KEY FACTORS DRIVING THE FORAGING ECOLOGY OF ORIBI: FEAR, CATTLE AND THE QUALITY AND QUANTITY OF FOOD

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ABSTRACT

Body size and digestive physiology are two factors that influence herbivores foraging behaviour, habitat use and potential to compete with other animals. The aim of this study was to determine how seasonal changes in grass quality, interactions with cattle, and perceived predation risk influenced oribi (*Ourebia ourebi*) foraging and landscape use. Oribi are one of the smallest pure grazing ruminants. As a result, they should select high quality vegetation. In line with this, I found that throughout the study oribi fed selectively over multiple spatial scales ranging from plant parts to habitats. By focussing on green grass within these different scales, oribi were able to maintain their crude protein intake needed for maintenance.

Throughout South Africa, oribi frequently interact with cattle. Due to their differences in body size and nutritional requirements, there should be sufficient resource partitioning to avoid competition. However, I found that the nature of the interspecific interactions (i.e. competition or facilitation) between these species depended on season and cattle stocking rates. During the wet season, cattle facilitated oribi by providing high quality regrowth. However, at high stocking rates, cattle indirectly competed with oribi during the dry season via the impacts of their wet season grazing. Specifically, intense wet season grazing by cattle reduced the availability of high quality grass for oribi in the dry season. This was not the case at low and intermediate stocking rates.

Differences in food availability and predation risk across habitats can influence how herbivores utilise landscapes. I found that predation risk greatly affected oribi foraging behaviour, with oribi preferring to feed in safer rather than riskier habitats. However, when food availability increased in these risky habitats, oribi increased their risk-taking behaviour at both small- and large-scales within these risky areas. Ultimately, this suggests that oribi trade-off between predation risk and food availability. Finally, to link my results to the management and conservation of this vulnerable antelope, I applied the knowledge I gained from the above research to a case study.

Male oribi antelope (*Ourebia ourebi*)

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DECLARATION

I, Keenan Stears, declare that

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Keenan Stears

December 2014

PREFACE

The work described in this thesis was carried out at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa, from January 2012 to December 2014, under the supervision of Dr. Adrian Morgan Shrader. This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Pietermaritzburg, represents original work by the authors and has not been submitted in any form to another university. Where use of other work was made, it has been acknowledged in the document

All work was approved by the University of KwaZulu-Natal's Animal Ethics Committee and permits were obtained from Ezemvelo KZN-Wildlife for working in protected areas.

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Throughout the last three years I have interacted with the Oribi Working Group, who are determined to help with conservation of oribi. Many of the ideas that are included in this research started as discussions in this group. My first challenge was to find suitable field sites to conduct my research. Without the Oribi Working Group I would not have known where to start. Thank you to the following members Dr. Athol

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CHAPTER 1

Introduction

The foraging behaviour of herbivores determines where they feed, their diet selection and ultimately their nutritional intake rate. However, the manner in which they feed can be influenced by predation risk (e.g. Ripple and Beschta 2004) and potential competition with coexisting herbivores, (see Arsenault and Owen-Smith 2002). Oribi antelope (*Ourebia ourebi*) are Africa's smallest pure grazer (Brashares and Arcese 2013). They live in grasslands both within and outside of protected areas across their distributional range. In South Africa, they are listed as vulnerable, despite their regional red listing being that of least concern (Shrader et al. In press). Despite a number of studies focusing on the foraging and habitat selection of oribi (Everett et al. 1991; Everett and Perrin 1992; Mduma and Sinclair 1994; Perrin and Everett 1999), none have explored foraging in relation to nutritional requirements, habitat use with regard to predation risk, or how these antelopes cope with living and feeding in areas dominated by cattle (*Bos taurus*). To explore these gaps, I have focused my study so that it addresses the following broad aim and objectives.

Broad aim:

To determine how seasonal changes in grass quality, interactions with domestic livestock (i.e. cattle) and perceived predation risk determine oribi food selection and ultimately their utilisation of the landscape.

Objectives:

1. Determine how Africa's smallest grazing antelope adjusts its foraging such that it can survive the dry season.

2. Determine whether cattle compete with or facilitate oribi foraging and how these interactions change across seasons and cattle stocking rates.
3. Explore how perceived predation risk influences oribi large-scale habitat selection and small-scale foraging behaviour.

Motivation for research

The main research topics for my study were developed from concerns raised by the Oribi Working Group with regard to the population and habitat viability of oribi in southern Africa. In South Africa, oribi are listed as vulnerable (Shrader et al. In press). and some of the major threats to oribi have been identified as inappropriate management, predation risk and interspecific competition (Coverdale et al. 2006). Before any useful management on oribi can be implemented, an understanding of the ecology of the species is needed. Therefore, the goal of this research is two-fold. First, I aim to understand the ecology behind how a small pure grazer survives the dry season, while interacting with cattle and predators. Second, to supplement current management with useable information gained from my research on oribi.

To understand how a herbivore survives, one needs to understand how it forages because foraging behaviour provides a link between species performance and food resources in an environment (Owen-Smith 1994). Moreover, understanding small-scale foraging decisions provides insight into large-scale patterns such as habitat use and dispersal (Shipley 2007). However, information on how a small herbivore should forage is lacking because the majority of studies have focused on medium to large grazers (e.g. Bergman et al. 2001; Fortin et al. 2002; Shrader et al. 2006), most likely due to the difficulties observing small herbivores. Oribi are pure grazers and do not incorporate higher quality browse into their diet, like other small herbivores (e.g. steenbok, *Raphicerus campestris,* and duikers, *Cephalophus* genus) (Gagnon and Chew 2000; Prins et al. 2006). Therefore, for oribi to overcome the nutritional homogeneity of grass they need to select for certain plant species and plant parts (Reilly et al. 1990). However, it is unclear how the constraints of body size and high metabolic requirements allow these small herbivores to meet their energetic requirements.

A possible cause of declining oribi populations has been identified as potential competition between oribi and other herbivores, both wild ungulates and livestock (Coverdale et al. 2006). However, competition is frequently blamed for declining populations without direct evidence to support it (e.g. O'Connor and Krüger 2003). The potential competition between cattle and oribi is especially important in South Africa because the majority of oribi occur outside of protected areas and frequently interact with cattle (Oribi working group unpublished data). However, research on the effects of cattle on oribi is lacking. Because cattle are bulk grazers they can remove large amounts of biomass, which can result in structural changes in the environment (Kutt and Fisher 2011). Consequently, it is important to understand how oribi deal with these changes caused by cattle feeding and how this influences their nutritional intake. Although farms are managed differently, understanding the interspecific interactions between cattle and oribi across different stocking rates may improve the co-existence of oribi and cattle on rangelands.

The main risk of predation to oribi has primarily focused on the direct predation by black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) (Brashares and Arcese 2002). Although direct predation influences fitness, the indirect effect of predation on foraging behaviour and habitat use may also impose fitness costs and can have important consequences for ecosystems and conservation of species (Lima 1998). By understanding how herbivores use their environment in relation to predation risk, one can identify key habitat features that oribi prefer and features they tend to avoid. Thus, providing valuable information to management to ensure the availability of key habitat features. In an attempt to answer the above concerns, this study was initiated.

Literature review

Section I: Foraging

Optimal foraging theory

The distribution of high quality resources varies both spatially and temporally across the landscape. As a result, the choice of where an individual feeds is a major concern for ruminant herbivores, which typically spend 70–96% of their time feeding (Langvatn and Hanley 1993). Optimal foraging theory provides a framework to assess the behavioural choices behind diet and patch selection. Owen-Smith and Novellie (1982) created a foraging model to test how a short-term maximiser for foraging performance selects a diet to maximise intake of a limiting nutrient. This model incorporated different nutrients and feeding styles (i.e. energy-maximiser and time-minimiser). Although the model did not match the foraging behaviour of kudu (*Tragelaphus strepsiceros*), it did provide valuable information on what factors influences diet selection of herbivores. There are two assumptions that need to be met before applying optimal foraging to herbivore foraging behaviour. These are, 1) herbivores must be able to rank food items according to their value (Pyke et al. 1977), and 2) the herbivore must be able to keep track of changing values of food items (Hanley 1982). However, a study on wapiti (*Cervus elaphus*) found that these herbivores spend a lot of time feeding in sub-optimal patches (Wilmshurst et al. 1995). This could be because of 1) differences in the nutritional requirements of animals (Belovsky 1978; Fortin et al. 2002), 2) bite size and cropping rate varies allometrically within grazers (Shipley and Spalinger 1992; Shipley et al. 1994), 3) error in selecting patches (Wilmshurst et al. 1995), and 4) sampling to update information on nutritional changes (Krebs and McCleery 1984). The use of optimal foraging by no means shows that foragers are optimal (Parker and Maynard Smith 1990), but rather provides a way to predict the type of diet an ungulate is likely to select (Hanley 1982).

Body size and digestive physiology

The major constraints of optimal foraging include feeding time, digestive capacity and nutritional requirements (Belovsky 1997). All of which are influenced by body size. Furthermore, the relationship between metabolic requirements and gut capacity to body size is important in explaining diet composition of herbivores (Bell 1971; Jarman 1974). The main reason for this is that metabolic requirements scale with body mass (M) raised to the power of three quarters ($M^{0.75}$). Thus, small herbivores require more protein and energy per day per unit body mass than large herbivores. Therefore, the plant characteristics of species in the diet and the manner in which herbivores forage should be different for large and small herbivores. This is termed the Jarman-Bell principle (Geist 1974).

For small herbivores to meet their high energetic requirements, they need to forage selectively and consume high quality vegetation. During the dry season when resources are limited, the ability of small herbivores to selectively feed on high quality vegetation may be difficult. However, daily foraging times scale almost independently of body size (Belovsky and Slade 1986; Owen-Smith 1988). Therefore, small herbivores likely take advantage of the greater time they have to forage and select high quality vegetation (Illius and Gordon 1999). In contrast, larger herbivores require a greater absolute quantity of nutrients and thus, have less time per nutrient unit to spend searching for high quality food resources than do smaller herbivores, which have lower total relative requirements (Hanley 1982; Demment and Van Soest 1985).

Although large herbivores consume lower quality diets compared to smaller herbivores (Clauss et al. 2013), a suggested advantage of a large body size is an increased digestive efficiency due to longer retention times in the gut, and as a result, a greater ability to digest food than smaller herbivores (Demment and Van Soest 1985). However, the concept of greater digestibility with an increase in body size has been challenged (Müller et al. 2013). A recent study compared the digestive efficiency of a number of species over a body mass gradient and found no effect of body size on digestive abilities (Steuer et al. 2014). Although large herbivores do not have an advantage over smaller species in their ability to digest consumed material, they are still able to consume lower quality vegetation without having to increase their digestive efficiency because their intake has a higher allometric scaling than their basal metabolism (Müller et al. 2013).

Differences in digestive physiology coupled with body size further influence the foraging behaviour of herbivores as well as the characteristics of consumed vegetation (Demment and Van Soest 1985; Belovsky 1997). For ruminant herbivores, an increase in the fibre content of forage decreases daily food intake (Foose 1982). This is due to a reduced rate of passage because fibre needs to be broken down into small particles before it can pass through the rumen and continue through the digestive tract (Mertens

1987). Furthermore, in small ruminants, gut fill is reached in a short period while feeding, which can further reduce daily intake on high fibre diets (Hanley 1982). Ultimately, this can lead to serious nutritional limitations for these small ruminants.

Non-ruminants are not limited by the passage rate of fibre (Janis 1976), but are not as efficient as ruminants in digesting the cell walls of plants (Koller et al. 1978). As a result, they are unlikely to gain as many nutrients per mouthful as ruminants, but they can eat more per day than ruminants. Thus, on low quality, high-fibre diets, non-ruminants are better able to compensate for their lower nutritional gains by increasing their daily intake rate compared to ruminants (Edouard et al. 2008). However, the degree to which non-ruminants can increase their intake rate can be different for herbivores within the same body size range (Clauss et al. 2013). For example, a hippopotamus (*Hippopotamus amphibious*) is more constrained in its ability to increase their food intake compared to an elephant (*Loxodonta africana*) due to differences in the passage rate of ingested food in relation to intake rate (Clauss et al. 2007).

For small herbivores to overcome the constraints imposed by body size and digestive physiology, they need to forage selectively (Jarman 1974; Demment and Van Soest 1985). At the lower end of the body size scale of mammalian herbivores, the majority of small ruminants tend to be mixed-feeders or browsers (e.g. suni, *Neotragus moschatus,* 4–6 kg and red duiker, *Cephalophus natalensis*, 12–14 kg) (Kingdon 1997). This is likely due to the higher digestibility of woody plants allowing these herbivores to have smaller rumens and yet still meet their nutritional requirements (Clauss et al. 2013). In addition, mixed feeders can shift their diet when resources are limited (e.g. dry season) to include higher quality browse (Gagnon and Chew 2000). This, however, is not an option for pure grazers. Fibre content in grass is generally higher than in browse

(Owen-Smith 1982). Therefore, the need to forage selectively is greater for small grazers. As oribi are one of the smallest pure grazing ruminants (~15 kg), they likely represent an extreme case with regard to the constraints that grazers face when trying to maintain nutritional intake during periods of limited food quality. For this reason, they are an ideal species to study.

The degree of selectivity that a herbivore can exhibit is determined by mouth size (Hanley 1982). In addition, the mouth morphology of a herbivore influences the bite size that it can achieve on different vegetation (Shipley 2007). For example, wildebeest (*Connochaetes taurinus*) with their wide muzzles obtained twice the intake rate on short grass swards compared to narrow-muzzled topi (*Damaliscus lunatus*). However, on taller swards the narrow muzzle of topi allowed them to selectively remove green leaves and achieve a higher nutritional intake compared to wildebeest that could not feed as selectively (Murray and Illius 2000).

Hierarchical foraging

The distribution of high quality vegetation varies both spatially and temporally within the landscape. As a result, herbivores interact with resources over multiple scales (Senft et al. 1987). Because high quality vegetation is spatially distributed, the decision of where a herbivores feeds can influence its intake rate (Ungar and Noy-Meir 1988) and its ability to forage selectively (Sinclair and Gwynne 1972). Hence, determining where a herbivore feeds has implications for nutrient gains and time budgets (Langvatn and Hanley 1993). Senft et al. (1987) combined optimal foraging, landscape ecology and hierarchy theory to explain herbivores foraging distributions. The foraging decisions of herbivores are based off hierarchical decisions that span a range of scales, usually from large- to small-scale (Senft et al. 1987; Bailey et al. 1996). At a landscape scale, a herbivore decides in which habitat or area of its home range to feed in. Within this area and at a smaller scale, a herbivores selects a patch to utilise, and finally, within this patch a herbivores selects for a feeding station (the area a herbivores can feed in without moving its feet (Goddard 1968)) and the species it will consume.

What is important to herbivores is deciding what patches to visit and how long to stay in each patch. Patch choice can be predicted by identifying what morphological and physiological characteristics influence the intake of food (Spalinger and Hobbs 1992; Fryxell 2008). For example, a study on Thomson's gazelles (*Gazella thomsoni*) compared the relationship between foraging rates and food availability using the foraging model of Spalinger and Hobbs (1992) (Bradbury et al. 1996). This model predicts that the cropping rate of grazers should shift from being constrained by search time to handling time (i.e. chewing and swallowing) as the density of food in patches increases. In the dry season, Thomson's gazelle bite rates were positively correlated with green biomass and protein densities (Bradbury et al. 1996). In contrast, in the early wet season, there was a negative correlation between bite rates and protein density. The correlation between bite rate and protein density was a result of sward height and increased bite mass (Bradbury et al. 1996). Similarly, sheep (*Ovis aries*) maximised their intake rate on tall swards (Illius et al. 1992). These results suggest that food abundance can influence patch selection and distribution of this species.

A further study on Thomson's gazelle found that their daily energy intake was constrained at grass biomass levels >25 g/m^2, whereas at a lower sward biomass, energy intake was constrained by cropping rates (Wilmshurst et al. 1999a). Consequently, Thomson's gazelles should select from patches of intermediate to low forage biomass, while avoiding high biomass patches (Wilmshurst et al. 1999a). Wilmshurst et al. (2000) modelled the trade-off between food abundance and quality and predicted that optimal sward height should scale allometrically with body size. They found that the sward biomass that resulted in optimal energy gain was a positive, decelerating function of body size. This relationship is a result of relaxed digestive constraints (Meissner and Paulsmeier 1995) as well as increased bite size (Gross et al. 1993) with an increase in body mass. For example, cattle selected for patches of tall grass, which allows them to increase their bites size (Laca et al. 1992) and ultimately their intake rate (Distel et al. 1995). A study in the Serengeti supported the findings that patch selection is influenced by the allometric scaling in gut passage and cropping in ruminants (Wilmshurst et al. 2000).

Once a forager has selected a patch, the amount of time it spends feeding in the patch can be predicted by the marginal value theorem (Charnov 1976). The theory states that a forager should stop feeding in a patch once its harvest rate for that patch drops to the average harvest rate for that habitat and a forager should spend more time in a more profitable patch. However, other factors such as metabolic costs, missed opportunity costs and predation risk can also influence patch selection and the amount of time a forager spends in a patch (Kotler 1984; Brown 1988; Embar et al. 2011).

At the smallest scale of selection (i.e. feeding station) herbivores can either consume or avoid certain plant species as well as plant parts. Different grass species vary in their nutritional concentrations (Owen-Smith 1982). In grasses, the majority of digestible matter is contained in the leaves, whereas the stems are mostly fibre (McDonald et al. 1981). The foraging goals of a herbivore (e.g. maximise intake rate of protein, energy, or minerals) dictates its diet selection. For example, bison (*Bison bison*) selected for meadows as well as feeding sites within meadows to consume plant species that allowed them to maximise their instantaneous energy intake rate (Babin et al. 2011). Furthermore, as plants grow, their nutritional quality decreases due to an increase in fibre (Miller et al. 1965). As a result, as biomass increases so does handling and digestion times (Spalinger and Hobbs 1992; Pastor et al. 1999). Thus, herbivores should feed in patches where they can maximise their intake rate and energy digestibility while reducing their intake of fibre (Fryxell 1991). In line with this suggestion, a study on wapiti found that they selected patches of intermediate biomass and fibre when presented a range of different biomasses as these patches allowed the wapiti to maximise their daily rate of energy gain (Wilmshurst et al. 1995).

Oribi foraging

Oribi are Africa's smallest pure grazer (Brashares and Arcese 2013). Thus, due to its body size and digestive physiology (outlined above) they should be selective grazers. A study looking at the diet of oribi in KwaZulu-Natal Province of South Africa found that oribi selected certain plant species and plant parts seasonally (Everett and Perrin 1992). Because of their high degree of selectivity, oribi avoided low quality vegetation even when it dominated above ground biomass. Although oribi diet was comprised mainly of grass, oribi did increase their use of forbs and sedges during the wet season (Everett and Perrin 1992).

A study at Golden Gate Highlands National Park in South Africa, agrees with the findings of Everett and Perrin (1992) that oribi show seasonal selection in plant species and plant parts (Reilly et al. 1990). However, in contrast to Everett and Perrin (1992), oribi at Golden Gate consumed grass inflorescences and flowers of forbs (Reilly et al. 1990). Unfortunately, these authors do not provide information as to what season inflorescences and flowers were consumed. Therefore, it is difficult to determine the reason for selecting these plant parts.

The habitat requirement suggested for oribi is the combination of short and tall grass. It is generally agreed that oribi utilise the short grass for feeding and the tall grass for predator avoidance (Oliver et al. 1978; Everett et al. 1991; van Teylingen and Kerley 1995). However, evidence is lacking as to whether oribi utilise taller grass swards for feeding. Due to their small size and selective foraging, oribi should be able to maximise their intake rate of high quality green leaves on taller grass swards (Owen-Smith 1988). It is possible that the oribi’s observed preference to short grass may be a result of visibility bias, due to the difficulty in locating oribi in tall grass because of their small size, rather than a true preference for feeding on short grass (Everett et al. 1991; Mduma and Sinclair 1994).

The concept of landscape complementation can also provide a theoretical framework to help explain oribi patch selection. A landscape consists of a number of different resources and a single species requires a certain number of critical resources to survive. However, these resources may not occur within the same patch. As a result, a herbivore must travel between patches to obtain these resources. Landscape complementation occurs when patches in close proximity to each other contain the critical resources needed for survival of a species, and thus, supports a greater number of species than a landscape where these resources are spatially far apart (Dunning et al. 1992). For oribi, these critical resources are high quality food and nearby tall grass to avoid predators. Therefore, oribi should select for patches of high quality vegetation in close proximity to tall grass.

Although studies show oribi to be selective and forage on certain species and plant parts, (e.g. van Teylingen and Kerley 1995), there are marked differences in which species are actually consumed in different areas. This, however, is not surprising because of different grass species compositions across the different sites. However, because of the way data were collected in these studies no information is provided as to the reasons (i.e. grass greenness, changes in nutritional quality) for oribi making these seasonal adjustments in their diet. Therefore, it is difficult to expand these findings to different sites. However, by identifying what factors drive oribi diet selection, foraging predictions and management recommendations can be applied across sites.

Rainfall is another important factor that can influence oribi foraging behaviour because of its influence on the availability of green grass during the dry season. Because of their small size, oribi need to focus on selecting high quality green grass in order to meet their high energetic requirements. Therefore, during high rainfall periods, oribi likely easily meet their nutritional requirements. However, during periods of low rainfall when the availability of green grass is low, oribi may need to make a number of behavioural changes to their foraging behaviour to try and meet their energetic requirements.

Section II: Competition

Interspecific interactions

Competitive interactions occur when one species incurs a cost on another species (du Toit 2011). This can occur through competition for limited resources (Wiens 1989), structural changes in habitats (Kutt and Gordon 2012), or when one species prevents another from occupying a habitat that it would have exploited (Rosenzweig 1981).

Furthermore, for competition to occur there must be a high degree of overlap in the use of spatial and temporal resources (Prins and Olff 1998).

The diversity of herbivores in African savannas can largely be explained through resource partitioning, high productivity and a long evolutionary history (Murray and Illius 1996; Prins and Olff 1998). Resource partitioning can be defined as the differential use of resources such as food and space by two individuals (Schoener 1974), so that these individuals can coexist despite overlap in ecological requirements. Competition is the driving factor behind resource partitioning because of its negative effects on fitness (Schoener 1986; Gordon and Illius 1989). In relation to the long evolutionary history of wild ungulates, the introduction of cattle into these systems is relatively recent (Voeten and Prins 1999). As a result, in many cases there has been insufficient time for resource partitioning to occur between cattle and wildlife. Furthermore, in most cases the grazing style of cattle is different from native herbivores (Searle and Shipley 2008), which can enhance the potential for competition.

The competitive interactions between cattle and wildlife through direct competition for shared resources and changes in habitat use have been well documented (Loft et al. 1991; Fritz et al. 1996; Voeten and Prins 1999). For example, in Laikipia, Kenya, the presence of cattle influenced the use of plots by zebra (*Equus quagga* and *E. grevyi*) (Young et al. 2005). Zebra utilised plots that had high grass cover, suggesting they tracked food abundance. However, grazing by cattle reduced the dominant grass species as well as total cover (Young et al. 2005). Thus, zebra were forced to use plots not being used by cattle. Furthermore, the high dietary overlap between cattle and zebra (Voeten and Prins 1999) suggest they compete for food.

If competition is important in structuring communities, then body size provides a means by which these herbivores can differentially use the same resource (Demment and Van Soest 1985). Body size ratio predicts that small herbivores will not compete with larger herbivores because of niche differentiation (Illius and Gordon 1992; Belovsky 1997). This lack of competition for different sized herbivores is related to metabolic costs and different requirements for food quality and quantity (Demment and Van Soest 1985). Interestingly, smaller herbivores may out-compete larger herbivores by being able to survive on a grass that is too short to support large herbivores (Clutton-Brock and Harvey 1983). Moreover, they may even exclude large-bodied herbivores, by reducing the availability of high quality green grass within areas during the dry season (Illius and Gordon 1987). Smaller herbivores tend to be selective foragers and select for high quality isolated vegetation, whereas larger herbivores can utilise more abundant lower quality vegetation (Bell 1971; Jarman 1974). However, grazing pressure by cattle can remove large amounts of biomass and reduce the availability of dry season green leaves. For example, heavy grazing by cattle reduced the dry season green grass availability for tsessebe (*Damaliscus lunatus lunatus*) (Dunham et al. 2003). Furthermore, the heavy grazing of cattle in addition to drought conditions further reduced dry season grass greenness by causing a shift in species composition from leafy grasses to species with short, wiry leaves. The shortage of dry season forage caused a decline in the tsessebe population (Dunham et al. 2003).

The muzzle size of herbivores can also influence the resource use patterns of herbivores and consequently the nature of interspecific interactions between species (Murray and Brown 1993). Herbivores with narrow muzzles can selectively remove green leaves from taller grass swards, effectively competing with larger species by reducing the nutritional quality of the vegetation through removal of green leaves (Murray and Illius 2000). In contrast, species with wide muzzles that are adapted for grazing on short swards can reduce the availability of taller swards to the detriment of other species. For example, the removal of hippopotamus in Queen Elizabeth Park in Uganda resulted in an increase of elephant, buffalo (*Syncerus caffer*) and waterbuck (*Kobus ellipsiprymnus*) due to an increase in the availability of tall grass (Eltringham 1974). Hippopotamus can transform tall grasslands into grazing lawns and maintain these areas in this short state through continued use (Verweij et al. 2006).

In contrast to competition, there may be facilitation between co-existing species. A number of studies have found that cattle facilitate the foraging behaviour of smaller wild herbivores (Gordon 1988; Bakker et al. 2009). Feeding facilitation can occur when one species makes grass more accessible to other species by removing taller vegetation (Vasey-Fitzgerald 1960; Bell 1970, 1971). Facilitation can be further enhanced if this removal of tall grass results in grass regrowth, which enhances the nutritional quality of another species (Gordon 1988).

When assessing the interspecific relationships between herbivores the seasonal variation in resource use needs to be taken into account (Arsenault and Owen-Smith 2011), because the foraging decisions such as diet selection change with food availability. For example, in Lake Nakuru National Park, dietary overlap between buffalo and impala (*Aepyceros melampus*) was 58% in the late wet season and 81% in the dry season (Mwasi 2002). This change in dietary overlap relates to differences in resource utilisation as a function of decreasing nutritional quality of vegetation in the dry season. Despite the overlap in both seasons, competition may only be occurring in the dry season when resources are limited (e.g. Odadi et al. 2011). In addition, the intensity of grazing should also be considered when assessing interspecific interactions. For example, there may be an interaction between food availability and the importance of cover from predators (Bakker et al. 2009). At low intensity grazing, cattle may facilitate smaller herbivores, but as the intensity of grazing increases the reduction of tall grass may reduce food availability and increase potential predation risk.

Section III: Predation risk

The non-lethal effects of predation

The majority of foraging models predict that foragers should select patches that maximise their nutritional intake rate per unit time (Owen-Smith and Novellie 1982; Belovsky and Slade 1986). However, one of the major constraints of patch selection predicted by optimal foraging models is the risk of predation (Lima and Dill 1990). It is unlikely that a herbivore has perfect knowledge of the whereabouts of predators or when a predator is near. As a result, an evolutionary stable strategy is to maintain underlying fear of predation (Brown et al. 1999). It is this fear that drives the actions of herbivores in response to predation risk at both small and large spatial scales. For example, a number of studies have shown how foraging behaviour changes when predation risk is altered (Sih 1980; Lima et al. 1985; Zimmer et al. 2011). An experiment on gerbils (*Gerbillus andersoni allenbyi*) showed that sightlines were important in reducing predation risk (Embar et al. 2011). In patches where sightlines were reduced, gerbils spent less time feeding and harvested fewer seeds in these riskier patches because vigilance was less effective at detecting predators (Embar et al. 2011). Therefore, maximising energy intake may not account for all foraging decisions. Predation risk can influence foraging behaviour in a number of ways, such as when to feed, where to feed, foraging selectivity, how to handle food, and the distance a forager is willing to travel to a feeding site, reviewed by (Lima and Dill 1990). By altering patch conditions and measuring patch use, this gives an indication of the foraging costs associated with that patch.

At a large scale, different habitats can influence predation risk. This could be a result of the hunting style of the predator. For example, puma (*Puma concolor*) killed more mule deer (*Odocoileus hemionus*) at forest edges compared to open areas (Laundré and Hernández 2003) because the edges provided cover for pumas to stalk their prey (Hornocker 1970). Furthermore, habitat shifts to safer areas can result in reduced feeding efficiency (Barnier et al. 2014). When wolves (*Canis lupus*) were reintroduced into Yellowstone National Park, elk shifted from using their preferred open habitats to less preferred wooded habitats, which resulted in a lower quality diet (Hernández and Laundré 2005). This highlights that predation risk can have a cascading effect on the nutritional status of herbivores and restricts use of lower quality areas (Hernández and Laundré 2005). The reduced browsing pressure by elk in avoided high risk areas resulted in an increase growth of young cottonwood trees (*Populus* spp.) (Ripple and Beschta 2003).

At a smaller scale, landscape variables within habitats can alter predation risk. Free ranging goats (*Capra hircus*) preferred to feed from patches that were far from potential ambush sites, had favourable escape substrate and where other herd members were visible (Shrader et al. 2008). Patch use by a central place forager—the European rabbit (*Oryctolagus cuniculus*) decreased as the distance from its burrow increased (Bakker et al. 2005). When the quality of the patches increased, rabbits increased their use of patches irrespective of their distance from the burrow. Furthermore, when the predation risk of each patch was altered by adding mink (*Mustela vison*) dung pellets, rabbits did not alter their spatial use of patches, but they altered their temporal use of patches (Bakker et al. 2005). Rabbits were generally nocturnal but the addition of mink pellets, (nocturnal predator) caused rabbits to shift and use patches equally during the day and night.

The availability and the quality of food, coupled with differences in perceived predation risk results in a non-uniform use of the landscape with animals preferring certain areas more than others (Butler et al. 2005; Hannon et al. 2006). This spatial use of a landscape in relation to predation is termed the landscape of fear (Laundré et al. 2001). Whether a forager feeds in a certain patch is determined by its potential foraging efficiency in that patch (Langvatn and Hanley 1993) and its perceived predation risk (Creel et al. 2005). As a result, there may be a trade-off between food quality and predation risk so that foragers may feed in low quality patches if the risk of predation is low (e.g. Cowlishaw 1997). Alternatively, foragers may risk feeding in areas with high predation cost if there is abundant high quality food. For example, a study using two gerbiline rodents (*G. allenbyi* and *G. pyramidum*) showed that they preferred to utilise safer bush habitats compare to higher risk open areas (Kotler and Blaustein 1995). Interestingly, when food availability in the risky patches increased, so did the utilisation of these patches by gerbils. Using behavioural titrations, they determine that the riskier patches needed to be 4 to 8 times richer than the safer habitats for these two habitats to be of equal value and for gerbils to display risk taking behaviour (Kotler and Blaustein 1995). If risky habitats benefit predators, changing the landscape of fear by reducing risky areas could improve habitats before the reintroduction of species (Laundré et al. 2010).

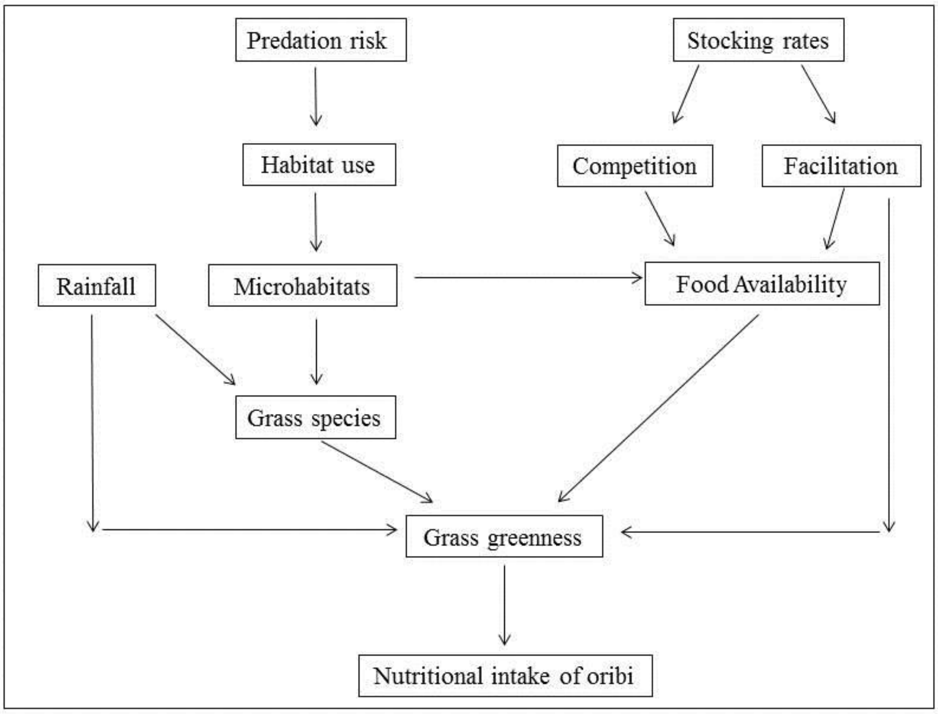

Figure 1: Conceptual model of the factors that influence the nutritional intake rate of oribi

Thesis structure

The research chapters in this thesis have been written up as stand-alone scientific papers with each chapter containing an Abstract, Introduction, Methods, Results, and Discussion. The rationale behind this approach is that I intend to submit each chapter to an international peer-reviewed journal, and by using this approach I can speed up the process. I have included a single reference list at the end of the thesis to reduce potential repetition and help with the ease of examination. However, before submission to journals, the amount of information in certain sections may need to be reduced to meet journal specifications.

Chapter one forms the introduction and outlines the aims and objectives for my research chapters. It also provides a review of the key literature relating to each question. Chapter two and three are closely related and follow on from each other. Chapter two provides an in depth foraging study of oribi antelope with the focus on determining how oribi survive through the dry season. This research highlights how changes in the quality and abundance of food influences the behavioural decisions behind patch and diet selection. By setting up how oribi forage, chapter three investigates the nature of interspecific interactions between cattle and oribi and how these interactions influence the foraging behaviour and performance of oribi. The effects of cattle are investigated in both the wet and dry seasons across a range of cattle stocking intensities.

Chapter four determines how food availability and predation risk influences habitat use of oribi. Furthermore, it explores whether large- or small-scale variables influence predation risk and how increases in food availability can cause oribi to take greater risks over multiple scales when foraging. This chapter has been submitted for publication to the journal Oikos.

Finally, chapter five is split into three sections. The first section provides a summary of the conclusions from this work and highlights important ecological outcomes. The second section is a case study applying the findings from the previous three chapters using the Fort Nottingham Commonage. At this site, the oribi population has decrease from ~35 to less than 10 over the last 8 years. Due to it locality, poaching is very low and is most likely not the cause of the decline. However, the area is grazed by cattle. As a result, I use the information gained from the previous chapters about habitat use and the impact of cattle on oribi forage and heterogeneity to provide a possible explanation for the decrease in oribi numbers, and how the area could be improved so that it would be more suitable for oribi. Lastly, these findings are used to develop key management criteria and how these can be implemented across a range of sites to ensure the conservation of viable oribi populations.

CHAPTER 2

How does a small, selective grazer survive the dry season? Multi-scalar selective foraging and the nutritional intake of oribi antelope

Small ruminant herbivores require high quality vegetation in order to survive. However, as the seasons progress the availability and quality of vegetation declines. The manner in which a small selective grazer forages to meet its energetic requirements when resources are limited has scarcely been explored. To address this, I focused on the foraging behaviour of oribi antelope (*Ourebia ourebi*), the smallest (<15 kg) African grazing antelope. I used field observations to determine how oribi foraged selectively and how this influenced bite mass, bite rate, intake and nutritional intake rates in the dry season and how these measures changed in the transitional and wet seasons. I found that oribi were selective over multiple spatial scales. Firstly, oribi selected for specific microhabitats, such as vlei areas and firebreaks, within grasslands. The proportional availability of firebreaks was relatively low and only slightly increased the availability of crude protein and crude protein: organic matter digestibility. However, heavy utilisation of firebreaks increased the protein concentration in consumed forage by ~4.5 times and ~1.5 times for crude protein: organic matter digestibility. As a result, foraging on firebreaks allowed oribi to more than double their crude protein intake rate compared to their protein intake on unburnt grasslands during the same period. Secondly, at the patch scale (i.e. feeding station), oribi selected for green grass and focused on patches with high availability of green grass. Thirdly, within patches, oribi selected for specific grass species as well as plant parts (i.e. grass leaves). In addition to foraging selectively, oribi also increased their diet breadth and altered their use of species across the different

season. To further compensate for nutritional declines, oribi increased their dry matter intake rate as the dry season progressed. Although oribi utilised a number of behavioural mechanisms to forage selectively, they barely maintained their metabolic requirements during the dry season when they were not feeding on firebreaks. Ultimately, these results highlight the energetic costs of being small, and how these herbivores adjust their foraging across multiple scales to overcome these costs during the dry season.

Introduction

The spatial and temporal distribution of high quality vegetation in grasslands can influence food intake, dietary selection and movements of herbivores (Demment and Van Soest 1985). As the dry season progresses, grass species senesce and thus, the availability of high quality green grass declines (Owen-Smith and Novellie 1982). As a result, protein content, which is a limiting nutrient for grazers, decreases (Sinclair 1975). Therefore, for grazers to survive, they need to select vegetation that yields an adequate rate of intake of energy, protein and other essential nutrients (Owen-Smith and Novellie 1982; Robbins 1993; Belovsky 1997).

Foraging behaviour and diet selection are of major importance within grazing systems because they determine the nutrient intake of herbivores (Prache et al. 1998). The ability of a forager to determine what food it selects, and its ability to digest this food is influenced by body size, digestive physiology, plant characteristics, and mouth size (Hanley 1982; Belovsky 1997). It is the interaction of these factors that makes the process of understanding diet selection at the plant species level so complex (Hanley 1997). For example, bite size influences dry matter intake rate as well as the nutritional quality of the bite. The combination of bite size and plant species influences rumination time, passage rate, and digestion. The nutritional quality of vegetation varies and as a result, the behavioural decisions behind diet selection ultimately affect quantity and quality of food intake. This then influences the time required for feeding as well as the nutritional status of herbivores (Langvatn and Hanley 1993; Hanley 1997). Therefore, it is important to understand how the foraging behaviour of a herbivore allows it to meet its nutritional requirements throughout the seasonal cycle.

The diet selection and foraging behaviour of medium and large bodied grazers has been well documented (e.g. Thomson's gazelles, *Gazella thomsoni* (Bradbury et al. 1996), wildebeest, *Connochaetes taurinus* (Wilmshurst et al. 1999b), Bison, *Bison bison* (Fortin et al. 2002), and white rhinoceros, *Ceratotherium simum* (Shrader et al. 2006)). However, the manner in which small ruminant grazers forage has scarcely been explored. One of the major constraints of a small herbivore is its high mass-specific metabolic requirements (Jarman 1974). These requirements influence the way in which small herbivores feed, because of their need to consume high quality vegetation (Hanley 1982; Illius and Gordon 1992). In addition, there are conflicting theories as to how small herbivores should forage (Kerley et al. 2010). These two conflicting theories are the body constraint hypothesis and the optimal foraging theory. The constraints associated with body size suggest that small ruminants should forage selectively and maintain a narrow diet by only selecting for high quality vegetation (Jarman 1974). However, optimal foraging suggests that as the availability of high quality resources decrease, foragers should increase their diet breadth (Stephens and Krebs 1986; Owen-Smith 1994). Therefore, I ask, how do small ruminant grazers feed and how does this relate to their energetic requirements?

The limitations of small body size of ruminant herbivores can be further constrained by the passage rate of high fibre diets (Demment and Van Soest 1985). As the fibre content of the diet increases, the daily intake rate of forage declines (Bell 1971; Hanley 1982). This decline is related to the slow passage rate of fibre through the rumen because fibrous food takes longer to break down to the small particle size that is needed for matter to pass from the rumen to the rest of the digestive tract (Foose 1982; Demment and Van Soest 1985). Therefore, the combination of these factors forces small ruminants to 1) select a diet that is high in rapidly digestible cell contents (Demment and Van Soest 1985), and/or 2) feed selectivity when faced with mature, fibrous plant material (Jarman 1974).

Optimal foraging provides a theoretical framework to assess the behavioural choices behind diet selection, patch selection and movements (Bailey et al. 1996). According to optimal foraging theory, herbivores should forage in patches that maximise their energy return per unit time (Charnov 1976; Stephens and Krebs 1986). Different grass species and parts of grasses differ in their nutrient contents (Owen-Smith and Novellie 1982). Therefore, small ruminants can maximise their nutritional intake at a patch scale (i.e. feeding station) by selecting for patches that have a large availability of high quality grass species (Senft et al. 1987; Bailey et al. 1996). At a smaller scale, foragers may select for the most nutritious plant parts (e.g. green leaves) of a number of different grass species (Senft et al. 1987; Bailey et al. 1996). For example, the narrow muzzle of topi (*Damaliscus lunatus*) allows them to selectively remove the green leaves of medium-height grass swards (Murray and Illius 2000) and avoid old mature leaves that are higher in fibre. By selecting at both of these scales, foragers can obtain higher quality intake compared to the general vegetation than what is available (Owen-Smith and Novellie 1982).

However, during the dry season the availability of high quality vegetation decreases. Therefore, the ability of small ruminant herbivores to maintain a high quality diet is limited by the time required to find high quality food and the energy requirements of walking between dispersed patches of high quality food (Demment and Van Soest 1985). To compensate for the time and energy constraints of finding high quality vegetation, foragers can expand their diet breadth during the dry season. For example, sable antelope (*Hippotragus niger*), which are primarily grazers, increased their diet breadth during the dry season by increasing the proportion of browse in their diet (Hensman et al. 2012). This was a result of declining food availability. Although small ruminants have a high turnover rate of food, the inclusion of less palatable species into the diet (i.e. high fibre) may limit the rate of food passage through their gastrointestinal tract and thus restrict their daily consumption of additional forage. In addition, in small ruminants, rumen fill is reached rapidly which also limits the intake of forage. As a result, the addition of lower quality forages into the diet may limit the ability of small ruminants to meet their daily energetic requirements by reducing the rate of passage of food through the gut (Luna et al. 2013).

To compensate for the inclusion of lower quality vegetation, herbivores can increase their intake rate (Laca et al. 1994). An increased intake rate can be associated with an increase in bite size (or bite mass) or an increased bite rate (Shipley 2007). To increase bite mass, herbivores would have to forage on patches with taller grass swards or higher bulk density (Wilmshurst et al. 1995; Shrader et al. 2006). By foraging on taller grass, foragers would increase their intake of low quality food (i.e. increase fibre) (Van Soest 1994; Wilmshurst et al. 1999a), which would ultimately limit their daily food intake (Mertens 1987; Bergman et al. 2001). In addition, mouth dimensions limit the amount of food that can be cropped in a single bite and thus, limits the rate at which grass can be consumed (Illius and Gordon 1987; Spalinger and Hobbs 1992; Shipley et al. 1994). Moreover, dry matter fill has been found to correlate with body size (Luna et al. 2013). As a result, the ability of small ruminants to increase their instantaneous intake rate may be limited by the time taken to process the increase in fibre in the diet. Therefore, forage selection is a trade-off between intake rate and diet quality (Hanley

1997). During the dry season, larger intake rates likely result in greater intake of poor quality vegetation (e.g. brown leaves and high fibre stems). In contrast, increasing selectivity reduces bite mass, but may maintain both instantaneous and daily nutritional intake via the selective intake of limited high quality plant parts (e.g. green leaves).

At a broader scale (i.e. landscape), herbivores can alter their seasonal movements and habitat choice by increasing their home range during the dry season in an attempt to find suitable foraging areas (McNaughton 1978; Mysterud et al. 2001; Hebbelmann 2013). In doing so, they can take advantage of green flushes on recently burnt areas, or vegetation flushes in areas that have received sporadic winter rainfall. The use of fire is an important management tool that can reduce the nutritional stress of grazers during the dry season (Vemeire et al. 2004). A study on sable antelope showed that dry season burns helped sable overcome the nutritional limitations experienced during the dry season (Parrini and Owen-Smith 2010). In the dry season, these green flushes caused by patch mosaic burning can limit the distance that herbivores need to travel to obtain high quality vegetation and therefore, reduce the energetic costs of travel because these burnt areas offer more green grass than the surrounding unburnt grasslands.

To determine how small ruminants obtain high quality forage, I focused on the foraging behaviour of Africa’s smallest (~15 kg) pure grazing antelope, the oribi (*Ourebia ourebi*, Zimmerman 1783). Oribi are an interesting species because they seem to be on the limit of how small a pure grazer may be. For example, other herbivores of similar or smaller body weight that also belong to the Neotragini, such as the dik-diks (*Madoqua* genus) and steenbok (*Raphicerus campestris*), tend to be browsers or mixed feeders that utilise higher quality browse during the dry season (Gagnon and Chew

2000). In the KwaZulu-Natal province of South Africa, oribi occur within the mistbelt and highlands sourveld areas, where winters are severe and food quality and food availability is at its lowest (Rowe-Rowe and Scotcher 1986). As a result, the low quality food during winter was identified as a major limiting factor for oribi (Oliver et al. 1978; Rowe-Rowe 1983). Therefore, the behavioural decisions behind diet selection of oribi are key to their survival.

In my study, I aimed to determine how oribi forage through the seasonal cycle. From this I estimated seasonal changes in nutritional intake of oribi in relation to the nutrients required for maintenance. Based on body size (high mass-specific requirements) and digestive physiology (slow passage rate of high fibre diets), I predicted that oribi would forage selectively (i.e. high protein, low fibre diet) throughout the seasonal cycle, which would result in seasonal changes in dietary preference. On a large scale (i.e. landscape level), oribi should select for microhabitats (i.e. firebreaks) that provide green grass of high nutritional quality. On a small scale (i.e. a patch), oribi should select for grass greenness categories of certain species to maximise their nutritional intake. Furthermore, oribi will only select for grass leaves and avoid other plant structures (i.e. culms) that are higher in fibre. Alternatively, oribi could shift and utilise energy-rich grass inflorescences. During the dry season, oribi should likely broaden their diet breadth to include additional species because of the decreasing availability of high quality vegetation. These species would likely include forbs and sedges because of the higher nutritional quality of these plants compared to grasses (Codron et al. 2007). In contrast, oribi could maintain the same diet and still meet their nutritional requirements by feeding only on green leaves. In addition to selective foraging, oribi may increase their intake rate by either increasing their bite size (bite mass) or increasing their bite rate. However, this would likely increase their intake of non-digestible or low quality plant parts (e.g. brown leaves and high fibre stems). As a result, I predicted that oribi would most likely not increase their instantaneous intake rate to compensate for lower quality vegetation, because of their need to ingest high quality forage. Alternatively, the abundance of green leaves may decrease to a point where oribi may have to shift and forage on lower quality vegetation and by increasing their intake rate may allow them to maintain some level of nutritional intake. Finally, during the wet season when green grass is abundant, I predicted that oribi would increase their instantaneous intake rate as a means of compensating for decreased daily nutritional intake obtained during the dry season.

Methods

Study site

The study was conducted at Chelmsford (Ntshingwayo) Dam Nature Reserve (2852 ha), KwaZulu-Natal, South Africa (S 27.9540° E 29.9470°) from the beginning of June 2012 to the end of February 2013. The geology of Chelmsford Dam is dominated by mudstone, sandstone and shales of the Beaufort and Ecca groups of the Karoo Supergroup (Mucina and Rutherford 2006). Vegetation in this area has been classified as Northern KwaZulu-Natal Moist Grassland (Mucina and Rutherford 2006). Dominant grass species include *Hyparrhenia hirta* and *Themeda triandra*. Although the study site is grassland, there are microhabitats within the grassland such as vlei (i.e. marsh) areas. These areas maintain soil moisture and therefore grass greenness late into the dry season. These areas are also dominated by different grass species such as *Paspalum* *urvillei*, *Arundinella nepalensis*, *Hemarthria altissima*, and *Leersia hexandra*. These vlei areas represent about 30 ha (~1 %) of the study site.

The rainy season at Chelmsford Dam extends from September or October to March, which is then followed by a cold dry period when frost is common from April or May to August. Long-term mean (mean ± SD) annual wet season rainfall (1995–2014) for the Chelmsford Dam area is 513 ± 187 mm (South African Weather Services). The wet season rainfall (September 2011 to March 2012) prior to the start of the dry season during the study was below the long-term mean (434 mm) and only slightly above (534 mm) during the wet season of October 2012 to March 2013. For this study, I categorised the months into dry (June–August), transitional (October) and wet (November–February) seasons (Figure 4). I based these subdivisions on natural breaks in the data for mean rainfall and mean grass height (dry: 6 ± 7 mm; 46 ± 3 cm, transitional: 95 mm; 20 ± 12 cm, and wet: 71 ± 24 mm; 46 ± 9 cm). Dry season data is split into foraging on unburnt grassland and on burnt firebreaks within the reserve. These firebreaks are strips of land that are burnt in the dry season to control and prevent run away fires. In July 2012, firebreaks (~300 ha) were burnt, providing a green flush, which lasted until the start of the rainy season in September. However, the severe frosts during the dry season caused a number of species to senesce shortly after flushing. In September 2012 ~1000 ha was block burnt, which provided a second green flush after the start of the rains.

During the study, there were roughly 220 oribi on the reserve (Ezemvelo KZN Wildlife 2012 oribi count). Estimates of other species included 240 plains zebra (*Equus quagga*), 65 black wildebeest (*Connochaetes gnou*), 357 springbok (*Antidorcas marsupialis*), 132 blesbok (*Damaliscus pygargus phillipsi*), 86 red hartebeest

(*Alcelaphus buselaphus caama*), 17 common reedbuck (*Redunca arundinum*), 9 common/grey duiker (*Sylvicapra grimmia),* and 4 steenbok (*Raphicerus campestris*).

Figure 1: Map of Chelmsford Dam. The red line denotes the boundary of the study site.

Figure 2: An oribi feeding in unburnt grassland in the dry season.

Figure 3**:** Green flush on a firebreak during the dry season.

Data collection

The vlei areas and firebreaks represented microhabitats within the grassland system. As a result, I noted the number of times oribi fed within these microhabitats as well as the number of times they fed in the grassland.

Oribi foraging data

To collect foraging data, I located oribi in the early mornings and afternoons when they were most active (Coverdale et al. 2006). I found oribi by driving along the reserve's roads (~20 km). Each day a different route was chosen. To prevent bias towards observing oribi in areas where they could be more easily seen, I spent equal amounts of time in different parts of the reserve. Furthermore, I did not drive the same roads in the morning and afternoon. This ensured that similar numbers of samples were obtained from the different areas in the reserve. When an oribi was spotted, I observed it from a stationary vehicle using binoculars (Pentax 8x42 DCF) and/or a spotting scope

(Bushnell XLT 20-60x 65mm). Data were collected from all adults of both sexes that were encountered.

Upon locating an oribi, data collection began at the first sign of feeding. If oribi showed vigilance towards the vehicle, I terminated the observation. The position of each oribi was determined using nearby landmarks (e.g. (Arsenault and Owen-Smith 2011). Each foraging observation spanned five feeding steps and started with the movement of one of the front feet. Each foraging observation resulted in five separate feeding stations (i.e. one per step). A feeding station is an area in which an animal can forage without taking a step (Ruyle and Dwyer 1985). Although each observation could include non-feeding steps, a minimum of five feeding steps was necessary for each observation. Preliminary observations indicated that the average area in which an oribi fed before taking a step was about 0.16 m^2. Thus, I represented each feeding station using a 0.4 x 0.4 m quadrat.

To reduce the disturbance of oribi, I waited for them to move off ~50 m from the five feeding stations before I approached the foraging area on foot. Once the foraging path was found, I placed the quadrat over the first set of bites. This represented a feeding station. For each of the five quadrats in a foraging observation, I differentiated newly foraged grass species from older use by the white appearance of the damaged cuticle (Arsenault and Owen-Smith 2011). For each bite, I recorded the plant species consumed, sward height and grass greenness using the surrounding ungrazed grass of the same species as an estimate (Shrader et al. 2006; Arsenault and Owen-Smith 2011). I estimated grass height for each bite of the consumed grass species using five measurements from surrounding un-grazed tufts of the same species within the feeding station. I then averaged these measurements for each bite. For each foraging observation, I then averaged the grass height of consumed grass for each bite to determine the mean grass height grazed by oribi. Each bite was allocated a grass greenness category according to Walker's (1976) eight-point scale of grass greenness (0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99%, and 100%). Each bite typically ranged from a single blade up to four blades of grass. In addition to the species eaten, I also recorded the species the oribi avoided in each quadrat as well as their greenness.

In some cases, finding all five feeding stations for each foraging observation was not possible. However, in these cases I included the data from observations where at least three feeding stations could be found. This resulted in a total of 226 foraging observations being recorded from over 100 individual oribi. Due to the difficulty in locating foraging paths, I was only able to obtain one foraging observation from any single oribi per session. As a result, this ensured that there was no serial autocorrelation between observations.

Bite rate, bite mass and intake rate

I calculated the bite rate for each foraging observation by dividing the total number of bites along the five feeding steps by the time required for the oribi to take these bites. In addition, I determined the bite mass for each bite by using hand plucking (see Bonnet et al. 2011). Hand plucking was the best technique to use because oribi are very selective. Moreover, there was a lot of variation between bites because they could comprise between one and four leaves. Thus, using average bite masses would likely provide unreliable estimates. I simulated oribi bites by using the surrounding un-grazed grass of the same species to hand pluck a grass sample that represented a single oribi bite. The simulated bite was plucked to the same level to which the oribi had grazed. Each of these bite mass estimates (N = 2463) were then dried at 60°C for 48 hrs and weighed to four decimal places, due to the small size of bites. I then calculated the mean bite mass for each foraging observation by averaging the total number of bite masses found in each foraging observation. For every foraging observation, I calculated the dry matter intake rate (g/min) by multiplying the mean bite mass from the five feeding steps with the corresponding bite rate. This resulted in 226 intake rate estimates from over 100 different oribi.

Selection of sward structure

To relate oribi foraging to the grass greenness categories that were available, I walked five 2 km transects every month (N = 8 months). This allowed me to determine the seasonal changes in the availability of grass in the different grass greenness categories across the study site. Every 50 m (N = 3280) along each of these transects, I randomly placed two quadrats. Within each quadrat, I measured the sward height of the tallest grass species and the percentage of green grass using Walker's (1976) eight-point scale.

Data analysis

Habitat use

I determined differences in habitat use across seasons using the proportion of foraging observations that occurred in vlei areas compared to the number that occurred out of vlei areas in the grassland. I compared proportional use of vlei areas (dependent variable) using a General Linear Model with season as the independent variable. Data were Arcsine transformed to meet the assumptions of normality.

Dietary contribution

The dietary contribution of consumed species was determined within each feeding station (i.e. quadrat) for each foraging observation. I determined the dietary contribution for each species in each season (i.e. dry – unburnt and burnt firebreaks, transitional, and wet) by dividing the number of bites of that species in that time period by the total number of bites of all species in that time period.

Acceptability

To establish the seasonal preference oribi have for each consumed species, I determine the acceptability indices of the different species. I limited this analysis to species that occurred in ten or more quadrats per season. Acceptability was calculated by dividing the number of quadrats in which a certain species was eaten by the total number of quadrats in which that species occurred (Owen-Smith and Cooper 1987). In addition, I calculated 95% binomial confidence intervals for the acceptance frequencies of each grass species in each time period. I grouped consumed plant species according to their acceptability indices in each season as favoured (AI > 0.5), eaten (0.3 < AI > 0.5) and avoided (AI < 0.3) (Owen-Smith 2002).

Selection of grass species, greenness, and their combination

I used a χ^2 test and Bonferroni confidence intervals (Byers et al. 1984) to determine whether there was a significant difference between the expected utilisation of grass and forb species compared to the observed frequency of their use (i.e. do oribi select for species in proportion to their availability in each period). The confidence intervals allowed me to determine whether there was a positive or negative selection for certain grass species.

The availability of each grass and forb species was calculated as the number of times a species was present in a feeding station divided by the total occurrence of all species. Within each season, availability was only determined for species that occurred in ten or more feeding station quadrats. In the χ^2 test, the number of times a species was eaten was compared to the expected utilisation for that species. The expected use was determined by multiplying the total number of feeding stations for all grass species by the proportional availability of each species within each seasonal period. This process was repeated for grass greenness and grass greenness categories for each species.

I determined selectivity at the species, grass greenness, and the species-specific grass greenness levels using the S index (McNaughton 1978). Selectivity values range between 0 and 1, with 0 indicating no selection (i.e. eating in relation to availability) and 1 indicating maximum selection.

Bite rate, bite mass and intake rate

I used a Generalised Linear Model (Gamma distribution and log link function) to determine the seasonal changes in bite rate, bite mass and intake rate of oribi. I ran a separate model for each dependent variable (bite rate, bite mass, and intake rate) with season (dry – unburnt grassland and burnt firebreaks, transitional, wet) as the independent variable. Furthermore, to determine if oribi increased their intake rate during the dry season to compensate for the declining nutritional quality of vegetation, I ran another Generalised Linear Model (Gamma distribution and log link function). The dependent variable was intake rate and the independent variable was month (June, July, August) in the dry season. For this model, I excluded all data obtained from observations of oribi foraging on firebreaks. Because intake rate is influenced by bite rate and bite mass, I used two Generalised Linear Models (Gamma distribution and log link function) to determine if changes in bite rate or bite mass (dependent variables) across the dry season months (independent variable) influenced dry season intake rates.

Chemical analysis

Once I determined the seasonal diet of oribi, I collected grass samples (N = 250) of the top five contributing species (>80%) to oribi diet in each of the different seasons. For the dry season, this included the top five contributing species in unburnt grasslands as well as the top five species on burnt firebreaks. This totalled nine grass species and one sedge (see Results; Table 1). Because oribi were very selective and only foraged on leaves, I only collected grass leaves for each species so the samples were a representation of what was consumed by the oribi. Furthermore, I collected these grass samples from areas in which I had observed oribi foraging. All collected grass samples were oven dried at 60°C for 48 hours and then milled through a 1 mm sieve.

I used Near Infrared Reflectance Spectroscopy (NIRS) to assess crude protein (CP), and organic matter digestibility (OMD) of the collected grass samples (see Appendix I for nutritional values). NIRS spectra were calibrated off a database of South African grasses that were analysed using wet chemistry by the Wallon Agricultural Research Centre, Belgium. For the wet chemistry, nitrogen was determined using the macro-Kjeldahl procedure and digestibility was determined using the enzymatic-cellulase method. I was able to estimate measures of CP and OMD for each sample because the averaged standardized H value (distance between a sample and the centroid of the group) was lower than or close to 3.0 for each predicted parameter (Shenk and Westerhaus 1991).

I was unable to use NIRS for one of the main contributing species, a sedge from the Cyperaceae Family, because I did not have a database of wet chemistry for this species. As a result, I used wet chemical analyses using techniques outlined by the AOAC (1990). Nitrogen was extracted using the macro-Kjeldahl procedure by the Analytical Laboratory at Cedara Agricultural College and converted to crude protein by multiplying by 6.25. ADF and NDF were determined using the van Soest method in the laboratory at the University of KwaZulu-Natal. Digestibility was then calculated using the equation: %DDM = 88.9-(0.779 x %ADF) (Saha et al. 2013).

Nutrient content of the diet in relation to nutritional availability

Because oribi forage selectively (see Results), I compared the %CP, digestibility, and the ratio of CP to digestibility consumed by oribi to what was available on the reserve in each season. To calculate available %CP and digestibility, I used the grass greenness estimates from my transect data. I calculated the availability of each grass greenness category and multiplied it by the corresponding nutritional quality. At each quadrat, I did not record species, only grass greenness. As a result, I determined the nutritional quality for each grass greenness category by averaging the nutritional quality of the collected grass samples for the corresponding grass greenness category. When oribi utilised unburnt grassland in the dry season, I used transect data from June, July, and August with all data points with firebreak data omitted. For firebreaks, I only used dry season data from July and August incorporating all data points that fell within the firebreaks. For the transitional and wet seasons I used the respective monthly transect data.

I calculated the %CP and the digestibility of the consumed species in the diet by multiplying the proportion of each species in the diet for each grass greenness category by its respective nutritional quality for crude protein and digestibility. I then summed each of these values to calculate the mean %CP consumed and the digestibility for each season. For this analysis, I only used the nutritional quality of the top ten consumed species because they contributed to over 80% of an oribi's diet. I calculated the ratio of CP to digestibility by dividing CP by its corresponding digestibility value.

I used a Generalised Linear Model with a Gamma distribution and a Log link function to test for seasonal differences in the nutritional quality of the diet in relation to availability. Furthermore, I also tested for differences between the nutritional content and availability within each sampling period. For this analysis, the dependent variables were crude protein, digestibility, and crude protein: digestibility. Independent variables included sampling period (dry season – unburnt grasslands and burnt firebreaks, transitional, and wet season), preference (consumed or available), and their interaction.

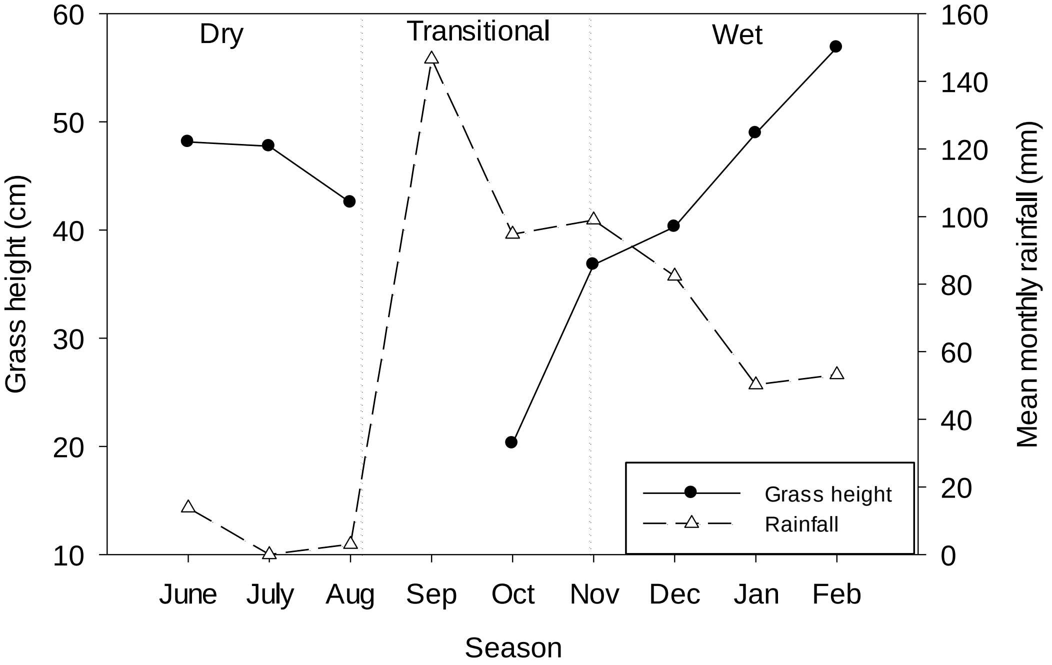

Figure 4: The study period was divided into three seasons based on natural breaks in the data for mean grass height and mean monthly rainfall; dry (June-August), transitional (October), and wet (November-February).

Protein intake relative to minimum and reproductive requirements.

Crude protein is a major limiting resource for grazing ruminants and the minimum concentration of protein in the diet required for maintenance is 5% (Sinclair 1975). To determine if the selective foraging (consuming forage that has higher nutrient levels than what is available) of oribi allows them to meet their minimum requirements, I calculated their nutritional intake rate of protein and compared it to the minimum requirements of 5%.

I determined the nutrient concentration of bites by using the estimates of CP for each grass species in the respective grass greenness category. For bites that did not contain one of the top species that was chemically analysed, the mean nutrient concentration of the analysed grasses for that grass greenness was assigned. The intake rate (g/min) of CP was determined by multiplying the nutrient concentrations of the grass by bite mass. I then established the mean nutrient concentration per foraging observation which was then multiplied by the respective bite rate to give the nutritional intake rate (g CP/min). To determine the percentage of crude protein in the oribi diet for each season, I converted intake rates (g/min) obtained from each foraging observation, for that season, into daily intake rates (g/day). On average, oribi foraged for roughly 36% (518 min) of a 24 hr period (Arcese 1999). Therefore, each intake rate was multiplied by 518 min to convert them into daily intake rates. I applied the same approach to the nutritional intake rates to convert them into daily nutritional intake rates (e.g. g CP/day). To determine seasonal changes in the actual percentage crude protein in the diet (%CP DM), I divided the mean nutritional intake rate by the mean intake rate for each month.

In addition, I compared the daily protein intake rate of oribi to the protein requirements needed for reproduction. Nutritional demands on females peaks during early lactation. During this time, protein requirements may be more than double the protein requirements needed for maintenance (see Clutton-Brock et al. 1989; Chan-McLeod et al. 1994) in (Owen-Smith 2002). Therefore, pregnant females may require more than 10% CP in their diet.

I ran a Generalised Linear Model (Gamma distribution and Log Link function) to determine if there were seasonal differences in the protein content of the diet. The dependent variable was percentage crude protein intake in the diet (% CP DM) and the independent variable was sampling period (dry season – unburnt grasslands and burnt firebreaks, transitional, and wet season). I ran an additional Generalised Linear Model (Gamma distribution and log link function) to compare the difference in percentage crude protein intake when oribi fed on firebreaks compared to when they fed on unburnt grasslands during the same period. The dependent variable was protein intake (%CP DM) and the independent variable was firebreaks versus unburnt grasslands. For this analysis, I only used data from July and August when firebreaks were present. All statistical analyses were performed using SPSS version 22.

Results

Habitat use

In the dry season, 40% of foraging observations occurred within vlei areas (~1 % of the total area). As the dry season progressed into the wet season and the availability of green grass increased, oribi decreased their use of vlei areas with only 12% of foraging observations occurring within these areas (ANOVA: $F_{1;5} = 8.192$, $P = 0.035$).

Diet contribution

Throughout the study period, the majority of oribi diet consisted of grass (>90%) with only a few forbs and sedges being consumed (<10%). The transitional period had the highest use of forbs and sedges (13%), followed by the wet season (11%) and finally in the dry season (~1%). The Cyperaceae sedge was the only non-grass species that was consumed enough to contribute to the top consumed species across the seasons. Interestingly, this is in contrast to my initial predictions that oribi would consume more forbs during the dry season.

Oribi increased their diet breadth as the dry season progressed into the wet season to incorporate previously avoided species (Table 1). By changing their seasonal diets, oribi were able to maintain a narrow selective diet with five species contributing to over 80% of the diet in each season. During the dry season, oribi encountered 55 different species along their foraging paths. Of these species they only consumed 20 species and avoided 35. During the dry season, the five species that contributed to 92% of the diet were *Hyparrhenia hirta* (53%), *Pennisetum clandestinum* (15%), *P. urvillei* (11%), *Themeda triandra* (7%), and *Heteropogon contortus* (6%) (Table 1). When oribi utilised firebreaks in the dry season, they encountered 11 species but only fed on three of them, *Andropogon appendiculatus* (57%), *H. hirta* (34%), and *H. altissima* (9%) that comprised 100% of the diet. Interestingly, oribi did not feed on the flush of all the encountered species on firebreaks.

During the transitional period, oribi encountered 41 different species but only consumed 19 of these species. *H. hirta* (57%), the Cyperaceae sedge (8%), *T. triandra* (7%), *L. hexandra* (5%), and *H. altissima* (4%) comprised 81% of the diet. During the wet season, oribi encountered 59 species but only consumed 20 species. *H. hirta* (59%), *Diheteropogon amplectens* (16%), the Cyperaceae sedge (11%), *L. hexandra* (4%), and *T. triandra* (3%) contributed to 92% of the diet. Of all the grass species, *H. hirta* was the only top contributing species that was consumed year round. In each season, it contributed to over 56% of the diet, except when the oribi fed on the firebreaks where it only contributed to 34% of their diet.

Table 1: Seasonal dietary contribution and availability of the top consumed species to oribi diet.

	Dry - unburnt		**Dry - firebreak**		**Transitional**		**Wet**	
Grass species	Dietary contribution	Availability	Dietary contribution	Availability	Dietary contribution	Availability	Dietary contribution	Availability
Hyparrhenia hirta	0.53	0.56	0.34	0.46	0.57	0.50	0.59	0.45
Pennisetum clandestinum	0.15	0.11	0	0	0	0	0	0
Paspalum urvillei	0.11	0.09	0	0	0	0.04	0	0.02
Themeda triandra	0.07	0.07	0	0	0.07	0.05	0.03	0.04
Heteropogon contortus	0.06	0.06	0	0	0	0	0	0.01
Cyperaceae sedge	0.01	0.02	0	0	0.08	0.13	0.11	0.12
Hemarthria altissima	0.003	0.003	0.09	0.09	0.04	0.04	0.01	0.03
Andropogon appendiculatus	0	0	0.57	0.45	0.01	0.01	0.001	0.02
Leersia hexandra	0	0	0	0	0.05	0.04	0.04	0.04
Diheteropogon amplectens	0	0	0	0	0	0	0.16	0.12

Acceptability of grass species

The acceptance and avoidance of species varied across the seasons, reflecting the selective nature of oribi foraging. The acceptance of consumed species in the oribi diet varied across seasons (Figure 5 a-d). Species such as *P. clandestinum* (acceptability = 0.9) and *P. urvillei* (acceptability = 0.67) that provided green leaves during the dry season were only consumed during this period, despite being encountered in the other seasons. The only grass species that had a favourable acceptance across all seasons was *H. hirta*. The transitional and wet seasons were the only periods where sedges, such as the Cyperaceae sedge, were favoured by the oribi.

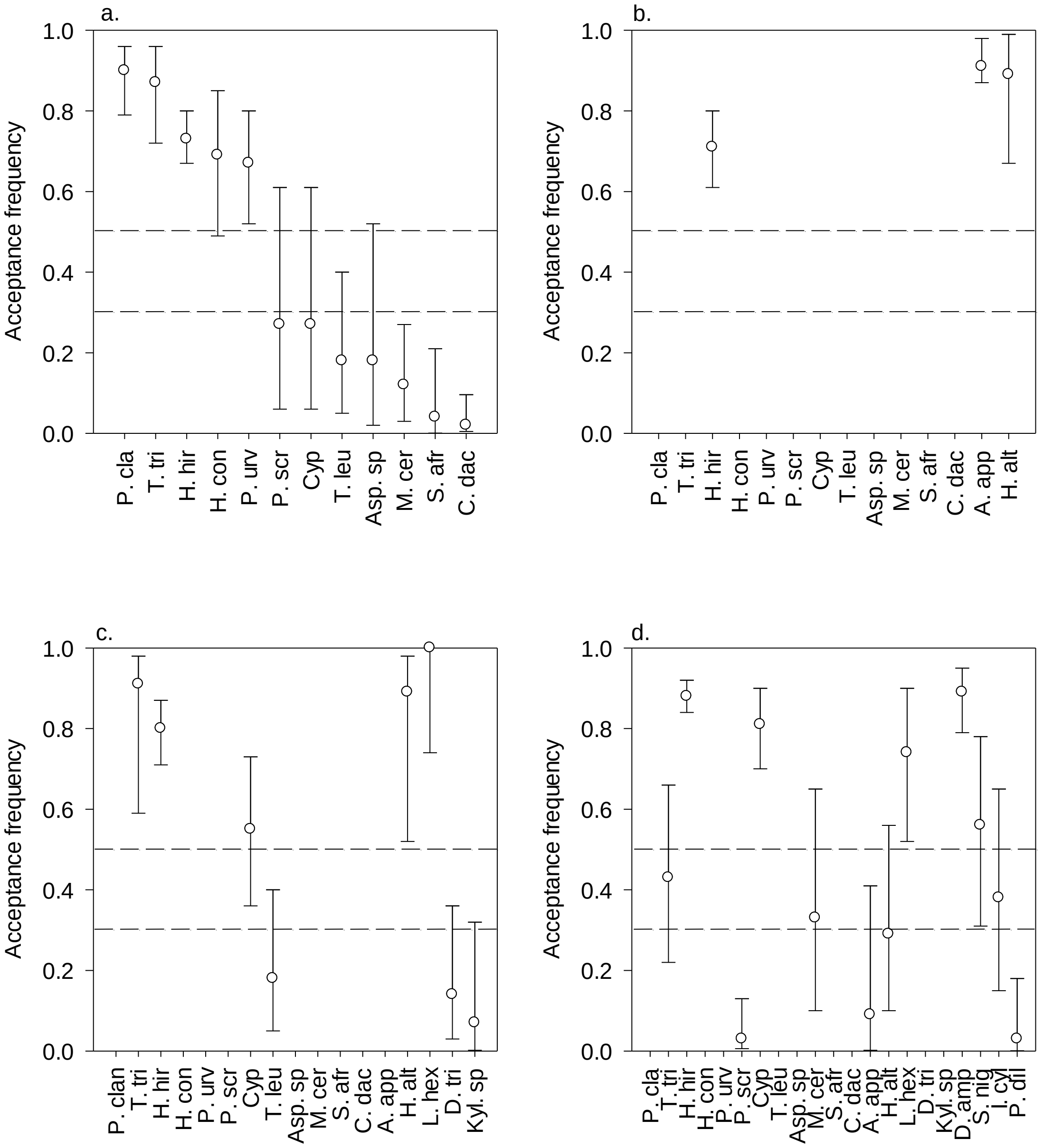

Figure 5 a-d: Acceptance (mean ± 95 CI) of consumed species by oribi during a) the dry season (June to August, b) firebreaks (July and August), c) transitional period (October), and d) the wet season (November to February). Grass species are P. clan (*Pennisetum clandestinum*), T. tri (*Themeda triandra*), H. hir (*Hyparrhenia hirta*), H. con (*Heteropogon contortus*), P. urv (*Paspalum urvillei*), P. scr (*Paspalum scrobiculatum*), Cyp (Cyperaceae sedge), T. leu (*Tristachya leucothrix*), Asp. sp. (*Asparagus* species), M. cer (*Monocymbium ceresiiforme*), S.afr (*Sporobolus africanus*), C. dac (*Cynodon dactylon*), A. app (*Andropogon appendiculatus*), H. alt (*Hemarthria altissima*), L. hex (*Leersia hexandra*), D. tri (*Digitaria tricholaenoides*), Kyl. sp. (*Kyllinga* species), D. amp (*Diheteropogon amplectens*), S. nig (*Setaria nigrirostris*), I. cyl (*Imperata cylindrica*), and P. dil (*Paspalum dilatatum*).

Selection of grass greenness

At the landscape scale (i.e. across habitats), oribi utilised green grass in proportions greater than its availability for each month (Figure 6). During the early dry season (June and July) oribi consumed mainly green and very green grass even though these greenness categories were not available during this period at the quadrat scale. This is because oribi select only for green leaves within a quadrat while foraging, and available greenness was determined at the sward level. When firebreaks were burnt during August, the proportion of mainly green and very green grass increased. By heavily utilising firebreaks, oribi used green grass ~4 times greater and very green grass ~52 times greater than their availabilities. In the transitional and wet season periods, oribi fed exclusively on very green grass although mainly brown, mainly green, and very green grass were available during October and November. However, only mainly green and very green grass was available from December to the end of February (wet season).

Overall selectivity for grass greenness at the patch scale remained relatively low throughout the study period (dry season unburnt grasslands S = 0.11, dry season burnt firebreak S = 0.15, Transitional S = 0.05, and wet season S = 0.03). Despite this, oribi selected for specific grass greenness levels throughout the dry season (Chi square: $\chi^2 = 19.70$, $df = 5$, $P < 0.001$), firebreak (Chi square: $\chi^2 = 30.794$, $df = 3$, $P < 0.001$), and transitional periods (Chi square: $\chi^2 = 5.683$, $df = 1$, $P = 0.02$). During the wet season, oribi did not show a preference for specific grass greenness levels because the majority of the grass was green during this period (Chi square: $\chi^2 = 1.573$, $df = 1$, $P = 0.21$).

During the dry season, oribi only selected for the greenest grass greenness categories that were available 26–35%, 51–65%, and 76–90%, while they avoided grass that was the <25% green (see Appendix II Table 1). Three grass greenness categories

(36–50%, 66–75% and 100%) were not recorded during the dry season. While foraging on firebreaks, oribi only ate grass that was >76% green (see Appendix II Table 1). During the transitional period, oribi only selected for grass that was 91–99% green, while avoiding 100% green grass (see Appendix II Table 1). The other greenness categories were not available during this period. Finally, during the wet season, oribi selected grass that was 91–99% green, but avoided grass that was 100% green (see Appendix II Table 1). At the patch scale, all other greenness categories did not occur even though they were available at the landscape scale (Figure 6a) during this period. This highlights that oribi selected feeding areas in relation to grass greenness

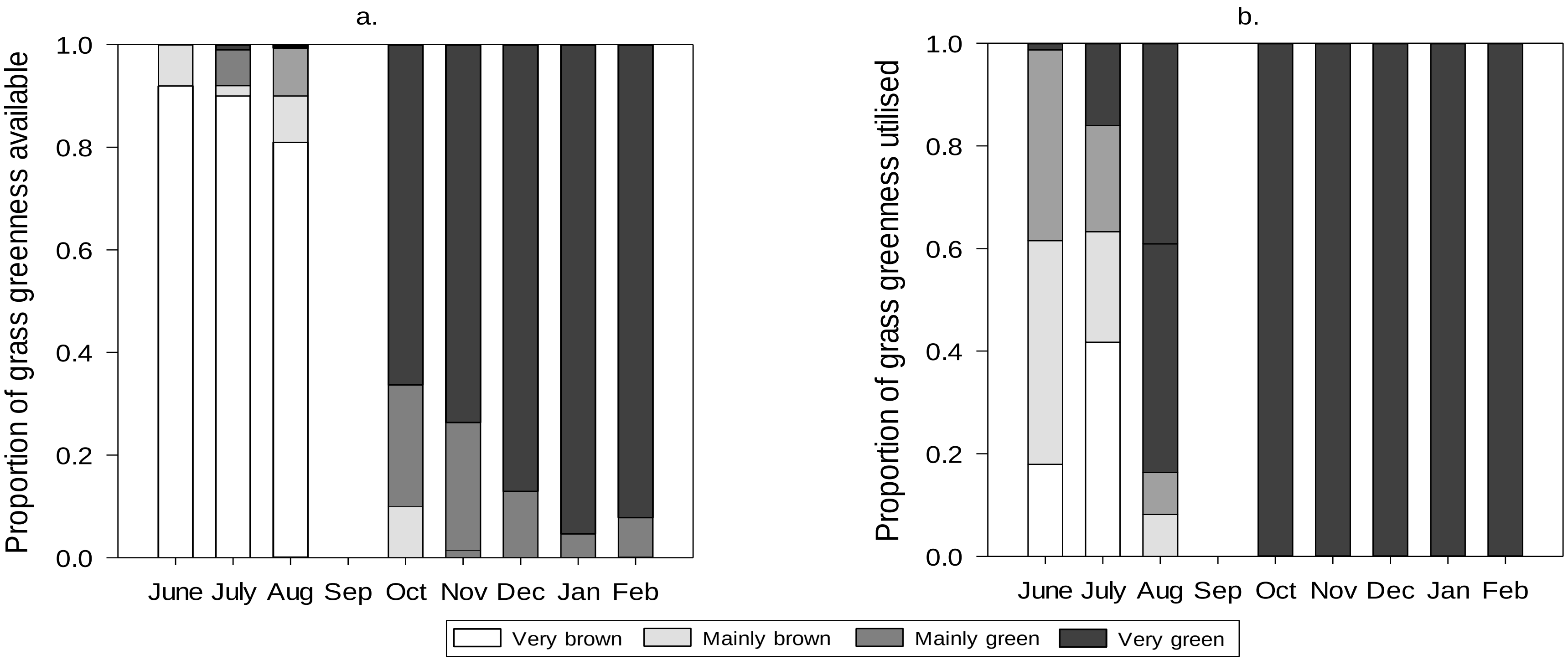

Figure 6: a) Availability and b) utilisation of grass in the different grass greenness categories (very brown 0–10%, mainly brown 11–50%, mainly green 51–90%, and very green 91– 100%). Availability was determined using the number of quadrats in each greenness category from monthly transect data (*N* = 410 quadrats for each month). Proportion of use was determined using the grass greenness of each quadrats obtained in monthly foraging observations June *N* = 74, July *N* = 184, August *N* = 223, October *N* = 174, November *N* = 170, December *N* = 96, January *N* = 91, and February *N* = 67.

Selection of grass species

Throughout the study, overall selectivity for grass species was surprisingly low (dry season unburnt grasslands S = 0.24, dry season burnt firebreaks S = 0.06, transitional S = 0.21, and wet season S = 0.17). However, at the species scale, the oribi did not feed on species in relation to their availability. Rather, they selected for specific grass species throughout the dry season (Chi square: $\chi^2 = 88.341$, $df = 11$, $P < 0.001$), transitional (Chi square: $\chi^2 = 30.500$, $df = 7$, $P < 0.001$), and wet season periods (Chi square: $\chi^2 = 78.371$, $df = 12$, $P < 0.001$). As expected, there was no significant difference in the utilisation and the availability of grass species when oribi fed on the green flush on firebreaks during the dry season (Chi square: $\chi^2 = 3.010$, $df = 2$, $P = 0.22$).

In the dry season, oribi selected for *H. hirta, T. triandra*, *H. contortus*, *P. clandestinum,* and *P. urvillei* while they avoided *P. scrobiculatum*, *Tristachya leucothrix*, the Cyperaceae sedge, an *Asparagus* sp., *Monocymbium ceresiiforme*, *Cynodon dactylon*, and *Sporobolus africanus* in unburnt grasslands (See Appendix II Table 2). While feeding on firebreaks during the same period, oribi selected for all three of the species they ate (*H. hirta, H. altissima* and *A. appendiculatus,* see Appendix II Table 2). During the transitional period oribi selected for *H. hirta*, *T. triandra*, *H. altissima*, and *L. hexandra*, while avoiding the Cyperaceae sedge, *T. leucothrix*, *Digitaria tricholaenoides,* and *Kyllinga* sp. (See Appendix II Table 2). During the wet season, oribi selected for *H. hirta*, *D. amplectans*, the Cyperaceae sedge, and *L. hexandra,* while avoiding *T. triandra*, *Setaria nigrirostris*, *Imperata cylindrical*, *M. ceresiiforme*, *H. altissima*, *A. appendiculatus*, *P. dilatatum*, and *P. scrobiculatum* (See Appendix II Table 2). Surprisingly, oribi did not feed on any grass or forb species in proportion to its availability.

Selection of grass species and greenness

As with the overall selection of grass greenness, selection for grass greenness categories of specific species remained relatively low throughout the study period (dry season unburnt grasslands S = 0.21, dry season burnt firebreak S = 0.02, transitional S = 0.17, and wet season S = 0.14). For each grass species, oribi showed preferences for green leaves throughout the dry (Chi square: $\chi^2 = 71.82$, $df = 13$, $P < 0.001$), transitional (Chi square: $\chi^2 = 30.943$, $df = 5$, $P < 0.001$), and wet season periods (Chi square: $\chi^2 = 54.633$, $df = 11$, $P < 0.001$). However, there was no selection when oribi fed on firebreaks (Chi square: $\chi^2 = 0.245$, $df = 2$, $P = 0.88$).

During the dry season (see Appendix II Table 3), oribi selected for all available grass greenness categories (0%, 1–10%, and 11–25%) of *T. triandra*. However, they only ate the greenest leaves that were available for *H. contortus* (1–10%), *P. clandestinum* (51–65%), *H. hirta* (26–35%), and *P. urvillei* (76–90%). Finally, oribi avoided *P. scrobiculatum*, *T. leucothrix*, the Cyperaceae sedge, *M. ceresiiforme*, *C. dactylon*, and *S. africanus* irrespective of greenness during the study.

While utilising firebreaks, oribi consumed the greenness grass available in relation to its availability for *A. appendiculatus* and *H. altissima* (see Appendix II Table 3). Interestingly, oribi avoided the 91–99% green leaves of *H. hirta*. During the transitional period, oribi selected for the greenest grass available for *L. hexandra*, the Cyperaceae sedge, and *H. hirta* (see Appendix II Table 3). However, oribi avoided *T. leucothrix, D. tricholaenoides*, and a *Kyllinga* sp. irrespective of their greenness.

Finally, during the wet season, oribi selected for *D. amplectens* when it was >91% green and the Cyperaceae sedge when it was 100% green. Oribi only consumed *H. hirta* when it was 91–99% green, but avoided grass that was 100% green. Green leaves of *L. hexandra* were consumed in relation to their availability. Oribi avoided *S. nigrirostris, I. cylindrical, T. triandra, H. altissima, P. dilatatum,* and *P. scrobiculatum* irrespective of greenness (see Appendix II Table 3).

Bite rate, bite mass and intake rate

Oribi increased their intake rate (g/min) as the seasons progressed from dry to wet (Generalised Linear Model: $\chi^2 = 182.174$, $df = 3$, $P < 0.001$). They obtained their lowest intake rate (mean ± SE) in the dry season (0.35 ± 0.02 g/min), which then increased to 0.43 ± 0.02 g/min in the transitional period, and finally, oribi obtained the highest intake rate in the wet season (0.72 ± 0.03 g/min). In contrast to my prediction, oribi increased their intake rate as the dry season progressed from June to August (Generalised Linear Model: $\chi^2 = 21.797$, $df = 2$, $P < 0.001$), likely as a means of compensating for reduced nutritional quality. During this time, oribi obtained this increased intake rate by increasing their bite mass (Generalised Linear Model: $\chi^2 = 98.081$, $df = 2$, $P < 0.001$) and not their bite rate (Generalised Linear Model: $\chi^2 = 0.374$, $df = 2$, $P = 0.829$).

When oribi utilised firebreaks during the dry season, they obtained similar intake rates (0.50 ± 0.03 g/min) to the transitional period. Oribi obtained similar bite masses throughout the dry season, irrespective of whether they fed on unburnt grasslands (0.009 ± 0.0002 g) or burnt firebreaks (0.009 ± 0.0002 g), and also during the transitional period (0.009 ± 0.0002 g). Therefore, the increase in intake rate from feeding on unburnt grasslands in dry season to feeding on firebreaks and the transitional period is likely a result of increased bite rates, due to the abundance of high quality vegetation. Oribi obtained the highest bite rates (mean ± SE) while feeding on firebreaks during the dry season (58.56 ± 1.60 bites/min), then the transitional period

(49.92 ± 1.40 bites/min), followed by the wet season (40.90 ± 0.72 bites/min), and finally they obtained the lowest bite rate on unburnt grassland during the dry season (39.22 ± 0.87 bites/min). However, the high intake rate obtained in the wet season is a result of increased bite mass (0.18 ± 0.0002 g) and not bite rate.

Nutrient content in relation to availability

By foraging selectively, oribi were able to obtain higher levels of %CP, digestibility, and CP: OMD compared to what was available in each of the sampling periods (Generalised Linear Model CP: $\chi^2 = 1763.088$, $df = 3$, $P < 0.001$; OMD: $\chi^2 = 1532.052$, $df = 3$, $P < 0.001$; CP: OMD: $\chi^2 = 1807.481$, $P < 0.001$) (Figures 7 a-c). The nutrient content (mean ± SE % CP) of consumed forage during the dry season was 4.94 ± 0.09 %CP, which was about ~3 times higher than the mean available crude protein (1.72 ± 0.04 %CP). Positive selection for high quality green leaves of *P. urvillei* and *P. clandestinum* during the dry season enabled oribi to obtain higher protein intake and digestibility. Burning firebreaks only slightly increased the available crude protein to 2.70 ± 0.04 %CP because the availability of the green grass in relation to unburnt areas was low. However, the oribi showed a strong selection for the green flush on firebreaks when they were available which resulted in the oribi obtaining ~4.5 times the amount of crude protein (12.84 ± 0.30 %CP) and ~1.5 times more digestible forage compared to what was available on the reserve. Even during the transitional and summer periods when the majority of the grass was green, the selective foraging of oribi allowed them to maintain higher levels of crude protein and digestibility intake compared to what was available (Figure 7 a & b). Finally, oribi maintained higher levels of CP: OMD in their diet than what was available. The heavy utilization of firebreaks increased the ratio of

CP: OMD so that there was no significant difference in CP: OMD when oribi were foraging on firebreaks, the transitional period, and the wet season (Figure 7c).

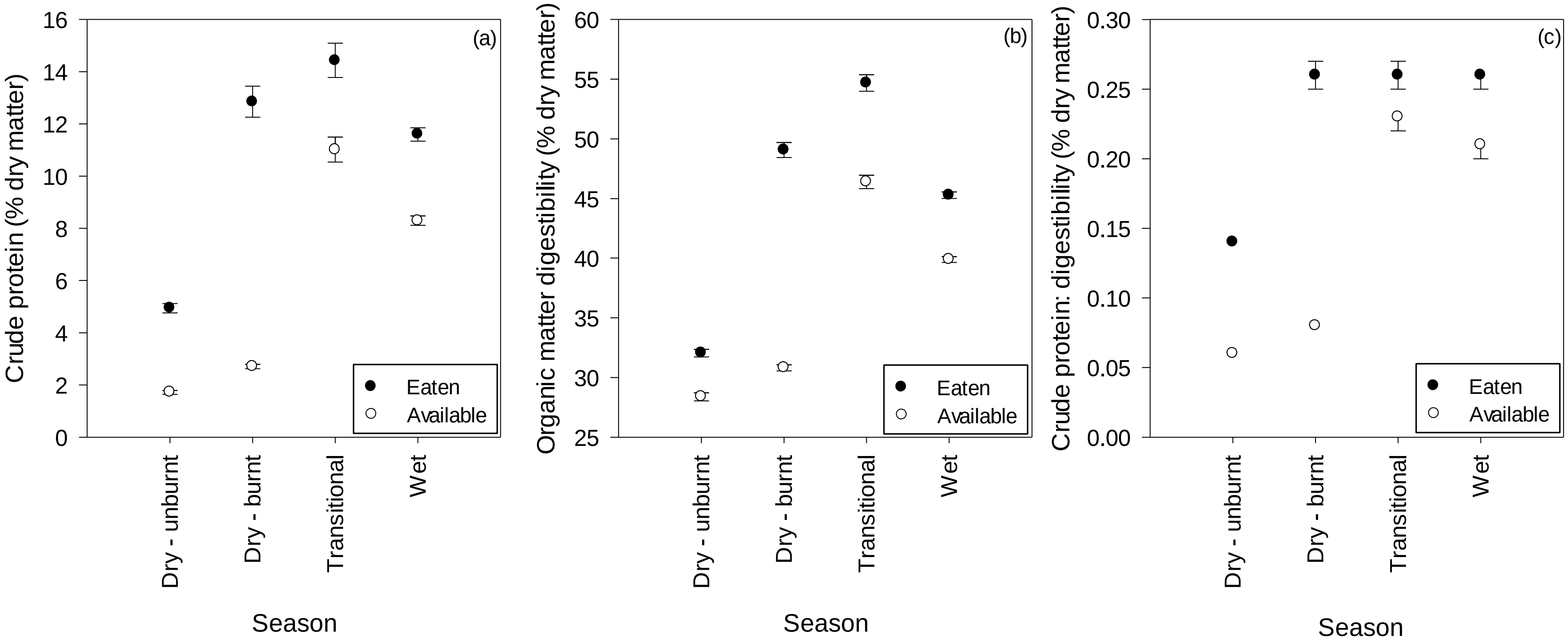

Figure 7 a-c: Mean (± 95% CI) seasonal variation in a) the protein concentration of consumed forage in relation to protein concentration of available forage, b) organic matter digestibility concentration of consumed forage in relation to the organic matter digestibility concentration of available forage, and c) crude protein: organic matter digestibility concentration of consumed forage in relation to the crude protein: organic matter digestibility concentration of available forage

Protein intake relative to minimum and reproductive requirements

There was a significant difference in the protein intake (%DM) across the different periods (dry season, firebreaks, transitional, and wet season) (Generalised Linear Model: $\chi^2 = 559.498$, $df = 3$, $P < 0.001$). Oribi obtained the lowest protein intake during the dry season (5.16 ± 0.16 %CP DM), which then increased to 12.81 ± 0.49 %CP DM when oribi fed on the firebreaks burnt during this season. By heavily utilising the green flush provided by firebreaks oribi were able to obtain greater intake rates of crude protein (mean ± SE: 12.43 ± 0.52 %CP DM), compared to when they fed on unburnt grass (4.93 ± 0.21 %CP DM) during this period (Generalised Linear Model: $\chi^2 = 240.504$, $df = 1$, $P < 0.001$). Oribi achieved the highest intake of protein during the transitional period (14.19 ± 0.56 %CP DM). During the wet season, protein intake declined to 10.17 ± 0.25 %CP DM, as the grasses matured.

When I compared the monthly intake of protein to the minimum requirement for maintenance (i.e. 5%), I found that during June (early dry season) the mean protein intake (i.e. 6.03%) was above the 5% minimum requirement needed for maintenance (Figure 8). If firebreaks were not available in July and August, the mean protein intake in the diet (4.94% and 4.86% respectively) would have been around the oribi’s minimum requirements. However, by utilising firebreaks in July and August (middle to end of dry season), oribi were able to more than double their protein intake and thus exceed the minimum of 5% needed for maintenance (Figure 8). During the transitional and summer periods, the %CP in the diet (14% and ~10% respectively) were more than double the minimum requirements (Figure 8).

During the dry season, the monthly intake of protein was far below (4.86% to 6.03%) the minimum requirement needed for reproduction (i.e. 10%). However, when oribi fed on firebreaks they were able to exceed the protein needed for reproduction (Figure 8). Furthermore, in the transitional and wet season, oribi were able to maintain or exceed these requirements.

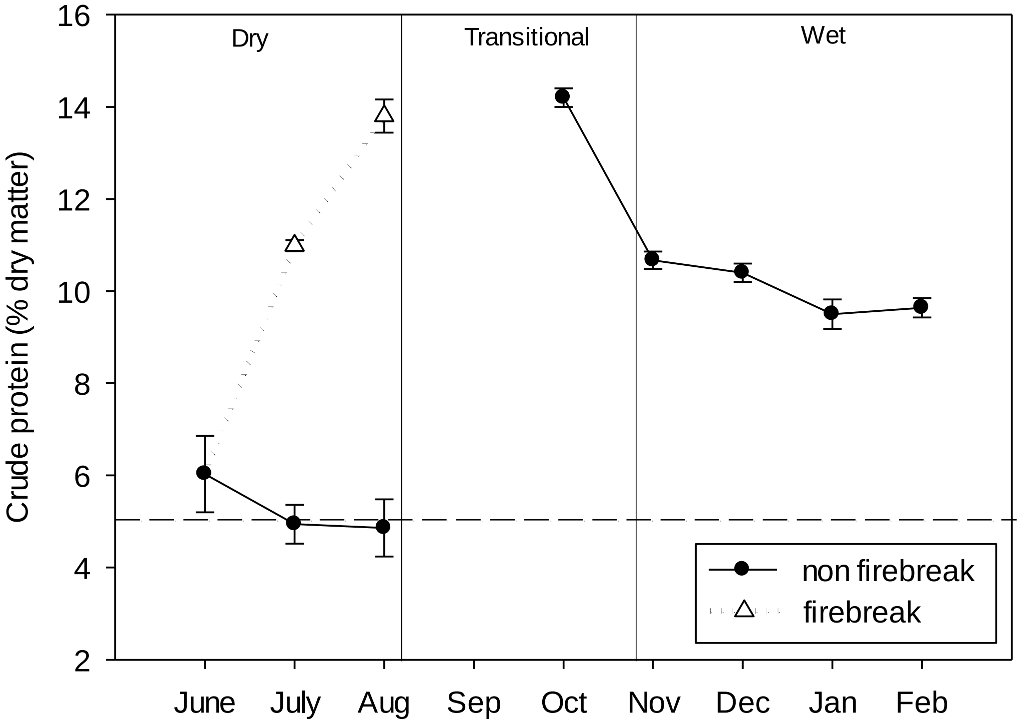

Figure 8: Mean (± SE) monthly variation in protein concentration in the diet of oribi in relation to the minimum 5% protein concentration required for maintenance.

Discussion

Small ruminant grazers are limited by their high energetic requirements and digestive physiology such that they need to consume high quality vegetation (Jarman 1974). However, the availability of this vegetation decreases during the dry season. Therefore, for these grazers to meet their high energetic requirements, they likely need to feed selectively over a range of spatial scales (Bailey et al. 1996). I found oribi foraged over multiple spatial scales. At a landscape scale, oribi selected for certain microhabitats such as vlei areas and firebreaks where high quality green grass was readily available. By heavily utilising firebreaks, oribi were able to far exceed their minimum protein requirements needed for maintenance during the dry season. At the patch scale, oribi increased their diet breadth as well as altered their feeding strategy, by increasing their use of forbs during the transitional and wet seasons. By making seasonal shifts in their diet selection, oribi were able to maintain a nutritional intake above their metabolic requirements. Interestingly, in addition to being highly selective, oribi also increased their intake rate of dry matter as the dry season progressed. This increase progressed into the wet season.

A number of studies have shown that herbivores increase their diet breadth to compensate for declines in nutritional quality of vegetation (Brown and Doucet 1991; Owen-Smith 1994; Kerley et al. 2010). For example, kudu (*Tragelaphus strepsiceros*) increased their diet breadth during winter to include evergreen and unpalatable deciduous woody species, which were avoided during the wet season (Owen-Smith 1994). However, this increase in diet breadth alone did not allow kudu to satisfy their daily energetic requirements. A possible explanation for this could be by incorporating lower quality vegetation into the diet, foragers become limited by the passage rate of the food (Belovsky 1981; Shipley and Spalinger 1992), which ultimately limits the intake of additional forage.

For small grazing herbivores, the quality of grass is generally lower and more seasonally variable than browse (Owen-Smith and Novellie 1982). Furthermore, the gut anatomy of browsing ruminants allows a higher rate of passage of undigested fibrous vegetation than is the case for grazers (Hoffman and Stewart 1972). As a result, browsers may be better suited to increase the amount of lower quality vegetation in the diet compared to grazers. For grazing ruminants, food intake is constrained by the rate of fibre digestion, and thus passage rate, and with low quality diets the daily intake rate may be as little as 1.3% of live mass (Stanley-Price 1978). The added constraints of being small, such as small digestive tracts, and high rates of passage means that small grazing ruminants need to forage on high quality vegetation and they cannot afford to consume low quality forage (Luna et al. 2013).

As with other herbivores, oribi seasonally increased their diet breadth. Moreover, they also seasonally shifted their feeding strategy. My initial prediction was that oribi would alter their feeding strategy to include more forbs in the diet during the dry season. However, less than 1% of the diet consisted of forbs. The reason for this was that all the forbs had already senesced by the start of the dry season and the nutritional quality of these senesced forbs was lower than the nutritional quality of some of the green grasses that were available. During the transitional period, oribi did shift their feeding strategy to include more forbs in the diet (13%). The start of the rains and the block burning in September caused both grass and forb species to flush. During this time, oribi increased their consumption of forbs, which had equal or higher nutritional values compared to grasses that were available. This shift in feeding strategy is consistent with the foraging behaviour of other small ruminants. For example, red duiker (*Cephalophus natalensis*), common duiker (*Sylvicapra grimmia*) and suni (*Neotragus moschatus*) all showed major dietary shifts than included altering the proportion of browse and graze in their diet (Prins et al. 2006).

As part of adjusting their diet breadth, oribi also altered their preference for different species. They achieved this by foraging selectively at two spatial scales.

Preferences for favourable foraging conditions can help explain patterns of habitat selection (Bjørneraas et al. 2012). At the landscape scale, oribi selected for microhabitats that provided green grass. For example, during the dry season, they concentrated their feeding in vlei areas where *P. urvillei* was common, which provided the greenest grass during the dry season. After the dry season, this species was not consumed again, nor was it encountered along foraging paths even though it was still available. This is because oribi shifted away from the vlei areas after the dry season to consume more available species. This then resulted in nutritious species such as *L. hexandra* and *D. amplectans* to be consumed during the transitional and wet seasons. These species were available during the dry season but only had brown leaves. Thus, this suggests that oribi first make large-scale decisions about which habitat to feed in, and then make small-scale decisions about where to feed within a habitat.

Firebreaks also provided microhabitats with green grass. Only a small proportion of the reserve (~10%) was burnt as firebreaks, which resulted in only a small increase in the available crude protein and organic matter digestibility. However, by selecting for this microhabitat, oribi were able to greatly increase their crude protein in their diet and far exceed the 5% crude protein needed for maintenance. This suggests that these microhabitats do not have to be large to benefit oribi. As a result, oribi likely can obtain the same benefit from green flushes caused by winter rainfall because of its direct influence on food availability. For example, grass production in grazing lawns, which are of major importance to grazers because they provide high quality vegetation (Verweij et al. 2006), is correlated with rainfall (Bonnet et al. 2010). During the dry season, the resurgence of grazing on grazing lawns was a result of increased production of grass after a rainfall event and not due to an increased production from grazing activity (Bonnet et al. 2010).

At the patch scale, oribi did not feed on species in relation to their availability. Rather, they maintained a narrow, selective diet breadth with five species contributing to over 80% of the diet across all seasons. In addition to selecting for specific plant species, oribi also selected the plant part that they consumed. Throughout the study, oribi only consumed grass leaves and where possible selected for new green shoots and avoided high fibre plant structures such as culms and stems. This supports the feeding style where oribi should show seasonal variation in their diet, select for highly nutritious species as well as plant parts (Jarman 1974).

Interestingly, oribi increased their dry matter intake as the dry season progressed. This increase was due to them increasing the bite mass of consumed species. In contrast, as the dry season progressed, oribi maintained a constant bite rate. Because the availability of high quality food is sparsely distributed in the dry season, the intake rate of herbivores is limited by search time. Seeing that the bite rate of oribi did not increase suggests that they are limited by the time it takes to find high quality vegetation. Instead of increasing their bite rate and incorporating additional lower quality species, oribi increased their bite mass of the highest quality vegetation that was available. Because of this, oribi maintained a similar nutritional intake between July and August. As a result, it seems that oribi increased intake rate (via larger bites of high quality food) as a way to compensate for overall decreasing nutritional quality of the available vegetation.

Although oribi increased their bite mass during the dry season, the bites were still smaller than the bites obtained during the wet season. This suggests that during the dry season, the small bites taken by oribi were not a result of being limited by the size of bites that they could take. There are two possible reasons why oribi did not take as big a bite during the dry season as they did in the wet season. Firstly, by increasing their bite size oribi may increase the amount of low quality brown grass they obtain in each bite. This would then decrease the nutritional quality of each bite. Unfortunately, I was unable to determine whether the increasing bite sizes during the dry season resulted in an increase in the ingestion of brown grass. However, as the oribi bites were so small, if they did increase the amount of brown grass in each bite, the proportion of brown grass to green grass ingested would likely not be large enough to greatly decrease the nutritional quality of each bite. This is reflected in the fact that oribi were able to maintain similar nutritional intakes between July and August, even though the availability of green grass declined. Secondly, the size of bites that oribi could achieve were most likely limited by the chewing time required for fibrous vegetation (Shipley and Spalinger 1992) because the bigger the bite, the greater the handling time. By keeping bites of fibrous vegetation small, oribi could have reduced the handling time required to chew the food and therefore, maintain their intake rate.

Ultimately, my results agree with previous studies that indicate that oribi forage selectively (Reilly et al. 1990; Everett and Perrin 1992). However, this is the first study that relates the foraging behaviour of oribi to their nutritional requirements. Interestingly, in this study oribi just maintained their minimum requirements for crude protein during the dry season, despite being selective at the landscape and patch scales. This highlights the energetic costs of being small and that selective foraging is essential for small ruminants to survive. The significant differences in crude protein levels between what is available on the reserve and what is actually eaten by oribi suggests that if oribi were not selective and foraged on species in relation to their availability, they would not be able to cope with the decreasing nutritional quality available during the dry season.

Although oribi would survive the dry season, their ability to obtain enough protein for reproduction may be limited without the inclusion of firebreaks. Oribi have a seven month gestation period and birth peaks are associated with high rainfall (Jongejan et al. 1991). Therefore, if oribi give birth anywhere from October to January they will likely be pregnant during the dry season. If this is the case, then the high crude intake available on firebreaks may allow these females to achieve a nutritional intake that would cope with the high nutrient demands associated with pregnancy and lactation.

Protein has been identified as a major limiting nutrient for grazing ruminants during the dry season (Sinclair 1975). However, there are other nutrients such as sodium and phosphorous (du Toit et al. 1940) that may be limiting during the dry season. Unfortunately, testing for these nutrients was beyond the scope of the study. The increased nutritional intake rate obtained during the wet season may have allowed oribi to compensate for reduced nutrients in the dry season. However, it is unlikely that oribi maintained this high intake throughout the wet season purely to compensating for limited nutrients in the dry season.

The mean rainfall for the wet season prior to the start of the dry season sampling period (434 mm) was below the long term mean (513 mm). Therefore, the availability of green grass in the dry season that was sampled may have been lower than during periods of normal or above average pre-dry season rainfall. If this is the case, the average nutritional intake of oribi would have increased because of their high selectivity for green grass. This increase would raise the nutritional intake rate higher above the 5

% minimum requirement. However, it is unlikely that the increase in the availability of green grass would have been high enough for oribi to obtain an intake rate that was need for reproduction, without the use of firebreaks. Therefore, firebreaks are essential for oribi to reproduce even during periods of normal wet season rainfall.

Interestingly, there are a number of years where the wet season rainfall is even lower than the rainfall experienced during the study period. This would decrease the availability of green grass even further and it is unlikely that oribi would be able to survive the dry season. In addition, during these periods of extremely low rainfall, the importance of firebreaks as a means to increase the nutritional intake rate of oribi may be limited. For firebreaks to produce a green flush there needs to be sufficient soil moisture (Parrini and Owen-Smith 2010) and after a dry wet season there remaining soil moisture on the dry season may not be high enough to sustain a green flush in the middle of the dry season.

Conclusions

These results suggest that oribi (Africa’s smallest grazing antelope) use a number of behavioural mechanisms to maintain their high energetic requirements during the dry season. Despite their small size, and thus likely ability to focus seasonal adjustments primarily at small spatial scales (e.g. plant parts), oribi adjusted there foraging across a number of different spatial scales to meet their nutritional intake requirements. Firstly, oribi selected for favourable habitats in which to feed and then selected for certain species to consume. By altering habitat use, oribi increased their overall diet breadth and only consumed particular species during certain seasons. As a result, oribi were able to maintain a selective seasonal diet. In addition, oribi increased their dry matter intake rate as the dry season progressed. They achieved this by increasing their bite mass of consumed species and not by increasing their bite rate, and thus avoiding the incorporation of avoided species. Although oribi utilised several ways to meet their energetic requirements, they just maintained the minimum protein requirement needed for maintenance. By utilising firebreaks oribi were able to greatly increase their crude protein intake to a level where they exceed the requirements needed for reproduction. This highlights the energetic constraints imposed on small herbivores and the fitness benefits provided by green flushes during the dry season.

CHAPTER 3

Friend or foe? The influence of season and stocking rate on the nature of interspecific interactions between cattle and oribi.

Domestic herbivores forage alongside wildlife in many parts of the world. Through their feeding, domestic herbivores can greatly impact wildlife. However, these impacts are not always negative. I explored the influence of cattle stocking rates and season on the foraging behaviour and the resulting nutritional intake rates of oribi antelope (*Ourebia ourebi*), in a South Africa rangeland. During the wet season when cattle (*Bos taurus*) and oribi utilised the same feeding areas, there was high dietary overlap and both species fed from swards of similar height. At low stocking rates (1.7 ha/AU), relative grass regrowth was high enough for oribi and cattle to utilise the same species and grass height. However, in the high stocking rate camp (0.94 ha/AU) there was less relative regrowth. In response, oribi adjusted their feeding and focused on the green leaves available in taller grass swards not used by cattle. This adjustment allowed these oribi to achieve the same nutritional intake as oribi in the lower stocking rate camps. Overall, oribi maintained higher crude protein intake rates feeding with cattle than they did when feeding in ungrazed camps. Thus, cattle facilitated oribi during the wet season. During the dry season, oribi obtained their lowest crude protein intake in the high stocking rate camp, while oribi obtained higher, but similar crude protein intake rates when feeding in camps with low and intermediate stocking rates. Moreover, the high intensity wet season grazing by cattle in the high stocking rate camp reduced the availability of high quality grass for oribi in the dry season. Thus, wet season cattle feeding competed with

oribi dry season feeding. Finally, across both seasons, cattle grazing altered grass height and structural heterogeneity, which could potentially increase the predation risk of oribi.

Introduction

Mammalian herbivores within a community share a number of resources. However, resource partitioning due to differences in body size, morphology, and digestive physiology allow these herbivores to occupy different parts of the ecosystem (van Wieren and Bakker 2008). In eastern and southern Africa, the majority of native large herbivores occur outside protected areas (Ottichilo et al. 2000) and frequently interact with cattle (*Bos taurus*) (Young et al. 2005; du Toit 2011; Odadi et al. 2011). The introduction of livestock at high numbers can influence native ungulates through the modification of habitats and competition for food (du Toit and Cumming 1999; van Wieren and Bakker 2008). However, resource partitioning has the potential to minimise competition so that cattle production and wildlife conservation can be compatible (Hopcraft 2000).

Competition occurs when the exploitation of a shared resource by two or more species leads to a reduced performance of at least one species (Prins 2000). Although herbivores can compete for food resource, they can also compete for habitats (Rosenzweig 1981). Large herbivores can alter vegetation structure so that habitat conditions are changed for other species. For example, cattle grazing reduced the available food supply and the structural component understory needed for predator avoidance by female mule deer (*Odocoileus hemionus*) (Loft et al. 1987). In response, these females altered their habitat use in the presence of cattle during late summer when resources in habitats were limited (Loft et al. 1991).

Habitat modifications, however, are not always detrimental. For example, habitat changes through reduced grass height and removal of stems by one species may make grass more accessible to other species, resulting in facilitation rather than competition (Vasey-Fitzgerald 1960). However, a more likely example of facilitation is when the foraging of one species stimulates high quality grass regrowth that increases the nutritional quality of forage for another species (McNaughton 1984; Arsenault and Owen-Smith 2002). The benefits obtained through facilitation can have an immediate influence (i.e. high quality regrowth during the wet season), or they may occur across seasons. For example, red deer (*Cervus elaphus*) preferred to feed in areas that had been grazed by cattle the previous winter (Gordon 1988). The winter grazing by cattle resulted in a higher proportion of green grass to dead material compared to areas without winter grazing by cattle. However, the influence of summer grazing by cattle on the performance of wildlife during the dry season has scarcely been explored.

The extent to which species are affected by changes in vegetation structure and composition through grazing pressure will depend on the biology of the species concerned (Bakker et al. 2009; Kutt and Gordon 2012). Large herbivores belong to either a grazing or a browser guild (Cerling et al. 2003) and it is this grazer–browser guild that promotes resource partitioning (McNaughton and Georgiadis 1986). However, coexisting species within a specific guild do not necessarily compete with each other because body size and/or digestive physiology influences preference for grass height and diet quality (Bell 1970; Demment and Van Soest 1985; Prins et al. 2006). Small species require higher quality vegetation and select for short grasses, while larger herbivores can tolerate lower quality, taller vegetation. As a result, small herbivores may out-compete larger herbivores by being able to survive on grass biomass levels too low to support larger herbivores (Illius and Gordon 1987; Arsenault and Owen-Smith 2002). In addition, small herbivores may have a competitive advantage over larger species because of their ability to survive on sparse or limited high-quality resources (Prins and Olff 1998).

Furthermore, muzzle size also influences the selective ability of herbivores and their ability to crop grass of different heights (Illius and Gordon 1987). In addition, small herbivores with narrow muzzles are able to selectively remove green leaves from tall grass swards, effectively decreasing the forage quality for larger less selective herbivores (Illius and Gordon 1987; Murray and Illius 2000). Because small herbivores require high quality forage, they tend to occur in specialised habitats that provide such resources (Jarman 1974; du Toit and Owen-Smith 1989). As a result, their ability to compete with larger herbivores tends to be confined to these specialised habitats. In contrast, larger species can out-compete smaller herbivores because of their wider feeding tolerance (du Toit and Cumming 1999). Thus, larger herbivores tend to be more evenly spread throughout the ecosystem, exploiting a wide range of habitats (du Toit and Cumming 1999). This results in large herbivores foraging in the high quality areas that are used by smaller herbivores, which can reduce the availability of food left to support small herbivores during the dry season (Arsenault and Owen-Smith 2002).

Interspecific interactions between herbivores are also density dependent (McCullough 1999). For example, low and medium grazing intensities can promote high quality regrowth that may facilitate the foraging of another species. However, as the grazing intensity increases, net primary production decreases (Hilbert et al. 1981), especially during periods of low rainfall (Fynn and O'Connor 2000). As a result, facilitation under low to medium stocking rates may change to competition under high grazing intensities. Furthermore, moderate grazing intensities of cattle can create structural heterogeneity through the heavy utilisation of certain patches interspersed with light to medium grazed patches (Bailey et al. 1998). As a result, other herbivores can take advantage of potential regrowth from the grazed areas, while the lightly grazed areas could provide cover from predators.

In contrast, high stocking rates reduce grass height and structural heterogeneity (Fuhlendorf and Engle 2001), which can increase predation risk by reducing hiding cover (Loft et al. 1987), even though they may provide large amounts of high quality regrowth. Therefore, competitive exclusion may occur because the negative effects associated with an increased predation risk of an unsuitable habitat negate the benefits of high quality vegetation. For example, in the Hluhluwe-iMfolozi Park in South Africa the abundance of a large bulk grazer—the white rhinoceros (*Ceratotherium simum*), resulted in a decrease in species such as reedbuck (*Redunca arundinum*) and waterbuck (*Kobus ellipsiprymnus*), which are dependent on tall grass (Owen-Smith 1988). Because white rhinoceros promote the existence of grazing lawns, grazers that prefer short grasses such as wildebeest (*Connochaetes taurinus*) and warthog (*Phacochoerus africanus*) increased in their abundance.

Whether coexisting herbivores compete or facilitate each other can depend on the season. A study that explored the effect of wild herbivores on cattle production found that wild herbivores compete with cattle during the dry season when resources are limited (Odadi et al. 2011). This competition was attributed to lower food intake of cattle as a result of zebra (*Equus quagga* and *E. grevyi*) and cattle competing for the same grass species (Odadi et al. 2011). In contrast, wild ungulates facilitated cattle production in the wet season through an enhanced crude protein and digestible organic matter: crude protein associated with the removal of dead grass stems by zebra as well as stimulated regrowth.

One species that interacts with cattle extensively in South Africa are oribi antelope (*Ourebia ourebi*). Yet, surprisingly very little research has focused on the interactions between these two herbivores (Coverdale et al. 2006). Oribi are pure grazers that occur within the mistbelt and highlands sourveld areas in the KwaZulu-Natal province of South Africa (Rowe-Rowe and Scotcher 1986). Within South Africa, oribi are listed as vulnerable. Moreover, throughout their distribution, the majority of oribi occur outside of protected areas and frequently interact with cattle (Oribi working group unpublished data). It is common farming practice in South Africa for cattle to graze on natural rangelands during the wet season and then be removed from the wet season grazing areas. Therefore, on many rangelands cattle and oribi only interact during the wet season. As a result, understanding the interspecific interactions between cattle and oribi are of major conservation importance. Current literature suggests that smaller herbivores are competitively superior because they can survive on sparse high quality resources. However, this competitive superiority is not always supported. For example, in Zimbabwe, impala (*Aepyceros melampus*) competed with cattle, which lead to impala altering their habitat preference to utilise refuge habitats during the wet and hot dry seasons (Fritz et al. 1996).

Therefore, the aims of this study were to 1) explore the interspecific interactions between cattle and oribi and how these interactions influenced the performance (i.e. nutritional intake rate) of oribi across different cattle stocking rates in the wet season, and 2) determine how the wet season foraging by cattle influenced the dry season performance of oribi. I predicted that the type of interspecific interaction (i.e. competition or facilitation) that cattle impose on oribi would be dependent on season. During the wet season, cattle would facilitate oribi whereas in the dry season, grazing by cattle in the wet season would have a competitive effect on oribi. If facilitation took place in the wet season, I predicted that cattle would facilitate oribi foraging by providing high quality regrowth. Even if dietary overlap was high, there could still be facilitation because of regrowth that cattle and oribi both utilise. Alternatively, at high stocking rates, I predicted that cattle would compete with oribi because of the rapid removal of potential regrowth. Moreover, cattle have the ability to influence the structural heterogeneity of grass through their foraging, which is important to oribi (see Chapters 2 & 4). I predicted that as stocking rates increase there would be a decrease in average grass height and structural heterogeneity, which could ultimately influence the availability of tall grass for oribi to use as cover for predator avoidance (see Chapter 4).

Although cattle and oribi do not directly interact during the dry season, I predicted that the foraging behaviour of cattle in the wet season would negatively affect oribi foraging in the following dry season. This would be the result of high dietary overlap between cattle and oribi during the wet season reducing the availability of dry season food for oribi. However, this competition would only be apparent in areas with high wet season cattle stocking rates because of the higher removal of vegetative biomass.

Methods:

Study site

I conducted these experiments at Arundel Farm (~770 ha) in Ixopo, KwaZulu-Natal, South Africa (S 30°11.557 E 30°12.199) during the dry season (June–August 2013) and the wet season of January–February 2014. Mean rainfall for the area was 725 mm

(1995–2013), South African Weather Services). The wet season extends from October to April and the dry season is from May to September.

The vegetation type is defined as Midlands Mistbelt Grasslands, which is dominated by sour *Themeda triandra* grasslands that are invaded by *Aristida junciformis* (Mucina and Rutherford 2006). Other species include *Hyparrhenia hirta*, *Sporobolus africanus, Heteropogon contortus, Setaria nigrirostris, S. sphacelata* var. *torta*, *Cymbopogon excavatus, Eragrostis plana* and *Paspalum dilatatum.*

Arundel farm focuses primarily on beef production and is stocked with ~370 (240 adults and 130 heifers) Sussex Bonsmara, which are an Afrikaner, Hereford, and shorthorn cross-breed. The cattle are managed using a continuous grazing policy where the cattle remain in each natural grassland camp throughout the grazing season. The farm is divided roughly in half with one half of the area being used solely for wet season grazing for the cattle and the other half for dry season grazing. During the wet season (October–April) the cattle are in the summer grazing camps (~380 ha) where the majority of the oribi also occur (N = ~21). During the dry season (May–September), the cattle are moved from the wet season camps to the dry season grazing camps (~380 ha). However, the oribi are resident and remain in the wet season camps throughout the year. As a result, oribi and cattle only occur in the same camps during the wet season.

The wet season grazing is divided into four camps, but the majority of the oribi only occur in three of these camps. These three camps are different sizes and have different numbers of cattle. I calculated the stocking rate for each camp using the following equation: land area/number of animal unit, which gives a stocking rate of ha/AU. To calculate animal units I used the standard conversion of one adult beef cow is equal to one animal unit (Meissner et al. 1983). One camp contained adult cows as well as heifers, which equal 0.7 animal units. Therefore, the stocking rates for the different camps were: 1.7 ha/AU, 1.5 ha/AU and 0.95 ha/AU. To simplify this, these camps will be referred to as low, intermediate and high stocking rates throughout the manuscript. Oribi are monogamous, territorial and occur in small herds (average herd size *N* = 2.7 with juveniles) (Adamczak and Dunbar 2007). Therefore, each camp have resident herds of oribi, which remain in each camp throughout the year (Camp 1: three herds, *N* = 7 oribi, camp 2 has two herds: *N* = 8 oribi, and camp 3 has two herds: *N* = 6 oribi). Furthermore, these camps are all adjacent and receive equal amounts of rainfall.

The grass species composition across the three stocking rate camps differs slightly. The low and intermediate stocking rate camps were dominated by *H. hirta*, *A. junciformis*, *T. triandra*, *S. nigrirostris*, and *P. dilatatum.* The high stocking rate camp was dominated by the previous species as well as *H. contortus*, *S. sphacelata* var. *torta*, and *C. excavatus.*

Figure 1: Map of Arundel Farm, Ixopo, South Africa. The solid line denotes the study site boundary and the dashed lines represent internal fences. 1 = low stocking rate camp, 2 = intermediate stocking rate camp, and 3 = high stocking rate camp.

Data collection

To determine seasonal changes in sward structure and grass greenness, I walked one 2 km transect in each of the three camps per month (*N* = 5 months). During the wet season, this allowed me to determine the influence of different stocking rates of cattle on the structure and availability of green grass. During the dry season, these transects allowed me to compare the structure and available green grass as a consequence of cattle grazing that took place during the wet season. Every 50 m along each of these transects, I randomly placed two quadrats. Within each quadrat (*N* = 1230), I measured the sward height of the dominant grass species and the percentage of green grass using Walker's (1976) eight-point scale (0%, 1–10%, 11–25%, 26–50%, 51–75%, 76–90%, 91–99%, and 100%). Prior to analysis, I combined estimates of green grass into four categories: very brown (0–10%), mainly brown (11–50%), mainly green (51–90%), and very green (91–100%).

In addition, I also determined whether cattle influenced the availability of tall grass, which oribi require to hide from predators (Mduma and Sinclair 1994). In each camp, I compared the average height of grass that oribi chose to hide in. Whenever oribi were found hiding, I took five height measurements from the surrounding grass (in a 1 m radius from where the oribi was hiding) to calculate the average grass height in which the oribi hid. These hiding areas were marked and data were only collected once the oribi moved off from their hiding place.

Cattle foraging observations

During the wet season when oribi and cattle were in the same camps, I collected foraging data for cattle in the mornings and afternoons. The cattle were accustomed to the presence of humans, so I was able to observe the foraging behaviour of cattle from about 10–15 m away with no visible effect on behaviour. I spent equal amounts of time in each stocking rate camp to obtain similar numbers of foraging observations per stocking rate. Cows were the dominants sex. As a result, I only collected data from foraging adult females.

Each foraging observation spanned five feeding steps and started with the movement of one of the front feet. Each foraging observation resulted in five separate feeding stations (i.e. one per step). A feeding station is an area in which an animal can forage without taking a step (Ruyle and Dwyer 1985). Although each observation could include non-feeding steps, a minimum of five feeding steps was necessary for each observation. Each feeding station was represented by a 1.5 x 1.5 m quadrat, which is the average area in which a cow feeds without moving its feet (pers. obs.).

Once the foraging individual moved off, I placed the quadrat over the first set of bites along the foraging path. This represented a feeding station. Each feeding station did not overlap, thus each station was an independent observation. For each of the five quadrats in a foraging observation, I differentiated newly foraged grass species from older use by the white appearance of the damaged cuticle (Arsenault and Owen-Smith 2011). For each bite, I recorded the plant species consumed, sward height and grass greenness using the surrounding ungrazed grass of the same species as an estimate (Shrader et al. 2006; Arsenault and Owen-Smith 2011). I estimated grass height for each bite of the consumed grass species using five measurements from surrounding un-grazed tufts of the same species within the feeding station. I then averaged these measurements for each bite. For each foraging observation, I then averaged the grass height of consumed grass for each bite to determine the mean grass height grazed by oribi. Each bite was allocated a grass greenness category according to Walker's (1976) eight-point scale of grass greenness. This resulted in a total of 42 foraging observations.

Cattle bite rate, bite mass and intake rate

For the above foraging observations, I calculated the bite rate, mean bite mass and intake rate for cattle. I calculated the bite rate for each foraging observation by dividing the total number of bites along the five feeding steps by the time required for the cattle to take these bites. In addition, I determined the bite mass for each bite by using hand plucking (Bonnet et al. 2011). While feeding, cattle took different bite types depending on grass height, biting method and bite size (see Bonnet et al. 2011). For each of the different observed bite types, I collected 45 replicates to calculate the mean bite mass per bite type. I simulated cattle bites by using the surrounding un-grazed grass of the same species to hand pluck a grass sample that represented a single bite. The simulated bite was plucked to the same level to which the cattle had grazed. Each of these bite mass estimates (*N* = 225) were then dried at 60°C for 48 hrs and weighed. I then calculated the mean bite mass for each foraging observation by averaging the total number of bite masses found in each foraging observation. For every foraging observation, I calculated the dry matter intake rate (g/min), as a measure of biomass removal, for each observation by multiplying the mean bite mass from the five feeding steps with the corresponding bite rate.

Grass regrowth per stocking rate

Cattle are bulk feeders and have larger bites and intake rates compared to oribi. As a result, they can influence the amount of regrowth that occurs under different stocking rates. To compare the amount of relative regrowth per stocking rate, I ran a regrowth trial from 19 January to 25 February 2014. In each stocking rate camp, I selected 30 swards of *H. hirta*, which was the most consumed grass species by oribi (see Results). All swards were similar in size (~8 cm in diameter) and were selected to form a 6 x 5 grid, with each sward being separated by ~1.5 m. To ensure the same sward was always measured, I marked each sward using orange nails that were flush with the ground next to each sward. All swards were measured every three days. For each observation period, I averaged five measurements of each sward to obtain an estimate of grass height. For each cattle stocking rate, I determined the average net relative regrowth (i.e. [ln final grass height – ln initial grass height] (Evans 1972)) and the resulting average grass height at the end of the experiment, as well as the average number of times a sward was grazed (see below).

Because each stocking rate was unreplicated, I conducted a clipping experiment during the same period as the observations of *H. hirta* regrowth described above. The experiment assisted in two ways. First, it aided in interpreting whether the differences I observed in grass net regrowth at each stocking rate, resulted from differences in cattle grazing pressure rather than site-specific differences unrelated to cattle grazing among the camps. Second, the experiment potentially enabled a generalisation of the results for cattle to other bulk feeders (e.g. wildebeest and zebra) that may co-occur with oribi elsewhere.

The clipping experiment I conducted was designed to determine if the observed net regrowth (i.e. the amount of regrowth in each stocking rate camp) was similar to the expected amount of net regrowth under known clipping intensities (i.e. clipping experiment with different defoliation intensities). Because I was making comparisons between the clipping experiment and the regrowth experiment at different stocking rates, I used the same grass species and sward diameter (i.e. *H. hirta* swards that were ~8 cm in diameter) selected to form a 4 x 10 grid. These swards used in the experiment were in a camp that was not exposed to grazing by cattle but that was adjacent to the stocked camps. For this experiment, I used a blocked design, with each block (4 x 10 grid of grass swards) containing all four defoliation intensity treatments. These treatments were: no clipping, one clip every two weeks (i.e. 3 clipping events during the experiment), one clip every week (5 clipping events), and two clips a week (10 clipping events). I clipped each sward to a height of 8 cm above the ground, which was the average height, at the start of the experiment, to which cattle reduced grass swards post grazing (pers. obs.). There were three blocks with each treatment having ten replicates per block. Each sward was marked (as above) and measured every three days (i.e. grass swards in the regrowth and clipping experiment were measured on the same days). As before, my metric was the average of five measurements of grass height of each sward for each observation period. For each clipping intensity, I determined the number of times a sward was clipped over the experimental period (set by my clipping frequencies), the relative regrowth, and the resulting grass height at the end of the experiment.

Oribi foraging observations

To determine if cattle foraging behaviour influenced the way in which oribi fed, I collected the same foraging data for oribi as I did for cattle. I located oribi in the early mornings and afternoons when they were most active (Coverdale et al. 2006). I found oribi by driving along the farm’s roads (~3 km) as well as off road around the perimeter of each camp. Because I wanted to make comparisons across camps (i.e. stocking rates), I spent equal amounts of time in each camp. This ensured that similar numbers of samples were obtained at each stocking rate. When an oribi was spotted, I observed them from a stationary vehicle using binoculars (Pentax 8x42 DCF) and/or a spotting scope (Bushnell XLT 20-60x 65mm). Data were collected from all adults of both sexes that were encountered.

Upon locating an oribi, data collection began at the first sign of feeding. If oribi showed vigilance towards the vehicle, I terminated the observation. The position of each oribi was determined using nearby landmarks (e.g. Arsenault and Owen-Smith 2011). As with the cattle, each foraging observation spanned five feeding steps and started with the movement of one of the front feet. Each foraging observation resulted in five separate feeding stations (i.e. one per step). Although each observation could include non-feeding steps, a minimum of five feeding steps was necessary for each observation. Preliminary observations indicated that the average area in which an oribi fed before taking a step was about 0.4 m^2. Thus, I represented each feeding station using a 0.4 x 0.4 m quadrat.

To reduce the disturbance of oribi, I waited for them to move off ~50 m from the five feeding stations before I approached the foraging area on foot. Once the foraging path was found, I placed the quadrat over the first set of bites. This represented a feeding station. At each feeding station, I followed the same experimental procedure and collected the same foraging data (outlined above) for oribi as I did for cattle. A feeding station was placed over the bites that were taken per feeding step and never overlapped. This included, consumed and avoided species, sward height and grass greenness using the surrounding ungrazed grass of the same species as an estimate (Shrader et al. 2006; Arsenault and Owen-Smith 2011). Each bite typically ranged from a single blade to multiple blades (maximum four blades) of grass. This resulted in 39 foraging observations in the wet season and 63 oribi foraging observations in the dry season.

Bite rate, bite mass and intake rate

To determine if different stocking rates influenced grass structure, and therefore, the way oribi feed, I determined the bite rate, bite mass and intake rate for oribi. I calculated the bite rate for each foraging observation by dividing the total number of bites along the five feeding steps by the time required for the oribi to take these bites. In addition, I determined the bite mass for each bite by using hand plucking (see Bonnet et al. 2011). Hand plucking was the best technique because oribi are very selective. There was a lot of variation between bites because they could comprise between one and four leaves. I simulated oribi bites by using the surrounding un-grazed grass of the same species to hand pluck a grass sample that represented a single oribi bite. The simulated bite was plucked to the same level to which the oribi had grazed. Each of these bite mass estimates (N = 1802) were then dried at 60°C for 48 hrs and weighed to four decimal places, due to the small size of bites. I then calculated the mean bite mass for each foraging observation by averaging the total number of bite masses found in each foraging observation. For every foraging observation, I calculated the dry matter intake rate (g/min) for each observation by multiplying the mean bite mass from the five feeding steps with the corresponding bite rate.

Data analysis

To determine the influence of stocking rate on average grass height, I used a Generalised Linear Model (Gamma distribution and Log link function) to compare the average grass height in each camp during the wet season. I ran another Generalised Linear Model (Gamma distribution and Log link function) to determine if wet season grazing influenced the average grass height during the dry season when cattle were not present. The dependent variable was grass height and the independent variable was camp (i.e. stocking rate).

Although grass height is important, it is the structural heterogeneity in grass height that is a key feature of oribi habitat. As a result, I calculated the coefficient of variation (CV = (standard deviation/mean) x 100%) as a measure of structural heterogeneity per camp. The greater the variations in grass height, the greater the CV. These values ranges from zero (no structural heterogeneity) to 100 (maximum heterogeneity). I used the transect data for each month to calculate average seasonal heterogeneity values for each camp.

The average grass height and structural heterogeneity can influence the availability of tall grass that oribi use to avoid predators. As a result, I ran a General Linear Model to determine whether different stocking rates influence (independent variable) the average grass height that oribi select for hiding (dependent variable) in both the wet (N = 53) and dry season (N = 38). The data did not need to be transformed to meet the assumptions of normality.

Cattle foraging behaviour

The dietary contribution of consumed species was determined within each feeding station (i.e. quadrat) for each foraging observation. I determined the wet season dietary contribution for each species by dividing the number of bites of that species by the total number of bites of all species in that time period. In addition, I ran two Generalised Linear models (Gamma distribution and Log link function) to determine if stocking rates (independent variable) influenced: 1) the grass height (dependent variable) that cattle select, and 2) the post grazing sward height (dependent variable).

Prior to the cattle bite mass analysis, I ran a Generalised Linear Model (Gamma distribution and Log link function) to determine if the different bite types were significantly different across the different stocking rates. I found that the different stocking rates did not influence the mass of bites within the same bite type (Generalised Linear model Stocking rate x bite type: $\chi^2 = 15.126$, $df = 8$, $P = 0.057$). As a result, I pooled the bite mass data from the different stocking rates for each bite type to calculate the mean bite mass range for cattle.

I determined the proportional use of green grass by cattle in the wet season using the grass greenness of each bite. For each stocking rate, the number of bites in each grass greenness category was divided by the total number of bites obtained for that stocking rate camp.

Grass regrowth experiment

To compare the amount of net regrowth under different stocking rates, I calculated the relative growth of each sward for the duration of the experiment (i.e. 38 days). To do this, I calculated the natural log of the height of grass at the end of the experiment and subtracted the natural log of the grass height at the start of the experiment (Evans 1972). This statistically controlled for possible differences in absolute change in height as a function of sward height. I used a Generalised Linear Model (Gamma distribution and Log link function) to compare the relative grass regrowth (dependent variable) across the different stocking rates (independent variable). Because these swards were grazed by cattle, the average net relative regrowth was negative for some swards. As a result, I transformed the data by adding the lowest negative relative regrowth value to each net relative regrowth value to remove all negative values from the dataset.

For the regrowth experiment, there was no statistically significant difference in grass regrowth for each treatment across replicated blocks (Generalised Linear Model: Block x treatment: $\chi^2 = 3.995$, $df = 6$, $P = 0.677$). As a result, I pooled the data across the three blocks and ran a Generalised Linear Model (Gamma distribution and Log link function) to compare the difference in relative regrowth (dependent variable) per clipping treatment (independent variable).

To compare the observed relative growth under different stocking rates (i.e. my field trial) to the expected growth rates due to variation in grazing pressure, I plotted the net relative growth from the clipping experiment against the number of times the swards were clipped during the experiment (i.e. 3, 5, and 10). For this analysis, I excluded the no clipping treatment because I was only interested in regrowth of swards that could have been grazed. The experimental data was well fitted by a linear relationship, which yielded the following equation: $y = -0.0606x + 0.6502$, $r^2 = 0.89$, where y is the relative regrowth and x is the number of times the sward was clipped during the experiment. The equation provides an estimate of the predicted net relative regrowth as a function of grazing pressure (i.e. how frequently a sward is eaten). To obtain an empirical estimate of how many times a sward was eaten per stocking rate I used the above trend line to fit a relationship between stocking rate and relative regrowth (i.e. I used the relative regrowth in each camp and solved for x). For statistical and graphical representation the relative regrowth was back transformed into percentage growth. All statistical analyses were performed using SPSS version 22.

Oribi foraging behaviour

I calculated the diet of oribi in each stocking rate for the wet and dry seasons. To determine if oribi and cattle consume the same species during the wet season, I calculated dietary overlap at each stocking rate using Schoener's index: $O_{jk} = 1\text{-}1/2\sum|P_{ij}–P_{ik}|$ where O_{jk} is the dietary overlap between ungulate species j and k; P_{ij} and P_{ik} are the utilisation of the ith resource by the jth and kth species (Schoener 1968). In addition, I calculated the dietary overlap of the dry season diet of oribi with that of cattle during the wet season. This allowed me to determine if wet season foraging by cattle could potentially reduce the availability of species that oribi consume during the dry season. Furthermore, I also compared the dietary overlap between the oribi's wet and dry season diet at each stocking rate. This allowed me to determine if stocking rates influenced grass species selection between seasons. However, cattle are less selective and could potentially have a wider diet breadth, so the comparing the total dietary overlap may result in an underestimation of dietary overlap. As a result, I recalculated the dietary overlap using just the main contributing grass species to the cattle and oribi diets.

Due to the large bites of cattle, they have the ability to reduce grass height. As a result, I used a Generalised Linear Model (Gamma distribution and log link function) to compare the height of the grass sward in which oribi feed at different stocking rates for each season (i.e. wet and dry season). To determine whether oribi and cattle compete for the same grass height when feeding together, I compared the sward height in which cattle and oribi fed across the different stocking rates during the wet season. Furthermore, I ran another Generalised Linear Model (Gamma distribution and log link function) to determine if wet season grazing by cattle influenced the sward height on which oribi fed during the dry season. The dependent variable was grass height and the independent variable was stocking rate (i.e. camp).

The different stocking rates influenced the availability of green grass in the dry season (See Results and Figure 1). To determine if this reduced availability influenced the proportion of green grass consumed, I compared the proportion of green grass in the diet (dependent variable) across the different stocking rates (independent variable) using a General Linear Model. For this analysis only the mainly green and very green categories were used because oribi did not eat grass that was very brown or mainly brown. Proportion of use of green grass was Arcsine transformed.

Oribi bite rate, bite mass and intake rate

I used a General Linear Model to determine if different stocking rates influenced the bite rate, bite mass and intake rate of oribi. I ran a separate model for each dependent variable (bite rate, bite mass, and intake rate) across the different stocking rates (independent variable) for each season (i.e. wet and dry). Bite rate data met the assumptions of normality, but bite mass was log transformed and intake rate was square root transformed.

Chemical analysis

Once I determined the seasonal diet of oribi, I collected grass samples (*N* = 112) of the top contributing species (> 90%) to oribi diet at each stocking rate for each season. This totalled six grass species (see Results; Table 1). Because oribi were very selective and only foraged on leaves, I only collected grass leaves for each species so the samples were a representation of what was consumed by the oribi. Furthermore, I collected these grass samples from areas in which I had observed oribi foraging. All collected grass samples were oven dried at 60°C for 48 hours and then milled.

I used Near Infrared Reflectance Spectroscopy (NIRS) to assess the crude protein content (CP) of the collected grass samples (see Appendix III for nutritional values). NIRS spectra were calibrated off a database of South African grasses that were analysed using wet chemistry by the Wallon Agricultural Research Centre, Belgium. I was able to estimate measures of CP for each sample because the averaged standardized H value (distance between a sample and the centroid of the group) was lower than or close to 3.0 for each predicted parameter (Shenk and Westerhaus 1991).

Nutritional intake rate

I determined the nutrient concentration of bites by using the estimates of CP for each grass species in the respective grass greenness category. For bites that did not contain one of the top species that was chemically analysed, the mean nutrient concentration of the analysed grasses for that grass greenness was assigned. The intake rate (g/min) of CP was determined by multiplying the nutrient concentrations of the grass by bite mass. I then established the mean nutrient concentration per foraging observation which was then multiplied by the respective bite rate to give the nutritional intake rate (g CP/min).

I ran a General Linear Model to determine if stocking rates influences the crude protein intake rate of oribi. I ran a separate model for each season (wet and dry) with crude protein intake rate as the dependent variable and stocking rate as the independent variable. In addition, to determine if cattle facilitate oribi foraging I used a General Linear Model to compare wet season crude protein intakes obtained from camps grazed by cattle and ungrazed camps with no cattle for the last few months. Crude protein intake rates were log transformed for normality.

Results

Seasonal changes in grass height and the availability of green grass

During the wet season, the average grass height for the study site was 22 cm with a range of 11–47 cm and a resulting CV (i.e. structural heterogeneity) of 53%. As the wet season progressed into the dry season some addition grass growth occurred and the average grass height increased to 29 cm with a range of 11–51 cm with a CV of 51%. In each camp, the cattle stocking rates during the wet season influenced the average grass height in each camp (Generalised Linear Model: $\chi^2 = 23.625$, $df = 2$, $P < 0.001$). As the stocking rate increased the average grass height as well as the structural heterogeneity decreased (low: 23 cm with a range of 12–37 cm and 58% CV; intermediate: 24 cm with a range of 13–47 cm and 55% CV; high: 18 cm with a range of 10–29 cm and 47% CV; see Appendix IV Figure 1). The wet season stocking rates also influenced the average grass height (Generalised Linear Model: $\chi^2 = 121.107$, $df = 2$, $P < 0.001$) and structural heterogeneity in the dry season per camp low: 34 cm with a range of 17–52 cm and 53% CV; intermediate: 34 cm with a range of 11–48 cm and 53% CV; high: 21 cm with a range of 12–30 cm and 46% CV; see Appendix IV Figure 2). Although stocking rates influenced the average grass height across camps, it did not influence the height of grass (mean ± SE) that oribi hid in to avoid predators in the wet (low = 40 ± 1.1 cm; intermediate = 41 ± 1.7 cm; high = 41 ± 1.6 cm ANOVA: $F_{2,50}$ = 0.120, P = 0.887) and the dry seasons (low = 49 ± 1.0 cm; intermediate = 47 ± 1.0 cm; high = 45 ± 1.2 cm; ANOVA: $F_{2,35}$= 2.435, P = 0.102).

The proportional availability of green grass decreased from the wet season into the dry season (Figure 2a-c). During the wet season, all camps were similar in the availability of green grass and were dominated by very green (>80% availability) and mainly green grass. However, the intensity of wet season grazing by cattle had a marked effect on the availability of green grass in the dry season. In the dry season, the camps that had low and intermediate wet season grazing had higher availabilities of green grass (35% and 32% respectively) than the high stocking rate camp (23%). In addition, the high stocking rate camp had no very green grass and was the only area that had very brown grass during the dry season.

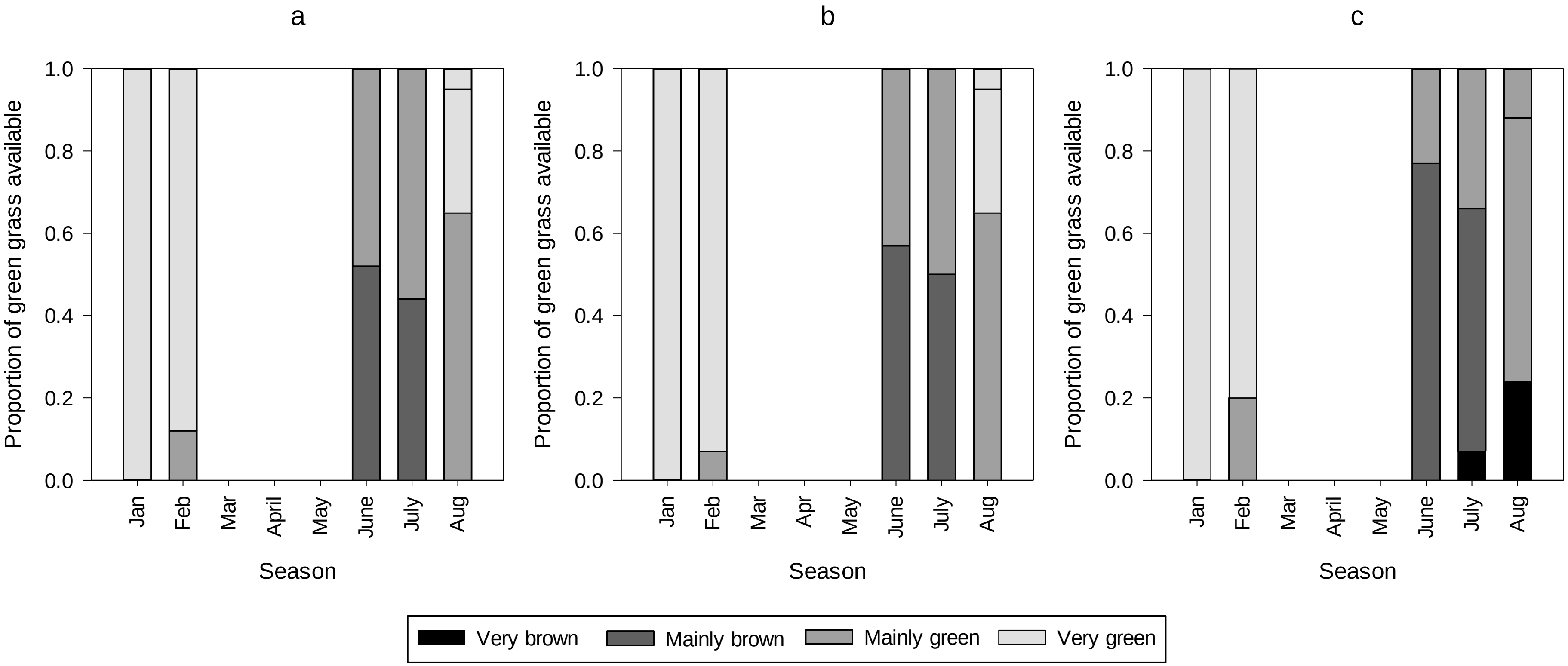

Figure 2: Seasonal differences in the availability of green grass in the different grass greenness categories across a) low stocking rate 1.7 ha/AU, b) intermediate stocking rate 1.5 ha/AU, and c) high stocking rate 0.95 ha/AU. Greenness categories are very brown 0–10%, mainly brown 11–50 %, mainly green 51–90%, and very green 91–100%. Availability was determined using the number of quadrats in each greenness category from monthly transect data (*N* = 246 quadrats for each month).

Cattle foraging behaviour

The majority of cattle diet, irrespective of stocking rates, comprised of grass species (~94%), with only a few forbs being consumed. During the wet season in the low stocking rate camp cattle consumed nine different species. However, 95% of the diet comprised of six species *H. hirta, A. junciformis, P. dilatatum, P. scrobiculatum, S. africanus* and *T. triandra*. In the intermediate stocking rate camp cattle consumed 17 species with six species *H. hirta, A. junciformis, Pennisetum clandestinum, P. scrobiculatum, Tristachya leucothrix* and *T. triandra* contributing to over 85% of the diet. Similarly, in the high stocking rate camp cattle consumed 13 species, with five species *H. hirta, S. sphacelata* var. *torta, S. nigrirostris, S. africanus* and *T. triandra* comprising over 92% of the diet. Cattle only consumed grass that was very green (91–100% green), irrespective of stocking rates. Irrespective of stocking rates, cattle selected for the same grass height (11.83 ± 0.20 cm; Generalised Linear Model: χ^2 = 0.102, *df* = 2, *P* = 0.950) and reduced grass to the same post grazing height (4.91 ± 0.10 cm; Generalised Linear Model: χ^2 = 5.147, *df* = 2, *P* = 0.076). The average cattle bite (mean ± SE) ranged from 0.11 ± 0.003 g (*N* = 45) for the smallest bites to 1.74 ± 0.05 g (*N* = 45) for the largest bites, which resulted in an average intake rate of 12.79 ± 0.73 g/min.

Grass regrowth and clipping experiment

Notably, compared to the assumed ‘low’ stocking rate camp, my data indicate that the ‘intermediate stocking rate camp’ had a slightly lower realized grazing pressure over the period of observation that resulted in a corresponding slightly greater re-growth and final grass height. As a result, the estimated average number of times a grass sward was grazed (using the clipping trial trend line) over the 38 day observation period did not match the assumed stocking rate of each camp (low stocking rate = ~4 times, intermediate stocking rate = ~3 times, and high stocking rate = ~14 times) (Figure 3). However, there was still a significant difference in the relative net regrowth of grass across stocking rates (Generalised Linear Model: $\chi^2 = 85.508$, $df = 2$, $P < 0.001$). The low and intermediate stocking rates camp had positive relative regrowth that were relatively similar (+46% and +56% respectively), whereas the high stocking rate camp showed negative growth (-20%). Furthermore, the average grass height at the end of the experiment declined with increases in stocking rates. The low stocking rate camp had an average grass height of 16.7 ± 0.55 cm; the intermediate stocking rate camp had 17.1 ± 0.56 cm and the high stocking rate camp 11.6 ± 0.39 cm at the end of the experimental period.

For the clipping experiment, relative net regrowth declined with increases in clipping frequency (Generalised Linear Model: $\chi^2 = 577.548$, $df = 3$, $P < 0.001$). The average regrowth for the no clipping treatment (+56%) and the clip every two weeks (3 clips total) treatment (+59%) were similar, but lower regrowth was obtained from the one clip (5 clips total) (+42%) and two clips a week (10 clips total) treatment (+4%).

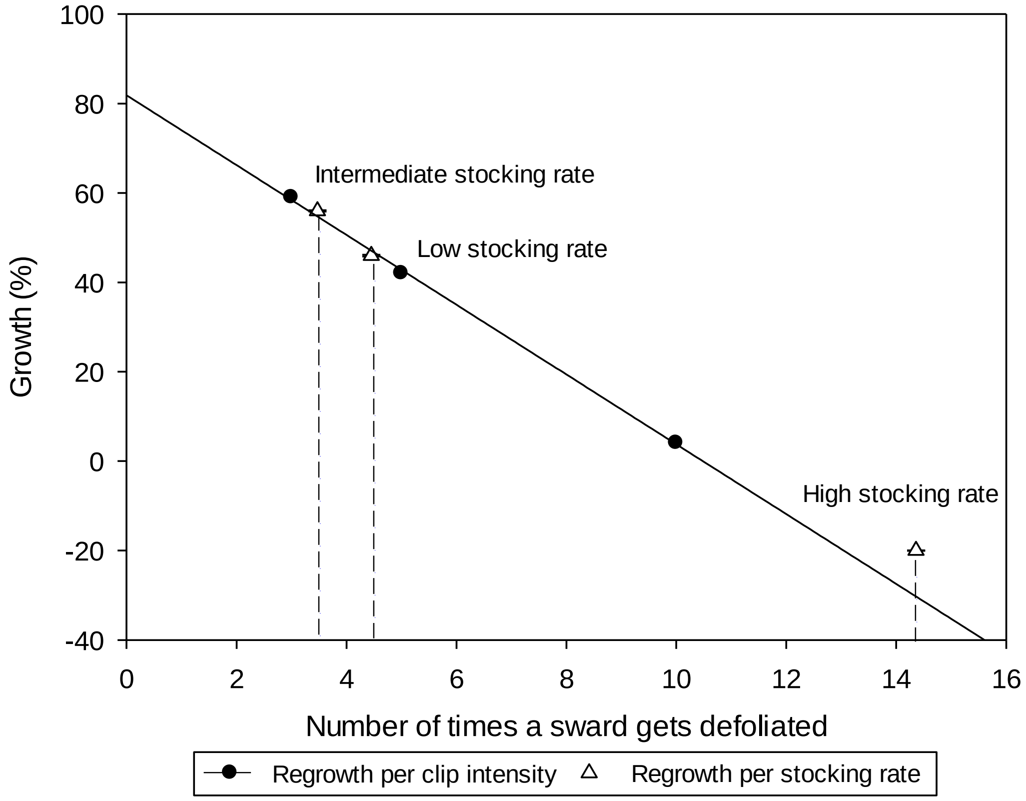

Figure 3: Comparison of the percentage growth per stocking rate to the expected regrowth under known clipping intensities (i.e. clipping experiment with different defoliation intensities). By substituting the percentage growth for each stocking rate into the trend line can be used to predict the number of times a sward was eaten in each stocking rate camp.

Oribi foraging behaviour

As with the cattle, the overall diet of oribi comprised of grass species (~96%; Table 1). During the wet season, oribi consumed 11 different species of which four made up roughly 92% of the diet. These top contributing species included *H. hirta, P. dilatatum, S. nigrirostris* and *T. triandra*. During the dry season, oribi were more selective and only consumed five species with four species *H. hirta, P. clandestinum, P. dilatatum* and *T. triandra* contributing roughly 99% of the diet. As a result, oribi expanded their diet breadth to include *P. clandestinum* as well as increase their use of *H. hirta,* which was the highest contributing species during the wet season.

In the intermediate stocking rate camp, oribi consumed five species during the wet season. Three of these species *H. hirta, S. nigrirostris* and *T. triandra* contribute to about 97% of the diet. During the dry season, oribi consumed more species than during the wet season in the intermediate stocking rate camp. Oribi consumed 7 species with 4 of these species *H. hirta, P. clandestinum, P. dilatatum* and *T. triandra* contributing 94% of the diet. The contribution of *H. hirta,* the species that contributes most to the diet in each season, remains similar from the wet season to the dry season. However, the proportional use of *P. dilatatum* and *P. clandestinum* increased in the dry season. In contrast, the contribution of *T. triandra* was reduced by half as the wet season progressed into the dry season.

During the wet season in the high stocking rate camp, oribi consumed 7 species with 3 species *H. hirta, S. nigrirostris* and *T. triandra* contributing about 96% of the diet. During the dry season, oribi consumed 6 species with 3 of these *H. hirta, H. contortus* and *T. triandra* making up about 96% of the diet. Oribi increased their utilisation of *H. hirta* and *T. triandra* in the dry season compared to the wet season. Interestingly, *H. contortus* was only a major contributor to oribi diets in the high stocking rate camp even though oribi did consume this species (~3%) in the low stocking rate camp (Table 1).

Table 1: Changes in the dietary contribution of consumed grass species from the wet into the dry season at low (1.7 ha/AU), intermediate (1.5 ha/AU), and high stocking rates (0.95 ha/AU). Species in bold represent the top contributing species to the overall diet of oribi.

	Low stocking rate		Intermediate stocking rate		High stocking rate	
	Dietary contribution (%)		Dietary contribution (%)		Dietary contribution (%)	
Grass species	Wet	Dry	Wet	Dry	Wet	Dry
Hyparrhenia hirta	63.92	88.69	79.95	72.43	35.29	57.68
Paspalum dilatatum	10.82	3.62	0.55	8.5	0	0
Setaria nigrirostris	10.57	0	4.95	0	36.65	0
Themeda triandra	6.44	2.71	12.09	6.45	21.72	24.72
Paspalum scrobiculatum	2.06	0	0	0	0	0
Tristachya leucothrix	1.8	0	0	0	0.9	0
Chloris gayana	1.55	0.9	0	1.47	0	0
Cyperaceae species	0.77	0	0	0	0	0
Eragrostis plana	0.77	0	0	0	0	0
Ledebouria species	0.77	0	0	0	0	0
Pennisetum clandestinum	0.52	4.07	0	6.74	0	0
Iridaceae species	0	0	2.47	0	0	0
Digitaria eriantha	0	0	0	0	2.71	0
Setaria sphacelata var. *torta*	0	0	0	0	1.36	0
Sporobolus africanus	0	0	0	0	1.36	2.25
Eragrostis curvula	0	0	0	1.17	0	0.74
Heteropogon contortus	0	0	0	3.23	0	14.23
Cymbopogon excavatus	0	0	0	0	0	0.37

Dietary overlap between cattle and oribi

During the wet season the highest dietary overlap occurred between cattle and oribi at the low stocking rate camp (75%), followed by the intermediate stocking rate camp (52%), and finally, the lowest overlap (44%) in the high stocking rate camp. However, the dietary overlap for the top contributing grass species was a much greater in all the camps (low stocking rate = 90%, intermediate stocking rate = 77%, and high stocking rate = 75%; Table 2). There was also a high degree of overlap when the wet season diet of cattle was compared to the dry season diet of oribi (low stocking rate = 62%, intermediate stocking rate = 55%, and high stocking rate = 40%). Again, the degree of overlap was greater when the top contributing species were compared. The low stocking rate camp had a 77% overlap, followed by the intermediate stocking rate with 74%, and 70% overlap in the high stocking rate camp. This suggests that the wet season foraging of cattle may influence the availability of top contributing grass species for oribi in the dry season.

A comparison of the dietary overlap of the top contributing species between the wet and dry season diet of oribi was lowest at the high stocking rate (62%), compared to 75% and 83% in the low and intermediate stocking rates, respectively. The low overlap highlights a larger shift in diet selection of oribi at high stocking rates. Ultimately, this was a result of oribi adding *H. contortus* into their diet during the dry season at high stocking rates (Table 1).

Table 2: Dietary contribution of the top consumed grass species for cattle and oribi and the resulting dietary overlap at low (1.7 ha/AU), intermediate (1.5 ha/AU) and, high stocking rates (0.95 ha/AU) during the wet season.

	Low stocking rate		Intermediate stocking rate		High stocking rate	
	Dietary contribution (%)		Dietary contribution (%)		Dietary contribution (%)	
Grass species	Cattle	Oribi	Cattle	Oribi	Cattle	Oribi
Hyparrhenia hirta	56.07	63.92	36.86	79.95	11.21	35.29
Paspalum dilatatum	9.82	10.82	0	0	0	0
Paspalum scrobiculatum	10.4	0	6.27	0	0	0
Aristida junciformis	8.09	0	5.49	0	0	0
Sporobolus africanus	5.78	0	0	0	7.88	0
Themeda triandra	5.20	6.44	10.2	12.09	25.15	21.72
Setaria nigrirostris	0	10.57	0	4.95	6.36	36.65
Pennisetum clandestinum	0	0	14.90	0	0	0
Tristachya leucothrix	0	0	7.06	0	0	0
Setaria sphacelata var. *torta*	0	0	0	0	42.12	0
Dietary overlap	90%		77%		75%	

Grass height and grass greenness of consumed species

Although cattle fed on similar grass heights across camps (12 ± 0.2 cm), the different stocking rates significantly influenced the grass height that the oribi selected (Generalised Linear Model: $\chi^2 = 435.354$, $df = 2$, $P < 0.001$). As the stocking rates increased, oribi fed on taller grass swards. In the lowest stocking rate camp, oribi selected grass that was 12 ± 0.15 cm, followed by 13 ± 0.17 cm in the intermediate stocking rate camp. In both these camps, oribi and cattle selected for the similar grass heights (cattle: 11.83 ± 0.20 cm). However, the low relative growth rate caused by heavy utilisation of short grass in the high stocking rate camp, caused oribi to shift and feed on taller grass swards, including *H. contortus*, that were 18 ± 0.31 cm (Figure 4a).

The wet season cattle grazing significantly influenced the grass height that oribi consumed during the dry season (Generalised Linear Model: $\chi^2 = 33.726$, $df = 2$, $P < 0.001$). Oribi in the low and intermediate stocking rate camps increased the sward height in which they fed (low: 20 ± 0.57 cm, intermediate: 20 ± 0.45 cm) compared to the wet season. However, in the high stocking rate camp, oribi maintained their feeding on the same sward height as they did in the wet season and fed from grass that was 17 ± 0.43 cm (Figure 5a).

When the availability of green grass was high in the wet season, both oribi and cattle only consumed grass that was very green (91–100%), irrespective of stocking rates. The higher removal of biomass in the high stocking rate camp in the wet season (lower relative regrowth) influenced the availability of green grass in the high stocking rate camp in the dry season (Figure 2). This is reflected in the difference in the proportion of green grass used by oribi in the dry season (ANOVA: Proportion of green grass consumed x stocking rate: $F_{2,12} = 11.558$, $P = 0.002$). In the low and intermediate stocking rate camps, oribi had similar proportions of mainly green (0.65 and 0.64 respectively) and very green grass (0.35 and 0.36 respectively) in their diet. Although oribi in the high stocking rate camp also consumed mainly green and very green grass, their proportional use of mainly green grass increased to 0.99, while the low availability of very green grass reduced the proportional use to 0.01.

Bite rate, bite mass and intake rate

The presence of cattle at different stocking rates during the wet season had a significant effect on bite mass (ANOVA: $F_{2,970} = 4.353$, $P = 0.013$, Figure 4b) and bite rate (ANOVA: $F_{2,36} = 6.143$, $P = 0.005$, Figure 4c) of oribi during the wet season. In the low stocking rate camp, oribi took large bites, despite feeding on short grass, as well as maintaining a high bite rate. In the intermediate stocking rate camp, oribi achieved the lowest bite mass because of the short grass they were consuming. As a result, oribi achieved a high bite rate. In the high stocking rate camp, oribi took large bites because of the tall grass they were feeding on, but maintained low bite rates. Although stocking rate influenced the bite rate and bite mass of oribi during the wet season, it did not result in significant differences in the dry matter intake rate of oribi in the different camps (ANOVA: $F_{2,36} = 1.865$, $P = 0.170$, Figure 4d).

During the dry season when the cattle were absent, the previous wet season stocking rates resulted in oribi obtaining different bite masses in the different camps (ANOVA: $F_{2,826} = 4.765$, $P = 0.009$, Figure 5b). Specifically, oribi in the low and intermediate stocking rate camps achieved similar bite masses (Tukey’s Post hoc test: $P = 0.935$). In the high stocking rate camp, oribi had smaller bites than in the low and intermediate stocking rate camps, even though they fed on similar grass heights.

However, there was no significant difference in the bite rate of oribi across stocking rates (ANOVA: $F_{2,60} = 0.922$, $P = 0.403$, Figure 5c). In addition, the wet season stocking rates did not influence the dry matter intake rate of oribi during the dry season (ANOVA: $F_{2,60} = 2.563$, $P = 0.085$, Figure 5d).

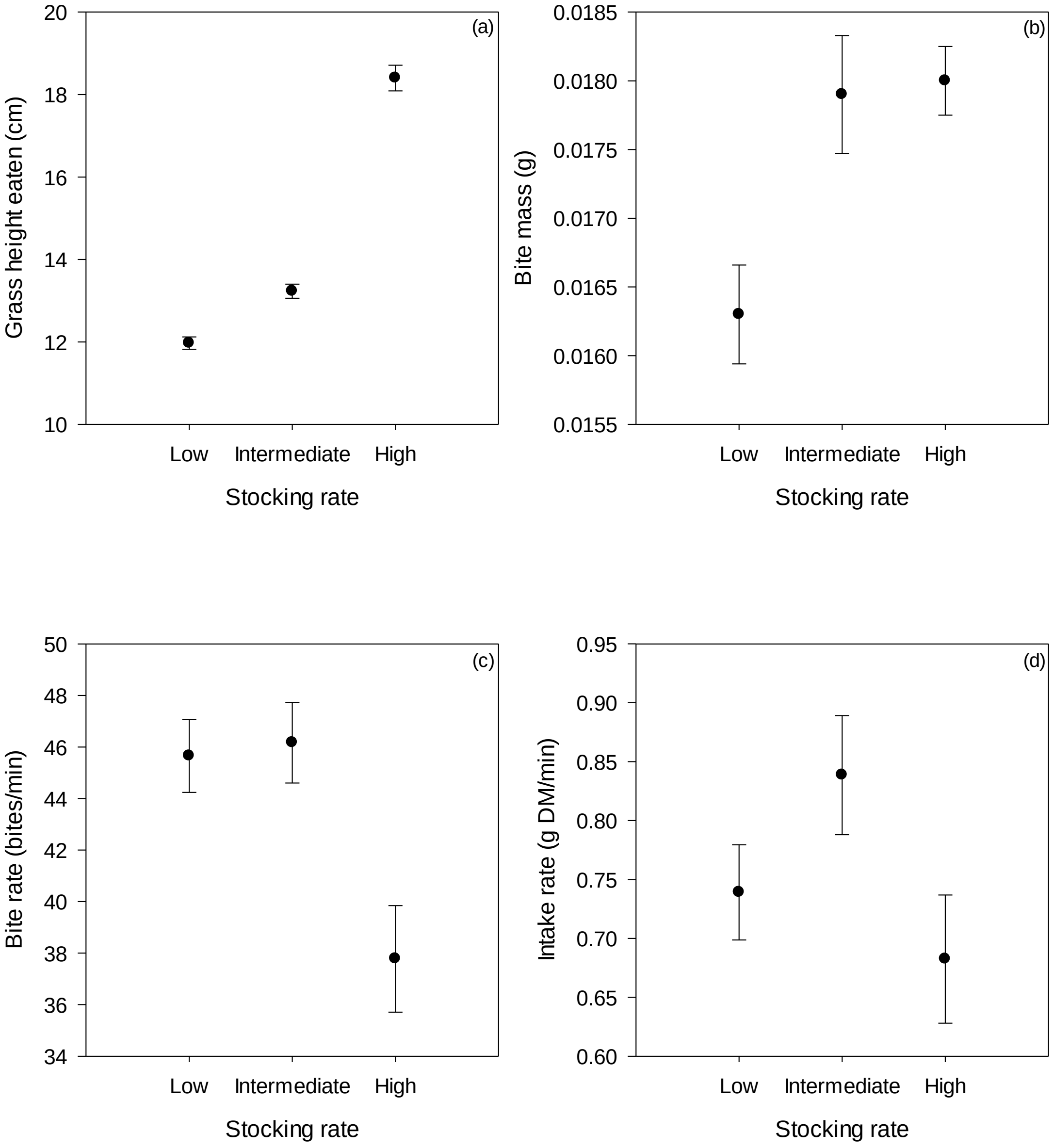

Figure 4: Average (mean ± SE) for a) grass height eaten, b) bite mass, and c) bite rate, and d) intake rate of oribi at low (1.7 ha/AU), medium (1.5 ha/AU) and high stocking rates (0.95 ha/AU) during the wet season..

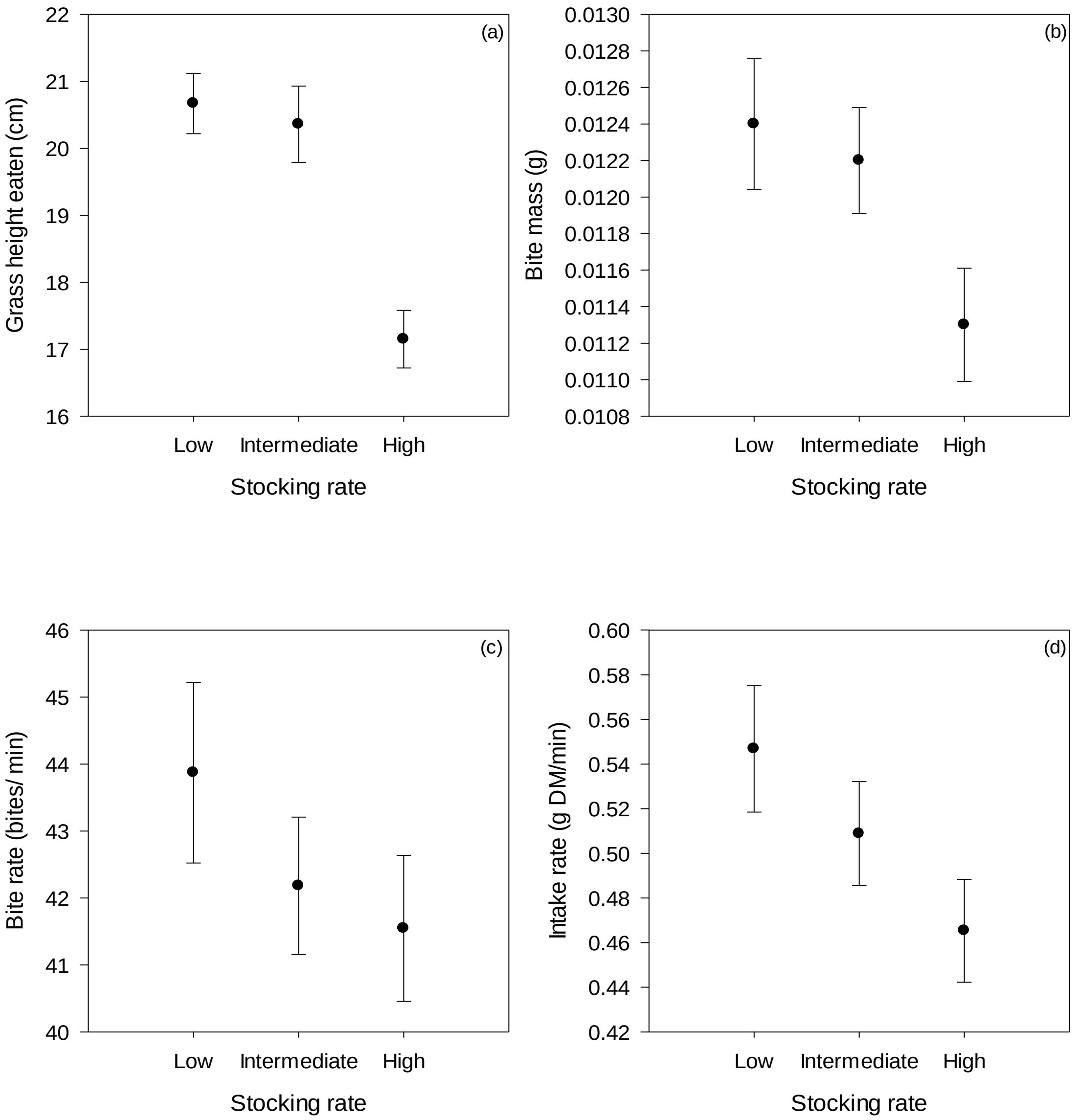

Figure 5: Average (mean ± SE) for a) grass height eaten, b) bite mass, c) bite rate, and d) intake rate of oribi at low (1.7 ha/AU), medium (1.5 ha/AU) and high stocking rates (0.95 ha/AU) during the dry season.

Nutritional intake rate of oribi

During the wet season, oribi obtained similar crude protein intake rates irrespective of the different cattle stocking rates (ANOVA: $F_{2,36} = 0.002$, $P = 0.998$, Figure 6a). When oribi fed in camps grazed by cattle they maintained higher crude protein intake rates (0.07 g CP/min) compared to when foraging in a camp not grazed by cattle (0.05 g CP/min) during the same period (ANOVA: $F_{1,44} = 12.832$, $P < 0.001$). Thus, cattle facilitated oribi in the wet season.

Although cattle were removed from the camps during the dry season, the greater removal of biomass, and possibly green leaves, at high stocking rates in the previous wet season significantly influenced the crude protein intake of oribi during the dry season (ANOVA: $F_{2,60} = 3.543$, $P = 0.035$, Figure 6b). Oribi that foraged in the camp that had high summer stocking rates obtained the lowest mean CP intake rates (0.29 g CP/min), while oribi obtained higher, but similar crude protein intake rates when feeding in camps with low (0.40 g CP/min) and intermediate (0.40 g CP/min) summer stocking rates (Tukey's Post hoc test: $P = 0.997$).

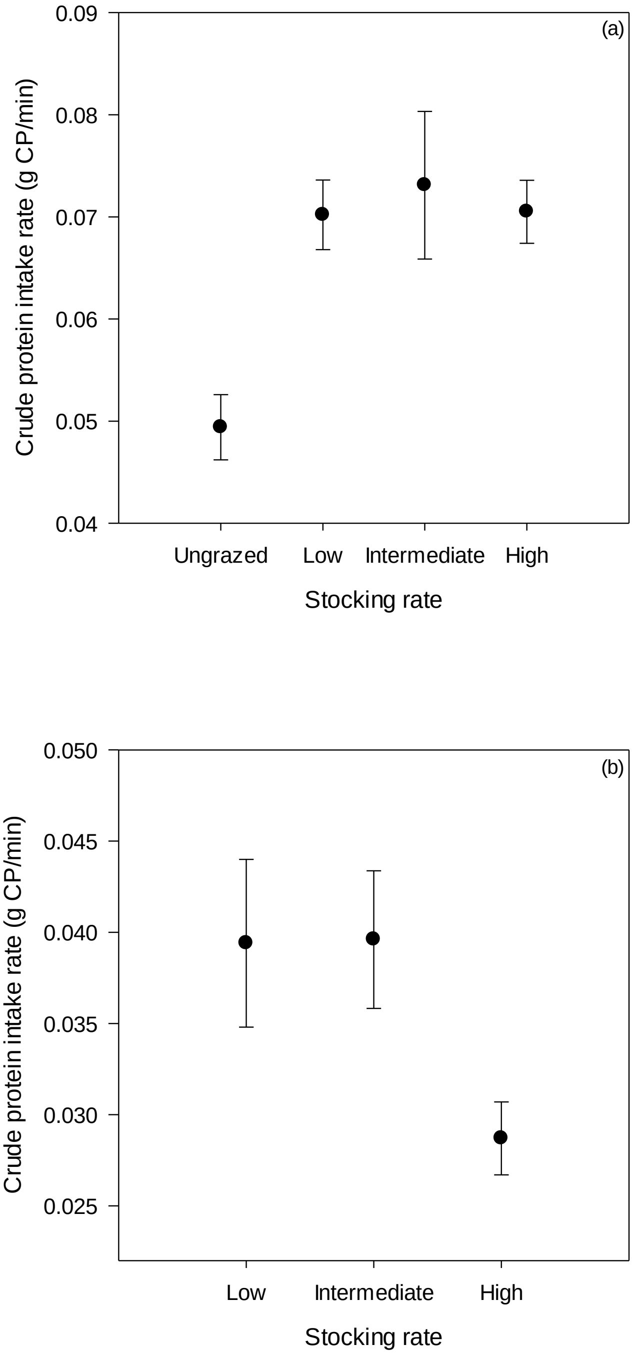

Figure 6: Average (mean ± SE) crude protein intake rate of oribi at low (1.7 ha/AU), medium (1.5 ha/AU) and high stocking rates (0.95 ha/AU) during a) the wet season, and b) the dry season. The wet season also includes the crude protein intake that oribi obtained when cattle grazing was absent, indicating the degree of facilitation obtained through grazing cattle.

Discussion

Resource partitioning due to body size and mouth morphology are means to reduce potential interspecific competition (van Wieren and Bakker 2008). Large and small herbivores should be able to co-exist due to differential use of resources. However, my results show that oribi and cattle largely utilise the same grass species, greenness categories, and feed from grass of similar heights during the wet season. At low and intermediate stocking rates, oribi and cattle do not compete with each other because their shared grass species were not limited. During my study, cattle grazing facilitated oribi grazing by providing high quality regrowth. Furthermore, the low stocking rates resulted in sufficient net regrowth that allowed both oribi and cattle to share the same grass species. However, in the high stocking rate camp, oribi had to adjust their foraging behaviour and shifted to consume taller grass swards and species not being used by cattle. Despite feeding on taller grass, oribi maintained the same nutritional intake as oribi in the lower stocking rate camps by selecting for green leaves in the taller swards. High intensity wet season grazing by cattle significantly reduced the nutritional intake of oribi by reducing available biomass of high quality grass of the top consumed species in the dry season. Although cattle facilitate and compete with oribi for food, their ability to change landscape structure reduced the structural heterogeneity of grasslands in both the wet and dry season, potentially increasing the perceived predation risk of oribi (see Chapter 4).

Changes in habitat structure as a result of cattle grazing can result in facilitation or competition with oribi. Structural heterogeneity is a key component in oribi habitat selection (see chapter 4). Oribi require both short and tall grass, with the distribution of tall grass influencing the feeding intensity or oribi. As the distance from tall grass increases, the utilisation of these areas for feeding decreases (see Chapter 4), due to an increase in perceived predation risk (e.g. Kotler et al. 1994). During the wet and dry season, increasing cattle stocking rates decreased overall grass height, and the resulting structural heterogeneity. This reduced structural heterogeneity was a result of an overall shorter grass height and larger areas of short grass (<15 cm) due to high intensity grazing (See Appendix II Figure 1 and 2). As a result, this reduced heterogeneity may influence the distribution and the amount of suitable foraging habitat for oribi because of the greater distance between tall grass patches. Interestingly, the differences in grass height and structural heterogeneity across stocking rate camps did not significantly influence the height of grass that oribi hid in to avoid predators. This could be due to two reasons. First continuous grazing creates areas of heavily grazed patches interspersed with intermediate and ungrazed patches (Fuhlendorf and Engle 2001). These ungrazed patches persist even at higher stocking rates because cattle repeatedly select for the same grazing areas, although they may be more spatially dispersed across the landscape. Secondly, oribi physically seek out tall grass for predator avoidance, and select for the tallest grass available.

Although cattle and oribi fed largely on the same species, and selected for the same grass greenness categories at the low and intermediate stocking rates, there was no evidence of competition. This is evident in that oribi obtained the same nutritional intake rate across these two stocking rates. Ultimately, the net regrowth in the low and intermediate stocking rates allowed both oribi and cattle to feed on the same species, greenness and grass height with limited to no competition because grass regrowth was not a limiting resource (Putman 1996; Mysterud et al. 2001). In fact, the net regrowth during the wet season from grazing cattle facilitated oribi foraging by providing them with an increase in availability of high quality vegetation.

Similarly, in the high stocking rate camp, there was a large overlap in the diet of cattle and oribi as well as the grass greenness both herbivores selected. However, the higher stocking rates resulted in a lower net growth rate. Therefore, cattle were reducing the grass height faster than any regrowth could occur, thus preventing oribi from utilising this resource. As a result, oribi shifted their foraging behaviour and fed on taller grass and grass species not being used by the cattle. Although oribi fed from taller grass, there were no significant differences in dry mater intake rate and nutritional intake rates across the different stocking rate camps. This may be due to the selective feeding of the oribi.

Herbivores with narrow muzzles, such as topi (*Damaliscus lunatus*) and mountain reedbuck (*Redunca fulvorufula*) feed mainly on medium to tall grass by selectively feeding on green leaves (Irby 1977; Murray and Illius 2000). Oribi feed in the same way (Oliver et al. 1978; Reilly et al. 1990), which likely explains why they were able to maintain their nutritional intake rate even when feeding on taller grass in the high stocking rate camps. Oribi are able to take small bites and can feed most effectively in relatively tall grass by selecting for green leaves (Owen-Smith 1985). My results suggests that due to the small bite size of oribi, they can utilise both short (~10 cm) and taller grasses (>20 cm) just as efficiently. Because oribi shifted their foraging to where they fed from vegetation not being used by cattle, suggests that the cattle directly competed with oribi at high stocking rates during the wet season. However, the ability of oribi to forage selectively and only consume green leaves likely allowed them to compensate for not being able to feed on their preferred species. As a result, by restricting their feeding to green leaves of less preferred species, they were able to achieve the same nutritional intake as oribi feeding at lower stocking rates.

During the dry season, oribi and cattle do not interact. However, the wet season grazing by cattle significantly reduced the nutritional intake of oribi at high stocking rates during the dry season. This is due to a number of reasons. Firstly, the wet season cattle foraging influenced the structural component of each stocking rate camp and the grass height that oribi consumed. In the low and intermediate stocking rates, oribi shifted and fed on taller grass swards compared to the wet season. A possible explanation for this is both cattle and oribi utilised shorter grass in the wet season, thereby reducing the food availability in these shorter swards. In contrast, the lower utilisation of taller swards during the wet season meant that leaves (and even green leaves) were still available on these taller swards during the dry season. As a result, oribi shifted to feed from this taller grass to maintain their nutritional intake by feeding on available green leaves. In contrast, in the high stocking rate camp, oribi were unable to utilise short grass in the wet season because of the heavy grazing. Thus, oribi were forced to feed on the remaining tall grass swards avoided by the cattle. Then, in the dry season oribi continued to use these tall grass swards as this provided the only source of food. However, the continued use of these taller swards likely reduced the availability of green grass, especially during the dry season when grasses are dormant (Murray and Illius 2000).This may explain why oribi expanded their diet breadth to include previously avoided grass species of both oribi and cattle.

Secondly, high cattle stocking rates in the wet season can result in competition through exploitation. In the wet season, cattle only selected for very green grass and the low net regrowth of heavily grazed swards suggests cattle can exclude oribi by reducing the availability of certain grass species though the removal in biomass (Treydte et al. 2013). Furthermore, there is a high overlap of the top consumed species of oribi and cattle. This suggests that the wet season foraging of cattle can reduce the availability of preferred species for oribi to consume in the dry season. As a result of this lingering competitive effect, oribi showed the greatest shift in species selection in the high stocking rate camp. The reduced availability of top consumed species for oribi, caused by cattle grazing, resulted in oribi adding *H. contortus* into their diet in the late dry season. Oribi included *H. contortus* into their diet because it was not consumed by cattle in the wet season, and was therefore high in abundance in the dry season. Similarly, a study on the mountain ungulate bharal (*Pseudois nayaur*) showed that a high dietary overlap with cattle resulted in a shift in the diet of the bharal (Mishra et al. 2004). In winter, the depletion in grass availability due to cattle caused bharal to select for herbs, while cattle remained feeding on grass. The fact that oribi maintained their dry matter intake rate across stocking rates, but had lower nutritional intake rates in the high stocking rate camp, highlights that the major effect of competition on oribi was the reduction in the availability of high quality food.

The good fit between the net regrowth obtained between the clipping experiment and the stocking rate camps provides confidence that differences in sward performance was due to differences in cattle grazing intensities. As a result, this experimentally derived relationship between grazing pressure and regrowth is potentially a general tool that can be applied to other bulk and selective feeders that co-exist with oribi. For example, oribi commonly coexist with zebra, wildebeest and impala. During the wet season in the Serengeti-Mara region of East Africa, wildebeest were observed feeding on grass swards 10 cm tall, while zebra and impala utilised grass 25 cm tall (Sinclair

1985). During the dry season, wildebeest and zebra increased their use of taller grass ranging from 10–25 cm and 50 cm, respectively. In contrast, impala utilised shorter grass about 10 cm in height. This range of grass used by other species throughout the wet and dry seasons limits the ability of oribi to shift and feed in taller grass like they did in the high stocking rate camp in the wet season. These seasonal shifts in preferred grass height have been found in other parts of southern Africa as well (e.g. Voeten and Prins 1999; Arsenault and Owen-Smith 2008). This highlights the potential for competition in areas where oribi coexist with a range of other mammalian herbivore species.

In the regrowth experiment per stocking rate, the realized grazing pressure and sward regrowth did not rank with stocking rate. Intermediate stocking rates had the lowest measured grazing pressure and the highest sward regrowth. A potential reason for this is that at low and intermediate stocking rates, cattle do not graze uniformly over the landscape, which is common for continuous grazing systems (Fuhlendorf and Engle 2001). At the high stocking rate camp, the average number of times a sward was defoliated was very high. The high stocking rate is roughly double the low and intermediate camps. As a result, you would expect the sward to be eaten twice as much. However they were eaten ~5 times as much. A possible explanation is that the observed regrowth may not be entirely due to direct defoliation, but the long term heavy grazing could potentially influence regrowth after defoliation. An experiment using *T. triandra* showed that swards in areas of intensive grazing showed lower regrowth potential than swards in non-grazed patches at the start of the wet season (Lutge et al. 1996). This could be an important factor for high intensity rotational grazing systems where heavy grazing reduces the rate of regrowth even after cattle have been removed.

Rainfall is an important factor that can influence the nature of interspecific interactions between herbivores. During the study period, cattle and oribi did not compete during the wet season because grass regrowth was not a limiting factor, and there was enough green grass in taller swards in the high stocking rate camp. However, during drought years, grass regrowth could become limiting so that competition occurs irrespective of stocking rates. Furthermore, the availability of green grass in taller swards may also be reduced due to the drought conditions. Alternatively, the availability of tall grass could be reduced if cattle shift and feed on tall swards in response to a reduction in grass regrowth. Therefore, oribi would not be able to shift and feed on the taller grass swards as they did during the study period. During the dry season, the availability of green grass would be even lower because of the wet season grazing by cattle. Therefore, I would expect competition to occur in all camps, with the highest degree of competition occurring in the high stocking rate camp.

Conclusions

Despite differences in body size and mouth morphology, cattle competed with oribi. This was a result of competition for food resources and structural changes to the environment. The nature of interspecific interactions (i.e. competition and facilitation) for resources was seasonal and density dependant. Competition due to structural differences in heterogeneity as a result of cattle was also density dependent and occurred in both seasons. Therefore, there is a trade-off between competition and facilitation. Oribi survive and reproduce in the high stocking rate camp (pers. obs.), so the benefits obtained through facilitation may outweigh the costs of competition. This may be due to the productivity of the farm as a result of rainfall and mild winters. In less productive areas, however, competition may be more severe and may outweigh the benefits of facilitation. Oribi are predominantly found in areas with cattle. My results suggest that cattle can negatively affect oribi populations through their competitive interactions, especially at high stocking rates. Competition occurs through the removal of food, and structural changes that can influence habitat use and potential predation risk.

CHAPTER 4

Increases in food availability can result in oribi antelope taking greater risks at both large and small spatial scales

Differences in food availability and predation risk across habitats can influence how herbivores utilise landscapes. As a result, trade-offs between the costs and benefits associated with a certain habitats will influence habitat and patch selection. To determine how oribi antelope (*Ourebia ourebi*) weigh up these costs and benefits when making both large- and small-scale foraging decisions, I measured patch level foraging decisions using artificial foraging patches and measuring giving up densities (GUDs). First, I determined large-scale habitat use and second explored how patch variables (e.g. aspect, slope, distance to cover, sight lines, and distance to ambush sites) explained patch use within habitats. When the availability of food within patches across the different habitats was equal, oribi preferred to feed in short and tall grasslands and avoided woodlands. Furthermore, the avoidance of woodlands extended out into the surrounding grasslands resulting in oribi feeding less intensively in grassland areas within 15 m of the woodlands. Within the grassland habitats, oribi preferred to feed in patches close to tall grass (i.e. escape cover) and where they could see beyond 2 m, irrespective of slope or aspect. These results suggest that oribi select habitats and patches in relation to perceived predation risk (i.e. predation costs outweigh potential food intake benefits). However, when I increased food availability within woodlands, oribi increased their large-scale risk-taking behaviour and fed in the unsafe woodlands. Furthermore, this increased risk-taking extended to small-scale foraging decisions whereby within these woodlands oribi fed closer to potential ambush sites and ate more

from these patches as food availability increased. Ultimately, these results highlight how changes in food availability can determine the degree to which herbivores are willing to increase their risk-taking behaviour, and how these changes can affect overall landscape use.

Introduction

Animals do not utilise landscapes uniformly because of spatial and temporal variability in the quality and availability of food (Milne et al. 1989; Whittingham et al. 2006). Availability and the quality of food, coupled with differences in perceived predation risk associated with landscape features (Shrader et al. 2008; Druce et al. 2009) drive animals to favour some areas more than others (Cowlishaw 1997). Animals utilise habitats according to their foraging efficiency (Langvatn and Hanley 1993) and the perceived predation risk of that habitat (Creel et al. 2005). This spatial utilisation of the landscape in response to perceived predation risk is termed a ‘landscape of fear’ (Laundré et al. 2001). However, utilisation of areas can vary temporally because both food availability and predation risk are not static, but rather vary over both space and time (Lurz et al. 2000; Tolon et al. 2009).

A number of studies have shown that perceived predation risk is the driving force behind habitat selection (e.g. Hernández and Laundré 2005; Abu Baker and Brown 2012). For desert rodents, the predation cost of foraging was more than 75% of the total foraging cost (Brown et al. 1994). As a result, many animal species avoid high quality, high risk habitats and spend more time foraging in safer, poor quality habitats to reduce predation risk. For example, desert baboons (*Papio cynocephalus ursinus*) spent more time foraging in safer environments compared to risky habitats (Cowlishaw 1997). In addition, baboons displayed the same pattern of habitat use when resting and grooming, which is consistent with an anti-predator strategy (Cowlishaw 1997).

Habitats vary in their cost of predation due to structural differences (i.e. cover versus no cover) and predator abundance. As a result, the behavioural response of many species to predation risk is to avoid certain habitats or to alter their use of habitats because habitat structure affects visibility (Tchabovsky et al. 2001), ease of escape (Lima 1992) and ambush opportunities of predators (Hopcraft et al. 2005). When mule deer (*Odocoileus hemionus*) were subjected to predation risk by mountain lions (*Puma concolor*) they responded to predation risk by biasing their feeding efforts at the scale of habitats and microhabitats and by altering their habitat-specific patterns of vigilance behaviour (i.e. higher vigilance in risky habitats such as forest edges)(Altendorf et al. 2001).

Additionally, within habitats, a herbivore’s perception of safe and unsafe areas may change over short distances as a result of different terrain features affecting the risk of predation. For example, the gully depth next to an adjacent foraging site influenced the feeding intensity of elk (*Cervus elaphus*), with feeding intensity decreasing as the gulley depth increased (Ripple and Beschta 2003). Deep gullies can influence the ability to detect a predator as well as decrease the probability of escaping a predator if attacked (Ripple and Beschta 2003).

When different habitats within a landscape differ in their predation risk, this may result in distinct boundaries between these habitats (Abu Baker and Brown 2012), especially if one habitat is avoided (i.e. higher risk) and the other is preferred (i.e. lower risk). Furthermore, the properties of the avoided habitat may have negative effects that extend beyond the avoided habitat into the preferred habitat (Lidicker 1999). For example, four-striped grass mice (*Rhabdomys pumilio*) avoided wooded patches even when they provided feeding opportunities due to their high foraging costs (Abu Baker and Brown 2012). In addition, the negative effect of the wooded patches extended 1–3 m into the surrounding suitable habitat. Similarly, mule deer utilised edge habitats less and obtained higher vigilance levels compared to open and wooded habitats, which suggests that deer are responding to an increased predation risk in edge habitats (Altendorf et al. 2001).

Food quality and availability can also influence habitat and patch use (Langvatn and Hanley 1993). Wilmshurst et al. (1995) found that wapiti (*Cervus elaphus*) selected for grass patches where they could maximise their daily rate of energy gain. However, this energy gain was constrained by both grass biomass and grass fibre content. As a result, wapiti fed on patches with an intermediate biomass, yielding the highest rate of daily energy gain (Wilmshurst et al. 1995). Langvatn and Hanley (1993) found that red deer (*C. elaphus*) selected patches in relation to protein gain. However, a re-evaluation of their findings showed that patterns of patch use by red deer were better explained by simultaneous increases in both protein and energy intake (Wilmshurst and Fryxell 1995). As a result, behavioural preferences for favourable foraging conditions can help explain patterns of seasonal aggregations in herbivores (Wilmshurst et al. 1995) and habitat selection (Bjørneraas et al. 2012).

Interestingly, some habitats have contrasting functions. For example, woodlands can have high levels of predation risk (Altendorf et al. 2001), but may also provide higher quality vegetation to grazers (i.e. islands of fertility) (Belsky et al. 1989). An experiment in eastern and southern Africa found that the sub-canopy grass layer had higher leaf nitrogen and phosphorous content, as well as a more favourable grass structure (lower ratios of stem: leaf biomass and dead: living leaf material), compared to grasses outside the canopy (Treydte et al. 2007). Foraging animals tend to select for the higher quality sub-canopy grass, which may be particularly important for rare antelope species (Treydte et al. 2007).

A number of studies have shown that habitat choice of foragers is a compromise between safety and food reward (reviewed in Lima and Dill 1990). Therefore, a forager may feed in an area where it obtains a lower energy gain if it also receives lower predation risk, instead of foraging in a manner that maximises energy gain or food acquisition. Alternatively, a forager may feed in a risky habitat if it offers greater benefits (i.e. higher energy gains). To do this, a forager must assess risk in terms of energy or other resources (Brown and Kotler 2004). As a result, I can ask, under what circumstances will the potential food benefits outweigh the potential predation costs? By asking this, I can explore the conditions under which animals are willing to increase risk-taking behaviours. For example, an experiment using two gerbil species (*Gerbillus allenbyi* and *G. pyramidum*), Kotler and Blaustein (1995) showed that gerbils preferred bush (i.e. lower GUDs) to open microhabitats. However, as the quality of the risky open habitat increased, so did the use of these patches. For the gerbils, the benefits in the risky open habitat had to be 4 to 8 times richer than the bush microhabitat for these two habitats to be of equal value and for the gerbils to display risky behaviour and feed from the better quality patch (Kotler and Blaustein 1995).

To test the influence of predation risk and food availability on habitat selection I focused on habitat use by oribi antelope (*Ourebia ourebi*). Oribi are a suitable species to explore these factors because they are susceptible to a range of predators (e.g. caracal (*Caracal caracal*) and black-backed jackal (*Canis mesomelas*)) due to their small size (~14 kg), and food quality and availability have been shown to influence habitat selection (Brashares and Arcese 2002). Because both predation risk and food availability are important to oribi, this provides us with an opportunity to determine how changes in risk and food availability influence habitat selection as well as the foraging intensity within habitats.

In this study, I aimed to quantify patterns of habitat use of oribi across different scales and relate these choices to food abundance and perceived predation risk. Furthermore, I aimed to determine how oribi trade-off between food and perceived predation risk and how increasing food availability influences this trade-off. I tested landscape use across two scales: 1) large-scale habitat use and 2) small-scale within habitat patch use. In addition, at the patch scale, I explored how patch variables affected foraging within the patches. I predicted that when food availability was similar between two habitats, but predation risk differed, oribi would select habitats with the lowest predation risk. Furthermore, I predicted that oribi would utilise safe habitats with poor food patches over risky habitats with good food patches. At the smaller patch scale, I predicted that oribi would avoid feeding in patches where landscape variables (e.g. slope, distance to cover) increased predation risk. Alternatively, if food availability was the main driver, I predicted that oribi would utilise high risk habitats when they provided good quality patches. Moreover, the small-scale selection of patches would depend on food availability within a patch and not the landscape variables that may increase predation risk. Finally, if the benefits of food availability eventually outweigh the potential costs of predation, I predicted that as patch quality increased within risky habitats, there would eventually be a break point where oribi will increase their risk-taking behaviour. In addition, this increase in risk-taking behaviour may be reflected in both large-scale habitat selection and small-scale patch selection within habitats.

Methods

Study site

I conducted these experiments from 1 June to 30 August 2013 at Arundel Farm (~770 ha) in Ixopo, KwaZulu-Natal, South Africa (S 30°11.557 E 30°12.199). The majority of the property (~ 700 ha) is comprised of grasslands consisting of a mosaic of short and tall grass dominated by species such as *Aristida junciformis*, *Hyparrhenia hirta*, *Themeda triandra* and *Sporobolus africanus*. However, throughout the grasslands, there are scattered woodland areas. These areas have a ground layer of grass including *Pennisetum clandestinum, Paspalum dilatatum, Hyparrhenia hirta*, *Aristida junciformis, Themeda triandra* and *Sporobolus africanus* while *Acacia karroo*, *A. nilotica, A. mearnsii*, *Rhus rehmanniana*, *Ziziphus mucronata and Rubus cuneifolia* dominate the woody component. Woody species vary in size from small shrubs (~1.5 m) to large trees (2–6 m). Other herbivores found on the farm include common duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*), impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), reedbuck (*Redunca arundinum*), zebra (*Equus quagga*) and bushpig (*Potamochoerus larvatus*). Potential predators include black-backed jackal, caracal, and stray/feral dogs (*C. familiaris*). Black-backed jackals have a bigeminous activity pattern (crepuscular and nocturnal periods) and are cursorial pack hunters (Kaunda 2000). In contrast, caracal are solitary and mainly nocturnal hunters that stalk and ambush their prey (Kingdon 1997).

I conducted this experiment across three sites within the property. Sites were separated by at least 1 km, which is greater than the year-round territory size of 0.1–0.9 km^2 for male oribi (Brashares and Arcese 1999). This ensured that each site contained a separate group of oribi (site 1: N = 3 oribi; site 2 and 3: N = 4 oribi) and thus data were independent. At each site, I tested three habitats: short grass, long grass, and woodland habitats. These habitats differed in their potential predation risk. Only three photos (from trail cameras) across the sites captured predators in grasslands compared to eleven photos of predators in woodlands.

Giving up densities

To determine large-scale habitat use and small-scale patch use, I measured giving up densities (GUDs) in artificial patches (Brown 1988). A giving up density is the amount of food that a forager leaves behind after it has ceased feeding in a patch (Brown 1988). Thus, lower GUDs (i.e. greater feeding effort) reflect greater preference (Brown and Kotler 2004). An advantage of using GUDs is that they provide a quantifiable measure of the costs of feeding within a patch (Brown 1988, 1992). Theoretically, a forager should feed in a patch until its harvest rate no longer compensates for the energetic (C), predation (P), and missed opportunity costs (MOC) of foraging in that patch ($H = C+P+MOC$) (Brown 1988, 1992). Given that harvest rate is a function of patch quality, GUDs are a reflection of the forager’s quitting harvest rate (Schmidt et al. 1998). Because artificial patches are set up the same (i.e. same amount of food and diminishing returns), they can be set out across the landscape to determine both spatial and temporal differences in perceived costs (Druce et al. 2009). Moreover, by manipulating habitat characteristics and then measuring GUDs, it is possible to understand how different landscape features affect foraging decisions (Morris et al. 2009).

Prior to the start of the experiments, I habituated the oribi to the artificial food patches. I did this by exposing the oribi to these patches and used camera traps to identify consistent oribi foraging before I started the experiments. The artificial patches consisted of plastic trays (500 x 340 x 120 mm) with a 1 x 2 grid of 2 mm galvanized wire over the top of each tray. To create diminishing returns (Kotler and Brown 1990), I filled each patch with 9 L of an inedible medium of dried corncobs. For all experiments, I put in 300 g of commercial sheep pellets (Complete Sheep Finisher, Meadow Feeds, South Africa) into each patch. Because other herbivores were present in the study site, I used trail cameras (Bushnell Trophy Cam) in the habituation period as well as throughout the experiments to ensure that I only measured the GUDs of oribi. In addition, each camera trap was positioned an a pole ~1 m above the ground a few meters from a feeding tray to avoid changes in foraging behaviour caused by the camera. Because multiple experiments were run at the same time, each experiment had two cameras. However, these cameras were orientated on opposite sides of the experimental area to cover as many GUDs as possible.

Large-scale habitat use

To test for habitat selection, I placed a 3 x 3 grid of artificial patches in three different habitat types at each site replicated across the three sites (i.e. $N = 9$ grids of artificial patches). Within each grid, I spaced the different artificial patches 15 m apart. Habitats comprised, 1) long grass that ranged from 38–113 cm in height, 2) short grass ranging between 5–28 cm in height, and 3) woodland areas that contained both grass and trees. Within the woodlands, which ranged from 0.36 ha–0.72 ha in size, shrubs and broken branches provided potential ambush sites for predators and reduced visibility for oribi, which could potentially increase perceived predation risk (Lima and Dill 1990).

Small-scale patch use

Within all three habitat types, I recorded patch variables that could influence foraging decisions at each tray within the grids. These variables included aspect (North, East, South, West) and slope (0–5°, 6–10°, 11–15°, 16–20°, >20°), sight lines (i.e. whether the visibility from the patch was blocked within a 2 m radius of the patch by tall grass or shrubs –yes or no), and distance to escape cover (long grass).

To determine the influence of patch variables on oribi foraging, I collected data for seven consecutive days. I obtained GUDs by leaving the artificial patches out for 24 hours. At ~7h00 the following day, I then sifted out the remaining food and refilled the patches with 300 g of food. I then weighed the remaining food in each patch to determine the GUD.

Fear of woodlands

Wooded areas were highly avoided (see Results). As a result, I tested to see if the avoidance of these areas extended into the surrounding grassland habitats. To do this, I ran two transects of four patches each from the edge of a wooded area into the surrounding grassland. For each transect, I placed the first artificial patch at the edge of the wooded area (0 m) and the others at 15 m, 30 m and 45 m into the surrounding grassland away from the wooded area. I placed the transects extending from one woodland patch and separated them by ~30 m. I set up a pair of transects at each of the three sites ($N = 3$ wooded areas). I then collected GUDs by using the same experimental protocol as in the first experiment (i.e. 300 g of food per patch, patches left for 24 hours, experiment ran for 7 days).

Changes in risk-taking behaviour

I ran an additional experiment to determine if oribi would overcome their fear of woodlands with an increase in food availability. For this experiment, I used the same wooded areas and artificial patch grids from the habitat and patch use experiment. This allowed me to make direct comparisons between these different experiments. To determine if greater food availability would increase risk-taking behaviour, I increased the amount of food in each patch within the woodlands to 500 g. As above, I left the artificial patches out for 24 hours before collecting the GUDs, and ran the experiment for 7 days. I then ran the experiment again, but this time I increased the amount of food in the woodland patches to 750 g. I followed the same experimental protocol, but was only able to run this experiment for 3 days.

As in the first experiment, I collected patch variables that could influence patch use. These variables included distance to edge of wooded area, distance to potential ambush site, and site lines (i.e. whether the visibility from the patch was blocked within a 2 m radius of the patch). Because I used the same wooded areas and patch positions from the first experiment, I was able to compare the importance of the landscape variables across the different food availability treatments.

Data analysis

To determine oribi habitat preference, I analysed GUDs (dependent variable) with a Generalized Linear Model. I used a Gamma distribution with a Log link function. Habitat (short grass, long grass and woodlands) and tray nested within habitat were independent variables. Day was a blocking variable with number of oribi as a covariate.

Blocking by day made each day independent and removed the variability due to daily differences and tested for the main effect, the influence of habitat on foraging intensity.

I used a second Generalised Linear Model to determine the influence of patch variables on GUDs. Because the oribi avoided woodlands (see Results), I limited this analysis to the long and short grass habitats. I generated mean GUDs (dependent variable) for each tray from the data collected over the seven days within the two habitats and combined these data into a single data set. By using mean GUDs across days I avoided possible non-independences between days. Therefore, I did not have to use a blocked design. Independent variables included sight lines, slope, aspect and distance to cover (long grass). In addition, I ran a regression analysis to determine the relationship between mean GUDs and distance to cover. Distance to cover was normally distributed.

I had an overrepresentation of unused patches at the edge of woodlands, which resulted in difficulty in normalising the data. Therefore, I ran a Generalised Linear Model to determine the influence of distance from woodlands on feeding intensity (i.e. GUDs) of oribi. I calculated mean GUDs for each tray position per day from the two transects in each wooded area. In the analysis, mean GUD was the dependent variable, day was the blocking variable and distance to wooded area (0 m, 15 m, 30 m, 45 m) the independent variable. Number of oribi per site was a covariate.

To explore whether oribi increased their utilisation of wooded area as food availability increased, I analysed GUDs (dependent variable) using a blocked design Generalised Linear Model. Treatment (300 g, 500 g, and 750 g) and tray nested within treatment were the independent variables. Day was the blocking variable and the number of oribi as a covariate. Number of oribi was not significant so I removed it from the model.

To determine the influence of the patch variables on GUDs and thus risk-taking behaviour, I used a Generalised Linear Model. I limited this analysis to the wooded areas across the different treatments (i.e. 300 g, 500 g, 750 g). I converted the GUDs to proportions of food left (dependent variable) to make the three treatments comparable. I generated mean GUDs (dependent variable) for each tray from the data collected over the seven days within the wooded habitat for each treatment and combined them into a single data set. Independent variables included treatment, sight lines, distance to edge of wooded area, distance to potential ambush site, treatment x sight lines, treatment x distance to edge, and treatment x distance to potential ambush site. The interaction term of treatment x distance to potential ambush site was the only significant variable (see Results) that influenced patch selection. To explore this interaction, I used a Generalised Linear Model because the data were non-normal. For the analysis, I converted distance to ambush site into distance categories. These categories included close (0–5 m), intermediate (6–10 m), and far (<11 m). I then used distance to ambush site as an independent variable in the models. I ran three separate models and plotted the marginal means and 95% CI for each distance category across the different treatments. All statistical analyses were done using SPSS version 22.

Results

Habitat and patch selection

The feeding intensity (i.e. GUDs; mean ± SE g) of the oribi was significantly different across the three habitats (Generalised Linear Model: $\chi^2 = 642.349$, $df = 2$, $P < 0.001$;

Figure 1). Oribi equally preferred feeding in the short (mean GUD = 252 ± 1.4 g, N = 189) and long grass habitats (mean GUD = 253 ± 1.4 g, N = 189), but avoid woodlands (i.e. high GUDs) (mean GUD = 299 ± 1.7 g, N = 189). The different number of oribi at the three sites resulted in significant differences in the GUDs achieved (Generalised Linear Model: $\chi^2 = 99.763$, $df = 1$, $P < 0.001$). Nevertheless, the pattern of habitat preference and avoidance was the same across the sites.

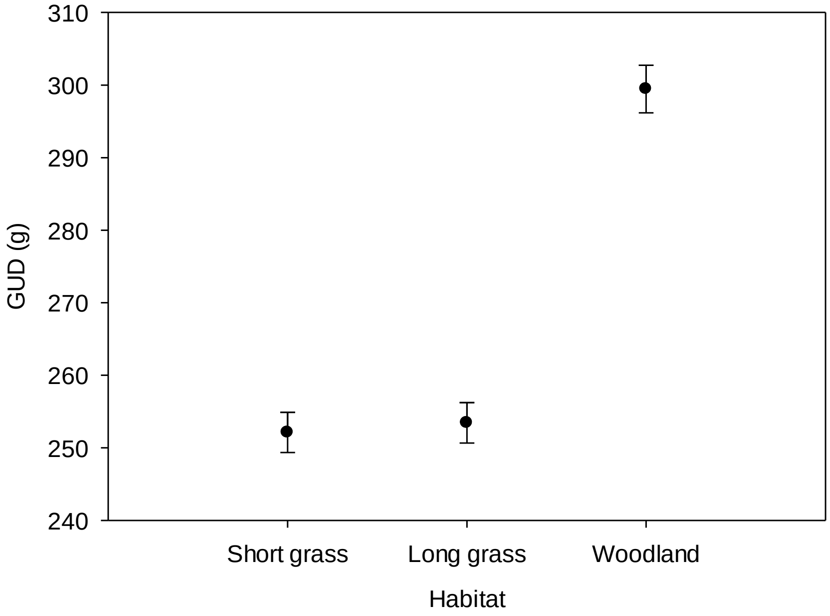

Figure 1: Giving up density (g) (mean ± 95 % CI) for oribi across habitats. Overlapping confidence intervals show equal preference for both short and long grass habitats, while woodlands were avoided.

Within the long and short grass habitats, sight lines and distance to cover (long grass) were the only variables that influenced patch selection of oribi (Table 1). Oribi ate more intensively (i.e. achieved lower GUDs) from patches where they could see > 2 m (mean = 246 ± 3.5 g, N = 43) compared to patches where they could only see < 2 m (mean = 290 ± 7.5 g, $N = 11$). As the distance to escape cover (i.e. tall grass) increased, oribi fed less intensively from the patches (Regression: $\beta = 0.728$, $t = 5.305$, $P < 0.001$) (Figure 2). Distance to cover also explained a significant proportion of variance in GUDs (Regression: $r^2 = 0.53$, $F = 28.142$, $P < 0.001$).

Table 1: Results of the Generalised Linear Model showing the influence of habitat variables on feeding intensity (measured as GUDs) in both the short and long grass habitats. Variables included whether sight lines from the patches (i.e. whether visibility from the patch was blocked by tall grass or shrubs within a 2 m radius of the patch), slope, aspect, and the distance from escape cover (long grass).

	χ^2	*df*	*P*
Long and short grass tray variables (N = 54)			
Sight lines	30.056	1	< 0.001
Slope	2.203	4	0.698
Aspect	2.87	3	0.412
Distance to cover	6.06	1	0.014

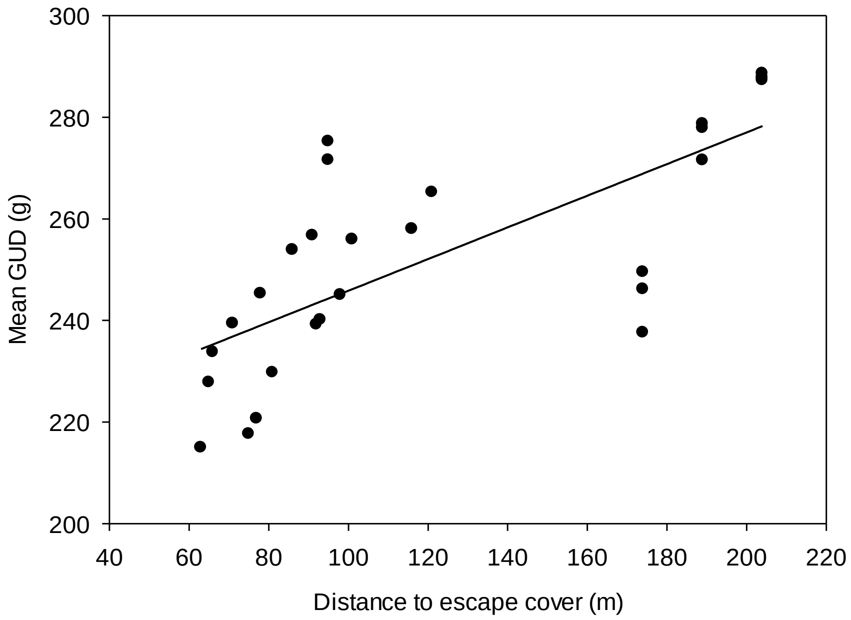

Figure 2: Mean giving up density (GUD) for each artificial food patch increased as distance to escape cover (long grass) increased. Low GUDs indicate greater feeding intensity and thus greater preference, whereas high GUDs indicate low feeding intensity (i.e. avoidance).

Not only did I find that oribi avoid woodlands, but they also fed less intensively in the grasslands close to these woodlands (Figure 3). Specifically, the oribi did not forage at the edge of the woodlands, and only increased their feeding intensity as they got farther away from the edge of the woodlands (Generalised Linear Model: $\chi^2 = 2728.700$, $df = 3$, $P < 0.001$) (Figure 3). The number of oribi at each site significantly influenced GUDs (Generalised Linear Model: $\chi^2 = 5.866$, $df = 1$, $P = 0.015$).

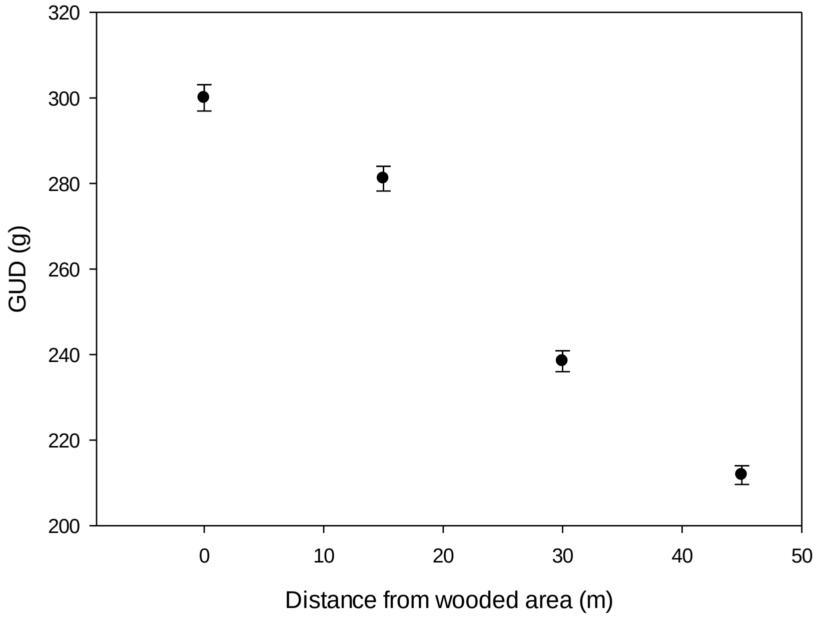

Figure 3: Giving up density (g) (mean ± 95 % CI) in artificial food patches as distance from woodlands increased. Oribi did not feed at the edge of the woodlands and only starting foraging (i.e. achieve lower GUDs) in patches placed 15 m from woodlands.

Changes in risk-taking behaviour

As food availability increased in the woodlands, oribi significantly increased their utilisation of these areas (Generalised Linear Model: $\chi^2 = 1077.366$, $df = 2$, $P < 0.001$). The mean percentage of food left declined as food availability increased from 300 g (99.8 ± 0.17 %), to 500 g (97.7 ± 0.16 %), and finally to 750 g (89.4 ± 0.26 %).

Within woodlands, distance to ambush site was the only single variable that explained the small-scale foraging decisions of oribi (Table 2). As the distance from potential ambush site increased, oribi fed more intensively (i.e. obtained lower GUDs). However, the interaction of food availability and distance to ambush site was also significant (Table 2). Specifically, oribi ate closer to ambush sites and ate more (i.e. achieved lower GUDs) from the artificial patches close to these ambush sites as food availability within the patches increased (300 g: χ^2= 3068.533, df = 2, $P < 0.001$; 500g: χ^2 = 42.454, df = 2, $P < 0.001$; 750 g: χ^2 = 9.049, df = 2, P = 0.011) (Figure 4).

Table 2: Results of the Generalised Linear Model showing the influence of habitat variables on feeding intensity (measured as GUDs) in wooded areas across three food availabilities (300 g, 500 g and 750 g). I tested the main effects as well as their interactions to determine the importance of the different small scale variables on GUDs as patch quality increased.

	χ^2	df	P
Wooded area tray variables (N = 81)			
Food availability	61.289	2	< 0.001
Sight lines	0.011	1	0.917
Distance to edge	3.406	1	0.065
Distance to ambush site	26.812	1	< 0.001
Treatment x Sight lines	0.513	2	0.774
Treatment x Distance to edge	2.331	2	0.312
Treatment x Distance to ambush site	8.664	2	0.013

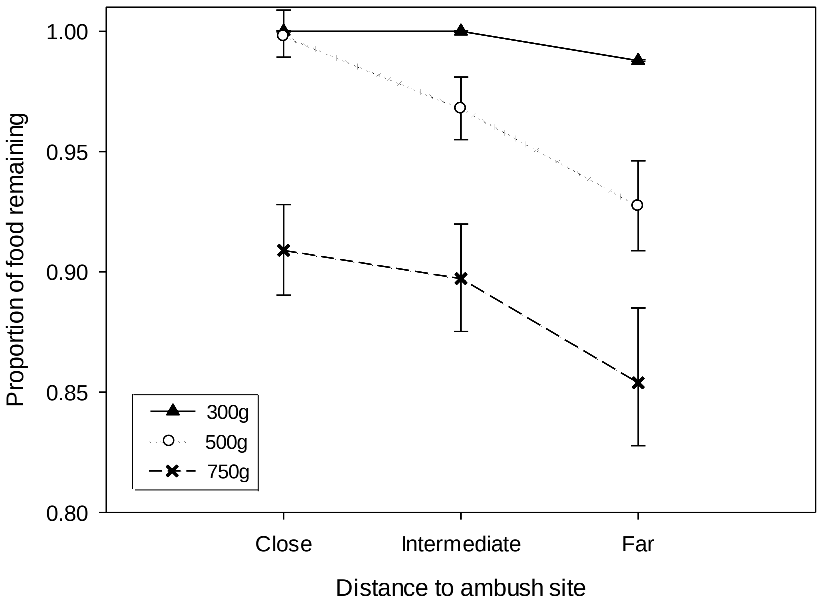

Figure 4: Proportion of food remaining (mean ± 95 % CI) in artificial food patches that I placed close to (0–5 m), intermediate (6–10 m), and far (>11 m) from ambush sites. This experiment was replicated across three (300 g, 500 g, and 750 g) initial food densities. Increases in food availability resulted in increases in both large (i.e. feeding in woodlands) and small-scale risk-taking behaviour (e.g. feeding closer to potential ambush sites).

Discussion

By using GUDs to measure habitat and patch selection, I found that oribi utilise different habitats in relation to perceived predation risk. On a large scale, oribi preferred foraging in grasslands (both long and short), but avoided woodlands. Utilisation within these grasslands, however, was not uniform. Oribi made small-scale patch selection decisions based on small-scale landscape variables (i.e. distance to escape cover and sight lines), rather than large-scale variables (i.e. aspect and slope). Additionally, oribi did not utilise grassland areas that were within 15 m of woodlands. However, feeding intensity increased as oribi fed further away from woodlands. When I increased food availability within these avoided woodlands, oribi made a large-scale shift and started feeding with the woodlands. This suggests that the risk-taking was driven by perceived benefits of greater food intake outweighing the potential cost of predation. Furthermore, as I increased food availability in the woodland patches, oribi took more small-scale risks and fed from artificial patches that were closer to potential ambush sites.

Habitat and patch selection

Similar to other studies (Shackleton and Walker 1985; Perrin and Everett 1999), I found that oribi preferred feeding in grasslands and avoided woodlands. However, contrary to these studies, I found that oribi did not just use the long grass to hide in, but rather, they foraged equally in both short and long grass habitats. The oribi likely avoided woodlands due to higher levels of perceived predation risk. Woodlands are dangerous for oribi due to a combination of having a greater number of potential ambush sites (i.e. shrubs) and the fact that a number of oribi predators prefer to move through and utilise woodlands (e.g. caracal). Moreover, shrubs within these woodlands not only reduce the detection of predators (Lima and Dill 1990), but, unlike tall grass, may also reduce escape paths. These factors, coupled with the results, support my initial hypothesis that when the food availability is equal in habitats, oribi will select and feed within the safer habitat.

The variability in the structure of habitats can influence the level of predation risk (Hannon et al. 2006), and thus small-scale patch use. Within grasslands, distance to cover and sight lines were the only variables that influenced small-scale patch selection in my study. Distance to cover is very important for oribi because they have a cover-dependent escape tactic and normally hide in grass to avoid predators (Jarman 1974). If oribi forage in short grass, they would need to retreat to tall grass to hide and thus reduce predation risk. The further away from long grass oribi forage, the earlier they would have to flee to avoid a predator (Dill and Houtman 1989). Although fleeing may enable a forager to escape predation, it does incur a cost in terms of reduced foraging (Ydenberg and Dill 1986). As a result, foraging further away from cover increases predation risk, which would result in an increase in vigilance at the expense of foraging efficiency (i.e. higher GUDs) (Lima and Dill 1990; Brown 1999).Therefore, it is not surprising that oribi fed more intensively near long grass. Similarly, Nubian ibex (*Capra nubiana*) perceive cliffs as areas of safety and GUDs increased as the distance from the refuges increased (Kotler et al. 1994). This avoidance of open areas far from cover may explain why oribi tend to avoid homogenous agricultural land, such as oats *Avena sativa* and rye grass *Lolium perenne* pastures, as a source of supplementary food during winter (Perrin and Everett 1999).

One of the main ways in which prey species reduce predation risk is through early detection of predators before they attack (Sorato et al. 2012). Thus, objects that block sightlines can increase predation risk (Shrader et al. 2008; Camp et al. 2012). In my study, oribi reduced feeding intensity in grassland patches where they could not see beyond two metres. Thus, by avoiding patches with limited visibility, oribi likely reduced their predation risk because they would be better able to assess the characteristics of approaching predators (e.g. speed and direction of approach), and thus make better escape decisions (Braun et al. 2010; Bateman and Fleming 2011). Similarly, bighorn sheep (*Ovis canadensis*) prefer to feed in open areas where they could easily detect approaching predators (Risenhoover and Bailey 1985). Moreover, by feeding in patches with unrestricted sightlines, oribi would be able to observe other group members, and thus further reduce predation risk via collective detection (Elgar et al. 1986; Shrader et al. 2008).

The avoidance of woodlands by oribi suggests that they perceived this habitat to contain a greater predation risk than grasslands. This is likely due to the higher predator presence in this habitat, and the vegetation structure (e.g. shrubs) creating increased ambush opportunities. One of the main predators of oribi is caracal (Coverdale et al. 2006; Grey-Ross et al. 2009), which is an ambush predator (Kingdon 1997). Thus, caracal could take advantage of these ambush sites which increases predation risk to oribi. In response to this possibility, oribi, when feeding within woodlands, fed more intensively in patches farther away from ambush sites. However, in grasslands, oribi did not avoid feeding next to tall grass, which could also act as an ambush site. This may be due to the lower predator density that I recorded within the grasslands and thus a lower perceived risk. However, it may also be that unlike shrubs and fallen branches found within woodlands, grass tufts are less of an obstacle preventing the oribi from fleeing cursorial predators such as jackal. The density of predators as well as the encounter rate between predators and prey can influence the antipredator response of herbivores. Although it was not possible to determine the encounter rate between oribi and their predators at the study site or the relative densities of the different predators, pictures from the trail cameras show that predators are present within wooded areas. Due to prey uncertainty about predators, prey should avoid risky areas well after predators have left the area (Sih 1992). Therefore, predator density or encounter rate between predator and prey does not necessarily have to be high to illicit strong antipredator behaviour and avoidance of risky areas.

Importantly, the perceived predation risk associated with woodlands was not restricted to woodlands, but extended out into the surrounding grasslands irrespective of the size of the woodland I tested (0.36 ha–0.72 ha). Therefore, even small woodlands can reduce the amount of suitable grasslands to oribi. Thus, the oribi did not use the entire grassland habitat within the study area. Abu Baker and Brown (2012) found similar patterns for the four-striped grass mice. In their study, the mice avoided wooded habitats and grassland areas next to the woodlands.

Changes in risk-taking behaviour

Despite greater perceived predation risk, woodlands can sustain greener vegetation, with increased production and increased nitrogen, longer into the dry season compared to open grasslands due to the microhabitats they create (Treydte et al. 2007). As a result, this higher quality vegetation could attract oribi to feed within these habitats. When I increased the amount of food within woodlands, I found that oribi increased both their large- and small-scale risk-taking behaviour. Specifically, when food availability increased, oribi shifted and fed within the woodlands (i.e. large-scale habitat shift). Additionally, with increasing food availability, oribi increased the number of patches in which they fed within woodlands and increased risk-taking behaviour by feeding closer to potential ambush sites (i.e. small-scale shift). This suggests that the perceived increase in food intake outweighed the potential costs of predation (Brown 1992). This supports my alternative hypothesis that when the availability of food increases, oribi will shift and feed within risky habitats.

Foraging animals use a hierarchy of decisions making, which usually ranges from large- to small-scale decisions: where to feed, when to feed, and what to eat (Lima and Dill 1990). Each of these hierarchal levels may in itself represent a large- to small-scale hierarchy. For example, where to feed could be large-scale (i.e. habitat level) or small-scale (i.e. patch level within a habitat). Because foraging decisions can occur over large- and small-scales, one would expect that risk-taking behaviour would also occur over both scales. However, the majority of the literature only explores risk-taking behaviour over a single scale. Foragers can either increase their risk-taking behaviour by altering their large-scale use of habitats (Kotler and Blaustein 1995) or their small-scale use of patches within habitats (Bakker et al. 2005) with an increase in food availability. To my knowledge, my results are the first to show that risk-taking behaviour occurs simultaneously over both large- and small-scales. Not only do oribi start utilising risky habitats, but their feeding behaviour also changed within this habitat. As a result, oribi were able to take further advantage of this high-reward habitat by increasing the number of feeding sites within the habitat. The concurrent assessment of habitat and patch use by foragers provides a better understanding of how animals utilise the environment to balance predation risk and food availability.

One factor that might push animals to take greater risks is if they are hungry (Brown 1999). This, however, is unlikely to explain my findings because I conducted my experiments over a relatively short period (i.e. 58 days). Over this period, the availability of food across the environment was unlikely to severely decline. As a result, the energetic state of oribi was unlikely to change throughout my experiments. Therefore, my results demonstrate that benefits of greater food availability can even tempt non-hungry animals to increase risky behaviour over both large- and small-scales.

Conclusions

My results indicate that predation risk is a major factor that influences oribi foraging behaviour. Oribi prefer to feed in both habitats (large-scale) and patches within habitats (small-scale) that have lower levels of perceived predation risk. I found that small-scale landscape variables (i.e. distance to cover for oribi, visibility around a foraging site, and the distance to potential ambush sites for predators) reduced perceived predation risk while large-scale landscape features (i.e. aspect and slope) do not. However, with an increase in food availability, oribi increased risk-taking behaviour over two spatial scales. First, oribi showed greater large-scale use of unsafe woodland habitats. Second, oribi extended their small-scale foraging decisions whereby within these woodlands oribi fed closer to, and ate more from, patches close to potential ambush sites as food availability increased. Ultimately, my results highlight how changes in food availability can determine the degree to which herbivores are willing to increase their risk-taking behaviour, and how these changes can affect overall landscape use.

CHAPTER 5

Section I:

Conclusion

The broad aim of this project was to determine how seasonal changes in grass quality, interactions with domestic livestock (i.e. cattle) and perceived predation risk determine oribi (*Ourebia ourebi*) food selection and ultimately their movement and utilisation of the landscape. To answer these questions, I had the following objectives, 1) determine how one of Africa's smallest grazing antelopes adjusts its foraging such that it can survive the dry season, 2) determine whether cattle compete with or facilitate oribi and how these interactions change across seasons and cattle stocking rates, and 3) Explore how perceived predation risk influences oribi large-scale habitat selection and small-scale foraging behaviour.

The degree to which a herbivore feeds selectively, and its ability to digest this food is influenced by body size, digestive physiology, plant characteristics, and mouth size (Hanley 1982; Belovsky 1997). A number of studies have investigated the foraging behaviour of medium to large herbivores (Laca et al. 1994; Bergman et al. 2001; Fortin et al. 2002). However, the foraging behaviour of small ruminants, especially small grazers like oribi, is lacking. Oribi are unique because the majority of small ruminants are either browsers or mixed feeders that incorporate woody vegetation into their diet when resources are limited (Gagnon and Chew 2000). Oribi, however, are pure grazers, thus they continue to feed on grass throughout the year, even when the availability of green grass is limited. To explore this, I focused chapter 2 on how one of the smallest, pure grazers survives the dry season. Quite simply, oribi meet their nutritional requirements by being highly selective foragers. During the dry season, oribi foraged over multiple spatial scales and increased their dry matter intake rate. At a large spatial scale, oribi utilised high quality microhabitats within grasslands, such as vleis and firebreaks, which provided nutritious green leaves during the dry season. Importantly, these areas did not have to be large to provide sufficient food to increase the nutritional intake of oribi. For example, at Chelmsford dam, the firebreaks only covered ~10% of the area. Due to the small muzzle size of oribi, they were able to successfully utilise these areas even when regrowth was minimal. As a result, the protein intake rate of crude protein doubled when oribi fed on firebreaks compared to unburnt areas during the dry season. Although oribi maintained their minimum requirements for maintenance without utilising firebreaks, the protein intake was below the levels required for reproduction.

At the smaller patch and feeding station level, oribi selected for green grass, specific grass species and certain plant parts. Throughout the study, oribi only consumed grass leaves, primarily from the grass species *H. hirta*. This grass species was a key food source for oribi during the dry season, because it is able to maintain green leaves in tall swards even during periods of frost (*pers. obs.*).

In addition to foraging selectively, oribi also increased their dry matter intake rate during the dry season. They achieved this by increasing their bite mass while maintaining the same bite rate throughout the dry season. This allowed oribi to maintain their crude protein intake despite decreasing grass greenness. Ultimately, the results from chapter 2 highlight the importance of high quality vegetation for oribi. As a result, the distribution of high quality vegetation can explain the distribution and habitat use of these small grazers.

Within South Africa, a majority of oribi are found on private land (Coverdale et al. 2006). As a result, they frequently live and feed in areas also utilised by domestic livestock. High quality vegetation is important for oribi, however, cattle foraging can influence the availability and distribution of high quality resources. Therefore, the results of Chapter 3 build on from Chapter 2 by determining how cattle influence the foraging behaviour of oribi across seasons and stocking rates. My findings indicate that the nature of interspecific competition between oribi and cattle is determined by season. In the wet season, cattle facilitated oribi at low and intermediate stocking rates. They did this by providing high quality regrowth despite a high dietary overlap and consuming grass of similar heights. However, at the high cattle stocking rate, oribi adjusted their foraging behaviour and fed from taller grass not utilised by the cattle. This was likely due to the higher grazing intensity in the high stocking rate camp reducing the grass regrowth to where this resource became limited. Despite feeding on taller grass, oribi in this camp still maintained the same nutritional intake as the oribi feeding in the lower stocking rate camps by selecting for green leaves in taller grass swards. Ultimately, this foraging strategy highlights the adaptive nature of oribi and their ability to obtain a high nutritional intake when foraging on either short or tall grass.

Competition, however, was not restricted to direct interactions between the cattle and oribi. The high dietary overlap between the wet season diet of cattle and the dry season diet of oribi, coupled with the high cattle grazing intensity during the wet season, greatly reduced available grass biomass in the dry season. Moreover, the cattle also reduced the dry season availability of preferred species for the oribi in the high stocking rate camp. In response, oribi in this camp showed a greater shift in species selection compared to the lower stocking rate camps. Most importantly, in the high stocking rate camp the oribi added *H. contortus* to their diet in the late dry season. The inclusion of *H. contortus* is likely because it was still available in the dry season as the cattle did not eat it.

Not only did the cattle remove potential food for oribi, but they also altered the grass height and structural heterogeneity. Areas with heavy grazing had shorter grass and less structural heterogeneity. The lower heterogeneity was due to large areas of heavy grazing with only a few patches of taller grass interspersed throughout the grazing area. This reduction in the availability of tall grass can potentially influence the distribution of oribi as they shift away from open areas of short grass to utilise microhabitats that provide taller grass. Moreover, it is likely that the large areas of short grass increase the perceived predation risk for oribi because they use tall grass to avoid predators (Everett et al. 1991). To explore this idea, I focused Chapter 4 on how oribi balance food availability and predation risk when making both habitat and patch selection decisions.

Differences in food availability and predation risk across habitats can influence how herbivores utilise landscapes. Chapter 2 showed the importance of high quality vegetation in determining landscape utilisation. Chapter 3 showed how other herbivores can alter the availability of high quality resources as well as the availability of tall grass that oribi utilise for avoiding predators. Therefore, the aim of chapter 4 was to determine how food availability and predation risk influence large- and small-scale foraging behaviour. A number of studies have determined the large-scale habitat features that oribi prefer and which ones they tend to avoid (Oliver et al. 1978; Rowe-Rowe 1983; Everett et al. 1991; Perrin and Everett 1999). Favourable habitat variables include: open grasslands dominated by *T. triandra*, north and east facing slopes, and gently sloping terrain or plateaus with a slope of less than 15 degrees. Avoided variables include: lowland areas and south and west facing slopes. However, predation risk can vary over much smaller spatial scales (Ripple and Beschta 2003). As a result, in Chapter 4 I tested whether oribi do in fact prefer certain large-scale habitat variables, and what influence some small-scale variables have on patch use within these habitats. In contrast to previous studies, I found that the large-scale variables of aspect and slope did not influence oribi habitat or patch selection. Rather, the small-scale variables such as distance to cover (i.e. tall grass), sightlines and distance to ambush sites were the key factors that influenced oribi patch selection.

Ultimately, the results from chapter 4 indicate that predation risk is a major factor that influences oribi foraging behaviour. When the availability of food within patches was equal across the different habitats, oribi preferred to feed in short and tall grasslands and avoided woodlands. During the dry season, woodland grasses tend to remain greener longer, thus they tend have higher nitrogen content compared to grasses outside the canopy (Treydte et al. 2007). However, woodlands also tend to have higher potential predation risk (Altendorf et al. 2001). To determine how oribi trade-off between food availability and predation risk, I increased the availability of food within previously avoided woodlands. As the food availability increased, oribi took greater risks and fed from within this previously avoided habitat. Furthermore, oribi fed closer to potential ambush sites within these woodlands and ate more from these patches as food availability increased.

Overall, there are a few key findings from the study. First, oribi require high quality vegetation in order to meet their high mass-specific metabolic requirements imposed on them by their small body size (Jarman 1974). I addition, they require a grassland habitat that consists of a mosaic of tall and short grass patches. However, the availability of high quality resources as well as tall grass can be reduced by large numbers of cattle and potentially native ungulates. Ultimately, changes in both habitat structure and food availability can change an oribi's "landscape of fear". The logical next step is to determine whether the information that I have obtained from my study can be applied towards the conservation and management of oribi. To explore this, I link my results to a case study of a declining oribi population at Fort Nottingham, South Africa.

Section II:

Fort Nottingham Commonage: a case study

The Fort Nottingham commonage is a ~778 ha grassland found in the Natal midlands and is used primarily for livestock production. The commonage has a mean rainfall of 950 mm per year with the majority of that occurring from October to February. The vegetation is classified as Drakensburg foothill moist grassland and is dominated by forbs, *Themeda triandra* and *Tristachya leucothrix* (Mucina and Rutherford 2006).

The whole area is leased to local farmers for cattle grazing during the wet season (September–April). However, in the dry season (May–August) the cattle are removed. The cattle on the commonage are managed using intensive rotational grazing. In 2006, the commonage had a population of ~30 oribi. However, over the last 8 years the population has steadily declined to where now there are estimated to only be 7 individuals (Ezemvelo KZN Wildlife oribi census data). Not surprisingly, this decrease has raised concerns and questions as to the possible reasons for the decline.

The most relevant potential causes of declining oribi numbers include, 1) habitat destruction (loss and fragmentation), 2) over-utilisation due to illegal hunting, and 3) inappropriate/poor farm management (Shrader et al. In press). Because the size and shape of the commonage has not changed since 1984 (Boothway et al. 2012), habitat loss and fragmentation does not explain the decline in oribi numbers. In other parts of South Africa, the main cause of declining populations is illegal dog hunting. However, the commonage is on a plateau surrounded by steep topography so access is limited. Moreover, illegal hunting has not been reported on the commonage, thus it is unlikely to be the reason for the decline.

One reason for the decline suggested by the management staff of the commonage was an increase in jackal (*Canis mesomelas)* numbers (R. Tabernor, 2013, *pers. comm.*[1]). It was thought that with increasing predator numbers, that both adult and young oribi were being killed. However, no observations of jackals killing oribi were made, and no carcases were ever found. Moreover, a recent study showed that oribi only contribute a small proportion of the diet of jackal in the Fort Nottingham area (Humphries 2014). In addition, jackals are present, and possibly found in even higher numbers in the areas surrounding the commonage, where there are stable oribi populations (R. Tabernor, 2013, *pers. comm.*[1]). Although predation cannot be excluded completely, it seems that other factors are likely playing a larger role in driving the population decline of oribi on the commonage.

The last potential explanation for the declining oribi population on the Fort Nottingham commonage is poor management of the area with regards to oribi ecology and habitat requirements. Because the area is leased there is generally poor cattle

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management. In approximately 2005, stocking rates of cattle on the commonage were reported to have increased. Due to poor management it is difficult to quantify this increase in cattle numbers. This was roughly the same time as oribi numbers started to decrease. From the regrowth experiment in the high stocking rate camp from Chapter 3, I found that high intensity cattle grazing can reduce net relative regrowth which ultimately influences grass height. Thus, cattle have the ability to remove key habitat features for oribi (i.e. remove tall grass and increase the distance between patches of tall grass), and ultimately their distribution. Furthermore, the entire commonage gets burnt to promote grazing capacity. This large-scale burning reduces overall grass height and structural heterogeneity.

Despite the knowledge that oribi require both long and short grass, habitat suitability is not often raised as a potential factor that can lead to a decline in oribi population size. Key explanatory variables in predicting habitat suitability for oribi include habitat quality (Chapter 2), structural heterogeneity (Chapters 2 & 4), and average grass height (Chapters 2 & 4). To explore whether poor habitat management could potentially explain the decline in the oribi population at the Fort Nottingham commonage, I did a habitat suitability assessment using the knowledge I gain from my previous experiments (Chapters 2–4). Using the insight gained from these chapters, I generated three potential alternative hypotheses to explain how the oribi are using the commonage and thus gain insight into why the oribi population had declined. First, I hypothesised, that the availability of high quality food would influence the distribution of oribi, with oribi occurring in the highest quality camps, especially during the dry season. Alternatively, I hypothesised that the structural heterogeneity would influence oribi distributions on the commonage, with oribi selecting areas of greatest heterogeneity. Finally, I hypothesised that the average grass height would influence oribi distribution across the commonage because it provides oribi with food and shelter from predators.

Methods

I assessed the grass height and structural heterogeneity of Fort Nottingham commonage (S 29.40481° E 29.89263°) during August (late dry season) of 2013 and in March (late wet season) 2014. Due to the low numbers of oribi on the commonage ($N = 7$), it was not feasible for me to determine the diet quality from foraging observations (as in Chapter 2). Fortunately, a habitat condition assessment for each grazing camp on the commonage was conducted in 2012 (Botha et al. 2012). I used these habitat condition scores as a proxy for the availability of high quality vegetation (i.e. high habitat conditions scores represent high quality vegetation). For these assessments, each species is ranked according to its nutritional quality, with high quality species having higher rankings. The rank of a species is then multiplied by its abundance. The overall score is calculated by summing these values and comparing it to a benchmark site (a site in pristine condition) that has a pre-calculated habitat quality value. The higher the score, the higher the quality of the habitat.

To determine the distribution of tall grass and structural heterogeneity on the commonage, I used the same technique as in chapters 2 and 3. I walked a 2 km transect in each cattle grazing camp. The size of these camps ranges from 40–230 ha. Every 50 m along these transects, I randomly placed two quadrats. In each quadrat, I measured the grass height of the tallest grass. Along these transects, I also recorded all locations of oribi. I then plotted these positions onto a map using QGIS. This allowed me to determine if oribi distributions were influenced by habitat quality, structural heterogeneity and/or grass height.

Data analysis

To determine whether habitat quality influenced the presence or absence of oribi in each camp, I ran a Generalised Linear Model (Binomial distribution and Logit link function). My dependent variable was the present or absence (1 or 0) of oribi with veld condition score, season (wet and dry), and their interaction as the independent variables.

I used the grass height from the quadrats in each transect to calculate the coefficient of variation (CV = (standard deviation/mean) x 100%) as a measure of structural heterogeneity per camp. The greater the variations in grass height, the greater the CV. These values range from zero (no structural heterogeneity) to 100 (maximum heterogeneity). I also ran a Generalised Linear Model (Binomial distribution and Logit link function) to determine if the presence or absence (1 or 0) of oribi from certain areas was influenced by structural heterogeneity, season, and their interaction. To determine if grass height, season and their interaction influenced the presence or absence of oribi, I used another Generalised Linear Model.

Results

Oribi numbers

Over the last 8 years the oribi numbers at Fort Nottingham have decreased (Figure 1). The missing values for 2007 and 2009 do not reflect the absence of oribi but rather no submissions of oribi count data to the oribi census database (Oribi working group unpublished data).

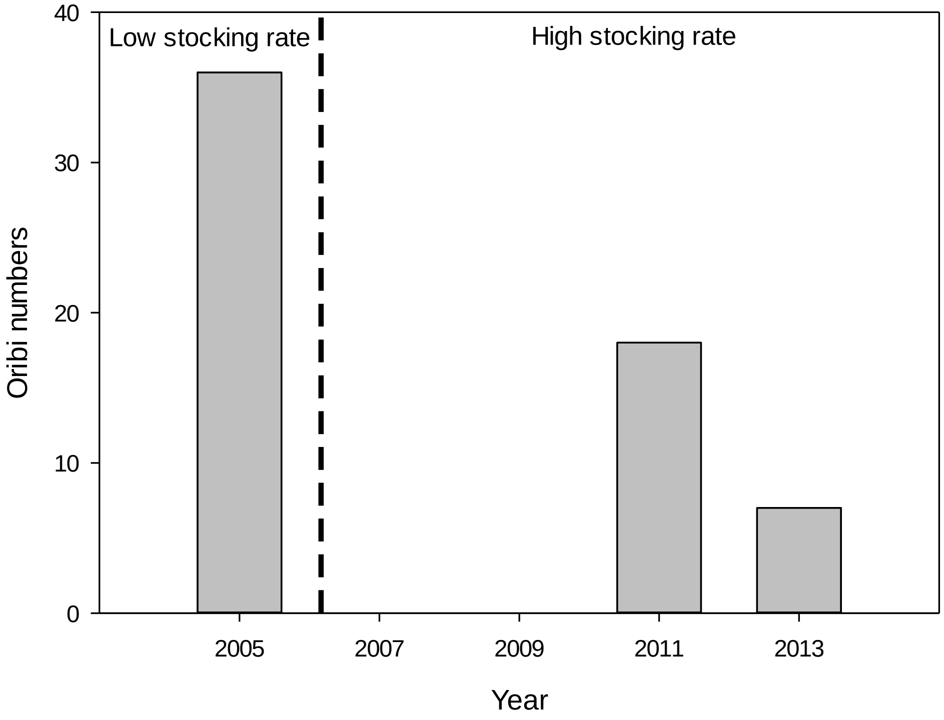

Figure 1: The decrease in oribi numbers over the last 8 years coincides with an increase in stocking rates (dashed line) at the Fort Nottingham Commonage.

Hypothesis 1: habitat quality

The average habitat condition score for the commonage was 71% with the different camps ranging from 61–91%. Despite this range, the presence or absence of oribi was not influenced by the quality of the habitat (Generalised Linear Model: $\chi^2 = 0.006$, $P = 0.941$). Furthermore, oribi did not select habitat in relation to habitat quality across seasons (Generalised Linear Model: $\chi^2 = 0.056$, $P = 0.812$).

Hypothesis 2: Structural heterogeneity

The distribution of oribi was significantly influenced by the structural heterogeneity in grass height, with oribi selecting for areas with higher heterogeneity (58 ± 1.3%) than surrounding areas (39 ± 0.9 %; Generalised Linear Model: $\chi^2 = 21.377$, $P < 0.001$).

Moreover, there was no significant interaction between heterogeneity and season, suggesting that oribi always use areas with the highest available heterogeneity in both the wet and dry seasons (Generalised Linear Model: $\chi^2 = 0.0000007$, $P = 0.999$; Figures 2 and 3).

Hypothesis 3: average grass height

Oribi selected for areas that on average had taller grass (26 ± 0.5 cm) and avoided areas with shorter grass (14 ± 0.3 cm) (Generalised Linear Model: $\chi^2 = 43.585$, $P < 0.001$). There was no significant difference in the interaction between grass height and season, showing oribi selected for the tallest grass height in both seasons (Generalised Linear Model: $\chi^2 = 0.0601$, $P = 0.806$; Figures 4 and 5).

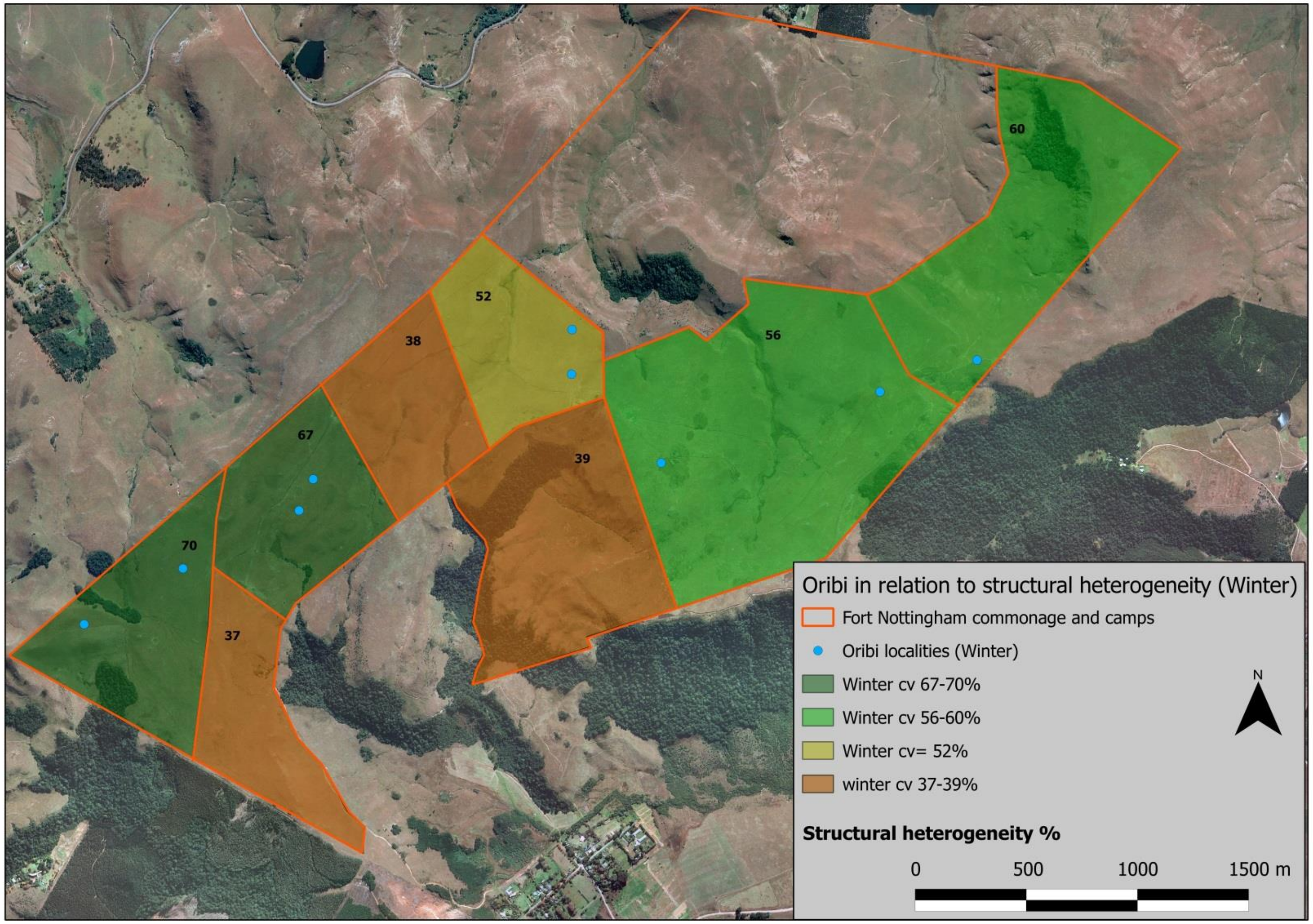

Figure 2: The distribution of oribi at Fort Nottingham Commonage in relation to structural heterogeneity during the dry season. The blue dots indicate oribi locations. The number in each camp refers to the structural heterogeneity of that camp.

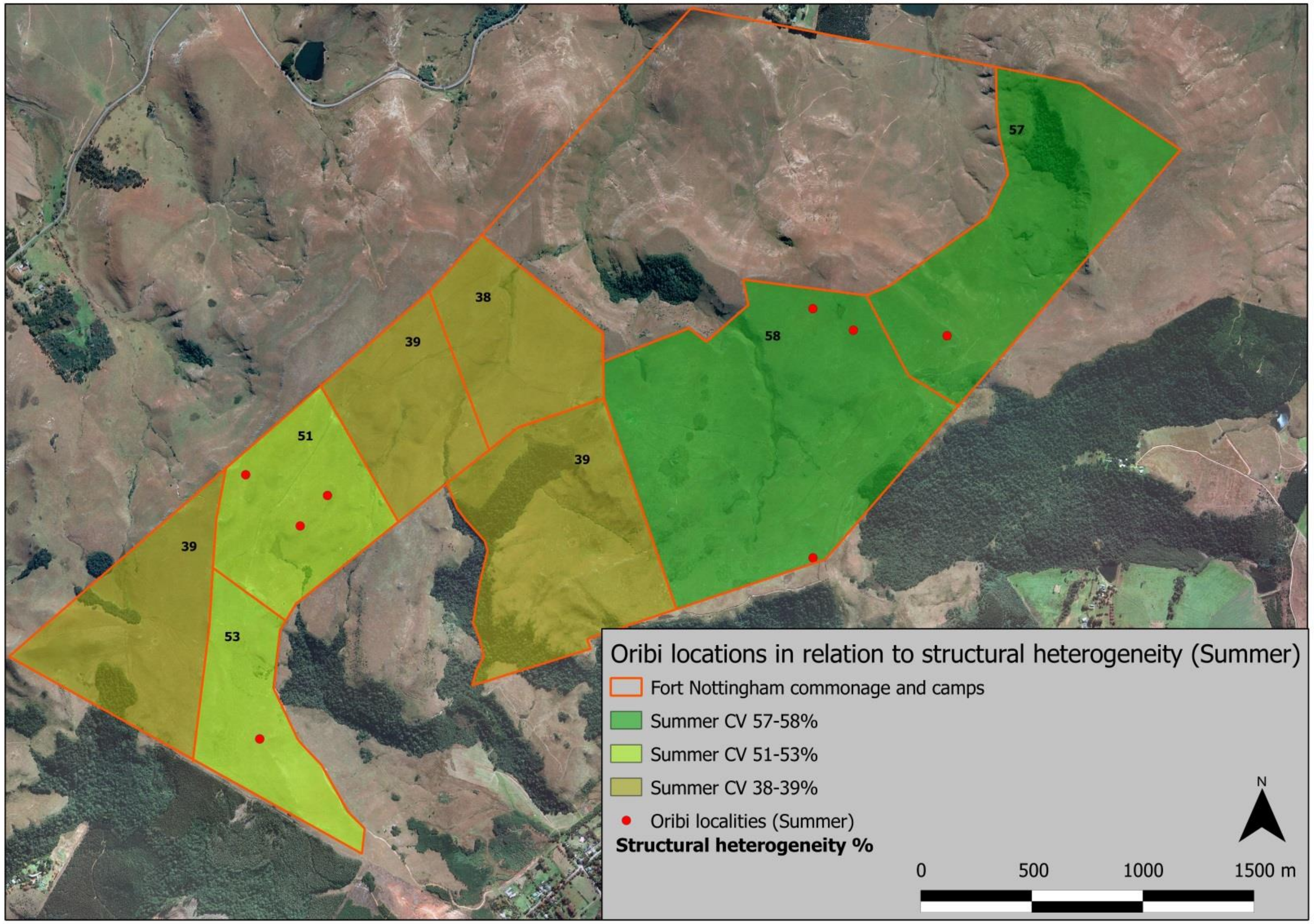

Figure 3: The distribution of oribi at Fort Nottingham Commonage in relation to structural heterogeneity during the wet season. Red dots indicate oribi locations. The number in each camp refers to the structural heterogeneity of that camp.

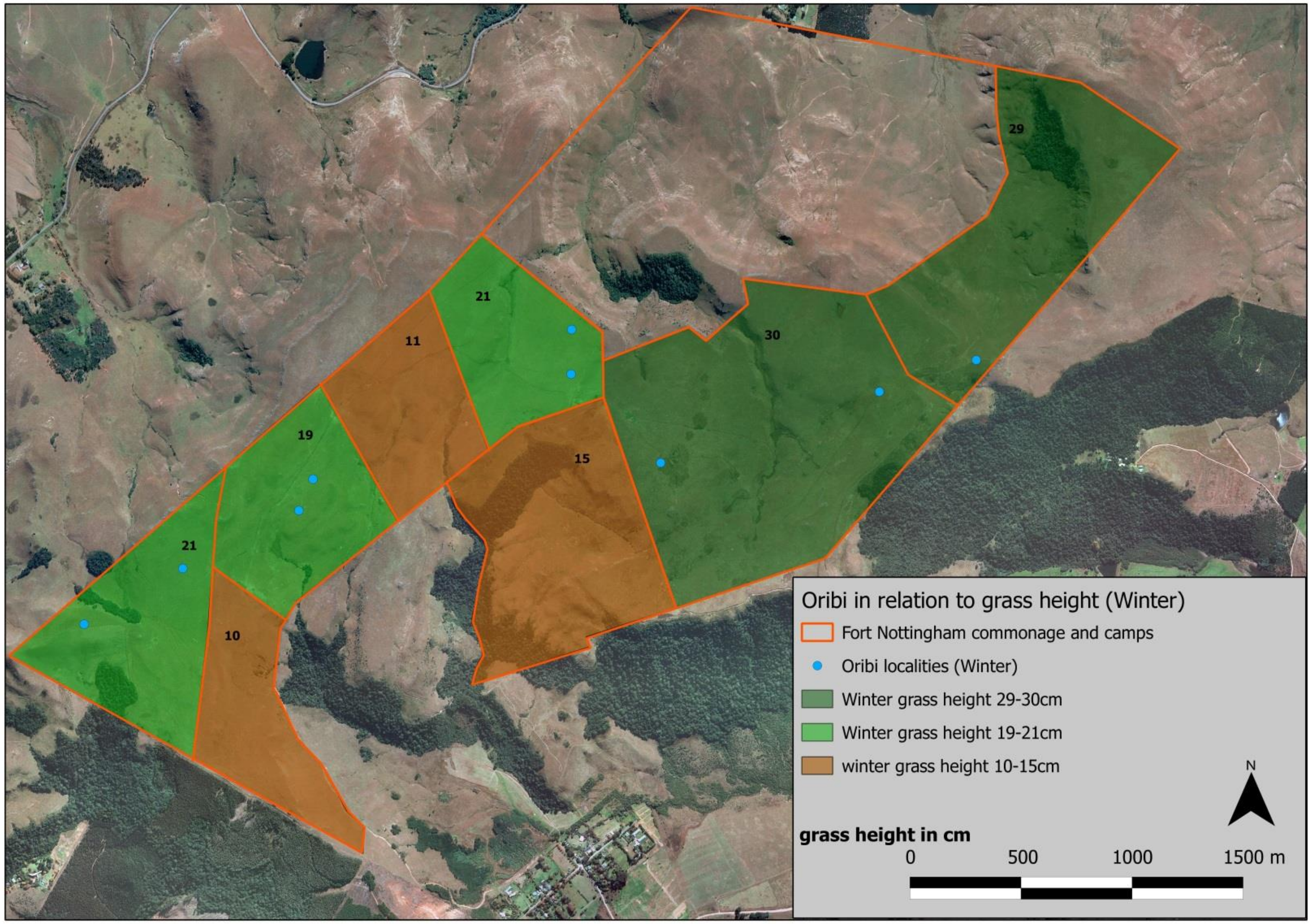

Figure 4: The distribution of oribi at Fort Nottingham Commonage in relation to grass height during the dry season. The blue dots indicate oribi locations. The number in each camp refers to the grass height of that camp.

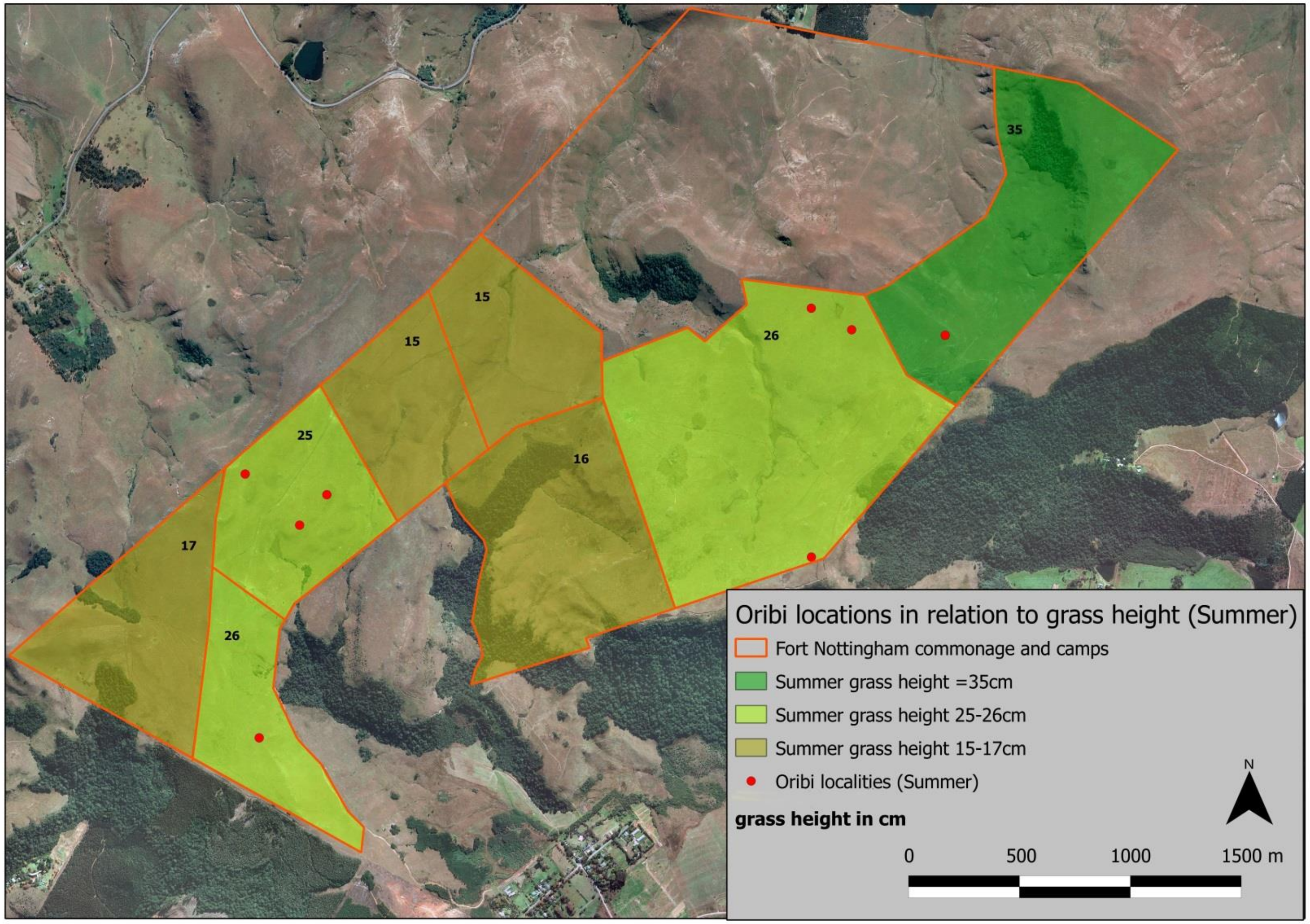

Figure 5: The distribution of oribi at Fort Nottingham Commonage in relation to grass height during the wet season. The red dots indicate oribi locations. The number in each camp refers to the grass height of that camp.

Discussion:

The distribution of herbivores across the landscape can be explained by food availability and perceived predation risk (Holbrook and Schmitt 1988; Butler et al. 2005). However, using the Fort Nottingham commonage as a case study, I found that factors that influence predation risk such as long grass and structural heterogeneity overrode the importance of high quality food availability. Thus, the knowledge I gained during my study (Chapters 2–4) can help explain the distribution of oribi on the commonage. Moreover, these findings have implications for management on how to improve oribi habitat to allow for increased distribution and utilisation of the landscape. Finally, they also may shed light onto the reasons for the historical decline in oribi numbers.

The habitat quality in the area that oribi occurred on the commonage was not different from the areas that they avoided. Thus, as with the situation in Chapter 4 when oribi avoided woodland areas, this pattern may be due to perceived predation risk. The camps in which oribi avoided on the commonage had shorter grass and less structural heterogeneity. Thus, distance to tall grass (i.e. cover) was limited. As a result, the utilisation of these short grass areas was likely low because as the distance from tall grass increases the utilisation of areas decreases (Chapter 4). Moreover, the results of Chapter 4 highlight that oribi can trade-off food availability and predation risk. In doing so, they will feed in riskier habitats when food availability is high. However, despite feeding in riskier areas, it is unlikely that that will establish territories in these areas because of the long-term costs of predation (Brown et al. 1999; Altendorf et al. 2001). Furthermore, oribi time their births with peak grass biomass (i.e. height) and not nutritional quality (Sinclair et al. 2000). Thus, this emphasises the importance of tall grass for hiding young. A limited availability of tall grass when offspring are born could decrease the probability of survival of offspring as predators could easily find them. In an attempt to maximise the survival of their young, and thus their reproductive success, oribi are likely to move away from these areas. Ultimately, the movement of oribi away from the heavily grazed commonage may explain the long-term reduction of oribi numbers. Furthermore, the lack of firebreaks during the dry season, limits the availability of high quality green grass that could attract oribi into these riskier areas.

Although there is no information available about stocking rates and the intensity of grazing in each camp, comparing these findings to the results from chapter 3 allows me to make some inferences. First, in contrast to the oribi at Ixopo (Chapter 3), during wet season, oribi only occurred with cattle in one of the camps. This camp had large tufts of *Eragrostis curvula* that was avoided by cattle most probably due to its size and lower nutritional quality compared to the grazed grass. Furthermore, this camp also had invasive forb species (Bramble, *Rubus cuneifolius* and Curry's post weed, *Phymaspermum acerosum*) that were not consumed by cattle. The tufts of *E. curvula* and the invasive forb created enough heterogeneity and grass height for cattle and oribi to occur in the same camps. The other three camps did not have this heterogeneity, thus oribi avoided them. This suggests that impacts on grass height and structural heterogeneity from cattle feeding could be the main drivers that influence whether oribi utilise the different camps.

By comparing the average grass height and structural heterogeneity in the high stocking rate camp in Ixopo, I estimated the impact of cattle on oribi on the commonage. On average, the avoided areas on the commonage had lower grass height and structural heterogeneity (14 cm; 38%) than the high stocking rate camp in Ixopo (20 cm; 46%). These lower values suggest higher stocking rates, and thus, greater potential for competition between cattle and oribi. One of the ways in which oribi avoided competing with cattle in Ixopo, was to shift their feeding to where they focused on taller grass swards not utilised by the cattle. However, the lower average grass height on the commonage may limit the ability of oribi to shift their foraging behaviour to compensate for competition. Thus, the heavy cattle grazing can reduce food availability, grass height and structural heterogeneity.

Across the seasons cattle movement can cause shifts in the availability and distribution of tall grass as well as heterogeneity. As a result, oribi on the commonage alter their use of camps and followed the distribution of tall grass and heterogeneity (Figure 2–5). However, oribi are territorial (Brashares and Arcese 1999) and thus are limited in their ability to track changes in grass height over large distances. At Fort Nottingham, oribi were able to shift between adjacent camps but not over larger scales. This highlights the importance of scale when assessing the distribution of grass height and structural heterogeneity. For tall grass to benefit oribi it has to be within their home range. As much of the commonage comprised short grass <15 cm high, oribi lacked access to the degree of heterogeneity for habitat conditions to be favourable. Moreover, the few isolated patches where the oribi were present, were areas where grass heterogeneity was greatest and tall grass/forbs were present. Thus, adjusting the location and grazing intensity of cattle such that grass height and heterogeneity increases over both large and small scales, would increase the amount of suitable habitat on the commonage, which could increase the distribution and size of the oribi population. Ultimately, by adjusting habitat heterogeneity and grass height, one would be applying the knowledge gained from Chapters 2–4 for the management and conservation of this locally vulnerable species.

Section III:

Management recommendations

From the onset of this research, one of the goals of this study was to supplement current management with useable information gained from my research on oribi. Each chapter provides important management information that can be implemented across a broad scale to increase the habitat quality for oribi, reduce potential competition from other grazing ungulates, and increase oribi numbers. Moreover, this research also provides information about what key points to consider when assessing habitat for oribi relocations.

Firebreaks

The use of firebreaks to provide high quality vegetation during the dry season can increase the crude protein intake of herbivores. At Chelmsford dam, oribi were able to maintain their minimum requirement of crude protein without utilising firebreaks. However, oribi have a seven month gestation period (Jongejan et al. 1991) and synchronise births with peak biomass in the wet season (Sinclair et al. 2000). As a result, a proportion of the gestation period occurs over the dry season. However, in my study crude protein intake of oribi was far below that needed for reproduction without firebreaks. As a result, the absence of the high quality regrowth found on firebreaks can potentially reduce the ability of oribi to reproduce. This highlights the potential importance of firebreaks for the reproduction of oribi.

Habitat requirements

Oribi require both short and long grass and avoid woodlands (Chapters 2–4). Oribi utilise the short and long grass for feeding, while tall grass is also used for predator avoidance, and is a key component to oribi habitat. More importantly, it is the distribution of short and long grass across the landscape that makes grasslands suitable for oribi. A recommendation coming from the results of my study is to maximise the heterogeneity in grass height over both small (within home ranges) and large spatial scales (landscape). Below I provide a list of recommendations that would increase grassland structural heterogeneity in different grazing systems.

1. Rotational grazing systems: the main goal of rotational grazing is to reduce selective grazing by increasing the grazing pressure on small proportions of grassland (Tainton et al. 1999). Cattle are managed by rotating them from one camp to the next so that not all camps are simultaneously grazed. Heavy grazing within a camp can potentially reduce heterogeneity required for oribi. This impact, however, can be reduced following a few recommendations. 1) Keep livestock at conservation stocking rates and not agricultural stocking rates. Conservation stocking rates are generally lower and have decreased forage utilisation, than agricultural stocking rates. As a result, conservation based stocking rate systems balance cattle production and alternative management objectives (i.e. wildlife conservation) (Hurd et al. 2007). Whereas, agricultural stocking rates have a high grazing pressure for the sole purpose of maximising grass utilisation, and therefore, cattle production (Fuhlendorf and Engle 2001). 2) Ensure adjacent grazing camps are not being grazed at the same time. For example, a camp being grazed by cattle should be next to a camp that is being

rested. This creates spatial heterogeneity, which benefits oribi by providing high quality regrowth from cattle grazing nearby to long grass for predator avoidance.

2. Continuous grazing: this grazing system generally has a lower stocking rate than rotational grazing (Tainton et al. 1999) and when managed under intermediate stocking rates can promote heterogeneity. Thus, by maintaining stocking rates at a level that promotes heterogeneity, the landscape should remain suitable for oribi.
3. Patch burning: burning like grazing can reduce heterogeneity if done incorrectly. The correct use of fire can create a patch mosaic of heterogeneity as well as provide high quality resources for oribi. This should be done using block burning design that creates a mosaic and ensuring that adjacent camps are not under the same burning frequency.

Competition between ungulates

One of the main ways to reduce competition between cattle and oribi is to reduce stocking rates of cattle. As stocking rates increase, the removal of potential food for oribi increases and the structural heterogeneity decreases, increasing predation risk. Alternatively, if rotational grazing is implemented ensure that adjacent camps are not under the same management (i.e. one camp should be rested while the other camp is grazed). This provides oribi with the opportunity to shift and feed from taller vegetation that is not being used by cattle. Furthermore, this allows oribi to take advantage of facilitation from grazing cattle.

In addition to cattle, oribi could also compete with other herbivores. One way to reduce this is to ensure areas are not overstocked with grazers (e.g. zebra (*Equus* *quagga*), wildebeest (*Connochaetes gnou*), springbok (*Antidorcas marsupialis*) and blesbok (*Damaliscus pygargus phillipsi*)). If oribi are in an area that is overstocked, they can alter their foraging behaviour to feed from taller vegetation that is not being utilised by other herbivores. However, if oribi are feeding with a wide range of herbivores that utilise different grass heights such as zebra, wildebeest and impala (*Aepyceros melampus*) (Arsenault and Owen-Smith 2008), their ability to alter their foraging behaviour may be limited.

Overall, the findings of this study have contributed to the ecological theory of how a small ruminant grazer survives during the dry season. This understanding of how oribi forage sets the framework to determine how other herbivores have the ability to compete with or facilitate oribi. Ultimately, the interaction of forage availability, other herbivores and perceived predation risk can be used to predict the best habitats and areas for oribi. Thus, the successful conservation of oribi lies in managing factors that reduce grass height and structural heterogeneity.

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APPENDIX I

Nutritional quality of grass: Chelmsford Dam

Table 1: Seasonal mean % crude protein per grass species in the different grass greenness categories for Chelmsford Dam Game Reserve, South Africa.

Season	Species	Greenness (%)	N	Mean %CP	SE %CP
Dry	*Hyparrhenia hirta*	0	11	2.12	0.28
		1-10	7	2.26	0.23
		26-50	5	3.78	0.28
	Themeda triandra	0	6	0.96	0.07
		1-10	2	1.63	0.35
		11-25	2	2.36	0.12
	Heteropogon contortus	0	4	0.91	0.30
		1-10	5	0.84	0.23
	Paspalum urvillei	0	4	1.71	0.14
		11-25	1	3.06	-
		26-50	2	8.96	0.74
		76-90	3	12.34	0.24
	Pennisetum clandestinum	0	3	3.31	0.25
		51-75	2	10	0.37
	Leersia hexandra	0	3	0.64	0.14
	Hemarthria altissima	0	4	2.31	0.16
	Andropogon appendiculatus	1-10	3	1.23	0.12
	Diheteropogon amplectans	0	3	0.88	0.03
	Cyperaceae sedge	0	5	3.96	0.00
Firebreak	*Hyparrhenia hirta*	91-99	6	12.79	0.44
	Hemarthria altissima	91-99	2	15.57	0.35
	Andropogon appendiculatus	76-90	4	12.45	0.72
Transitional	*Hyparrhenia hirta*	51-65	4	3.98	0.39
		76-90	5	5.96	0.52
		91-99	5	15.22	0.78

Table 1 continued

Season	Species	Greenness (%)	N	Mean %CP	SE %CP
Transitional	*Themeda triandra*	26-50	5	2.22	0.37
		51-75	4	3.5	0.40
		76-90	4	6.03	0.39
		91-99	3	9.68	0.10
		100	4	11.07	0.54
	Heteropogon contortus	51-75	5	3.23	0.50
		76-90	3	3.96	0.43
		91-99	3	12.2	0.37
	Paspalum urvillei	51-75	2	8.51	0.45
		76-90	2	7.84	1.10
		91-99	3	14.06	0.32
	Pennisetum clandestinum	76-90	4	13.16	0.26
	Leersia hexandra	100	3	15.41	0.52
	Hemarthria altissima	51-75	3	4.96	0.61
		76-90	3	5.29	0.19
		91-99	5	11.53	0.65
	Andropogon appendiculatus	26-50	2	1.65	0.24
		76-90	4	3.94	0.36
		91-99	4	12.66	0.25
	Diheteropogon amplectans	91-99	3	13.16	0.35
	Cyperaceae sedge	100	5	13.21	0.38
Wet	*Hyparrhenia hirta*	51-75	4	4.73	0.61
		76-90	4	4.9	0.13
		91-99	6	10.51	0.51
		100	4	11.38	0.92
	Themeda triandra	100	6	6.89	0.10
	Heteropogon contortus	91-99	5	6.72	0.49
		100	2	7.09	0.25

Table 1 continued

Season	Species	Greenness (%)	N	Mean %CP	SE %CP
Wet	*Paspalum urvillei*	91-99	4	8.31	0.33
	Pennisetum clandestinum	91-99	4	12	0.22
	Leersia hexandra	100	6	15.41	0.63
	Hemarthria altissima	100	4	7.76	0.29
	Andropogon appendiculatus	76-90	5	3.66	0.14
		91-99	3	7.89	0.33
		100	4	8.11	0.46
	Diheteropogon amplectans	91-99	5	7.65	0.21
		100	4	9.18	0.14
	Cyperaceae sedge	100	5	12.19	0.21

Table 2: Seasonal mean % organic matter digestibility (OMD) per grass species in different grass greenness categories for Chelmsford Dam Game Reserve, South Africa.

Season	Species	Greenness (%)	N	Mean %OMD	SE %OMD
Dry	*Hyparrhenia hirta*	0	11	26.97	0.80
		1-10	7	28.31	0.75
		26-50	5	27.99	1.09
	Themeda triandra	0	6	26.24	0.40
		1-10	2	30.2	1.79
		11-25	2	29.74	1.36
	Heteropogon contortus	0	4	25.49	1.63
		1-10	5	24.4	0.95
	Paspalum urvillei	0	4	30.07	0.85
		11-25	1	22.8	-
		26-50	2	41.22	2.26
		76-90	3	43.97	0.42
	Pennisetum clandestinum	0	3	32.82	1.22
		51-75	2	42.26	2.83
	Leersia hexandra	0	3	32.76	0.34
	Hemarthria altissima	0	4	38.81	0.54
	Andropogon appendiculatus	1-10	3	25.67	0.22
	Diheteropogon amplectans	0	3	35.18	0.52
	Cyperaceae sedge	0	5	44.59	2.06
Firebreak	*Hyparrhenia hirta*	91-99	6	49.74	1.13
	Hemarthria altissima	91-99	2	53.74	0.73
	Andropogon appendiculatus	76-90	4	47.94	1.36
Transitional	*Hyparrhenia hirta*	51-75	4	30.22	1.54
		76-90	5	35.99	0.69
		91-99	5	55.5	1.04

Table 1 continued

Season	Species	Greenness (%)	N	Mean %OMD	SE %OMD
Transitional	*Themeda triandra*	26-50	5	33.02	1.18
		51-75	4	32.04	0.65
		76-90	4	37.39	0.51
		91-99	3	47.14	2.33
		100	4	47.39	1.69
	Heteropogon contortus	51-75	5	30.08	1.43
		76-90	3	35.79	0.60
		91-99	3	47.58	0.32
	Paspalum urvillei	51-75	2	38.51	0.42
		76-90	2	43.97	1.81
		91-99	3	47.89	0.73
	Pennisetum clandestinum	76-90	4	46.98	0.87
	Leersia hexandra	100	3	56.28	0.46
	Hemarthria altissima	51-75	3	42.9	0.76
		76-90	3	46.01	1.56
		91-99	5	52.61	0.81
	Andropogon appendiculatus	26-50	2	28.12	0.06
		76-90	4	33.23	0.81
		91-99	4	48.35	0.75
	Diheteropogon amplectans	91-99	3	50.95	0.70
	Cyperaceae sedge	100	5	56.05	2.41
Wet	*Hyparrhenia hirta*	51-75	4	30.91	1.22
		76-90	4	35.05	0.55
		91-99	6	45.09	0.56
		100	4	45.07	0.71
	Themeda triandra	100	6	39.97	0.64
	Heteropogon contortus	91-99	5	36.44	0.64
		100	2	38.03	1.00

Table 1 continued

Season	Species	Greenness (%)	N	Mean %OMD	SE %OMD
Wet	*Paspalum urvillei*	91-99	4	37.67	0.35
	Pennisetum clandestinum	91-99	4	40.9	0.72
	Leersia hexandra	100	6	42.55	0.29
	Hemarthria altissima	100	4	46.01	0.56
	Andropogon appendiculatus	76-90	5	32.84	0.72
		91-99	3	37.85	1.26
		100	4	39.6	1.22
	Diheteropogon amplectans	91-99	5	38.77	0.41
		100	4	42.12	0.57
	Cyperaceae sedge	100	5	56.29	0.38

Appendix II

Seasonal selection values: Chelmsford Dam.

Table 1: Seasonal selection of grass greenness categories by oribi.

Season	Grass greenness	Proportional availability	Proportion of use	Bonferroni intervals
Dry	0%	0.198	0.143	0.137<p<0.143#
	1–10%	0.281	0.267	0.267<p<0.273#
	11–25%	0.086	0.043	0.038<p<0.042#
	26–35%	0.224	0.277	0.277<p<0.283*
	51–65%	0.135	0.173	0.167<p<0.173*
	76–90%	0.076	0.097	0.10<p<0.102*
Firebreak	0%	0.099	0	0#
	11–25%	0.052	0	0#
	76–90%	0.427	0.508	0.505<p<0.515
	91–99%	0.427	0.492	0.485<p<0.495
Transitional	91–99%	0.701	0.754	0.747<p<0.753
	100%	0.289	0.246	0.245<p<0.255
Wet	91–99%	0.626	0.657	0.656<p<0.658
	100%	0.372	0.343	0.341<p<0.345

* indicates selection and # indicates avoidance of species in relation to availability. Level of significance *P* = 0.05.

Table 2: Seasonal selection of consumed species by oribi.

Season	Species	Proportional availability	Proportion of use	Bonferroni intervals
Dry	*T. triandra*	0.072	0.110	0.107<p<0.113*
	H. contortus	0.055	0.066	0.064<p<0.068*
	P. clandestinum	0.112	0.176	0.172<p<0.179*
	H. hirta	0.560	0.478	0.475<p<0.481*
	P. scrobiculatum	0.021	0.010	0.009<p<0.011#
	P. urvillei	0.093	0.110	0.107<p<0.113*
	T. leucothrix	0.042	0.013	0.012<p<0.014#
	Cyperaceae sedge	0.021	0.010	0.009<p<0.011#
	Asparagus sp.	0.021	0.007	0.006<p<0.008#
	M. ceresiiforme	0.064	0.013	0.012<p<0.014#
	C. dactylon	0.106	0.003	0.002<p<0.004#
	S. africanus	0.045	0.003	0.002<p<0.004#
Firebreak	*A. appendiculatus*	0.451	0.508	0.503<p<0.513*
	H. altissima	0.089	0.096	0.092<p<0.010*
	H. hirta	0.460	0.395	0.390<p<0.400#
Transitional	*L. hexandra*	0.042	0.068	0.064<p<0.072*
	T. triandra	0.046	0.068	0.064<p<0.072*
	H. altissima	0.038	0.054	0.050<p<0.058*
	H. hirta	0.500	0.642	0.637<p<0.647*
	Cyperaceae sedge	0.130	0.115	0.110<P<0.120#
	T. leucothrix	0.092	0.027	0.024<p<0.030#
	D. tricholaenoides	0.088	0.020	0.017<p<0.023#
	Kyllinga sp.	0.063	0.007	0.005<p<0.009#
Wet	*D. amplectans*	0.121	0.151	0.149<p<0.153*
	H. hirta	0.451	0.559	0.557<p<0.561*
	Cyperaceae sedge	0.116	0.132	0.130<p<0.134*
	L. hexandra	0.039	0.040	0.039<p<0.041*
	S. nigrirostris	0.030	0.024	0.023<p<0.025#
	T. triandra	0.035	0.021	0.020<p<0.022#
	I. cylindrica	0.027	0.014	0.013<p<0.015#
	M. ceresiiforme	0.020	0.009	0.008<p<0.010#
	H. altissima	0.028	0.012	0.011<p<0.013#
	A. appendiculatus	0.018	0.002	0.001<p<0.002#
	P. dilatatum	0.049	0.002	0.001<p<0.002#
	P. scrobiculatum	0.067	0.002	0.001<p<0.002#

* indicates selection and # indicates avoidance of species in relation to availability. Level of significance *P* = 0.05.

Table 3**:** Seasonal selection of species specific grass greenness categories by oribi

Season	Grass species	Grass greenness	Proportional availability	Proportion of use	Bonferroni intervals
Dry	*T. triandra*	0%	0.024	0.025	0.019<p<0.021*
		1-10%	0.036	0.046	0.048<p<0.052*
		11-25%	0.031	0.046	0.048<p<0.052*
	H. contortus	1-10%	0.052	0.068	0.067<p<0.073*
	P. clandestinum	51-65%	0.121	0.181	0.176<p<0.184*
	H. hirta	0%	0.059	0.046	0.048<p<0.052#
		1-10%	0.175	0.167	0.166<p<0.174#
		26-35%	0.211	0.288	0.276<p<0.284*
	P. urvillei	76-90%	0.066	0.100	0.097<p<0.103*
	T. leucothrix	0%	0.036	0.014	0.009<p<0.011#
	M. ceresiiforme	0%	0.028	0.014	0.009<p<0.011#
		1-10%	0.052	0	0#
	C. dactylon	1-10%	0.081	0	0#
	S. africanus	1-10%	0.028	0	0.003<p<0.005#
Firebreak	*A. appendiculatus*	76-90%	0.492	0.508	0.505<p<0.515
	H. altissima	91-99%	0.098	0.096	0.096<p<0.104
	H. hirta	91-99%	0.410	0.395	0.395<p<0.405#
Transitional	*L. hexandra*	100%	0.052	0.079	0.075<p<0.085*
	H. hirta	91-99%	0.623	0.754	0.746<p<0.754*
	Cyperaceae sedge	100%	0.120	0.135	0.124<p<0.136*
	T. leucothrix	91-99%	0.063	0.024	0.017<p<0.023#
	D. tricholaenoides	91-99%	0.084	0	0#
	Kyllinga sp.	100%	0.058	0.008	0.006<p<0.010#
Wet	*D. amplectans*	91-99%	0.090	0.104	0.102<p<0.106*
		100%	0.042	0.055	0.053<p<0.057*
	H. hirta	91-99%	0.446	0.538	0.536<p<0.540*
		100%	0.050	0.047	0.046<p<0.048#
	Cyperaceae sedge	100%	0.123	0.139	0.137<p<0.141*
	L. hexandra	100%	0.042	0.042	0.041<p<0.043
	S. nigrirostris	100%	0.028	0.025	0.024<p<0.026#
	T. triandra	100%	0.022	0.020	0.019<p<0.021#
	I. cylindrica	91-99%	0.029	0.015	0.014<p<0.016#
	H. altissima	100%	0.024	0.007	0.006<p<0.008#
	P. dilatatum	91-99%	0.046	0	0.002<p<0.002#
	P. scrobiculatum	91-99%	0.057	0	0.002<p<0.002#

* indicates selection and # indicates avoidance of species in relation to availability. No symbol indicates utilisation in relation to availability. Level of significance *P* = 0.05.

APPENDIX III

Nutritional quality of grass: Arundel Farm (Ixopo)

Table 1: Seasonal mean % crude protein per grass species in different grass greenness categories across low (1.7 ha/AU), intermediate (1.5 ha/AU) and stocking rates high (0.95 ha/AU) at Arundel Farm, Ixopo, South Africa.

Season	Stocking rate	Species	Greenness (%)	N	Mean %CP	SE %CP
Wet	Low	*Hyparrhenia hirta*	91-99	5	8.1	0.18
		Paspalum dilatatum	100	5	15.38	0.20
		Setaria nigrirostris	100	5	12.06	0.52
		Themeda triandra	100	5	8.09	0.15
	Intermediate	*Hyparrhenia hirta*	91-99	5	8.22	0.11
		Setaria nigrirostris	100	5	12.38	0.27
		Themeda triandra	100	5	6.8	0.16
	High	*Hyparrhenia hirta*	91-99	2	7.35	0.37
		Setaria nigrirostris	100	5	12.37	0.48
		Themeda triandra	100	5	8.84	0.10
	Ungrazed	*Hyparrhenia hirta*	91-99	5	6.37	0.13
Dry	Low	*Hyparrhenia hirta*	76-90	5	5.65	0.14
			91-99	5	7.6	0.23
		Pennisetum clandestinum	91-99	3	14.1	1.86
		Paspalum dilatatum	91-99	5	12.36	1.70
		Themeda triandra	66-75	4	4.59	0.23
	Intermediate	*Hyparrhenia hirta*	76-90	6	6.52	0.18
			91-99	5	7.39	0.12
		Pennisetum clandestinum	91-99	3	13.9	1.76

Table 1 continued

Season	Stocking rate	Species	Greenness (%)	N	Mean %CP	SE %CP
Dry	Intermediate	*Paspalum dilatatum*	91-99	5	12.22	1.70
		Themeda triandra	66-75	4	4.49	0.21
	High	*Hyparrhenia hirta*	66-75	4	5.67	0.25
			76-90	5	7.74	0.14
		Heteropogon contortus	76-90	3	3.46	0.45
		Themeda triandra	66-75	3	5.71	0.59

APPENDIX IV

Seasonal variation in structural heterogeneity in relation to stocking rates for Arundel Farm, Ixopo, South Africa

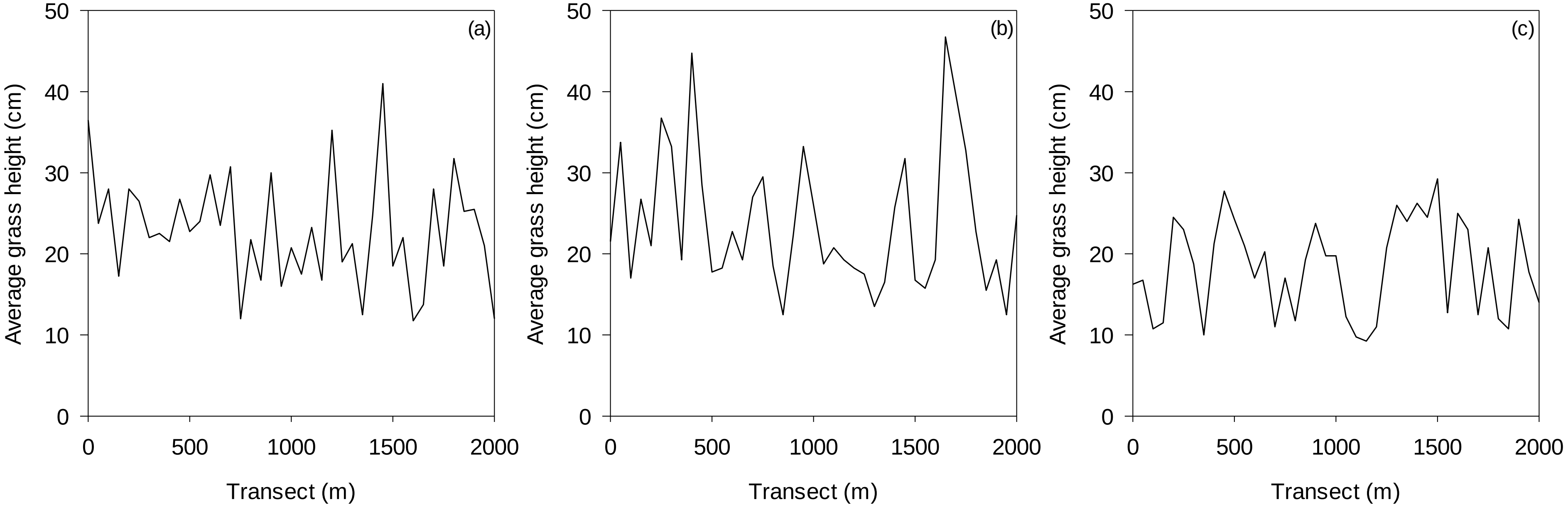

Figure 1: Graphical depiction of mean grass structural heterogeneity in the wet season for a) low stocking rate camp (1.7 ha/AU), b) intermediate stocking rate camp (1.5 ha/AU), and c) high stocking rate camp (0.95 ha/AU). Large spikes and troughs indicate greater variation in heterogeneity.

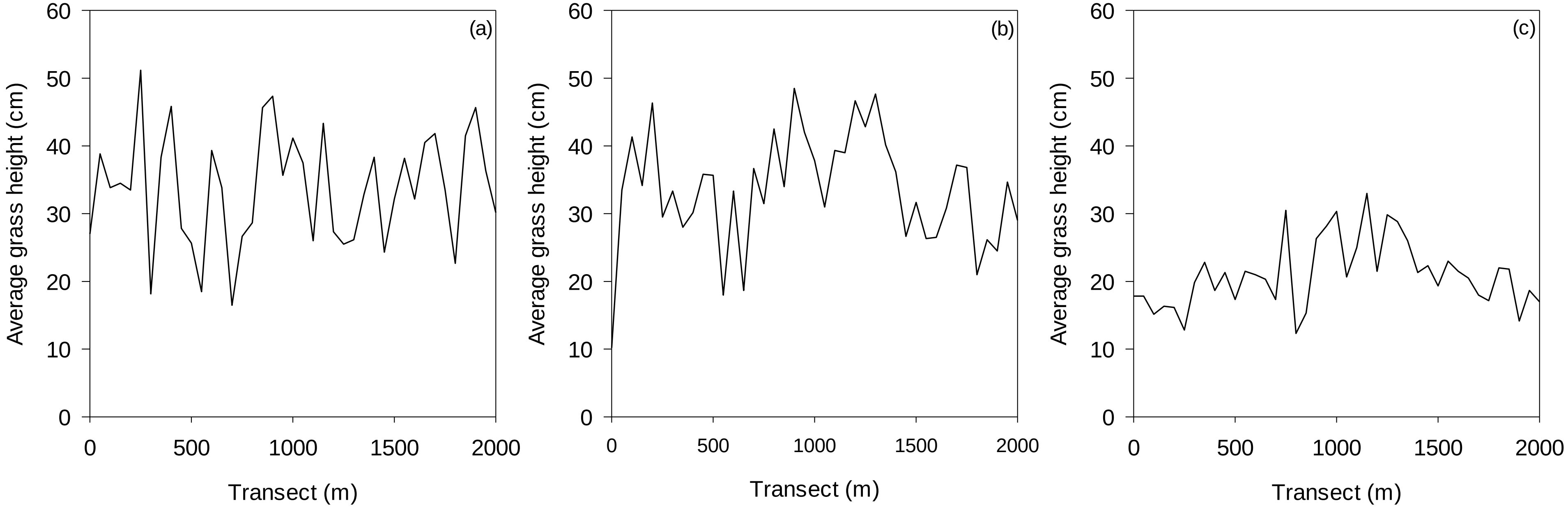

Figure 2: Graphical depiction of mean grass structural heterogeneity in the dry season for a) low stocking rate camp (1.7 ha/AU), b) intermediate stocking rate camp (1.5 ha/AU), and c) high stocking rate camp (0.95 ha/AU). Large spikes and troughs indicate greater variation in heterogeneity