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Ecology of South African large herbivores in a managed arid savanna: body mass, local distribution, and parasites.

White rhinoceros (*Ceratotherium simum*) | ©Nicolás Fuentes-Allende

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DECLARATION

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

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ABSTRACT

Large herbivores are an important natural resource for humans, but a high proportion of these species are classified as globally endangered. Current declines of these species are mainly caused by unsustainable harvesting and land use loss or conversion. These processes frequently increase herbivore mortality rates, and alter a species' behaviour and local distributions. Because of their importance, humans frequently attempt to manage large herbivores to assure their sustainable use and effective protection. Nevertheless, these actions usually focus on managing and monitoring target species, neglecting possible side effect on other species or components of the environment. In this thesis, I focus on studying both environmental and anthropogenic effects on a large herbivore community that inhabits a seasonal, human-modified arid savanna. Firstly, I propose a method to automate monitoring body mass variation of large herbivores over time and use this to explore seasonal mass changes. The method permitted continual body mass monitor of three species over an 18-month period. Animals lost weight during the dry season and gained weight during the wet season, though interesting sex-specific variation in mass change phenology occurred. Frequency of precipitation was the main predictor of annual mass variation. Such work has the potential to inform on the potential impacts of changing future climatic regimes on large herbivores. Secondly, I map the spatial abundance of 16 species using Distance Sampling and Density Surface Models. My results suggest that this highly diverse community of large herbivores can coexist in African savannas because they spatially differentiate their vegetation and water preferences within and between seasons. I found that both target and non-target hunted species avoided human activities at my study site, suggesting that management activities in the area are perceived as a threat, and that hunting has impacts beyond target species. Finally, I use Structural Equation Modelling to assess the simultaneous effects of prescribed fire on tick abundance, grass volume and large herbivore abundance. My results show that ticks decline in number during the first 12 months after burning, but then rapidly return to previous densities. Burning vegetation has a longer-lasting effect on grasslands, and grass volume only returned to pre-burn levels after three to four years.

My findings highlight the need for conservation managers to monitor the effects of target actions to assess impacts on both focal and non-focal organisms as well as on the health of the wider ecosystem. Here I have presented a tool to monitor the day-to-day condition of the larger wild ungulates of African savanna systems, which could inform management activities (such as relocating animals, provision of additional resource etc) based on real-time, empirical data. I have demonstrated that relatively inexpensive ground surveys can provide consistent, regular indices of the abundance of ungulate species. The role of human activities in altering herbivore use of the landscape indicates how reducing such activity might actually increase savanna ungulate carrying capacity. These findings, along with the more detailed understanding of the role of fires on the vegetation-grazer-parasite system that I present, should aid conservation managers and researchers in conserving such species, under both current and future scenarios.

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1. GENERAL INTRODUCTION

Plains Zebra (*Equus quagga*) | ©Nicolás Fuentes-Allende

1.1. Motivation

Since the emergence of humanity, large herbivores have been an important natural resource for them (Bonavia, 2009). This group of animals, particularly ungulate species, has been the main source of animal protein, wool, hides and many other materials that humans have used to develop their societies. Today, as a group, large herbivores are highly threatened, with a high percentage of them classified as globally endangered (Ripple et al., 2015). Around 58% of large herbivores species have declining populations, and approximately 60% are listed as threatened with extinction (IUCN, 2013). Current declines are mainly caused by human-related threats, particularly human activities related to the unsustainable use or harvest of these species (Turvey and Crees, 2019). Hunting, competition with livestock and habitat loss due to land-use change, human encroachment, agriculture, and deforestation are the main human-related threats to the conservation of large herbivores (Ripple et al., 2015). These lead to increased mortality rates (Radovani et al., 2015) and alter behaviour and local distributions (Stankowich, 2008). Climate change is another important threat for biodiversity conservation worldwide. Although climate change is a naturally occurring process that throughout earth history has caused mass extinction events, e.g. megafauna extinction in South America (Metcalf et al., 2016; Villavicencio et al., 2016), North America (Faith, 2011; Seersholm et al., 2020) and Eurasia (Lister and Stuart, 2008), the current accelerated rate of change is now widely acknowledge to be fuelled by humans and their disproportionate use of natural resources. Through producing shifts and contractions of distribution ranges (Thomas et al., 2004; Borges et al., 2019) and changing species interactions (Cahill et al., 2012), climate change increases extinction risk of species. Current studies predict that extinction rates will increase in the future because of climate change (Urban, 2015; Davidson et al., 2017).

Because large herbivores are crucial to almost all healthy terrestrial ecosystems and human societies (Ripple et al., 2015), humans frequently attempt to manage their populations to assure their sustainable use and effective protection (Gordon et al., 2004). These actions mainly focus on improving survival and reproduction rates, and enhancing their environments through, for example, modifying and protecting feeding sites (Bothma and du Toit, 2016; Weeber et al., 2020). Although these actions aim to benefit the target species, in some cases they could be detrimental to non-target species (Gallo and Pejchar, 2016), and can alter the balance of entire ecosystems (Apollonio et al., 2017; Speed et al., 2019). Managers tend to monitor the effects of their actions based solely on target species, often neglecting possible side-effects on other components of the environment. In this thesis, I focus on studying the effects of management actions, such as prescribed burning of vegetation, hunting, and human activity, on a large herbivore community that inhabits a seasonal and productive environment. My study system is a human-modified arid savanna of southern Africa, in which a highly diverse community of large herbivores are maintained for conservation and economic purposes. My mover-arching study aims are (i) to investigate the potential to monitor ungulates in savanna systems, in terms of both their condition and their populations as a means of improving management recommendations, and (ii) to evaluate the impact of current management activities such as burning to control diseases and improve grass condition, as well as the impact of human presence during the course of such management, on ungulate distributions. With my research, I hope to contribute to the better understanding of the ecology of these animals in managed environments, specially the maintenance of ungulates in African savanna systems where they are an important component of wildlife-based tourism in Africa. In this first chapter, I present and describe a general background to support my research, and then present, and briefly explain, the specific objectives of each of the studies that I present in my subsequent data chapters.

1.2. Background

1.2.1. African savannas

Savanna habitats are typified by a mixture of grassland and scattered trees and can contain species typical of both grassland and woodland biomes (Hirota et al., 2011), and usually dominate the tropics along with forest systems (Higgins and Scheiter, 2012; Aleman, Blarquez and Staver, 2016). They typically comprise a low percentage cover of tall woody plants that are scattered among a grass layer that often contains numerous C-4 species (Bouchenak-Khelladi et al., 2009). Although their dynamics differ between continents (Koerner et al., 2014), savannas are maintained by seasonal fluctuations in precipitation and fire (Sankaran et al., 2005). Seasonally-limited precipitation acts to maintain savanna vegetation (Hirota et al., 2011; Lehmann et al., 2011), with increased precipitation leading to the formation of more continuous woody cover (Sankaran et al., 2005). Fire also operates to limit the coverage of woody vegetation in savannas (Sankaran et al., 2008) and excessively frequent or intense fire can cause savanna to revert to grassland ecosystem (Staver et al., 2011). Herbivory is also important in maintaining savannas, with a similar effect to fire on vegetation, but typically with a lower impact (Staver et al., 2009).

During the late Pleistocene (100K-10K years ago), African savannas occurred extensively in areas with low rainfall and high soil fertility (Owen-Smith, 2013). Increased humidity and declining temperatures during the subsequent Holocene Climate Optimum period (9,000 to 5,000 years ago) led to extended woodlands coverage, often at the expense of savanna habitat (de Vivo and Carmignotto, 2004). In the Late Holocene, which started 2000 years ago, further changes in climate, fire regimes and anthropogenic impacts (Marlon et al., 2008) caused savannas to expand once again (Breman et al., 2012). Currently, savannas cover 20% of the Earth’s land (Lehmann, 2010) and can be classified as either stable or unstable (Sankaran et al., 2005). Stable savannas receive a mean annual precipitation (MAP) between 400 mm (Bucini and Hanan, 2007) and 650 mm (Sankaran et al., 2005), which limits woody encroachment and allows the habitat to persist. Unstable savannas usually occur when MAP is over 650 mm, which would usually promote woody cover (Sankaran et al., 2005). Consequently, in unstable savannas woody encroachment must be held in check by other factors, such as fire and herbivory (Bucini and Hanan, 2007).

Due to continuous climate change (Scholze et al., 2006) and overexploitation of savanna ecosystems (Foley et al., 2005), their stability can be uncertain (Breman et al., 2012). Increases in atmospheric CO_2 during the 20th century are thought to have promoted the encroachment of woody vegetation in South African savannas (Midgley and Bond, 2015). It is predicted that this woody encroachment will continue for the next 200 years, driven by changes in temperature and precipitation (Scholze et al., 2006). In addition, for centuries people have altered savannas and artificially extended their coverage (Bayon et al., 2012; Rohde and Hoffman, 2012) by using them for livestock grazing, crop production (Mbow et al., 2000) and tourism.

1.2.2. Fire in savannas

Fire is one of the most influential abiotic factors shaping vegetation (Bowman et al., 2009), being comparable to herbivory in its impact in some systems (Bond and Keeley, 2005) and being necessary for the maintenance of some ecosystems (Beckage et al., 2009). For example, fire can control woody encroachment and promote the proliferation of fire-tolerant vegetation in savannas (Uys et al., 2004; Ekblom and Gillson, 2010). However, fire can sometimes exceed tolerance thresholds (in either intensity or frequency), even for fire-tolerant species, resulting in detrimental impacts (Zida et al., 2005) and declines in plant diversity (Palmer et al., 2008). Changes in vegetation structure caused by fire have been observed in some savanna systems to last for just a few years before returning to pre-burn conditions (Owens et al., 2002; Sankaran 2005). However, changes in the frequency of fire regimes could have longer-term effects on nitrogen and carbon cycles (Coetsee et al., 2010).

Intrinsic characteristics that have been used to define a fire regime include the size, frequency (occurrence of fire over a time period of interest), intensity (the energy released), seasonality and extent of fires (Bond and Keeley, 2005; Archibald et al., 2013). These characteristics are controlled by factors such as climate, vegetation (biomass, dryness and structure), herbivory (Johnson, 2009) and human activities (Govender et al., 2006; Archibald et al., 2013). Both direct precipitation and moisture contained within vegetation affect the intensity, patchiness (Slocum et al., 2003) and spatial extent (Holdo et al., 2009) of fire regimes. By contrast, herbivores tend to affect fire regimes by changing the availability of fuel loads (Johnson, 2009).

The most important factors determining the extent of savannas are fire frequency and human population (Bucini and Hanan, 2007). People have historically modified savannas fire regimes for their convenience (Bond and Keeley, 2005). African fossil records indicate that increases in savanna cover and changes in fire regimes were related to human occupancy as far back as the Iron Age (Bayon et al., 2012). The main motivation of humans to burn savannas are to limit woody encroachment (Uys et al., 2004), to increase productivity of the grass layer (Sensenig et al., 2010) and to control parasites that affect livestock and humans (Cully, 1999).

1.2.3. Ungulates of the African Savanna

The high diversity of African ungulates that have persisted since the start of the Holocene are thought to have been driven by changes in climate (de Vivo and Carmignotto, 2004) and vegetation (Bouchenak-Khelladi et al., 2009) that increases environment heterogeneity during that period. This diversity is considered to have been maintained by the impact that these species have on the vegetation. The impact of African ungulates on vegetation depends upon their body size (Cumming and Cumming, 2003) and their feeding strategy (Bothma and du Toit, 2016). Ungulates have been shown to increase vegetation heterogeneity (Holdo et al., 2009; Johnson, 2009; Goheen et al., 2010), which generates niche opportunities for other species (Hobbs, 1996; Ripple et al., 2015).

Vegetation heterogeneity and landscape complexity (Venter et al., 2014) allow ungulates with different body sizes and body plans (Illius, 1997), both generalists and specialists (Woolnough and du Toit, 2001; Codron et al., 2007), to coexist with minimum competition (de Iongh et al., 2011). For example, tall trees in savannas allow giraffes *Giraffa camelopardalis* to feed without competing with smaller ungulates (Cameron and du Toit, 2007). When plant diversity declines, interspecific competition between large herbivores increases (de Iongh et al., 2011), leading to reduced vegetation quality (Stähli et al., 2015). By contrast, declining ungulate diversity in savannas can result in changes to vegetation structure (Koerner et al., 2014), as well as changing community interactions (e.g mutualistic and antagonistic interactions between arthropods and plants [Palmer et al., 2008]).

The impact of wild ungulates on livestock (e.g. in terms of food competition and ticks and disease transmission) is somewhat uncertain. Odadi et al. (2011) found that competition occurred only during the dry season. Parasite and disease transmission are not related to livestock-wild ungulate interactions (Cully, 1999; de Garine-Wichatitsky, 2002; Wesonga et al., 2006) and are better explained by vegetation cover (Cully, 1999) and taxonomic kinship (Romero-Castañón et al., 2008; Clifford et al., 2009).

1.2.4. Seasonal variation of body condition in large herbivores

Body condition of large herbivores inhabiting seasonal environments is affected by seasonal variation of resources (Ogutu et al., 2008; Marshal et al., 2012; Herfindal et al., 2014; Kornél and Lanszki, 2017; Lombardini et al., 2017). Variations of precipitation in particular can lead to changes in the availability of water and green vegetation, which are critical resources for large herbivores (Parker et al., 2009). These seasonal cycles of scarcity and abundance of resources can provoke seasonal changes in body mass of individuals. Resource scarcity has been shown to affect reproduction (Green et al., 2017; Newbolt et al., 2017; Peláez et al., 2017), survival (Parker et al., 2009), behaviour (Li, 2013; Brivio et al., 2014), parasite load (Debeffe et al., 2016) and home range size (Ofstad et al., 2016) in mammals. To maximize their fitness, large herbivores inhabiting seasonal environments have adapted to such seasonality by minimizing energy expenditure during periods of scarcity, e.g. only giving birth and mating when resources are abundant (Côté and Festa-Bianchet, 2001; Paoli et al., 2018), or by migrating when resources are scarce (Loarie et al., 2009; Killeen et al., 2014; Debeffe et al., 2017; Barker et al., 2019).

1.2.5. Fire regime effects on ungulate distribution

Fire can also serve to decrease densities of natural enemies of ungulates (e.g. predators [Riginos and Grace, 2008]; ticks [Cully, 1999]) and to increase habitat quality for grazers (Sensenig et al., 2010; Burkepile et al., 2013). Fire can result in lower local predator densities through removing the vegetation cover require for stalking and hunting (Riginos and Grace, 2008). A reduced tick burden can also result from changes in the woody vegetation cover (Gallivan and Horak, 1997). These reductions in ticks can allow ungulates to increase their numbers in more regularly burned environments, as well as their feeding time, because they require less time for grooming (Mooring and Hart, 1995) and vigilance (Burkepile et al., 2013).

Vegetation burning increases forage quality (Burkepile et al., 2013) and feeding opportunities for grazers in particular (Sensenig et al., 2010). For example, recently burned areas often quickly produce flushes of new, tender grass shoots, which attract herbivores to the easily digestible forage (Archibald and Bond, 2004; Sensenig et al., 2010). It can also reduce woody vegetation (Klop and Prins, 2008), which reduces forage, and niche opportunities for browsers (Cromsigt and Olff, 2006). Additionally, although grazers are usually the dominant herbivore in burned areas (Klop and van Goethem, 2008), woody vegetation can improve grazer habitat quality (e.g., grazers have been shown to feed preferentially near isolated trees over totally open areas [Treydte et al., 2011]). Consequently, the frequent burning of savannas can lead to declines in ungulate diversity (du Toit and Cumming, 1999) and changes in the structure and composition of the ungulate community (Klop and van Goethem, 2008).

1.2.6. When humans are perceived as predators

Predation is a strong evolutionary force (Lima and Dill, 1990) that has direct and indirect effects on prey species, at both individual and population levels (Kotler and Holt, 1989). The most direct effect of predators on prey is predation mortality, though indirect effects, such as resultant changes in behaviour and habitat preferences also occur (Brown et al., 1999; Lima and Dill, 1990). At the population level, indirect effects can have greater impact than mortality losses (Kotler and Holt, 1989; Brown and Alkon, 1990), affecting the fitness of survivors (Lima and Dill, 1990), and, thus, the maintenance of populations (Kotler and Holt, 1989). Depending upon the perceived predation risk, prey can reduce foraging (Brown et al., 1999; Benhaiem et al., 2008) and social interactions in order to spend more time performing anti-predator behaviours (Lima and Dill, 1990). Additionally, the risk of being predated influences feeding of prey (Lima and Dill, 1990), such that vegetation quality may not be the key determinant of foraging locality (Laundré et al., 2010). Characteristics of prey (e.g. size, health, sex, age), predators (e.g. speed, size) and the environment (e.g. refuge availability, vegetation), as well as previous experiences with predators influence prey perception of predation risk (Frid and Dill, 2002; Stankowich and Blumstein, 2005).

Irrespective of their activity, humans can be perceived as natural predators (Stankowich, 2008) and hence many animals avoid them (e.g. roe deer *Capreolus capreolus* [Benhaiem et al., 2008]; small and medium-sized carnivores [Grilo et al., 2009]; American black bear *Ursus americanus* [Switalski and Nelson, 2011]; lions *Panthera leo* [Valeix et al., 2012]; wolf *Canis lupus* [Lesmerises et al., 2013]). The “risk-disturbance hypothesis” suggests that animals can perceive human activities with different intensities of fear (Frid and Dill, 2002). Human presence can provoke behavioural changes in individuals, e.g. in feeding activities (Setsaas et al., 2007), anti-predator activities (Donadio and Buskirk, 2006; Malo et al., 2011) and in their local distribution (Setsaas et al., 2007; Benhaiem et al., 2008). At a population and community level, responses can lead to e.g. localised overgrazing (Frid and Dill, 2002), displacement of predators (Leighton et al., 2010) and impacts on sympatric species (Gallo and Pejchar, 2016).

Poaching and hunting activities are the most strongly avoided of human activities for large herbivores. Such human hunting avoidance has been observed in many species including guanaco *Lama guanicoe* and vicuña *Vicugna vicugna* (Donadio and Buskirk, 2006), impala *Aepycerus melampus* (Setsaas et al., 2007) and roe deer (Benhaiem et al., 2008). These activities can provoke even greater predation responses than do natural predators (e.g., red deer *Cervus elaphus*, wild boar *Sus scrofa*, roe deer and European bison *Bison bonasus* in Białowieża Forest, Poland [Theuerkauf and Rouys, 2008]; red deer in Canada [Ciuti et al., 2012]). Compared to hunting, ungulates often perceive tourism as a less threatening activity (Setsaas et al., 2007; Stankowich, 2008). With no human harassment some ungulates can rapidly become habituated to tourist activities (e.g. bison *Bison bison* and elk *Cervus elaphus* in Yellowstone National Park [Borkowski et al., 2006]; guanacos in Argentinian Patagonia [Marino and Johnson, 2012]). Although not reported for ungulates specifically, other types of prey species have been shown to benefit from local human activity because it repels predators (e.g., hawksbill sea turtles *Eretmochelys imbricata* [Leighton et al., 2010]; birds in cities [Møller, 2012]). However, tourism can also be deleterious to prey, by interfering with social interactions (e.g., reproductive events

[Frid and Dill, 2002]) or displacing individuals from feeding sites, as has been shown for mountain gazelle *Gazella gazella* and the Nubian ibex *Capra ibex nubiana* in Saudi Arabia (Wakefield and Attum, 2006).

In summary, large herbivores inhabiting managed arid savannas have to daily deal with natural enemies, seasonal variation of resources and anthropogenic management. These may cause changes to their body condition and spatial distribution, which could, in turn, be detrimental to reproduction and/or survival. In this thesis, I will study large herbivores inhabiting an African savanna system to explore the effects of ticks, seasonality and management itself, with the intention of improving management recommendations to conserve ungulates.

1.3. Chapter objectives

Below, I describe the specific objectives and structure of my thesis. In the thesis, I aim to address some of the gaps in our current understanding of ungulate behaviour and ungulate responses to management activities. Following a review of the literature (summarised above), I identified three key research gaps in relation to ungulate ecology and management in savanna systems: i) firstly, that little information exists relating to how ungulate condition changes across seasons and years, ii) secondly, that there has been limited exploration of the impacts of environmental and human drivers on the local distribution of African ungulates, and iii) finally, that although burning has been explored in terms of its impacts on ungulate distribution in Africa, the potential importance of burning in controlling ticks, as opposed to creating high quality forage, have rarely been explored. These separate studies all have the potential to inform management of such species, and hence to improve the management strategies to conserve these species in the future.

1.3.1. Chapter 1: Introduction Chapter.

This chapter provides an overarching context of the issues associated with ungulate management in savanna systems and a basis upon which the subsequent data chapters build in more detail.

1.3.2. Chapter 2: To monitor the variation of individual body mass in a seasonal environment.

This chapter explores seasonally changing body condition in ungulates utilising a novel technology to automatedly monitor the body mass of identified ungulate individuals during an 18-month period, across dry and wet seasons. In this chapter, I describe the method of monitoring individuals over time. I then relate body mass changes to seasonal variation of precipitation, vegetation productivity and phenological events for both male and female individuals. Monitoring short-term body mass variations within and between seasons may be useful for identifying future threats as well as for identifying potential solutions to deal with them. Today, reducing the impacts of resource scarcity on body mass in seasonal savannas is especially important considering that the current climate change crisis is making these environments drier thus more difficult for large herbivores (Trenberth, 2011; Engelbrecht et al., 2015).

1.3.3. Chapter 3: To identify the effects of resource and human-related drivers on the spatial abundance of a diverse community of large herbivores.

In this chapter, I use spatially explicit models to understand the effects of seasonal variation of resources, anthropogenic activities and human infrastructure on the spatial abundance of large herbivores that inhabit a managed arid savanna. I map the spatial abundance of different species within the study area, and explore the specific effects on abundance of vegetation type, water availability, burn-age, road traffic, and distance to roads and perimeter fence. I then discuss how seasonality, availability of resources and avoidance of humans shape the local distribution of individuals in managed lands, and question whether these effects are generalized among species. Finally, I discuss whether avoidance provoked by management actions is detrimental for management goals.

1.3.4. Chapter 4: To assess the effectiveness of burning vegetation for controlling ticks and its simultaneous impacts on hosts and habitat.

In this chapter, I assess the effectiveness of prescribed fire for controlling ticks in the environment from an ecosystem-level perspective. Using information on tick abundance, ungulate densities, vegetation structure and precipitation, I build path diagram models to identify impacts of burning on parasites, their hosts and habitat, and characterize effects by type, size and temporal extent of burn regimes. I then discuss the effectiveness of prescribed fire for controlling ticks in the environment. Additionally, considering the simultaneous effects of burning on tick hosts and their habitat, I discuss the role of burning for controlling parasites in arid savannas. I provide recommendations on how to improve tick control in savannas, whilst reducing undesirable effects on other components of the ecosystem.

1.3.5. Chapter 5: Discussion chapter.

In the final chapter of the thesis, I draw together the findings across all of my data chapters to provide an overarching summary of the contributions of the thesis to better understanding the ecology and management of ungulate species in savanna systems. I finish by discussing the potential for future research that could address outstanding issues that remain in our understanding of African ungulates, and highlight future research that could further develop the current work.

2. SEASONAL VARIATIONS OF BODY MASS IN ARID SAVANNA BOVIDS

Greater Kudu (*Tragelaphus strepsiceros*) | ©Nicolás Fuentes-Allende

2.1. Abstract

Large herbivores inhabiting seasonal environments often experience variations in body mass due to temporal changes in the availability of critical resources like water and green vegetation. Yet the role of seasonal resource variation on body mass of mammals of savanna habitats, which host the largest densities of grazing ungulates globally, has rarely been explored. To explore seasonal variation in mass, I used mineral baited cattle scales and camera traps to automatedly track the body mass of adult individuals from three bovid species through a period incorporating both wet and dry seasons in a South African savanna ecosystem. This novel approach allowed us to explore mass changes daily in relation to time, weather and resource availability. I found that, as expected, all species increased their body mass, by around 5-10%, during the wet season and lost mass, by around 5-12%, during the dry season. These changes were positively related to vegetation productivity (assessed using NDVI) and frequency of rains. This weighing approach resulted to increase and facilitate data acquisition, making the method easier to deploy concurrently over large areas, and being suitable for a wide range of ungulate species. Considering current climate change is resulting in longer and harsher dry seasons in such arid systems, tracking short-term variations of body mass may help managers and authorities to identify body mass reductions more rapidly, thus being better informed to prevent excess mortality during unfavourable periods.

2.2. Introduction

Animals inhabiting seasonal environments have to deal with regular changes in weather conditions, often associated with pulses of resource availability and sparsity. Seasonal variations of precipitation in particular can lead to changes in the availability of water and green vegetation, which are critical resources for large herbivores (Parker et al., 2009). Savanna ecosystems, which are typified by a hot, wet season and a cooler, dry season are a common biome in subtropical regions. Seasonal water scarcity results in extensive grasslands with scattered trees, supporting very high densities of grazing herbivores. To deal with resource scarcity and maximize their fitness, large herbivores inhabiting these environments have adapted to such seasonality by minimizing energy expenditure, e.g.

giving birth and mating when resources are abundant (Côté and Festa-Bianchet, 2001; Paoli et al., 2018), and migrating when resources are scarce (Loarie et al., 2009; Killeen et al., 2014; Debeffe et al., 2017; Barker et al., 2019).

In general, body mass varies according to availability of resources (Kornél and Lanszki, 2017), impacting the daily routine of individuals. For example, energy availability has been shown to affect reproduction (Green et al., 2017; Newbolt et al., 2017; Peláez et al., 2017), survival (Parker et al., 2009), behaviour (Li, 2013; Brivio et al., 2014), parasite load (Debeffe et al., 2016) and home range (Ofstad et al., 2016) of mammals. Despite the importance of the nutritional state of large herbivores for individual fitness (Parker et al., 2009; Luna et al., 2013; Festa-Bianchet et al., 2019), short-term body mass variation in wild animals inhabiting seasonal environments has been little studied. Studies that have explored these issues have focussed on monitoring body growth (e.g. Decristophoris et al., 2007; Bergeron et al., 2010; Brambilla et al., 2018), long-term changes in body size (Martin et al., 2018), and temporal variation during reproduction (Therrien et al., 2007). Seasonal changes of body mass have been monitored using data from hunted individuals (hence, non-repeated measures on individuals: Flores-Saavedra et al., 2018; Risco et al., 2018) and from limited capturing and weighing of live animals (which can only occur infrequently, in wild populations: Newbolt et al., 2017; Lemaître et al., 2018). However, such studies are rarely successful (never in terms of hunted animals) in describing the seasonal, short-term changes of body mass taking into account individual heterogeneity, because they usually cannot measure the same individuals through time at short-term intervals.

In order to assess the effect of seasonality on the temporal variation of body mass in large herbivores, I focus on adult individuals from three bovid species that co-occur in many of the savannas of sub-Saharan Africa; these being blue wildebeest *Connochaetes taurinus*, greater kudu *Tragelaphus strepsiceros* and red hartebeest *Alcelaphus buselaphus*. I used cattle scales (Bassano et al., 2003), baited with a mineral lick, to weigh individual animals in a South African wildlife reserve between April 2017 and October 2018. A similar method has been previously applied to temperate and temperate-montane species, including alpine ibex *Capra ibex* (e.g. Decristophoris et al., 2007; Bergeron et al., 2010; Brambilla et al., 2018), bighorn sheep *Ovis canadensis* (e.g. Pelletier and Festa-Bianchet, 2004; Moquin et al., 2010; Festa-Bianchet et al., 2019), mountain goat *Oreamnos americanus* (e.g. Mainguy et al., 2009; Godde et al., 2015; Castro et al., 2018), and white-tailed deer *Odocoileus virginianus* (Therrien et al., 2007). Camera traps were used to identify individuals and to follow their body mass changes throughout the time. I hypothesized that body mass would vary seasonally, being positively related to changing availability of forage and water. Finally, I discuss about the importance of monitoring these variations in seasonal environments within the context of the current climate change crisis (Trenberth, 2011).

2.3. Materials and Methods

2.3.1. Study Site

The research was conducted at Mankwe Wildlife Reserve (MWR; 25°13’39’’S 27°17’50’’E), a 3,875 ha private reserve located in the South African arid savanna. The reserve supports 18 ungulate species, which are principally managed for conservation and research purposes. However, being a relatively small reserve that lacks lions (*Panthera leo*), the only major predator of the larger ungulates, some hunting and capturing of ungulates for sale takes place to maintain populations within estimated carrying capacity limits (Table A2.1). The largest predators present [leopard (*Panthera pardus*) [rare], caracal (*Caracal caracal*), serval (*Leptailurus serval*) and brown hyaena (*Parahyaena brunnea*)] take relatively low numbers of the smaller ungulate species. Ungulates are mainly hunted in the dry season, between May and end of September, with males targeted more often than females. During this period, animals are also sold to other game ranches. A 3 m electrified perimeter fence around the site restricts ungulate movements in and out of the reserve. The reserve is mainly comprised of savanna grasslands, which covers 83% of its surface. The remainder of the reserve is made up of woodland, thicket, and seasonal water bodies, along with two permanent water bodies and several smaller artificial water points. Rains typically concentrate during the wet season that occurs from the beginning of October to the middle of the following May, after which little or no rains falls until the following October. For example, rainfall data from

MWR indicate that the dry season extended from the 15th of May to the 4th of October in 2017, and from the 15th of May to the 30th of September in 2018 (Figure 2.1a). This weather regime promotes changes in vegetation, which reaches its highest and lowest greenery peaks during wet and dry seasons respectively (Figure 2.1b).

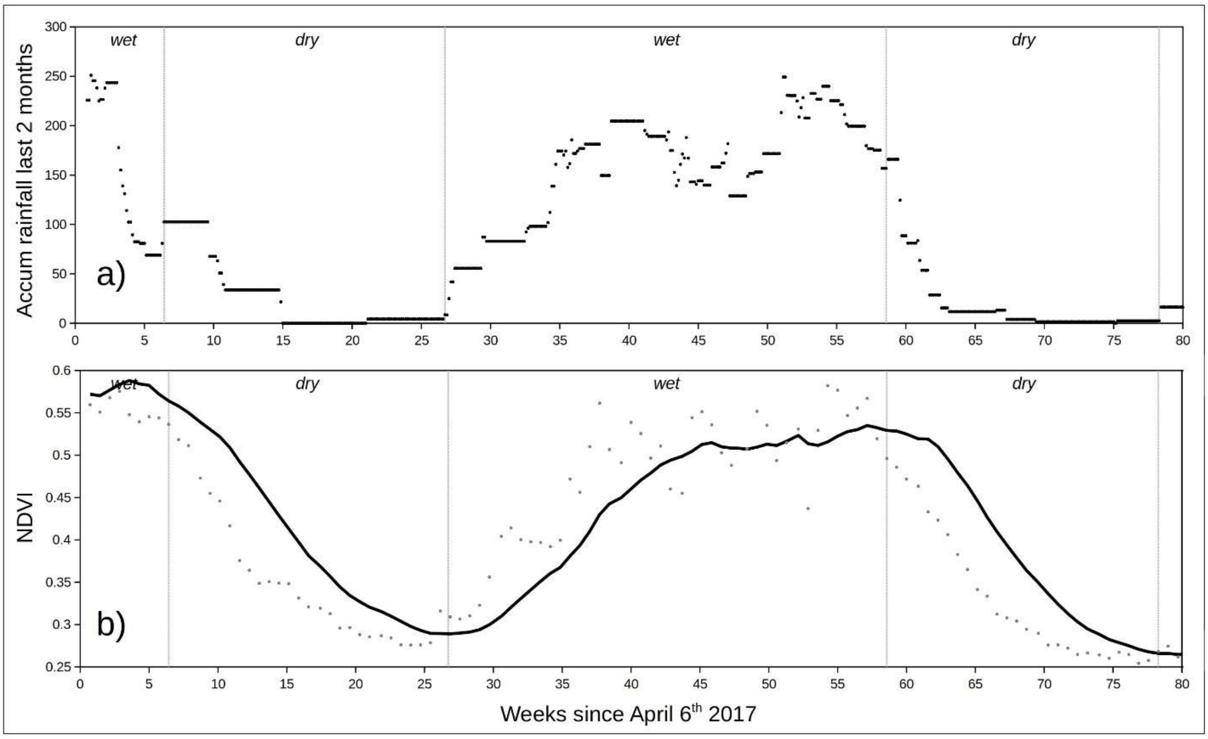


Figure 2.1. a) Accumulated rainfall over the study period, where black dots represent daily accumulated rainfall considering last 60 days. b) Mean grassland NDVI at MWR, where grey dots represent NDVI from previous five days, and black line represents the average NDVI considering last 60 days (Santangeli et al., 2018). Vertical grey dotted lines represent starts/ends of wet and dry seasons (defined as when precipitation events increase and reduce their occurrence).

2.3.2. Body mass and environmental data collection

Body mass data (kg) were collected between April 6th 2017 to October 8th 2018 at MWR, using two cattle weighing scales (± 0.5 kg) that were deployed close to artificial ponds where animals had access to drinking water throughout the year (Figure 2.2b). The setup comprised a 50 kg salt block to attract animals, a 1.5 x 1.5 m^2 metal platform scale (3-Ton Platform Scale LMI Ltd, http://www.lmi.co.za/wordpress/) with a reader (LS4F Readout Instrument LMI Ltd) that displayed the body mass of individuals standing on the platform, and a camera trap (Reconyx Hyperfire HC500) that captured photographs of animals along with their mass reading when using the scales (Figure 2.2a). Although animals were not tagged, most individuals were easily identified, during both day and night by unique patterns in horn shape and hair length, and by scars on their face, ears, neck, legs, and feet (Figure 2.2c). For individuals that could be uniquely identified, the mean body mass per week was calculated as the average of all daily mass readings from that individual. If the body mass was recorded more than once within a day, the average mass for that day was used. Only those individuals considered adults (Silva and Downing, 1995; Wilson and Mittermeier, 2011; Castelló et al., 2016), and those using the scale for a minimum period of three months, and with at least two weeks of readings within a season were included in the study.

Normalized Difference of Vegetation Index (NDVI) was used as a proxy of availability of high-quality forage (NDVI provides a measure of photosynthetic activity, derived from satellite sensors; Pettorelli et al., 2005). One hundred and nine images were downloaded to cover the entire study period, obtained from the AQUA sensor eMODIS NDVI V6 (United States Geological Survey; https://earthexplorer.usgs.gov/). Every five days, this satellite generates composite images with a spatial resolution of 250 m. As animals can forage across the entire reserve, I calculated the mean NDVI for grassland areas across the entire site. Only one image was discarded (21st February 2018) because more than 50% of the pixels with grassland were corrupted by atmospheric conditions (Agapiou et al., 2011). Animal measurements were assigned to the closest image, in temporal terms, that was captured before a weighing event. Mean NDVI for last 30 and 60 days prior to a body mass reading, defined as NDVI30 and NDVI60 respectively, were calculated (Santangeli et al., 2018), by averaging NDVI across all the images within the relevant period before a weighing event.

Accumulated rainfall for last 30 and 60 days prior to a weighing event, defined as RAIN30 and RAIN60 respectively, and frequency of rainy events (number of days with precipitations) during last 30 and 60 days, defined as FRAIN30 and FRAIN60, were used as indices of water availability (Ogutu et al., 2008; Santangeli et al., 2018). Daily rainfall (accuracy of +/1 mm per day) in the study area was obtained by averaging readings from five rain gauges deployed across the reserve. Then, these daily averaged readings were used to calculate accumulated values for the 30 and 60 days preceding each mass reading.

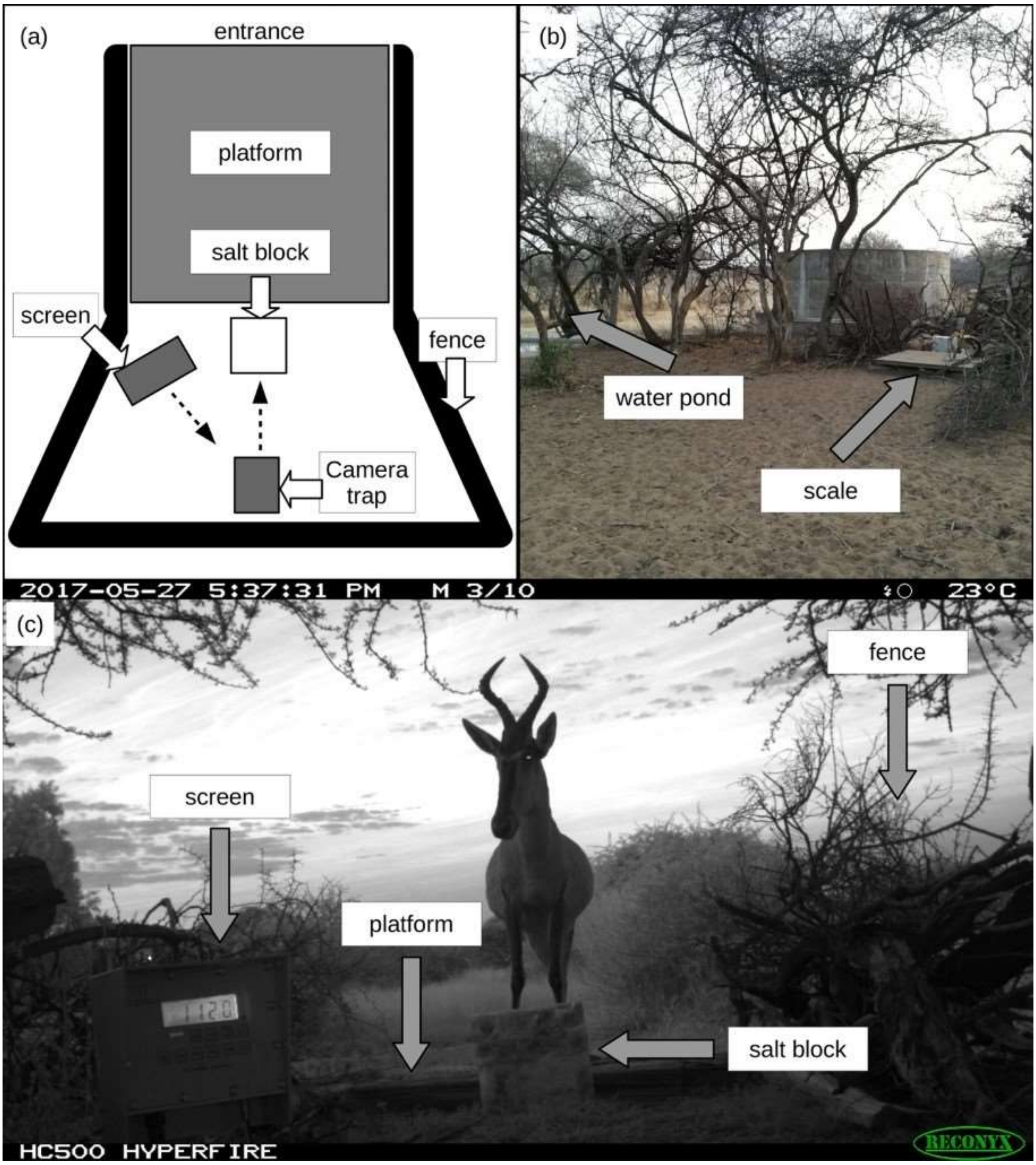


Figure 2.2. Body mass stations. a) Representation of the set-up from an aerial view, b) Location of one of the two scales next to an artificial pond, and c) Example mass reading of a female red hartebeest that was attracted to the scale.

2.3.3. Data Analysis

Hierarchical Generalized Additive Models (HGAMs, Pedersen et al., 2019) were used to explore weekly mass fluctuations in relation to date, NDVI, and water availability, for each analysed group. Groups were composed of uniquely indentifiable individuals of the same species and sex. Body mass was analysed as weekly relative body mass divided by mean body mass of the group. Hence, individual with a relative mass <1 weighed less than the mean of the group, those with a relative mass =1 had a mass equal to the group mean, and relative mass of >1 identified individuals heavier than the group mean. Individual identification was used as random intercepts to control for variability among individuals. Date was included in models as *weeks since April 6th 2017* (running from 1 to 79 weeks). HGAMs included penalized thin-plate regression splines as smooth terms (Wood, 2003) for date, availability of fresh forage (weekly mean NDVI, and NDVI30 and NDVI60) and water availability (RAIN30, RAIN60, FRAIN30, FRAIN60).

Models that included >1 smoother presented issues of concurvity (non-linear collinearity Hastie and Tibshirani, 1990; >0.5 Ramsay et al., 2003) which may bias predictions (Dominici et al., 2002). All models assumed a Gaussian distribution with identity link functions, and the smoothing selection was defined by marginal likelihood (Wood, 2011; Wood, 2017). The quality of models was checked using basis dimension assessments (BDAs; Wood, 2017), and visually inspecting plots of residuals, and plots of observed vs fitted values.

Two models were selected per group: (i) one with a smoother for date, to explore temporal variation, and (ii) one with a smoother for availability of resources (fresh forage and water). I used Akaike Information Criterion (AIC; Akaike, 1974) to rank models; all models with ΔAIC ≤2 of the top model were considered equivalent (Burnham and Anderson, 2002). Of these, the model with highest explained deviance was selected to assess the effect of availability of resources on body mass.

All analyses were performed using R version 3.5.2 (R Core Team, 2018), and the package ‘mgcv’ (Wood, 2019). Satellite images were processed using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

2.4. Results

Over the study period, 3,700 body mass records were registered (Figure 2.3). Species captured comprised: blue wildebeest (n = 435), Cape eland (*Taurotragus oryx*; n = 69), common reedbuck (*Redunca arundinum*; n = 1), common warthog (*Phacochoerus africanus*; n = 26), gemsbok (*Oryx gazella*; n = 160), giraffe (*Giraffa camelopardalis*; n = 4), greater kudu (n = 2,383), impala (n = 115), red hartebeest (n = 503) and white rhinoceros (*Ceratotherium simum*; n = 4). From those, 1838 records could be allocated to 58 individuals comprising: adult blue wildebeest (n = 6 females, 1 male), greater kudu (n = 29 females, 11 males) and red hartebeest (n = 10 females, 1 male) that used the scale between two and 38 weeks (mean number of recordings per individual = 31.69±27.74). Discarded data corresponded to records from either unmatured or individually unidentified individuals.

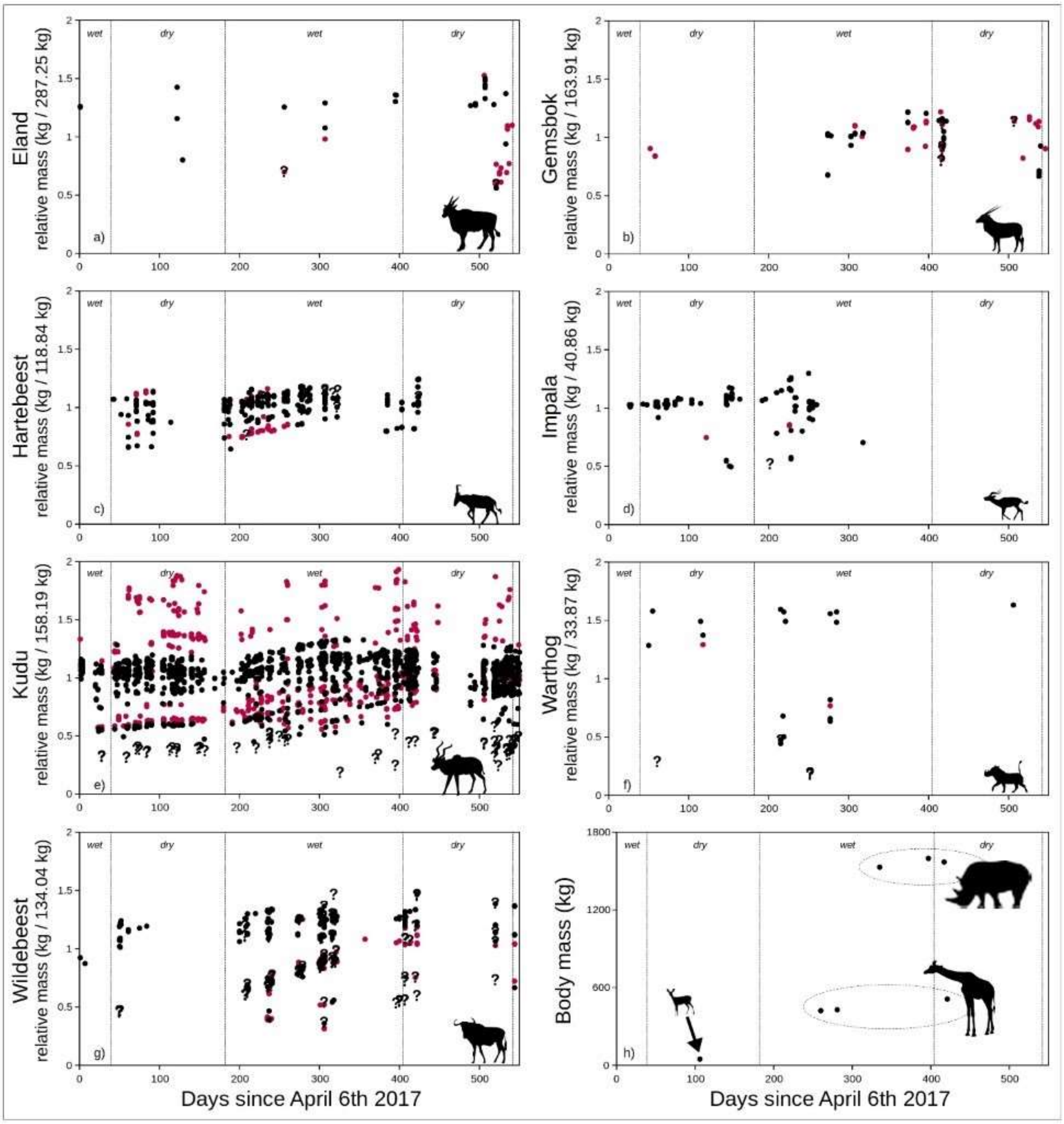


Figure 2.3. Total records of relative body mass in relation to the mean body mass of the species, where a) shows data for eland, b) gemsbok, c) hartebeest, d) impala, e) kudu, f) warthog, g) wildebeest, and h) shows specific body mass records for giraffe (n = 4), reedbuck (n = 1) and rhino (n = 4). Black dots represent records from females, red dots records from males, and "question marks" represent records from "unidentified sex" individuals. Vertical grey lines represent starts/ends of wet and dry seasons.

Averaging records from the same individuals for individual weeks resulted in a dataset of 609 weekly body masses for further analysis (Table 2.1, Figure 2.4). Male blue wildebeest and male red hartebeest were discarded from the analysis as only one individual per species used the scale for more than three months. Data included in the analysis corresponded to 40 weekly records of female blue wildebeest (from week 7 to 61), 389 weekly records of female greater kudu (from week 1 to 79), 96 weekly records of female red hartebeest (from week 10 to 61), and 70 weekly records of male greater kudu (from week 7 to 79).

Table 2.1. Summary of body mass records. (F) and (M) refer to females and males respectively. Ave ± SD refers to Mean ± Standard Deviation. "Individuals recorded / included" refers to total individuals that were identified using the scale for more than one week during the study period / individuals that complied with minimum requirements for being included in the analysis. "Data recorded / included" refers to total observations of individuals recorded and individuals that were included in the analysis.

Group	Individuals recorded / included	Data recorded / included	Range body mass (kg)	Ave ± SD body mass (kg)	Ave ± SD weeks per individual
Blue Wildebeest (F)	15 / 6	66 / 40	143.7 – 196.5	168.8 ± 11	6.7 ± 3.1
Greater Kudu (F)	49 / 29	448 / 389	121.8 – 209.9	166.3 ± 17.4	13.4 ± 8.3
Greater Kudu (M)	12 / 11	74 / 70	192.8 – 296.1	238.8 ± 29.9	6.4 ± 4.1
Red Hartebeest (F)	15 / 10	109 / 96	101.3 – 148	122.9 ± 9.8	9.6 ± 4.7

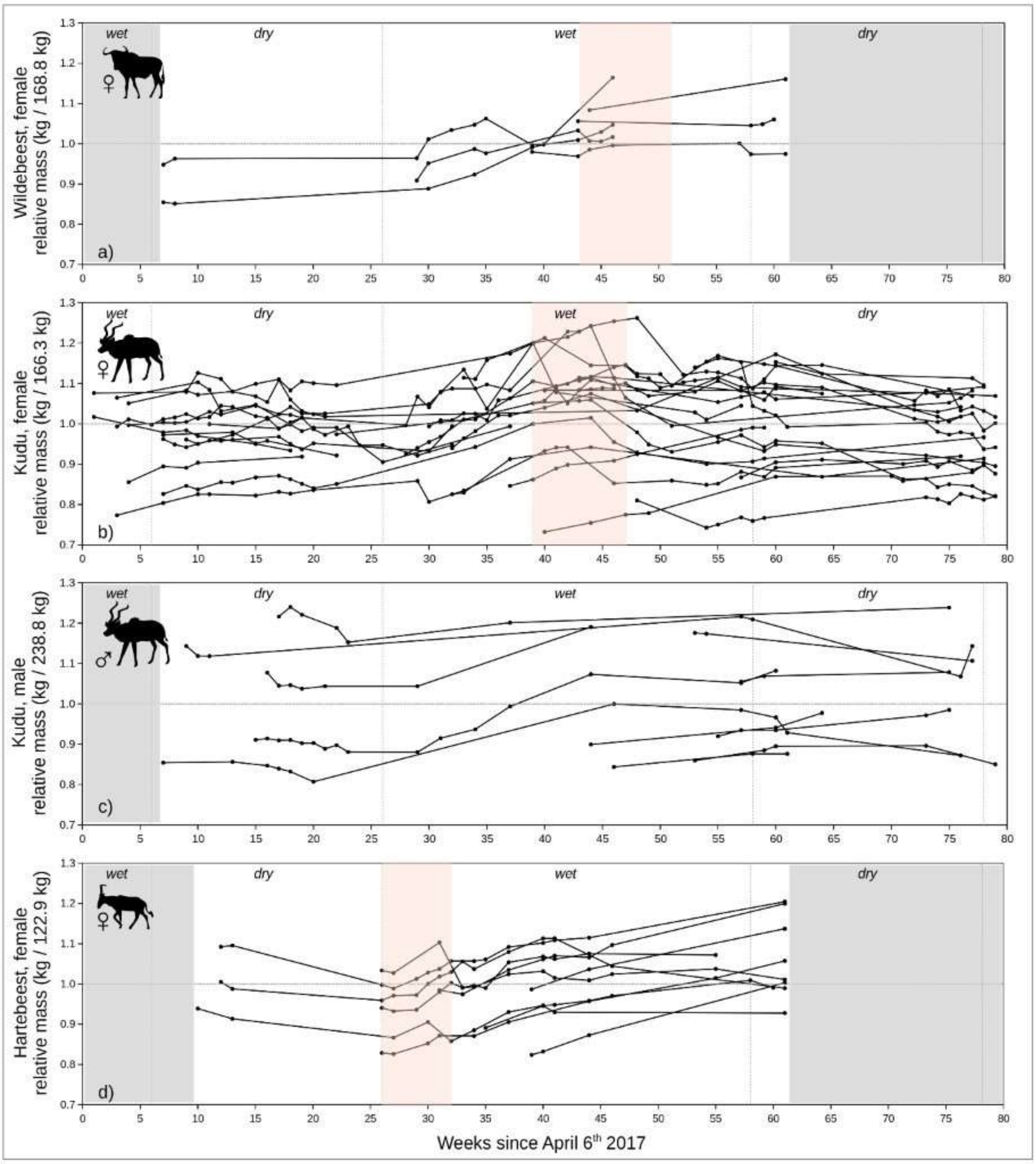


Figure 2.4. Fluctuations of the relative body mass in relation to the mean body mass of the group, where a) shows female blue wildebeest, b) female greater kudu, c) male greater kudu, and d) female red hartebeest. Black dots and lines to distinguish individual trends. Vertical grey lines represent starts/ends of wet and dry seasons, and horizontal grey lines represent the group mean. Grey areas visualize weeks beyond the first and

last records for each group. Peach areas visualize when calving peaks typically occurs for each species (Spinage, 1973; Estes, 1976; Nowak 1997; Perrin, 1999).

All models including a smoother for date were significant (Table A2.2 to Table A2.5), had the lowest AIC within their groups (Table 2.2), and predicted an increment on body mass during the wet season in relation to the mean body mass of their groups (Figure 2.5). Although animals started to gain weight just after the beginning of the rainy season, each species varied in terms of which date the peak of weight gain was reached. In terms of the role of resource availability, models containing NDVI60 (female blue wildebeest, greater kudu and red hartebeest) and FRAIN60 (male greater kudu) performed best at predicting body mass (Table 2.2; Table A2.2 to Table A2.5).

Table 2.2. Models fitted per groups. Models are organized from lowest to highest AIC. Bold text indicates the two selected models per group. "Predictor" indicates smoother included in the model, "DE" is deviance explained, "edf" is effective degrees of freedom, and "ΔAIC" is the difference with model of lowest AIC. Grey rows indicate models with a smoother that did not passed the basis dimension assessments (BDAs), therefore were not considered for analysis.

Group	Predictors	DE(%)	edf	Δ AIC
Blue Wildebeest (F)	**s(week)**	**83.1**	**3.01**	**0.00**
	s(NDVI60)	**85.1**	**5.96**	**0.00**
	s(FRAIN30)	54.8	1	33.59
	s(ndvi 5 days)	57.9	3.62	36.97
	s(RAIN60)	49.9	1	37.68
	s(NDVI30)	52.4	2.17	38.61
	s(RAIN30)	46.6	1	40.15
	s(FRAIN60)	43.5	1	42.30
Greater Kudu (F)	**s(week)**	**85.2**	**8.09**	**0.00**
	s(RAIN60)	did not passed BDAs		
	s(NDVI60)	**80.8**	**4.24**	**21.11**
	s(NDVI30)	80.6	4.95	27.87
	s(FRAIN60)	79.2	1	43.46
	s(ndvi 5 days)	79.6	3.23	43.90
	s(RAIN30)	77.7	2.49	75.97
	s(FRAIN30)	77.1	1	81.30
Greater Kudu (M)	**s(week)**	**95.9**	**6.03**	**0.00**
	s(NDVI30)	did not passed BDAs		
	s(ndvi 5 days)	did not passed BDAs		
	s(NDVI60)	did not passed BDAs		
	s(FRAIN60)	**88**	**1**	**6.50**
	s(RAIN60)	87.9	1	7.43
	s(FRAIN30)	85.7	1	19.09
	s(RAIN30)	85.2	1	21.40
Red Hartebeest (F)	**s(week)**	**80.8**	**3.86**	**0.00**
	s(NDVI60)	**77.7**	**1**	**0.00**
	s(NDVI30)	76.8	1	3.87
	s(ndvi 5 days)	77.5	4.78	10.80
	s(RAIN30)	70.4	6.84	40.02
	s(FRAIN30)	64.4	4.93	54.79
	s(RAIN60)	58.7	1	58.59
	s(FRAIN60)	58.2	1	59.74

2.4.1. Blue wildebeest

The model predicted female Blue Wildebeest to gain 6.75 ± 5.06 kg, on average, during the entire dry season in 2017 (from the 20th of May to end of September, 19 weeks), compared to 15.19 ± 5.06 kg during the first 15 weeks of the following wet season (from the beginning of October to mid-January 2018). After which, animals maintained their weight without variation until the end of the rainy season. It was not possible to model mass changes for the 2018 dry season as no wildebeest used the scales during that period (Figure 2.5a).

There was a positive relationship between body mass and NDVI60 (Figure 2.5b). The top candidate model predicted mass increases of 20.26 kg ± 3.38 kg as mean NDVI increased from 0.294 to 0.514. However, on average, animals lost up to 14% of their body weight (25.32 ± 5.06 kg) when mean NDVI increased from 0.514 to 0.55.

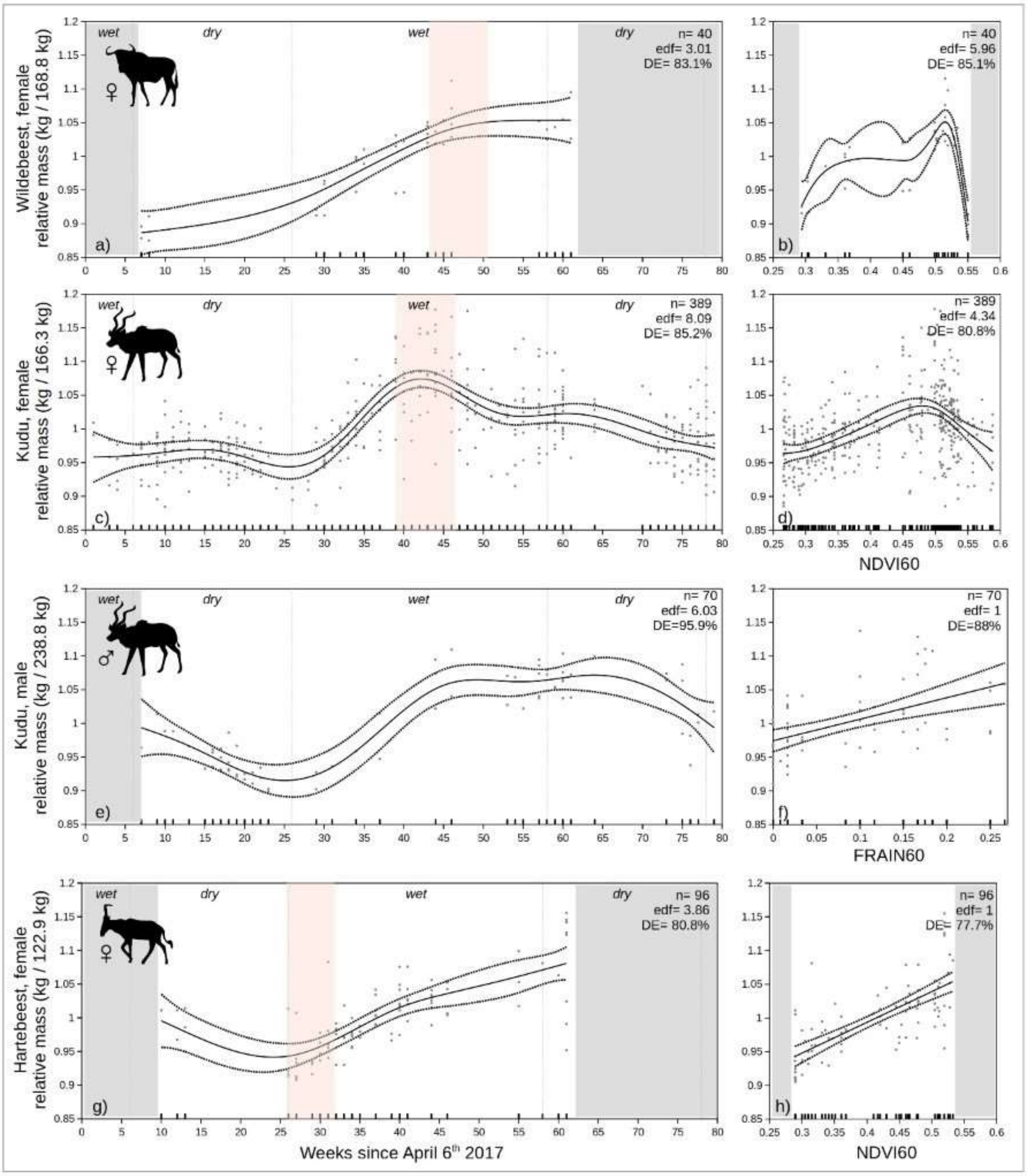


Figure 2.5. Modelled fluctuations of relative body mass over the study period, where a-b) shows fitted curves for female blue wildebeest, c-d) female greater kudu, e-f) male greater kudu, and g-h) female red hartebeest. Plots a), c), e) and g) show predictions for temporal trends, plots b), d) and h) predictions for NDVI60, and plot f) FRAIN60. Black continuous lines indicate fitted curves, black dotted lines are standard errors, grey dots are Pearson residuals, black marks at x axis indicate the x-location of residuals, and

vertical grey lines represent starts/ends of wet and dry seasons. Grey areas visualize weeks beyond the first and last records for each group. Red areas visualize when calving peaks typically occurs for each species (Spinage, 1973; Estes, 1976; Nowak 1997; Perrin, 1999).

2.4.2. Greater kudu (females)

Female kudu gained body mass during the wet season and lost mass during dry seasons (Figure 2.5c). In 2017, they maintained their body mass without variation from the beginning of the dry season (mid-May) to mid-July, after which body mass tended to decline. By the end of that season animals lost, on average, 4.99 ± 3.33 kg (end of September, 11 weeks). During the following wet season, they initially increased their body mass in 21.62 ± 3.33 kg from the beginning of October to mid-January 2018 (15 weeks), then lost around 8.32 ±1.66 kg during the next 12 weeks (beginning of April), and ended the season with a stable body mass from April to mid-May. During the 2018 dry season, body mass losses from mid-June to the end of September (16 weeks) were in the order of 8.32 ± 3.33 kg.

Despite seasonal fluctuation of body mass, animals increased mean mass between the beginning of the dry seasons of 2017 to 2018. Model predicted animals were 9.99 ± 1.66 kg heavier at the beginning of the dry season in 2018 compared to 2017, and 4.99 ± 3.33 kg heavier at the beginning of the wet season in 2018 compared to 2017.

There was a positive relationship between body mass and NDVI60 (Figure 2.5d). Model predicted increases of 11.64 kg ± 1.66 kg when average NDVI increased from 0.266 to 0.478. Similarly to blue wildebeest, animals experienced losses (11.64 ± 4.99 kg) when average NDVI was particularly high (from 0.478 to 0.589).

2.4.3. Greater kudu (male)

Males kudu experienced fluctuating body mass during the study period (Figure 2.5e). During the 2017 dry season, body mass reductions were continuous from the beginning to the end of the season, with mean mass loss per individual of 19.1 ± 4.78 kg in 19 weeks. Then, individuals increased their body mass by 26.27 ± 4.78 kg during the first 15 weeks of the following wet season (from the beginning of October to mid-January 2018). After that, animals maintained their mass without variation until the third month of the dry season in 2018 (mid-July), following which individuals experienced, on average, mass loss of 16.72 ± 7.16 kg over a 13-week period (end of September).

Despite seasonal fluctuation of body mass, on average kudu bulls increased mean mass from 2017 to 2018. Model predicted they were 16.72 ± 9.55 kg heavier at the beginning of the dry season in 2018 than 2017, and 19.1 ± 4.78 kg heavier at the beginning of the wet season in 2018 than 2017.

In male kudu, there was a positive linear relationship between body mass and FRAIN60 (Figure 2.5f). Model predicted a mean mass difference of 21.49 kg ± 7.16 kg when comparing readings from a period with no precipitations with one where individuals were exposed to 16 days with precipitations (FRAIN60 =0.27).

2.4.4. Red Hartebeest

During the 2017 dry season, on average females experienced a steady loss of body mass from the beginning to the end of the season, totalling 6.15 ± 2.46 kg over 16 weeks. During the following wet season, they increased body mass from the beginning to end of the season, gaining 15.98 ± 1.23 kg in 32 weeks. It was not possible to fit mass change curves for the 2018 dry season because there were no records of Hartebeest on the scales during that period (Figure 2.5g).

Regarding availability of resources, there was a positive linear relationship between body mass and NDVI60 (Figure 2.5h). Model predicted increases of 13.52 kg ± 1.23 kg when NDVI increased from 0.289 to 0.532.

2.5. Discussion

This study presented temporal variation of body mass in three arid savanna ungulates that were exposed to same changes in resource availability over an 18-month period. This highlights that this approach, previously only applied to temperate systems, and usually without remote data collection, can be applied to sub-tropical savanna systems to monitor the diverse community of ungulates that coexists there (e.g. from warthog piglets [6 kg] to adult white rhino [1598 kg]). Despite a similar method having been previously applied to temperate and temperate montane species (Bassano et al., 2003), mine is the first study, to my knowledge, that has focused on analysing the short-term variations of body masses in African ungulates that inhabits the seasonal tropics. Additionally, this is the first time that camera traps have been used to automate the data recording process, increasing the opportunities for data recording during periods when an observer may influence the data collection or cannot be present (e.g. at night, in harsh or remote environments or during unfavourable weather conditions), allowing the continuous monitoring of the body mass of individuals, and making the method easier to deploy concurrently over large areas. Considering the high number of threatened large herbivores in Africa (Ripple et al., 2015), the relevance of this group for ecosystems and societies (du Toit and Cumming, 1999), and the current projected climate changes in the region (Baker et al., 2015), such an evaluation of environmental impacts on condition is timely.

2.5.1. Seasonal changes in body mass

All species experienced changes in body mass throughout the year, with mass declining during dry seasons and increasing during wet season, as predicted. Although there are studies assessing seasonal changes in body mass of ungulates (e.g. effect of temperature on body mass of moose *Alces alces* in Norway van Beest and Milner, 2013; long-term body mass decline of Alpine chamois *Rupicapra rupicapra* in Italy Mason et al., 2014; long-term seasonal changes of bighorn sheep body mass in Canada, Douhard et al., 2018; associations between winter mortality and body mass of white-tailed deer in USA, Kautz et al., 2019), there are no studies to date describing seasonal effects on temporally finely resolved changes in body mass of African ungulates. Regarding African species, very few studies exist on mass changes in small and medium sized mammals (the only ones I could locate being for Madagascan rousette *Rousettus madagascariensis* [50-70 g] Goodman et al., 2017; and Egyptian mongoose *Herpestes ichneumon* [1.8-1.9 kg] Bandeira et al., 2019). Despite these studies being on a frugivore and omnivore respectively, their findings tend to match with the patterns of mass change that I report here. Individuals reached their minimum body mass at the end of the dry season, when availability of high-nutritious green vegetation also reached their minimum (Figure 2.1b). In my study system I typically recorded losses of 3% to 8% of body mass loss during the harsher dry season. These losses were considerably lower than the typical 15 to 30% losses in body mass measured in ungulates inhabiting other seasonal environments, e.g. montane environments (Japanese Serow *Capricornis crispus*, Miura and Maruyama, 1986; mountain goat Festa-Bianchet and Côté, 2008), arctic environments (black-tailed deer *Odocoileus hemionus sitkensis*, Parker et al., 1993; barren-ground caribou *Rangifer tarandus granti*, Allaye Chan-McLeod et al., 1999). Considering the climatic stochasticity of African savannas, where episodic extreme droughts can cause mass mortality (Veldhuis et al., 2019), a temporally longer monitoring program is needed to determine whether the mass changes reported here are representative for these dryland systems. Animals may lose weight during unfavourable seasons in response to resisting harsh weather conditions (Lesage et al., 2001; Chang and Wiebe, 2016; Bonardi et al., 2017) when there is high scarcity of resources in the environment, thus requiring more calories to be burned than acquired (Young and Van Aarde, 2010; Wato et al., 2016). Unfortunately, this study cannot quantify whether the reduced mass losses at my study area (compared to e.g. ungulates of arctic or montane environment) were triggered by less harsh weather conditions or less scarce resources. One factor confounding such a generalisation is the fact that, at the study site, animals were likely also influenced by the anthropogenic control of ungulate density (via the hunting and sale of animals) that maintained populations below their carrying capacity on the reserve (Ogutu et al., 2012; Bonardi et al., 2017; Delciellos et al., 2018).

Female red hartebeest was the only group that continuously gained body mass during the wet season. In South Africa, this species gives birth at the beginning of the wet season

(October-November Spinage, 1973; Nowak 1997), when body mass has been deeply affected by the resource scarcity from the previous dry season. Despite the confounding negative effect of reproduction and resource scarcity on body mass, which makes difficult to assess their individual impacts on body mass, body mass gains during the first part of the wet season may be constrained by energy expenditure for maternal care. Female blue wildebeest and female greater kudu did not have a continuous increase of body mass during the wet season, which may also be explained by reproductive events. The timing and temporal extent of these losses match with when these species are calving (Spinage, 1973; Estes, 1976; Owen-Smith, 1993; Perrin, 1999) and intensively provisioning milk to their offspring in Southern Africa (intensive lactation occurs up to six to 10 weeks after birth, Kingdon and Hoffmann, 2013). Considering that, calving and maternal care may also explain the declines in body mass that both groups experienced when NDVI60 was at its highest values. This, in turn, is suggestive of the species timing their calving to coincide with peak foraging conditions. Mass loss during the wet season may be associated with physiological costs of reproduction (Borowske et al., 2018; Ayotte et al., 2019; Festa-Bianchet et al., 2019), because in seasonal environments animals tend to give birth at the beginning or during the favourable season (Berkeley and Linklater, 2010; Ogutu et al., 2013; Ogutu et al., 2015; Cucco and Bowman, 2018), and they continue losing weight because of maternal care (Ayotte et al., 2019).

Despite seasonal changes in body mass, models predicted that both females and males of greater kudu became heavier in the period from 2017 to 2018. This may, in part, be driven by natural maturity of individuals or may represent a genuine improvement in condition of individuals between those years. It is important to highlight that these findings portray body mass changes that individuals experienced during those 18 months of data collection, and a longer period of study is needed to elucidate long-term trends. Studies on other ungulates have demonstrated continued mass gain from birth to senescence, [e.g. bighorn sheep (Pelletier and Festa-Bianchet, 2006), mountain goat (Mainguy and Côté, 2008) and Alpine ibex (Brivio et al., 2014)], which could be consistent with observations recorded here for kudu.

2.5.2. Availability of resources

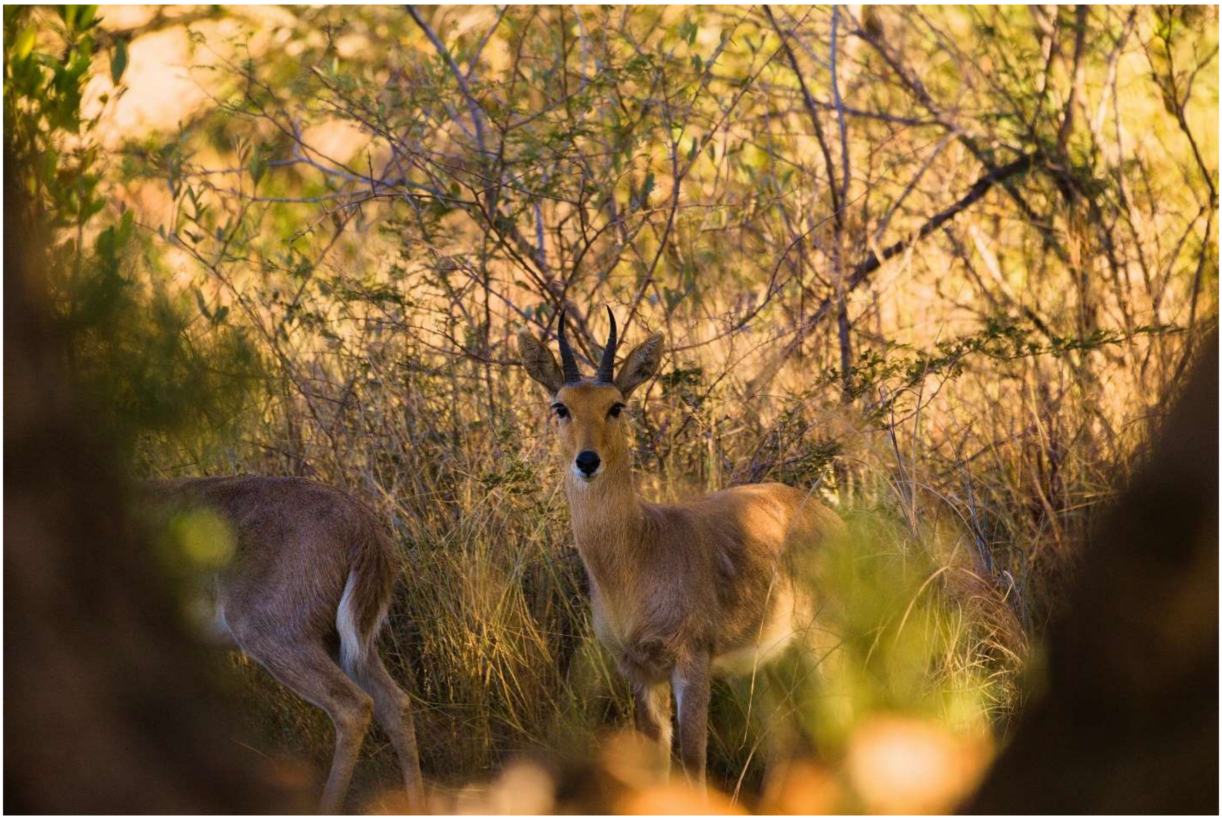
Average NDVI and the frequency of precipitation prior to a weighting event were positively related to increases in body mass. NDVI was reported to have a positive effects of on the nutritional status of red deer in the Iberian Peninsula (Santos et al., 2018) using the Kidney Fat Index (KFI; Riney, 1955), and on the body mass of hunted calves and yearlings of moose in Norway (Herfindal et al., 2014). Rainfall has also been positively related to the survival and reproduction of African ungulates in Kenya (Ogutu et al., 2013), and the survival of Apennine chamois *Rupicapra pyrenaica* in central Italy (Ferretti et al., 2019). In seasonal environments, reproduction often occurs only during seasons when NDVI is high (Côté and Festa-Bianchet, 2001; Paoli et al., 2018), implicitly indicating that there are abundant resources that can help individuals to reach their best nutritional condition for breeding and investing in maternal care (Wittemyer et al., 2007; Berkeley and Linklater, 2010; Ogutu et al., 2013; Ogutu et al., 2015; Peláez et al., 2017; Cucco and Bowman, 2018).

Current changes to seasonality associated with climate change have included documented reductions in precipitation events and extended dry seasons in some areas, both globally (Trenberth, 2011) and in Southern Africa (Engelbrecht et al., 2015). Longer periods of water scarcity and periods lacking nutritious vegetation may impact body condition to the point of affecting survivorship of individuals. This may be especially true for grazers and mixed feeders that rely on seasonal vegetation pulses (Abraham et al., 2019), as well as for migratory species that may have to travel longer distances looking for vegetation of high nutritional value (Perkins, 2019). Although not focused on ungulates, Brawn et al. (2016) reported reduced survival of tropical birds that inhabit seasonal environments because of climate change, and Howard et al. (2018) predicted that pathways of migratory birds will become longer under future scenarios of climate change. Under the current and future climatic contexts, monitoring short-term changes of body mass becomes crucial to keep managers and authorities informed about when to support individuals, e.g. supplying water and palatable vegetation during unfavourable seasons, in order to reduce body mass losses that may result in lower survival of high value species. This is especially true when natural migratory pathways for African ungulates have been lost due to land-use development fragmenting natural landscapes, combined with the fact that many populations are now preserved in fenced areas.

2.5.3. Conclusions

My study showed it is possible to monitor and model seasonal variations of body mass in wild African ungulates on a near-daily basis taking into account individual variability. The methods I utilise here provides an easy means to continually monitoring body mass of a diverse range of wild ungulates, which could be used by site managers to rapidly identify times of body condition changes and alter management plan accordingly to aid survival (Douhard et al., 2019) or reproduction (Lombardini et al., 2017; Newbolt et al., 2017; Podofillini et al., 2019) of high value species. Monitoring body mass variations may be critical for protecting large herbivores that inhabit seasonal environments (van der Merwe et al., 2014; Wato et al., 2016; Abraham et al., 2019), especially considering the current projections of climate change scenarios that consider precipitation events will be reduced and less frequent in the near future (Trenberth, 2011).

3. FOOD RESOURCES AND FEAR OF HUMANS DRIVE SPATIAL ABUNDANCE OF LARGE HERBIVORES IN A SOUTH AFRICAN ARID SAVANNA



Mountain reedbuck (*Redunca fulvorufula*) | ©Nicolás Fuentes-Allende

3.1. Abstract

African savannas hold many species of large herbivores living in sympatry, which reduces interspecific competition by spatial segregation. This segregation is mainly driven by availability of resources (vegetation and water) and perception of predation risk. Past experience of predation makes preys build mental landscapes of fear of their surroundings, thus avoiding areas where they perceive higher probabilities of encountering predators. While large herbivores often perceive humans as predators in areas where they are hunted, it remains unclear whether non-target species are affected by human presence. In this study, I focus on a community of large herbivores within a fenced protected area that lacks the largest predators of the South African arid savanna. Here, a subset of these species is either hunted at a low intensity throughout the year or rounded up and sold to maintain populations within the site's carrying capacity, while others are not. For the reserve area, I modelled the seasonal variation of spatial abundance of 16 large herbivores using Density Surface Models, and identified the effects of vegetation, water, and human movement and infrastructure on spatial abundance. I found that species were differently affected by natural resources, which may be explained by dietary differences, and by human infrastructure and movement. Human activity (road traffic) and infrastructure (proportion of roads and distance to perimeter fence) negatively impacted occurrence of eight species, irrespective of whether or not they were a hunted species. These findings highlight a potentially overlooked role of humans in generating a perceived landscape of fear even in species that are not impacted negatively by people. Minimising large herbivores' perception of fear to their surroundings could be an important management tool to maximize species' carrying capacity, and could be a key factor in reducing carrying capacity at well visited sites for some species of conservation concern.

3.2. Introduction

Africa holds nearly 90% of the world's large herbivore species (Ripple et al., 2016) and savanna and grassland habitats in particular have many species living in sympatry (Hempson et al., 2015). Diet partitioning and spatial segregation help individuals to reduce interspecific competition and to increase their fitness (Hutchinson, 1959; Jarman, 1974). This is mainly driven by species traits (body size, morphology, behaviour; Veldhuis et al., 2019) and availability of resources (vegetation Schuette et al., 2016; Djagoun et al., 2020; water Kihwele et al., 2020). In African savannas, sympatric large herbivores deal with interspecific competition and resource scarcity by modifying foraging behaviours, and selecting specific resources and areas to exploit (Owen-Smith, 2019). Type of diet (grazers, browsers and mixed feeders; Du Toit and Cumming, 1999; Pascual-Rico et al., 2020) and water dependence (Hempson et al., 2015) can result in permanent or temporal segregation (Roberts et al., 2017; Hall et al., 2018). Temporal segregation between sympatric species has been widely studied in seasonal environments, where resources change from being scarce and patchily distributed during unfavourable seasons to being abundant and widely spread in the environment during favourable ones. Temporal segregation may be expressed by switching feeding areas (Nakashima et al., 2020; Owen-Smith et al., 2020), food items (McSchea et al., 2019), and/or diurnal foraging timing (Pascual-Rico et al., 2020).

Perception of predation risk is another factor that influences spatial distribution of large herbivores (top-down control; Koerner et al., 2017). The “ecology of fear” theory proposes that perception of predation risk results in prey species modifying their behaviours and spatial distribution in accordance with perceived risk (Brown et al., 1999). Depending on previous experience, prey map their surroundings according to perception of predation risk (“landscape of fear” Laundré et al., 2010), avoiding areas with high perception of risk (Gaynor et al., 2019) or increasing anti-predatory behaviours when roaming within risky areas (Krishna et al., 2016; Smith et al., 2019).

While species have different strategies to cope with predators (Brown et al., 1999), how they respond to human disturbances remains unclear. Responses vary between species and contexts, from avoiding humans, when they are identified as predators (Frid and Dill, 2002; Koerner et al., 2017), to becoming habituated (Marino and Johnson, 2012; Schroeder et al., 2018) or even be attracted to them (Muhly et al., 2011), when there is no harassment or when humans can serve as a shield against natural predators (Berger, 2007; Atickem et al., 2014; Nowak et al., 2014). These wildlife reactions to humans have been documented based upon direct encounters with people (Lahkar et al., 2020) as well as in relation to indirect measures of human presence, such as the presence of livestock (Schieltz and Rubenstein, 2016; Harris et al., 2019; Crego et al., 2020), infrastructure (Nickel et al., 2020), or buildings (Koerner et al., 2017). Avoidance of humans may be detrimental for large herbivores inhabiting arid environments (Rivas et al., 2015), where water and forage are scarce and patchily distributed across the landscape; human disturbances have been shown to cause wild ungulates to avoid preferred feeding sites and instead to make use of sub-optimal habitats (Frid and Dill, 2002; Journeaux et al., 2018). By contrast, attraction to areas near humans may promote overgrazing (Frid and Dill, 2002; Muñoz et al., 2015) and spread of exotic grasses (Stokely et al., 2020), while making hunting more difficult for natural predators (Leighton et al., 2010; Muhly et al., 2011; Valeix et al., 2012).

In the present study, I explore the effects of environmental and anthropogenic variables on the spatial distribution of 16 sympatric large herbivores that inhabit a fenced protected area in the South African arid savanna. This is an isolated area which lacks large ungulate predators, but which undertakes limited hunting of a few species for management purposes, while others are maintained for conservation purposes. In addition to controlled hunting that normally occurs next to roads when managers are riding their vehicles, poaching involving dogs and snares is sporadically reported near the perimeter fence. Using data collected at the end of dry and wet seasons from 2016 to 2018, I build density surface models (DSM; Miller et al., 2013), a spatially explicit approach that uses distance sampling (Buckland et al., 2001) and generalized additive models (HGAMs; Pedersen et al., 2019) to model spatial distribution of abundance, to identify key drivers in the spatial abundance of large herbivores in the reserve. I hypothesize that species, in addition to being affected by vegetation structure and water availability, are influenced by human presence and their infrastructure. I also explore if animals’ responses toward humans are similar among exploited and non-exploited species within the reserve, and identify which may be the main anthropogenic factors driving variation on spatial abundance. I finally propose recommendations for management strategies that might increase carrying capacity.

3.3. Methodology

3.3.1. Study site

The work was conducted at Mankwe Wildlife Reserve (MWR; 25°13’39’’S 27°17’50’’E), a 3,875 ha private reserve located in the South African arid savanna. The site is a convenient system to test human impacts on the spatial abundance of large herbivores, because (i) there are 19 large herbivores species living in sympatry that are maintained for conservation, research and, to a lesser extent, hunting purposes, (ii) migration in and out of the reserve is restricted by a 3 m electrified perimeter fence, (iii) natural predation by larger predators is marginal (leopard is the largest predator within the reserve, though only an irregular visitor), with typical large predators of the regions such as lion, cheetah (*Acinonyx jubatus)*, wild dog (*Lycaon pictus)* and spotted hyaena (*Crocuta crocuta)* being absent, (iv) carrying capacity is maintained mainly by low-intensity hunting and capturing for sale of a few species (blesbok *Damaliscus pygargus*, blue wildebeest, greater kudu, impala, plains zebra *Equus quagga*). In addition to controlled hunting, non-selective poaching of small and medium-sized herbivores using snares, dogs and firearms occasionally occurs in the proximity of the perimeter fence. Abundance of large herbivores is monitored yearly via helicopter strip counts, undertaken at the end of dry seasons. As is typical for arid savannahs, rains concentrate during the wet season, occurring from the beginning of October to the middle of the following May (Yarnell et al., 2007), followed by little or no rain until the following October. This weather regime promotes intense seasonal changes in vegetation and water availability, where resources are more abundant and nutritious during the wet season than the dry season. Approximately 83% of the reserve is covered by savanna grasslands, with the reminder comprising woodland, thicket, and natural/artificial water bodies. Each year, up to approximately a quarter of the grasslands are burned during the dry season, using slow-burn techniques against the wind (Yarnell et al., 2007). The pattern of burning follows a rotational block fire regime (Brockell et al., 2001), such that most areas of grassland are burned every 4-5 years. On occasion, when a dry season follows a wet season with much-reduced precipitation, burning is suspended or spatially reduced. Burning is used as a means of enhancing sward palatability for large herbivores and to reduce tick densities.

In addition to the block burning regime, firebreaks between blocks and around the perimeter fence are burned yearly.

Data were collected over five sampling campaigns that occurred at the end of dry (August-September) and wet (April-May) seasons from August 2016 to October 2018.

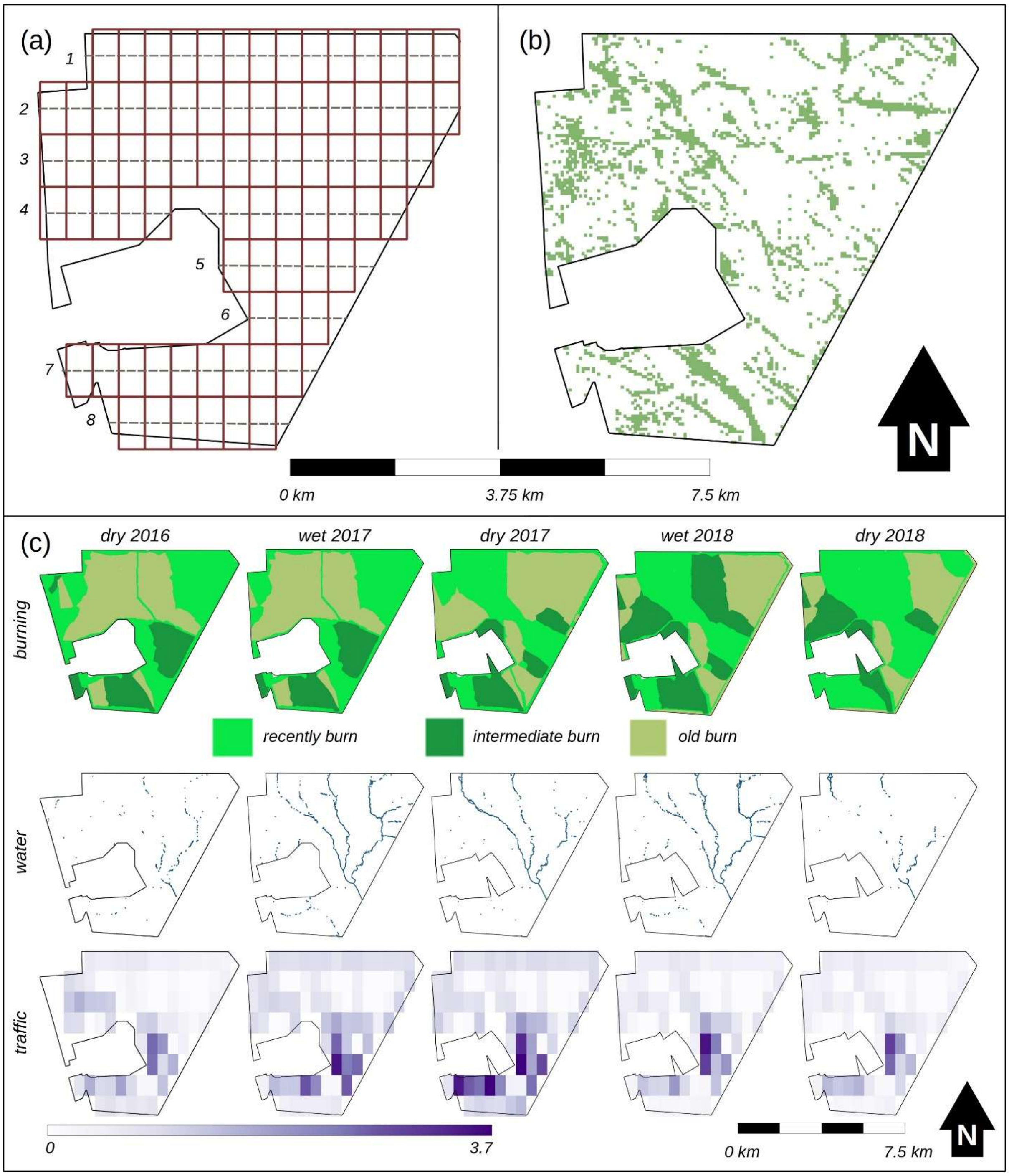


Figure 3.1. Study Area. Map a) shows the walked transects (dashed lines) and segments (red rectangles). Numbers indicate transect id, and black line shows perimeter fence. Map b) shows distribution of woody vegetation (green area) considering at a 50x50 m^2 resolution. Maps c) indicate distribution of burn-ages (top row), availability of water

(middle row), and road traffic at each segment (bottom row) for each sampling campaign (columns one to five). Areas with different intensities of green at first row maps show distribution of recently burn (burned no later than two wet seasons ago), intermediate burn (burned from three to four wet seasons ago) and old burn (not burned for at least five preceding wet seasons). Blue on the middle maps indicates the presence of water (50x50 m^2 resolution). White to purple areas on the lower maps indicate different levels of road traffic (intensity of colours indicates mean numbers of vehicles per hour for the whole sampling campaign).

3.3.2. Estimating Animal Abundance

Large herbivore densities were estimated using line transects. Eight line transects were walked during early mornings (one transect per day, between 6-11am) by one observer recording sightings of all larger (>2kg) herbivorous mammals, plus ostrich *Struthio camelus*. The latter was included as it is also a large (ca 110 kg) herbivorous species in African savannas. Mammals recorded ranged in size from steenbok *Raphicerus campestris* (mean mass 11.2 kg) to white rhino (mean mass 2196 kg). Transects ran in parallel, were east-west oriented and located 950 metres from neighbouring transects (Figure 3.1a). Northern and southernmost transects were located 475 metres away from northern and southern fences, respectively. Transect lengths varied from 1.8 km to 7.7 km, and each transect was walked 21 times in total (five times during the first season, then four times during each of the subsequent seasons), totalling 816 km walked during the whole study period. Transects were repeated every 10 to 14 days within a season, and neighbouring transect surveys were separated by at least two days to avoid potential displacement and double counting effects. Transects were walked in a different direction (i.e. E-W or W-E) on subsequent visits to minimise time-related biases in detectability.

Animals were sighted by eye on both sides of transects. When an encounter occurred, species herd size, sex and age composition were described using binoculars (each event being referred to as a ‘cluster’; Buckland et al., 2001). The location of each cluster was additionally recorded as being within either an open landscape (high visibility) or a wood/thicket area (low visibility), in order to explore potential detectability impacts of habitat. The geographical position of the recorder on sighting a cluster was recorded using a GPS (Garmin GPSMAP® 60CSx), and the azimuth and distance to the locality of first sighting of the cluster was recorded with a compass (Suunto 2015 KB-20/360R G) and a rangefinder (Leica Rangemaster CRF 1600-B) respectively. Using the geographical location of the recorder, along with the azimuth and distance to a cluster, the position of animals was later plotted using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

3.3.3. Spatial covariates

To determine environmental covariates that may influence the spatial abundance of herbivores, transects were first divided into 80 segments of 475 m length (Figure 3.1a). When combined with the mid-distance (475m) between transects on either side of the survey line, this resulted in a rectangular grid-cell of approximately 45 ha (950m x 475m). These cells covered the 93.16% of the protected area. To ascribe water extent, proportion of vegetation burned, presence of woody vegetation, physical infrastructure and road traffic to each cell, I summed the extent of each trait that intersected a cell. Given 80 cells x five seasons, this resulted in 400 cell descriptions. To estimate water availability within cells, all riverbeds and natural ponds within the reserve were surveyed before and after performing each transect cycle. When water was found, its geographical location was recorded and assigned to cells. To estimate water availability, cells were described using both the proportion of their surface covered with water (using a spatial grain of 50 m), and its frequency of occurrence, with frequency classified as: (i) “no water”, if no water bodies were found within the segment during the whole campaign, (ii) “occasional water”, when water bodies were found in at least one of the walking visits, or “permanent water” when water was always present in the segment (Figure 3.1c). The proportion of a cell’s area that had been burned at different time was categorised in terms of areas of “recently burned” habitat (burned no later than two wet seasons ago), “intermediate burn” habitat (burned from three to four wet seasons ago), and “old burn” habitat (not burned for at least five preceding wet seasons) (Figure 3.1c). Cells were also described by the proportion covered by woody vegetation (Figure 3.1b). Each cell was divided by 200 squares of equal size that were individually classified as with woody vegetation if more than half of the surface was covered by trees using Satellite images (©Google LLC). The minimum distance from the central point of each cell to the nearest perimeter fence and roads, as well as proportion of the cell covered by roads were also calculated. Road traffic use coinciding with transects was recorded for each segment by setting GPS loggers (i-gotU GT-600 and Canmore GT-730FL devices) on all vehicles that transited within the reserve. Devices recorded vehicle locations every three minutes from one hour before walking a transect to one hour after (5-12am). Then the mean number of vehicles per hour for the whole sampling campaign was calculated for each segment (Figure 3.1c). All spatial analyses were done using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

3.3.4. Herbivore Spatial Abundance Analysis

Density Surface models (DSM; Miller et al., 2013) were used to estimate spatial abundance of large herbivores in the reserve. DSMs combine a two-stage approach, incorporating both a detection function (Distance Sampling; Buckland et al., 2001) and Generalized Additive Model (GAM; Wood, 2006) in order to model spatial abundance of species within the protected area.

3.3.4.1. Detection function for herbivore abundance

Detection functions estimate the decline in detectability with increasing distance from the observer (Buckland et al., 2001). Here, detectability was calculated using perpendicular distance from sightings to transect lines for all the species that were recorded in at least 40 events during the 21 walking repetitions (Buckland et al., 2015). Recording events for common duiker (*Sylvicapra grimmia*) and steenbok did not pass this threshold. However, as both species have similar morphological and ecological characteristics (both are small, retiring, occur only solitarily or in pairs, are principally crepuscular/nocturnal, and typically flush from close range), observations from both species were grouped together to estimate detectability. In this situation, “species” was incorporated as a covariate of the detection function to explore species-specific variation in detectability (Alldredge et al., 2007). For all species, truncation distance was limited to 475 m in order to keep detection functions within a cell; this limit was appropriate for almost all species, as it is suggested that the most distant 10 percent of observations can usually be discarded in distance sampling, and across all species the mean distance of the 90th percentile of observations was 640 m. A total 17 candidate detection functions were fitted per species. Candidate detection functions considered three potential key functions (uniform, half-normal, hazard-rate; Thomas et al., 2010), and also included three covariates that could have affected detectability of individuals (Marques et al., 2007). The latter three variable comprised: cluster size (continuous variable), visibility when sighting a cluster (a factor with four levels; observer within thicket, sighting within thicket, both within thicket, both at open landscape), and season (a factor with two levels; dry season, wet season). All detection functions were compared using Akaike Information Criterion (AIC; Akaike, 1974). Candidate models with ΔAIC ≤2 were considered as equivalent (Burnham and Anderson, 2002). Model selected for further predictions was the one that excluded uninformative parameters (Arnold, 2010; Richards et al., 2011), passed goodness-of-fit tests (Buckland et al., 2015) and fit the highest detection probability for the species-specific data. All statistical analyses were performed using “Distance” package (Miller, 2020) in R (R version 3.5.2; R Core Team, 2018).

3.3.4.2. Density surface model

After determining the best detection function for each species, the second modelling stage involved building species-specific hierarchical generalized additive models (HGAMs; Pedersen et al., 2019) that considered cells as sampling units (*n*=400) in order to model spatial abundance of herbivores within the reserve. Models were built per species and included the number of its sightings, the selected detection function and the spatial covariates measured at the cell level (Miller et al., 2013), while taking into account that transects (and hence cells) were repeatedly visited across five sampling campaigns. Sightings and cell information from the fifth walking repetition during the dry season in 2016 were discarded for the analysis in order to keep a balanced sampling effort across seasons (4 walking repetitions per sampling campaign). As was done with the Distance sampling, all sightings >475 m from a transect line (and hence falling into a more distant cell) were discarded. The remaining sightings were assigned to cells, and sampling effort was calculated as distance walked per transect considering all sampling campaigns.

A total of 134 DSM candidates that varied on the spatial covariates that included were proposed for each species. All candidate models were built with a base model that included: (i) geographic coordinates (in metres) as a bivariate covariate with a soap film group-level smoother (two levels: dry and wet seasons) that allowed consideration of the perimeter fence as a barrier for animal movement (Wood et al., 2008), (ii) season as a factor with two levels (dry season, wet season), and (iii) segment id as random intercepts. Candidate models varied from one that did not include any extra covariates more than the base model to models including up to four extra covariates. Extra covariates were grouped in four categories, and only one covariate per category was considered at a time to prevent collinearity. Categories were (i) water availability (proportion of the segment with water and frequency of water availability), (ii) thicket (proportion of woody vegetation), (iii) burn-age (proportion of recently burned, intermediate burn, old burn), and (iv) human impact (distance to fence, distance to roads, proportion of roads, and road traffic). Unless they were factors, extra covariates had group-level (season) penalized thin-plate regression splines as smooth terms (Wood, 2003). All models assumed a Tweedie distribution (Candy, 2004; Shono, 2008; Peel et al., 2012), and the smoothing selection was defined by marginal likelihood (Wood, 2011; Wood, 2017). The quality of models was checked using basis dimension assessments (Wood, 2017), visually inspecting plots of residuals and plots of observed vs fitted values as well as checking correlograms for spatial autocorrelation. Candidate models were ranked based on AIC and deviance explained. The one with the lowest AIC, that excluded uninformative parameters (within ΔAIC ≤2), and had highest deviance explained was selected as the best model. All statistical analyses were performed using “dsm” package (Miller et al., 2020) in R (R version 3.5.2; R Core Team, 2018).

3.3.4.3. Estimations of spatial abundance

Seasonal spatial abundance and seasonal total abundance (pooling estimations from all cells together) were estimated using the best density surface model for each species.

These total population estimates were compared with abundance estimations from helicopter strip counts conducted towards the end of the dry season each year. Species-specific variance propagation and coefficient of variation were calculated using the delta method approach (Cañadas et al., 2018). Abundance maps were generated using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

3.4. Results

3.4.1. Field data and detection functions

3,975 observations of 19 species were collected during the five sampling campaigns. Species comprised 13 grazers (African buffalo, *Syncerus caffer*; blesbok; blue wildebeest; common ostrich; common reedbuck; common warthog; common waterbuck, *Kobus ellipsiprymnus;* gemsbok; plains zebra*;* red hartebeest; sable antelope, *Hippotragus niger;* white rhino; tsessebe, *Damaliscus lunatus),* four mixed feeders (common eland, *Tragelaphus oryx*; greater kudu; impala*;* steenbok), and two browsers (common duiker; giraffe). From those, a total of 3,201 observations (17 species) were considered for building detection functions (Table 3.1). These observations correspond to sightings registered no farther than 475 m away from transects, and from species that had more than 40 records for the whole study period. African buffalo (*n*= 6) and sable antelope (*n*= 7) were discarded from the analysis. Common duiker (*n*= 22) and steenbok (*n*= 33) were grouped together for estimating detectability, as explained in the methods. All selected detection functions passed quality assessments and goodness-of-fit tests. Apart from giraffe, red hartebeest and common reedbuck, all detection functions included at least one covariate. Figure 3.2 shows average detection functions and histograms for the 17 modelled species, and Figure A3.1 shows goodness-of-fit tests for each species.

Table 3.1. Selected detection functions per species. “n TOT” indicates total observations, “n DF” indicates observations considered when building detection functions, “C-vM p-value” indicates Cramér-von Mises p-value, “Pa ± SE” indicates average detection function ± standard error., “CV” coefficient of variation, and “ΔAIC” refers to difference between the selected model (considering nested models and deviance explained), and the model with lowest AIC.

Species	n TOT	n DF	Key function	Covariates	C-vM p-value	Pa ± SE	CV	Δ AIC
Blesbok	535	414	Half-normal	season + roughness	0.27	0.69 ± 0.03	0.04	1.72
Buffalo	7	6	not enough observations					
Duiker - Steenbok	57	55	Half-normal	species + size	0.42	0.16 ± 0.02	0.12	0.00
Eland	176	141	Half-normal	roughness	0.98	0.63 ± 0.05	0.08	0.42
Gemsbok	130	105	Hazard-rate	season + roughness	0.90	0.19 ± 0.08	0.41	0.00
Giraffe	137	104	Uniform (1)	-	0.87	0.75 ± 0.07	0.10	1.80
Hartebeest	188	152	Half-normal	-	0.72	0.66 ± 0.05	0.07	1.70
Impala	543	472	Hazard-rate	season + roughness	1.00	0.39 ± 0.03	0.08	0.00
Kudu	200	166	Half-normal	roughness	0.54	0.43 ± 0.02	0.06	1.51
Ostrich	360	273	Hazard-rate	roughness	0.98	0.68 ± 0.05	0.07	2.00
Reedbuck	77	76	Half-normal (cos 2,3)	-	0.99	0.25 ± 0.03	0.11	0.00
Rhino	74	62	Hazard-rate	Season + size + roughness	0.16	0.39 ± 0.08	0.20	1.93
Sable	7	7	not enough observations					
Tsessebe	228	200	Half-normal	roughness	0.49	0.6 ± 0.08	0.14	0.00
Warthog	142	139	Hazard-rate	season	0.97	0.12 ± 0.02	0.15	0.26
Waterbuck	273	233	Hazard-rate	size + roughness	0.48	0.5 ± 0.10	0.20	0.00
Wildebeest	531	390	Hazard-rate	season + roughness	0.70	0.6 ± 0.05	0.09	1.84
Zebra	310	219	Hazard-rate	size + roughness	0.95	0.68 ± 0.05	0.08	0.00

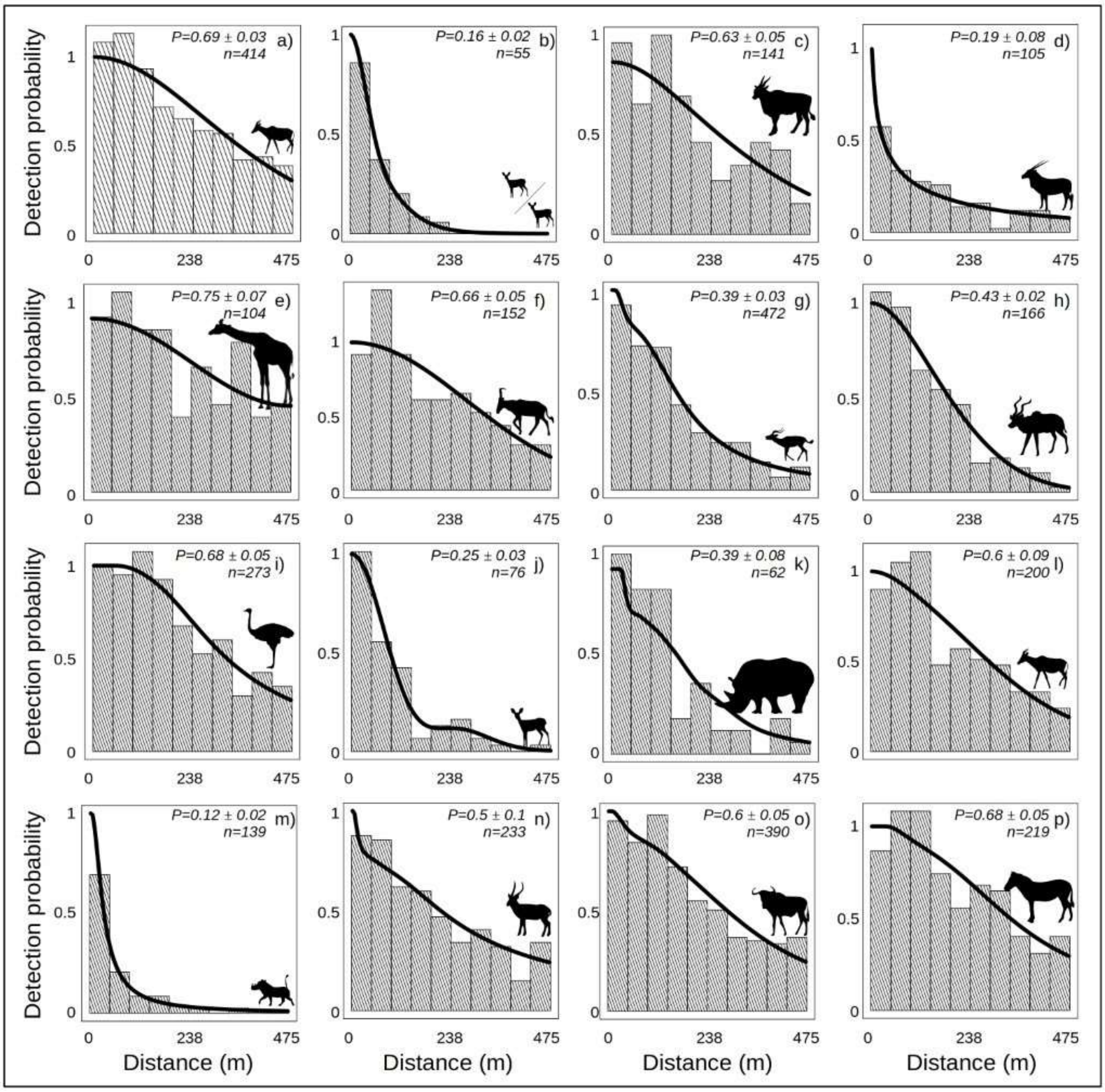


Figure 3.2. Histograms and detection functions of selected models, where a) blesbok, b) duiker/steenbok, c) eland, d) gemsbok, e) giraffe, f) red hartebeest, g) impala, h) greater kudu, i) ostrich, j) reedbuck, k) white rhino, l) tsessebe, m) warthog, n) waterbuck, o) blue wildebeest, p) zebra. Black lines represent mean detectability curves. P and n at right upper corners indicate value of detection function (mean ± standard error) and sampling size respectively.

3.4.2. DSMs and abundance estimations

2,955 observations were assigned to cells and considered for building DSMs. Apart from the warthog model, which only included geographic coordinates and seasons, all selected models included at least one additional spatial covariate (Table 3.2). Waterbuck was discarded for further analyses because none of its candidate models passed spatial autocorrelation assessments.

Apart from greater kudu and blue wildebeest, mean abundance estimations from the wet season were always lower than those from the dry season (mean proportion=0.288 lower than dry season; max proportion=0.55 lower in duiker; min proportion=0.09 lower in ostrich). Additionally, estimations from the dry season were more alike to estimations from helicopter counts: with a mean difference of 30.9% between mean helicopter counts and distance sampling estimations per species, amax difference of 76% for warthog (mean counts from helicopter counts during the dry season considered 74.6 warthogs in the study area, and distance sampling estimations predicted 131.41 individuals during the dry season) and a min difference of 0.3% for impala (mean estimation from helicopter count considered 407.5 individuals, and distance sampling predicted 408.65 individuals). Apart from duiker, gemsbok, impala, common reedbuck and warthog, line transects predicted fewer animals in the reserve than helicopter counts. According to mean abundance estimates, impala (dry season 408.65 ± 47.24 individuals; wet season 342.24 ± 39.56 individuals), blue wildebeest (dry season 204.74 ± 25.86 individuals; wet season 246.01 ± 31.07 individuals), blesbok (dry season 187.73 ± 19.81 individuals; wet season 117.45 ± 12.39 individuals), zebra (dry season 186.98 ± 22.74 individuals; wet season 102.16 ± 12.42 individuals) and warthog (dry season 131.41 ± 24.17 individuals; wet season 105.68 ± 19.44 individuals) were the most abundant species in the reserve (Figure 3.3; Table 3.2). Further details of the DSMs are presented at Table 3.2.

Abundance maps show that the core occupied areas for the 16 modelled species occur in quite different areas within the reserve, and hence they seem to seasonally and permanently partition their distributions from each other, despite the apparent habitat uniformity at a coarse scale (Figure 3.4). Maps illustrating the spatial abundance of species (and associated coefficients of variation) for each field campaign can be found in Figures A3.2 to Figure A3.7 in supplementary materials.

Table 3.2. Selected density surface models per species. "n" indicates observations considered when building the species-specific density surface model, "Covariates" indicates extra covariates that were included in the selected model, "R2" indicates adjusted R-squared, "DEV.EXP" indicates deviance explained, "ML" marginal likelihood, "ΔAIC" refers to difference between current model and model with lowest AIC, "CV" coefficient of variation, and "Abun ± SE" indicates mean abundance ± standard error for the whole study period. Grey cells indicate species that were discarded for further analysis.

Species	n	Covariates	R^2	DEV.EXP	ML	ΔAIC	CV (%)	Abun ± SE	Helicopter
Blesbok	391	Prop recently burn + Freq water + Prop road	0.44	0.47	936.30	0.00	10.53	183.02 ± 19.3	226
Duiker	21	Prop water + Dist road	0.07	0.23	105.77	0.00	25.02	10.77 ± 2.7	10.6
Eland	130	Prop old burn + Prop thicket + Traffic	0.16	0.28	484.78	1.57	14.9	36.47 ± 5.43	59.5
Gemsbok	96	Prop recently burn + Dist fence	0.31	0.50	429.09	0.40	43.92	40.57 ± 17.82	33.8
Giraffe	91	Prop old burn + Dist fence	0.14	0.30	365.06	0.00	17.75	20.61 ± 3.66	27.8
Hartebeest	143	Prop intermediate burn + Prop thicket + Dist fence	0.12	0.33	489.79	0.00	15.01	40.37 ± 6.06	69.4
Impala	435	Prop recently burn + Prop thicket + Traffic	0.19	0.31	1292.90	0.00	11.56	382.08 ± 44.18	407.5
Kudu	145	Prop old burn + Freq water + Prop road	0.14	0.25	506.02	0.00	12.54	37.52 ± 4.71	115.9
Ostrich	247	Prop recently burn + Prop thicket + Prop road	0.29	0.40	650.65	0.00	10.84	37.47 ± 4.06	50.6
Reedbuck	73	Prop intermediate burn + Prop thicket + Freq water	0.7	79.5	127.47	0.00	14.43	23.28 ± 3.36	20.5

Rhino	49	Prop old burn	0.19	0.36	221.44	1.64	25.83	10.51 ± 2.72	15.2
Steenbok	31	Prop intermediate burn + Traffic	0.09	0.24	117.35	0.00	21.69	6.53 ± 1.42	11.4
Tsessebe	181	Prop thicket	0.25	0.37	534.80	1.15	16.95	30.08 ± 5.1	43.4
Warthog	127	-	0.09	0.14	636.15	0.00	18.39	121.12 ± 22.27	74.6
Waterbuck	220	Discarded because models did not pass spatial autocorrelation assessments							
Wildebeest	365	Prop old burn + Prop thicket + Traffic	0.30	0.50	1044.90	0.00	12.63	221.25 ± 27.94	280.8
Zebra	210	Dist fence	0.32	0.44	767.06	0.00	12.16	153.05 ± 18.61	205.4

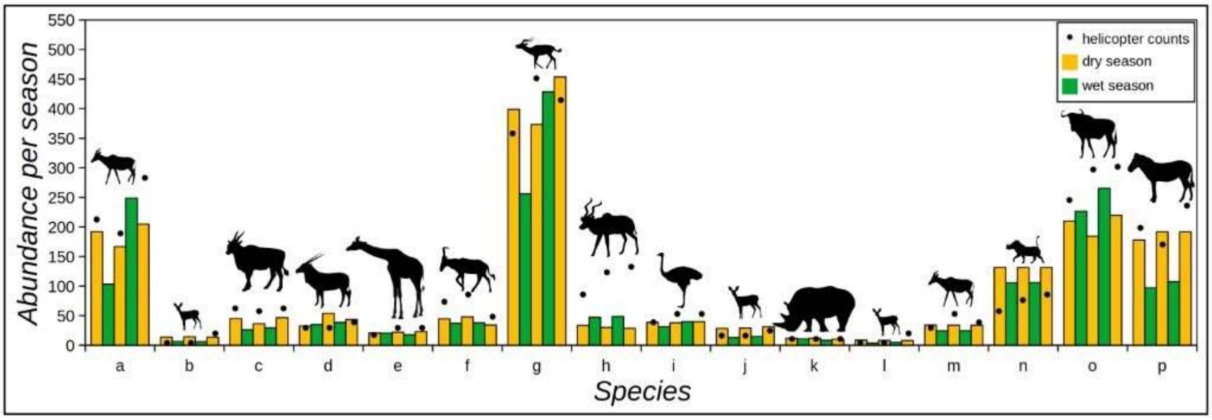


Figure 3.3. Abundance estimations at study site per species: a) blesbok, b) duiker, c) eland, d) gemsbok, e) giraffe, f) red hartebeest, g) impala, h) greater kudu, i) ostrich, j) reedbuck, k) white rhino, l) steenbok, m) tsessebe, n) warthog, o) blue wildebeest, p) zebra. Yellow and green bars represent abundance estimations for dry and wet seasons respectively, from the first (the leftmost bar) to the fifth (the rightmost bar) field campaigns. Black dots represent counts from helicopter surveys that were obtained at the end of dry seasons.

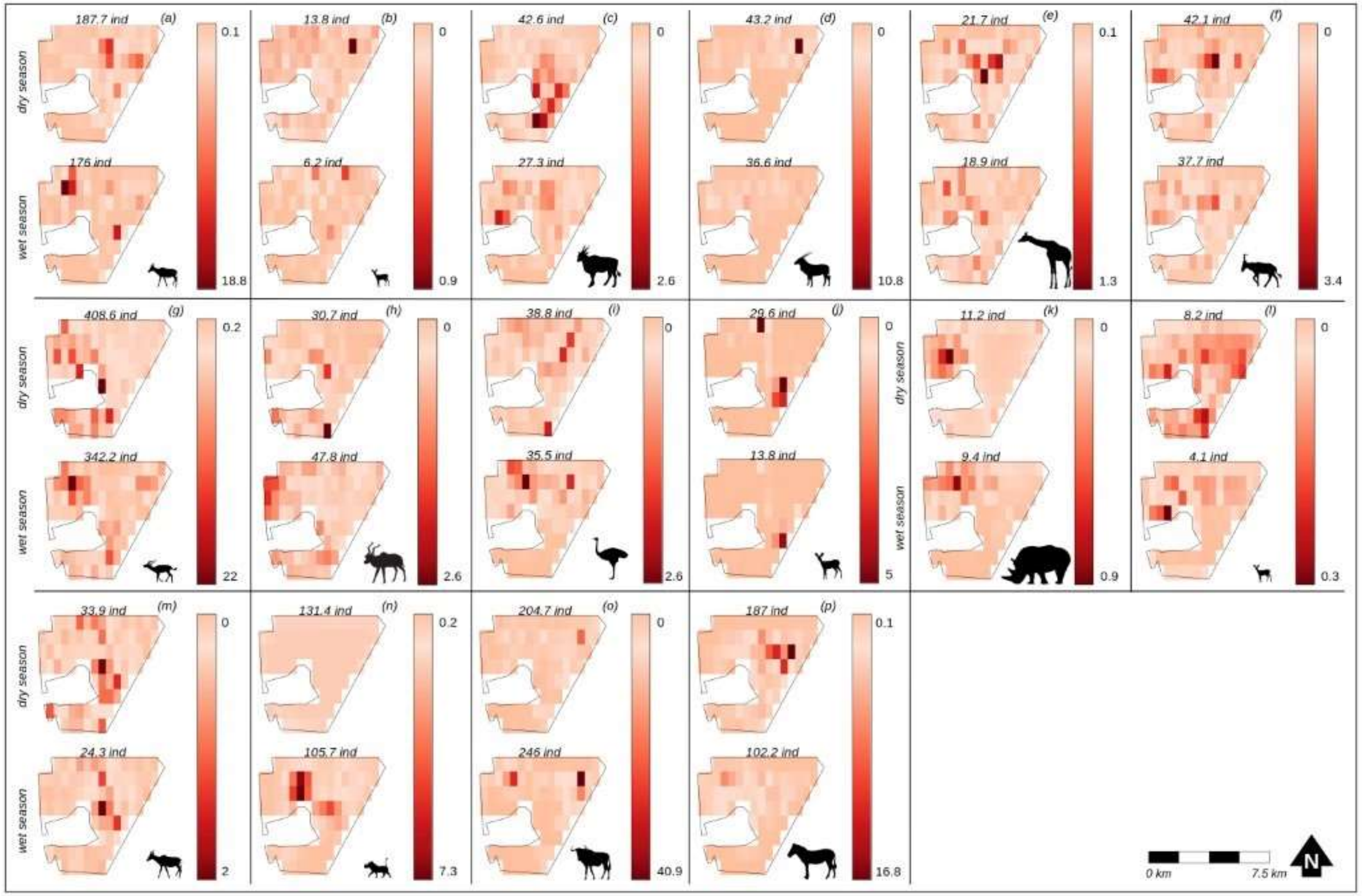


Figure 3.4. Average spatial abundance for dry (upper row) and wet seasons (second row), where a) blesbok, b) duiker, c) eland, d) gemsbok, e) giraffe, f) red hartebeest, g) impala, h) great kudu, i) ostrich, j) reedbuck, k) white rhino, l) steenbok, m) tsessebe, n) warthog, o) blue wildebeest, p) zebra. Numbers above maps are average estimations of total abundance considering sampling campaigns at dry and wet seasons separately. Intensity of red refers to mean density of individuals at each segment.

3.4.3. Partial effects of environmental covariates

3.4.3.1. Human infrastructure and movement

Variables related to anthropogenic disturbances were included in the selected models for 12 species, and they had partial significant effects on 10 of them. When significant, proximity to perimeter fence and road traffic always displayed a negative effect on abundance, but there was not a common trend in relation to proportion of roads. Distances to perimeter fence had a positive linear effect on the abundance of gemsbok during the dry season (edf=1; *F*=4.726; *p*<0.03; Deviance explained=50.3%; Figure 3.5a), giraffe during the wet season (edf=1; *F*=4.978; *p*<0.026; Deviance explained=30.4%; Figure 3.5d), red hartebeest during dry (edf=1; *F*=5.663; *p*<0.018; Deviance explained=33.2%; Figure 3.5g) and wet seasons (edf=1; *F*=4.143; *p*<0.043; Deviance explained=33.2%; Figure 3.5g), and a positive non-linear effect on zebra during the dry season (edf=2.65; *F*=12.872; *p*<0.001; Deviance explained=44.2%; Figure 3.5j) and a positive linear effect during wet season (edf=1; *F*=8.575; *p*<0.004; Deviance explained=44.2%; Figure 3.5j). Road traffic had a negative linear effect on the abundance of eland during the dry season (edf=1; *F*=5.429; *p*<0.02; Deviance explained=28%; Figure 3.5c), blue wildebeest during dry (edf=1; *F*=7.750; *p*<0.006; Deviance explained=49.9%; Figure 3.5i) and wet seasons (edf=1; *F*=13.459; *p*<0.001; Deviance explained=49.9%; Figure 3.5i), and a negative non-linear effect on the abundance of impala when the mean number of vehicles per hours was <1.5 (edf=2.391; *F*=3.291; *p*<0.019; Deviance explained=30.7%; Figure 3.5f). The proportion of a cell covered with roads had a positive linear effect on the abundance of greater kudu during the dry season (edf=1; F=20.467; p<0.001; Deviance explained=25.1%; Figure 3.5e), and a positive non-linear effect on ostrich during the dry season (edf=3.313; *F*=3.117; *p*<0.02; Deviance explained=40.1%; Figure 3.5h). By contrast, it had a negative linear effect on the abundance of blesbok during the dry season (edf=1; *F*=24.737; *p*<0.001; Deviance explained=46.9%; Figure 3.5b), and a non-linear effect during the wet season: being negative when proportion was <0.2, and positive effect when it was >0.2 (edf=2.854; *F*=11.543; *p*<0.001; Deviance explained=46.9%; Figure 3.5b).

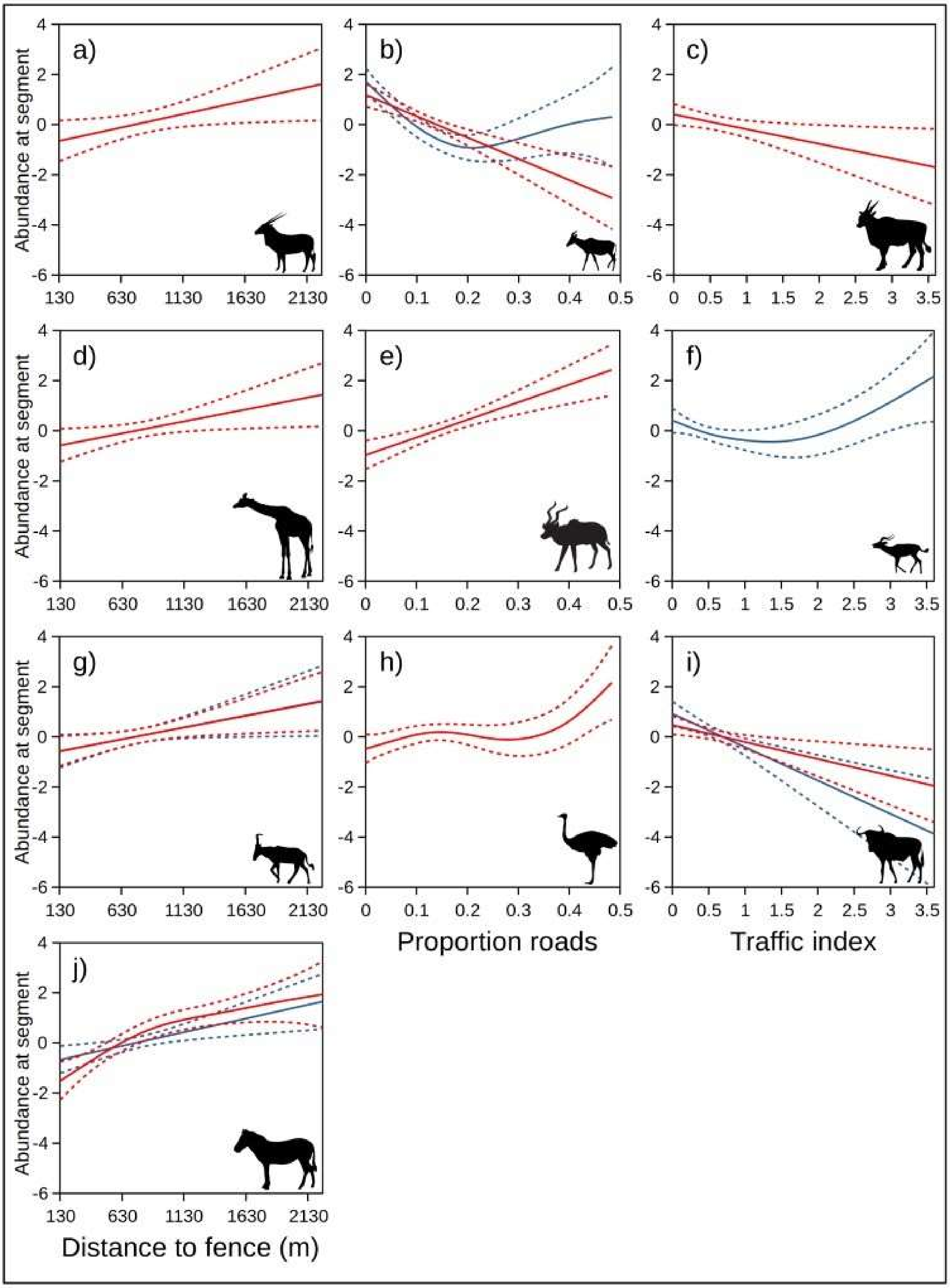


Figure 3.5. Predicted partial effects of distance to fence (a,d,g,j), proportion of roads

(b,e,h) and road traffic (c,f,i) on the abundance of large herbivores at segment level (50 ha). Where: a) gemsbok, b) blesbok, c) eland, d) giraffe, e) greater kudu, f) impala, g) red hartebeest, h) ostrich, i) blue wildebeest, j) zebra. Straight and dotted lines are predicted effects with their standard errors respectively. Red and blue lines indicate predicted effects for dry and wet seasons respectively. Only significant effects are shown.

3.4.3.2. Proportion of burn

Proportion of burn (recently, intermediate and old burn) was included in the models of 12 species, and it presented partial significant effects on 9 of them. Species abundance was differently affected by burn-age, and there was not a common trend among different species. Proportion of recently burn had a positive linear effect on the abundance of blesbok during dry (edf=1; *F*=8.935; *p*<0.003; Deviance explained=46.9%; Figure 3.6a) and wet seasons (edf=1; *F*=32.552; *p*<0.001; Deviance explained=46.9%; Figure 3.6a), and on impala during the wet season (edf=1; *F*=14.452; *p*<0.001; Deviance explained=30.7%; Figure 3.6f). On the contrary, it had a negative linear effect on the abundance of gemsbok during the dry season (edf=1; *F*=8.329; *p*<0.004; Deviance explained=50.3%; Figure 3.6d), and a non-linear effect on ostrich during the wet season: being negative when it was <0.2, and positive when it was >0.8 (edf=2.042; *F*=3.445; *p*<0.021; Deviance explained=40.1%; Figure 3.6h). Proportion of intermediate burn had a positive linear effect on the abundance of red hartebeest during the dry season (edf=1; *F*=4.51; *p*<0.034; Deviance explained=33.2%; Figure 3.6b). Proportion of old burn had a positive linear effect on the abundance of giraffe during the wet season (edf=1; *F*=7.577; *p*<0.006; Deviance explained=30.4%; Figure 3.6e), and on greater kudu during the dry season (edf=1; *F*=5.636; *p*<0.018; Deviance explained=25.1%; Figure 3.6g). Additionally, it had a non-linear effect on the abundance of eland during the wet season, being positive when the proportion was >0.6 (edf=2.201; *F*=4.003; *p*<0.012; Deviance explained=28%; Figure 3.6c), and on white rhino during the wet season, being positive when the proportion was >0.8 (edf=1.889; *F*=4.026; *p*<0.016; Deviance explained=35.5%; Figure 3.6i).

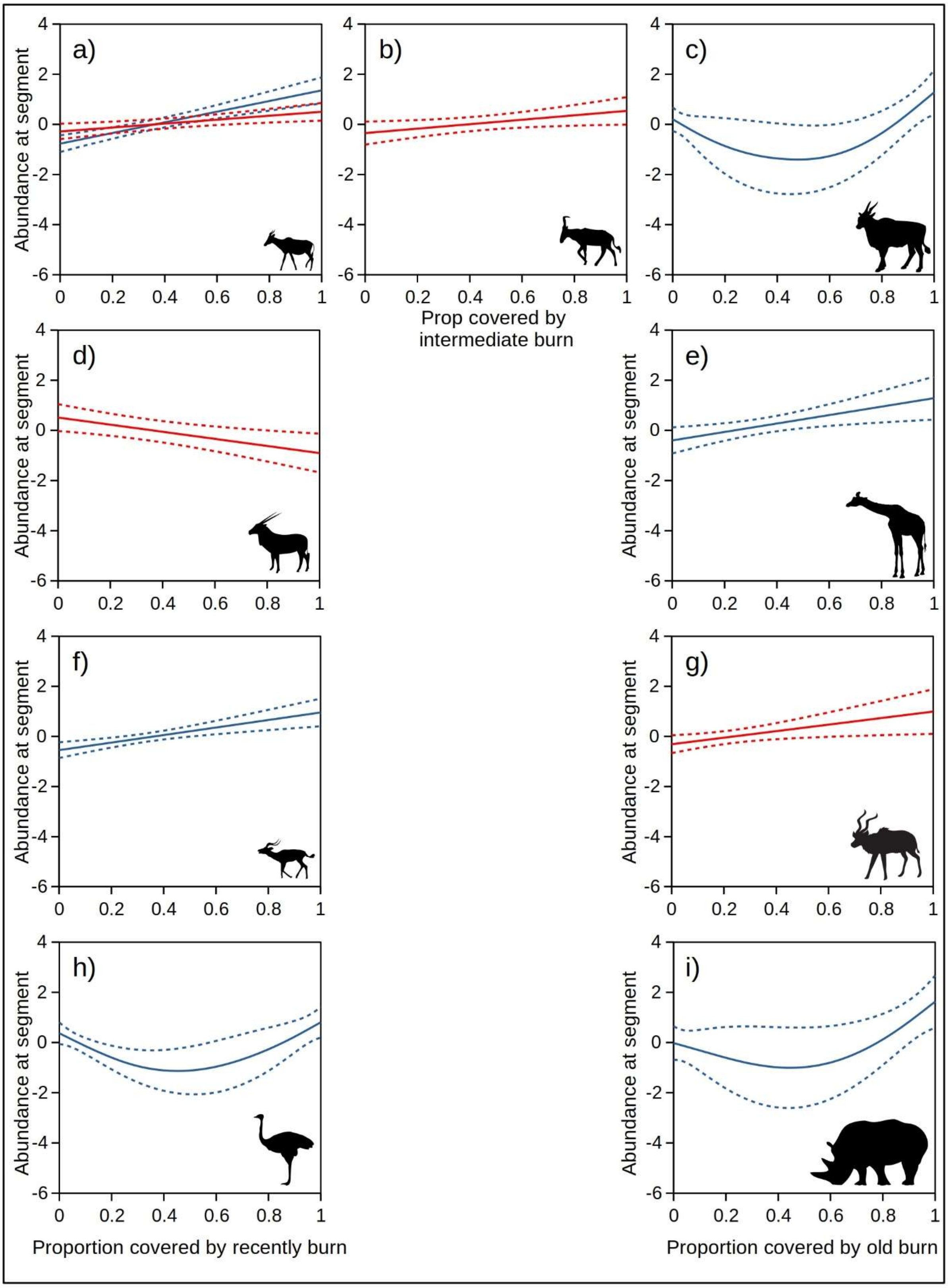


Figure 3.6. Predicted partial effects of proportion of recently (a,d,f,h), intermediate (b)

and old burn (c,e,g,i) on the abundance of large herbivores at segment level (50 ha). Where: a) blesbok, b) red hartebeest, c) eland, d) gemsbok, e) giraffe, f) impala, g) greater kudu, h) ostrich, i) white rhino. Straight and dotted lines are predicted effect with their standard errors respectively. Red and blue lines indicate predicted effects for dry and wet seasons respectively. Only significant effects are shown.

3.4.3.3. Proportion of thicket

Proportion of thicket was included in the best model for seven species, and it presented significant partial effects on six of them. Species abundance was differently affected by thicket, and there was not a common trend among different species. It had a negative linear effect on the abundance of four species: red hartebeest during the dry season (edf=1; F=9.987; p<0.002; Deviance explained=33.2%; Figure 3.7a), ostrich during the dry season (edf=1; F=7.233; p<0.008; Deviance explained=40.1%; Figure 3.7c) , common reedbuck during dry (edf=1; *F*=20.245; *p*<0.001; Deviance explained=50.6%; Figure 3.7d) and wet seasons (edf=1; *F*=20.245; *p*<0.001; Deviance explained=50.6%; Figure 3.7d), and tsessebe during the dry season (edf=1; *F*=9.818; *p*<0.002; Deviance explained=36.7%; Figure 3.7e). On the contrary, it had a positive linear effect on the abundance of impala during the dry season (edf=1; *F*=6.35; *p*<0.012; Deviance explained=30.7%; Figure 3.7b), and a non-linear effect during the wet season: being a positive effect when proportion of thicket was <0.2, and negative effect when it was >0.2 (edf=2.857; *F*=5.972; *p*<0.001; Deviance explained=30.7%; Figure 3.7b). Similarly, proportion of thicket had a non-linear effect on the abundance of blue wildebeest during the wet season: being a positive effect when the proportion was <0.2, and a negative effect when it was >0.2 (edf=2.804; *F*=4.004; *p*<0.006; Deviance explained=49.9%; Figure 3.7f).

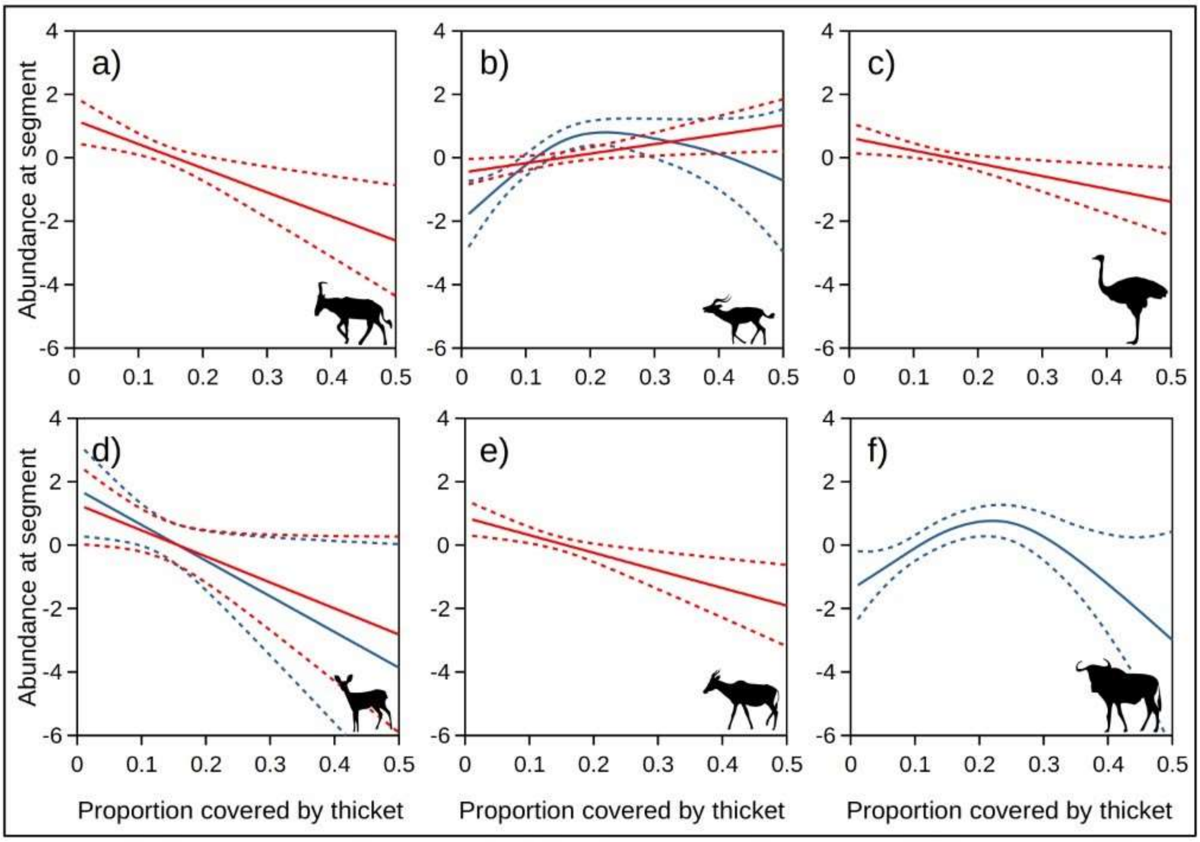


Figure 3.7. Predicted partial effects of proportion of thicket on the abundance of large herbivores at segment level (50 ha). Where: a) red hartebeest, b) impala, c) ostrich, d) reedbuck, e) tsessebe, f) blue wildebeest. Straight and dotted lines are predicted effect with their standard errors respectively. Red and blue lines indicate predicted effects for dry and wet seasons respectively. Only significant effects are shown.

3.4.3.4. Water availability

Variables related to water availability (proportion and frequency of water) were included in models for four species, but only one of them had significant partial effects on abundance. Frequency of water had significant effects on the abundance of common reedbuck. After Tukey comparisons with 95% confidence level, common reedbuck was similarly abundant in segments with occasional and permanent water (permanent-occasionally= 0.06 ± 0.43; z-value=0.145; p=0.99), but less abundant in segments with no water (permanent-no water= -1.51 ± 0.64; z-value=-2.35; p=0.048 // occasionally-no water= -1.57 ± 0.64; z-value=-2.45; p=0.04). Table 3.3 summarizes effects of spatial covariates on abundance.

Table 3.3. Seasonal effects of spatial covariates on abundance. “Tot cov” indicates total spatial covariates in the density surface model. Grey cells indicate covariates included in the model, “+” indicates that the covariate had a significant positive linear effect on abundance, “-” indicates that the covariate had a significant negative linear effect on abundance, “nl” indicates that the covariate had a significant non-linear effect on abundance, and “ns” indicates that the covariate had a non-significant effect on abundance. Direction, type and significance of seasonal effects are presented as follows “(effect during dry season / effect during wet season)”.

Species	Tot cov	Prop recent burn	Prop inter burn	Prop old burn	Prop thicket	Prop water	Freq water	Dist fence	Dist road	Prop road	Traffic
Blesbok	3	(+ / +)					(ns)*			(- / nl)	
Duiker	2					(ns / ns)			(ns / ns)		
Eland	3			(ns / nl)	(ns / ns)						(- / ns)
Gemsbok	2	(- / ns)						(+ / ns)			
Giraffe	2			(ns / +)				(+ / ns)			
Hartebeest	3		(+ / ns)		(- / ns)			(+ / +)			
Impala	3	(ns / +)			(+ / nl)						(ns / nl)
Kudu	3			(+ / ns)			(ns)*			(+ / ns)	
Ostrich	3	(ns / nl)			(- / ns)					(nl / ns)	
Reedbuck	3		(ns / ns)		(- / -)		(s)*				
Rhino	1			(ns / nl)							
Steenbok	2		(ns / ns)								(ns / ns)
Tsessebe	1				(- / ns)						
Warthog	0										
Wildebeest	3			(ns / ns)	(ns / nl)						(- / -)
Zebra	1							(nl / +)			

3.5. Discussion

This study presents seasonal variations in the spatial abundance of 16 large herbivores species that co-occur in a fenced arid savanna. Previous studies have used Density Surface Models to reveal spatial abundance of single herbivore species (e.g. roe deer in Spain, Valente et al., 2016; Svalbard reindeer *Rangifer tarandus platyrhynchus* in Norway, Le Moullec et al., 2017; guanaco in Argentina, Schroeder et al., 2018; Antún and Baldi, 2020), competition with livestock (e.g. guanacos and livestock in Argentina Schroeder et al., 2014; African ungulates and livestock in Kenya Tyrrell et al., 2017) or considering a few coexisting species from more diverse environments (four African ungulates in Kenya Tyrrell et al., 2017), but to date these models have not been applied to highly diverse communities of large herbivores. Using this approach, I detected subtle differences in individual species' preferences for habitat structure and water availability, and that these preferences varied between seasons in some species. Such subtle variation in preferences probably facilitate the coexistence of such large numbers of ungulate species, and results in their quite different spatial utilisation of what, at first appearance, might be considered a relatively uniform site. Spatial segregation of sympatric species with similar requirements have been reported before in large herbivores, such as red deer and Alpine Chamois in Switzerland (Anderwald et al., 2016), feral horse *Equus caballus*, pronghorn *Antilocapra americana* and mule deer *Odocoileus hemionus* in USA (Hall et al., 2018), bighorn sheep and mountain goat in USA (Lowrey et al., 2018), four duiker species in Gabon (Nakashima et al., 2020), and for aoudad *Ammotragus lervia* and Iberian ibex *Capra pyrenaica* in Spain (Pascual-Rico et al., 2020).

Spatial abundance models for multiple coexisting species have been produced before for different species, e.g. marine birds (Winiarski et al., 2014; Fifield et al., 2017), forest species (Devenish et al., 2017) and marine mammals (Herr et al., 2009; Dellabianca et al., 2016; Nichol et al., 2017). The simultaneous estimation of abundance and its spatial distribution may be useful for improving the management and conservation of target species (Miller et al., 2013), especially for species with confined distributions and seasonal movements.

3.5.1. Availability of resources (bottom-up influence on spatial abundance)

All selected models in this study included a covariate that described either vegetation structure or water availability, highlighting the key role of natural resources in the spatial abundance of these animals (Veldhuis et al., 2019; Kihwele et al., 2020; Owen-Smith et al., 2020). Large herbivores were each affected differently by vegetation structure and water, and these responses may be influenced by niche specialization, in terms of diet and water dependence, as well as by their energy requirements (Pansu et al., 2018; Boyers et al., 2019; McShea et al., 2019; Kihwele et al., 2020). While some responses clearly reflect food preferences; for example browsers such as eland, giraffe and greater kudu were attracted to non-burned areas where woody vegetation may be better preserved. By contrast, the grazers blesbok, impala and ostrich were attracted to grass flushes at recently burned sites (O'kane and Macdonald, 2018), and other grazers avoided areas with higher proportion of woody vegetation where palatable grass may be more scarce. Different responses to the environmental variables among species within the same feeding guild (i.e. grazers, browsers, mixed feeders) could reflect strategies for reducing interspecific competition (Kihwele et al., 2020; Nakashima et al., 2020; Pascual-Rico et al., 2020). Variability in responses may also reveal strategies for avoiding predators (Gaynor et al., 2019; Smith et al., 2019), which may indirectly help to regulate exploitation of resources (Tablado et al., 2016; Otieno et al., 2019; Owen-Smith, 2019).

3.5.2. Fear to humans (top-down influence on spatial abundance)

The distribution of around two thirds of the modelled species (blesbok, eland, gemsbok, giraffe, red hartebeest, impala, greater kudu, ostrich, blue wildebeest and plains zebra) appeared to be significantly affected by anthropogenic infrastructure (roads and perimeter fence) and road traffic. Distance to perimeter fence and road traffic had a negative effect on abundance among herbivores, regardless of body mass (ranging from impala 49.1 kg to giraffe 1117.5 kg) or whether the species were targeted for hunting. Despite the frequent occurrence of habituation by species when hunting/harassment is absent (Marino and Johnson, 2012; Mulero-Pázmány et al., 2016; Schroeder et al., 2018), my results suggest that the negative perception of humans by mammals may be transversal and echoed across the whole ecological guild in the study area, regardless of whether or not they are hunted. This is the first study to my knowledge that reports negative impacts of humans on the occurrence of a wide range of non-target species. It must also be borne in mind, however, that illegal hunting of other species (e.g. poaching of rhino, illegal hunting of warthogs by local communities), which tend to occur in the proximity of perimeter fence, may also shape the human response across a wider component of the ungulate guild. Previous studies have reported negative effects on non-target species when hunting with dogs (for roe deer in Italy Grignolio et al., 2011; porcupine *Hystrix cristata* in Italy Mori, 2017), which may explain avoidance of poaching areas by non-target species, but there is no reported negative impacts on non-target species near roads, which may be the situation for eland in areas with high road traffic. There was no common trend among species, in terms of their response to the presence of roads. This may suggest that utilization of roads (road traffic) could better explain perceived fear towards humans than the presence of roads itself.

Smaller abundance estimations for greater kudu and blue wildebeest from walked transects compared to helicopter strip counts could be a result of avoidance of humans on the ground. Both are hunting-target species within the reserve; thus, they may perceive humans as a threat and be adjusting their behaviours to reduce encounters with them or not being seen by them (Ciuti et al., 2012). Other research has shown that when combined with negative impacts, species behaviours are consistent with a perceived fear of humans, their activities as well as buildings and infrastructure (Nickel et al., 2020), and this can be similar to their perceived fear of natural predators (e.g. Neotropical rainforest mammals, Mendes et al., 202; wild boar in Germany, Johann et al., 2020; carnivores in the USA, Nickel et al., 2020) or even exceed it (e.g. elk in Canada, Ciuti et al., 2012).

Managers must consider that hunting and poaching may provoke a negative non-lethal effect on entire communities, regardless of whether all species are hunted or not. Illegal and controlled hunting may reduce the ability of herbivores to exploit all areas of a reserve to the full, thereby limiting carrying capacity. I recommend that hunting must be predictable for animals, and temporally and spatially planned, e.g. limiting hunting to specific seasons, time during the day and areas, to reduce the generalized perception of fear that animals may have towards humans within their landscape, such as avoiding feeding sites (Frid and Dill, 2002; Journeaux et al., 2018). Spatial planning of hunting may help herbivores to find temporal and spatial refugia, and to prevent affecting their feeding. Managers must keep on mind that reducing large herbivores perception of fear to their surroundings will help to maximize their carrying capacity.

3.5.3. Burning regime

My results show that burning vegetation can contribute increasing landscape heterogeneity, which can help maximizing the abundance and richness of large herbivores in protected areas. Nevertheless, managers must implement this action with caution. When overused, in terms of frequency and spatial extent of burning, it may reduce landscape complexity (Connell, 1978; Veldhuis et al., 2019). This can reduce niche opportunities and thereby increase interspecific competition (Diplock et al., 2018; Pansu et al., 2018; Alves et al., 2020). Despite was not included in my study, it has been documented that vegetation burning and creating artificial water points, can also negatively affect non-target species (Gallo and Pejchar, 2016). Such negative by-products of management have been recorded for small mammals (Yarnell et al., 2007), invertebrates (Radford and Andersen, 2012; Bhaskar et al., 2019), and birds (Saab and Powell 2005; Docherty et al., 2020). Additionally, the attraction of large herbivores to recently burned areas (“magnet effect”) or artificial water points may promote detrimental overgrazing (McNaughton, 1984; Archibald et al., 2005; Fuhlendorf et al., 2009; Smit and Archibald, 2019; Westlake et al., 2020).

3.6. Conclusions

Abundance maps can help to visualize spatial segregation of sympatric large herbivores in highly diverse arid savannas. Here spatial abundance may be defined by trade-offs between choosing areas with high-quality resources and reducing encounters with humans. Managers must keep on mind that reducing large herbivores perception of fear to their surroundings, apparently caused by illegal and controlled hunting, may help animals to reduce their spatial avoidance to roads and fences, thus to maximize their carrying capacity at protected areas. Regarding feeding opportunities, prescribed fire in the study area seems to contribute to landscape heterogeneity and to increase density and diversity of large herbivores.

4. THE IMPACTS OF PRESCRIBED BURNING REGIMES ON GRASS VOLUME AND TICK ABUNDANCE IN AN ARID SAVANNA: A COMMUNITY-LEVEL APPROACH

Steenbok (*Raphicerus campestris*) | ©Nicolás Fuentes-Allende

4.1. Abstract

Ticks act globally as vectors to spread a large variety of disease-causing agents. In grassland habitats, burning is often used to reduce their numbers. However, little consensus exists regarding the effectiveness of this management. Management methods, habitat type and ecological traits of the tick species may all influence the outcomes of control attempts. Additionally, management effectiveness is usually assessed in terms of tick reductions without considering wider community impacts. Here, path diagram models, built using data from 126 grassland sampling locations from a South African protected area, were used to assess the simultaneous effects of patch burning and precipitations on ticks, ungulates and grass communities. Models indicated that tick abundance was significantly lower within the first year after burning, but thereafter there were no significant effects. Burning also negatively impacted grass volume for three to four years following a burning event. Rainfall had a positive effect on both tick abundance and grass volume, and the latter also had a positive effect on tick abundance. Prescribed fire had no effect on local density of ungulates, but animals tended to disperse when rainfall increased. The results suggest that tick abundance is mainly influenced by fire, vegetation and precipitation, but not by density of their hosts, and that local density of ungulates and usage of their feeding sites was influenced by precipitation. Managers must keep on mind that controlling ticks may change composition and/or structure of ecosystems, thus monitoring simultaneous effects of their actions on non-target components is needed to assure long-term stability of their environments.

4.2. Introduction

Ticks are a concern worldwide for human health (Eisen et al., 2016; Kilpatrick et al., 2017; Mac et al., 2019), welfare of domestic and wild animals (Randolph 2000; Mansfield et al., 2017; de la Fuente et al., 2017; Spare et al., 2020), and economic activities (Jabbar et al., 2015). They parasitise every class of terrestrial vertebrates (Sonenshine and Roe 2014), and are important vectors in the spread of many disease-causing agents (Jongejan and Uilenberg 2004; Spare et al., 2020), such as viruses, parasites, and bacteria (Mansfield et al., 2017). Annual global financial losses caused by ticks have been estimated at between $14–$19 billion (Jabbar et al., 2015; Mac et al., 2019) with higher impacts in developing countries (Kivaria 2006; Narladkar 2018; Shuaib et al., 2020).

The most common methods for reducing infestation risk by ticks are habitat modifications, patch burning, acaricides (substances poisonous to mites or ticks), tick traps, and creating exclosures to separate wild and domestic hosts (White and Gaff 2018). Patch burning uses fire to create variation in the composition and structure of the plant community (Polito et al., 2013) and is often used to reduce tick densities in the environment (Cully 1999). However, its effectiveness in tick management has been questioned and may depend on the ecological traits of ticks (Mather et al., 1993; Horak et al., 2006) and their hosts (Horak et al., 2006; Allan 2009), as well as on habitat (Drew et al., 1985) and landscape (Simpson et al., 2019) variables, as well as on the fire regimes themselves (Davidson et al., 1994; Stafford et al., 1998; Cully 1999; MacDonald et al., 2018). Independently, there is consensus that long-term patch-burning regimes can keep both environmental tick density and host infestation risk low (Gleim et al., 2013; Polito et al., 2013; Gleim et al., 2019; Hodo et al., 2020). Implicitly, patch burning is a disturbance that produces changes in whole environments; its performance in pest control usually focuses on directly killing ticks, without estimating the simultaneous effects on vegetation, tick hosts, and the relationships between them.

Here I address this potential oversight by building path diagram models to assess the effectiveness of prescribed fire on ticks, and the simultaneous effects on their hosts and on vegetation. I collected data on ticks, ungulates, vegetation structure, and water availability in a South African arid savanna that has been managed long-term using regular block-burning (Docherty et al., 2020). Data were collected from patches of different burn-ages and visited from 2016 to 2018 at the end of wet and dry seasons. I hypothesised that fire would be effective controlling ticks in the environment, but with unknown impacts on other components of the ecosystem. The aim of the research was to provide evidence to managers of savanna sites on the implications of burning on different components of the environment.

4.3. Methodology

4.3.1. Study area

Data were collected at Mankwe Wildlife Reserve (MWR) (25°13’39’’S 27°17’50’’E; Figure 4.1), a 3,875 ha private game reserve located in the South African arid savanna. MWR is home to over 2,000 ungulates of 19 species, maintained principally for conservation and research purposes. The reserve does not practice direct (acaricide) tick management on animals, and their movement in and out of the reserve is prevented by a 3 m electrified perimeter fence. Rains typically concentrate during a wet season, occurring from the beginning of October to the middle of the following May (Yarnell et al., 2007), and there is limited rainfall in the period May-October. The reserve consists largely of savanna grasslands (83% cover), which are managed with a rotational block fire regime (Brockell et al., 2001). Burning is motived primarily to increase grass palatability for large herbivores, though reducing tick density is a potential secondary benefit. Each year, managers aim to burn approximately 25% of the grasslands at MWR during the dry season, using slow-burns against the wind (Yarnell et al., 2007). Each block burn is repeated every four to five years. In addition, firebreaks between blocks and around the perimeter fence are burned annually (Figure 4.1e). Non-grassland areas, such as woodland, thicket, and seasonal wetlands, are not burned as part of the prescribed fire management.

4.3.2. Tick and vegetation data

Data for ticks and vegetation were collected from 126 systematically distributed sites (Figure 4.1a) that were sampled once at the end of each dry (August-September) and wet (April-May) season from August 2016 to September 2018, resulting in five sample periods per site (three dry seasons and two wet seasons). Sites sampled all burn block areas and were separated from other sites by 500-700 m. Depending on burn-age, points were grouped in five categories, those burned: i) within the past 12 months, ii) between one and two years ago, iii) between two and three years ago, iv) between three and four years ago, and v) burned more than four years ago (Figure 4.1e). Sampling of ticks occurred during the afternoon (between 2pm and 7pm), avoiding midday high temperatures that might reduce tick activity (Walker et al., 2003), and avoiding periods of unsuitable weather (rain and windy days) or when the vegetation was wet (Cully 1999; Mierzejewska et al., 2015).

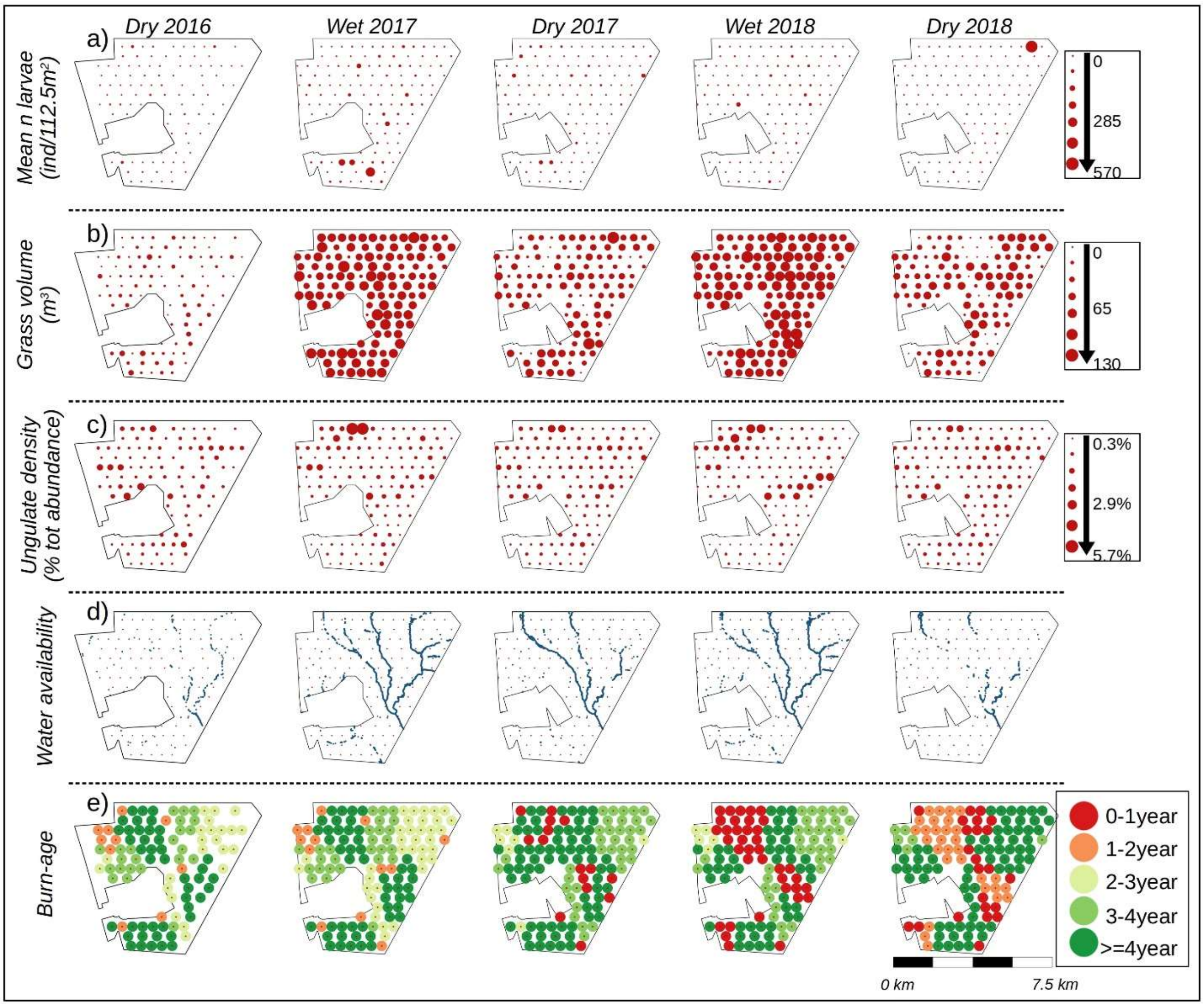


Figure 4.1. Study area. Dots indicate sample locations for the five sampling campaigns (From Dry season 2016 to Dry season 2018), and black lines represent the perimeter fence. Size of dots represents a) mean number of tick larvae, b) grass volume, and c) local density of ungulates per season. Section d) shows variation of water availability along seasons, and e) burn-age at sample location.

Ticks that are host-seeking, typically referred to as questing ticks (Rulison et al., 2013), are considered a good proxy for tick burdens on animals (Gilbert et al., 2017). Hard ticks, belonging to the family Ixodidae, were sampled at each point by drag sampling (Piesman et al., 1986; Carroll and Schmidtmann 1992; Newman et al., 2019). Drag sampling entailed dragging a 1.5 m x 1.5 m flannel cloth over the grass layer and ground litter along two parallel transects of 75 m length with randomly selected directions from the sampling location (north, south, east, west, north-west, north-east, south-west and south-east). After dragging, ticks were immediately collected from both sides of the cloth using a lint roller with an adhesive surface and stored in plastic bags for later identification. Ticks were classified, using a dissecting microscope (Olympus SZ Stereo Microscope) by life stage (larvae, nymph and adults) and species using the identification key from Walker et al., 2003. Tick abundance was calculated as the mean number of ticks in the sampling site considering both transects.

Vegetation sampling was performed after tick collection, sampling in same direction of the first drag sampling. Grass cover, defined as the area physically covered by plant parts (Herrick et al., 2005), and grass height were estimated for each point using point-intercept transects (Elzinga et al., 1998; Herrick et al., 2005; Godínez-Alvarez et al., 2009). Grass cover and grass height were recorded at 1.5 m intervals along the transect for 75 m (Elzinga et al., 1998). At each point, a vegetation sampling pin was dropped vertically, and the height of the tallest grass contacted by the pin recorded (Herrick et al., 2005). Bare ground was recorded wherever grass cover was absent or dead. Proportional grass cover was calculated as the proportion of pins that recorded at least one grass contact. In order to explore the combined effect of both grass cover and grass height on tick abundance, I included in my analysis the mean grass volume (m^3) in the sampling site (Figure 4.1b).

4.3.3. Ungulate and water data

I In addition to tick and vegetation information from sample points, data on ungulate density (see Chapter 3), the distance from a point to the nearest non-dry stream/water point, and accumulated rainfall were also collected, as described below. Ungulate density was estimated, using Density Surface Models (DSM; Miller et al., 2013) with 45 ha of spatial resolution (equivalent to a circle of radius 380 m), for each field campaign. In order to keep ungulate density comparable between sampling seasons, I calculated the proportion of ungulates at sampling sites in relation to the predicted abundance for the whole reserve for each field campaign (Figure 4.1c). Distance to nearest non-dry water sources was included as it was considered that water proximity would be related to ungulate usage/passage through an area. It was obtained from surveying all riverbeds and ponds within the reserve and georeferencing non-dry water bodies every 10 days, over the entire course of the sampling period, then measuring the distance in metres from sampling locations to the nearest water source (Figure 4.1d). Accumulated rainfall (measured in mm) for the previous 60 days prior to visiting each sampling point was obtained averaging data from four rain gauges that were located across the reserve. I considered the previous 60 days in order to capture seasonal changes in precipitation.

4.3.4. Data analysis

Structural Equation Modelling (SEM; Grace 2006) was used to estimate the simultaneous effects of burning on ticks, ungulates and grasslands from a path diagram perspective. This is a multivariate modelling approach where variables are connected to each other by causal paths, they can be both predictors and responses, and effects on response variables are estimated considering contribution of all variables simultaneously (Grace, 2006). I used a piecewise SEM approach (Lefcheck, 2016), a variation of classical SEM that allows random effects and consists of separate sub-models which are combined and linked into one global SEM.

An ecologically plausible SEM was proposed (“full model”, Figure 4.2), which included six variables (burn-age, accumulated rainfall over the last 60 days, distance to the nearest natural water source, abundance of ticks, density of ungulates, and grass volume). This consisted of four sub-models that predicted: (i) distance to nearest water source, (ii) density of ungulates, (iii) grass volume, and iv) tick abundance; and the following relationships: (i) rainfall as a predictor for distance to nearest water source, grass volume, abundance of ticks, and ungulates, (ii) distance to nearest water source as a predictor for grass volume, tick abundance and density of ungulate, (iii) burn-age as a predictor for abundance of ticks, ungulates, and grass volume, (iv) ungulate density as a predictor of grass volume and tick abundance, and v) grass volume as a predictor of tick abundance (Figure 4.2). The path diagrams were built considering positive correlations between rainfall and tick abundance (Walker et al., 2003), and rainfall and grass volume (Bucini and Hanan, 2007), a negative correlation between rainfall and density of ungulates at sampling locations (precipitations increase availability of palatable vegetation which allows ungulates to reduce local densities and spread around), and a negative correlation between distance to nearest non-dry water source and tick abundance, ungulate density and with grass volume.

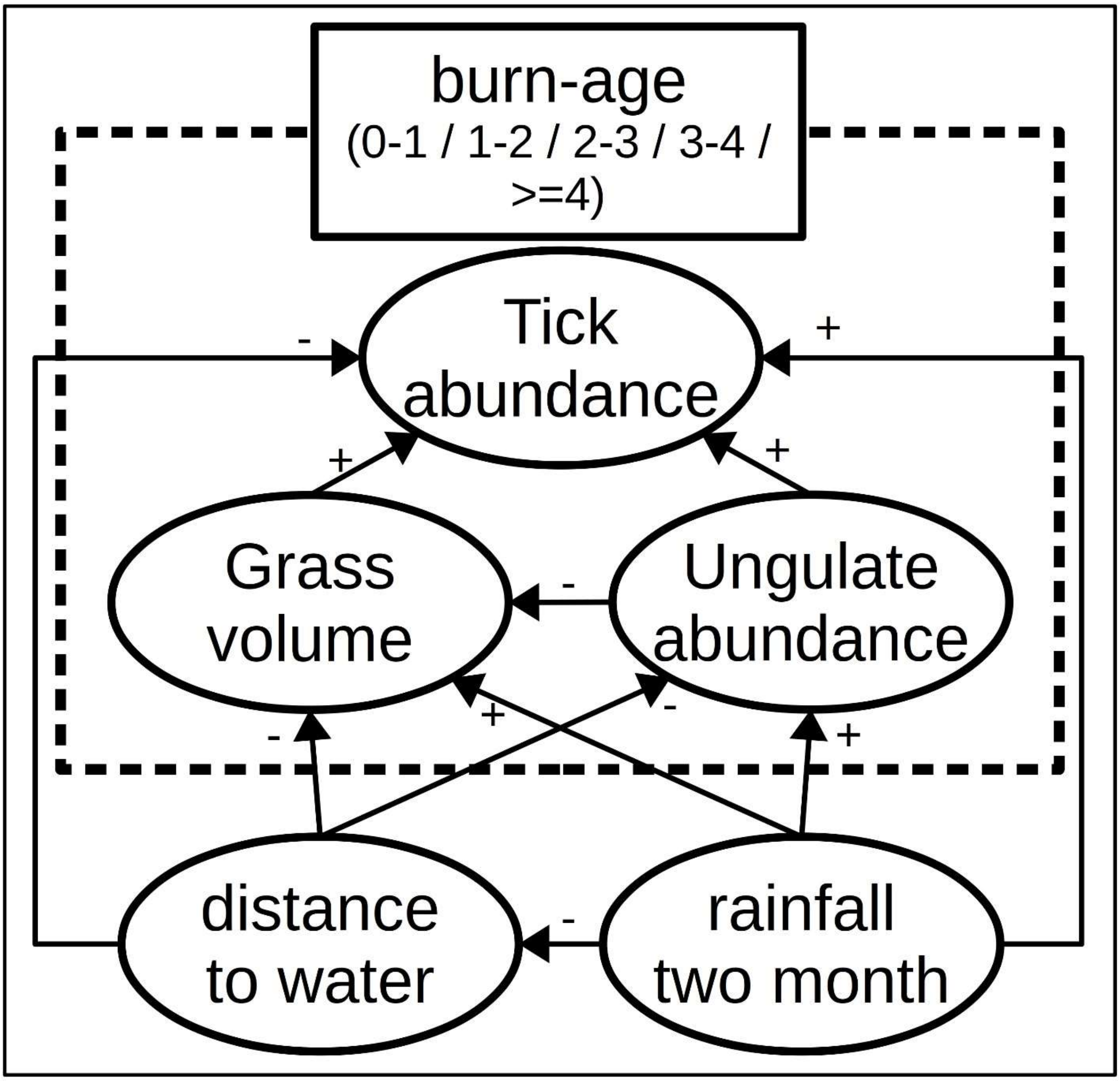


Figure 4.2. Path diagram of the hypothesized structural equation model (Full Model),

where arrows indicate pathways going from explanatory to response variables. Dashed black line encloses variables affected by burn-age. Plus and minus signs indicate positive and negative correlation between variables, respectively.

All sub-models were linear mixed-effects models LMMs with sampling points as random intercepts, and used maximum likelihood for fitting. Model quality was evaluated by observing Q-Q plots. Variables were log- (abundance of ungulates and ticks) or square root-transformed (distance to water body and accumulated rainfall) to meet normality assumptions, and scaled ($x-\bar{x}/\sigma x$) to produce standardized and comparable coefficients among predictors.

A backward stepwise approach was used to find a reduced model that best explained the data. Starting from the proposed "full model", I eliminated one term at a time and compared models with and without the term using Akaike Information Criterion (AIC; Akaike, 1974). AIC was calculated using Fisher's C statistic (Shipley, 2013). If AIC of a reduced model was smaller than or equal to the one from a previous step, I continued one more step discarding relationships. Models that did not passed directional separation tests (Fisher's C statistic P values < 0.05; Shipley 2009) were discarded. The model with the lowest AIC was considered for analysis. Models with ΔAIC <2 were considered as equivalent (Burnham and Anderson, 2002) with the one that contained the fewest relationships between variables chosen (Arnold, 2010; Richards et al., 2011).

Once a model was chosen, I estimated coefficients and described the effects of burn-age on tick abundance, ungulate density, and grass volume as well as effects of rainfall and distance to water sources and between them. Similarly, using the same selected top model, I ran a multi-group analysis by grouping data by burn-age to assess if relationships between variables differed between burn-age categories. In order to assess if my results differed between seasons, I ran the analysis three times: (i) considering all data together (global analysis), (ii) considering only dry season data, and (iii) considering only wet season data. All statistical analyses were performed using R (R version 3.5.2; R Core Team 2018). LMMs were implemented with the "lme" function of the "nlme" R package (Pinheiro et al., 2014). Piecewise SEMs and multigroup analyses were run with the "psem" and "multigroup" functions of the "piecewiseSEM" R package (Lefcheck 2019).

Estimated marginal means were calculated using “emmeans” function of the “emmeans” R Package (Lenth et al., 2020). All spatial analyses were performed using QGIS 3.4.6-Madeira (QGIS Development Team, 2019).

4.4. Results

604 out of 623 sampling locations visited were included in the analysis (352 sampling locations during the dry season, and 252 sampling locations during the wet season). Points that were excluded were confounded by anthropogenic actions outside of the described study parameters (e.g. vegetation was removed for building roads or they were fenced to exclude ungulates from their surroundings). In total, 23,801 questing ticks were collected during the five field campaigns. As a result of the low number of adults/nymphs collected (2.89% of total individuals), only larvae (23,112 individuals) were considered in the analysis. Adult tick species found were *Rhipicephalus microplus* (*n* = 619 individuals), *Rhipicephalus appendiculatus* (*n* = 32), *Rhipicephalus evertsi* (*n* = 31), and *Ixodes* spp. (*n* = 6). Due to the occurrence of a severe drought from 2015- 2016 no burning was undertaken during the dry season of 2016. Consequently, it was not possible to collect data from early post-burn points at the beginning of the study (see Table 4.1 for information about field campaigns and data collected).

None of the selected ‘best’ models fitted to global, dry and wet season data included (i) ungulate density as a predictor of tick abundance, or (ii) rainfall as a predictor of distance to water source as it was suggested (Figure A4.1). Additionally, the best model fitted to wet season data excluded the effect of grass volume on tick abundance. Table 4.2 shows further information about the candidate and selected ‘best’ models for each set of data. The effect of ungulate density on grass volume was not significant for any of the three models, and the effects of (a) distance to water source, and (b) rainfall, on grass volume were not significant in the wet season model (Figure 4.3). The selected global model showed i) significant negative effects of distance to nearest water source on grass volume and tick abundance, but a significant positive effect on ungulate density, ii) positive effects of accumulated rainfall on tick abundance and grass volume, but a significant negative effect on ungulate density, and iii) a significant positive effect of grass volume on tick abundance.

Table 4.1. Field campaigns information. Columns 1-5 show visits 1-5. Column “All visits” shows aggregated information from all campaigns. “Mean ± SD” refers to mean values ± Standard Deviation. “points in analyses” refers to points that were included in analyses. “ind/45ha” refers to ungulate individuals per 45 ha.

Field campaign	1	2	3	4	5	All visits
Season	dry	wet	dry	wet	dry	-
Year	2016	2017	2017	2018	2018	-
Date (day/month)	31/08 – 05/11	05/04 – 21/05	27/08 – 12/10	10/04 – 18/05	25/08 – 24/09	-
Accumulated rainfall (mm)	25	818	56	574	20	1492
Sampling points visited (points in analyses)	119(100)	126(126)	126(126)	126(126)	126(126)	623(604)
Total points burn-age 0-1 years old	0	0	15	37	23	75
Total points burn-age 1-2 years old	12	13	0	0	30	55
Total points burn-age 2-3 years old	31	36	7	6	0	80
Total points burn-age 3-4 years old	26	27	36	36	6	131
Total points burn-age >4 years old	50	50	68	47	67	282
Mean ± SD distance water (m)	726 ± 451	330 ± 240	372 ± 245	389.6 ± 307.1	1033.9 ± 901.6	568.7 ± 564.8
Total larvae	1586	11622	4424	3592	1888	23112
Mean (±SD) larvae	13 ± 28	92 ± 369	35 ± 57	29 ± 43	15 ± 101	37 ± 177
Mean ± SD cover grass (proportion)	0.4 ± 0.16	0.91 ± 0.11	0.67 ± 0.23	0.92 ± 0.1	0.62 ± 0.29	0.71 ± 0.27
Mean ± SD height grass (m)	0.36 ± 0.16	0.8 ± 0.19	0.62 ± 0.2	0.8 ± 18	0.67 ± 0.19	0.66 ± 0.24
Mean ± SD volume grass (m^3)	17.8 ± 12.5	82.3 ± 23.3	50.1 ± 25.3	83.7 ± 21.7	50.1 ± 27.9	58.1 ± 33
Mean ±SD ungulates (ind/45ha)	17.3 ± 7.8	14.1 ± 9.4	18.5 ± 9.3	18 ± 15.9	19.1 ± 9	17.4 ± 10.8

Table 4.2. Path diagram models fitted for Global data, Dry season data and Wet season data. Highlighted cells indicate the selected model for the global analysis, the dry season data and wet season data. “name” refers to the name of models, “Discarded” shows which relationships between variables that were included in the “full model”, were eliminated at the candidate models, where: “dw~r” refers to effect of rainfall on distance to water source, “”t~u” refers to effect of ungulate density on tick abundance, “u~r” refers to effect of rainfall on ungulate density, “u~dw” effect of distance to water source on ungulate density, “t~g” effect of grass volume on tick abundance. “AIC” refers to AIC value. “R2” is adjusted R2 for: distance to nearest water source, tick abundance, ungulate density and grass volume.

name	Discarded	AIC	R^2 dist water	R^2 ticks	R^2 ungu	R^2 grass
Global model (n=602 \\ 5 visits)						
semFULL	-	73.53	0.43	0.24	0.68	0.50
sem1	dw~r	60.00	na	0.24	0.68	0.50
sem2	dw~r / t~u	58.81	na	0.24	0.68	0.50
Dry season model (n=352 \\ 3 visits)						
semdryFULL	-	76.57	0.27	0.29	0.93	0.37
semdry1	dw~r	60.00	na	0.29	0.93	0.37
semdry2	dw~r / t~u	58.52	na	0.29	0.93	0.37
semdry3	dw~r / u~r	58.80	na	0.29	0.93	0.37
semdry4	dw~r / t~u / u~dw	59.88	na	0.29	0.93	0.37
semdry5	dw~r / t~u / u~r	57.32	na	0.29	0.93	0.37
semdry6	dw~r / t~u / u~dw / u~r	58.90	na	0.29	0.93	0.37
Wet season model (n=250 \\ 2 visits)						
semwetFULL	-	73.64	0.88	0.33	0.82	0.35
semwet1	dw~r	60.00	na	0.33	0.82	0.35
semwet2	dw~r / t~g	60.86	na	0.32	0.82	0.35
semwet3	dw~r / t~u	59.35	na	0.33	0.82	0.35
semwet4	dw~r / u~r	60.43	na	0.33	0.83	0.35
semwet5	dw~r / t~g / t~u	60.05	na	0.32	0.82	0.35
semwet6	dw~r / t~g / u~r	61.29	na	0.32	0.83	0.35
semwet7	dw~r / t~u / u~r	59.78	na	0.33	0.83	0.35
semwet8	dw~r / t~g / t~u / u~r	60.48	na	0.32	0.83	0.35

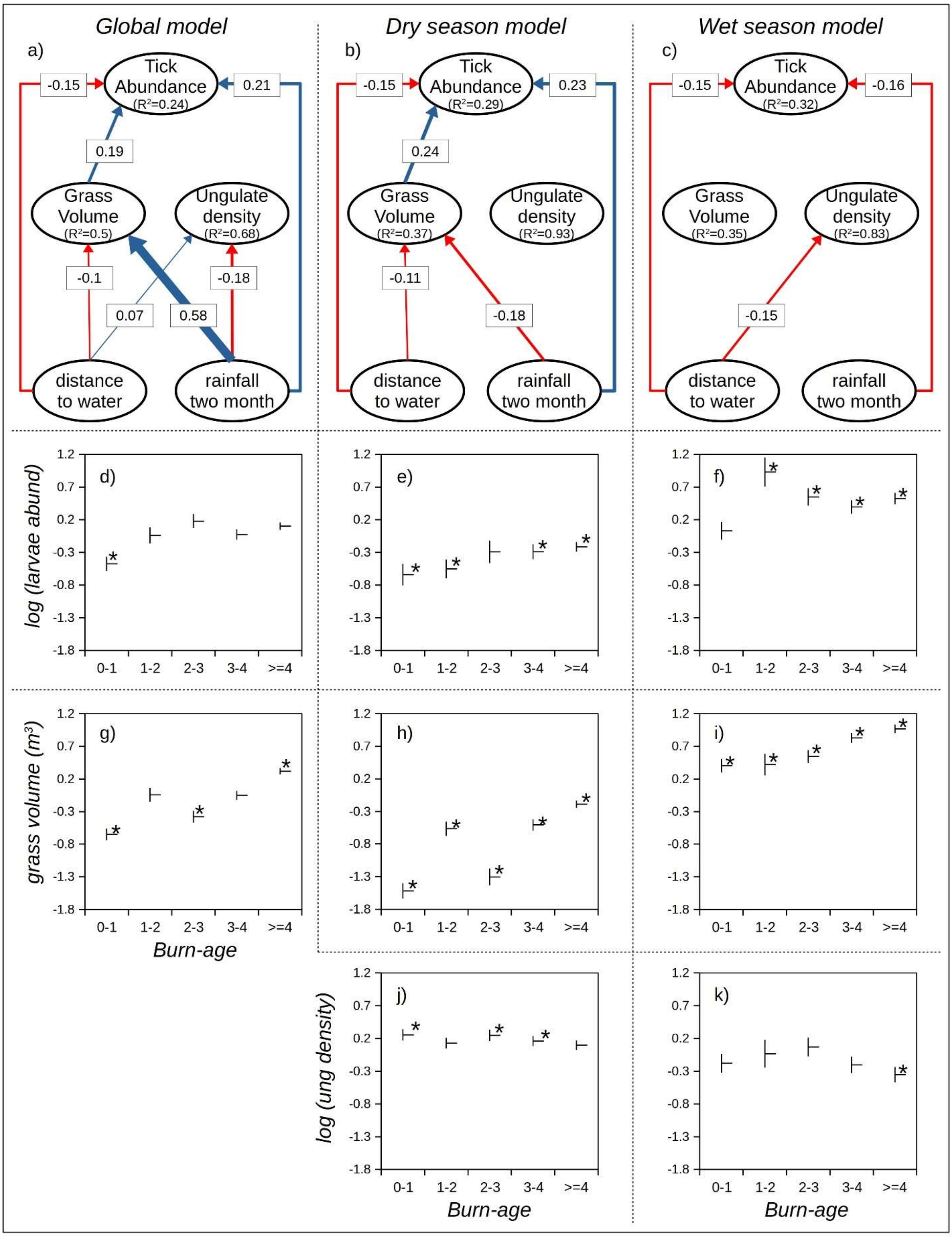


Figure 4.3. Best piecewise SEM fitted for the global model (a,d,g), dry season data (b,e,h,j), and wet season data (c,f,i,l). Path diagrams (a,b,c) only showing significant

effects. Arrows indicate unidirectional effects, where blue and red lines indicate positive and negative effects respectively. Thickness of lines depends on effect size. R2 is adjusted R2. Graphs d), e) and f) show significant estimated marginal means for larvae abundance, g), h) and i) for grass volume, and j) and k) for ungulate density respectively for differing burn-ages. Vertical lines represent standard errors and asterisks indicate significant effects. All coefficients were standardized.

In the dry season model, rainfall had a significant negative effect on grass volume. In the wet season model distance to water source had a negative effect on ungulate density, and rainfall had a significant negative effect on tick abundance.

With respect to burning, fire provoked significant changes in the abundance of ticks and grass volume for the three sets of data, and significant changes to ungulate density in the dry and wet season models.

Considering the global model, prescribed fire had a significant negative effect on tick abundance for a period of 12 months following the burning event, after which point tick numbers recovered and did not change further over subsequent time (Figure 4.3a). Additionally, the global model suggested a negative effect of burning on grass, with grass volume increasing year-on-year even four years after a burning event (Figure 4.3a). Regarding size of effects in the global model, accumulated rainfall on grass volume as well as burning within the first 12 moths on ticks and grass volume were the most influencing. On the other hand, effects of distance to water source on grass volume and ungulate density had the smallest effect size. Further details from wet and dry seasons models can be seen in Figure 4.3b-c. Finally, multi-group analysis showed that the impact of grass volume on tick abundance, and accumulated rainfall on grass volume become weaker at older burn-ages (Figure 4.4a-b). In general, rainfall had a positive effect on grass volume, but this effect was particularly high at burn-age 0-1 and 2-3 (Figure 4.4b).

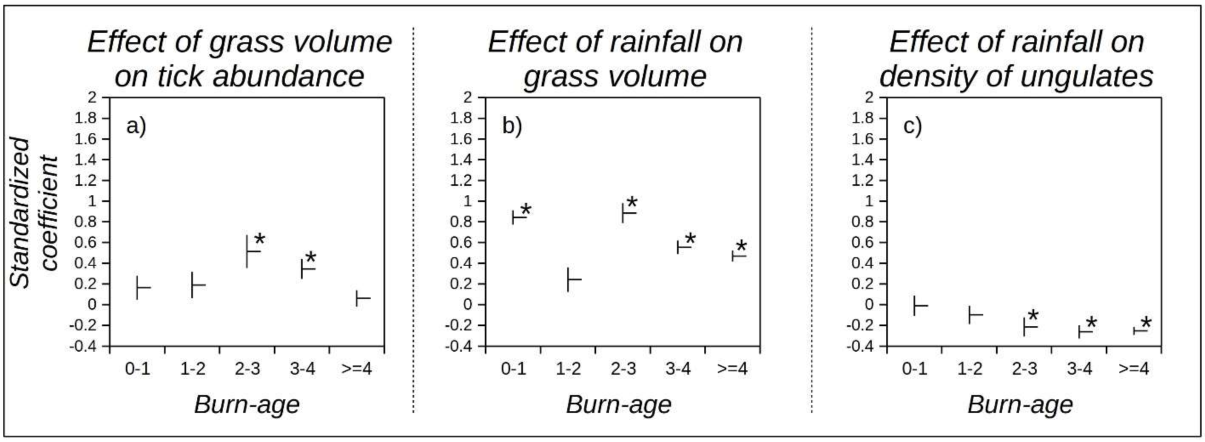


Figure 4.4. Effect of a) grass volume on tick larvae abundance, and of accumulated rainfall for different burn-ages on b) grass volume, and b) ungulate density. Values represent estimated marginal means, vertical lines are standard errors, and stars indicate significant effects. All coefficients were standardized. Graphs represent estimations for multigroup analysis of the "global model".

4.5. Discussion

To my knowledge, this study is the first to use an ecosystem approach to evaluate the effectiveness of prescribed fire on tick control as well as its host species and habitat. I show that prescribed fire is a disturbance that provokes simultaneous changes on ticks and grasslands of the savanna ecosystem, and that rainfall was also a key driver of changes in grass volume, tick abundance and ungulate density. The modelling also indicates that the magnitude and duration of the fire effects differed among the affected components, being especially detrimental to grass 'biomass'. Path diagrams were useful for assessing the simultaneous effects of patch burning on different components of grassland ecosystems. Although not considered in this study, other biotic components of savanna grasslands such as low mobility animal species (e.g. small mammals: Yarnell et al., 2007; invertebrates: Radford and Andersen 2012) and birds (Saab and Powell 2005; Docherty et al., 2020) may be affected by fire and have shown to be easy to monitor at these ecosystems. Soil nutrients should be also important to monitor when burning vegetation, because soils may become poorer if fire releases nutrients to the atmosphere

(Coetsee et al., 2010; Ponette-González et al., 2016; Verma et al., 2019) or if precipitation wash them away from just burned areas (Pereira et al., 2018).

4.5.1. Ticks

Our study shows that burning effectively reduces tick abundance for the first 12 months, following which they rapidly recovered in numbers and maintained their abundance between subsequent burn-ages. Similar results of numeric declines in ticks numbers during the first 12 months following burning, and subsequent recovery, have been widely reported in North American prairies (Barnard 1986; Wilson 1986; Mather et al., 1993; Davidson et al., 1994; Stafford 1998; Cully 1999; Allan 2009). This impact of fire on ticks may be influenced by characteristics of the burn regime employed, e.g. frequency of burning (Davidson et al., 1994; Cully 1999; Polito et al., 2013), time of year of burn (Stafford et al., 1998), and intensity of fire (Stafford et al., 1998; MacDonald et al., 2018). Gleim et al. (2013) found that, when executed over a long period of time, burn regimes can reduce the overall abundance of ticks in the environment. Although I did not evaluate tick abundance at other sites, it is possible that MWR has lower numbers of ticks than nearby unmanaged/natural places because the burning program has been running for more than 20 years in this protected area and animals are isolated inside the reserve. A comparison of ticks loads between grassland at MWR and similar sites with less regular burn regimes (e.g. Pilanesberg National Park) would be a useful follow-on piece of work to explore the role of burn regularity on tick numbers.

Rainfall, through increasing grass volume as well as its direct effects on ticks, was the main factor that positively increased tick abundance (McCabe and Bunnell 2004; Burtis et al., 2016). This may be explained by precipitations increases grass biomass, thus microhabitat for ticks. Rainfall may also influence density of key hosts (Ostfeld et al., 2006), nevertheless I could not find a significant effect of ungulate density on tick abundance. A North American study on lone star ticks (*Amblyomma americanum*) found fire was effective in reducing tick numbers, but these numbers were not related to presence of their ungulate host (bison; Cully 1999). My results at MWR are consistent with this finding. Future research may include multiple techniques for collecting ticks from the environment (White and Gaff, 2018; Newman et al., 2019). Tick drag methodology seemed to be effective over grass cover, but its effectiveness was reduced over bare ground and shrub cover.

4.5.2. Grasslands

Grass volume was the variable in the models that was most affected by fire, with burning having a negative impact on volume for up to three to four years. In addition to that, some large herbivores are certainly attracted to feed on newly re-growing grasses following burning events (O'Kane and Macdonald 2018), as some regrowth is suggested to be more nutritious (van Oudtshoorn, 2014). Despite that, I did not find significant effects of ungulate density on grass volume. Both concatenate events may suggest managed grasslands are kept under a continuous pressure in the study area, caused by frequent patch burning and subsequent foraging pressure from large herbivores, and this may be negatively affecting grass volume. Although fire can promote diversity in savanna ecosystems (Cowling et al., 1997; Govender et al., 2006; Driscoll et al., 2010), when burn regimes are not well executed, they can reduce richness and increase dominance of generalist and invasive species (Favier et al., 2004; Uys et al., 2004). This negative impact may be amplified by high concentrations of ungulates grazing recently burned areas which could become dominated by grazing tolerant species (Du Toit and Cumming 1999), at the expense of those species considered most palatable (Sankaran 2005; Klop and van Goethem 2008).

4.5.3. Ungulates

Increases in rainfall were negatively related to ungulate density. Considering rainfall is positively related to grass volume, the overabundance of new and highly palatable grass when rainfall increases may explain the recorded decreases on local ungulate density. Animals have no need to congregate and feed at specific sites if high nutritious grasses are growing everywhere at the local scale (area-restricted search; Curio 1976; Kareiva and Odell 1987). Surprisingly, I did not find significative relationships between local density of ungulates and abundance of ticks. My results suggest that the main drivers of tick abundance are precipitation and grass characteristics. Nevertheless, density of other key hosts that were not monitored in this study, such as rodents and other small mammals (Ostfel et al., 2006), may be influencing tick density in the environment. Further research, that includes monitoring the broad community of tick hosts in savanna ecosystems, is needed. My findings also suggest that rainfall has a negative effect on ungulate usage of older burned areas (from two years after being burned to never burned). Reductions in density at old patches may be motivated by the flushes of nutritive vegetation after precipitation events in recently burned areas (O'kane and Macdonald, 2018). Grazers and mix-feeders prefer to feed on grasslands if palatable grass can be found there, and only browsers keep using old-burned areas (Staver and Hempson, 2020).

4.6. Conclusions

Prescribed fire reduces questing ticks in the environment for a period of approximately 12 months after its application, but it is also detrimental to the grass layer with a negative effect on grass volume for up to three to four years after burning. My well documented impacts on changes to the grass layer should make managers wary of repeat burning areas too frequently in savanna ecosystems. Regarding my findings, prescribed fire in the study area may not be efficient controlling ticks in natural savannas, thus it may be reviewed. The extent to which different inter-burn intervals may affect soil and vegetation composition at a longer term is a subject worthy of more research effort. Such research would provide a better understanding of how a balance might be obtained between the potential beneficial effects (on ungulates) of nutrient return to the soils, and hence nutritious regrowth, and reduced tick burden versus longer term changes to the nutritional quality of the vegetation sward. In addition to monitoring tick abundance, I also recommend that managers monitor the state of grasslands when implementing burning programs, as well as to monitor other potential hosts (e.g. small mammals, carnivores, birds) and the quality of soils (Driscoll et al., 2010; Corey et al., 2019). Fires are needed for keeping the natural cycle of African savanna (Cowling et al., 1997; Burrows, 2008). From my results, I cannot confirm that abundance of ticks in the environment relates to density of ungulates. I recommend density data from other key tick hosts should be included in future studies to investigate associations between density of hosts and ticks. Parasites are a component of ecosystems, therefore any effort to control them have consequences on other components. Managers must keep on mind that controlling ticks may change composition and/or structure of ecosystems, thus they have to monitor simultaneous effects of their actions on non-target components if they want to keep long-term stability of their environments.

5. GENERAL DISCUSSION

Waterbuck (*Kobus ellipsiprymnus*) | ©Nicolás Fuentes-Allende

In this thesis, I have evaluated the effects of seasonal variation of essential resources, human-caused fires and human presence on the field ecology of large herbivores, their parasites, and their habitat in a managed arid savanna. The findings should advance our understanding of the functioning of managed savanna ecosystems (especially African savannas), help managers to improve the effectiveness of their management actions, as well as identifying any negative side effects of management on non-target species or components of the ecosystem. Management of large herbivore populations is widespread and motivated by various interests, such as academic research (Clutton-Brock et al., 2002), protecting threatened populations (Cosse and González, 2013), maintaining populations as a natural resource (Milner-Gulland et al., 2004), minimizing negative effects on humans (Hubbard and Nielsen, 2009) or the environment (Russell et al., 2001), and for economic reasons (Conover, 2002). In this closing chapter I will start by describing the main findings for each one of my particular studies, and then discuss the findings in relation to the management of large herbivores in seasonal environments, and their fear of humans in non-hunted species. I will go on to discuss the benefits of monitoring the effects of prescribed fire at an ecosystem scale (considering more than just immediate targets of management), and the importance of conducting long-term studies for monitoring the management of large herbivores. I will end the chapter by briefly considering more holistically what the combined results of the individual chapters mean for the management of large herbivores, and for the field of ecology and conservation more generally. I will also discuss how future research could build on the findings of the thesis.

5.1. Summary of main findings

In Chapter 2, I proposed and tested a novel technology to automatically and remotely monitor the body mass of identified (or non-identified) ungulates over time, and without human presence, using weighing scales in the field. The proposed method was tested in the South African arid savanna, and was shown to monitor successfully the changing body mass of eight ungulate species of contrasting mass and ecology. Red hartebeest, blue wildebeest and greater kudu were the three species that used the scale most, and hence permitted the most detailed studies of body mass phenology within and across seasons. I found that variation in body mass was correlated to seasonality, decreasing during the dry season, when water and green vegetation are scarcer, and increasing during the wet season when natural resources are more abundant. I also found that variation in body mass matched with the phenological events of individuals (Côté and Festa-Bianchet, 2001; Loarie et al., 2009; Killeen et al., 2014; Debeffe et al., 2017; Paoli et al., 2018; Barker et al., 2019), such as females losing weight during the calving season (Borowske et al., 2018; Ayotte et al., 2019; Festa-Bianchet et al., 2019) or animals getting heavier from one year to the next due to annual body growth (Pelletier and Festa-Bianchet, 2006; Mainguy and Côté, 2008; Brivio et al., 2014). A similar method has been previously applied in temperate and temperate montane species: alpine ibex (e.g. Decristophoris et al., 2007; Bergeron et al., 2010; Brambilla et al., 2018), bighorn sheep (e.g. Pelletier and Festa-Bianchet, 2004; Moquin et al., 2010; Festa-Bianchet et al., 2019), mountain goat (e.g. Mainguy et al., 2009; Godde et al., 2015; Castro et al., 2018), and white-tailed deer (Therrien et al., 2007). Nevertheless, those studies have focused on the long-term changes of body mass, and the data collection has not been totally automated as it was here. There is great potential for such automated weighting stations to be used across sites that manage large ungulates to monitor the health of populations. The technology is relatively low-cost and easy-to-deploy and maintain and has been proven to work successfully for monitoring large herbivores. This permitted, for the first time (to our knowledge) an assessment of the changing body condition of savanna ungulates on a near-daily basis. Such data has the potential to revolutionize management of wild savanna ungulates, as changes such as the rapid loss in body condition across a population, and hence the need for management interventions, could be identified as very early stages before severe negative impacts occur. There is scope for future development of the weighing site site-up to encourage a greater diversity, or different suite of animals to use such systems. More open scale system (i.e. without surrounding brush to funnel individuals onto the scales) might encourage species that avoid enclosed areas to use the scales, as might simply situating the scales on natural walkways to, for example, water. The salt blocks could easily be replaced by carrion to attract and monitor carnivores onto the scales and more careful levelling of the base of the scales with surrounding land,

and the use of matched covering substrate might also encourage more skittish animals to use the system. It was notable that Impala, as the commonest ungulate on the reserve, were rarely recorded on the sets of scales. The use of smaller, more mobile scales could make rapid deployment of scales, and extended deployment of scales in different areas more feasible, which could permit finer-scaled understanding of factors determining body condition in species.

In Chapter 3, I mapped the seasonal distributions of 16 large herbivore species in a private game reserve in South Africa, and explored the environmental and anthropogenic factors that may explain their spatial abundance. I found, rather unexpectedly, that animals were non-uniformly distributed within the reserve, in terms of their core areas of occupancy, with spatial abundance differing among species and seasons. Before this study, our expectation was that species of similar feeding guilds would respond to management in a relatively uniform way. Hence, more specialist feeders were expected to track recent burns, bulk feeders would focus their time around older, long swards and browsers would tend to stick to the same areas of high bush/tree cover, though avoiding newly burned areas. Instead I found that there was no common trend in distribution and abundance that could be related to vegetation structure and water availability. This could be a consequence of niche segregation theory which states sympatric species can coexist because they differentiate their preferred food items and habitats to reduce interspecific competition (Pansu et al., 2018; Boyers et al., 2019; McShea et al., 2019; Kihwele et al., 2020). However, such theory does not necessarily dictate that species would be spatially segregated. Anthropogenic factors were found to impact the spatial abundance of seven species. These species, which had highly variable body masses and likelihood of being targeted for hunting, tended to avoid areas with high vehicle traffic and areas in the proximity of perimeter fences, often with quite extensive avoidance distances. Such avoidance of humans, or human structures, among species has rarely been reported and, for impacted species, this could markedly affect carrying capacities in fenced reserves, and be particularly acute in smaller reserves where it is not so easy to remain distant from fence-lines. Given the increased preponderance of smaller, fenced protected areas in the landscapes of developing nations, this effect merits further future research. The mechanism by which this avoidance occurred was unknown but may be influenced by controlled hunting occurring more frequently near roads, illegal poaching near perimeter fences, or might simply reflect an avoidance of more disturbed areas. My findings suggest human activities, which may include hunting and poaching, may affect the whole community of large herbivores in multi species environments, and be detrimental for the management of non-hunting target species, because fear towards humans may reduce their fitness through displacement to sub-optimal areas or reducing foraging behaviours as in hunting target species.

Finally, in Chapter 4, I used path diagram models to explore the simultaneous effects of prescribed fire on ticks, grasslands and large herbivores that inhabit a seasonal arid savanna. I found that prescribed fire significantly reduced the abundance of ticks in the environment during the first year after its use, but that tick numbers bounced back to previous densities within 12 months. In contrast, the impacts of fire on grass volume lasted for three to four years after the burning event. Importantly, at the densities of wild ungulates present across the study site, there was no impact at all of typical ungulate densities in a region on tick abundance. This might be a response of a lagged effect between ungulate numbers in previous seasons and tick numbers (which merits further exploration), or it might be that other factors, such as habitat conditions determine tick abundance. We can conclude however that burning is relatively ineffective in controlling tick numbers in block burn regimes such as occurred in our study system. Rainfall, by contrast, was the most important factor contributing to increased tick abundance and grass volume. Tick abundance was significantly affected by rainfall, grass volume and prescribed fire. Both this study and the study presented in chapter 3 highlight the importance of monitoring non-target components when assessing the success of management actions, especially if these actions may have impacts across an ecosystem.

5.2. Management of large herbivores in seasonal environments

Precipitation regimes define livestock and large herbivores production in many seasonal environments (Derner et al., 2020; Raynor et al., 2020). Variability in precipitation can change the productivity of vegetation and affects water availability, both of which impact upon the dynamics of large herbivores, both directly and indirectly (Malpeli et al., 2020).

This makes seasonal environments challenging for managers of sites that host large herbivores because they continuously have to match animal demands with forage availability (Illius et al., 1998, Reid et al., 2014; Apollonio et al., 2017).

Managers of isolated sites must monitor precipitation on a yearly basis for calculating the large herbivores annual carrying capacity of their lands, because the first will inform them about the vegetation biomass production for the year. If annual density is above the annual carrying capacity, population sizes can be artificially reduced by various means, including culling, hunting or translocation off-site [the latter often via wildlife auctions in South Africa] (Raynor et al., 2020). The alternative is to allow the system to naturally regulate and result in increased mortality and declining condition of many individuals. In small, fenced sites, natural regulation approaches run the potential risk of widespread population collapse and even local extinction. An alternative strategy for coping with annual variations in scarcity of resources is to artificially provide those resources, such as creating man-made water points (Chamaillé-Jammes et al., 2016; Weeber et al., 2020) or burning grassland to maximize its production (Bothma and du Toit, 2016). Climate models can help managers and researchers to predict the amount and variability of precipitation in the long-term (Raynor et al., 2020), and managers usually have strategies to cope with resource scarcity in areas of high variability. However, anthropogenic climate change is making precipitation less predictable in seasonal savannas and other productive environments (Trenberth, 2011; Engelbrecht et al., 2015), which brings with it the risk of novel climatic conditions forming, for which managers have no prior experience. Modelling of changing body conditions in relation to environmental conditions could help to predict what the impacts of such changes might be, on both individuals and populations.

The impacts of recent and future climate change on large herbivores will vary greatly across the world. It is predicted that climate change will increase foraging areas for arctic ungulates which, as a result, could increase local densities and/or modify migration routes (Rivrud et al., 2019). It has even been suggested that enhancing large herbivore numbers in some arctic regions could help to limit climate change impacts by restricted scrub growth and hence increasing albedo (Zimov, 2005). It has also been suggested that large herbivores trampling of snow in such regions could reduce the insulating effects of snow-cover and hence reduce permafrost thaw (with consequent enhanced emission of the 'super greenhouse gas' methane).

By contrast, climate change is increasing desertification in many arid environments (Malakoutikhah et al., 2019), as a result of shorter and drier rainy seasons (Engelbrecht et al., 2015) and increasing drought frequency (Knapp et al., 2008). This directly impacts vegetation productivity in these ecosystems, especially affecting the grass layer (Abraham et al., 2019). Special care will be needed to sustain grazer numbers in these ecosystems (Abraham et al., 2019; Staver and Hempson, 2020). In other semi-arid areas increases in scrub cover have been attributed to changed carbon dioxide levels, which favour some vegetation types (e.g. Stevens et al., 2016). When forage is scarce many grazers migrate to alternate areas where nutritious vegetation can be found. Given that climate change is predicted to reduce precipitation across whole biomes, grazers may be forced to increase migratory distances or to concentrate in, and over-exploit, remaining feeding areas (Perkins, 2019). Moreover, the increased fragmentation and fencing of remnant natural areas mean that many former migratory ungulates can no longer migrate to avoid harsh conditions and instead must survive year-round at a single site, potentially resulting in lower overall carrying capacities at a landscape scale. In South Africa, springbok and black wildebeest both formerly undertook large over-land seasonal migrations in response to changing seasonal availability of resources. The prevention of such natural migrations led to the near extinction of Black Wildebeest, possibly contributed to the extinction of the Quagga, and has likely resulted in much reduced populations of blesbok and springbok in South Africa (Harris et al., 2009).

Although managers are largely unable to control the impacts of climate change on grasslands, they could reduce other stressors on grazers such as enhancing water availability (Fullman et al., 2017), and also work to open up former fenced areas to permit migrations among sites of variable resources. Such fence removal has occurred very successfully around Kruger National Park, most notably resulting in the development of the Greater Limpopo Transfrontier Park. At a more local scale to the study site uses in this thesis, the adjacent Pilanesberg National Park was part of a ambitious local plan to link it to another large but distant national Park (Madikwe National Park, Ndabeni et al., 2007) but this ‘game corridor seems now to have been all but abandoned due to competition with platinum mines in the connecting land.

Unlike grazers, mixed-feeders may be more adaptable to the current and future seasonal regimes in savanna environments. Their dietary plasticity could facilitate alteration to food preferences to minimise impacts of periods of scarce grazing. Instead of seeking nutritious grazing in drought periods, they may be able to switch to browsing woody vegetation, which typically accesses deeper soil-water than do grasses and hence can often produce forage in dry periods. This may allow browsers to become more dominant in savanna environments (Abraham et al., 2019; Staver and Hempson, 2020).

5.3. Fear of humans in non-hunted species

Fear of humans is a non-lethal impact (often a result of hunting) on large herbivores (Frid and Dill, 2002; Stankowich, 2008). Perceived fear of humans can even exceed fear of natural predators (Ciuti et al., 2012), and induces avoidance. In order to reduce the perceived predation risk caused by humans, many large herbivores modify their behaviour to avoid people (Teckentrup et al., 2018). They can also alter their habitat selection (Grignolio et al., 2011), home ranges (Brown et al., 2020) and local distributions (Frid and Dill, 2002; Journeaux et al., 2018) to minimise human interactions. When such modified behaviour is not warranted, these modifications likely carry costs for individuals (Spitz et al., 2019; Brown et al., 2020), which may reduce their survival and reproduction rates. Even though perceived fear towards humans has been used in management strategies for reducing human-wildlife conflicts (Cromsigt et al., 2013), pest control (Krijger et al., 2017; Bedoya-Pérez et al., 2019) and protecting threatened species (Gaynor et al., 2020), the unintended effect on non-target species has not been widely explored and is still poorly understood. Individuals from the same (Grignolio et al., 2011; Spitz et al., 2019) and different species (Mendes et al., 2020; Nickel et al., 2020) that are not a target for hunting but share an environment with hunting-targeted individuals may also perceive humans as predators, and therefore could be indirectly threatened by hunting activities. Such behaviours were observed in Chapter 3, where four species that are not hunted at the study site (eland, gemsbok, giraffe and red hartebeest) nonetheless avoided areas where hunting/poaching tended to occur and responded similarly to hunting-target species. This unintended effects of hunting on non-target species might be considered by managers in areas where hunting occurs and where they aim to maximize carrying capacity of large herbivore populations. Despite habituation to humans being common in protected areas and other lands where there is no anthropogenic harassment (Marino and Johnson, 2012; Schroeder et al., 2018), the transition period for changing from human avoidance to tolerance has been little studied and is an area of potential future research. The effect of hunting on non-target species may be a constraint for increasing their population sizes, and therefore oppose management goals. Managers should consider these hereto unintended consequences of hunting in multi-species environments, as this could be detrimental for the whole community of large herbivores. Assessing the 'ecology of fear' dynamics for all the species of the community is necessary to better anticipate and mitigate unintended consequences for non-target species (Gaynor et al., 2020). Actions such as restricting hunting areas, altering method of hunting and hunting dates, particularly during important reproductive periods, and identifying and understanding the stimuli that provokes fear in non-target species may help to mitigate unintended risk effects on non-target individuals (Gaynor et al., 2020).

It is necessary to clarify that I did not directly measure hunting/poaching activities in the study area, and its association to specific spatial characteristics was assumed considering both personal and staff observations. Hunting was usually executed by the manager when driving his car on main roads during daytime, and poaching occurred near the perimeter fence by external people using dogs and rifles at night. Poaching with snares was also identified as a type of hunting occurring in the reserve, nevertheless finding these traps was opportunistic and rare which made impossible to estimate its spatial distribution (Mudumba et al., 2021). Future studies should focus on directly measuring hunting/poaching activities instead of proxies of their presence to improve our knowledge about how fear to humans modifies the spatial distribution of large herbivores.

5.4. Using an ecosystem approach to monitor effects of prescribed fire

Prescribed fire is an ecosystem disturbance that is used to accomplish diverse management goals, such as controlling undesired species (Waldrop and Goodrick, 2012), ecosystem restoration (Izbicki et al., 2020), maximising biodiversity (Archibald and Hempson, 2016; Beale et al., 2018), modifying wildlife habitat (Hunter and Robles, 2020), and hazardous fuel reductions (Fernandez-Carrillo et al., 2019). Although its application may cause alterations at the ecosystem level, and may promote undesired impacts on soils (Fonseca et al., 2017; Akburak et al., 2018; Klimas et al., 2020), water quality (Harper et al., 2018; Hahn et al., 2019), and biodiversity (Fultz et al., 2016; Harper et al., 2018; Hunter and Robles, 2020), assessments of the 'success' of burn management normally focuses on measuring impacts on the components of interest only. Hence, for many years burning to promote higher quality forage for ungulates in savanna wildlife systems have focussed on the impacts on ungulates only, with almost no consideration of the impacts on other key taxa such as other mammals (Yarnell et al., 2007), birds (Docherty et al., 2020), insects, reptiles and amphibians.

By considering the reported simultaneous effects of burning (to enhance ungulate forage) on ungulates, ticks and the grass coverage, I highlighted that the differential response of the various affected elements and their very different recovery times. Fire provokes ecosystem-level impacts, therefore its success must be monitored at an ecosystem level. As an example, my findings suggested that prescribed fire helps maintain a diverse community of large herbivores in my study area through increasing vegetation heterogeneity. However, fire was ineffective in controlling parasites in the environment, and resulted in detrimental impacts on the grass layer (even if it did improve forage quality in the short to mid-term). To better understand the effects that prescribed fire may have on their lands managers could usefully monitor changes in the composition and structure of the vegetation layer, as well as tracking impacts on, for example: species with low mobility, such as reptiles, arthropods, amphibians and small mammals. Also of key importance in understanding the effects of burning grasslands is its impact on the chemical and physical composition of the soil, and on water quality and occurrence in the environment. By removing dead litter, burning will almost certainly increase temperatures at ground level and maybe more extensively, and will remove valuable shade shelter for many species. Hence, burn management is likely to have unintended, and poorly documented consequences on both microclimates and microhabitats in the landscape.

5.5. The value of long-term studies to monitor the management of large herbivores

Management actions are usually motivated by an immediate need, and associated research is usually short-term in nature. As a result, the effectiveness of actions are usually assessed only over the near-term. Despite my research has only gathered field information from three consecutive years, this period of monitoring allowed me to detect some undesirable effects of management actions on both large herbivores and on the structure of the grasslands themselves. Previous research at the same site (Docherty et al., 2020) has also identified short-term impacts of burning on non-target bird species. Management actions also often have long-term effects that are not always clear in the short-term. Such long-term effects have been shown in terms of population dynamics (Coulson et al., 2004; Bocci et al., 2012), structure and species composition of large herbivore communities (Speed et al., 2019), herbivore-plant interactions (Lecomte et al., 2016) and trophic cascade effects at the ecosystem level (Kiffner et al., 2017). Maintaining long-term monitoring programmes for large herbivores is difficult, because of budget constraints and due to the fact that objectives may change over time. However, those long-term monitoring programmes of wild herbivores that do exist have been useful for understanding population dynamics (e.g Soay sheep *Ovis aries,* Coulson et al., 2001; red deer, Clutton-Brock et al., 1982; bighorn sheep, Coltman et al., 2003; moose, Vucetich and Peterson, 2004; review Clutton-Brock and Sheldon, 2010), and have helped improve management strategies. Long-term studies may help managers to monitor their performance and adapt their strategies to confront future scenarios (Raynor et al., 2020). Such studies can provide information that helps reduce future uncertainties, and to increase the success and sustainability of their actions. These programmes have also allowed us to understand the effects that natural factors have on populations, like those related to weather (Boyce et al., 2006; Gaillard et al., 2013), and the population itself (e.g.

density, Owen-Smith, 2006; age structure Coulson et al., 2001), as well as to understand the effects that management itself could have on non-target components of ecosystems (Apollonio et al., 2017). Long-term studies are necessary for monitoring the management of large herbivores, because it allows managers to understand and prevent unwanted results (Apollonio et al., 2017), help them to be better informed about how to adapt to future scenarios (Raynor et al., 2020), as well as to prevent the degradation that their actions may have over their ecosystems (Lecomte et al., 2016).

Due to their value as both a wildlife tourism and as a harvesting resource, large ungulates have been well monitored in many of the numerous small game reserves that now occur across South Africa. The potential for such monitoring (at least in terms of population numbers) to continue long-term, and for the costs of which to be covered by site managers, as part of their operations, opens up the possibility for novel long-term study datasets to be established in African savannas. Such long-term studies would help provide new insight into the management of these valuable ecosystems which, to date, are often managed on the basis of short-term studies. There is great, but potentially under-exploited opportunities to establish cost-effective long-term monitoring studies in African savanna systems.

Large herbivores inhabiting managed savannas are affected by seasonal changes in the availability of food resources and the effects of human activities on them and their environments. Each one of the research chapters from this thesis has shown that monitoring and analysing information from environmental and anthropogenic factors can help researchers to better understand the ecological dynamics in these environments as well as the impacts on the fitness, survival and reproduction of individuals. Improving our knowledge of seasonality, fear of human, and the effects of management actions on different components of the ecosystem will be essential to enhance the management of such systems. Further research is needed to better understand the effects of such factors on the large herbivores that inhabit managed lands or that are managed. Future work should consider large herbivores communities that inhabit both managed and unmanaged savanna habitats, In this way, researchers will be able to compare the effects of human activities on large herbivores with similar natural processes (e.g. predation) and improve the management of these species in both managed and unmanaged environments.

5.6. Conclusions

Throughout my thesis I have shown that ecological management of large herbivores in seasonal environments is challenging. Despite the fact that there is much information concerning the creation and maintenance of highly productive savannas (Bothma and du Toit, 2016), more research is needed to understand how such management impacts on the ecology of both large herbivores and the rest of the ecosystem. Variations in seasonality and the impacts of management actions over focal and non-focal components of the ecosystem oblige managers to be continuously adapting their strategies to accomplish their management goals. In addition, there is an urgent need to consider more fully the potential impacts of anthropogenic climate change on these fragile and finely balanced savanna ecosystems. The methods that I have piloted and developed in thesis should go some way towards improving our understanding of how these systems might alter when faced with novel conditions, which in turn should help managers to prevent degradation of savannas and to ensure their future continuity.

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APPENDIX

Common Warthog (*Phacochoerus africanus*) | ©Nicolás Fuentes-Allende

Table A2.1. Total large herbivores hunted and captured to sell during study period (2016-2018). “M” refers to male, “F” to female, “TH” to total hunted, “C” to captured.

Species	***Scientific name***	**2016**				**2017**				**2018**			
		M	**F**	**TH**	**C**	**M**	**F**	**TH**	**C**	**M**	**F**	**TH**	**C**
African Buffalo	*Syncerus caffer*	0	0	**0**	**0**	0	0	**0**	**0**	1	0	**1**	**0**
Blesbok	*Damaliscus pygargus phillipsi*	26	4	**30**	**0**	41	62	**103**	**61**	33	28	**61**	**35**
Blue Wildebeest	*Connochaetes taurinus*	61	46	**107**	**40**	26	49	**75**	**52**	45	50	**95**	**50**
Common Duiker	*Sylvicapra grimmia*	0	0	**0**	**0**	0	1	**1**	**0**	0	0	**0**	**0**
Common Eland	*Taurotragus oryx*	4	0	**4**	**2**	6	7	**13**	**5**	4	2	**6**	**0**
Common Warthog	*Phacochoerus africanus*	0	2	**2**	**0**	4	4	**8**	**0**	6	4	**10**	**0**
Gemsbok	*Oryx gazella*	2	1	**3**	**0**	1	2	**3**	**0**	0	3	**3**	**0**
Giraffe	*Giraffa camelopardalis*	1	0	**1**	**0**	0	1	**1**	**0**	0	0	**0**	**0**
Greater Kudu	*Tragelaphus strepsiceros*	9	9	**18**	**4**	12	13	**25**	**9**	3	2	**5**	**5**
Impala	*Aepyceros melampus*	30	4	**34**	**0**	39	6	**45**	**0**	48	39	**87**	**42**
Ostrich	*Struthio camelus*	0	0	**0**	**0**	1	1	**2**	**0**	1	0	**1**	**0**
Plains Zebra	*Equus quagga*	47	11	**58**	**0**	8	26	**34**	**27**	15	16	**31**	**18**
Red Hartebeest	*Alcelaphus buselaphus caama*	3	3	**6**	**0**	3	7	**10**	**4**	13	14	**27**	**19**
Sable Antelope	*Hippotragus niger*	0	0	**0**	**0**	0	0	**0**	**0**	1	0	**1**	**0**
Southern Reedbuck	*Redunca arundinum*	2	1	**3**	**0**	2	0	**2**	**0**	2	1	**3**	**0**
Tsessebe	*Damaliscus lunatus*	1	1	**2**	**0**	3	0	**3**	**0**	3	2	**5**	**0**
Waterbuck	*Kobus ellipsiprymnus*	4	1	**5**	**0**	5	13	**18**	**14**	3	15	**18**	**14**
	Total	**190**	**83**	**273**	**46**	**151**	**192**	**343**	**172**	**178**	**176**	**354**	**183**

Table A2.2. Description of models selected for female blue wildebeest. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

s(week)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	1.0059	0.01868	53.84	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(week)	3.014	3.531	22.5	7.74E-10
		s(ind id)	4.488	5	13.68	5.47E-09
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.791	-72.288	0.0008806	40	6
s(ndvi 2 months)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	1.0072	0.01788	56.34	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(ndvi 2 months)	5.963	6.953	11.94	1.95E-08
		s(ind id)	4.486	5	13.14	1.54E-08
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.797	-65.994	0.0008569	40	6

Table A2.3. Description of models selected for female greater kudu. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

s(week)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	0.99374	0.01744	57	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(week)	8.088	8.772	25.98	<2e-16
		s(ind id)	27.368	28	62.1	<2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.837	-603.83	0.001794	389	29
s(ndvi 2 months)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	0.99233	0.01698	58.43	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(ndvi 2 months)	4.338	5.35	18.53	<2e-16
		s(ind id)	27.191	28	47.57	<2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.791	-570.06	0.002297	389	29

Table A2.4. Description of models selected for male greater kudu. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

s(week)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	0.99088	0.04231	23.42	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(week)	6.028	7.183	19.36	<2e-16
		s(ind id)	9.892	10	117.81	<2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.946	-112.04	0.0008442	70	11
s(rain freq 2 months)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	1.00504	0.03639	27.62	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(rain freq 2 month)	1	1	18.18	7.03E-05
		s(ind id)	9.676	10	41.31	< 2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.859	-95.573	0.0022137	70	11

Table A2.5. Description of models selected for female red hartebeest. “edf” is effective degrees of freedom, “Ref.df” is reference degrees of freedom, “ML” is marginal likelihood, “Scale est.” is estimated scale parameter, “n” is sample size, and “ind” is number of different individuals.

s(week)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	0.98167	0.02318	42.35	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(week)	3.864	4.667	21.59	8.04E-15
		s(ind id)	8.65	9	30.71	< 2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.778	-155.82	0.0014221	96	10
s(ndvi 2 months)	*Parametric coefficients*	*Parametric term*	*Estimate*	*Std. Error*	*t. value*	*Pr(>|t|)*
		Intercept	0.98296	0.02286	43.01	<2e-16
	Approx significance smooth terms	*Smooth term*	*edf*	*Ref.df*	*F*	*p-value*
		s(ndvi 2 months)	1	1	82.24	1.85E-15
		s(ind id)	8.605	9	26.78	< 2e-16
		R-sq(adj)	*ML*	*Scale est*	*n*	*ind*
		0.752	-157.14	0.0015899	96	10

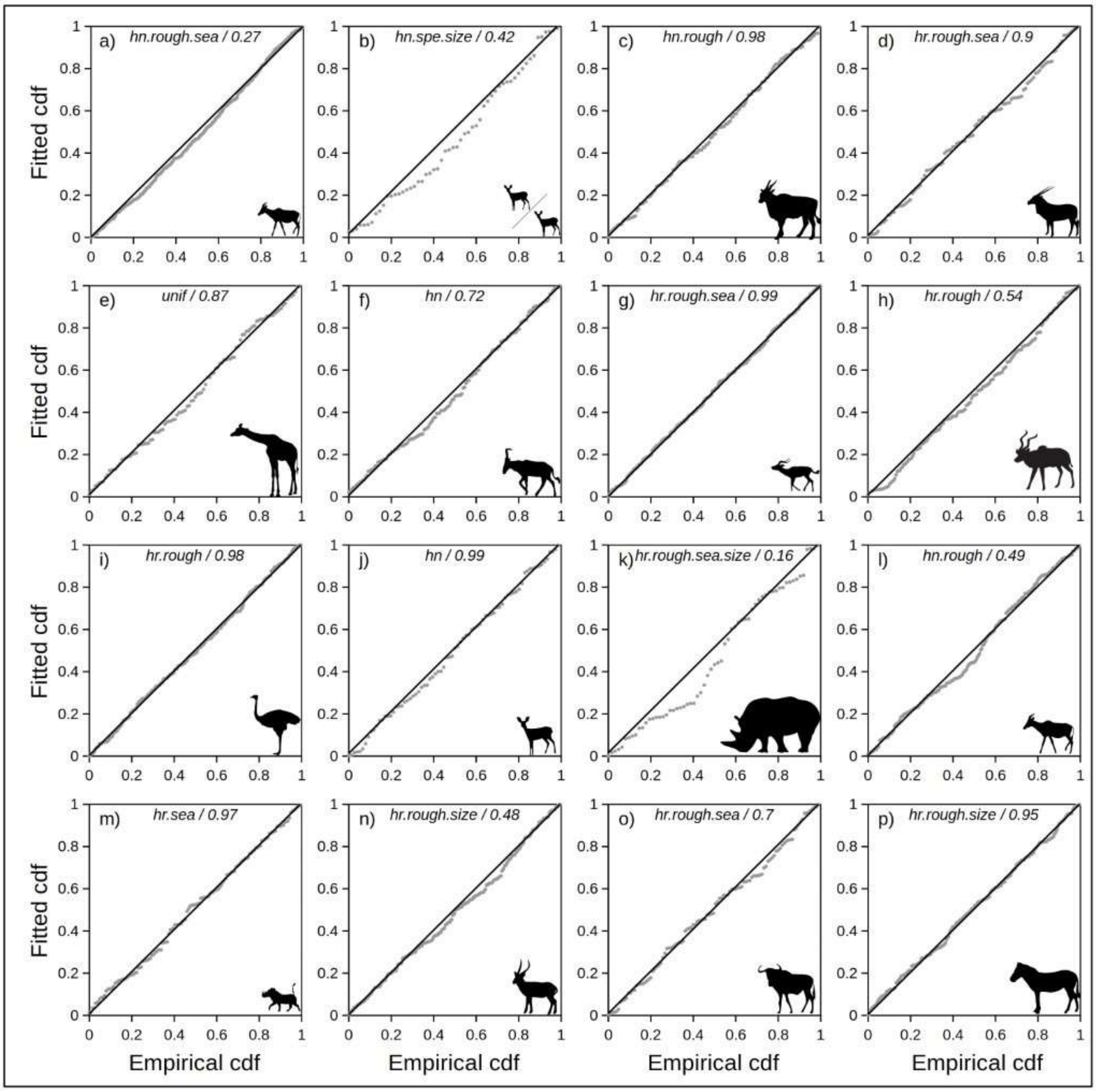

Figure A3.1. Q-Q plots of selected detection functions, where a) blesbok, b) duiker/steenbok, c) eland, d) gemsbok, e) giraffe, f) red hartebeest, g) impala, h) great kudu, i) ostrich, j) reedbuck, k) white rhino, i) tsessebe, m) warthog, n) waterbuck, o) blue wildebeest, p) zebra. Name of model selected / Cramer-von Mises p-value are indicated at upper side of each plot.

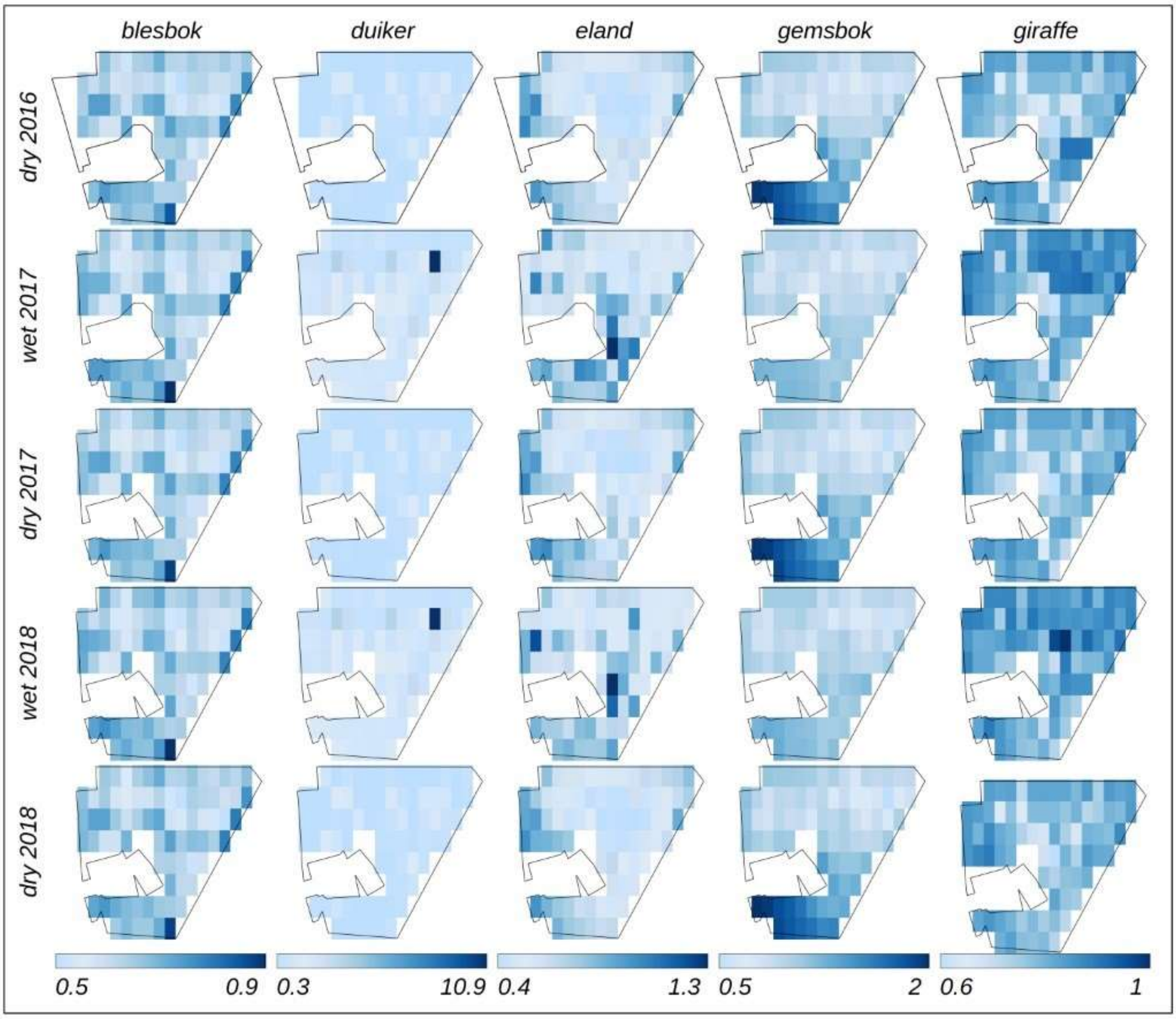

Figure A3.2. Distribution of the coefficient of variation for blesbok, duiker, eland, gemsbok and giraffe (columns) for each sampling campaign (rows).

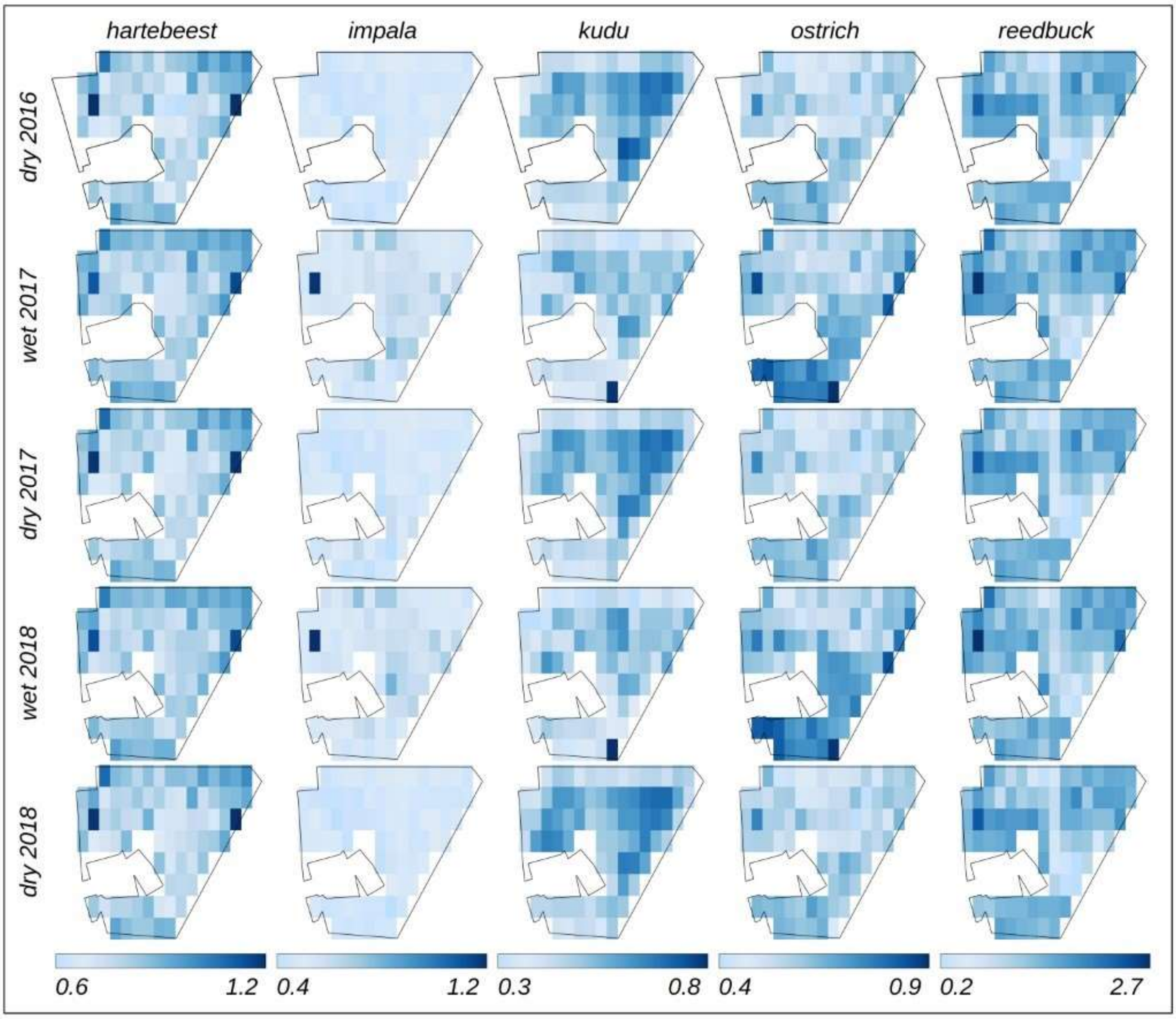

Figure A3.3. Distribution of the coefficient of variation for red hartebeest, impala, greater kudu, ostrich and reedbuck (columns) for each sampling campaign (rows).

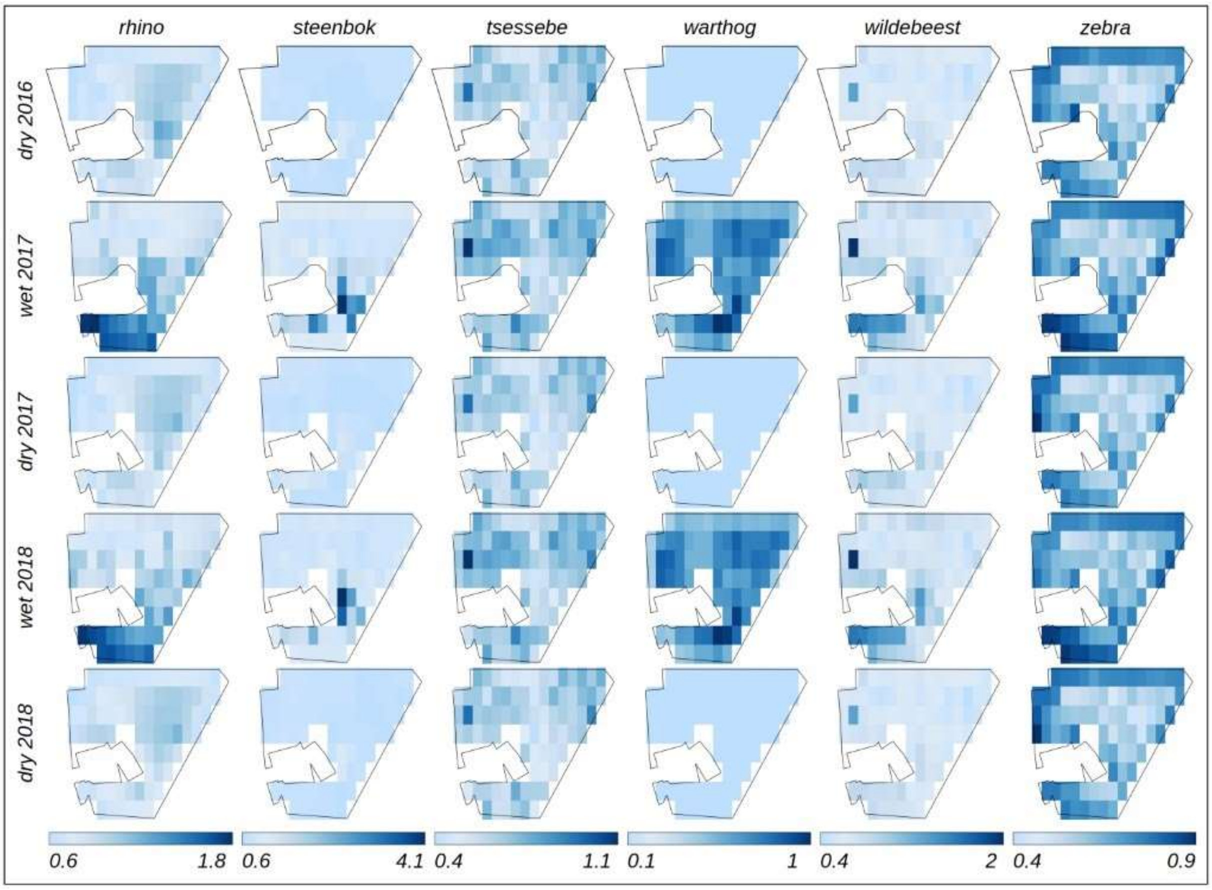

Figure A3.4. Distribution of the coefficient of variation for white rhino, steenbok, tsessebe, warthog, blue wildebeest and zebra (columns) for each sampling campaign (rows).

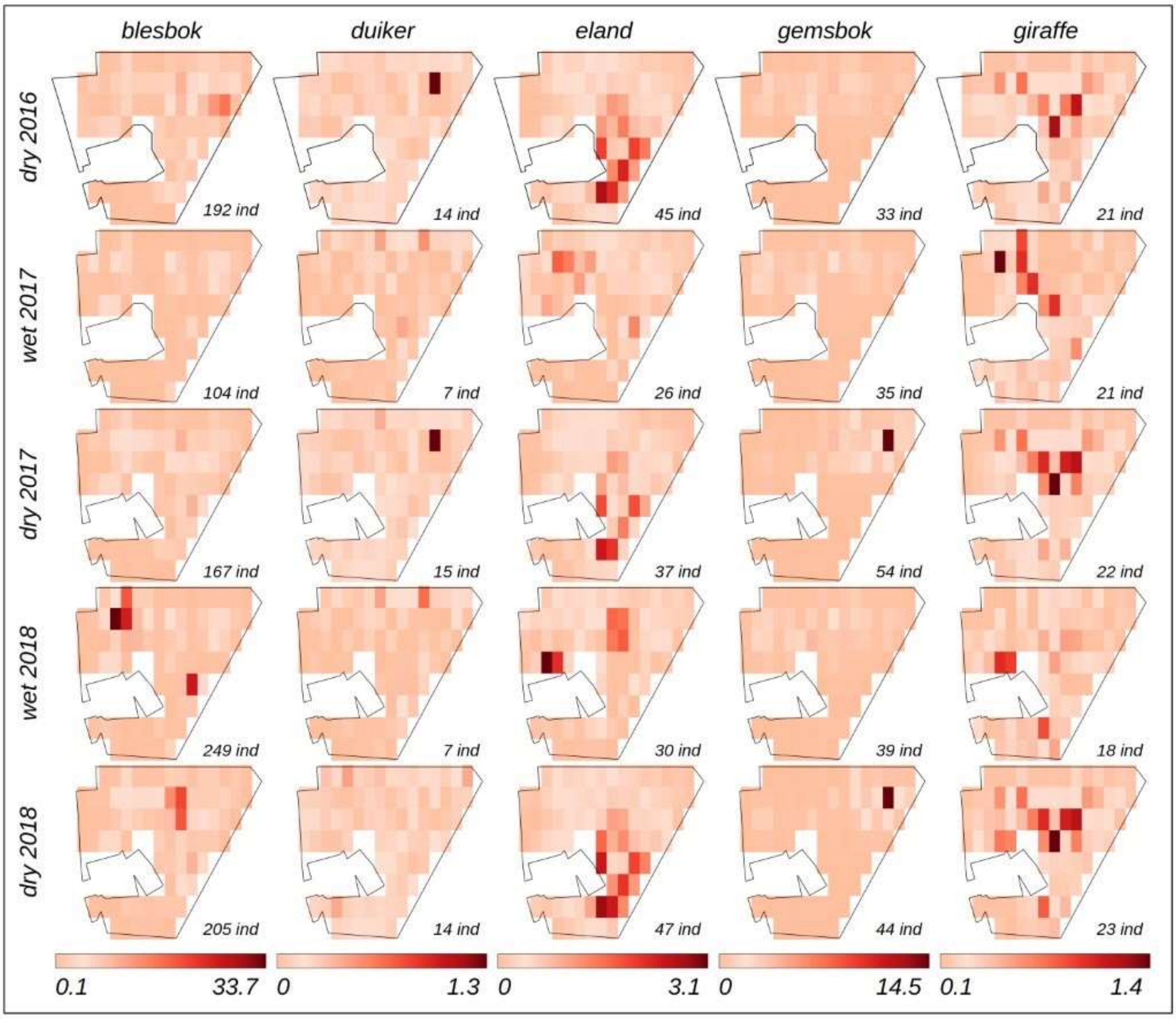

Figure A3.5. Spatial abundance of blesbok, duiker, eland, gemsbok and giraffe (columns) for each sampling campaign (rows). Values at the right of each map indicate total abundance predicted for the sampling campaign. Intensity of red indicates number of animals per segment.

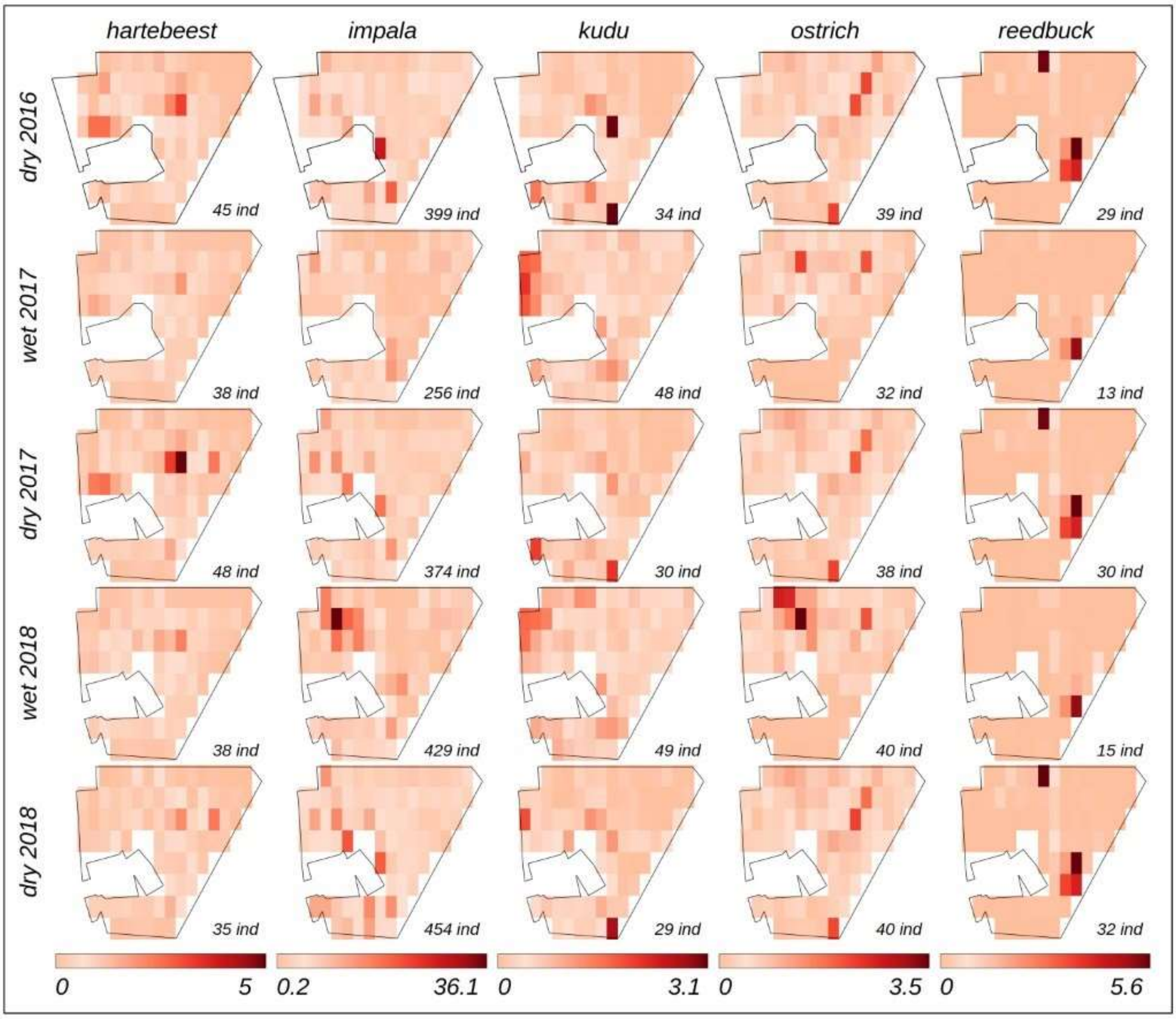

Figure A3.6. Spatial abundance of red hartebeest, impala, kudu, ostrich and reedbuck (columns) for each sampling campaign (rows). Values at the right of each map indicate total abundance predicted for the sampling campaign. Intensity of red indicates number of animals per segment.

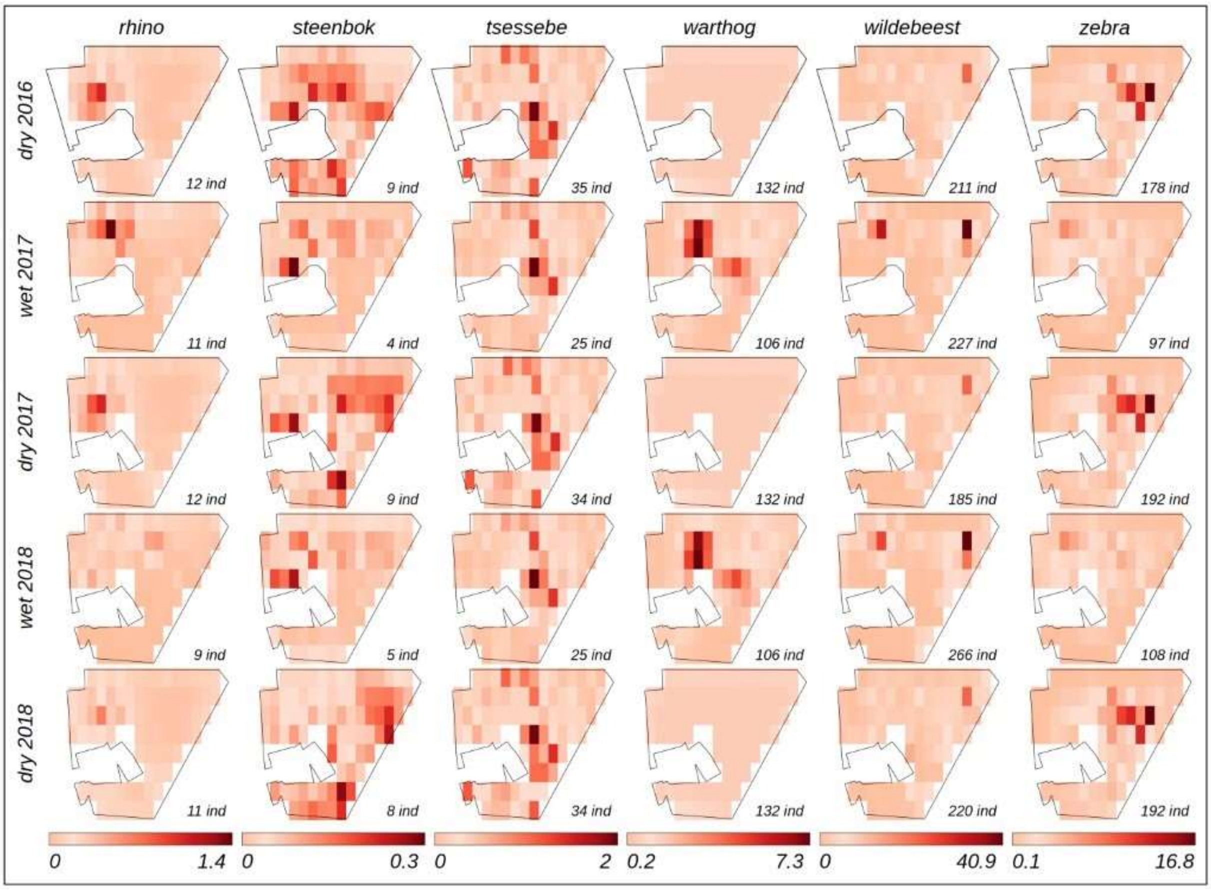

Figure A3.7. Spatial abundance of white rhino, steenbok, tsessebe, warthog, blue wildebeest and zebra (columns) for each sampling campaign (rows). Values at the right of each map indicate total abundance predicted for the sampling campaign. Intensity of red indicates number of animals per segment.

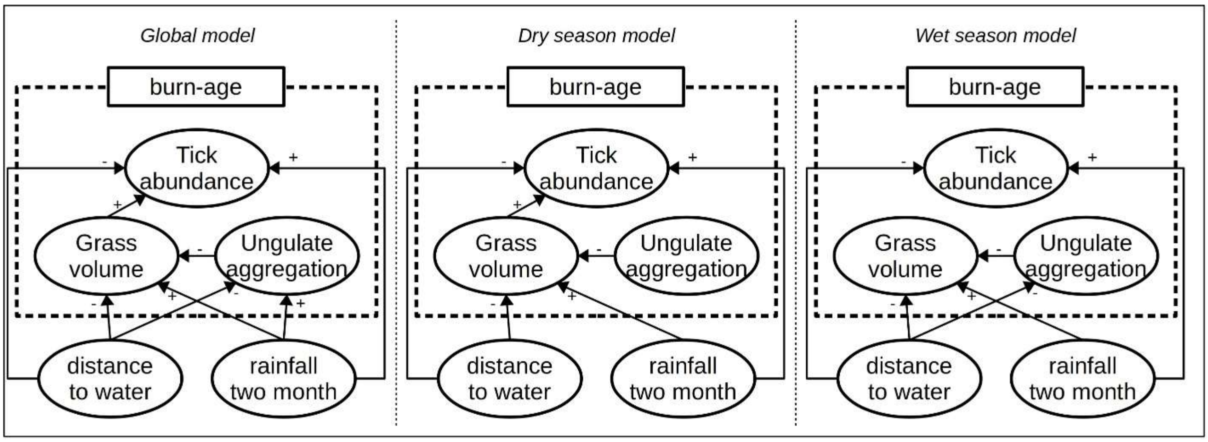

Figure A4.1. Best path diagram of the hypothesized structural equation model for the global model, dry season data, and wet season data, where arrows indicate pathways going from explanatory to response variables. Dashed black line encloses variables affected by burn-age. Plus and minus signs indicate positive and negative correlation between variables, respectively.