazing lawns may be modulated indirectly by the feeding behaviour of elephants.

Megaherbivore Impacts on Grazing Lawns

Elephants and white rhinos are considered ecosystem engineers (Owen-Smith 1988). Their interaction not only has cascading effects on mesoherbivores in terms of foraging and vigilance behaviour, but will directly influence the dynamics and composition of these grazing lawns, upon which this interaction has been observed. Since, white rhinos play an important role in the creation and maintenance of grazing lawns (Waldram et al. 2008), what should happen to the grazing lawn if they (or other) herbivores are prevented from maintaining these lawns in their short grass state? Chapter 3 of this thesis investigates how elephants may indirectly regulate the impacts of grazers on grazing lawns in African savannas, providing insight into the heterogeneity and complexity of this ecosystem.

Drought

The 2015-2016 wet season, the period during which this study took place, ranks among the worst drought in at least the last 30 years in southern Africa and led to extensive drought across Mozambique, Zambia, Zimbabwe, South Africa and southern Madagascar (Liberto 2016). In KwaZulu Natal, South Africa, HiP and surrounding areas were severely affected and major rivers such as the Umfolozi River dried up (Kaplan and Zitzer 2016). Since the data were collected during this severe drought, it is likely that white rhino shifted their feeding patterns to longer grasses as the grass quality and abundance of grazing lawns is known to decline during dry periods (Owen-Smith 1988; Perrin and Brereton-Stiles 1999), which may explain the low visitation by white rhino. Similarly, as predicted, white rhino foraged less with increasing levels of woody debris. This is most likely due to limited food availability because of the drought and not necessarily the inaccessibility of white rhino to grass directly beneath those branches and in between branches lying closely together. Manoeuvring through high levels of woody debris would be challenging for white rhino due to their large body size comprising large limbs and broad muzzles (Owen-Smith 1988). However, there were no observations recorded of white rhino moving branches out of their way to access forage.

Conclusion

In conclusion, my study provides evidence for the megaherbivore-megaherbivore interaction where African elephant indirectly affect the foraging opportunities for white rhino as well as the megaherbivore-mesoherbivore interaction where the African elephant indirectly affect the foraging opportunities for nyala. My work adds to a growing body of literature on the complexity of top-down (predation risk) or bottom-up (forage quality/quantity) forces on herbivore behaviour. However, this study calls for similar approaches in assessing predation risk under different levels of elephant impact. This would give us a more complete picture of how herbivores deal with gathering food versus avoiding predation in areas impacted by elephants. This will also provide grazing lawn ecologists with a better understanding of how the dynamics of grazing lawns are influenced by herbivore interactions.

CHAPTER 3: EVALUATING THE EFFECTS OF ELEPHANT-DEPOSITED WOODY DEBRIS ON THE STRUCTURE OF GRAZING LAWNS

INTRODUCTION

Grazing lawn grass species respond to herbivory in a variety of ways such as having their important structural components (e.g. stems and buds) below the reach of grazers (i.e.: beneath the soil; Hempson *et al*. 2014). Any build-up of accessible leaf material above the soil becomes a high-quality forage resource for grazers due to the grasses' higher leaf to stem ratio and the higher foliar N levels than surrounding bunch grasses (Stock, Bond and van de Vijver, 2010). Defoliation also stimulates foliar regrowth rates as frequent grazing allows insufficient time for leaf blade tips to senesce, meaning that bites are largely composed of the phenologically young and actively photosynthesising leaf material for as long as the grass sward is continually regrowing (i.e. in the wet season; McNaughton 1985; Bonnet *et al*. 2010). These factors are crucial in maintaining a cycle of regular grazing, which leads to the prevention of invading tall-grass species, which results in the persistence of the grazing lawn. This study focuses on the megaherbivore-megaherbivore interaction wherein foraging by elephants is hypothesized to indirectly influence foraging by other herbivores therefore ultimately having the potential to mediate these herbivores' effects on the persistence of grazing lawns.

Herbivory by elephant is a primary disturbance structuring savanna woodlands (Cumming 1982; Owen-Smith 1988). Elephants are mixed feeders, consuming both browse and grass depending on seasonal availability (Kerley *et al*. 2008). Wood deposited onto the ground by elephant during foraging exerts ecological influences on the area upon which it lands (Spies and Cline 1988; Stokland 2001). Consequently, the depositing of discarded branches by elephants may have profound, cascading influences on local species richness and composition, possibly influencing savanna ecosystem functioning (Huntly 1991) but studies on the effects of elephant-deposited woody debris are few (e.g.: Kerley *et al.* 2008; Rutina and Moe 2014; Maqatsa 2016).

Here, I hypothesize that woody debris deposited onto grazing lawns has the potential to influence the foraging behaviour of another megaherbivore, the white rhino, thereby leading to changes in the grass composition and structure of grazing lawns. The white rhino is a megagrazer whose impact on grass communities may be as large as that of the elephants on tree communities (Waldram *et al.* 2008). White rhinos are specialized grass feeders with low-slung heads, wide mouths and broad, sensitive upper lips suitable for plucking grass (Owen-Smith 1988). Repeated grazing by white rhino and other grazers leads to the establishment and maintenance of a type of short grassland called a grazing lawn (Owen-Smith 1988, Cromsigt *et al.* 2017). These lawns stand out as intensely grazed patches of stoloniferous, grazing-tolerant grass species (Cromsigt and Olff 2008). During periods of disuse, such as if white rhino or other herbivores are prevented from maintaining these lawns (Vesey-

Fitzgerald 1969; McNaughton 1976), grass height will increase, tall-grass species will invade and the lawn is likely to change its state from a short grassland to a taller bunch grass community (Waldram *et al*. 2008; Hempson *et al.* 2014).

As seen in Chapter 2, in Hlhluwe-Imfolozi Park (HiP), increasing levels of woody debris on grazing lawns reduced the probability of foraging by white rhino. This was further confounded by the drought which likely affected foraging availability for both white rhino and mesoherbivores. Since repeated grazing was generally prevented, the effects of this on grazing lawn composition and structure are unknown, especially under different levels of elephant impact and different sizes and positions of elephant-deposited woody debris.

In this chapter, my objective is to investigate how grass structure and composition varies within a grazing lawn patch in the presence of elephant-deposited woody debris (Fig. 3.1). Therefore, I tested the hypothesis that the grass composition and structure of a grazing lawn is altered by the deposit of woody debris due to the browsing activities of elephants. This led to the following predictions: at a rhino foraging patch scale, (1) heavy disturbance by elephants, as indicated by a large amount of discarded branches and fallen trees, leads to increased height of surrounding grasses; (2) grass height beneath woody debris will increase as the space between that piece and the ground increases (as seen in Fig. 3.1 where toppled trees do not always lie directly on the ground and some may lean on their canopies creating space for grass growth); and (3) as the amount of woody debris increases, the occurrence of lawn-forming grasses will decrease and the occurrence of tussock-forming grasses will increase.

Figure 3.1. Grass grew out underneath a fallen tree canopy pushed over by elephants whereas grazing occurred underneath the tree trunk leaning above the ground at a grazing lawn in Hluhluwe-iMfolozi Park, KwaZulu Natal, South Africa.

METHODS

Study Site

This study was conducted in similar areas as described in Chapter 2, with specific sites indicated in Fig 2.1.

Study Design and Sampling

This study was set up in 2013 within a high elephant impact site comprising an *Acacia burkeii* woodland and a low elephant impact site in an area dominated by tall *Dichrostachys cinere*a shrubs (Fig. 3.2). In each of these, five 15 m x 15 m grazing lawn plots with varying scales of elephant impact were selected in each site. Sampling occurred at the end of the wet season in March 2013, 2014 and 2015. In each plot, I laid out sixteen 15 m transects spaced 1 m apart. Every 50 cm along each transect (496 points per plot) I recorded whether the point was covered with wood, bare soil, forbs, lawn and/or tussock grass. A grid resolution of 50 cm between points along a transect was selected based on three measurements: (1) the bite width of white rhino of 20 cm (Owen-Smith 1988); (2) woody debris encountered in this study with widths between 0.5 cm and 40 cm; and (3) space next to woody debris available for grass growth. The table height of the functional grass types (lawn or tussock), measured from the ground to the tallest sward of the tuft, was also recorded at each point. If wood was present, the size (height, length and width), type (bark, branch, log and tree canopy) and height underneath wood (i.e. the height that is available for vegetation to grow underneath) was recorded.

Site Selection Verification

The two sites were initially selected based on observed high versus low intensity of use by elephants (J.P.G.M. Cromsigt, *personal observations*). To verify this, we used data on presence of elephants and white rhino at the two study sites from a separate study running concurrently (Le Roux 2016). In Le Roux (2016), sites were monitored using camera traps between May 2014 and January 2015. The images captured were used to calculate a visitation index for each site for each of the two megaherbivore species. The visitation index was calculated as the number of visits to the area divided by the sampling effort, which was the number of trap days divided by the number of days the camera was active for. This produced a visitation rate of the number of visits per day of filming at each site. The high elephant impact site had a significantly higher elephant visitation index (mean = 1.00 ± 0.57; Fig. 3.3) than the low impact site (mean = 0.26 ± 0.12) and this was significant at $p < 0.1$ (t = -1.96, df = 8, $p = 0.086$; Fig. 3.4). Furthermore, the visitation by white rhino was not significantly different for both the low and the high elephant impact sites (mean = 1.77 ± 0.6 and mean = 1.92 ± 0.44, respectively; t = 0.48, df = 8, $p = 0.64$).

Figure 3.3. A photograph of the low impact site sampled in this study in Hluhluwe-iMfolozi Park, South Africa.

Figure 3.4. A photograph of the high impact site sampled in this study in Hluhluwe-iMfolozi Park, South Africa.

Data Analyses

For all analyses involving mixed effects models, if the numeric values of a variable were on a very different order of magnitude to other variables within the same model, that variable was scaled using the “scale” function in R, which calculates the mean and standard deviation of the dataset in question, then "scale" each element by those values by subtracting the mean and dividing by the standard deviation (Crawley 2007). Collinearity among main effects was investigated using variance inflation factors (VIFs) in the *car* package (Fox and Weisberg 2011). Model selection was performed on the candidate models using a modified version of Akaike information criteria (AICc) which approximates AIC at large sample sizes if the sample size is small ($n/k < 40$; Simonds and Moussalli 2010) using the R package *AICcmodavg* (Mazerolle 2016). The model with the lowest AICc value was selected, but model averaging using the *MuMln* package (Barton 2016) was performed if the delta AICc value of models differed by less than 2 (Burnham and Anderson 2002). The distribution family was specified as Poisson, which is appropriate for count data (Crawley 2007), and the random effects, if used have been stipulated below, fulfilled their role of assigning repeated measures (Zuur *et al*. 2009).

Difference in woody debris amount between impact areas

I compared the amount of woody debris on grazing lawns between the high and low elephant impact sites by constructing a candidate set of generalized linear models (GLMs) using the *lme4* package (Bates *et al.* 2015), with the amount of woody debris as the response variable. The amount of woody debris was calculated as the number of points per plot covered with woody debris. I included site (two levels: low and high) and year (three levels: 2013, 2014 and 2015) as fixed effects.

Effect of woody debris volume on grass height

I looked at the effect of the volume of single pieces of woody debris (cm^3) on grass height surrounding each piece of woody debris. The height of grasses growing directly next to or within 50 cm of the pieces of wood were averaged so that there was one grass height measurement per piece. I then modelled trends of the volume and height underneath wood as fixed effects on the response variable of average grass height using linear mixed effect models (LMMs) where I specified that plot nested within impact site was random. The residual errors of the selected model met the normality assumption (Crawley 2007). The *car* package was used to compute p-values via a Type II Wald chi-square test because the *lmer* function in the *lme4* package does not produce p-values (Bates *et al.* 2015). I compared the results to the line of unity, where grass height would increase at the same rate that the height above the ground increased.

Effect of woody debris amount on average grass height

I used LMMs to look at the effect of the amount of woody debris on the average grass height. The amount of woody debris was calculated as the number of points per plot covered with woody debris. Grass height was recorded at each point and averaged across the entire plot. I specified that the amount of points covered by woody debris, year (a repeated measure)and its interaction were fixed, and that site was random.

Effect of woody debris position on grass height in 2015

I tested three positions of the woody debris in relation to the ground against grass height in 2015. These positions included above ground (a toppled tree leaning above the ground and balancing on its canopy); touching ground (a branch lying directly on the ground); and tree canopy (the area beneath a fallen tree canopy that allows grass growth in between the branches, thorns and leaves) (Fig. 3.1). I used a non-parametric Kruskal-Wallis test to assess if grass height varied significantly depending on the position of woody debris. This was done because the response variable of grass height did not meet the normality assumption of a one-way ANOVA and wood position was a categorical variable (McDonald 2008). I then ran a Dunn’s Test (*dunnTest* function in the *FSA* package) as an appropriate post hoc test following the rejection of the null hypothesis (Zar 2010).

Effect of woody debris amount/volume on ground cover types

I tested how the amount of woody debris (measured as the frequency of occurrence of the number of points per plot covered with woody debris) as well as the volume of woody debris influenced variation in cover of the four cover types (bare soil, forbs, lawn and tussock). A candidate set of generalized linear mixed effects models (GLMMs) was used, where I specified that the amount of woody debris and year were fixed and site was random.

Results

Difference in woody debris amount between sites

Multicollinearity was not of concern (impact site: VIF = 1; year: VIF =1). Model fit was best for model 3 (Table 3.1). There was less woody debris in the low impact site than in the high impact site in all three years (β = -2.23; SE = 0.12; z-value = -17.95; $p < 0.05$).

Table 3.1. Summary results after model selection of the candidate model set where the response variable is the amount of woody debris tested against year, impact and their interaction.

Candidate Models	*K*	*AICc*	*ΔAICc*	*AICcWt*	*Cum.Wt*	*LL*
Model 3: Impact Site + Year	4	384.58	0	0.93	0.93	-187.49
Model 4: Impact Site * Year	6	389.77	5.19	0.07	1	-187.06
Model 2: Impact Site	2	434.05	49.47	0	1	-214.8
Model 1: H_0	1	984.15	599.57	0	1	-491

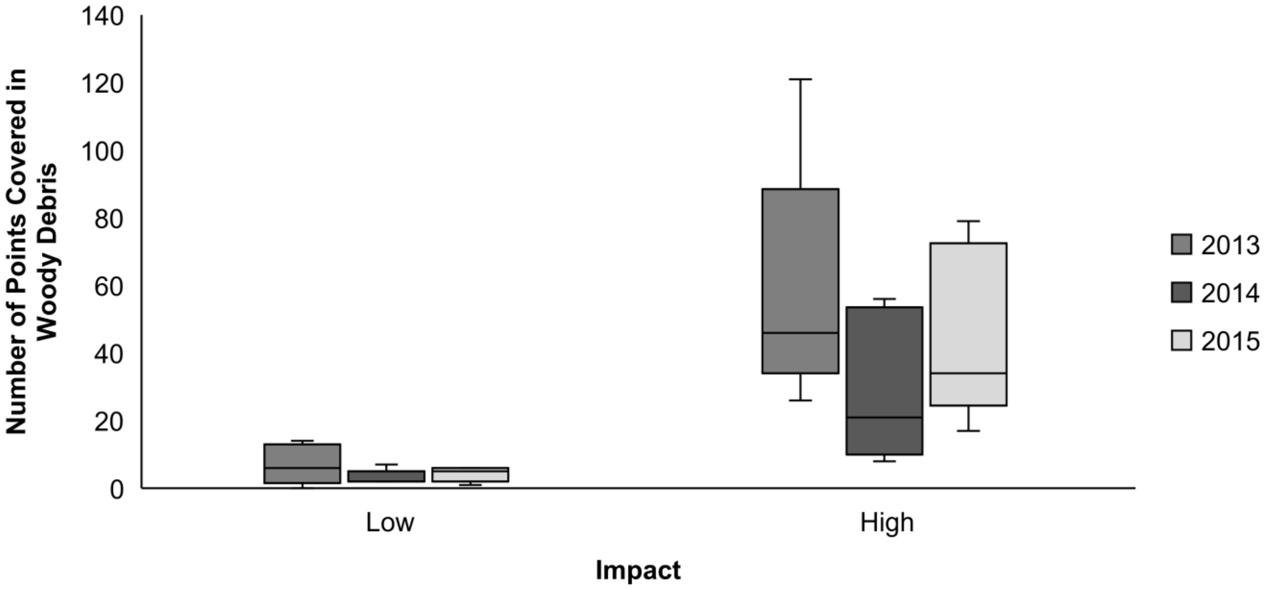

Figure 3.5. Graph showing the number of points covered with woody debris in the low elephant impact site and in the high elephant impact site in all three years.

Effect of woody debris volume on grass height

Multicollinearity was not of concern (volume: VIF = 1.26; height under debris: VIF = 1.26). Model 3 and 4 differed by an AICc value of 1.46. Model averaging was performed (Table 3.2). The resulting analysis showed that an increase in wood volume did not significantly affect grass height (β = -0.99; SE = 0.94; z-value = 1.06; p = 0.29). Grass height does not exceed the line of unity (Fig 3.6.A).However, grass height significantly increased as the height underneath woody debris increased (β = 10.93; SE = 0.81; z-value = 13.41; $p < 0.05$) (Fig. 3.5.B). However, some grasses stayed below typical lawn grass heights (< 7 cm - Waldram *et al*. 2008) despite this being less than the height beneath the woody debris (Fig 3.5.C).

Table 3.2. Summary results after model selection and averaging of the top models containing wood volume and height underneath woody debris as fixed effects on the response variable of grass height. Averaged models are shaded in grey.

(a) Candidate Models	*K*	*AICc*	*ΔAICc*	*AICcWt*	*Cum.Wt*	*LL*
Model 4: Height underneath Wood + Wood Volume	5	968.21	0	0.68	0.68	-478.88
Model 3: Height underneath Wood	4	969.67	1.46	0.32	1	-480.69
Model 2: Wood Volume	4	1091.11	122.9	0	1	-541.4
Model 1: H_0	3	1098.93	130.71	0	1	-546.37
(b) Component Models	*df*	*LogLik*	*AICc*	*ΔAICc*	*Weight*	
Wood Volume; Height underneath Wood	5	-478.88	968.21	0	0.68	
Height underneath Wood	4	-480.69	969.67	1.46	0.32	

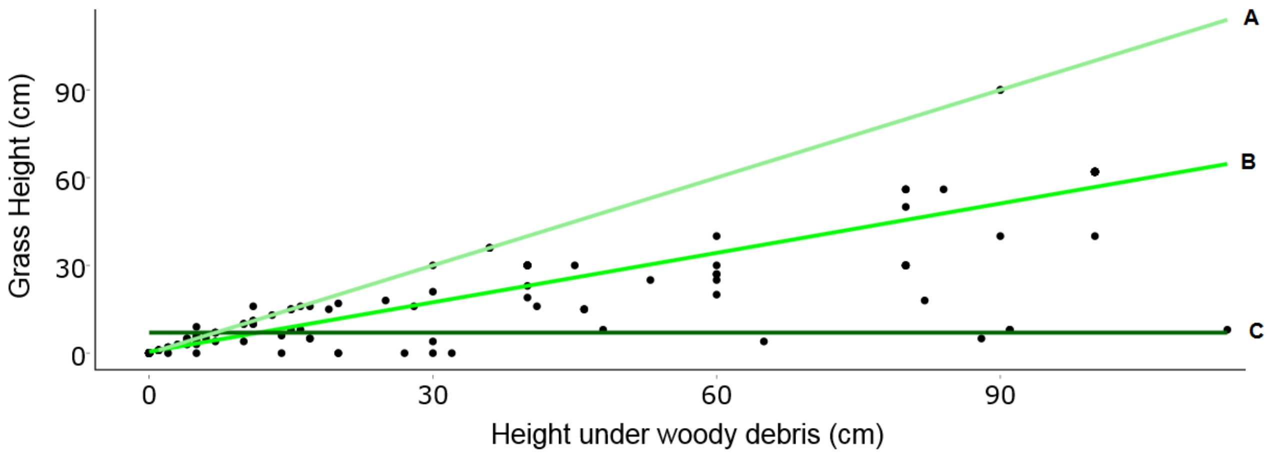

Figure 3.6. Relationship between the height of grass and height underneath woody debris, showing that grass height did not exceed the line of unity, which is the height above which grasses would extend above the woody debris) (A). As per the selected model, grass height significantly increased as the height underneath woody debris increased (B; $\beta = 10.93$; SE = 0.81; z-value = 13.41; $p < 0.05$). Some grasses stayed below typical lawn grass height (C = 7 cm) as described by Waldram *et al.* 2008.

Effect of woody debris amount on average grass height

The delta AICc values of all five models differed by less than 2 therefore model averaging was performed (Table 3.3). The amount of woody debris was not a significant predictor of average grass height in 2013 ($\beta = -0.4$; SE = 0.84; z-value = 0.46; $p = 0.65$); 2014 ($\beta = -1.05$; SE = 1.67; z-value = 0.614; $p = 0.54$) and 2015 ($\beta = -0.52$; SE = 1.006; z-value = 0.5; $p = 0.62$).

Table 3.3. Summary results after model selection of the candidate model set where the response variable is the amount of woody debris (WD) tested against year. Model averaging was performed of all models shaded in grey.

Candidate Models	*K*	*AICc*	*ΔAICc*	*AICcWt*	*Cum.Wt*	*LL*
Model 3: Year	5	167.88	0	0.25	0.25	-77.69
Model 5: WD * Year	8	167.89	0.01	0.24	0.49	-72.52
Model 4: WD + Year	6	168.34	0.47	0.2	0.69	-76.34
Model 1: H_0	3	168.5	0.63	0.18	0.87	-80.79

Model 2: WD	4	169.1	1.23	0.13	1	-79.75

Effect of woody debris position on grass height

The mean rank of grass height differed significantly among the three different positions of woody debris ($\chi^2 = 153.76$; $p < 0.05$) and multiple comparisons were conducted between the grass height in different woody debris positions using Dunn’s Test (Dunn 1964) where p-values were adjusted with the Bonferroni method. Grass height was significantly higher growing through the fallen tree canopy than in areas without woody debris (mean = 19.86 cm; SD = 11.07 cm; Z = 2.7; $p < 0.05$). Grass height was low in areas without woody debris (open: mean = 7.38 cm; *SD* = 9.01 cm) and for grasses surrounding woody debris when it was leaning above the ground (above ground: mean = 10.99 cm; *SD* = 15.22 cm).

Effect of woody debris volume on ground cover types

For the year 2015, the volume of woody debris per plot was not a significant predictor of the amount of bare soil (VIF < 1.1; $\beta = -0.23$; SE = 0.21; z-value = -1.1; p = 0.27), forbs (VIF < 1.1; $\beta = -0.09$; SE = 0.3; z-value = 0.28; p = 0.78) and tussock (VIF < 1.1; $\beta = -0.27$; SE = 0.16; z-value = -1.76; p = 0.08). However, as the volume of woody debris increased, the amount of lawn increased (VIF < 1.1; $\beta = 0.3$; SE = 0.13; z-value = 2.32; $p < 0.05$). These cover types were dependant and only four out of eight were analysed.

Effect of woody debris amount on ground cover types

For bare soil, lawn and tussock, the model with the interaction between the amount of woody debris and year had the lowest AICc value and was selected (Table 3.4). For forbs, the model with the amount of woody debris and year and the model with their interaction had AICc values that differed by less than 2, therefore model averaging was performed (Table 3.4). Results of these models are displayed in Table 3.5 and are displayed graphically in Fig. 3.7.

Table 3.4. Results of model comparison using AICc (a) and component models of model averaging (b) where the response variable is the number of points covered with (1) bare soil, (2) forbs, (3) lawn and (4) tussock. Selected models are shaded in grey.

1. Bare Soil						
(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 3: Woody Debris * Year	7	261.95	0	1	1	-121.43
Model 4: Woody Debris + Year	5	525.49	263.54	0	1	-256.5
Model 2: Woody Debris	3	1255.95	994	0	1	-624.51
Model 1: H_0	2	1425.37	1163.42	0	1	-710.46
2. Forbs						
(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 3: Woody Debris * Year	7	195.97	0	0.68	0.68	-88.44
Model 4: Woody Debris + Year	5	197.45	1.48	0.32	1	-92.48
Model 2: Woody Debris	3	288.61	92.64	0	1	-140.84
Model 1: H_0	2	347.79	151.83	0	1	-171.67
(b) Component Models	***df***	***LogLik***	***AICc***	***ΔAICc***	***Weight***	
Woody Debris; Year; Woody Debris * Year	7	-88.44	195.97	0	0.68	
Woody Debris; Year	5	-92.48	197.45	1.48	0.32	
3. Lawn						
(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 3: Woody Debris * Year	7	442.51	0	1	1	-211.71
Model 4: Woody Debris + Year	5	646.73	204.22	0	1	-317.12
Model 2: Woody Debris	3	1122.55	680.04	0	1	-557.82
Model 1: H_0	2	1140.1	697.59	0	1	-567.83
4. Tussock						
(a) Candidate Models	***K***	***AICc***	***ΔAICc***	***AICcWt***	***Cum.Wt***	***LL***
Model 3: Woody Debris * Year	7	442.51	0	1	1	-211.71
Model 4: Woody Debris + Year	5	646.73	204.22	0	1	-317.12
Model 2: Woody Debris	3	1122.55	680.04	0	1	-557.82
Model 1: H_0	2	1140.1	697.59	0	1	-567.83

Table 3.5. Results of the GLMMs showing whether the amount of woody debris was a significant predictor of the amount of (1) bare soil, (2) forbs, (3) lawn and (4) tussock at a 95% confidence level.

Cover Type	Year	*Estimate*	*SE*	*Z-value*	*P-value*
1. Bare soil	2013	0.2864	0.05709	5.017	$p < 0.05$
	2014	-0.0441	0.06146	-0.72	0.47
	2015	-0.78663	0.06773	-11.61	$p < 0.05$
2. Forbs	2013	-0.711	0.3052	2.288	$p < 0.05$
	2014	-1.2115	0.2257	5.18	$p < 0.05$
	2015	-1.1177	0.2311	4.6	$p < 0.05$
3. Lawn	2013	-0.14605	0.01842	-7.93	$p < 0.05$
	2014	0.02328	0.0324	0.72	0.47
	2015	0.21811	0.02451	8.9	$p < 0.05$
4. Tussock	2013	-0.09466	0.04781	-1.98	$p < 0.05$
	2014	-0.34537	0.07532	-4.586	$p < 0.05$
	2015	-0.14363	0.05052	-2.843	$p < 0.05$

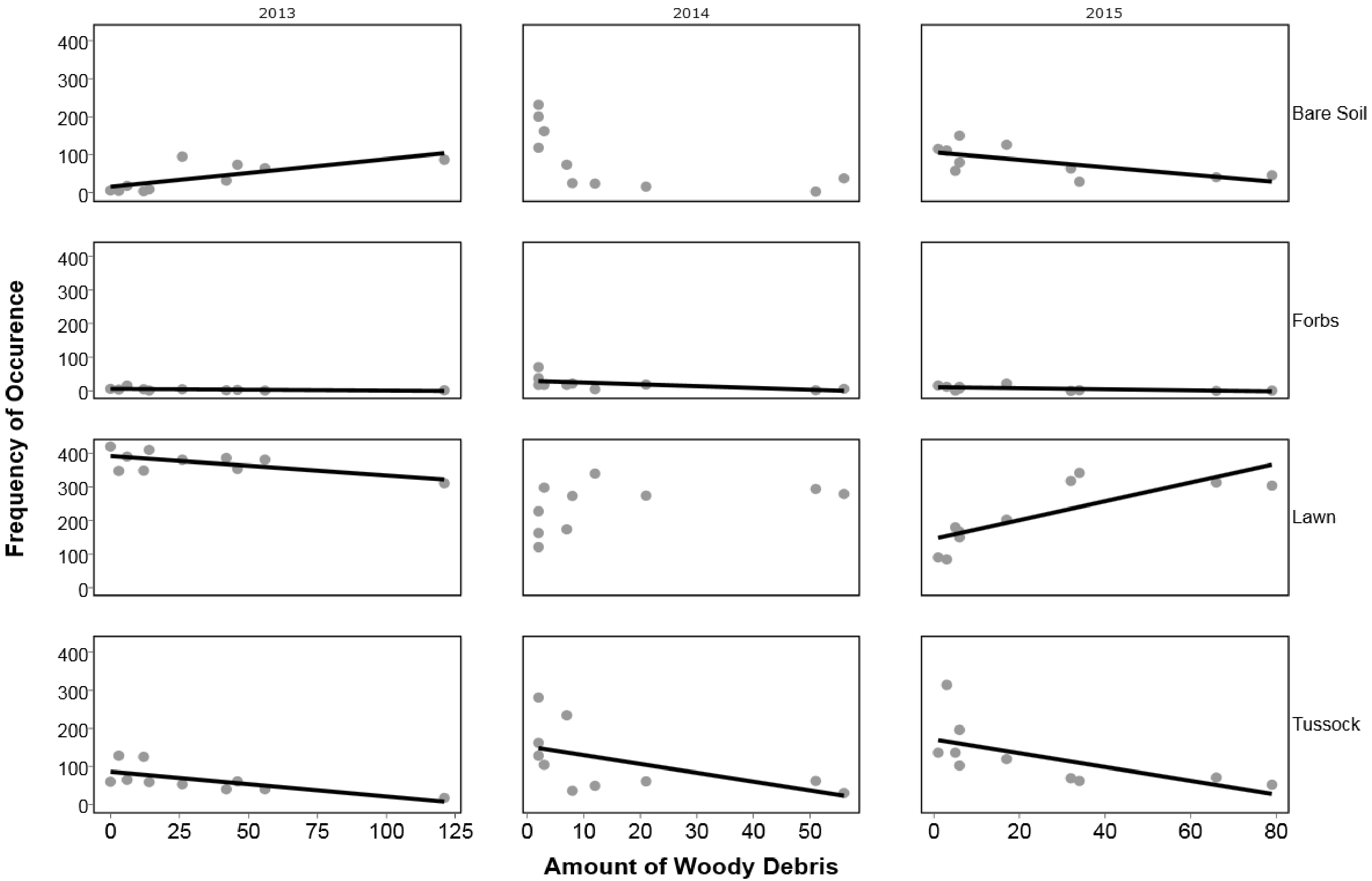

Figure 3.7. Relationship between the amount of woody debris and the frequency of occurrence of the four different ground cover types (bare soil, forbs, lawn and tussock) in each of the 3 years. The relationship was not significant for bare soil and lawn in 2014.

DISCUSSION

The sites for this study were selected based on a perceived intensity of use by elephants and white rhino. The high impact area had more woody debris than the low impact area, despite both areas being in woodlands s with woody debris available for depositing. The selection was validated by the low visitation index of the low impact area meaning that this area was less utilized by elephants. The opposite was true for the high impact area, which was highly visited by elephants and this was the possible cause of the high levels of woody debris. The white rhino visitation index was similar for both the low and the high elephant impact areas, suggesting that plots were visited regularly by white rhino throughout the study.

My results partly support the hypothesis that the composition and structure of a grazing lawn is altered by the deposit of woody debris due to the browsing activities of elephants. As determined in this chapter, areas with high visitation by elephants will have more woody debris than those with low visitation by elephants. The amount of woody debris did not influence average grass height as was thought. As hypothesized, the position of woody debris in relation to the ground influenced grass height as grasses growing underneath woody debris lying above the ground and growing through a fallen tree canopy were higher than those in areas without woody debris. Woody debris volume has a positive relation with the amount of lawn but did not affect the amount of bare soil, forbs and tussock in 2015. I predicted that the occurrence of lawn-forming grasses will decrease with increasing amount of woody debris. This effect was supported for 2013 but not 2014 or 2015. I also predicted that the occurrence of tussock-forming grasses will increase with increasing woody debris, however this was not the case as the amount of tussock decreased with increasing woody debris and this effect was the same in each year.

The Role of Mesoherbivores and Insects

I predicted that high levels of elephant-deposited woody debris onto grazing lawns would lead to a reduction in grazing pressure as grass underneath the woody debris would be inaccessible to the broad-muzzled, short-grass specialists, such as white rhino, and they can therefore not maintain these patches as permanent stoloniferous grazing lawns (Owen-Smith 1988; Hempson *et al*. 2014). This interaction between woody debris and plants may be modulated by the potential influence of woody debris traits on surface moisture availability (Haughian and Frego 2017) as well as the creation of associational refuges, whereby focal plant individuals grow near neighbours that physically impede herbivore access thereby reducing herbivory damage (Milchunas and Noy-Meir 2002). Despite these refuges, average grass height did not increase with amount of woody debris as I had hypothesized (Fig. 3.4) but the amount of lawn increased instead. In the high impact area, trees toppled by elephants did not always land directly onto the ground (Fig. 3.1), resulting in space available for grass growth. My results showed that increased height underneath woody debris led to increased grass height at a grazing lawn patch scale. However, some grasses remained below typical lawn grass height (< 7 cm - Waldram et al. 2008) indicating that grazing was still occurring. White rhino would not be able to fit their heads under most of these toppled trees leaning above the ground nor their muzzles in-between pieces of woody debris. Therefore, as seen in the results of chapter 2, mesoherbivores may play an important role in maintaining these patches as grazing lawns – despite the presence of woody debris. Cromsigt and Olff (2008) proposed that a diverse community of herbivores promote grazing lawn formation and that mesoherbivores keep the grass short and promote colonization of stoloniferous grazing lawn species after an initial disturbance by a megaherbivore. Less conspicuous yet highly diverse are the communities of herbivorous insects (such as grasshoppers) that share the same food (van der Plas and Olff 2014) and consume a substantial part of the plant biomass in these savannas (Sinclair 1975).

Another major player in the ecology of savannas are the litter-feeding termites, which move large quantities of litter, soil and nutrients through the landscape (Goudie 1988). These agents of savanna heterogeneity may have played a major role in keeping the grass short in the grazing lawns in this study. Buitenwerf *et al*. (2011) found that there are positive effects of large herbivores on termites in the dry areas of HiP, where termite foraging intensity was higher in areas with a high abundance of mammalian grazers, i.e.: grazing lawns. Grazers improve accessibility of vegetation to termites through trampling and by increasing litter-fall by dropping plant fragments whilst grazing (Cumming and Cumming 2003). Termites are very common in semi-arid savanna ecosystems and play a critical role in leaf-litter removal as well as dead and decaying plant material such as woody debris (Bignell and Eggleton 2000; Fornara and Du Toit 2008). Termite abundance and consumption increase with increasing rainfall due to the increase in food availability (Picker *et al*. 2007). It is thought that the positive association between herbivores and termite consumption may change from facilitation to food competition during droughts (Buitenwerf *et al*. 2011) which may have been the case in my study as it took place during a severe drought ranking among the worst in at least the last 30 years in southern Africa (Liberto 2016). Given their smaller size, mesoherbivores and herbivorous insects such as termites may have a competitive advantage over white rhino in grazing lawns with high levels of elephant-deposited woody debris.

Limitations

I did not identify vegetation down to species, however since grass species respond differently to herbivory and environmental conditions (Hempson *et al*. 2014), I recommend that lawn grasses, tussock grasses and forbs are identified down to species in future studies. This would provide greater insight into possible changes in richness and diversity under different levels of elephant impact. The unexpected differences in the amount of vegetation types recorded in my study may be attributable to observer bias: each year was sampled by different observers whose ability to distinguish between lawn and tussock grasses varied. In this case, grass height is then a more reliable and objective measure. Another limitation possibly contributing to these results is the relatively low frequency of sampling: the two sites were sampled once a year for three consecutive years. In such a dynamic ecosystem, it would perhaps be more appropriate to measure over a shorter time scale to account for temporal and seasonal variability.

Conclusion

In conclusion, elephant impact through the deposit of woody debris affects grazing lawn dynamics in savanna grasslands. To retain and manage heterogeneity in savannas, it is becoming increasingly necessary to develop a predictive understanding that can provide protected area managers with the necessary input for developing and implementing action plans (Archibald *et al.* 2005). The growing elephant population in Hluhluwe-iMfolozi Park has been perceived as posing an immediate threat to the integrity of biodiversity, specifically priority species such as the white rhino, among others (Druce *et al*. 2017). Although our results demonstrate the impacts of woody debris on grazing lawns in HiP, it is important to develop a greater understanding of the ecological threshold of grazing lawns to woody debris, that is, the amount of woody debris at which grazing lawns can no longer be maintained by grazers. It would also be important to assess the occurrence and extent of elephant impact on grazing lawns across the park as this has the potential to predict the location and intensity of use by white rhino, which is necessary to inform the white rhino management plan.

Chapter 4: General Discussion

Elephants indirectly impact foraging opportunities for white rhino

The central focus of my thesis was to determine whether woody debris discarded by elephants onto grazing lawns influenced visitation by and foraging behaviour of white rhino and subsequently, the availability and structure of lawn grasses. Through my experiment, I confirmed my main objective by showing that the foraging probability of white rhino decreased as the amount of woody debris increased. I was also able to show that increasing levels of woody debris led to increased grass height around pieces of woody debris. Grass height also increased when woody debris was toppled over and lying above the ground as well as in between branches of toppled tree canopies. However, despite the presence of woody debris, short grasses persisted, potentially because of reduced grazing pressure as tussock-grasses outcompeted lawn grasses. I showed that the amount, type and volume of woody debris has the potential to influence foraging opportunities for white rhinos.

Drought

Regarding the questions set out in the introduction of this thesis: my results did not provide strong evidence for the hypothesis that browsing activities of elephant indirectly affect white rhino foraging behaviour and the structure and composition of grazing lawns in HiP. In 2015, South Africa received the lowest amount of rainfall since records began in 1904 (Piesse 2016). Fig. 4.1 shows one of my sites (S1) in January 2015 during an average rainfall year and one year later in January 2016 during the drought. The possible reduction of suitable habitats for white rhino due to the persistent severe drought may explain the low visitation by white rhino during the experimental component of my study between January and March 2016. White rhino would have shifted their feeding patterns to areas of longer grasses as the grass quality and abundance of those grazing lawns are likely to have declined during this study period as they do over the dry season (Owen-Smith 1988; Perrin and Brereton-Stiles 1999). While my study did not allow me to properly separate the effects of elephant-deposited woody debris from the severe lack of rainfall on grass response and subsequently herbivore foraging behaviour, my experiment still provided valuable insights – the lack of rain inhibited grass growth and this may explain the lack of response by grasses to woody debris.

Figure 4.1. Photographs showing a difference in the grass presence of a grazing lawn site (S1) in (a) January 2015 during the observational component and in (b) January 2016 during the experimental component of my study in the Hluhluwe Section of Hluhluwe-iMfolozi Park, South Africa.

Predation Risk

The risk of predation is thought to exert a strong influence over the foraging behaviour of potential prey (Lima and Dill 1990). The need of prey to gain access to sufficient resources must be balanced against avoiding areas where predation risk is high (McNamara and Houston 1987). This may be exacerbated in many African savannas that are strongly influenced by seasonal rainfall differences. Le Roux (2016) found that predation risk affected local herbivore community structure at a grazing lawn patch scale in HiP. Grazing lawns are typically considered to provide refuge from predation due to the short stature of the grass community and the absence of woody cover inside the lawn (Hempson *et al.* 2014). However, even with the addition of woody debris, my results did not confirm our hypothesis that increasing levels of woody debris may lead to an increased level of vigilance as branches may act as escape impediments to nyala and zebra thereby increasing perceived predation risk. During this drought period where resources are extremely limited, I found that in terms of vigilance behaviour, nyala and zebra responded less or not at all to risk factors such as woody debris, which is in line with the risk allocation hypothesis (Lima and Bednekoff 1999). Similarly, Valeix *et al*. (2009) found that during an average rainfall year, buffalo avoided risky waterholes characterised by a high long-term risk of encountering lions. During a dry year, buffalo were forced into shifting the trade-off between exposure to predation risk and necessity to access water. Thus, in years when water access is limited, they will visit riskier waterholes despite a higher predation risk. Since prey respond differently to different temporal variations in the risk of predation (Creel and Winnie 2005), further work is needed to fully explore this in a grazing lawn scenario exposed to the indirect impact of elephants and their cascading effects on behaviour patterns of prey species.

Herbivorous Insects

Herbivorous insects (such as grasshoppers and termites) share the same food as mammalian herbivores and consume a substantial part of the plant biomass in these savannas (Sinclair 1975). Given their smaller size, mesoherbivores and herbivorous insects may have a competitive advantage over white rhino in areas with high levels of elephant-deposited woody debris. My study showed that some grasses remained below typical lawn grass height (< 7 cm - Waldram *et al.* 2008) and that grazing-sensitive bunch grasses were displaced by grazing-tolerant sprawling lawn grass species thereby indicating that grazing still occurred. Repeated grazing pressure is essential for grazing lawn persistence (McNaughton 1979; Hempson *et al*. 2014). Since white rhino would not be able to fit their heads under most of the toppled trees leaning above the ground nor their muzzles in-between pieces of woody debris, I expect that mesoherbivores and herbivorous insects such as termites may play a rather important role in maintaining these patches as grazing lawns. Termites remove leaf-litter as well as dead and decaying plant material such as woody debris (Bignell and Eggleton 2000; Fornara and Du Toit 2008). Herbivores and termites may compete for food during droughts (Buitenwerf *et al*. 2011) which may have been the case in my study as it took place during a severe drought (Liberto 2016). The presence of woody debris as well as the increase in forage associated with it would likely have attracted mesoherbivores and termites during this study.

Fire

Woody debris has the potential to influence the effects of fire and fire has the potential to mediate the effects of elephant-deposited woody debris on grazing lawns. Elephants and fire are important processes in savannas that facilitate the coexistence of trees and grasses (Higgins *et al.* 2000). The grass layer is the dominant fuel in savannas that carries and supports a fire and its availability as a dry season fuel is influenced by differences in rainfall patterns (Trollope 1984) as well as herbivory (O'Connor and Bredenkamp 1997). An interesting interaction between elephants and fire may exist where elephant-deposited woody debris would in one-way act as fuel for fires resulting in high flammability and temperature especially during dry periods. In another way, fire may assist in the removal of woody debris deposited by elephant on grazing lawns due to fire's capacity to consume dead plant material (Bond and Keeley 2005). Consumption of woody debris by fire would depend on the fire regime of HiP, such as frequency, type, intensity and season of burn (Trollope 1984), since it is in a mesic savanna that experiences considerable variation in rainfall (Balfour and Howison 2002).

Megaherbivore-Megaherbivore Interaction

This study is only a second demonstration of foraging interactions between two species of megaherbivores. Landman and Kerley (2013) demonstrated the key role of elephants in facilitating browsing opportunities for black rhino through the formation and spread of elephant pathways in otherwise impenetrable thicket of the Addo Elephant National Park, South Africa. My study gives valuable insight on this interaction for the first time (1) between elephants and white rhino and (b) in a savanna ecosystem. I found that elephant-deposited woody debris reduced white rhino foraging, however I expected that a decline in grazing lawns would occur as well. This was not the case during my study and was most likely due to the drought. So, what would happen in an average to higher rainfall year? Firstly, I would expect that woody debris would not limit access to forage by white rhino since food is no longer limited and more readily available. Grass would also be able to respond more quickly to a reduction in grazing pressure and therefore, lawn grasses would increase in height due to less intensive cropping and be outcompeted by bunch grasses. This suggests that my original hypothesized effect of the indirect impacts of elephants on white rhino foraging and grazing lawn dynamics could still hold. This key hypothesis that I was unable to test under ‘normal’ conditions due to the drought is still valid and could be functionally important for understanding the ecosystem processes driving grazing lawn formation, persistence and composition in African savannas where elephants and white rhinos coexist.

Limitations

Reduced data quality such as the lack of consistency in methods used for data collection by different observers restrains the outcome of my study and can have important effects on the results. I believe that observer error accounted for inaccuracies in physical measurements of woody debris in 2013 and 2014, hence the use of 2015’s data alone when calculating woody debris volume. A finer scale for measuring points within a plot comprising a grid is needed and this should be consistent for each year (50 cm x 100 cm in 2013, 2014 and 2015 compared to 25 cm x 25 cm in 2016). With regards to the method of acquisition and analysis of camera trap photographs, *behaviour* should be quantified in terms of duration as opposed to proportion, as this will provide actual data on time spent foraging versus vigilance in response to different levels of woody debris.

Conclusion

In conclusion, my study contributes to a growing body of evidence that the impacts of elephants, as ecosystem engineers, have cascading effects on savanna ecosystems. My study showed that elephant impact mediates the foraging behaviour of white rhino during low rainfall periods. This suggests that my key hypothesis that I was unable to test under ‘normal’ conditions due to the drought has validity and may be functionally important, and that elephants should mediate the ecological impacts of white rhino in average to high rainfall years. An interesting outcome is the increasingly important role of mesoherbivores on grazing lawn persistence during occasions where maintenance by white rhino is prevented. Further research is necessary to understand the effects of rainfall (or the lack thereof), predation risk, herbivorous insects, fire, decomposition of woody debris and woody debris-facilitated inflorescence production and the possible interactions among these variables on the persistence of grazing lawns. The coexistence of and interactions between elephants and white rhinos is an important aspect to consider in obtaining a greater understanding of the ecosystem processes driving grazing lawn formation, persistence and composition in African savannas.

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