Potential ecological factors contributing to springbok (*Antidorcas marsupialis*) population declines in the southern Kalahari, Botswana

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Disclaimer

I declare that this work was completed by myself at the Okavango Research Institute (University of Botswana) and was carried out in accordance with the University of Botswana regulations. The dissertation is an original work except where reference is made and it has not been submitted for any award at other universities.

Signature:

Date:

Dedication

To my favourite women; my mother Itumeleng Moatswi for the support throughout my life and believing in me; and to my late grandmother Neo Moatswi for raising me to be the person I am today.

Abstract

The springbok (*Antidorcas marsupialis*) population in the southern Kalahari, Botswana has declined precipitously in recent years, but the primary causes of this decline are not known. Springbok play an important role in the ecosystem, so understanding the possible causes of their decline is essential for conservation of the species and ecosystem management. This study identifies possible factors that could contribute to the declining springbok population in the southern Kalahari. Most of the remaining springbok inhabit the Schwelle area of the southern Kalahari, with a small proportion of that population in Mabuasehube. The study was conducted in both locations.

Herd composition counts and demographic ratios were used to quantify seasonal changes in recruitment rates by comparing the ratios of each demographic category to adult females. The effects of season and location on herd size, herd composition and demographic ratios were assessed. Larger herds were recorded during the wet than the hot and cold dry seasons. The effects of season and location were significant for herd composition and demographic ratios. The reduction in the juvenile: adult female ratio recorded in this study from 0.37 during the wet season months to 0.10 during the cold dry season suggests a low recruitment rate that could be contributing to low springbok numbers. A high ratio of juvenile: adult female was recorded in the Schwelle, so the results highlight the importance of protecting this region as a wet season calving range.

We sampled vegetation characteristics in sites used by and available to springbok to determine forage selection criteria. Springbok used sites with diverse, short grass species in all seasons. Short, diverse shrubs characterised springbok browsing sites. Highly selective species like springbok may experience nutritional stress when forage is scarce and this could compromise reproductive success and survival.

Seasonal changes in resource availability determine the location of home ranges, daily movements and habitat selection; these were studied using data from GPS collars that were deployed on five herds of springbok. Home range sizes were larger during the wet than the hot and cold dry seasons. Springbok covered longer distances during the wet than the hot dry season. Movement may have been restricted by high temperatures during the hot dry season, among other factors. High quality resources and reduced predation risk associated with pans were probably important determinants of springbok habitat use.

These results highlighted the importance of protecting habitats like pans, which offer critical resources, for conservation of springbok and the ecosystem. The decline in springbok numbers could be caused by low recruitment rate. A lack of rain could lead to low forage quality especially during the late months of pregnancy and during lactation when the nutritional demands for females are high. This could lead to low recruitment of juveniles. More studies on recruitment rates over a longer time period using marked individuals should be conducted. Movement between key habitats should be maintained to facilitate migration between wet and dry season ranges. A declining springbok population could have cascading impacts on the resident large predators, with possible ecosystem wide consequences. Predicted impacts of climate change in Botswana, including higher temperatures and lower rainfall, could exacerbate these problems and cause further declines in arid-adapted antelopes such as springbok.

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Thesis outline

Chapter One provides a general background about the study and the Kalahari ecosystem. The chapter discusses the different factors that influence population demographics, foraging behaviour and habitat selection patterns of herbivores. The chapter also introduces the study, and provides the problem statement, objectives of the study, and a brief description of materials and methods. Chapter Two presents results on seasonal changes in springbok herd composition and age structure in the Mabuasehube and Schwelle regions of the Southern Kalahari with a focus on herd composition counts, herd sizes and demographic ratios. The chapter highlights the importance of protecting the Schwelle as a wet season range for herbivores in the southern Kalahari. It also gives an overview of factors that could lead to low recruitment rates of juveniles. Chapter Three identifies forage characteristics that determine springbok foraging patterns. It compares forage characteristics between sites used by and available to springbok and between habitats in each season. The results highlight the importance of functional resource heterogeneity in springbok foraging sites. Chapter Four presents results on seasonal changes in springbok home range sizes, daily distance movements and habitat selection ratios. The chapter highlights the importance of springbok movement between different pans for productive springbok populations. Chapter Five presents a synthesis to the overall study, management implications of the results to springbok conservation, limitations of the study and recommendations for future research.

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Chapter One - General introduction

1.1 Introduction

African savannas are important in supporting a high diversity and abundance of wild herbivores (Smithers, 1983; Scholte et al., 2007). However, these species face population declines caused by factors such as anthropogenic pressures and climate change (Lande, 1993). Historically, there was co-existence between pastoral communities, their domestic animals and wildlife, however changes in land use and developments have disrupted movements of both domestic and wild herbivores (Boyce, 2006; Bartlam-Brooks et al., 2011; Fynn, 2012). Most protected areas are limited in supporting the needs of migratory species that access seasonal resources by moving between habitats that offer functionally different resources (Harris et al., 2009; Fynn and Bonyongo, 2011). These movements are important as adaptive responses to environmental gradients and patchy rainfall, thereby maintaining the carrying capacity of both domestic and wild animal populations (Owen-Smith, 2004; Fryxell et al., 2005).

Habitat loss and fragmentation

Arid and semi-arid environments experience patchy rainfall, frequent droughts and hot dry seasons (Ellis and Swift, 1988) that force wildlife populations to depend on their mobility to access spatio-temporally heterogeneous habitats to cope with environmental variability (Illius and O'Connor, 1999; Fryxell et al., 2005). This involves adaptive movements between habitats varying in forage quality and quantity to meet seasonal nutritional requirements for survival and reproduction (Fryxell et al., 2005). Habitat loss and fragmentation prevent populations from moving between habitats, thus restricting animals to a small portion of land (Brook et al., 2008).

Increasing human populations and developments result in human wildlife conflict by encroaching into some habitats and fragmenting connected landscapes (Newmark, 2008; Fynn and Bonyongo, 2011), resulting in isolated wildlife populations (Primack, 2002). Habitat loss and fragmentation restrict access to key seasonal resources and decrease habitat quality, which could affect species survival and cause population declines (Brook et al., 2008) and possible extinction (Rybicki and Hanski, 2013).

The decline in wildlife populations in Africa is attributed to land use and habitat changes (Ogutu et al., 2016). In Kenya, the decline is caused by the lack of effectiveness of wildlife conservation policies, strategies and practices (Ogutu et al., 2016). In Botswana, an increase in the number of cattle posts and veterinary cordon fences disrupted ungulate movements across the Kgalagadi (Verlinden and Masogo, 1997; Mbaiwa and Mbaiwa, 2006). Cattle posts and settlements make it difficult for wildlife to access their historical wet season range, known as the Schwelle region, which has good grazing pastures and nutritious resources (Verlinden and Masogo, 1997). Past studies have emphasised the importance of protecting the Schwelle, which forms part of the Wildlife Management Areas (WMAs) of southern Kalahari (Williamson et al., 1988; Selebatso et al., 2018b).

Seasonal herbivore foraging behaviour

Seasonal variation in forage influence habitat selection (Owen-Smith, 2002; Valeix et al., 2009) and cause seasonal changes in diet (Manousidis et al., 2016) as animals strive to meet daily and seasonal resource requirements for survival and reproduction (Fryxell et al., 2005). Herbivore populations adapt to variation in forage resources and surface water availability by selecting different habitats in different seasons (Zweifel-Schielly et al., 2009; Sianga et al., 2017). In tropical systems seasonal migrations between wet and dry habitats are governed by water (Muposhi et al., 2016) and are important in maintaining individual fitness and a stable population (Illius and O’connor, 2000; Owen-Smith, 2004). During the wet season, rain fills seasonal pans and herbivores move from their dry into their wet season ranges, undertaking the reverse journey at the beginning of the dry season (Sianga, 2014). In addition to water availability, forage quality plays a role in determining herbivore distribution and habitat selection patterns (McNaughton, 1988).

Forage quality and quantity in habitats determine diet selection and intake rates (Farnsworth and Illius, 1998) thus influencing survival and the ability to meet nutritional requirements. Short grasses are highly digestible and richer in nutrients than tall grasses, so they are selected by herbivores during the wet season to maximise energy and protein intake rates, particularly for pregnant and lactating females for reproduction and growth (Kreulen, 1975; Parker et al., 2009). In the Kalahari, Botswana, short saline grasslands in pans are key wet season habitats for blue wildebeest (*Connochaetes taurinus*) and springbok (Selebatso et al., 2018b), while the Serengeti Plains are a key wet season habitat for herbivores in East Africa (Kreulen, 1975; Maddock, 1979). When forage quality declines during the dry season, herbivores tend to feed on plants that are less preferred in the wet season (Knight, 1991; Ben-Shahar and Coe, 1992).

Herbivores cope with changing resource availability over the annual cycle by foraging on functionally different plant species in different habitats and seasons (Owen-Smith, 2002). Thus, functional wet season habitats provide high quality resources of sufficient energy, nutrients and minerals for reproduction, growth and maintenance requirements during the wet season. Functional dry season habitats provide forage that acts as reserve resources, usually eaten during the late dry season after favoured resources have been depleted or are not accessible. Dry season resources are generally low quality resources that can buffer herbivore populations during drought periods, thus preventing starvation and ensuring survival (Illius and O'connor, 2000; Owen-Smith, 2002). Reducing access to heterogeneity by restricting movement, habitat loss and fragmentation could therefore affect population viability.

Predation

Predation does not affect all herbivores equally: large predators consume large prey species, while small predators consume small prey, however, small prey are more vulnerable because they are easier to capture and kill and both large and small predators can consume them (Hopcraft et al., 2010). Predation can exert a greater impact on small herbivores when they are hunted by both small and large predators (Hopcraft et al., 2010). In declining populations, predation could lead to overall population declines, especially when there is a high removal of juveniles (Mills and Mills, 2016). The impact of predation on herbivores is not only on the number of individuals hunted but also on the age distribution of the kills (Sinclair et al., 2003). During the mating season males are searching for mates so they are more likely to be detected and hunted by predators (Mysterud et al., 2005). Predation of lactating females increases mortality of females and offspring and prevents reproduction and recruitment into the adult stage (Rughetti and Festa-Bianchet, 2014).

Predation can regulate herbivore populations (Ogutu and Owen-Smith, 2005) and it influences vigilance (Underwood, 1982) and distribution of herbivores (Russell et al., 2003). Large groups of individuals are more vigilant because many eyes see more and increase the chances of early predator detection (Childress and Lung, 2003). Small groups are vulnerable to predation because they are less vigilant (Burger et al., 2000). Some herbivores favour wooded habitats where predation risk is low (Creel et al., 2005), while in landscapes dominated by ambush predators, prey species select open habitats that offer greater visibility for predator detection (Hay et al., 2008; Massé and Côté, 2009). Predation pressure can drive herbivore movements to areas with lower predation rates and migrants may experience lower predation rates than resident species (Hebblewhite and Merrill, 2009). Some African herbivores reduce predation risks by moving to open areas for early predator detection (Valeix et al., 2009).

Anthropogenic factors

Herbivores must access different habitats in different areas to obtain diverse resources (Owen-Smith, 2002). However, fences (Boone and Hobbs, 2004) and development activities have disrupted these movements and could cause population declines (Holdo et al., 2011). Developments and agricultural activities block migratory routes to areas with key seasonal resources (Bartlam-Brooks et al., 2011; Fynn, 2012). Blue wildebeest in Nairobi National Park, Kenya declined because of urbanisation, fencing and developments blocking access to areas with abundant wet season resources (Ogutu et al., 2013). The restriction of wildebeest movement in the Serengeti, Tanzania, could affect the population by preventing migration to seasonally productive areas (Holdo et al., 2011). Natural processes such as drought, diseases, floods and competition for resources are uncontrolled and they affect population numbers and could also contribute to low recruitment rate (Sinclair et al., 2007; Western et al., 2009; Geldmann et al., 2013).

Anthropogenically-induced climate change can increase temperatures, frequency of droughts and also change seasonal rainfall patterns (Ogutu and Owen-Smith, 2003), which can cause alterations in the growth, abundance and distribution of plant species (Wang et al., 2002). This can change habitat selection and distribution of herbivores (Luzhang et al., 2005), cause shifts and changes in home ranges sizes (Hu and Jiang, 2011) and impact population dynamics (Wang et al., 2002). Lack of nutritious forage following scarce rainfall may force animals to forage on areas of low nutritional value (Marshall et al., 2009). Climate change predicts high temperatures which may limit animal movement further and restrict access to areas with better forage quality therefore compromising fitness and reproduction (Martin et al., 2015). Climate change may cause changes in ecosystem health, functioning and impact particular herbivore populations (Hu and Jiang, 2011).

1.2 Problem statement

The 2012 and 2015 nationwide aerial censuses of Botswana conducted by the Department of Wildlife and National Parks (DWNP, 2012; 2015) highlighted a 71% decline in the springbok population and a contraction of their range between 1992 and 2012, but the primary causes of this decline remain unknown. Further research is required to understand the reasons behind this downward population trend and recommend appropriate management responses. In Botswana, the majority of the springbok population inhabits the Schwelle area of the Kgalagadi region, with a small proportion of that population in Mabuasehube. However, the population declined across all protected areas, including in the Central Kalahari Game Reserve (CKGR; DWNP, 2012).

Lion (*Panthera leo*) and cheetah (*Acinonyx jubatus*) likely exert some influence on springbok populations, with springbok representing 29.4% of lion kills in South Africa and Namibia (Hayward and Kerley, 2005) and 26.3% of cheetah kills in nine study sites in South Africa and Namibia (Hayward et al., 2006). In the Southern Kalahari, springbok comprised 86.9% of cheetah kills, with males being the most targeted demographic category (Mills, 1984b). No evidence suggests that diseases caused the decline (Skinner and Moss, 2004). Increased effects of habitat loss and poaching also contribute to declining mammal species across the world (Harris et al., 2009). This study seeks to understand the causes of the observed springbok population decline. Stake-holders, including scientists, conservationists and policy managers, can then develop measures that can help recover the springbok population. Fynn and Bonyongo (2011) highlighted the need to identify movement patterns, dry and wet season resource requirements, threats to ungulate movement, and habitat use to know which resources wildlife need for survival.

There have been few studies focused on springbok ecology in Botswana and very few ecological studies have been conducted anywhere across their range. In addition, very few studies have collared springbok to understand space use. Currently most wildlife research in Botswana is concentrated in the north, with only a few studies in the south. The majority of the springbok population is found in the Kgalagadi but little research on their spatial ecology has been done in the area. The results of this study will inform the conservation of this iconic species. The Botswana DWNP has developed a Wildlife Conservation Research Strategic Plan (2016-2020) that highlights the need for adaptive management and applied research projects within Botswana. Following from that, the main aim of this study is to provide sound ecological information that will assist the long-term conservation and management of the Kalahari springbok population, and indeed springbok in all the protected and management areas within their distribution in Botswana.

1.3 Theoretical Framework

The study is guided by the functional habitat heterogeneity framework. Functional habitat heterogeneity recognises that habitat types vary in their provision of resources, and herbivores must access a variety of habitats at different seasons of the year to meet their resource requirements (Owen-Smith 2002, 2004; Hopcraft et al., 2010). Some habitats provide energy, nutrients and minerals to meet the requirements of lactating females and growing calves (Parker et al., 2009; Hopcraft et al., 2010), while others provide water, shade and high visibility (Bjorneraas et al., 2012; Giotto et al., 2015; Hopcraft et al., 2010). Dry season habitats provide nutrients and energy that are important in maintaining the population during resource limited periods to minimize reliance on body stores (Fynn, 2012). Restricting movement, fragmenting habitats or restricting access to resources can lead to animals being unable to meet their resource requirements and therefore to population declines.

Functional heterogeneity is represented by a mixture of areas providing high quality resources during the wet season and other areas that can provide sufficient forage to sustain animals during the dry season (Owen-Smith, 2002; Fynn, 2012). Loss of wet and dry season resources may lead to population crashes (Owen-Smith, 2004). Functional wet season habitats provide short, digestible, green grass rich in energy and nutrient content to meet the demands of lactation, calf growth and body condition maintenance (Hopcraft et al., 2010; Owen-Smith, 2004; Fynn, 2012). Functional, dry season habitats have soils that can hold water for a long time and maintain green leafy plants at a time when other habitats cannot (Illius and O'Connor, 1999; Fynn, 2012). In the Kgalagadi melons and underground storage organs form a critical dry season resource (Williamson, 1987).

Springbok must move between different habitats at different times of the year because those habitats have different levels of productivity. Saline pans cannot maintain greenery during the dry season, salinity can lead to severe osmotic stress which may threaten the development, growth and productivity of species (Kawasaki et al., 2001). Therefore, springbok will move to key functional habitats that will meet their resource requirements. During the wet season, when grass is growing, springbok may choose to forage on pans with high levels of forage productivity, whereas during the dry season they rely on browse species that occur in off-pan habitats. Denying animals' access to key functional habitats may cause mortalities because animals do not get enough nutrients from their diet and could eventually lead to population declines.

1.4 Objectives

The general objective of the study was to identify factors that contribute to declining springbok numbers in the southern Kalahari of Botswana. The study was guided by the following specific objectives:

1. To investigate springbok seasonal recruitment rate.

2. To determine the forage characteristics that govern springbok seasonal foraging patterns.

3. To determine the seasonal patterns of springbok habitat selection.

1.5 Study area

The Kgalagadi Transfrontier Park (KTP), part of the Kalahari Desert, is located in the Kgalagadi district of Botswana and shared by South Africa and Botswana (Van Rooyen, 2001). The Kalahari is the largest extent of sand in the world, extending into Botswana, Namibia, South Africa, Angola and the Democratic Republic of Congo (Van Rooyen 2001).

The southern Kalahari region is an arid savanna that includes the Mabuasehube and the Kgalagadi Schwelle in Botswana and lies between 22° and 28° S and 20° and 23° E (Barker, 1983). It covers approximately 38,000 km^2 of the Kalahari ecosystem (Wallgren et al., 2009). The southern Kalahari is dry, receiving an annual rainfall of 200 – 250 mm (Mills and Retief, 1984a). The area experiences cold winters, with lows of -10 °C, and hot summers, with highs of 45 °C (Van Rooyen et al., 1990). Owing to the low, unpredictable rainfall distribution of the region, Kalahari ungulates are extremely mobile in search of grazing resources (Williamson et al., 1988). The main wet season range for herbivores, the Schwelle, lies between the CKGR and KTP, and contains a high density of saline pans (Parris, 1976). The study was conducted in the Mabuasehube portion of KTP and the adjacent part of the Schwelle (Fig 1.1) from August 2017 to June 2018.

1.6 Seasons

I identified three seasons based on rainfall and temperature patterns: the wet season (December-March) when most rainfall occurs and there is enough forage of sufficient quality to meet the demands of lactation (Sinclair et al., 2000); the cold dry season (April-August) when temperatures drop; and the hot dry season (September-November) when temperatures increase (van Rooyen and van Rooyen, 1998) and forage quality may drop below maintenance levels (Owen-Smith, 2004).

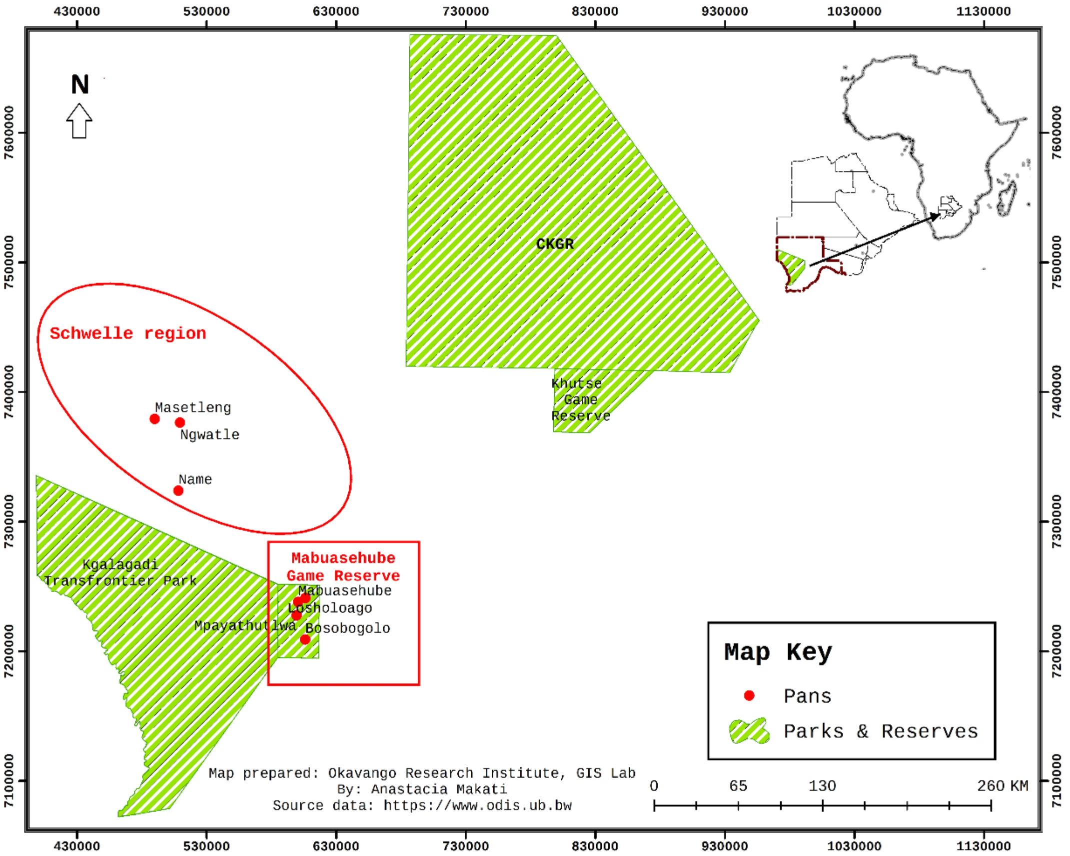

Figure 1.1: Map of southern Kalahari, Botswana showing pans in Mabuasehube Game Reserve and part of the Schwelle Region, pan dots refer to saline pans located in the landscape.

1.7 Habitat types

Vegetation in the area is comprised of shrub savannah, characterised by bushes and grassland (Skarpe, 1986). The dominant woody plants in the area include *Terminalia sericea*, *Vachellia erioloba*, *Boscia albitrunca*, and *Senegalia mellifera*, while the dominant grass species include *Stipagrostis uniplumis*, *Aristida meridionalis*, *Eragrostis pallens*, *Anthephora pubescens*, and *Schmiditia kalahariensis* (Van Rooyen, 2001).

I identified three habitat types based on herbaceous and woody vegetation: pan, pan-edge, and off-pan (Fig 1.2). Pan was characterised by short grassland. Pan habitat is dominated by *Sporobolus ioclados, Enneapogon desvauxii*, *Chloris virgata* and *Cenchrus ciliaris*. Shrubby grassland with dwarf shrubs, herbs and forbs was found in the pan-edge habitat. *Rhigozium trichotomum* and *Catophractes alexandrii* are dominant on the pan-edge habitat. The off-pan habitat was dominated by a combination of the vegetation found on the pan and pan-edge habitats and expanses of *Senegalia, Vachellia* and *Grewia* species. *Anthephora pubescens, Schmidtia pappophoroides, Stipagrostis uniplumis* and *Urochloa trichopus* are dominant in off-pan habitats. I identified four focal saline pans in Mabuasehube (Bosobogolo, Losholoago, Mabuasehube and Mpayathutlwa) and three in the Schwelle (Name, Ngwatle and Masetleng; Fig 1.1) that springbok were observed to use extensively.

The wildlife population includes herbivores such as blue wildebeest, eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*) and springbok. Large predators in the southern Kalahari are lion, spotted hyena (*Crocuta crocuta*), brown hyaena (*Hyaena brunnea*), cheetah, and leopard (*Panthera pardus*; Mills, 1984a). Meso-predators are black-backed jackal (*Canis mesomelas*), bat-eared fox (*Otocyon megalotis*), and caracal (*Caracal caracal*; Blaum et al., 2009; Mills and Mills, 2013). Large predators occur in relatively low numbers in the southern Kalahari ecosystem (Castley et al., 2002; Skinner and Moss, 2004). Livestock found in the area include goat (*Capra hircus*), cattle (*Bos taurus*), horse (*Equus caballus*), donkey (*Equus asinus*), and sheep (*Ovis aries*). The area has limited rainfall, so humans and livestock get most of their water from boreholes (Wallgren et al., 2009). Communal grazing land, settlements and ranches also form part of the southern Kalahari.

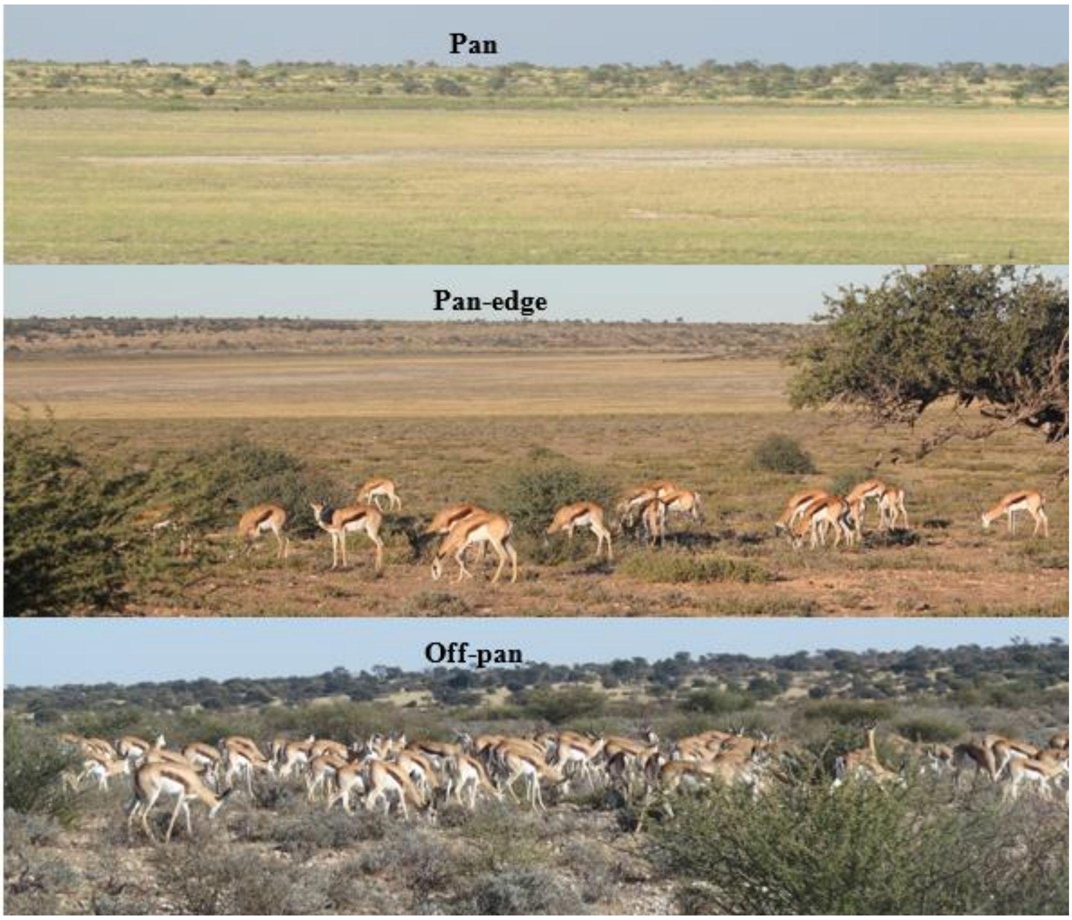

Figure 1.2: Habitat types for springbok in the southern Kalahari, Botswana

1.8 Study species

Arid-adapted antelopes synonymous with the Kalahari region, springbok play an important role in the ecosystem through the cycling of nutrients and as a prey source for predators (Cain et al., 2004) such as cheetah (Mills and Mills, 2016), leopard (Hayward and Kerley, 2008), black-backed jackal (Klare et al., 2010), and lion (Stander, 1992). Springbok herd sizes vary seasonally (Stapelberg et al., 2008). During the dry season (April - October), springbok usually form small herds that increase in size, sometimes into the thousands, during the wet, summer months, when they move in search of suitable grazing (Nagy and Knight, 1994; Roche, 2008). Springbok breed throughout the year with a peak during the cold dry season (Wilson and Reeder, 2005). After a gestation period of five to six months new lambs are born (Skinner and

Louw, 1996) often synchronising their births with rainfall during the wet season when resources are abundant (Wilson and Reeder, 2005).

Restricted to the arid semi-deserts of southern Africa, springbok occur across most of Namibia, through much of Botswana, in north western South Africa, and into western Angola (Lehmann, 2015; Castelló, 2016). The total springbok population in southern Africa is between 2 and 2.5 million (IUCN, 2018). The Kgalagadi in southern Botswana includes a portion of the KTP and Mabuasehube, which are both protected areas, and the surrounding Wildlife Management Areas (WMA's), which are part of the Schwelle region (Fig 1.1). The Schwelle is the main wet season range for Kalahari ungulates because of its high density of saline pans that support vegetation high in nutrient content and provide salt licks for ungulates (Williamson et al., 1988). The highest springbok population in Botswana is found in the Schwelle region (Verlinden, 1998; Stapelberg et al., 2008). However, the Kgalagadi district saw a major decline in springbok numbers between 1994 and 2005 (Gaobotse, 2008).

1.9 Brief description of the materials and methods

In order to address the objectives of this study the following methods were used for each objective:

1. To determine the juvenile: adult female ratio in different seasons as a measure of springbok recruitment rate

Springbok congregate on open pans, where they are easily observed. At each pan, the total count of the springbok population was recorded, including demographic categories. Herd size and composition were recorded and the number of males, females, sub-adults and juveniles were quantified in every opportunistically encountered herd in each season.

2. To determine the forage characteristics that govern springbok seasonal foraging patterns

Springbok were observed feeding and the vegetation characteristics of the feeding sites were sampled. Available sites where there were no observations of springbok feeding were also sampled for comparison.

3. To determine the seasonal patterns of springbok habitat selection

Springbok in different herds were darted and fitted with satellite-enabled GPS collars. Pseudo-random sampling method was used to select the study animals. GPS data collected by the collars was used to identify key habitats used by springbok.

Chapter two - Seasonal changes in springbok herd composition and age structure in the southern Kalahari, Botswana

Summary

Population demographics studies are important for wildlife management because they can be useful in assessing demographic trends. Most of the springbok population in Botswana inhabits the Schwelle area of the Kgalagadi, with a small proportion in Mabuasehube. The study was conducted in both areas. Age, sex and herd size were recorded from springbok herds in each season at each study pan over a one year period. Generalised linear mixed models in R were used to assess the effects of season and location on herd size, herd composition and demographic ratios. Larger herd sizes were recorded during the wet than during the hot dry season. Herd composition varied across seasons and locations due to a variation in sub-adult and adult male categories, with the proportion of the latter being highest during the hot dry season and that of the former being highest in the Schwelle. A high juvenile: adult female ratio was recorded in the wet season months in the Schwelle and a decline in the subsequent cold dry season, indicating a low recruitment rate that could be contributing to the springbok population decline.

2.1 Introduction

The world is experiencing a loss of biodiversity and many species face extinction from anthropogenic pressures and climate change (Lande, 1993). African ungulate populations, in general, are declining (Owen-Smith and Mills, 2006; Bolger et al., 2008; Western et al., 2009), possibly because Africa's conservation areas do not always include migration routes and seasonal habitats, which are important for productive ungulate populations (Fynn and Bonyongo, 2011). In addition, increasing human populations adjacent to conservation areas lead to rising poaching and human-wildlife conflict in unprotected areas that often contain key seasonal resources (Williamson et al., 1988). Habitat loss and fragmentation may decrease habitat quality, which could affect the survival rates of species and cause population declines (Brook et al., 2008), and even extinction (Rybicki and Hanski, 2013).

Most herbivores reproduce seasonally, with birthing timed to coincide with peak resource availability (Post, 2003) when there is enough forage of sufficient quality to meet the demands of lactation and growth (Sinclair et al., 2000). However, potential shifts in timing of plant growth caused by climate change could negatively impact the reproduction period of some herbivores due to a lack of nutritious forage from new plant tissues (Clutton-Brock, 1991). Climate change can alter the timing of productive forage availability by, for example, delaying rainfall, which facilitates the growth of new plants that most species depend on for reproduction; therefore, reproduction may not be synchronised with forage availability (Clutton-Brock, 1991). In tropical systems, birthing coincides with rainfall, when new grasses are abundant and provide high quality forage that increases survivorship of offspring (Moe et al., 2007). In unfavourable climatic conditions, adult females may sacrifice offspring survival in favour of their own to ensure that they continue reproducing in the future (Clutton-Brock, 1991).

Predation can influence access to resources (McLoughlin et al., 2010) and cause a reduction in population size (Sinclair et al., 2003). Predation of lactating females affects population dynamics because it increases mortality of females and orphaned offspring (Rughetti and Festa-Bianchet, 2014). Predation of young prevents recruitment to adult life stages (Mysterud et al., 2005; Mason et al., 2011), but adult mortality has the largest impact on the population size because it prevents reproduction (Mysterud et al., 2005).

Information on population age and sex structure is vital for wildlife management (Rughetti, 2016) because animals in different demographic categories have temporally varying energetic demands, which depend on reproductive costs, growth, and behaviour (Clutton-Brock, 1988). These costs and benefits vary according to sex and age classes (Conradt and Roper, 2000) and influence herd composition since the allocation of time to various activities differs between classes (Silk, 2007). Climate change can alter the cost-benefit balance (Conradt and Roper, 2000) by changing foraging behaviour, reducing suitable habitat, altering plant phenology, and affecting species’ calving areas (Singh and Milner-Gulland, 2011).

Herd size varies with environmental conditions: small herds occur in areas of limited resource availability (Korte, 2008) and during periods of resource scarcity (Isvaran, 2007). Large herds can form during periods of forage abundance (Jarman, 1974), which is during the wet season in African savannas (Wilmshurst et al., 1999). Herd composition and age ratios can be used as a proxy for studying recruitment rate and can be useful in population growth studies to assess demographic trends (Harris et al., 2008), although accurate quantification of population growth requires long-term monitoring of marked individuals (Gaillard et al., 1998; Bonenfant et al., 2005). The juvenile: adult female ratio can be affected by predation (Linnell et al., 1995), late parturition (Singer et al., 1997), and juvenile and adult female survival (Gaillard et al., 1998).

Recruitment rate, calculated from temporal changes in the ratio of juveniles: adult female (Gaidet and Gaillard, 2008), represents the combined vital rates of young survival and adult female fecundity (Bonenfant et al., 2005). Recruitment rates and demographic ratios are important in population growth studies and are affected by environmental pressures (Gaillard et al., 1998). Adult females are used as the reference category for age and sex ratios (McCullough, 1994) because they form the core of breeding herds (Prins, 1996) and move freely between territories that contain key resources (Ritter and Bednekoff, 1995). Adult females suffer lower mortality rates than adult males and juveniles as a result of sex differences in the rate of senescence (Clutton-Brock and Isvaran, 2007) and their survival rates are resistant to changes in environmental conditions (Gaillard et al., 1998). McCullough (1994) argues that even though adult females are used as the reference category, they are not a perfect denominator because of temporal variation in their numbers. However, adult females are unlikely to leave herds through emigration so they remain the best reference category (Owen-Smith, 1993).

Adult male springbok defend territories that contain key resources (Ritter and Bednekoff, 1995). During the breeding period adult males are intolerant of each other's presence (Clutton-Brock and Huchard, 2013). Larger males compete for females and the dominant ones mate (Kappeler, 2012). Prior to mating, breeding males engage in rutting behaviour when females come into oestrus (Skinner, 1996). Mating follows the rut and there are fewer breeding males in herds with a variable number of females and their offspring (Bigalke, 1972). During mating, sub-adults are evicted from the group (Wolff, 1993) and can experience high levels of mortality before they are integrated into a new group (Lukas and Clutton-Brock, 2011).

2.1.2 Hypotheses

1. Herd sizes will be larger in the Schwelle than in Mabuasehube during the wet season because that is where majority of springbok congregate.

2. Herd composition will vary between seasons and location with a higher juvenile: adult female ratio in the Schwelle, a calving area for Kalahari ungulates.

3. The ratio of adult male: adult female will decrease during the cold dry season when territorial males defend herds of breeding females from other males.

2.2 Methods

I recorded population demographics from all springbok herds encountered in open areas because they offered the highest visibility, so minimised sight bias (Ogutu et al., 2006). Animals were counted when the herd was moving in one direction to avoid errors. When necessary, Steiner 10x44 peregrine XP binoculars were used to identify gender. Animals were classified into demographic categories using body size, shape and size of the horns, and external genitalia (Rautenbach, 1971; Table 2.1). Each animal in every herd was assigned to a demographic category: juvenile (Fig 2.1), sub-adult (Fig 2.2), adult male (Fig 2.3) or adult female (Fig 2.4). Data were recorded from herds in every saline pan in each season.

Table 2.1: Criteria used to classify springbok into demographic categories, according to Rautenbach (1971).

Category	Age	Horns
Juvenile	0 – 6 months	Very short, curved forward
Sub-adult	7 – 21 months	Short, tips curved forward
Adult male	> 21 months	Long, thick, curving sharply backward from the base, tips tilted backward
Adult female	> 21 months	Long, slender, tilted backward, tips curving in/outward

Figure 2.1 Juvenile

Figure 2.2 Sub-adult

Figure 2.3 Adult male

Figure 2.4 Adult female

2.2.1 Data analysis

For each sighted herd, the saline pan name and its location were recorded, the latter as Mabuasehube or Schwelle. The effects of season and location on herd size were assessed using generalised linear mixed models with pan name as the random effect (GLMMs: lme4 package) (Bates et al., 2015) using a poisson error distribution and a log link function for positive count data (Crawley, 2007). To account for over-dispersion in the model, an observation-level random effect was included (Harrison, 2014). A global model was run with herd size as the dependent variable and the full interaction effects of season and location as fixed predictor variables. The dredge function in the MuMIn package was used to perform automated model selection (Barton, 2009) using the global model based on Akaike Information Criterion (AIC) values (Akaike, 1974). Herd sizes were compared between the hot dry – cold dry, hot dry – wet and wet – cold dry seasons to determine whether they varied seasonally.

There were no juveniles recorded during the hot dry season. To account for missing values in juvenile counts the zeros were replaced with juvenile replacement values. The juvenile replacement value (x) was calculated using the minimum replacement value (min) and the maximum replacement value (max), which was calculated as follows (Fry et al., 2000):

$$x = \text{min}/\text{max}$$

where: min = 1 (the minimum positive number of juveniles in any herd)

max = the number of adult females in each herd.

To avoid the effect of zeros in other categories and deviation of the data set (Martín-Fernández et al., 2000), 11 small herds were removed from the analysis.

Herd composition was analyzed using compositional data analysis. The test assumes proportional data are positive and sum to one (Van Der Boogaart and Tolosana-Delgado, 2006). A change in a proportion of one category affects the proportion of other categories, so the data are not independent (Van Der Boogaart and Tolosana-Delgado, 2006). The ‘compositions’ package in R version 3.5.2 was used to transform the data into log ratios and used the ‘mvtnorm’ package in R to test data for multivariate normality (Hothorn, 2001). Multivariate Analyses of Variance (MANOVAs) were used to assess the effects of season and location on herd composition to determine whether the proportion of different demographic categories varied significantly between seasons and location.

The ratios of each demographic category to adult females were calculated. The effects of season and location on adult male: adult female and sub-adult: adult female ratios were assessed. For juveniles, month was used instead of season to allow ratios to be related to recruitment rate. Adult male: adult female and juvenile: adult female ratios were used to identify breeding and birthing periods (Bigalke, 1972). GLMMs (lme4 package; Bates et al., 2015) with binomial distributions were used to determine seasonal effects on the ratios of each category to adult females. The binomial distribution assumes that data are bounded between zero and one, as is the case for proportional data (Bates et al., 2015). Models were run with demographic ratio as the dependent variable and season, location and full interaction effects between the two factors as fixed predictor variables. Saline pan name was the random variable.

2.2.2 Model selection

Models were run with all possible combinations of predictors to identify the best model based on the lowest AIC value (Akaike, 1974). The dredge function in the MuMIn package was used to perform automated model selection using the global model based on AIC values (Barton, 2009).Models were considered to be competitive if their AIC values were within two units of the best model and less competitive if they were above three (Burnham and Anderson, 2002). All data analyses was conducted in R (R Development Core Team, 2018).

2.3 Results

2.3.1 Herd size

Thirty-two herds were used in the analyses: 17, seven, and eight herds in the hot dry, wet, cold dry seasons, respectively. Sixteen herds were counted each in Mabuasehube and the Schwelle. The hot dry was compared to the wet and cold dry seasons. The most parsimonious model included only the effect of season on herd size (AIC = 347.0, AICω = 0.75). The effect of location and season was less competitive (ΔAIC = 2.86, AICω = 0.18). There was a seasonal variation between the hot dry and cold dry seasons (Z = -3.001, P = 0.003) and between the hot dry and wet seasons (Z = 2.72, P = 0.01) and no variation between the cold dry and wet seasons (Z = 1.05, P = 0.30), indicating smaller herd sizes in the hot dry season and larger during the wet and cold dry seasons (Fig. 2.5).

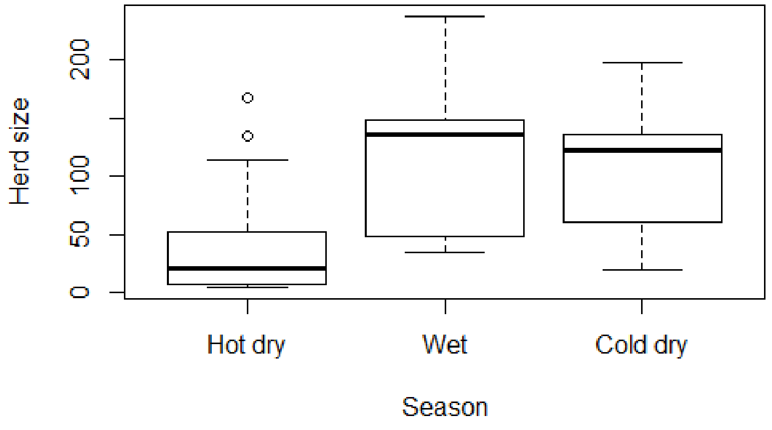

Figure 2.5. Springbok herd sizes in Mabuasehube and the Schwelle, Botswana according to seasons from 2017-2018. Error bars represent ± standard error.

2.3.2 Herd composition

The most parsimonious model included the interaction effect of season and location on herd composition (AIC = 84.78, AICω = 0.71). No other model was competitive. Detailed examination of the MANOVA results showed that the significant interaction effect was caused by variation in the sub-adult and adult male categories (Table 2.2), with the proportion of the latter being highest during the hot dry season (Fig 2.6A) and that of sub-adults being highest in the Schwelle (Fig 2.6B). The interaction effect of season and location was not significant for juveniles or adult females (Table 2.2).

Table 2.2: MANOVA effects of season and location on springbok herd composition in Mabuasehube and the Schwelle, Botswana from 2017-2018. An asterisk (*) marks a significant result.

Category	Season : location
Juvenile	F = 0.35, P = 0.71
Sub-adult	F = 4.17, P = 0.03*
Adult male	F = 7.84, P < 0.001*
Adult female	F = 0.55, P = 0.58

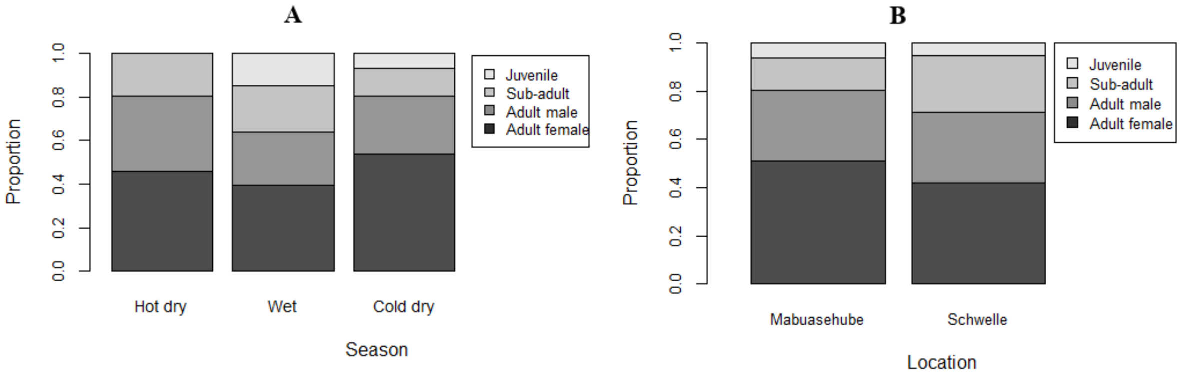

Figure 2.6. Proportion of demographic categories in springbok herds in Mabuasehube and the Schwelle, Botswana from 2017-2018 according to A) seasons and B) location.

2.3.3 Demographic ratios

For adult male: adult female ratios, there were two competitive models (Table 2.3).

Table 2.3*:* Competitive and null models explaining the effects of season and location on springbok demographic ratios in Mabuasehube and the Schwelle, Botswana from 2017-2018. ω = AIC weights; k = number of parameters.

Demographic ratio	Model	ΔAIC	ω	k	Deviance
Adult male: adult female	Season + location	0.00	0.50	7	150.3
	Season : location	0.47	0.40	2	144.0
	Null	15.75	0.00	2	174.2

Model averaging of two competitive models identified the effect of season and location on adult male: adult female ratio as significant, indicating that this ratio varied across seasons and location (Table 2.4).

Table 2.4: Model averaged parameter values explaining the effects of season and location on adult male: adult female springbok demographic ratios in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 are significant.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Season	0.57	0.23	0.12, 1.03	1.00
Location	0.47	0.22	0.02, 0.91	1.00
Season: Location	-0.56	0.24	-1.07, -0.06	0.44

The adult male: adult female ratio in Mabuasehube was highest during the hot dry season and in the Schwelle it was highest in the cold dry season (Fig 2.7A). For sub-adult: adult female ratios, the most parsimonious model was the null model (AIC = 241.8, AICω = 0.66), indicating no significant difference in the ratio of sub-adult: adult female between seasons or location. For juvenile: adult female ratios, the most parsimonious model included the full interaction effect of month and location (AIC = 136.4, AICω = 0.91), indicating that this ratio varied across months and locations. There were no juveniles recorded in the Schwelle in June. The juvenile: adult female ratio was higher in the Schwelle in December and February then higher in Mabuasehube from March into the cold dry months (Fig 2.7C). Mean monthly juvenile: adult ratios were calculated to compare with other studies. The mean ratio ± S.D. was 0.37 ± 0.10 during the wet months and 0.10 ± 0.01 during the cold dry months.

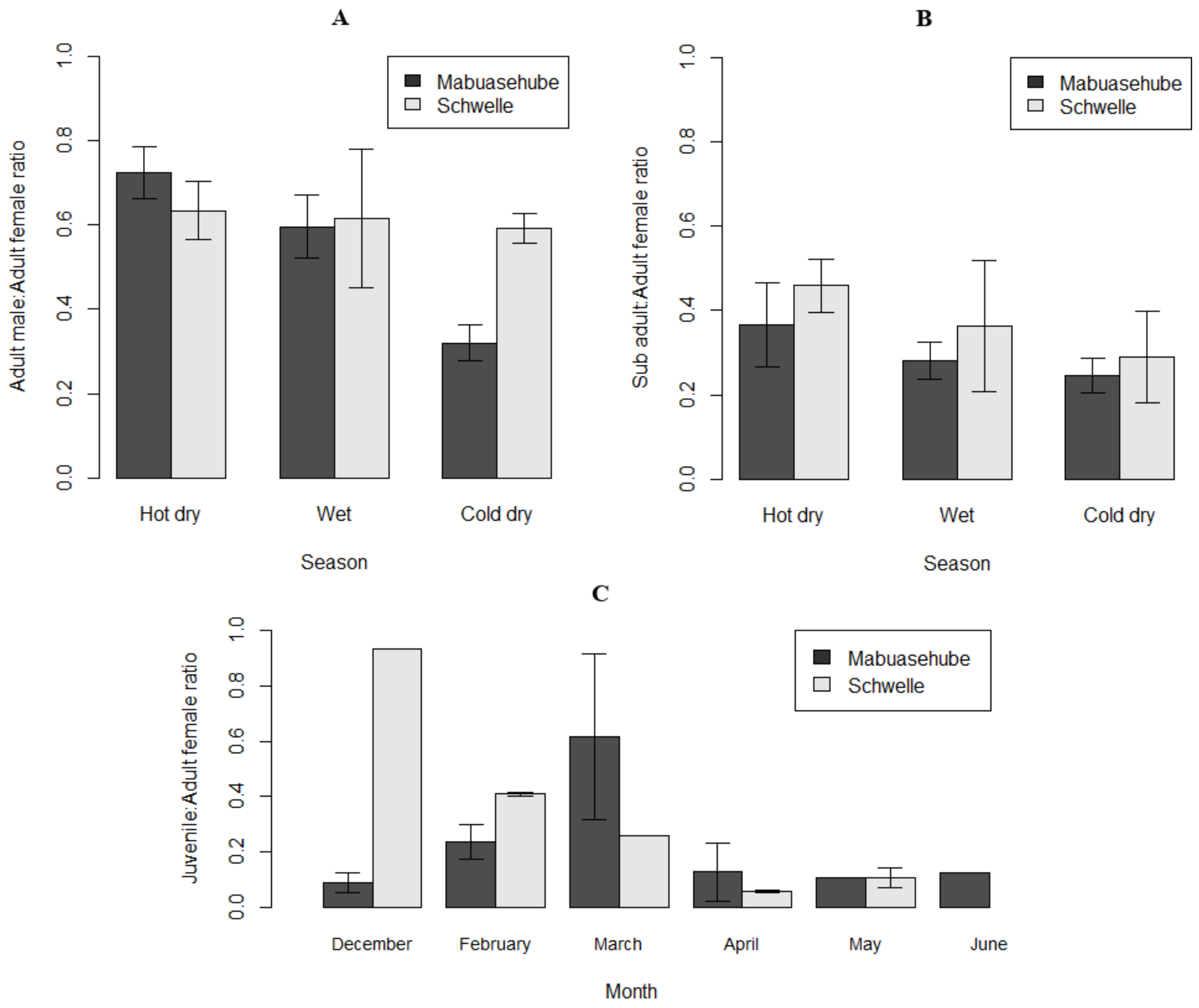

Figure 2.7. Springbok age ratios according to seasons, month and location, in Mabuasehube and the Schwelle, Botswana from 2017-2018 where A= adult male: adult female ratio, B= sub-adult: adult female ratio and C= juvenile: adult female ratio. Error bars represent ± 1 standard error.

2.4 Discussion

Springbok herd sizes are linked to rainfall patterns and forage quality and quantity (Stapelberg et al., 2008). Larger herd sizes recorded during the wet and cold dry seasons coincide with patterns reported by other studies (Jackson et al., 1993; Stapelberg et al., 2008). Although forage scarcity might limit herd size (Korte, 2008), predation pressure also influences the formation of herds (Jarman, 1974). In springbok, large herd size is important for predator detection because all members of the herd can be vigilant (Shorrocks and Cokayne, 2005). Small herds are vulnerable to predation because of reduced vigilance (Burger et al., 2000). The decrease in forage quality during the hot dry season could induce springbok to form smaller herds as animals separate to look for profitable habitat patches (Nagy and Knight, 1994; Stapelberg et al., 2008). Springbok congregate and form larger herds during the wet season when grasses are younger and higher in succulence and nutrient content (Nagy and Knight, 1994). The congregation of springbok coincides with the main lambing period, therefore increasing protection of lambs from predation (Bigalke, 1970).

Herd composition varied across seasons and locations. A lack of juveniles in the hot dry season could be due to high mortality of springbok juveniles or they could all have been as big as sub-adult after six months. However, this study began in the hot dry season, so there is no information about birth or survival rates from the previous birthing period. In springbok, only territorial males mate and they chase other males out of the herd, which then consists of females and juveniles (Smithers, 2012). The proportion of adult females was therefore expected to be high relative to other categories, as in impala (Murray, 1982). The nutritional quality of forage and climatic variations may influence the timing of breeding period (Furstenburg, 2006). This study found a significant effect of season and location on sub-adult contribution to herd composition. Some mammal species show high levels of sub-adult mortality during the breeding period (Wolff, 1993; Lukas and Clutton-Brock, 2011). Adult male springbok and juveniles are particularly vulnerable to predators (Mills and Mills, 2013). The proportion of adult males in herds was highest during the hot dry season in Mabuasehube and decreased in the wet season. The proportion of adult males decreased during the cold dry season as expected because territorial males defend herds of breeding females from intruding males.

Springbok historically moved into the Schwelle region for calving prior to the wet season (Williamson et al., 1988; Verlinden, 1998). During the late months of pregnancy, females need minerals, proteins and other nutrients to enable foetal development and growth (Kelly, 1992), which forage in the Schwelle provides (Williamson et al., 1988). The study found a strong interaction effect of month and location on juvenile: adult female ratio, which was highest in December, February and March. The Schwelle had a higher juvenile: adult female ratio in December and February while a higher ratio in Mabuasehube was recorded in March and April. The peak in the proportion of juveniles in herds in the wet season would have coincided with the period of high forage abundance, when there was enough forage of sufficient quality to meet the demands of lactation (Sinclair et al., 2000). A decline in forage availability following limited rainfall the previous season (O'Kane and Macdonald, 2016) can cause low birth weights of new-borns (Belkacemi et al., 2010) and lead to high mortality rates of juveniles in the early stages of life (Owen-Smith, 2008a).

The ratio of juvenile: adult female dropped in the cold dry season in both areas, suggesting that the young may not be surviving. Juveniles are more likely to be killed by predators in the early stages of life; these juveniles then have no opportunity to survive and reproduce (Mysterud et al., 2005; Mason et al., 2011), so there can be a negative impact on the overall population. According to previous studies, juvenile: adult female ratios ≥0.28 indicate a greater chance of an increasing population and a ratio <0.12 indicates a decreasing population (Harris et al., 2008), so the reduction in ratio recorded in this study from 0.37 during the wet season to 0.10 during the cold dry season suggests a decreasing population.

The decline in the ratio of juvenile: adult females indicates a low recruitment rate that could be contributing to the observed population decline. During the lambing season cheetah (Mills and Mills, 2016) and jackals (Kamler et al., 2012) kill many springbok juveniles. Adult female springbok carrying near-term foetuses are vulnerable to cheetah predation in the Kalahari (Mills and Mills, 2016), which could also contribute to population declines. In large populations, a high removal of juveniles may be compensated by breeding females, but in declining populations predation could reduce the overall springbok population (Mills and Mills, 2016). This, in turn, could lead to a decline in cheetah prey availability and a consequent decline in cheetah populations.

Black-backed jackals are the most abundant carnivore in southern Botswana (Kaunda and Skinner, 2003), with high densities in the KTP and Mabuasehube (Rutina and Ace Bachobeli, 2007) where the large carnivore density is low (Mills, 2015). Predation on springbok lambs is probably higher in Mabuasehube where a high number of black-backed jackals were observed within herds during the wet season (pers. obs.). Springbok juveniles are preferred prey for jackals during the birthing period (Krofel, 2008; Klare et al., 2010; Mills and Mills, 2013). Jackals were observed hunting springbok in the KTP (Mills and Mills, 2013) and in Etosha National Park (Krofel, 2008), and jackal predation on impala lambs depressed the impala population in Mokolodi Nature Reserve, Botswana (Kaunda and Skinner, 2003). Black-backed jackals predation impacts on springbok populations appear to be substantial in African savannas (Klare et al., 2010). More research is required to explore the impact of jackals, and carnivores in general, on springbok population dynamics, especially recruitment.

2.5 Conclusion

The study shows that the Schwelle area is important for the springbok population, re-inforcing the concept that protected areas alone may not be sufficient for conservation of some wildlife species. However, areas outside protected areas may expose animals to high levels of poaching brought by the expansion of settlements and growing human populations encroaching into protected areas. In western Africa, protected areas are faced with massive declines in mammal species due to a high level of poaching (Brashares et al., 2004). In the Karoo, South Africa human population growth exerted pressure on species by restricting movement and led to a decline in populations (Roche, 2008). In arid environments, rainfall drives resource availability, and so a lack of rain can lead to drought and forage scarcity (Mduma et al., 1999), causing population declines (Caughley and Gunn, 1993). Lack of nutritious forage forces females to utilise low quality forage, which might not meet their reproductive needs (Marshal et al., 2009). Natural processes, such as drought, diseases, floods and competition for resources, are uncontrolled and they affect population numbers and could also contribute to low recruitment rate (Western et al., 2009; Geldmann et al., 2013). Predation of lambs during the birthing season and low forage quality outside the rainy season could contribute to the low recruitment rates and eventual population decline. Low survival rate of juveniles could prevent population growth when juveniles are not recruited into the population. It is possible that jackal predation could also play a significant role in the decline of the springbok population. More research on jackal predation on springbok is needed in the Kalahari ecosystem to qualify and quantify this possibility. Long term monitoring of herd composition and demographic ratios using marked individuals could determine whether the low recruitment rate observed in this study contribute significantly to springbok decline in the southern Kalahari.

2.6 Link to next chapter

This chapter has shown that springbok herd sizes are linked to rainfall. The variation in herd composition was caused by the lack of juveniles during the hot dry season and the variation in sub-adult and adult male categories with season and location. A high ratio of juvenile: adult female ratio was recorded in the wet months in the Schwelle and the ratio declined in the cold dry season.

The next chapter compares the characteristics of herbaceous and woody species in sites used by and available to springbok to identify the forage characteristics that govern springbok seasonal foraging patterns.

Chapter three - Seasonal changes in forage characteristics in sites used by and available to springbok

Summary

Resources vary in space and time across landscapes, therefore herbivores must forage on profitable sites and avoid unproductive patches. This results in selection and avoidance of particular sites within habitats. Springbok feeding sites were identified from observations, and available sites were identified from remote sensing. At each grazing site, the vegetative characteristics of the herbaceous layer were recorded and compared with those in sites available to springbok using generalised linear mixed models in R with appropriate error distributions. For woody vegetation I only recorded the characteristics of used sites. Springbok selected grazing sites with low grass biomass and height, high species richness and high cover. Short, diverse shrubs characterised springbok browsing sites. There were no seasonal differences in springbok foraging patterns.

3.1 Introduction

The distribution of resources across landscapes determines the distribution of herbivores (Bailey et al., 1996) and of their predators (Valeix et al., 2010). Pressure (Parsons et al., 1997) and soil nutrients (Anderson et al., 2007) affect the structure of the herbaceous layer. For example, recently burned areas attract a large number of herbivores because new plant shoots that grow after fires have high nutrient levels and greater digestibility (Klop et al., 2007). Similarly, rainfall improves forage, as it leads to grass germination and growth (Levine et al., 2008), resulting in large increases in biomass (Bonnet et al., 2010), species richness and abundance (Haßler et al., 2010) during the wet season. During the wet season, regular grazing maintains productive grass growth (Bonnet et al., 2010) and prevents accumulation of low quality plant material (Frank et al., 1998). However, intensive grazing can alter the herbaceous layer, reducing the abundance and quality of the sward (Coughenour, 1991) and changing its composition (Ash and McIvor, 1998) by removing highly palatable species and allowing the dominance of less palatable species (Pastor et al., 1997). In addition, habitat productivity declines progressively as plants age at the end of the wet season (Georgiadis and McNaughton, 1990) until they reach a senescent stage when their digestibility is low (Zhang et al., 2005). Soil nutrients improve the quality of grass such that abundant, digestible, and nutritious grass is found in nutrient rich soils (Hopcraft et al., 2010), especially in pan habitats (Selebatso et al., 2018a) where soil fertility is high (Bergström and Skarpe, 1999a). Habitats with infertile soils yield less nutritious grass even when rainfall is high, so they provide high grass biomass and woody vegetation of low nutritional value, therefore supporting low densities of ungulates (Hopcraft et al., 2010).

The functional habitat heterogeneity concept recognises that habitat types vary in their provision of resources and herbivores must access a variety of habitats at different seasons to meet their requirements (Owen-Smith, 2002; Hopcraft et al., 2010). Some habitats provide animals with energy, protein, other nutrients and minerals to meet the requirements of lactating females and growing calves (Hopcraft et al., 2010), while other habitats provide water, shade, or high visibility (Hopcraft et al., 2010; Bjørneraas et al., 2012). Functional high quality resources enable animals to gain body weight and reproduce, reserve resources are reliable, adequate-quality forage that enable animals to maintain body weight over the dry season (Owen-Smith, 2004; Fynn, 2012).

During the wet season rainfall fill pans and herbivores may move adaptively from their dry to the wet season ranges and the reverse when the water in the pans get depleted (Sianga, 2014). In addition to water availability, forage quality and quantity determines selection and avoidance of habitats by herbivores (McNaughton, 1990, Murray 1995). Shallow soils and low rainfall regions have high quality forage than productive areas (Murray, 1995), as a result of low dilution effect that result in high concentration of minerals in the soil (Sianga, 2018). These low productivity habitats are dominated by short, high nutritious grasses while tall, less nutritious grasses are found in productive habitats (Sianga, 2018). These short and nutritious grasses are rich in energy and protein which are important for pregnancy and lactation (Murray, 1995; Packer et al., 2009). However, during the dry season high productive habitats offer adequate forage and water and they are selected by herbivores to minimise body store loss throughout the dry season (Fryxell et al., 1988; Sianga, 2018).

Forage quantity and quality determine food intake rates that influence the acquisition of nutritional requirements and play a major role in the distribution and abundance of different ungulates (Farnsworth and Illius, 1998; Hopcraft et al., 2010). Smaller bodied herbivores select fine, highly nutritious forage that is easy to digest to enhance their maintenance and reproductive requirements whereas larger bodied herbivores rely on more forage cover of low quality in response to higher demands for food associated with their body size (Steuer et al., 2014; Wilmshurst et al., 2000). Mouth anatomy can also affect forage selection (Arsenault and

Owen-Smith, 2008). Narrow-mouthed herbivores can selectively pick green plants of high quality, whereas broad-mouthed herbivores have a larger bite area and prefer to forage where the sward is dense (Arsenault and Owen-Smith, 2008). The different morphological and digestive adaptations allow herbivores to coexist through resource partitioning (McNaughton, 1985). Resource partitioning differentiates herbivore foraging patterns and reduces predation risks and diseases associated with large concentrations of herbivores (Arsenault and Owen-Smith, 2008).

Animals adapt to seasonal variability in resources by moving between habitats in different areas. (Owen-Smith, 2002). Seasonal variation in diet composition depends on seasonal forage availability and quality in different habitats (Owen-Smith, 2002; Selebatso et al., 2018b). To address this seasonal variability, some herbivores switch seasonally between grazing and browsing (Venter and Kalule-Sabiti, 2016); for example, springbok graze in the wet season and browse in the dry season (Bigalke, 1972; Selebatso et al., 2018c). These shifts in forage availability contribute to seasonal changes in diet and can lead to seasonal movement patterns (Manousidis et al., 2016). For example, in the Kalahari, many herbivore species engaged in seasonal migration in response to changes in water and forage availability (Crowe, 1995). The Kalahari’s Schwelle, in southwestern Botswana, attract migrating ungulates because it has a high density of saline, shallow, rounded pans holding water after rains (Bergström and Skarpe, 1999a), which vary in grass species composition and structure to the surrounding savanna and attract herbivores and their predators (Parris and Child, 1973).

3.1.2 Hypotheses

1. Springbok foraging sites will be characterised by high species richness, short grasses and cover in all seasons.

2. Pans and pan-edge habitats will contain more diverse forage in all seasons than off-pan habitats because of the higher soil fertility around pans.

3. Short shrubs and high species diversity will characterise springbok browsing sites.

3.2 Methods

3.2.1 Vegetation sampling

I observed opportunistically located herds of springbok until they began feeding in a patch and then moved them off once I was sure that they were feeding. Vegetation characteristics in those patches were recorded to identify the characteristics selected by springbok. For available sites, I used Google Earth (Mountain View, CA) to locate the main pans within the study area. I then created 100 m buffers around the points in ArcGIS 10.6 (ESRI). I generated 100 random points per saline pan within the buffers and pseudo-randomly identified four available points per habitat in each saline pan, ensuring that they fell within 200 m of a road for ease of access. Random sites were sampled to assess forage availability. The aim was to sample two used and two available sites in each habitat type in each pan per month, yielding 126 used and available sites sampled per season.

3.2.2 Grass sampling

A disc pasture metre (DPM; Bransby et al., 1977) was used to calculate grass biomass because it requires less time and effort than cutting grass samples for weighing in a laboratory. The DPM consists of an aluminium disc attached to a tube that slides over a rod with a calibrated measuring ruler. The central rod is placed perpendicular to the ground while the disc is held over the grass sward. The disc is then dropped onto the grass sward and the top of the tube is used to read a calibrated measure from the rod. The ground surface must be flat and drops on woody plants were avoided to prevent bias, since the DPM had only been calibrated for herbaceous vegetation. The DPM was dropped 50 times at 1 m intervals in a random pattern within 50 m of the location where springbok were grazing. DPM measurements were converted into biomass using the equation:

$$Y = -1633 + 1791\sqrt{X}$$

where X is the mean settling height of 50 DPM drops and Y is biomass in kg/ha (Trollope et al., 2000). The DPM calibration for grass dominated ecosystems in sites in Namibia and South Africa was valid for my study area (W Trollope, pers. comm., 2019).

Vegetation characteristics of herbaceous species were recorded after throwing a 0.5 x 0.5 m quadrat randomly four times in springbok used and available sites. Species richness, height, biomass and percentage cover was recorded for each sampled site. I took leaf height measurements from five different plants selected at random from within each quadrant. Biomass and height represented the abundance of vegetation, richness represented the diversity of the herbaceous layer and the physical attributes of the site were represented by percentage cover (Bennitt et al., 2015).

3.2.3 Woody vegetation sampling

Springbok are mixed feeders, so data from woody vegetation were also recorded. Pan-edge and off-pan habitats were sampled because pan habitats did not contain woody vegetation. Only used sites were sampled. The variable quadrat method was used, which minimises over- and under-sampling of short and tall height classes, respectively, as compared to a fixed plot method (Coetzee and Gertenbach, 1977; Sheil et al., 2003).

Woody vegetation was categorised according to height class: 0 - 0.5 m, 0.5 - 1.5 m and over 1.5 m. Two 30 m ropes, marked at 5 m intervals and crossing at the centre, were laid to create four quadrants. Quadrat sizes extended 5 x 5 m, 10 x 10 m and 15 x 15 m, depending on the characteristics of species contained within them. I counted the number of species in each quadrat as a measure of species diversity (i.e., species richness). The total number of species was also counted according to their height class in each habitat to determine species cover. To determine the appropriate quadrat size for each height class, at least one plant needed to occur within each of the marked quadrants, i.e. all four or the size of the quadrant was expanded incrementally until this was achieved.

3.2.4 Data analysis

Vegetation data were split and analysed according to seasons. Generalised linear mixed models in R (GLMMs: lme4 package) with appropriate error distributions (Bates et al., 2015) were used to compare forage characteristics between used and available sites (hereafter referred to as site type) and between habitats in each season. The effects of habitat and site type were assessed using the following error distributions: (i) Poisson with a log link function for species richness because it constituted positive count data, (ii) for biomass and grass height a gamma distribution was used because the data failed the assumptions of normality after a Shapiro-Wilk test on the data. Zero values for biomass were converted to very low values to allow the use of a gamma distribution with a reciprocal link function for positive, not normally distributed data, and (iii) percentages were converted to proportions prior to analysis to allow use of a binomial distribution with a logit link function for percentage cover (Crawley, 2007). The binomial distribution assumes that data are bounded between zero and one, as is the case for proportional data (Bates et al., 2015). Models were run with each forage characteristic as the dependent variable and the interaction effects of habitat and site type as fixed predictor variables. Saline pan name was the random variable. Individual site was used as a random effect to account for over-dispersion in some models (Harrison, 2014). The dredge function in the MuMIn package was used to perform automated model selection using the global model based on Akaike Information Criterion (AIC) values (Barton, 2009).

For woody species, species diversity and cover were compared between habitats and height classes in each season. The effects of habitat and height class on woody species diversity and cover were assessed using a Poisson error distribution with a log link function because they constituted positive count data (Crawley, 2007). Models were run with each forage characteristic as the dependent variable and the interaction effects of habitat and height class as fixed predictor variables. Saline pan name was the random variable and individual site was used as a random effect to account for over-dispersion in some models (Harrison, 2014). Models were run using the lme4 package (Bates, 2010). The dredge function in the MuMIn package was used to perform automated model selection using the global model based on AIC values (Barton, 2009).

All candidate models with ΔAIC <2 (Burnham and Anderson, 2002) were identified and model averaging in the MuMIn package was used to estimate model averaged parameters. Parameters with higher relative importance had a stronger effect on species diversity and abundance (Burnham and Anderson, 2002).

3.3 Results

For grass data, 314 and 378 used and available sites, respectively, from the seven focal saline pans were included in the analyses. For woody vegetation, data from 165 sites were used to run the analyses (Table 3.1). Woody vegetation was not present on the pans and springbok were not always observed browsing throughout the year.

Table 3.1: Number of sites sampled in each season in Mabuasehube and the Schwelle, Botswana from 2017-2018.

Forage type	Season	Habitat	Site type	Number of samples
Grass species	Hot dry	Pan	Available	42
			Used	19
		Pan-edge	Available	42
			Used	17
		Off-pan	Available	42
			Used	39
	Wet	Pan	Available	42
			Used	42
		Pan-edge	Available	42
			Used	42
		Off-pan	Available	42
			Used	26
	Cold dry	Pan	Available	42
			Used	42
		Pan-edge	Available	42
			Used	42
		Off-pan	Available	42
			Used	42
Woody species	Hot dry	Pan-edge	Used	36
		Off-pan	Used	40
	Wet	Pan-edge	Used	32
		Off-pan	Used	11
	Cold dry	Pan-edge	Used	36
		Off-pan	Used	10

3.3.1 Grass species richness

During the hot dry season, the most parsimonious model included the effect of site type only (AIC = 261.4, AICω = 0.81), indicating that species richness varied between used and available sites. No other model was competitive (Table 3.2). Species richness ranged between one and three in used sites and from zero to two in available sites (Fig 3.1A). During the wet season, two models were competitive (Table 3.2) and model averaging identified site type as the main factor determining grass species richness (Table 3.3), which ranged between two and four in used sites and from zero to four in available sites (Fig 3.1B). During the cold dry season there were two competitive models (Table 3.2). Model averaging identified site type as the main factor determining grass species richness (Table 3.3), which ranged between one and four in used sites and from zero to two in available sites (Fig 3.1C).

Table 3.2: Model selection table of seasonal vegetation characteristics in springbok foraging sites in Mabuasehube and the Schwelle, Botswana from 2017-2018.

Vegetation characteristic	Season	Model	AICc	ΔAIC	AICω
Grass species richness	Hot dry	Site type	261.4	0.00	0.81
		Null	278.5	17.06	0.00
	Wet	Site type	352.5	0.00	0.61
		Habitat + Site type	354.1	1.54	0.28
		Null	375.4	22.86	0.00
	Cold dry	Habitat + Site type	320.8	0.00	0.56
		Site type	321.7	0.89	0.36
		Null	343.4	22.65	0.00
Grass species biomass	Hot dry	Site type	1227.4	0.00	0.76
		Null	1234.0	6.65	0.03
	Wet	Habitat	1896.2	0.00	0.69
		Null	1906.1	9.90	0.01
	Cold dry	Habitat + Site type	2338.2	0.00	0.75
		Null	2379.0	40.74	0.00
Grass height	Hot dry	Habitat + Site type	1200.1	0.00	0.53
		Site type	1201.6	1.54	0.23
		Habitat : Site type	1201.0	1.79	0.22
	Wet	Habitat : Site type	1911.3	0.00	0.94
		Null	1937.5	26.23	0.00
	Cold dry	Site type	2273.5	0.00	0.46
		Habitat + Site type	2274.6	1.05	0.27
		Habitat : Site type	2274.6	1.05	0.27

Grass species cover	Hot dry	Habitat + Site type	811.1	0.00	0.77
		Null	849.5	38.39	0.00
	Wet	Site type	987.5	0.00	0.71
		Null	1052.0	64.48	0.00
	Cold dry	Site type	1236.4	0.00	0.74
		Null	1252.8	16.37	0.00
Woody species diversity	Hot dry	Height class	583.0	0.00	0.55
		Habitat + Height class	584.2	1.21	0.30
		Null	717.9	134.97	0.00
	Wet	Height class	385.3	0.00	0.44
		Habitat + Height class	385.4	1.10	0.42
		Null	401.1	15.77	0.00
	Cold dry	Height class	368.4	0.00	0.72
		Null	391.3	22.85	0.00
Woody species cover	Hot dry	Habitat : Height class	2286.8	0.00	1.00
		Null	5809.9	3523.12	0.00
	Wet	Habitat : Height class	854.2	0.00	1.00
		Null	4353.1	3498.84	0.00
	Cold dry	Height class	1160.8	0.00	0.48
		Habitat : Height class	1161.4	0.65	0.34
		Habitat + Height class	1162.7	1.93	0.18

Table 3.3: Model averaged parameter values explaining the effects of habitat and site type on mean grass species richness in springbok foraging sites during the wet and cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 had significant results.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Wet season				
Site type	0.64	0.14	0.36, 0.91	1.00
Habitat	0.23	0.24	-0.24, 0.70	0.32
Cold dry season				
Site type	1.05	0.30	0.46, 1.65	1.00
Habitat	-0.30	0.27	-0.83, 0.22	0.61

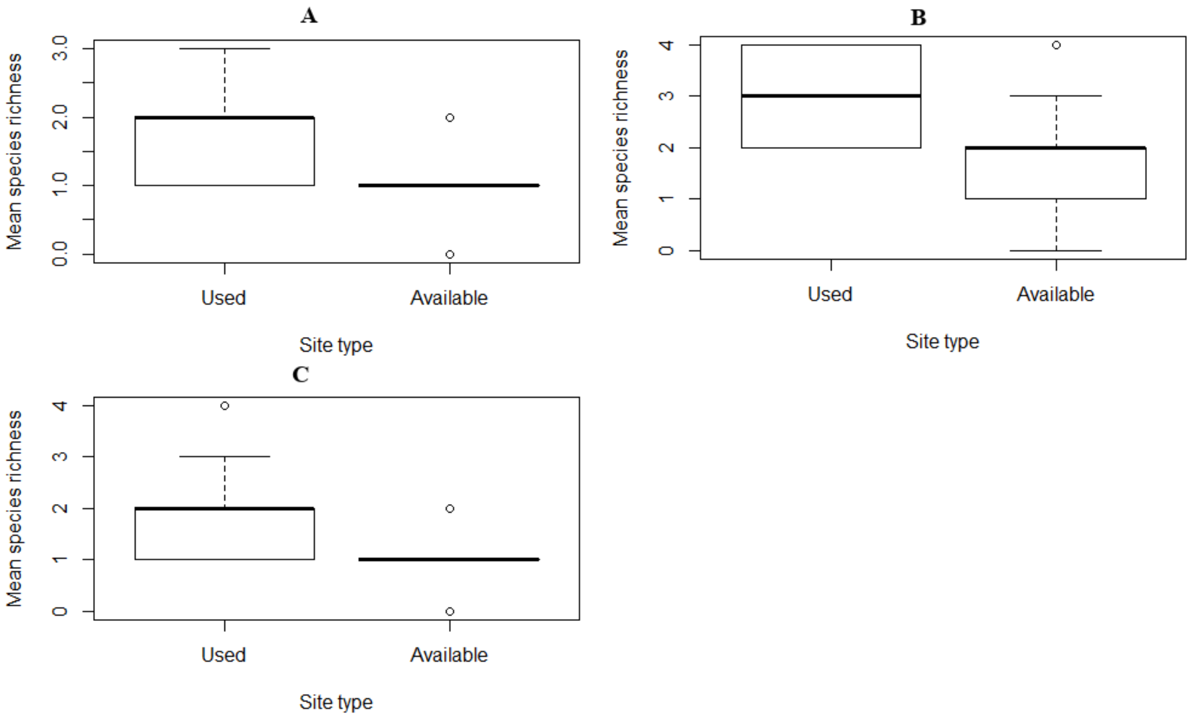

Figure 3.1. Effects of site type on mean grass species richness in springbok foraging and available sites during the A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.3.2 Grass species biomass

During the hot dry season, the most parsimonious model included the effect of site type (AIC = 1227.4, AICω = 0.76), indicating that grass biomass varied between used and available sites; no other model was competitive (Table 3.2). Biomass was lower in used than available sites (Fig 3.2A). During the wet season, the most parsimonious model included the effect of habitat (AIC = 1896.2, AICω = 0.69), indicating that species biomass varied between habitat types; no other model was competitive (Table 3.2). Biomass was lowest in pans, with increasing biomass to pan-edge and off-pan habitats (Fig 3.2B).

During the cold dry season, the most parsimonious model included the fixed effects of habitat and site type (AIC = 2338.2, AICω = 0.75), indicating that biomass varied between habitats and site type; no other model was competitive (Table 3.2).Biomass was lowest in pans and highest in off-pan habitats; it was also lower in used than available sites (Fig 3.2C).

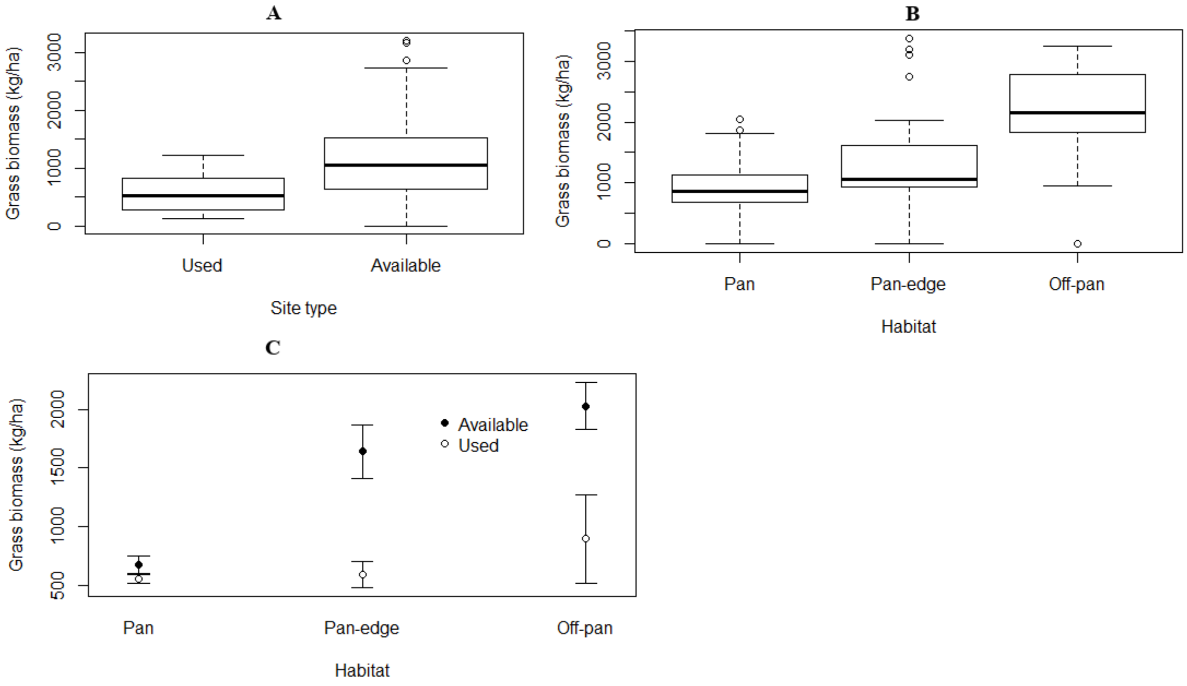

Figure 3.2. Effects of site type and habitat on grass species biomass in springbok foraging and available sites during the A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.3.3 Grass height

I found three competitive models during the hot dry season (Table 3.2). Model averaging identified site type as the main factor determining grass height (Table 3.3). Grass height was lower in used than available sites (Fig 3.3A).

Table 3.4: Model averaged parameter values explaining the effects of habitat and site type on mean grass species height in springbok foraging sites during the hot and cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 had significant results.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Hot dry season				
Site type	0.05	0.02	0.01, 0.09	1.00
Habitat	0.03	0.02	-0.00, 0.06	0.79
Habitat : Site type	-0.02	0.03	-0.09, 0.04	0.24
Cold dry season				
Site type	0.06	0.01	0.05, 0.08	1.00
Habitat	0.03	0.28	-0.01, 0.06	0.66
Habitat : Site type	-0.00	0.03	-0.06, 0.05	0.33

During the wet season, the most parsimonious model included the fixed effect of habitat and site type (AIC = 1911.3, AICω = 0.94), indicating that springbok used sites with lower grass heights in all habitats (Fig 3.3B). During the cold dry season there were three competitive models (Table 3.2). Model averaging identified site type as the main factor determining grass species height (Table 3.3), which was lower in used than available sites (Fig 3.3C).

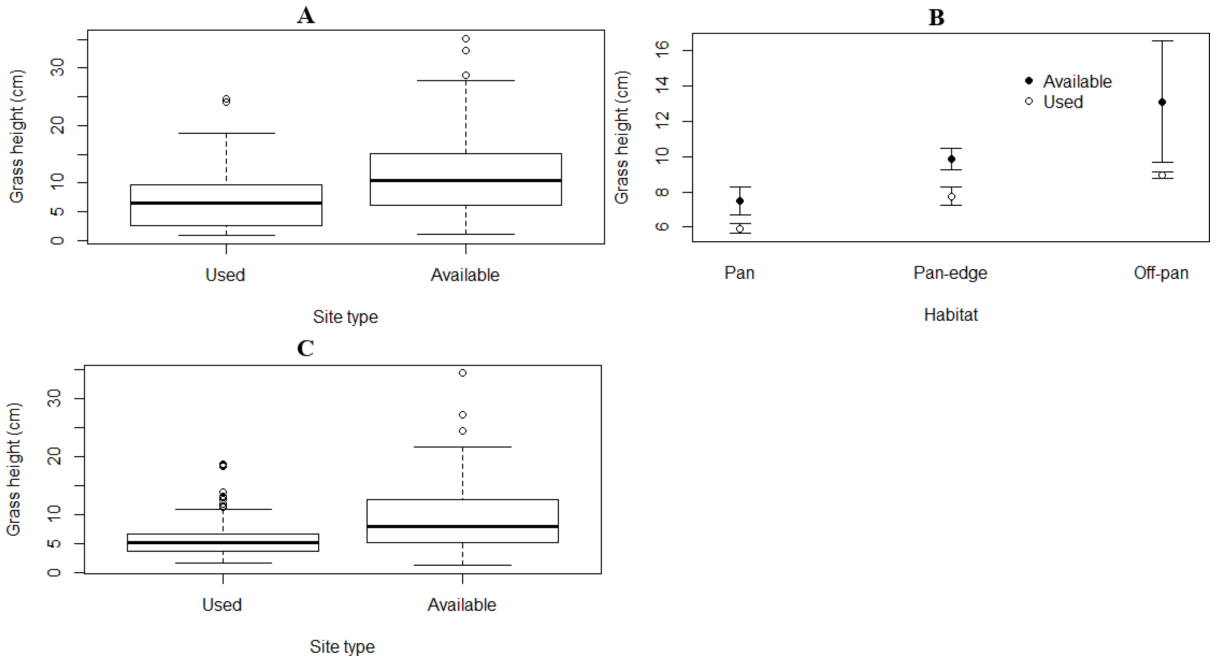

Figure 3.3 Effects of site type and habitat on grass species height in springbok foraging and available sites during A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.3.4 Grass species cover

During the hot dry season, the most parsimonious model included the effects of habitat and site type (AIC = 811.1 AICω = 0.77), indicating that percentage cover varied between habitats and site types; no other models were competitive (Table 3.2). Percentage cover was slightly higher in off-pan habitats than in pan and pan-edge habitats and was slightly higher in available than used sites (Fig 3.4A). During the wet season, the most parsimonious model included the effect of site type (AIC = 987.5, AICω = 0.71), indicating that species cover varied between used and available sites; no other models were competitive (Table 3.2). Percentage cover was higher in used than available sites (Fig 3.4B). During the cold dry season, the most parsimonious model included the effect of site type only (AIC = 1236.4 AICω = 0.74), indicating that species cover varied between used and available sites; no other models were competitive (Table 3.2). Cover was slightly higher in used than available sites (Fig 3.4C).

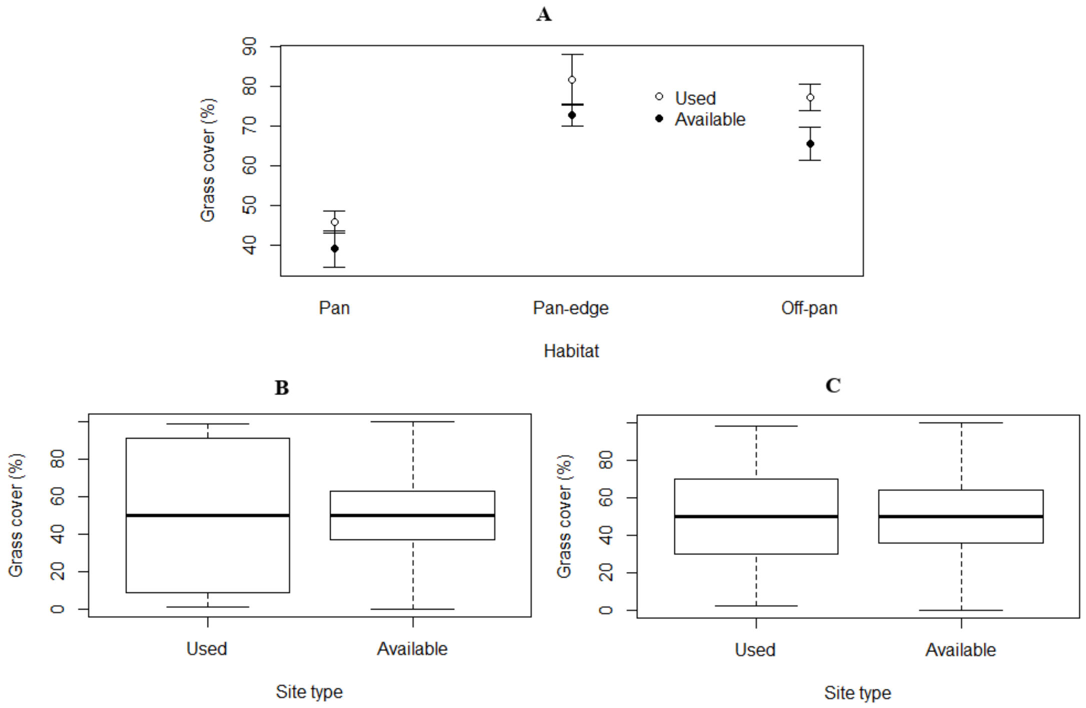

Figure 3.4. Effects of site type and habitat on grass species cover in springbok foraging and available sites during A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.3.5 Woody species diversity

During the hot dry season, there were three competitive models (Table 3.2). Model averaging identified height class as the main factor determining woody species diversity (Table 3.4).

Table 3.5: Model averaged parameter values explaining the effects of habitat and height class on woody species diversity in springbok foraging sites during the hot dry season in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 had a significant effect.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Height class	-0.83	0.14	-1.09, -0.56	1.00
Habitat	-0.10	0.12	-0.34, 0.13	0.45
Habitat : Height class	0.19	0.25	-0.30, 0.67	0.15

There was variation in woody species diversity between height classes during the hot dry season. A higher woody species diversity of up to five was recorded in the 0 – 0.5 m height class and a lower diversity of up to two species was recorded in the over 1.5 m height class (Fig 3.5A). During the wet season, there were three competitive models (Table 3.2). Model averaging identified height class as the main factor determining woody species diversity (Table 3.5).

Table 3.6: Model averaged parameter values explaining the effects of habitat and height class on woody species diversity in springbok foraging sites during the wet season in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 had a significant effect.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Height class	-0.56	0.19	-0.93, -0.19	1.00
Habitat	-0.16	0.18	-0.51, 0.20	0.56
Habitat : Height class	-0.17	0.35	-0.85, 0.51	0.15

A larger diversity of woody species was found in the 0 – 0.5 m height class than in the other two height classes (Fig 3.5B). During the cold dry season, the most parsimonious model included the effect of height class on woody species diversity (AIC = 368.4 AICω = 0.72), indicating that woody species diversity varied between height classes; no other models were competitive (Table 3.2). High diversity was found in the 0 – 0.5 m height class and low diversity in the other two height classes (Fig 3.5C).

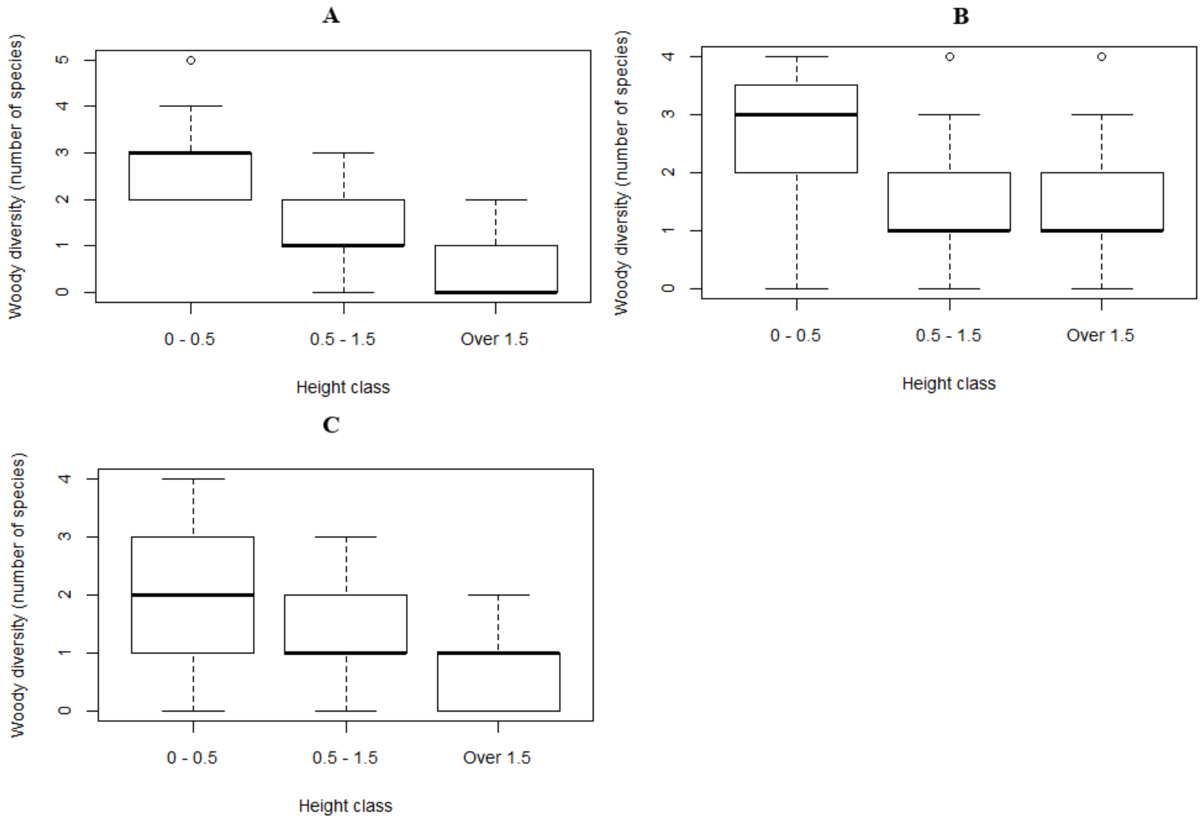

Figure 3.5. Woody species diversity according to height classes (metres) in springbok foraging sites during the A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.3.6 Woody species cover

The most parsimonious model included the interaction effects of habitat and height class during the hot dry season (ΔAIC = 2286.8, AICω = 1), indicating that species cover varied between habitats and height classes; no other models were competitive (Table 3.2). Two-way interaction plots were used for meaningful interpretation of the results. For the pan-edge habitat, woody species cover was highest in the 0 – 0.5 m height class and lowest in the > 1.5 m height class. For the off-pan habitat, woody vegetation in the 0 – 0.5 m height class was more abundant than in other classes (Fig 3.6A). During the wet season, the most parsimonious model included the interaction effect of habitat and height class (ΔAIC = 854.2 AICω = 1), indicating that species cover varied between habitats and height classes; no other models were competitive (Table 3.2). For the pan-edge habitat, woody species cover was highest in the 0 – 0.5 m height class and lower in the other two height classes. For the off-pan habitat, woody vegetation in the 0 – 0.5 m height class was more abundant than in other classes (Fig 3.6B). During the cold dry season there were three competitive models (Table 3.2). Model averaging identified height class as the main factor determining woody species cover during the cold dry season (Table 3.6). High woody species cover was found in the 0 – 0.5 m height class and low cover in the other two height classes. The lowest woody species cover recorded was in the height class over 1.5 m (Fig 3.6C).

Table 3.7: Model averaged parameter values explaining the effects of habitat and height class on woody species cover in springbok foraging sites during the cold dry season in Mabuasehube and the Schwelle, Botswana from 2017-2018. Parameters with relative importance of 1 had a significant effects.

Parameter	Estimate	Unconditional standard error	Confidence intervals	Relative importance
Height class	-1.71	0.13	-1.97, -1.44	1.00
Habitat	-0.11	0.16	-0.44, 0.21	0.52
Habitat : Height class	0.29	0.13	0.05, 0.54	0.34

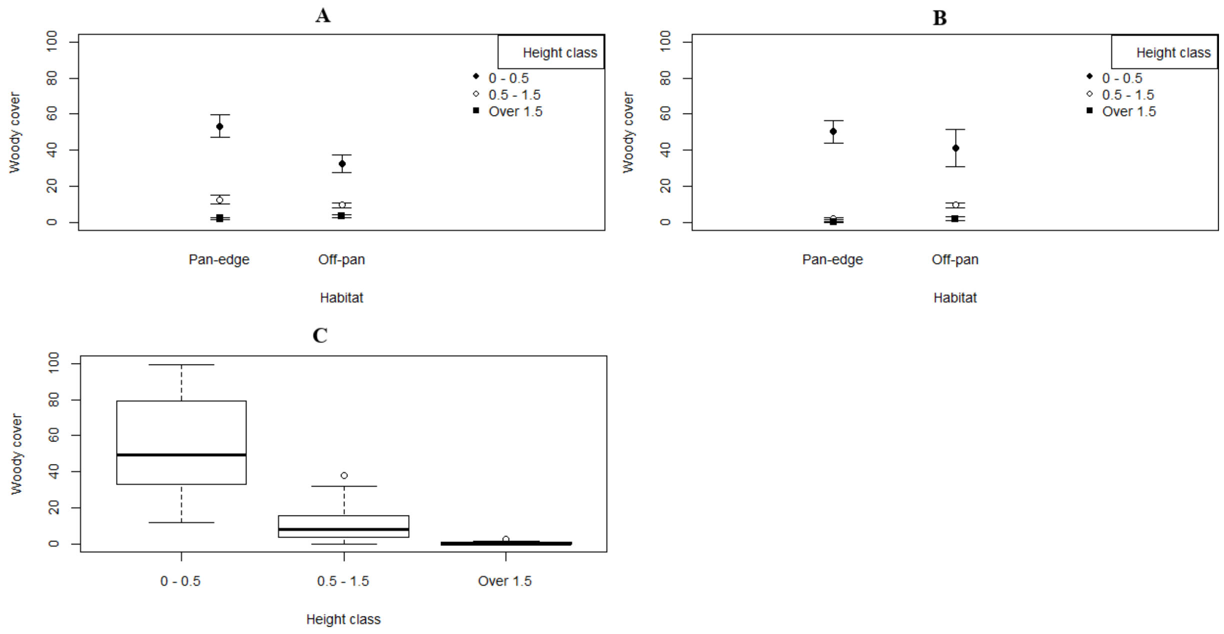

Figure 3.6. Effects of habitat and height class (metres) on woody cover in springbok foraging sites during the A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

3.4 Discussion

In agreement with functional resource and habitat heterogeneity concepts, springbok appeared to adapt to seasonal variation in resources. The results showed some differences in herbaceous forage characteristics between used and available sites throughout the year. The results also showed no effect of habitat therefore the hypothesis that pans would contain more diverse forage than other habitats is rejected.

Seasonal variations in resource availability determine the choice of particular foraging patches by herbivores (Owen-Smith, 2002), which need access to diverse resources provided by different habitats at varying times of the year. Springbok selected grazing sites that differed from available sites in terms of herbaceous abundance, height, diversity and percentage cover throughout the year.

Woody vegetation characteristics from available sites were not recorded, but across all browsing sites selected by springbok, diversity and cover of woody vegetation were greatest in short height classes, which provide an abundant selection of diverse woody species within reach of a foraging springbok. However, I cannot determine whether this structure was characteristic of the study site or of sites selected by springbok because I did not sample woody vegetation in available sites.

Springbok preferred sites with short grasses, high species richness and more ground cover in all seasons, therefore springbok selected sites where they could forage on a diversity of species that likely provided different nutrients (Holechek, 1984). Short, digestible green grass associated with pans (Selebatso et al., 2018) is rich in protein, energy and nutrient content to meet the demands of lactation, calf growth and body condition maintenance (Owen-Smith, 2004; Fynn, 2012). Tall grasses provide low forage quality while short grasses have higher quality forage (Fryxell et al. 2005; Owen-Smith, 2004). Thomson's gazelles (*Gazella thomsoni*) select short grass with high nutrient quality (Fryxell et al 2005). Wildebeest in the Serengeti, Tanzania, also prefer short grasses high in calcium and protein concentration (Kreulen 1975). Springbok prefer very short grasses which maintains their weight better because of their smaller body size (Wilmshurst et al., 2000).

High species richness and cover in pans during the wet season is associated with high soil fertility in pans, compared to the less fertile soils in off-pan habitats (Bergström and Skarpe, 1999a). During the cold dry season, ground cover declined as some grasses reached the senescent stage (Cain et al., 2017). Yet, the high density of saline pans found in the Schwelle area supported vegetation high in nutrient content, rendering this area a likely key wet season range for springbok and other Kalahari ungulates (Williamson et al., 1988).

High grass biomass during the wet season was expected as new grasses emerge and grow rapidly following the onset of rains (Levine et al., 2008) and reach maximum size by the end of the wet season in off-pan habitats, when forage abundance peaks (Owen-Smith, 2008b). Springbok favour such young, succulent grasses of higher nutritional value that are abundant during the wet season (Nagy and Knight, 1994). Grass senescence results in low grass biomass during the hot dry season (Zhang et al., 2005). During this period in the CKGR, a similar ecosystem to the southern Kalahari, springbok grazed less and increased browsing in off-pan habitats (Selebatso et al., 2018c), taking advantage of the higher protein and phosphorus content in browse than grass species during the dry season (Stapelberg et al., 2008; Mphinyane et al., 2015). Woody species provide important reserve resources for springbok and gemsbok in the CKGR (Selebatso et al., 2018c). Woody species remain green longer into the dry season and so likely provide more protein and energy than senescent grass species (Cain et al., 2017).

The pan-edge and off-pan habitats likely provide important habitats for springbok during the hot dry season, when herbaceous forage is senescent. Springbok favoured sites with a high cover and diversity of trees in the 0 – 0.5 m height class in pan-edge and off-pan habitats. A high woody species diversity and cover in the 0 – 0.5 m height class meant that springbok had access to a wide range of species diversity that likely provided different nutrients to meet their requirements. Short shrubs have small, green plant material that enables narrow mouthed herbivores like springbok to select and pick high quality forage (Arsenault and Owen-Smith, 2008). Springbok foraging on short shrubs might also be associated with their body height, which prevents them from reaching tall trees. During drought periods, when forage conditions deteriorate, herbivores overcome nutritional limitations by increasing their diet breadth and relying on key buffer forage resources that help to minimize the negative effects of climatically-induced declines in forage conditions (Cain et al., 2017).

3.5 Conclusion

Springbok need to move between key functional habitats that meet their changing resource requirements. Springbok displayed selection for sites with short grass, high species richness and more ground cover in all seasons, indicating a consistently high level of forage selection. Past studies emphasised that the Schwelle is important for productive ungulate populations, especially the southern and central Kalahari herbivore populations (Williamson et al., 1988; Verlinden, 1994). However, changing climatic conditions and anthropogenic disturbances can stop wildlife from reaching different habitats. Climatic patterns in arid and semi-arid regions of Africa are highly variable (Bassett and Crummey, 2003) and they can prevent access to spatio-temporal habitat heterogeneity to meet seasonal nutritional requirements (Fryxell et al., 2005). Restricted access to these resources can reduce a population's ability to respond to environmental variability and may lead to depletion of local resources and sustainability of the system (Noss, 2007). Restricted access to resources may result in low reproduction success, eventual population declines and possible local extirpation (Fahrig, 2007).

3.6 Link to next chapter

Springbok are highly selective in terms of species richness. Short, highly nutritious grasses associated with pans constitute springbok grazing sites and a high species diversity characterised springbok browse sites. Seasonal shifts in resource availability induce springbok to switch between grazing and browsing (Bigalke, 1972; Stapelberg et al., 2008). Variation in resource availability, predation risk determines the selection, location and extent of home ranges (Kie, 1999; Mitchell and Powell, 2007).

The next chapter will determine whether springbok home range size, daily distance movement and habitat selection ratios vary seasonally. The chapter also determines whether there is a seasonal variation in the day and night locations of springbok as a potential predation reduction strategy.

Chapter four - Seasonal variation in springbok home range size, daily distance movements and habitat selection ratios

Summary

Herbivore habitat use varies seasonally in response to resource availability. Seasonal variation in the distribution and availability of resources affects the location of home ranges, movement patterns and habitat selection. Seasonal variation in home range size, daily distance movement and habitat selection ratios were quantified in five springbok. Home range sizes were larger during the wet season. Springbok used habitats in proportion to their availability during the hot dry and wet seasons while during the cold dry season they selected pans and avoided off-pan habitats. Springbok daily distances were shorter and longer during the hot dry and wet seasons, respectively. Proportion of time spent in pans was higher at night than during the day and during the hot dry season springbok spent more time in off-pan habitats than in other seasons. Seasonal variation in forage and reduced predation risk offered by pans were probably important drivers of springbok habitat use. During the cold dry season three animals used the same pan, resulting in overlapping home ranges. Access to pans is important for springbok, as shown by the preferential use of this habitat during the cold dry season.

4.1 Introduction

The distribution of animals across landscapes is partly a result of the distribution of resources in space and time (Matthiopoulos, 2003). Most protected areas are limited in supporting the needs of all animal species, which access resources by moving between habitats that offer functionally different resources (Harris et al., 2009; Fynn and Bonyongo, 2011). Animals establish home ranges, defined as “an area used by an animal in its daily activities of foraging, mating and caring for young” (Burt, 1943, p. 351) and characterised by heavily revisited sites (Börger et al., 2008). Animals living in mostly stable herds share home ranges (Jarman, 1974), so an individual’s home range can be used as a proxy for the herd range (Cornélis et al., 2011). In resource abundant areas, animals can meet their resource requirements and restrict their movements to smaller home ranges (Buchmann et al., 2011). In resource limited areas, animals need to move frequently between profitable habitats to meet their daily food intake requirements, resulting in overlapping home ranges (Burt, 1943; Ryan et al., 2006; Mitchell and Powell, 2007).

Seasonal changes in resource availability influence home range size (Mitchell and Powell, 2007; Zweifel-Schielly et al., 2009) and can affect every habitat type differently (Zweifel-Schielly et al., 2009). Soil type (Mbatha and Ward, 2006a), rainfall (Zhang et al., 2005), nutrient concentration (Mutanga et al., 2004), and the interactions between these factors cause seasonal variation in forage quantity and quality (Kumar et al., 2002). The profitability of a habitat varies seasonally with differences in primary productivity (Zweifel-Schielly et al., 2009), climatic effects (Ramberg et al., 2006), and predation risk in foraging sites (Kie, 1999). In tropical systems, use of some habitat types is temporally constrained by access to water in the dry season (Redfern et al., 2003) and seasonal rainfall allows animals to make full use of habitats that are unavailable to them during other times of the year, resulting in a seasonal shift in habitat use (Illius and O’connor, 2000; Cornélis et al., 2011). Some herbivores undertake long distance movements to locate profitable foraging grounds and these movements may be repeated at different time scales (Bracis et al., 2018). Waterholes and foraging areas may be revisited at time scales that depend on habitat productivity and resource availability (Bracis et al., 2018). However, these recurring movements remain little studied, despite the improvement in field data collection brought by modern technology such as Global Positioning System (GPS) collars (Johnson et al., 2008; Bracis et al., 2018).

In arid and semi-arid environments, herbivore movement is restricted by water availability and high temperatures, which leads to herbivores moving less during the hot time of the day (Selebatso et al., 2017). These more extreme conditions affect animal feeding strategies and daily activity schedules and are worsened by increased temperatures and low rainfall brought by climate change (New et al., 2006; Valeix et al., 2009). Movement is another key mechanism allowing animals to cope with highly dynamic resource productivity (Martin et al., 2015) by migrating over large spatial scales to accommodate seasonal variation in forage production and retention (Cagnacci et al., 2011), especially in spatially and temporally heterogeneous environments.

Predation can influence access to resources (McLoughlin et al., 2010). Predation risk in foraging sites is an important factor that determines the choice of a habitat patch (Kie, 1999) and herbivores minimise predation risk by increasing vigilance in foraging sites (Ritter and Bednekoff, 1994). Predators like lions may concentrate near waterholes because of herbivore aggregations in the vicinity (Chamaillé-Jammes et al., 2007). Ambush predators also preferentially hunt in proximity to cover (Hopcraft et al., 2005), and more successfully at night than during the day (Martin et al., 2015).

Predation pressure can drive herbivores to areas with lower predation rates (Hebblewhite and Merrill, 2009). Areas with taller forage resources are perceived to confer higher predation risk. Therefore, the animals' ‘landscape of fear’, which describes the foraging cost of predation varies spatially with respect to resources in the landscape and drives the actions of prey in response to predation risk (Laundré et al., 2010). Herbivores tend to use more open habitats when predators are in their vicinity as an anti-predator behaviour and to improve vigilance (Valeix et al., 2009). African herbivores' vulnerability to predation is also influenced by body condition; animals in good condition are less susceptible to predation than those that are starving because they can evade predators than the weaker ones (Sinclair and Arcese, 1995).

In Botswana, Kalahari ungulates formerly made long distance movements from the CKGR and the KTP to the main wet season range known as the Schwelle, a region with a density of saline pans located between the CKGR and the KTP (Lancaster, 1978; Verlinden and Masogo, 1997). The saline pans of the Schwelle support vegetation high in nutrient content that enables pregnant and lactating females to meet their elevated nutritional demands (Williamson et al., 1988). During dry periods, springbok engage in long distance movements in search of suitable grazing (Roche, 2008) and blue wildebeest move between the Schwelle and the CKGR (Williamson et al., 1988). However fences, and human and livestock encroachment in the Schwelle have increasingly restricted access to these ranges (Cooke, 1985; Selebatso et al., 2018a). Despite the general understanding of animal movements in drylands ecosystems, springbok movement and habitat use have not been documented for the southern Kalahari.

4.1.2 Hypotheses

1. Springbok home range size will be smaller during the wet and larger during the hot dry season because of the abundance of high quality forage in pans during the former and limited forage resources during the latter.

2. Springbok will cover shorter daily distances during the wet than dry season and their movements would be focused around pans.

3. Springbok will select pans throughout the year, but the level of selection will be strongest at night and during the wet season.

4.2 Methods

4.2.1 Collaring and movement dataset

GPS satellite collars manufactured and programmed by Vectronic Aerospace, Germany and Followit, Sweden were fitted to four female and one sub-adult male springbok in different herds, each ranging in size from 20 to 70 individuals, between November 2017 and February 2018. All herds were located in pans at the time of capture. Every effort was made to dart and collar female springbok, however, the sub-adult male was darted by accident within a breeding herd and he was collared because he was unlikely to leave that herd until he reached sexual maturity. The study focused on females because they form the core of breeding herds (Prins, 1996). However, non-breeding and sub-adult males move freely with females between territories that contain key resources (Ritter and Bednekoff, 1995). GPS locations recorded by the collars were split by season but not all collars recorded data in every season. Although the individual collared springbok were in separate herds, some joined up for weeks within seasons, probably caused by herds congregating on profitable resources (Millspaugh et al., 1998). Collared animals used saline pans in Mabuasehube and other parts of the KTP (Fig 4.1).

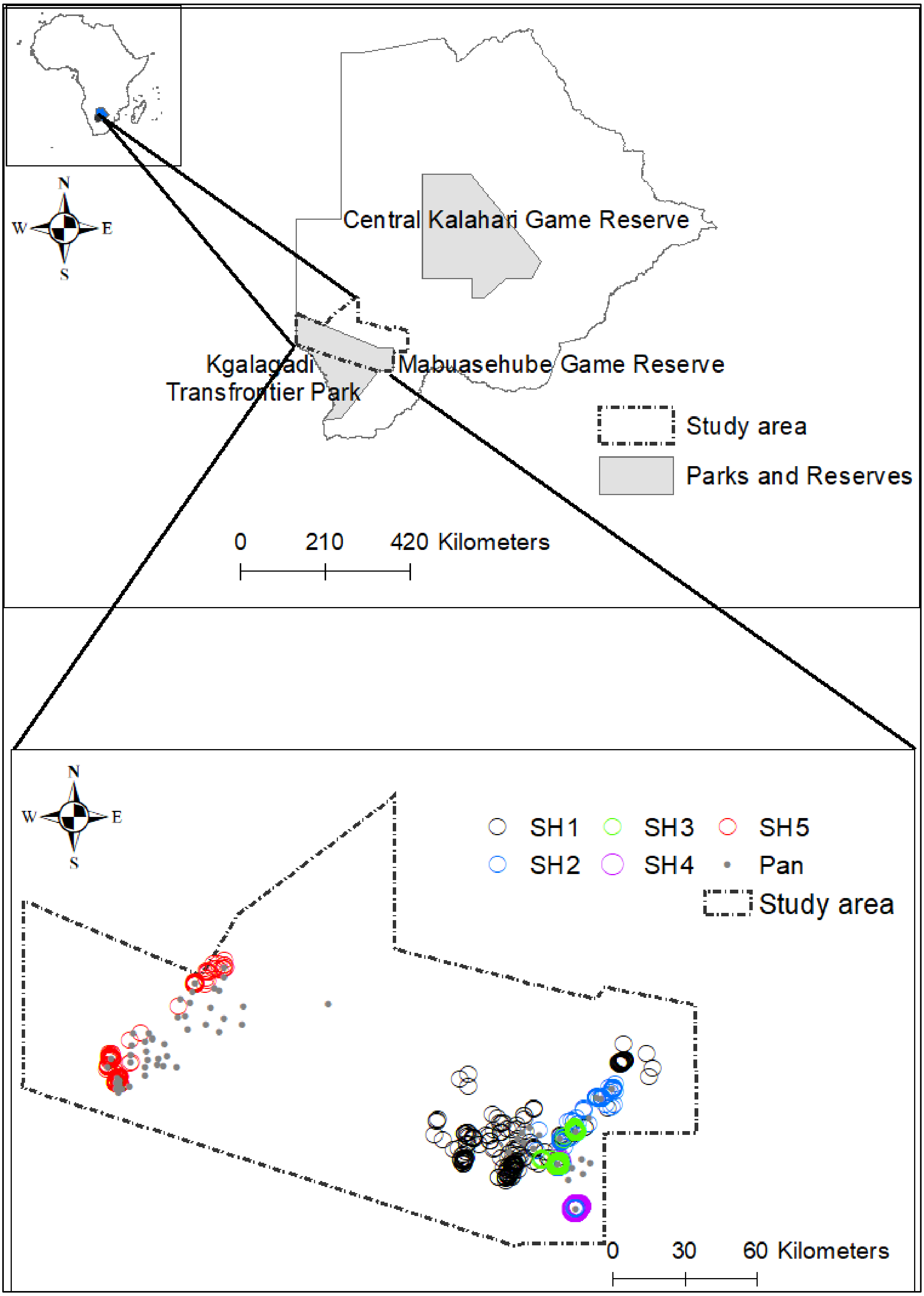

Figure 4.1. Map of study area showing Mabuasehube, the KTP and movement patterns of five collared springbok from 2017 to 2018.

One of two experienced wildlife veterinarians registered with the government of Botswana conducted the darting and collaring operations as approved by the Ministry of Environment, Natural Resources and Tourism through research and darting permits. Females were in good condition, without dependent young or obviously pregnant. Adjustments to the collars were made to ensure sufficient space between the neck and the collar to avoid abrasions. Collars weighed less than 350 g, <2 % of springbok body mass of 30-40 kg (Penzhorn, 1978). Stress to darted springbok and their herds was minimised. All animals were darted from a vehicle and darting during the hottest time and late hours of the day was avoided. I drove around herds until animals were comfortable with the vehicle before darting.

For the hot dry, wet and cold dry seasons, data from three (SH1, SH2, SH3), two (SH1 and SH2) and five animals (SH1, SH2, SH3, SH4 and SH5), were used, respectively. Only animals with data covering a full season were used (Table 4.1).

Table 4.1. Details of springbok satellite collars monitored in Mabuasehube and the KTP between October 2017 and December 2018.

Collar ID	Collaring date	Collar survival (months)	Number of fixes	Season with complete dataset	Fate of collar
SH1	October 2017	12	1174	Hot dry, Wet, Cold dry	Removed
SH2	October 2017	12	1138	Hot dry, Wet, Cold dry	Removed
SH3	February 2018	10	625	Hot dry, Cold dry	Collar failure
SH4	February 2018	5	233	Cold dry	Collar failure
SH5	February 2018	6	290	Cold dry	Collar failure

All animals were immobilised with Meditomidine (1 to 2 mg per animal) and Thianil (2 to 3 mg per animal), as well as 500 iu Hyalase per dart. The darted animals were reversed with Atipamazole at five times the dose of Meditomidine and Naltrexone at ten times the dose of Thianil. Each animal also received an antibiotic (Peni LA) and Kyroligo to prevent possible capture myopathy. Animals were monitored after drug reversal to ensure they re-joined and were accepted by the herd. All satellite collars were equipped with mechanical drop off systems so that collars would fall from the animals even if VHF and GPS transmission failed. Three of the five collars did not cover a full year and stopped transmitting signals. These animals were searched for when in the field, but they were not located to remove collars. Collars were programmed to record GPS positions every day at 7 am for a year. During the middle ten days of each month the fix frequency was increased to four fixes a day at 7 am, 1 pm, 7 pm and 1 am. All capture and handling procedures were approved by the University of Botswana Animal Care and Use Committee (UBR/RES/IRB/ACUC/004).

4.2.2 Data analysis

Home range size

The kernel density estimation (KDE) method from the adehabitat package in R (Calenge, 2006) was used to calculate 95 % kernel utilisation distribution for each animal (Benhamou, 2011) to allow a comparison of home range sizes between seasons. Kernel home range estimators were chosen over Minimum Convex Polygon (MCPs) because the latter do not provide the true outline of the home range, as they treat points rarely visited equally to those used extensively. Kernels produce similar estimates to LoCoH. However, LoCoH need a large sample size of GPS points in order to be accurate (Gertz et al., 2007) of which my sample size was not large enough to use this method. Kernels more accurately distinguish areas of intensive use (Worton, 1987). Individual animals’ home range areas were calculated using ArcGIS 10.6 (ESRI). The effects of season on home range size were analysed using generalised linear mixed models

(GLMMs) in R (lme4 package; Bates et. al, 2015) with a gamma distribution and a log link function for positive, not normally distributed data after running a Shapiro-Wilk test on the data. Models were run using home range size as the dependent variable and season as the fixed predictor variable. Individual animal was the random effect. AIC values from each model were extracted and compared to identify the most parsimonious model (Akaike, 1974).

Daily distance movements

Location data from the collars accessed online were used to calculate daily distance covered for each animal using the ‘move’ package in R (Kranstauber et al., 2017). The effects of season on daily distance movements were analysed using generalised linear mixed models (GLMMs) in R (lme4 package; Bates et. al, 2015) with a gamma distribution and a log link function for positive, not normally distributed data after running a Shapiro-Wilk test on the data. Models were run using distance as the dependent variable and the season as a fixed predictor variable. Individual animal was used as the random effect. The dredge function in the MuMIn package was used to perform automated model selection using the global model based on AIC values (Barton, 2009).

Habitat selection ratios

There was no habitat map for the study area and lacked the resources to create one, so habitat selection was based around pans within the landscape. Four springbok home ranges occurred in Mabuasehube and one in another part of the KTP, so two MCPs were created around the two sets of points and a 1 km buffer was added around each resulting polygon to allow for potential movements outside of the recorded range in between fixes. Google Earth (Mountain View, CA) was used to locate the main saline pans within the study area, including those that collared springbok did not use. Coordinates of the centre of each pan within the buffered polygon and location data from the collars were plotted in ArcGIS. Google Earth was used to calculate the radius of those pans, which had a primarily circular shape. The near tool in Arc GIS was then used to calculate the distance between the location of springbok and centre of the nearest saline pan. Pan radius was subtracted from the distance between pan centre and each springbok location. Distance <0 meant that the animal was in the pan and >0 indicated that the animal was off-pan. Distances between -50 and 50 were removed from the analysis to remove any ambiguous locations caused by irregular shaped pans. Only fixes that were in pan and off-pan habitats were identified because it was difficult to exactly identify pan-edge habitat.

The formula for calculating area of a circle

$$A = \pi r^2 \text{ where } A = \text{area}, \pi = \text{Pi and } r = \text{radius}$$

was used to calculate the area of each pan within the study area and summed to give a total pan area. The area of each MCP was calculated using the calculate geometry function in Arc GIS 10.6 and summed to give a total area. The total pan area was subtracted from the total study area to calculate the proportion of the study area that contained off-pan habitat. These habitat availability data were converted into percentages by dividing the area of pan and off-pan habitat by the total study area and multiplying by 100. Percentage habitat use for each animal was then calculated by dividing the number of fixes in pan or off-pan habitats by the total number of fixes and multiplying by 100.

The adehabitat HS package in R (Calenge, 2006) with a design III analysis was used to calculate seasonal habitat selection ratios by dividing the percentage of use by the percentage of availability for the two habitats for each animal (Manly et al., 2002). Values with confidence intervals >1 indicated selection and those <1 indicated avoidance (Neu et al., 1974).

Day and night locations

Locations recorded at 1 pm and 1 am were used to run a comparison between day and night habitat selection. The number of fixes on the pan and off-pan during the day and night were divided by the total number of fixes at each time and converted into proportions. The effects of season and time of day were analyzed using a GLMM in R (lme4package; Bates et al., 2015) with a binomial distribution and a log link function. Pan and off-pan habitats were coded 0 and 1, respectively, to allow the use of the binomial distribution (Bates et al., 2015). Models were run using habitat as the dependent variable and the interaction effects of season and time of day as fixed predictor variables. Individual animal was used as the random effect. AIC values from each model were extracted to compare models (Akaike, 1974).

4.3 Results

4.3.1 Home range size

The most parsimonious model included the effect of season; no other model was competitive (AIC =-240.71, AICω = 1). There was a seasonal variation in home range size between the hot dry and the wet ($t = 10.79$, $P < 0.001$), the hot and cold dry ($t = 8.38$, $P <0.001$) and the wet and cold dry seasons ($t = 14.10$, $P < 0.001$) indicating that home range size varied significantly across seasons. Home ranges were smaller during the hot (0.01 - 0.05 km²) and cold dry (0.01 - 0.07 km²) seasons than during the wet (0.02 - 0.15 km²) season (Fig 4.2).

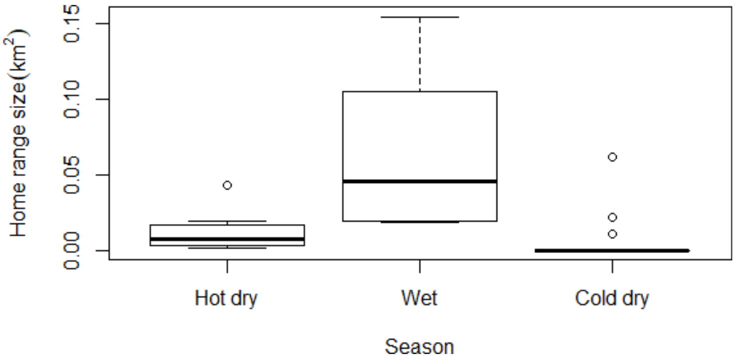

Figure 4.2. Springbok seasonal home range sizes in Mabuasehube and the Schwelle, Botswana from 2017-2018. Error bars represent ± 1 standard error.

Most home ranges were centred around saline pans, however springbok SH1 extended her home range beyond pans and occupied three different areas during the wet season (Fig 4.3B). SH2 and SH3 used two different areas during the hot dry season (Fig 4.3A). There were overlapping home ranges during the cold dry season for SH1, SH2, SH3 and SH4, indicating that springbok selected the same saline pans during the cold dry season (Fig 4.3C).

4.3.2 Daily distance movements

The most parsimonious model of factors influencing daily distance included the effect of season, no other model was competitive (AIC = 52327.02, AICω = 1). The hot dry (t = -7.61, P <0.001), the wet season (t = 2.40, P = 0.02) and the cold dry (t = 4.34, P = 0.01) caused the seasonal variation in distance, indicating that distance varied across seasons. Springbok covered shorter distances during the hot dry than during the wet and cold dry seasons (Fig 4.4).

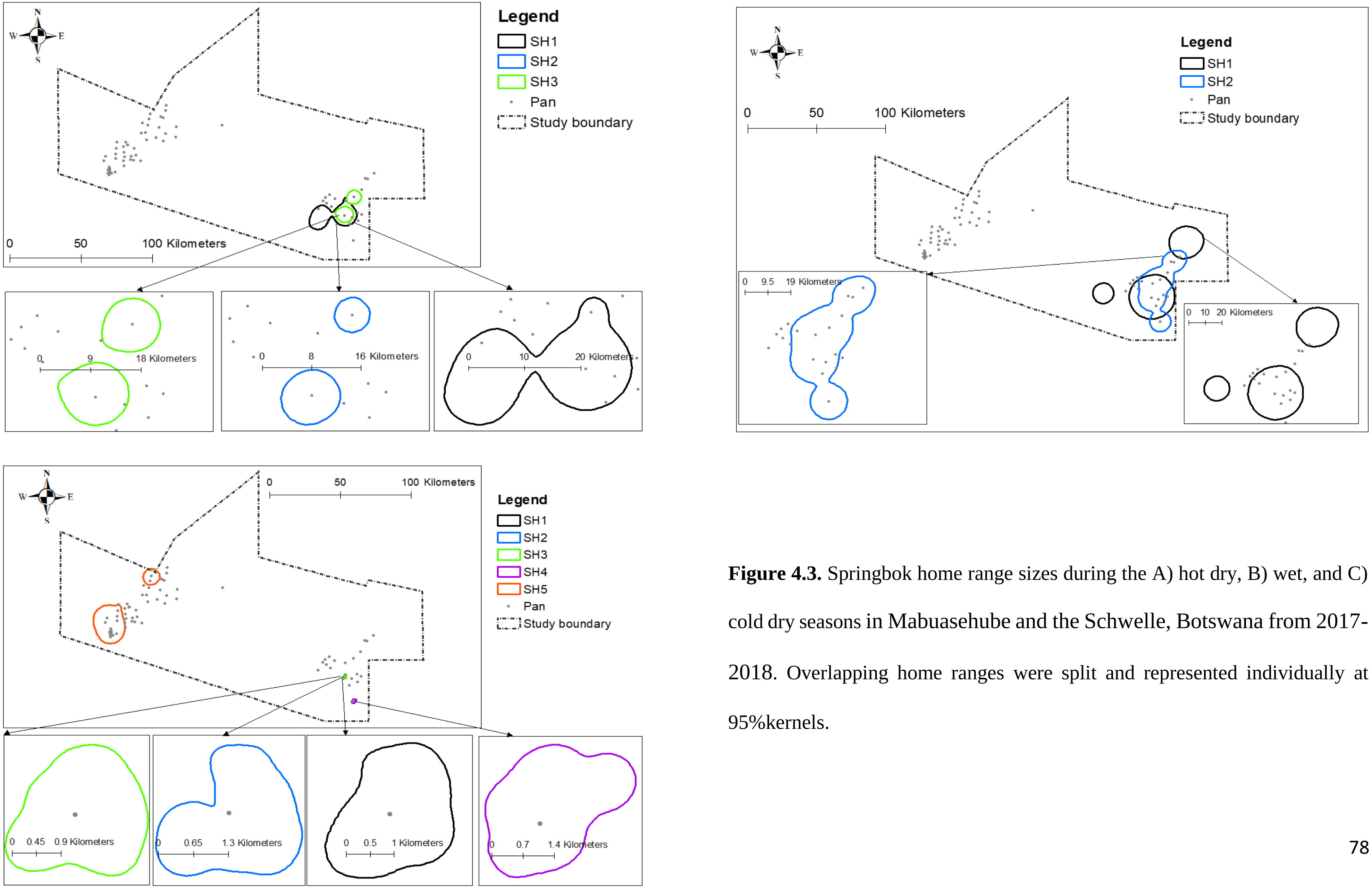

Figure 4.3. Springbok home range sizes during the A) hot dry, B) wet, and C) cold dry seasons in Mabuasehube and the Schwelle, Botswana from 2017-2018. Overlapping home ranges were split and represented individually at 95%kernels.

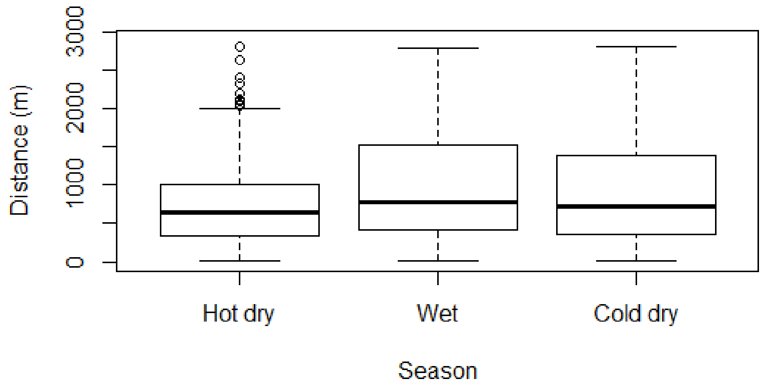

Figure 4.4. Springbok seasonal daily distance movements in Mabuasehube and the Schwelle, Botswana from 2017-2018. Outliers above 3000 metres are not included. Error bars represent ± 1 standard error.

4.3.3 Habitat selection ratios

Springbok did not select or avoid habitats in the hot dry or wet seasons, indicating that habitats were used in proportion to their availability. During the cold dry season, springbok selected pans and avoided off-pan habitats, as indicated by confidence intervals above and below 1, respectively (Table 4.2).

Table 4.2. Springbok seasonal habitat selection ratios in pan and off-pan habitats in Mabuasehube and the Schwelle, Botswana from 2017-2018. SE represents standard error of the selection ratio. Ratios with confidence intervals >1 and <1 indicate selection and avoidance of particular habitat types, respectively. Significant selection ratios are indicated in bold.

Season	Habitat	Selection ratio	S.E	Lower CI	Upper CI
Hot dry	Pan	8.29	3.77	-0.18	16.76
	Off-pan	0.87	0.07	0.73	1.02
Wet	Pan	6.30	2.88	-0.16	12.76
	Off-pan	0.91	0.05	0.80	1.02
Cold dry	Pan	**25.05**	**8.13**	**6.83**	**43.27**
	Off-pan	**0.60**	**0.13**	**0.31**	**0.89**

4.3.4 Day and night locations

The most parsimonious model included the effect of season and time of day (Table 4.3).

Table 4.3. Model selection table of factors influencing springbok day and night locations in Mabuasehube and the Schwelle, Botswana from 2017-2018.

Model	AIC	ΔAIC	AICω
Season + Time of day	605.8	0.00	0.88
Season : Time of day	609.8	4.02	0.12
Null	1291.5	685.77	0.00

Springbok used pans more than off-pan habitats in all seasons and at any time of the day. However, the proportion of time spent in off-pan habitats was higher during the hot dry season than in other seasons (Fig 4.5A). The proportion of time spent in pans was higher at night than during the day (Fig 4.5B).

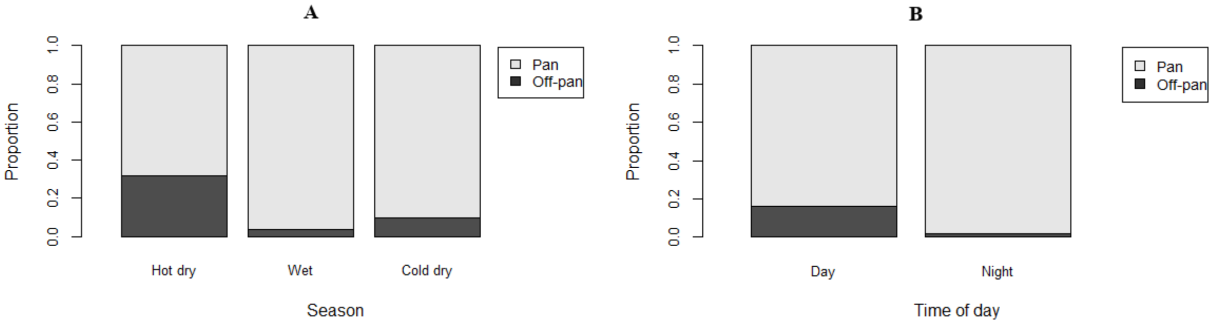

Figure 4.5. Proportions of springbok day and night locations according to A) seasons and B) time of day in Mabuasehube and the Schwelle, Botswana from 2017-2018.

4.4 Discussion

Seasonal shifts in forage quality and quantity determine habitat profitability and distribution of herbivores across the landscape (Bailey et al., 1996). Herbivores need food which is rarely available in one area in all seasons, resulting in selecting and avoidance of certain habitat types or migration from less productive to more productive habitats (D'Eon and Serrouya, 2005; Barraquand and Benhamou, 2008).

Herbivores must access different habitats that vary in characteristics to forage on diverse resources (Barraquand and Benhamou, 2008). According to Clutton-Brock’s (1989) hypotheses, the home range size of springbok breeding herds was expected to increase during the hot dry season when forage resources are limited, because females must move between habitats to obtain sufficient key resources (Ritter and Bednekoff, 1995). However, home range size increased during the wet season, a period when forage is abundant. Home range size depends on the animal’s nutritional requirements, the amount of energy and minerals provided by the resources within the habitat, and density-dependent competition (Kjellander et al., 2004). Energy and mineral requirements, particularly for lactating females, are highest during the wet season when they produce young; during dry periods animals might only meet a minimum resource threshold needed for survival (Kjellander et al., 2004). This means that during the wet season springbok need more energy and minerals to meet the demands of lactation and calf growth, and they should select habitats that will provide the best resources to meet their elevated nutritional requirements, hence occupying large home ranges. The larger home range sizes during the wet season may also be caused by movement between pans to meet the elevated nutritional requirements. During the hot dry season animals prevent dehydration because there is limited surface water hence occupying small home ranges (Selebatso et al., 2017).

Contrary to predictions, springbok daily distance movements were shorter in the hot dry than during the wet and cold dry seasons. During the hot dry season, forage availability is limited and temperatures are generally very high in the Kgalagadi region (Van Rooyen et al., 1990). Similar to other herbivores in this environment, springbok may attempt to conserve energy and avoid heat stress during the hot dry season when water availability is most limiting by minimising their movements (Selebatso et al., 2017). Springbok also seek shade under trees and shrubs during the hottest time of the day and revert to more nocturnal behaviour (Skinner, 1996). The wet season is characterised by an increase in foraging activity because of the higher nutritional demand associated with calving and lactating (Kreulen, 1975) and leads springbok to seek abundant mineral nutrients in grasses (Martin et al., 2015). Herbivores build enough body stores during the wet season when there is abundant forage and conserve them for survival during the dry season when forage resources are most limiting (Parker et al., 2009). Springbok should maximise foraging to meet their nutritional demands and accumulate enough body stores to take them into the dry season. Cooler days during the wet and cold dry season could enable springbok to forage and move throughout the day, increasing their daily distance movements and home range sizes.

The abundant forage during the wet season also provides energy that makes movement possible. Among ungulate species living in forested regions in the northern hemisphere, moose (*Alces alces*) respond to high temperatures by decreasing activity (Dussault et al., 2004). In the Kalahari, Botswana wildebeest suffered mortality when attempting to move long distances to seek alternative water sources during the dry season when artificial water holes dried up (Selebatso et al., 2018a). In Kruger National Park, South Africa, wildebeest travelled longer distances per day during the wet season when temperatures were lower than in other seasons (Martin et al., 2015).

There was no habitat selection or avoidance during the hot dry and wet seasons; however, during the cold dry season springbok selected pans and avoided off-pan habitat. Pans in the Kalahari have saline soils with high nutritional concentrations (Williamson et al., 1988).

Short grasses of high nutritional value associated with pans are favoured by springbok (Selebatso et al., 2018b). Kalahari ungulates select high quality habitats that can meet their nutritional demands, however, anti-predator behaviour also influences selection for pan habitats (Valeix et al., 2009; Yoganand and Owen-Smith, 2014). High visibility in pans reduces predation risk (Valeix et al., 2009) and may have contributed to selection of pans especially at night when most predators are active. Herbivores respond to predation by avoiding risky and selecting safer habitats (Valeix et al., 2009). In this study pans provided a safer habitat for springbok especially at night. Springbok browse in off-pan habitats during the hot dry season (Stapelberg et al., 2008), however they may have used this habitat more during the day than at night as an anti-predator strategy because predators can easily be seen and they are less active during the day than at night. Other activities like vigilance also play an important role in early predator detection (Valeix et al., 2009). In the Kalahari ecosystem, springbok and wildebeest meet their nutritional demands by foraging on open pans with high quality forage and low predation risk (Selebatso et al., 2018a).

The results showing that habitat selection only occurred during the cold dry season may have been caused by sample sizes, which were very low during the wet and hot dry seasons. Nevertheless, the results may have accurately represented springbok behaviour because the cold dry season is a transition from the wet into the hot dry season and some pans may have retained productive grasses of high quality. Springbok may have selected pans to take advantage of the remaining high quality grasses to meet the high energy requirements for lactation, which may well have continued from the wet into the cold dry season (Owen-Smith, 2004; Parker et al., 2009). During the wet season there is abundant, high quality forage across the landscape upon which herbivores can feed (Owen-Smith, 2008b), possibly explaining the lack of habitat selection: springbok were able to meet their nutritional demands by using habitats in proportion to their availability. The hot dry season is characterised by low grass quality, therefore springbok graze less and increase browsing in off-pan habitats to take advantage of the higher protein and phosphorus content in browse than grass species (Stapelberg et al., 2008; Selebatso et al., 2018a).

Springbok may attempt to conserve water by resting and avoid long distance movements, which might cost them more energy that is limited by scarce resources during the hot dry season. The study links springbok movement to habitats and highlights behavioural decisions made by springbok herds to exploit spatially and temporally heterogeneous resources in addition to reducing predation risk. The movement of springbok was likely constrained by extreme heat of the day, suggesting that heat stress influenced springbok foraging decisions during the hot dry season, coinciding with small home ranges occupied during the hot dry season. The suitability of pans for springbok populations in terms of high forage quality and reduced predation risk explain their preferential use of these habitats during the cold dry season.

4.5 Conclusion

Springbok move between pans, which are important for productive springbok populations because of their high soil and grass nutrient status (Selebatso et al., 2018; Milton et al., 1992). High quality forage in pans and reduced predation risk probably influence movement patterns of Kalahari springbok. However, resources in arid environments like the Kalahari are driven by rainfall. Lack of rain can lead to drought and forage scarcity (Mduma et al., 1999), which can lead to a decline in the productivity of pans that springbok depend on for resources, causing mortalities. A decline in forage availability during drought years means that springboks may not acquire their nutritional requirements, therefore compromising fitness and reproduction.

Pregnant females have elevated nutrient demands as they approach parturition (McDowell, 1985), which coincides with the time when the population struggles to get enough food to maintain body requirements. A delay in the onset of rains caused by climate change means that females go into the critical stages of pregnancy under resource limited conditions. These conditions may cause low birth weights of new-borns (Belkacemi et al., 2010), lead to mortality of lambs in the early stages of life (Owen-Smith, 2008a), and ultimately result in population declines (Caughley and Gunn, 1993).

Limited forage availability and high temperatures during the hot dry season could limit the daily movements, while forage and cooler temperatures during the wet season likely made movement possible. Climate change predicts hotter, drier conditions that could limit animal movement further (Martin et al., 2015).

4.6 Link to next chapter

Seasonal fluctuations in resource availability in addition to predation risk avoidance likely determine springbok home range size, daily distances and habitat use. Home range size increased with resource availability during the wet season because springbok needed high quality resources to meet their elevated nutritional demands. Temperature was an important factor determining springbok movement. High temperatures during the hot dry season restricted movement and springbok moved longer distances during the cool wet and cold dry seasons. Springbok selected pans and avoided off-pan habitats during the cold dry season. During the hot dry and wet seasons pan and off-pan habitats were used in proportion to their availability.

The last chapter brings together all the components of the thesis and summarizes them. The chapter highlights major findings, management implications and limitations of the study. Recommendations for future work are also suggested.

Chapter five - Synthesis

Two of the main factors driving population declines and loss of biodiversity are habitat loss and fragmentation (Owen-Smith, 2004; Fryxell et al., 2005; Harris et al., 2009) and the rising global effects of climate change (Post et al., 2009). Increasing human populations and associated land use demands continue to put pressure on wildlife species and their habitats because more people need land for agriculture and other development activities (Bergström and Skarpe, 1999b; Schieltz and Rubenstein, 2016). These effects are likely to increase given expanding human populations (Steffen et al., 2011).

The Kalahari herbivore population, like many dryland species, depends on mobility to access spatio-temporally varying resources (Williamson et al., 1988). Historically, springbok in the Kalahari would come together in herds of tens of thousands to migrate in search of suitable grazing resources (Roche, 2008), but these movements have increasingly been restricted by anthropogenic activities (Cooke, 1985). The main aim of this study was to determine possible factors that could contribute to the decline of the springbok population in the southern Kalahari. I found that these include the low survival rate of juveniles that can lead to low recruitment rates, limited forage availability to meet nutritional demands during the hot dry season, and high temperatures during the hot dry season that could limit movement to exploit spatially and temporally heterogeneous resources. This chapter discusses the major findings of the study and their implications for the Kalahari ecosystem management, identifies limitations of the study and suggests future research topics.

5.1 Major Findings and Discussions

The ecology of the Kalahari springbok is influenced among other things by changes in the region, such as environmental conditions. The most important factor is rainfall (Mills and Retief, 1984), which has an effect on herd size dynamics at a small scale and population dynamics at a large scale. Springbok herd sizes increase during the wet season in response to rainfall and grass growth and decrease during the hot dry season when there is limited forage in the landscape (Chapter Two) and could explain the observed differences in home range size (Chapter Four). Rainfall also has an indirect influence on springbok behaviour through changes in nutritional value of forage (Mbatha and Ward, 2006b). Springbok engage in long distance movements to areas where it rained to take advantage of the first green sprouts of vegetation (Bothma, 1972; Skinner and Moss, 2004). When the amount of rainfall is enough to stimulate forage growth, springbok might travel to those areas to forage on new plant shoots that grow immediately after rains. However, timing is important because springbok lambing coincides with rainfall (Bigalke, 1970) to meet the high nutritional demands for lactation and growth (Owen-Smith, 2004). During the wet months there is a higher ratio of juvenile: adult females in springbok herds than in the hot and cold dry seasons (Chapter Two), suggesting that rainfall and forage abundance may be the most important factors influencing herd size and proportion of juveniles. Springbok herd sizes decreased as they split to search for limited resources during the hot dry season, although they covered less distance than during other seasons (Chapter Four). Previous studies in the Kalahari also recorded larger springbok herd sizes during the wet than the hot dry season (Nagy and Knight, 1994; Stapelberg et al., 2008).

Springbok are selective mixed feeders (Skinner and Louw, 1996) and make use of grass and browse (Skinner and Smithers, 1990; Selebatso, 2018; Chapter Three). They prefer sites with short grasses, high species richness and diversity, and low biomass, where they can forage on a diversity of species that likely provide different nutrients (Chapter Three). Areas with tall grasses are avoided by springbok as an anti-predator strategy because some predators can easily attack them in tall grasses (Mills and Mills, 2013). Springbok respond to changes in the availability and nutritional quality of forage by altering their diet, feeding on grass during the wet season when forage quality is highest (Vorster, 1996), and on browse during the dry season when the nutritional quality of grass deteriorates (Bothma, 2002). Springbok are highly selective in terms of grass species on the pans and are able to survive with little or no water provided that their diet contains enough moisture from forage (Nagy and Knight, 1994; Stapelberg et al., 2008). Irrespective of their water independence, they have access to two waterholes in Mabuasehube, and they make use of natural licks to supplement their diet (Bergstrom and Skarpe, 1999). Past studies observed that springbok maximise water intake from foraging by feeding at night when plants retain moisture in their leaves, but nocturnal activity patterns are not yet fully understood and require further investigation (Nagy and Knight, 1994; Stapelberg et al., 2008). Selection behaviour of springbok can cause detrimental effects on the population during resource-limited and drought years when they cannot access a variety of resources, potentially leading to low reproduction success, starvation and population declines. Therefore, changing environmental conditions can prevent access to spatio-temporal habitat heterogeneity required to meet seasonal nutritional requirements (Fryxell et al., 2005).

The main predators of springbok in the southern Kalahari are cheetah (Mills and Mills, 2016), with some kills made by lions (Mills, 1984); however, the lion population of the southern Kalahari has declined over the past 20 years (Castley et al., 2002) and cheetah numbers have remained low over the past decades (Skinner and Moss, 2004). Declining large predator populations could lead to meso-predator release (Prugh et al., 2009) and black-backed jackals have been observed in high numbers in the southern Kalahari (Kaunda and Skinner, 2003), including within springbok herds during the birthing period (Chapter Two). High jackal predation on springbok juveniles was also observed elsewhere (Krofel, 2008; Klaire et al., 2010; Mills and Mills, 2013). In declining populations, predation of juveniles could reduce the overall springbok population (Mills and Mills, 2016). The springbok population dynamics in the southern Kalahari have not yet been studied in detail and more studies on predation impacts on the springbok population are needed.

Seasonal variation in the distribution and availability of resources and predation risk affected springbok home range size, movement and habitat selection. In this study springbok selected pans and avoided off-pan habitats during the cold dry season while habitats were used in proportion to their availability during the hot dry and wet seasons (Chapter Four). Pans were identified as critical habitats for springbok during the cold dry season in the study area. In addition, the proportion of time spent on pans was high compared to off-pan in all seasons which also explain the importance of this habitat (Chapter Four). Pans also offer the most visibility and it would have enabled springbok to reduce their exposure to predators especially at night (Valeix et al., 2009). However during the hot dry season there was a high proportion of time spent in off-pan habitat compared to other seasons mainly to complement their diet by browsing (Bothma, 2002).

During the wet season herbivore resource requirements are high and they need to meet their elevated nutritional requirements (Kjellander et al., 2004; Murray, 1995; Parker et al., 2009), therefore they need to move to profitable habitats, in this study it was indicated by more distances moved and larger home range sizes during the wet season (Chapter Four). During the most limiting season, animals need to meet a minimum resource threshold for survival therefore springbok may attempt to conserve the limited energy and minimise movement (Kjellander et al., 2004; Chapter Four).

The results are in agreement with the functional resource and habitat heterogeneity concept: springbok appeared to adapt to seasonal variation in resources by selecting and avoiding pans and off-pan habitats, respectively, during the cold dry season, grazing on pans with low biomass and in sites that differ in characteristics from available sites in terms of species richness, biomass, height and cover. The variation of habitat types in their provision of resources appear to be important for springbok.

5.2 Management implications and recommendations

The study shows that pans are important habitats for springbok in the arid ecosystem of the southern Kalahari as they provide access to abundant resource-rich forage. Losing access to the high density of resource-rich pans in the Schwelle limits the reproductive potential of the population and subjects the population to extended risks, extreme environmental effects and predation pressure, which would otherwise be avoided to ensure viability of the population. Therefore the study recommends the following;

1. Access to the rich pans in the Schwelle is important for productive springbok populations and should be maintained. Future management decisions should be aimed at maintaining free springbok movement within the southern Kalahari and between Mabuasehube and the Schwelle. Maintaining access to the Schwelle will insure that springbok continue to calve in the area. Restricted access to the Schwelle could compromise reproduction success, fitness and eventually contribute to population decline.

2. Areas with key resources for animals like pans and valleys should be taken into account when delimiting conservation zones. In addition to high forage quality provided by pans, springbok use pans for safety, especially at night for early predator detection.

3. Although this was not part of this study, springbok in the Schwelle could be disturbed by humans through poaching, which could be a factor leading to the observed decline. Therefore wildlife managers need to intensify their efforts to conserve springbok by having regular anti-poaching patrols in the KTP and the Schwelle areas. Although the International Union for Conservation of Nature (IUCN) Red List has springbok listed as Least Concern, one of their main predators, cheetah, are listed as Vulnerable by the IUCN and are declining across their

range (IUCN, 2018), and the decline in their main prey base could be a significant contributing factor. Kalahari lions (listed as Vulnerable by the IUCN) and wild dogs (listed as Endangered by the IUCN) also predate springbok, thus the carnivore guild would be negatively affected by reduced springbok numbers and should benefit from any actions that reverse this trend.

4. Collective action is important to get conservation working better outside protected areas. Community involvement in decision making and conservation design strategies will enable them to see the importance of conserving the springbok population. Also, communities living adjacent to protected areas should have better incentives derived from protected areas to encourage conservation. Community driven conservation initiatives that strives to protect key seasonal ranges, capacity building to come up with ways of making conservation socio-economically and ecologically sustainable should be encouraged (Kremen and Merenlender, 2018). For example, giving grazing concessions to non-sensitive parts of the protected area for communities to utilise resources at certain times of the year as suggested by Fynn et al., 2016. That is when the communities can realise the importance and benefits of conservation. There is need to come up with policies or government systems that support collective action. Involving communities would help come up with a working model at community level that will ensure co-existence between people and wildlife to enhance sustainability (Ostrom, 2009; Sayer et al., 2013). Legitimate policies and institutions enabling fair distribution of benefits and incentives among stakeholders will make communities realise the importance of conservation more especially local communities.

5. Community based tourism should be encouraged. In the case of the Schwelle the residents through the trust can earn income from tourists through camping at the pans where they can see diverse wildlife species. In addition to camping, residents could earn income from demonstrating their indigenous knowledge to tourists.

5.3 Limitations of the research

1. During the study period collar failures occurred for three of the five collared springbok. In most instances collars stopped recording and transmitting GPS fixes. The VHF stopped functioning as well, so it was impossible to track the animals to remove collars. Remote drop-off mechanism of two of the five collars functioned as planned. In some instances there were missing fixes. Substantial oscillation by the collar and weather conditions could have reduced the likelihood of maintaining contact between the satellites and the receiver for the time period necessary to record a GPS location.

2. There were efforts to deploy more collars in the Schwelle but the efforts failed as herds would not allow us to get close enough to dart, in contrast to animals inside the park that allowed us to approach them. Four attempts were made in different months and failed. While this was a problem, these events provided important information, as they reflected different behaviours between springbok inside and outside of the reserve.

3. There was no habitat map available for the study area and the resources were insufficient to create one. Lack of resources limited the capacity to create a map for habitat selection. There is need for a habitat map of the area.

4. The small springbok population in Mabuasehube reduced vegetation sample sites because in some instances springbok were not sighted in pans and springbok were not always observed browsing throughout the year.

5. Available data for woody vegetation was not collected because of lack of resources. The data would have given more insights on springbok selection for woody species.

6. Animals were counted in open areas, ie, pan and pan-edge habitats which mean that some may have moved into the off-pan habitats and were not counted.

7. Grass greenness was not measured due to time limitations.

5.4 Future research

1. This study highlights the potential influence of jackal predation on springbok juveniles during the birthing season, however, more research on this topic is needed in the Kalahari ecosystem to qualify and quantify this possibility.

2. More collars should be deployed in the Schwelle to determine how the springbok population uses the landscape close to settlements.

3. Springbok in the Schwelle are in close proximity to settlements and cattle posts, so there could be poaching pressure. There is great need to change people's attitudes toward unsustainable killing of wild animals for food. Future studies could use springbok as their flagship species by understanding people's perceptions about poaching and discussing the effect of poaching on declining springbok populations in an effort to change attitudes and reduce the levels of poaching in the study area.

4. Analysis of faecal samples can be used to monitor the nutritional value of springbok diet. This would help to understand seasonal changes in diet composition and general ecology, which will provide insights of the nutritional status of springbok. This would increase understanding of springbok ecology within the Kalahari system through detailed analysis of their resource requirements. The DWNP has identified this as a priority study to inform actions aimed at stopping springbok population declines; therefore, the results will be relevant to national conservation priorities.

5.5 Overall conclusions

There is little published knowledge on springbok ecology in Botswana, especially in the Kgalagadi, where most of springbok population occurs. Springbok ecology and predator-prey relationships require additional studies to halt and reverse the population decline. In addition, there is need for more research on interactions with other sympatric herbivores, especially in such spatially vast open pans and valleys of the southern Kalahari. Understanding ecosystem dynamics and functioning is important for ecosystem management, particularly for the continually fragmenting African habitats.

High quality forage and reduced predation rates associated with pans likely determine the movement patterns of springbok in the Kalahari. Findings from the study show that protected areas alone are insufficient for managing wildlife populations and the Schwelle appears to be an important habitat for productive springbok population. Securing the Schwelle is key because the high density of pans in the area have highly nutritious forage and open vegetation structure that are important determinants of springbok calving as well as reducing predation. Predation of juveniles during the birthing season and low quality forage during the hot dry season could lead to low recruitment rate that can cause a decline in springbok numbers. Low forage quality could compromise lamb survival. These findings call for a need to protect pans and corridors between them, especially those in the Schwelle, for the long term viability of Kalahari springbok and other ungulates in the dry land ecosystems. Human encroachment, expansion of settlements and cattle posts into the Schwelle should be minimised to allow unrestricted access of springbok and other ungulates into the area at any time of the year.

In the past ungulates were able to move between wet and dry ranges because of low human population densities (Ogutu et al., 2009). However, migration is slowly being restricted by population increases and developmental activities (Russell and Cuthill, 2009; Verlinden, 1997). In the past springbok engaged in long distance migration in search of suitable grazing

(Child and Le Riche, 1969; Skinner, 1993) but this migration has been disrupted by anthropogenic factors like livestock and human population increases, drought and fencing (Roche, 2008). During migration animal droppings play a major role in plant nutrient cycling, however animal movement restrictions have been predicted to reduce the rate of nutrient cycling in the landscape and will have an effect on plant composition, structure and ecosystem functioning (Augustine and McNaughton, 1998).

Connectivity between key habitats is important for species reliant on access to functional resources in different habitats. It is evident that springbok move between pans, probably due to the open nature of the pans and the different resources provided by different habitats at different times of the year. Short, high quality forage in pans is important to meet seasonal nutritional requirements. Declining forage quality during the hot dry season forces springbok to switch to browse species that retain moisture in leaves, however the available browse may not be able to meet their requirements. The onset of the wet season is critical for the fitness of the population as any delay in high quality forage may compromise reproductive success, survival rates and lead to population decline. During the hot dry season, springbok get limited moisture from forage and survive the heat by reducing activity as they attempt to conserve water by resting and avoiding long distance movements which could cost them more water and energy. Added to this is the effect of climate change that is predicted to have a large impact in Africa (IPCC, 2018).

High temperatures and reduced rainfall have been projected and African species may experience high extinction risks under climate change (Rabaiotti and Woodroffe, 2019). This may have huge impact on species in the hot arid environments given that reduced rainfall and high temperatures may impact survival and reproduction and lead to a decline and possible extinction. The predicted impacts of climate change will affect species and ecosystems (IPCC, 2018). Species occupying narrow ecological niches are vulnerable to changing climatic conditions and anthropogenic disturbances (Cowlishaw and Dunbar, 2000). Climatic patterns in arid and semi-arid regions of Africa are highly variable (Bassett and Crummey, 2003) and they are predicted to become more extreme in the future, so only species that can adapt to these changes will survive (Rudnick et al., 2012).

In addition to the impacts of climate change, predation could reduce the population of specialised species dependent on specific habitats because their locations are predictable. Low survival rate of juveniles could prevent population growth when juveniles are not recruited into the population. Animals in arid ecosystems may face more declines and possible extinction from increased risk of climate change and anthropogenic activities that might limit forage and water availability, reduce capacity for movement and lead to reduced food supply, destruction of the habitat and impacted survival.

In support of the functional habitat heterogeneity framework, springbok need access to different habitats to forage on. Foraging on a diversity of plant species distributed on different environmental gradients is an important strategy to obtain nutritional requirements from resources in that particular habitat (Stapelberg et al., 2008). Feeding behaviour and patterns are determined by species in the habitat which differ seasonally in addition to predation risk avoidance. Therefore springbok need to select habitats which meet their changing nutritional requirements in addition to predator risk avoidance.

Predation would be acting because of changes in ecological conditions making springbok more vulnerable to predators. Access to diverse forage resources in different habitats is important for productive springbok population. Dry season resources are important because they minimise the rate of decline in body stores during resource limited period whereas wet season resources are rich in energy, proteins and minerals to meet the demands of lactation, calf growth and body condition maintenance (Hopcraft et al., 2010; Owen-Smith, 2004; Fynn, 2012). Loss of access to these resources subjects the population to interspecific competition, predation pressure, and extended risks to extreme environmental effects, that could compromise the resilience of the population to environmental variability.

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