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Macandza, Valerio Antonio

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RESOURCE PARTITIONING BETWEEN LOW-DENSITY AND HIGH-DENSITY GRAZERS: SABLE ANTELOPE, ZEBRA AND BUFFALO

Valério António Macandza

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the Degree of Doctor of Philosophy.

Johannesburg, 2009

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

_____

(Signature of candidate)

_____day of _____2009

ABSTRACT

The issue of how the spatial scale and other aspects of food resources and habitat conditions may enable several species of grazing herbivores to coexist while using the same grass resources in the same region is of fundamental importance in ecology and management of herbivore communities. With this project I aimed at improving the understanding of the ecology of the tall-grass grazers assemblage, particularly how the spatial scale of resource use influenced resource partitioning between grazers that attain different regional density in the same region. Based on theories of patterns of species abundance, body size, feeding specialization and competition, I predicted that at all spatial scales the low density, smaller, resource specialist sable would be more narrowly selective for resources than the high density and generalist grazers buffalo and zebra, which I expected to be more broadly tolerant to resources at different spatial scales. I found that the grass species most preferred by sable were also preferred by the abundant species, but buffalo and zebra grazed a wider range of grass species than sable. Sable were narrowly selective for green grass whereas buffalo and zebra grazed grass within a wider range of phenological stages, including completely brown grass. The three grazers overlapped in habitat features prevailing in foraging areas and, contradicting expectations, the breadth of habitat features in areas used did not differ among grazers. The low density sable used resources that occurred in restricted areas of the landscape during periods of food abundance, but the resources required became sparser as the dry season progressed prompting sable to move notably more widely during the late dry season. Buffalo and zebra used space more evenly suggesting that resources supporting these high density grazers were abundant and widely distributed in the landscape year-round. The sections of the landscape supporting the low density sable were distinct from areas frequently used by high density grazers. Overall, results showed that resource partitioning occurred through spatial separation of core grazing areas, despite overlaps at lower spatial levels of resource use. The narrow tolerance of resources by sable at the grass species and grass features level suggests that the dry season is a more stressful period to sable than to more common grazers due to a progressive decrease in the availability of resources favoured by sable. This could contribute to explaining why sable occur in low density as well as the decline and the lack of recovery by the population.

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DEDICATION

This thesis is especially dedicated to you my daughter Nayra. I have not been there for you during your younger ages, but I trust this thesis will be an inspiration for your education.

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INTRODUCTION

THE NEED FOR THE STUDY

Species richness of natural biological communities and the rarity of species have been used widely in the species approach of setting priorities for biodiversity conservation (Bibby 1998; Margules and Pressey 2000). The diversity of the large herbivores in the Kruger National Park (KNP) is higher than in other protected areas, including low density and highly abundant species that coexist. However, the populations of sable antelope (*Hippotragus niger*) and other less common antelope species such as roan antelope (*Hippotragus equinnus*) and tsessebe (*Damaliscus lunatus*) have registered persistent declines since 1987 (Harrington et al. 1999; Grant and van der Walt 2000; Owen-Smith and Ogutu 2003). For instance, sable antelope numbers decreased from a peak of about 2240 in 1986 to about 550 individuals in 1996. Roan antelope and tsessebe experienced more severe decline than sable antelope (Grant and van der Walt 2000). This precipitous decline represents a management concern for biodiversity conservation in the KNP, because the observed declines are beyond the thresholds of potential concern (TPC) established according to population numbers and rate of decline, defined for adaptive management of low density antelope species in the KNP (Grant and van der Walt 2000). Therefore, there is a risk of these species being lost from the KNP biodiversity.

Harrington et al. (1999), Owen-Smith and Mills (2006) and Owen-Smith and Mills (2008) documented that elevated adult mortality due to predation by lion (*Panthera leo*) was the primary cause of the decline of low density antelope species. Harrington et al. (1999) and Owen-Smith and Mills (2006) suggested that the abundance of lions increased in the main range of low density antelope in the north of the park, following an immigration of plains zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) during the El Niño-related drought of 1982/3, because water was abundant and widely distributed in the form of artificial boreholes supplying drinking troughs to animals. African buffalo (*Syncerus caffer*) became more vulnerable to predation during the 1982/3 drought, but the population subsequently recovered in northern KNP (KNP Ecological

Aerial Survey), also benefiting from the artificial increase in water availability in habitats otherwise dry and not suitable for highly water dependent grazers such as buffalo. Deterioration of habitat conditions and forage resources associated with the persistence of annual rainfall below long term average, decrease in dry season rainfall and increase in temperature (Ogutu and Owen-Smith 2003; Owen-Smith and Ogutu 2003) might have contributed to the sable decline by reducing the availability of green forage during the dry season, which is potentially a period of nutritional stress for herbivores. Malnourished animals are weaker and more vulnerable to predation than well nourished animals (Owen-Smith and Ogutu 2003).

In addition to attracting and supporting the build up of the lion population and contribute to the sable decline through apparent competition (Holt 1977), zebra and buffalo have similar resource requirements to sable because the three grazers prefer to graze medium-tall grass (Skinner and Chimimba 2005). Therefore, zebra and buffalo could contribute to sable decline through depletion of food resources during the critical dry season. Putman (1996) suggested that opposite trends between populations of ecologically similar species may indicate competition for resources. However, the co-existence between the declining sable and the grazers that increased in abundance in northern KNP may indicate that resources are partitioned between these species reducing potential for competition.

Resource selection by animals occurs at different hierarchical spatial levels, ranging from the selection of geographical ranges to the selection of plant parts within feeding stations (Johnson 1980; Senft et al. 1987). However, the hierarchical level of resource use at which resource partitioning or competition among grazers effectively occurs has not been explicitly investigated. In addition, low density grazers have always been excluded from studies of resource partitioning. Therefore, the ecology of low density antelope species is poorly understood, specifically the issue of how these species coexist along with much more abundant and potentially competing species has not been addressed.

This project was designed as part of an umbrella research project of the Centre for African Ecology of the University of the Witwatersrand. The umbrella aim of this project was to improve the understanding of the ecology and identify the factors responsible for

the declining abundance of rare antelope species in the Kruger National Park. The aim of this specific study was to contribute towards a better understanding of resource partitioning between low and high density grazers at different spatial scales and thereby contribute to the conservation of low density species vulnerable to extirpation. The starting objectives of the study were as follows:

1) To assess diet separation between low density and high density grazers and assess diet breadth at the grass species and plant parts levels
2) To establish a comparative analysis of habitat use between the low density sable and the high density, zebra and buffalo
3) To establish distinctions in space use patterns between the low density, sable and the high density grazers, buffalo and zebra
4) To investigate competitive interactions between sable, buffalo and zebra in the use of space
5) To identify critical periods of the year for sable nutrition

LITERATURE REVIEW

Rare and low density species

Gaston (1997) defines rarity as a restriction in number or geographical distribution of a species caused by biological or physical factors; and defines low density species as those that occur over large geographic ranges but never abundant. Species are at most risk of extinction if they have limited distributions or occur at low local abundance (Johnson 1998). According to Rosenzweig and Lomolino (1997), the main causes of rarity and/or low density of a species may include species habitat selectivity and narrow tolerance, species dependency on habitats that become rare as a result of climate change and species vulnerability to competitive interactions or to predation.

Brown (1984) suggested that low density species use a narrower range of resources than high density species, but Seagle and McCracken (1986), Gaston and Kunin (1997) and Gregory and Gaston (2000) suggested that low density species might use a wide range of resources, but the resources most contributing to supporting the

population occur at low abundance or in more restricted areas, whereas high density species are supported by locally abundant and widespread resources. Therefore, to survive, low-density species need to be superior competitors if these species overlap in preferred habitats with high density species, otherwise low density species will be excluded from the preferred resources and forced to utilize alternative resources, which might lead to species decline and extinction (Rosenzweig and Lomolino 1997). Rosenzweig and Lomolino (1997) suggested that rare species might be quite common where they are not restricted to a subset of habitats by negative interactions, such as competition and predation.

For plants, Campbell et al. (1991) demonstrated that dominant species contributing most to the local plant biomass utilize soil mineral resources over a broad scale and tend to be common due to their ability to dominate resource capture. Subordinate species contributing less to local plant biomass are resource specialists that depend on the precision of exploitation of small patches of soil nutrients between patches depleted by dominant plants, and tend to be rare. According to Hodson (1993), common butterflies utilize more productive habitats than rare ones and butterflies that use a narrow range of food plants tend to be rarer than butterflies that exploit a wider range of food plants.

Temporal and spatial heterogeneity can reduce the average resource utilization by superior competitors and can create competition refuges, allowing inferior competitors to invade and persist (Atkinson and Shorrocks 1981; Hanski 1981; Hanski 1983). Accordingly, the pre-emption of small discrete patches by low density species could allow the coexistence between a low density and a competitively superior abundant species (Gaston and Kunin 1997). This suggests that heterogeneity and spatial scaling has an important role in resource partitioning and coexistence between low density and high density species.

Spatial scale of resource partitioning among large herbivores

Resource selection by large herbivores occurs at different hierarchical levels, including landscape, habitat or vegetation type, feeding patch, feeding station and plant level (Senft et al. 1987; Bailey et al. 1996; WallisDeVries et al. 1999). Decisions made by animals at these levels influence animal movements and hence the spatial distribution of populations (Turchin 1991). Therefore, resource partitioning and competition between foraging animals could take place at one or more of these levels of ecological resolution (Jarman and Sinclair 1979; Schoener 1986; Owen-Smith 1989). Furthermore, Senft et al. (1987), Bailey et al. (1996) and WallisDeVries et al. (1999) argued that, in order to select, herbivores must perceive differences among or within these levels so that they can discriminate and select among alternatives. The spatial dimension of each level of resource selection is influenced by body size and foraging strategy of the herbivore (Bailey et al. 1996; Ritchie 2002) and by group size (Fryxell 1991).

Body size determines the abundance of food resources that a species can perceive (Prins and Olff 1998; Ritchie and Olff 1999; Ritchie 2002). Larger herbivores require higher food quantity but can tolerate lower nutrient concentrations within their food and have greater range of acceptable food species than smaller species, which require less quantity of food, hence detect many small food patches, but require higher nutrient concentrations within it (Bell 1970; Jarman 1974; Geist 1974; Owen-Smith 1988). Owen-Smith (1989), Ritchie (2002) and Cromsigt and Olff (2006) stated that ecologically similar large herbivores may select the same habitat but differ in the dimension of habitat patch selected. Therefore, large herbivores can be limited by the availability in the environment of patches large enough to detect (Ritchie and Olff 1999). This results in larger herbivores using widespread resources and making little use of sparse resources and of resources occurring in small and discrete patches. du Toit and Owen-Smith (1989) observed that by feeding in habitats not selected by smaller species, larger species were found over a large range of habitats, whereas, smaller selective feeders tended to have smaller range of acceptable food items and used fewer available habitats.

Fryxell (1991) suggested that animals aggregate on habitat patches offering the highest quality of food and Ritchie (2002) pointed out that patchy distribution of food resources and habitats enhances coexistence through resource partitioning because spatial

heterogeneity at different hierarchical levels of resource selection suggests more choices available for foraging animals. Accordingly, establishing ecological separation among sympatric ungulates depends on the level of resource selection at which resource partitioning is evaluated.

At the broader landscape animals select home ranges, which may differ in size and location among herbivore species that differ in body size, among populations of the same species occupying areas that differ in the productivity of the available habitat and among individuals of the same population under different conditions of food availability and predation pressure (McLoughlin and Ferguson 2000). Accordingly, resource partitioning among grazers could be through spatial separation governed by differences in preferences or in tolerance to resource conditions and security prevailing in different sections of the landscape during the seasonal cycle. Within home ranges, the selection of vegetation types/habitat types is influenced by the quantity and quality of food resources, topography (catena position), proximity to water, proximity to salt licks and predation risk (Senft et al. 1987). Bell (1970) found that large herbivores differ in their proportional use of different catena positions because different levels of the catena differ in grass biomass, phenology and quality (Bell 1970; McNaughton 1985). Catena position also influences grazing succession (Vesey-FitzGerald 1960; Bell 1970), whereby larger grazers feeding on tall and fibrous grass such as zebra and buffalo move first from the nutritious short grass growing on uplands favoured during the wet season to graze the tall and fibrous grass prevalent on bottomlands during the dry season, creating separation and facilitating access to short grass for grazing by smaller short grass grazers that remain for longer periods in the uplands (Bell 1970). Grassland height, grassland species composition, woody canopy cover (Jarman and Sinclair 1979; Sinclair 1985; Ben-Shahar 1995; Owen-Smith 2002) and grass greenness (McNaughton 1985; Sinclair 1985) influence resources and/or habitat conditions for large grazers. Therefore, resource partitioning could be through distinct habitat preference (Rosenzweig 1991; Johnson et al. 2000; Owen-Smith 2002) associated with differences among species in preference for these habitat features.

Within the habitat patches selected, grazing herbivores might be ecologically separated by selecting different grass species, grass height or plant parts (Sinclair 1985;

Voeten and Prins 1999). For example, in the Hluhluwe-iMfolozi Park, South Africa, Kleynhans (unp.) reported that buffalo fed mainly on tall grass patches of mature *Themeda triandra*, while zebra also grazed tall grass but mainly *Panicum maximum*. Among large grazers, feeding specialization is generally revealed by the selective feeding on specific plant parts because plant parts differ in their nutritional quality (Bell 1970; Owen-Smith 1982; Fryxell 1991). Feeding specialization increases with decreasing body size because the high metabolic rate of smaller animals require plant parts with high concentration of protein and energy, whereas larger animals tolerate lower concentrations of nutrients within their food, hence have a greater range of acceptable plant parts than smaller herbivores (Bell 1970; Jarman 1974; Geist 1974; Owen-Smith 1988). Among large herbivores of similar body size, relatively narrow mouth grazers such as topi (*Damaliscus lunatus*) (Gordon and Illius 1988) select for green leaves over stems from tall grass swards (Duncan 1975; Owen-Smith 1982; Murray 1993; Murray and Brown 1993), whereas broad-mouthed grazers such as wildebeest (Illius and Gordon 1988) are less able to select for grass leaves from stems of tall grass, hence favour short grass (Bell 1970; Owen-Smith 1989; Murray 1993; Murray and Brown 1993; Arsenault and Owen Smith 2008). According to Owen-Smith (1982), ungulates that use their tongue to pull grass into the mouth, such as buffalo, are less able to select plant parts from grass tufts and ungulates with both upper and lower incisors such as zebra also have difficulties in selecting leaves between grass stems.

Competition

Mac Nally (1983) and de Boer and Prins (1990) pointed out that if species overlap in resource use and the resource supply is limited, these species might compete for the resources. According to Owen-Smith (1989, 2002), among large herbivores competition is mainly exploitative through the depletion of grass resources during seasons of food limitations. Because decisions on resource use occur at different hierarchical levels, competition should occur if ungulates overlap at all levels, i.e. home range, habitats, grass species and plant parts.

Rosenzweig (1973) suggested that species coexist because they have distinct resource preferences. However, differences in resources used by a species in the presence versus absence of potential competitors, demonstrated experimentally in rodents, suggest that coexisting species might be sharing preference for resources and the divergence in resource use might be a result of competition (Rosenzweig 1991).

Smaller herbivores are expected to be superior competitors to larger herbivores on high quality but sparse resources (Prins and Olff 1998; Owen-Smith 2002; Murray and Baird 2008), but should be out-competed by larger herbivores when food is abundant but of poor quality (Owen-Smith 2002). Non-ruminants are potentially out-competed by ruminants if food supply is limited, due to their low digestive efficiency and low food retention time in the gut (Illius and Gordon 1992). Gaston and Kunin (1997) suggested that low density species are fugitive species with lower competitive abilities than abundant species. Hanski (1983) and Wang et al. (2002) added that competitively superior locally abundant species can exclude locally rare species from local patches of resources. However, aggregation by superior competitors on discrete patches of resources enhances coexistence between species with different competitive abilities (Atkinson and Shorrocks 1981; Inouye 1999), because aggregation leaves out unoccupied patches that are exploited by inferior competitors as competition refuges (Inouye 1999). Accordingly, resource partitioning, although it might be a result of competition rather than distinct resource preference, results in coexistence among species and could explain the abundance and species richness of the African grazers assemblage despite sharing the same food resources (Jarman and Sinclair 1979; Prins and Olff 1998; Murray and Baird 2008).

Apart from exploitative competition, apparent competition, whereby some prey species support the build up of predator numbers, resulting in an increased predation pressure on other prey species (Holt 1977), might also influence resource use and spatial separation between the prey species sharing the predator. Owen-Smith and Mills (2008) documented that shifting from principal to alternative prey species by lions was the prime cause of decline of some ungulate populations in the KNP, including sable. Movements of ungulates to avoid concentrations of potential competitors and/or principal prey for

predators have been documented in East Africa (Sinclair 1985) and in North America (Johnson et al. 2000; Stewart et al. 2002; James et al. 2004).

RESEARCH DESIGN

I selected sable antelope to represent the low density grazer and buffalo and zebra to represent the high density grazers, based on data across their distribution ranges (Chapter 1). Sable antelope is a medium sized ruminant grazer, with a mean adult female weight of about 220 kg (Wilson 1968 cited by Owen-Smith 1988). It is a gregarious, sedentary species with a typical group size of 15-25 individuals (Estes 1991). Plains zebra is a medium sized non-ruminant grazer, with a mean adult female weight of about 310 kg (Wilson 1968 cited by Owen-Smith 1988; Skinner and Chimimba 2005). Plains zebra occur in non-territorial coherent groups of about 6-7 individuals on average, but these family groups may aggregate during the dry season to form larger groups (Estes 1991). Buffalo is a highly gregarious and non-migratory ruminant grazer with herd size of up to 2500 individuals (Skinner and Chimimba 2005); but occurring in herds of less than 500 individuals on average in the KNP (Winnie et al. 2008) and in neighbouring private nature reserves (Funston et al.1994; Ryan et al. 2006). The mean adult female buffalo body mass is about 520 kg (Pienaar 1969).

The three species share the trophic feature of all preferring to graze medium-tall grass (Skinner and Chimimba 2005) and have moderate differences in body mass, which suggests that the potential for competition among these grazers does exist. However, differences in group size and mobility may suggest differences in the spatial scale of foraging, which may enable these grazers to co-exist through resource partitioning. The other species that could compete for resources with medium-tall grazers is the mixed-feeder African elephant (*Loxodonta africana*). However, this species was excluded from the study because time would have been a constraint to collect data simultaneously on four species with the level of detail covered in this study.

The study was conducted to the south of the Punda Maria Rest camp in the far north-west of the Kruger National Park (KNP), South Africa, within an area comprising about 600 km^2 (Figure 1). This area was selected for the study because: 1) it is part of the

sable core distribution range in the park, 2) there was an increase in the abundance of zebra in this region after the 1982/3 drought and although buffalo declined during the drought this species remained abundant in this area and 3) the decline of sable in this region was more severe than further south in the park.

Data collection covered a period of 17 months (June 2006 – October 2007). However, while data on the use of space by each grazer and on species interactions in the use of space were collected through the entire period, collection of field data on habitat use, forage selection and nutrition was restricted to the dry seasons of 2006 (June – October) and 2007 (May – September) and to the first month of the early wet season of both years (November 2006 and October 2007). Fieldwork was limited to dry season and early wet season because these are the periods of lowest food quality and quantity during the seasonal cycle, respectively. Therefore, competition for food and nutritional limitations are more likely to occur during these periods than during any other time of the year.

THESIS OUTLINE

This thesis has been written in several chapters, each with a format of a draft manuscript for publication. Contrary to the traditional thesis format, this format will enable a prompt submission of papers for peer review and publication in scientific journals, after the submission of the thesis to the University.

In the introduction I justified the need for the study, presented the aim and objectives and reviewed the relevant literature on factors influencing patterns of species abundance, and on the influence of the spatial scale of foraging on resource partitioning and/or competition among large herbivores. Five main chapters were written, addressing resource use and interactions between grazers at different hierarchical spatial scales.

In chapter 1 I assessed whether resource partitioning between low density and high density grazers occurred through differences in diet selection. Accordingly, I presented distinctions or similarities between low density and high density grazers in tolerance to grass species and grass features, diet overlap and distinctions in diet breadth during periods of the dry season that differed in food availability.

In chapter 2 I investigated whether low density and high density grazers partition resources by using foraging areas with distinct habitat features or that these grazers potentially compete for forage resources due to similarities in habitats used. Therefore, I presented differences or similarities in habitat features prevailing in foraging areas used by sable and by the high density grazers, highlighting the habitat features most influential to ecological separation between grazers at the habitat level.

In chapter 3 I assessed how differences in precision and/or tolerance to forage resources at the grass species and grass features level influenced patterns of home range use by low density and high density grazers. Accordingly, I presented distinctions in the extent and location of the total and core range of the herd of the low density, specialist grazer sable and of herds of high density and generalist grazers buffalo and zebra in relation to the seasonal changes in availability and distribution of water and forage of adequate quantity or quality. I also presented distinctions in the intensity of metabolic use of space between grazers that differ in feeding specialization, body size and group size.

In chapter 4 I investigated whether resource partitioning between low density and high density grazers occurred through separation of core grazing areas or whether these grazers potentially compete for resources by using overlapping core grazing areas. Therefore, results presented in this chapter included separation or overlap in monthly and seasonal total and core ranges, spatial displacement of sable from core areas by abundant grazers and separation distances between sable and abundant grazers during foraging periods of the day. I also assessed whether differences in body size between sable and buffalo resulted in grazing facilitation to sable.

In chapter 5 I assessed whether low forage quality could be a contributory factor to the failure of the sable population to recover from the decline. I compared faecal nitrogen, phosphorus, sodium and crude fibre on the KNP sable populations with these indices of diet quality on populations of sable that are thriving elsewhere as well as with faecal concentrations of these nutrients on populations of similarly sized grazers grazing under similar conditions in the KNP and elsewhere.

In the general conclusion, I pointed out the main distinctions between sable, buffalo and zebra in resource use at different levels of resource selection that can help understand why sable occur in lower density than most other grazers. I summarised and

evaluated the findings of this research in relation to expectations based on published literature on resource partitioning within guilds and highlighted the importance of scale of assessment for a better understanding of resource partitioning and/or competition within species assemblages, particularly between species attaining different regional densities. I also presented the implications of the research findings for park management.

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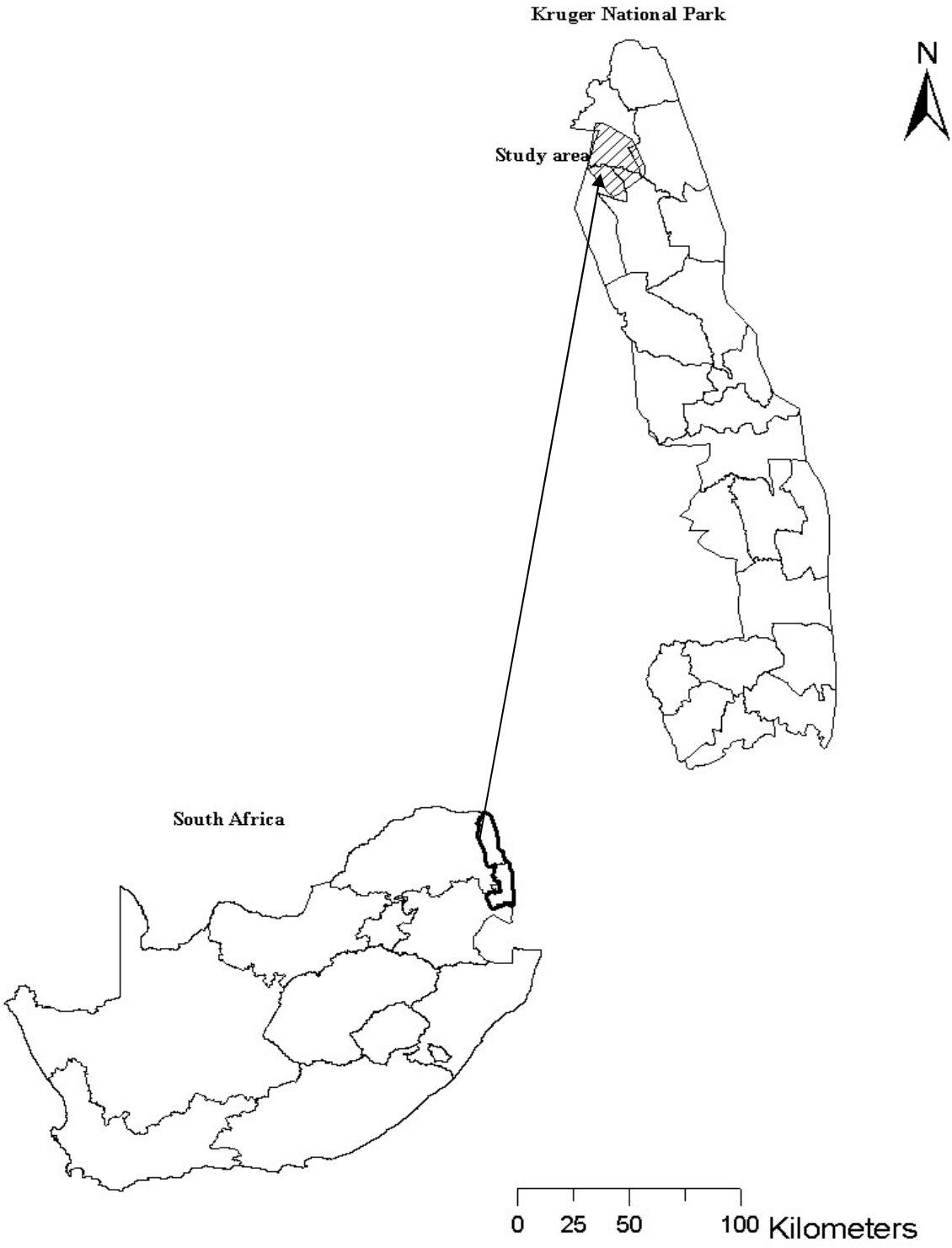


Figure 1. Location of the study area in the KNP and location of the KNP in South Africa

CHAPTER ONE

Precision versus tolerance in food niche of low-density and high-density grazers: sable antelope, zebra and buffalo

Abstract

The aim of this investigation was to assess diet breadth and diet overlap between the low density sable and the high density grazers buffalo and zebra occupying the same landscape during the same period. GPS-GSM collars were fitted on females from herds of these grazers and feeding sites were located by means of GPS tracking. Grass greenness, grass height, number of stems of grazed and ungrazed grass species and the number of bites taken from each grass species were recorded in feeding sites used by sable, buffalo or zebra during the dry seasons of 2006 and 2007. Distinctions between grazers in grass species selection were assessed by comparing the availability and acceptability of grass species in feeding sites using loglinear analysis. This analysis was also applied to establish the grass features that influenced the acceptability of grass, and hence establish tolerance or narrowness to plant parts by each grazer. Diet composition was determined as the proportion of bites taken on each grass species by each grazer and as the proportion of fragments of each grass species on faecal samples. Diet breadth was estimated using the Levins index and diet overlap was assessed using the Pianka's index. Sable were more selective for green and tall grass than buffalo and zebra, which were more tolerant for grass features. Sable showed a narrower range of highly accepted grass species than buffalo, but sable were less distinct from zebra in their acceptance to grass species. The acceptability of grass species by buffalo was more even across grass species than the acceptability by sable and zebra. The diet breadth did not differ among grazers; 4-5 grass species made up about 75% of the diet of the three grazers during all seasons. However, during periods of severe food limitations the diet of sable became more diverse because preferred food species were of limited availability, and the overlap in diet composition decreased during this time because the diet of buffalo and zebra remained dominated by the most abundant grass species. The overlap in diet composition suggests potential for food competition. The narrower selectivity shown by sable suggests that during years

with below average rainfall sable might be limited by the shortage of preferred grass species and green grass, which could have contributed to the decline or lack of recovery by the population. The more generalist feeding at grass species and plant parts levels could explain why buffalo and zebra occur at high density in the KNP and elsewhere.

Introduction

Species assemblages are composed by mostly rare species and few common species (Kunin and Gaston 1993). Two competing hypotheses explain patterns of species abundance within species assemblages, the niche breadth hypothesis (Brown 1984) and the niche position or resource availability hypothesis (Gaston and Kunin 1997; Gregory and Gaston 2000). According to Brown (1984) low density species are resource specialists that depend on a narrow range of resources, whereas abundant species are generalist consumers with broader ecological plasticity, and hence able to exploit a wide range of resources and environmental conditions. However, according to Gaston and Kunin (1997) and Gregory and Gaston (2000), low density species might use a wide range of resources, but the resources most contributing to supporting the population occur at low abundance or over more restricted areas, whereas abundant species are supported by locally abundant and widespread resources.

Campbell et al. (1991) demonstrated that dominant plant species contributing most to the local plant biomass utilize soil mineral resources over a broad scale and tend to be common. Subordinate species contributing less to local plant biomass are resource specialists that depend on the precision of exploitation of small patches of soil nutrients between patches depleted by dominant plants, and tend to be rare.

The vegetation in the tropics is heterogeneous in food resources supporting large herbivores, because it encompasses different plant forms and plant species with different chemical and physical properties (McNaughton 1983). This provides large herbivores with an opportunity to select some food types and avoid others. The diversity of food niches explains the coexistence among grazers feeding on the same grass resources (Prins and Olff 1998; Murray and Baird 2008).

The quality and quantity of food resources for large herbivores vary seasonally in response to seasonal variation in rainfall (Owen-Smith 1982; O'Reagain 2001). Food quality declines with the progress of the dry season due to a progressive reduction in the proportion of the more nutritious green leaves in the sward, whereas food quantity declines due to consumption of grass by grazers and progressive reduction in grass height during this period of grass dormancy (Owen-Smith 1982, 1988). Among large grazers feeding specialization decreases with increase in body size and is generally revealed by the selective feeding on specific plant parts because plant parts differ in their nutritional quality (Bell 1970; Owen-Smith 1982). Accordingly, specialist grazers select leaves in preference to stems and green leaves in preference to brown leaves (O'Reagain 2001). Ruminants have higher digestive efficiency but are less tolerant to fibre than non-ruminants of similar body size, which due to their hindgut fermentation tolerate plant parts with high fibre content (Bell 1970, 1971; Illius and Gordon 1992).

Differences between grass species in greenness retention, leaf production and quality lead grazing animals to prefer some grass species and neglect others (O'Reagain and Mentis 1989). Selective feeding results in a progressive reduction in the standing biomass of preferred grass species through the dry season until the first wet season rains promote the regrowth of these depleted grass species (Owen-Smith 2002). Foraging theory predicts that foraging animals widen their diets to incorporate less favoured food types, as the availability of preferred food resources declines towards the end of the dry season (Owen-Smith and Novellie 1982; Stephens and Krebs 1986). The widening of the diet by grazers could be through widening the range of grass species grazed (O'Reagain and Mentis 1989; Macandza et al. 2004), but also through increasing tolerance to brown grass, stems or less favoured grass height as the dry season progresses. Owen-Smith (2002) argued that hungry herbivores face the dilemma of how to be narrowly selective or broadly tolerant when food resources are abundant but most of which is of low nutritional quality such as during the late dry season.

Similarity in preferred food species and plant parts among co-occurring ungulates could result in competition during periods of limited food supply such as the dry season (Owen-Smith 1989; de Boer and Prins 1990; Prins 2000). Jarman (1971), Holbrook and Schmit (1989) and Owen-Smith (1989) suggested that competition could be weak during

the dry season if grazers use different alternative food resources when the availability of commonly preferred ones is limited. Ritchie (2002) stated that each species of mobile animal use some resource not used or less used by potentially competing species. Ritchie (2002) added that if that "exclusive resource" is abundant, the species can survive within the species assemblage regardless of the intensity of competition on shared resources. This reduces the intensity of competition and promotes coexistence and species richness of grazer communities (Prins and Olff 1998). However, changes in the range of resources used in the presence or absence of potential competitors demonstrated experimentally in rodents (Holbrook 1973; Holbrook and Schmitt 1989) suggest that coexisting species might be sharing preference for resources and the divergence in resource use might be a result of competition (Rosenzweig 1991).

Across their distribution range, sable antelope (*Hippotragus niger*, 220 kg) occur in lower regional density than most other grazers, including buffalo (*Syncerus caffer*, 520 kg) and plains zebra (*Equus burchelli*, 310 kg) (Figure 1). In the Kruger National Park (KNP, ~ 20000 km^2), South Africa, the general occurrence of sable at low density was accentuated by the precipitous decline that the population of this species suffered after 1987 (Grant and van der Walt 2000; Owen-Smith and Ogutu 2003; Ogutu and Owen-Smith 2005). Sable numbers dropped from a peak of 2250 animals (0.11 sable/km^2) in 1987 to about 550 individuals (0.03 sable/km^2) in 1996 (Owen-Smith and Ogutu 2003). By 2008, sable population in the park was probably less than 450 individuals. However, the larger ruminant buffalo and the non-ruminant zebra are more abundant in the park and occur in higher densities than sable (25 150 buffaloes, ~1.3 buffalo/km^2 and 32 000 zebras, ~ 1.6 zebra/km^2).

Food resources supporting the low density sable have been investigated by Grobler (1981), Parrini (2006) and Magome et al. (2008), whereas Macandza et al. (2004) documented buffalo diet during different stages of the dry season and Ben-Shahar (1991) and Bodenstein et al. (2000) studied zebra diet. These studies showed similarities among these grazers in the botanical composition of the diet and in favouring medium-tall and green grass for grazing. This suggests potential for food competition during periods of the year of limited food availability like the dry season. However, these studies were limited at documenting seasonal patterns in the use of food resources by each grazer

separately, without assessing the use of these resources by other grazers occupying the same regional landscape during the same time. Therefore, the aim of this paper was to assess the degree of diet overlap among grazers and to assess the diet breadth of low density and high density grazers at the grass species and plant parts level of resource selection. I hypothesize that:

1. Sable, being a low density, smaller ruminant should feed selectively on grass retaining a higher proportion of green leaves than the grass grazed by the high density larger ruminant buffalo and the non-ruminant zebra, which should be generalists at the plant parts level by tolerating a wider range of grass physical features, including brown grass
2. Following the niche position theory, the diet of the low density grazer, sable, should be composed by grass species occurring in low local availability, whereas the high density grazers, buffalo and zebra, should be supported by locally more abundant and widespread grass species
3. Following the niche breadth theory, the diet breadth of the low density grazer, sable, should be narrower than the diet breadth of the high density grazers buffalo and zebra
4. The diet overlap between sable and buffalo or zebra should decline with the shrinking availability of commonly favoured grass species as the dry season progresses

Methods

Study area

I conducted this study to the south of Punda Maria Camp (22°68'S, 31°018'E) in northern Kruger National Park (KNP), South Africa, within an area of about 600 km^2. I estimated the extent of the study area by joining the outer herd locations using a 100% Minimum Convex Polygon (MCP) in Geographic Information System (GIS) – ArcGIS 9.1, including locations of all collared herds of the three species during the study period (June 2006 – October 2007). The study area was limited by the KNP boundary in the west, by the Shisha River in the East, by the Punda Maria Camp in the North and

southwards the limit of the study area was between the Mphongolo and the Phugwane Rivers. The long term (1960-2007) mean annual rainfall (July-June) at Punda Maria Camp was 600 mm. At Shangoni section, to the south-west of Punda Maria, the long term mean rainfall was 573 mm; at Woodlands section in the south, the mean annual rainfall was 478 mm; whereas at Vlakteplaas in the south-east, the mean annual rainfall was 490 mm (Gertenbach 1980). During the seasonal cycle July 2005 – June 2006, rainfall in the study area was above average. For example, at Punda Maria Camp, rainfall (743 mm) was 24% above long term average and at Shangoni (765 mm) it was 34% above average. However, between July 2006 and June 2007 rainfall at Punda Maria (419 mm) was 30% below average and at Shangoni (284 mm) it was 50% below average. This means that the prevailing food and water conditions for herbivores were more favourable in 2006 than in 2007. About 80% of the rain falls during the wet season that spans from October to March. The dry season extends from April or May to September or October. In 2006 wet season rains began in early November, whereas in 2007 wet season rains began at the end of September (Figure 2). However, during the more severe year of 2007 the study area received dry season rainfall during the first week of July, being 2.6 mm at Punda Maria, 16 mm at Shangoni, 8.5 mm at Woodlands and 9.3 mm at Vlakteplaas.

Geologically the study area is underlaid by rocks of the Soutpansberg group, which consist of fine- to coarse-grained sandstone formations and medium-grained basalt formations (Schutte 1986; Venter 1990). There is also a portion of Ecca shale of the Karoo system in the east and a portion underlaid by granitic gneiss consisting of coarse sandy and loam soils towards the southern limit of the study area (Schutte 1986; Venter 1990; Joubert 2007). Based on woody vegetation species composition and physiognomy, Gertenbach (1983) described four landscape types covering the study area: (1) *Combretum* spp woodland on sandstone and granitic formations, (2) *Colophospermum mopane* woodland on Ecca shale, (3) *C. mopane*/*Acacia nigrescens* woodland mostly on granitic gneiss and (4) *Pterocarpus rotundifolius*/*Combretum* spp woodland on basalts of the Soutpansberg group.

In mid July 2006 a prescribed fire burnt 28% of the study area to the west, but no grass regrowth was available until the first wet season rains in early November. In mid September 2007, an accidental fire burnt the south east of the study area and grass

regrowth became available three weeks later, following rains at the end of September. Besides sable, buffalo and zebra, other ungulates feeding on the grass layer included grazers such as waterbuck (*Kobus ellipsiprymnus*) and white rhinoceros (*Ceratotherium simum*) and mixed feeders such as elephant (*Loxodonta africana*) and impala (*Aepyceros melampus*). The last total area Ecological Aerial Survey (EAS) in Punda Maria was conducted in 1993 and indicated that there were 19 sable antelope, 140 buffalos, about 570 zebra, about 100 elephants, 650 impala, 20 waterbuck and 3 white rhinoceros (KNP census data). Despite being relatively abundant and widespread in the study area, during the dry season elephant feed mainly on browse (Jarman 1971) and about 50% of the diet of impala during the dry season is also browse (Codron et al. 2007). Apart from occurring in low numbers, waterbuck and white rhinoceros are restricted to areas near the Mphongolo River in the south of the study area. Therefore, the grazing impact of these grazers is negligible, with the exception of elephant that can contribute to grass depletion when this species feed on grass during the wet season.

Research design

A total of nine Global Positioning System (GPS) - cellular phone (GSM) collars obtained from Africa Wildlife Tracking (http://www.awt.co.za) were placed on sable, zebra and buffalo at the end of May 2006. Three adult females from two sable herds, four adult females from four herds of zebra and two females in one buffalo breeding herd were fitted with collars. Collars were fitted on adult females to ensure that the movements of the individuals bearing the collar represented the movements of the herds because adult females remain within the breeding herds (Estes 1991; Skinner and Chimimba 2005), except during the calving period of sable when females move from the herd to the hidden calf and vice-versa (Estes and Estes 1974; Skinner and Chimimba 2005). On a sable herd numbering 13 animals two females were fitted with collars and on a smaller herd numbering 5 animals one adult female received a collar. However, the three collared females joined in July 2006 and remained together during the duration of this study, except for a few weeks during the early wet season when one of the collared females separated from the other two females. Therefore, there was only one sable herd

in the study area that occasionally split for short periods. In each zebra herd of about 6-7 animals, one adult female received a collar. In the buffalo herd of approximately 400 animals, collars were placed on two adult females. The two buffalo females bearing collars split in July 2006 between two groups, each assumed to have about 200 animals, and stayed apart for the rest of the dry season of 2006 and wet season of 2006/2007.

In June 2007, four additional collars were fitted, being one on sable, two on zebra and one on buffalo. Collars were fitted on female sable and buffalo from the same herds that had the collars fitted in May 2006 and on two female zebra from non-collared herds with home ranges overlapping with sable range. At the time of deploying these additional collars, the sable herd numbered 21 individuals. One zebra herd numbered 13 animals at the time of fitting the collar and one had 6 animals. However, the zebra herd of 13 animals split at the end of June 2007 to remain with 7 individuals. The buffalo collar was placed on the herd that had the animal bearing the collar AM152 fitted in May 2006. At the time of fitting the collar in June 2007, the buffalo herd numbered about 400 individuals, suggesting that the two groups of buffalo that were split during the dry season of 2006 and wet season of 2006/2007 had joined again. Fitting more collars was done to ensure that herd locations were obtained for at least one additional dry season in the case of eventual failure of the collars placed on animals in May 2006.

The GPS of the collar saved the geographical coordinates of the herd and through its cellular phone (GSM) component these coordinates were sent by Short Message Service (SMS) to a website (http://www.yrless.co.za) from which I downloaded these data. I initially scheduled the collars to record the GPS coordinates of the herds every six hours, at 2:00, 8:00, 14:00 and 20:00. Observations by Sinclair (1977) and Prins (1996) on buffalo, by Parrini (2006) and Magome et al. (2008) on sable and by Beekman and Prins (1989) and Robinson (unp.) on zebra suggest that most of the feeding by these grazers occur mainly in the morning and late afternoon. Accordingly, during days of observation of each herd I adjusted the schedule of the collar to record the GPS coordinates of the herd hourly to obtain detailed data on the spatial location of the herds during the main potential feeding periods for the animals in the morning (6:00 – 10:00) and late afternoon/early evening (16:00-20:00) and to ensure that feeding locations were obtained for the assessment of diet selection.

Population sizes for the study species within the study area were about 20 sable antelope, 200-300 zebras and 400 buffaloes. The populations of sable and buffalo were estimated as being equal to the combined sizes of the herds encountered during animal captures to deploy collars. At any time during this study 4-6 zebra herds were collared, corresponding to about 15-20% of the zebra herds encountered in the study area, whereas the remaining 80% of zebra herds that were encountered during field work were not collared. The total number of zebra herds, collared and non-collared was 30-40. I multiplied the number of herds by herd size of 7 animals, which resulted in a total estimate of 200-300 zebras.

Field data collection

I made plant-based feeding observations during the dry seasons of 2006 (June – October) and 2007 (May – September) and the early wet season of both years (November 2006 and October 2007). I conducted the study during these times because these are the times of limited food availability for large mammalian herbivores in African savannas (Scoones 1995; Owen-Smith 2008) and it is when exploitative competition among grazers is more expected. Therefore, result will reveal distinctions or similarities in the use of food resource during the critical periods of the year. I considered the critical period as ended and stopped feeding observations when the study area had received at least 20 mm of rainfall and more than 50% of the grass was green. Following these conditions, in 2006 rainfall began in early November and I collected feeding data until the end of November, whereas in 2007 rainfall began at the end of September and I collected data until the end of October. Therefore, data collected in November 2006 and October 2007 reflects food availability and patterns of diet selection during the early wet season period, which is of high food quality but low quantity.

To locate feeding areas I downloaded the GPS locations of areas used by the animals and went to these areas using a hand-held GPS unit. I visited sites used by the herds the previous day or at least a six hours lag was considered between the use of a feeding site by the animals and the recording of the grazing of grass species. This time lag ensured that fresh feeding could still be identified while avoiding encounters with the

study animals and interference with their movements. I visited areas used by each grazer two days each week and recorded feeding on 1-5 feeding sites (Bailey et al. 1996; Owen-Smith 2002) used by the herd during each morning or afternoon foraging session. Effort of data collection was distributed among collared zebra and buffalo herds, data were pooled across herds such that inference about diet selection was made at the population level (study design 1, Thomas and Taylor 1990). Distributing sampling effort between buffalo and collared zebra herds consisted of weekly alternating the herd of these species to be tracked for data collection, i.e. feeding observations were scheduled to include all the collared herds to obtain an unbiased sample of the diet of each of the study herbivore species.

From the position where the hand-held GPS unit indicated zero distance to the animal location at the time when the GPS coordinates were sent, hoof prints (tracks), signs of fresh feeding or fresh dung were sought to confirm the recent use of the area by the animals. The nearest signs of recent use of the area by the animal were generally found within less than 3 m radius from the locations provided by the collars, which means that the precision of the GPS location data was often within less than 3 m. However, the precision of the hand-held GPS unit that I used to track animals was within 5 m. Therefore, signs of fresh feeding were sought up to 10 m away from the GPS location. Fresh feeding was confirmed through the observation of fresh bites, identified by a lighter and brighter colour at the surface of the broken grass leaves and stems than old bites. If fresh foot prints or faecal samples of other grazers were present within the feeding site, the site was discarded in feeding observations, to ensure that only recent feeding by the species that provided the GPS herd location was recorded.

At the first identified sign of fresh feeding I placed a 0.7 m x 0.7 m quadrat to represent a feeding station. According to Novellie (1978) feeding station is the area that a foraging animal can harvest food resources without moving its from feet. Additional eight quadrats were placed in the surroundings of the central quadrat, being two quadrats for each cardinal direction (north, south, east and west) in relation to the central quadrat. Quadrats in the same cardinal direction were placed 2 m apart and could be flipped once to any side of the quadrat if there were signs of fresh grazing within 0.7 m from a quadrat that had no fresh grazing. Flipping quadrats was done to ensure that most feeding by the

animals within the feeding site was recorded (i.e. to minimize missing information on feeding, but objectively). If signs of fresh grazing were found in less than 5 out of the 9 quadrats sampled, additional quadrats were evaluated for feeding. These additional quadrats were placed only on the diagonals adjacent to quadrats without signs of feeding. Only one quadrat was placed at each diagonal and it was placed at the nearest sign of fresh grazing from the central quadrat along the diagonal. Therefore, quadrats on the diagonals could be in the north-east, north-west, south-east or in the south-west direction in relation to the central quadrat.

Plant-based feeding observations and measurements

To assess grass species acceptance, I recorded each grass species present within quadrats as grazed or ungrazed. I followed van Oudtshoorn (1999) for the identification and nomenclature of grass species. Grass species that were difficult to identify in the field were identified in the Herbarium of the KNP in Skukuza.

To establish the grass features influencing selection by herbivores, for each grass species (grazed or not grazed) within each quadrat, I recorded grass greenness, grass height and number of stems. I estimated grass greenness as the proportion of green leaves on the plants of each grass species within the quadrat and I classified according to the eight-point scale proposed by Walker (1976): 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100%. I estimated the grass height selected for grazing by each herbivore species by measuring the leaf table height of nearby ungrazed plants of the same species. This height represented the grass height that influenced the selection of the feeding station by the grazer. I classified grass height into four categories: short grass (<10 cm), medium (11-20 cm), medium-tall (21-40 cm) and tall (>41 cm). I estimated an average of the number of stems per tuft of each grass species within each quadrat and defined three categories of steminness: no stems, few stems (1-2) and many stems (≥3).

To assess the relative contribution of each grass species to the diet of each herbivore species, I counted the number of fresh bites taken from each grass species. Each bite was equated to the area of grazed grass leaves or stems that can be covered by a fist. This area approximates bite dimensions for sable and zebra, as estimated from the width of the incisor arcade of 5.66 cm and 5.26 cm, respectively (Gordon and Illius 1988,

Murray and Illius 1996), but the area covered by a fist is smaller than the potential maximum size of a buffalo bite (incisor breadth of 9.32 cm, Gordon and Illius 1988). I also collected composite fresh faecal samples for microhistological analysis of grass fragments following Stewart (1967) and Ego et al. (2003). From each composite faecal sample I identified 50 grass epidermis fragments by comparing the size and shape of the silica bodies, arrangement of cells, form of the stomata and presence or absence of hairs on grass fragments from the faecal samples with these structures from a reference collection prepared from the most common grass species occurring in the study area.

Data analysis

Seasonal subdivisions: I defined seasons for data analysis based on rainfall patterns and on the proportion of green leaves on the grass. For the two years, months when more than 50% of feeding sites used by sable had >10% of grass green were combined into the early dry season and months with no rainfall and more than 50% of feeding sites retaining <10% of grass green were grouped into the late dry season period (Chapter 2). Accordingly, I used the following seasons for data analysis: early dry season of 2006 (June-July), late dry season of 2006 (August – October), early wet season of 2006 (November 2006), early dry season of 2007 (May-July), late dry season of 2007 (August-September) and early wet season of 2007 (October 2007).

Sampling unit and calculations: I considered that the selection of grass species within quadrats that were 2 m apart was not independent, because according to Bailey et al. (1996) the acceptance of a particular food item is influenced by feeding events within the last few minutes. Separation distances between feeding sites used by the animals during successive hours averaged about 200 m for sable and zebra and about 1 km for the larger buffalo herds. Thus, I considered that the decision made by the animals to graze or not to graze a grass species encountered was an independent event between successive feeding sites. Accordingly, following Owen-Smith and Cooper (1987), I calculated site-based availability for each grass species as the number of feeding sites where the grass species was present divided by the total number of feeding sites assessed during each season (2006 and 2007 combined). I estimated site-based acceptability of each grass

species for each herbivore species by dividing the number of feeding sites where each grass species was grazed by the total number of feeding sites where the grass species was present. Due to the binomial distribution of acceptance/rejection values, I computed 95% binomial confidence limits for proportions. To establish distinctions between grazers in the breadth of tolerance of grass species I plotted the frequency distribution of the acceptance frequencies of each grazer during each season, with years combined. In the analysis of acceptability I only included grass species that were present in at least 10 feeding sites used by each grazer per season. I did this to secure large sample size and reliable comparison of acceptability of grass species between grazers.

To assess the effect of grass features on site-based acceptability, for each grazer I averaged the grass greenness, grass height and number of stems for each grass species present in each feeding site during a specific season. I averaged the midpoints of the categories recorded during plant-based feeding observations to obtain the average grass greenness, grass height and stemminness for each grass species in each feeding site. I then grouped the average greenness, combining grass species with same greenness, into the following categories: <5%, 6-10%, 11-20% and >20%. I combined all grass that had more than 20% of leaves green because these were less represented. Greenness in feeding sites used by sable and zebra during the early dry season was always above 5% and during the late dry season only sable found grass with more than 10% of leaves green. I used three categories for stemminness: no stems, few stems (1-2 stems) and many stems (≥3), but only two categories of grass height (<40 cm and > 40 cm) because grass was generally tall. Grass shorter than <20 cm was recorded on feeding sites that were on burnt areas during the first month of the early wet season. However, due to small number of feeding sites sampled, I excluded the early wet season in the analysis of factors influencing the acceptability of grass species.

To detect differences among grazers in tolerance to grass within different categories of grass greenness, I calculated the combined acceptability of grass that was within each category of grass greenness for each grazer, regardless of grass species. Despite differences in rainfall between the two years, the overall greenness available in feeding sites did not differ substantially between same seasons of both years (Chapter 2), with most grass species retaining >10% of leaves green during the early dry season, but

almost all grass species remaining with <10% of leaves green during the late dry season. This lack of difference was primarily because in the drier year of 2007 I started field data collection earlier (in May) than in 2006 (in June). In addition, in July 2007 the study area received rainfall (see study area description), which increased the proportion of green grass in the sward. Therefore, for the comparison of grazers in terms of relative tolerance of grass retaining different proportions of green leaves, I combined the data collected during the early dry season of 2006 and 2007 and combined data obtained during the late dry season of 2006 and 2007. To compare grazers in the monthly proportion of green and brown grass incorporated in the diet, I grouped bites taken by each grazer during each month into categories of grass greenness and calculated the proportions of bites within each category of grass greenness accordingly. To establish distinctions in tolerance to grass height and stemminess, I also calculated a combined acceptability of grass that was within each category of grass height and stemminess for each grazer per season, also combining years.

I considered each morning or afternoon foraging session as the independent sampling unit for the estimation of monthly and seasonal mean dietary contribution of each grass species to each grazer. Within each foraging session, I collected feeding data in up to 5 feeding sites, each including 9 quadrats. Accordingly, I estimated the dietary contribution by dividing the number of bites taken on tufts of each grass species by the total number of bites taken by each grazer during the morning or afternoon foraging session. The resulting proportions were averaged across foraging sessions to obtain the monthly and seasonal diet contribution of each grass species. I also estimated the proportional contribution of grass species to the diet by dividing the number of fragments of each grass species by the total of 50 grass epidermis fragments identified from each composite faecal sample, then averaging the proportions of fragments for each season.

Following Malmquist et al. (1992) I estimated diet breadth of each grazer during each month using the Levins (1968) index of niche breadth:

$$B = 1/\sum_{i}^{n} p_i^2$$

where:

B – diet breadth

p_i - proportion of bites taken on tufts of grass species ($_i$)

n – number of grass species.

According to Feinsinger et al (1981), this reciprocal of the Simpson diversity index, assesses not only the range of resources used, but also the relative frequency with which each resource was used, i.e. it is a measure of diet diversity and dispersion/evenness. The Simpson index varies between 0 and 1, with values closer to zero indicating high diversity and values closer to one indicating low diversity or even distributions of observations across species. Therefore, applying the reciprocal of the Simpson index suggests that a more diverse diet will have a higher value of *B* than a less diverse diet. A generalist grazer will have a more diverse diet than a narrowly selective grazer.

For the calculation of the index of diet overlap, i.e. overlap in grass species, I used Pianka's niche overlap formula (Pianka 1974):

$$O_{jk} = \sum_{i}^{n} p_{ij} * p_{ik} / \sqrt{\sum_{i}^{n} p_{ij}^2 * \sum_{i}^{n} p_{ik}^2}$$

where:

p_{ij} = proportion of bites by sable (*j)* recorded in grass species (*i)*

p_{ik} = proportion of bites by zebra or buffalo (*k)* recorded in grass species (*i)*

Only grass species that contributed ≥5% to the diet of sable during each month were included in the calculations of this index. Grass species with diet contribution <5% were grouped into the category of "other grass species" and were excluded from the analysis of diet overlap because these contributed little to diet separation between pairs of grazers. The overlap index varies from 0 to 1, overlap = 1 indicates complete diet convergence, whereas overlap = 0 indicates complete diet divergence.

Statistical analysis and model selection

Comparison of herbivore species in availability and acceptance of grass species

To compare the availability of grass species in feeding sites used by sable from the availability in feeding sites used by buffalo or zebra, I used a three-way loglinear

analysis (Agresti 1990) (herbivore x grass species x presence/absence). To compare the acceptance frequency of grass species I also used a three-way loglinear analysis between pairs of herbivore species (herbivore x grass species x grazed/not grazed). For these comparisons, I included in the analysis only grass species that were present in at least 30% of the feeding sites sampled during each season, because these grass species were the most common for the three grazers during all seasons. I used the likelihood ratio test for statistical significance. Therefore, from the three way interaction, I removed the factor herbivore and noted the loss in the fit of the model as indicated by the change in the likelihood chi-squared statistics. I did this analysis in SYSTAT 11.0 for Windows (SYSTAT Software, Inc., USA) at $p<0.05$. I examined z-scores from the SYSTAT output to identify cells of the contingency table that contributed to the lack of fit of the model, i.e. to identify the grass species with availability or acceptability that differed significantly between grazers.

To compare the distribution of acceptance values for grass species between grazers I used the Kolmogorov-Smirnov (K-S) two sample test between pairs of grazers during each season. The frequency distribution of acceptance values should differ between a generalist and a specialist grazer. A generalist grazer, i.e. with a broad tolerance to grass species should show an even spread of grass species within different acceptance categories, whereas specialist grazer should reveal a cluster of highly accepted and a cluster of neglected grass species.

Factors influencing the acceptability of grass species

Grass features likely to influence the acceptability of grass species were recorded as categorical predictors of grazing or not grazing each grass species when present in feeding sites. Therefore, I applied loglinear analysis to compare the frequencies of grazing or not grazing grass that was within each category of grass greenness, grass height and number of stems during each season, regardless of grass species. Because grass greenness between the two sampled early dry and late dry seasons did not differ considerably, I pooled data across early dry and across late dry seasons of 2006 and 2007. I did this analysis for each of the grazers separately to establish distinctions between grazers in the grass feature influencing the acceptability of the grass during each season.

Accordingly, the full model for each grazer was: grass greenness (3 levels) x grass height (2 levels) x stemminness (2 levels) x grazed/not grazed. For grass greenness, during the early dry season I used the following categories: <10%, 11-20% and >20% whereas during the late dry season I used <5% and 6-10%. For zebra the greenness category 6-10% was less represented and for buffalo this greenness category was absent during the late dry season. Therefore, I did not include grass greenness as predictor of acceptability of grass species by buffalo or zebra because there was little variation in grass greenness, with almost all grass plants present in feeding sites retaining <5% of leaves green during the late dry season. Even during the late dry season when grass depletion was expected, grass on feeding sites remained generally more than 20 cm tall. Therefore, I used only two categories of grass height for the three grazers during all seasons: medium-tall (<40 cm) and tall grass (>40 cm). For stemminness I also used two categories: few stems (<2 stems) and many stems (≥3) because the prevailing tall grass had supporting stems and grass without stems was less represented. From the full models, I removed factors or combination of factors and recorded the likelihood ratio chi-squared and the degrees of freedom of the model that hierarchically excluded each factor or combination of factors. I did this analysis in SYSTAT 11.0 for Windows (SYSTAT Software, Inc., USA).

To establish distinctions between herbivore species in features of grass that had been grazed, I compared herbivore species in grass greenness, grass height and stemminness only of grass tufts that were grazed by each of the herbivore species during each season using two-way loglinear analysis between pairs of herbivore species (sable vs buffalo and sable vs zebra). The models were: herbivore x grass greenness; herbivore x grass height and herbivore x stemminness. From these models, I removed the factor herbivore and noted the changes in the likelihood ratio chi-squared.

I applied Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to compare the relative weight of support by the data of models assessing the effect of different grass features or combinations of grass features on the acceptability of grass by each grazer. Following Agresti (1990, pg. 251) and Quinn and Keough (2002, pg. 390-396) I applied the following formula to calculate AIC from results of loglinear models:

$AIC = G^2-2df,$

where,
G^2 - log likelihood ratio chi-squared
df - degrees of freedom

The model with the lowest value of AIC is the best supported model (Anderson et al. 2000), i.e. the model that best explains the acceptability of grass by each grazer. Delta AIC (Δ AIC) is a measure of relative strength of support of each model compared to the best model and allows ranking the models. It is calculated as the difference in AIC values between the best model and each candidate model. Models with larger Δ AIC have less support by the data than models with smaller values of Δ AIC, but another data set could give a different ranking of models through chance sampling effects. If models are almost equally supported (Δ AIC <2), the model with the fewest predictors is the best model due to its parsimony/simplicity. Relative likelihood indicates the likelihood that the model is the best among the whole set of candidate models (Anderson and Burnham 2002; Hobbs and Hilborn 2006), it indicates the probability that another data set will rank a particular model as the best among a set of candidate models.

Results

Distinctions between grazers in the availability and acceptance of grass species

The overall availability of grass species in feeding sites differed significantly between sable and buffalo during both the early dry season (χ^2 = 66.32, df=8, p<0.001) and the late dry season (χ^2 = 80.19, df=7, p<0.001) as well as between sable and zebra during the early (χ^2 = 111.45, df=7, p<0.001) and late dry season (χ^2 = 49.82, df=6, p<0.001) (Figure 3a, b). Sable appeared narrower than buffalo and zebra in the grass species present in feeding sites, with the commonest grass species such as *Urochloa mosambicensis*, *Setaria incrassata,* and *Themeda triandra* being more prevalent in

feeding sites used by buffalo or zebra, whereas *Digitaria eriantha* was more present in feeding sites used by sable (Figure 3a, b).

With the exception of *P. maximum*, *Heteropogon contortus* and *T. triandra*, the acceptability of the most frequently encountered grass species by sable was lower than the acceptability of these species by buffalo during the early dry season (χ^2 = 113.17, df=8, p<0.001) and late dry season (χ^2 = 431.81, df=10, p<0.001) (Figure 4a). The acceptability of grass species also differed between sable and zebra during the early dry season (χ^2 = 63.04, df=7, p<0.001) and late dry season (χ^2 = 166.53, df=9, p<0.001) (Figure 4b). While the acceptance of *P. maximum* and *H. contortus* by sable was higher than by zebra, *S. incrassata* was more accepted by zebra than by sable. Sable and zebra did not differ significantly in the acceptance of *U. mosambicensis and D. eriantha* during the early dry season when grass was still green, but the two grass species became neglected by sable as the dry season progressed, while remaining commonly accepted by zebra and buffalo. The divergence in the most accepted grass species during the late dry season became evident because sable shifted selection in favour of less common grass species such as *P. deustum*, *Schmidtia pappophoroides* and *Ischaemum afrum* while the most common grass species remained highly accepted by zebra and buffalo (Figure 4a, b, Appendix 1).

Buffalo showed a more uniform acceptability across grass species and a wider range of highly accepted grass species than sable (Figure 5). This indicates that buffalo had a broader tolerance and generalist feeding at the grass species level, whereas sable were narrowly selective for particular grass species. However, sable and zebra were less distinct in the range of grass species highly accepted (Figure 5). During the early dry season, although sable neglected more grass species than buffalo, the difference in tolerance to grass species between sable and buffalo, as assessed by the frequency distribution of acceptance values, was not statistically significant (Figure 5; D.N. = 0.4, p=0.309, N=20). Out of 10 grass species, sable grazed 6 and buffalo grazed 9 grass species in more than 40% of the times when these species were present in feeding sites. However, sable became more narrowly selective for grass species than buffalo as conditions became harsher towards the end of the dry season, remaining with 6 grass species with acceptance >0.4 but increasing the cluster of grass species with acceptance

<0.4, while buffalo showed the opposite pattern increasing grass species with acceptance >0.4 to 13, out of 15 grass species present in feeding sites (D.N. = 0.412, p=0.06, N=30). Zebra appeared intermediate in tolerance to grass species, with 4 grass species showing acceptance values >0.4 during the early dry season, but increasing to 8 during the late dry season. The breadth of tolerance to grass species did not differ significantly between sable and zebra during the early (D.N. = 0.2, p=0.96, N=20) and late dry season (D.N. = 0.2, p=0.894, N=30).

Distinctions between grazers in grass features influencing the acceptance of grass species

During the early dry season the model assessing the effect of the interaction between grass greenness and grass height combined with the effect of the interaction between grass height and number of stems was the model most supported by the data in explaining the acceptance of grass by sable (best fit model, smallest AIC, Table 1a). During the late dry season, the model with four way interaction and the model including two three-way interactions (greenness x stems x grazed/not grazed + height x stems x grazed/not grazed) were both strongly supported by the data in explaining the acceptance of grass by sable (relative likelihood of 0.29 and 1.0, respectively, Table 1a). However, due to its simplicity, I consider the model including the two three-way interactions as the best model. The models assessing the effect of each grass feature separately were less supported by the data than the models including the effect of interactions between features. However, among single factors, grass greenness received relatively better support from the data in explaining the acceptance of grass by sable than grass height or number of stems during the early and late dry season (smaller ΔAIC, Table 1a). Sable were positively selective for grass greenness and grass height (Figure 6). The acceptance of grass that retained more than 10% of leaves green was higher (>0.7) than the acceptance of grass that had less than 5% of leaves green (<0.4). Sable favoured grass that was taller than 40 cm and neglected grass that was shorter than this. Sable tolerated grass with a wide range of stemminness, revealing no differences in acceptability between grass that had different numbers of stems (Figure 6).

Buffalo were broader than sable in tolerance of grass features, accepting grass that presented a wider range of greenness, height and number of stems during the early and late dry seasons (Figure 6). Among models assessing the effect of each grass feature, the number of stems was the best predictor of acceptability of the grass by buffalo during the early dry season. The acceptability of grass with 1-2 stems (0.93) was higher than the acceptability of grass with more than 3 stems (0.72) or with no stems (0.75). Grass height showed a week but positive relationship with acceptability, whereas grass greenness showed no clear influence on the acceptability of grass by buffalo. However, the overall best model included the effect of the interaction between grass greenness and grass height combined with the interaction between grass greenness and number of stems, indicating that each factor had an effect but also influenced the effect of other factors on the acceptance of grass by buffalo (Table 1b).

For zebra during the early dry season, the model including two three-way interactions (greenness x height x grazed/not grazed and greenness x stems x grazed/not grazed) was the most supported by the data in explaining the acceptance of grass by zebra and during the late dry season, grass height and number of stems as single factors explained the acceptance of grass (Table 1c). Grass height and grass greenness were positively associated with the acceptance of grass by zebra, but the relationship between acceptance and number of stems was negative (Figure 6).

Distinctions between herbivores in tolerance of grass features

Comparisons of grass grazed showed that sable were narrower in the use of grass greenness than buffalo (χ^2=116.0, df=3, p<0.001) and zebra (χ^2=91.6, df=3, p<0.001), generally neglecting grass with <10% of green leaves during the early dry season and with <5% of green leaves during the late dry season. Buffalo and zebra accepted grass within a wider range of grass greenness, including brown grass during both the early and late dry seasons (Figure 6). Even during the late dry season, sable still grazed grass that retained up to 20% of leaves green, which was not represented in feeding sites used by zebra or buffalo. Sable were also narrower than buffalo (χ^2=43.96, df=2, p<0.001) and zebra (χ^2=94.08, df=2, p<0.001) in the grass height grazed, favouring grass taller than 40

cm, whereas buffalo and zebra grazed grass of different heights (<40 cm and >40 cm) more evenly. However, when shorter grass became available on burnt areas following the first wet season rains, no distinction could be made among grazers in acceptance of short grass, with the three grazers grazing grass regrowth in the height range of 5 - 10 cm. Sable did not differ significantly from buffalo (χ^2=0.67, df=2, p=0.715) in tolerance of stems, but grazed grass that had many stems than the grass grazed by zebra (χ^2=41.48, df=2, p<0.001). However, differences between grazers in grazed grass height and number of stems could be because grass species neglected by sable during the late dry season such as *U. mosambicensis* and *D. eriantha* were generally shorter (<40 cm) and less stemmy (0-2 stems) than the most favoured ones.

Sable included a higher proportion of green grass in their diet than buffalo or zebra (Figure 7). Grass with more than 25% of leaves green made up about 50% of sable diet during the early dry season of 2006, but less than 20% of the diet of buffalo or zebra. During the early dry season of 2007 for the three grazers an average of about 40% of the diet consisted of grass with more than 25% of leaves green. However, zebra and buffalo became more tolerant of brown grass than sable as the dry season progressed. About 90% and 60% of the diet of zebra and buffalo, respectively during the critical late dry season months of October 2006 and September 2007 consisted of completely brown grass, whereas sable remained selective for green grass with only about 40% of bites taken on completely brown grass (Figure 7).

Distinctions between grazers in diet breadth

The overall diet breadth index (*B*) in terms of the range of grass species supporting the three grazers did not differ much, with an average index of 4.2 – 5.11 for the three grazers during both years (Figure 8). The diet of the three grazers was skewed towards few grass species, out of up to 23 grass species eaten by each of the grazers, only 4-5 grass species made up about 75% of the diet, with each of the remaining grass species representing less than 5% of the diet during all seasons (Figure 9a, b, c). The three grazers overlapped in the use of *P. maximum* because this grass species was among the 4-5 grass species contributing to about 75% of the diet of the three grazers during all

seasons, but the grazers were distinct in diet because while 75% of the diet of buffalo and zebra consisted of the most common grass species such as *U. mosambicensis*, *S. incrassata*, *D. eriantha* and *T. triandra* during all seasons, the diet of sable was more seasonally variable, being dominated by these common grass species plus *H. contortus* during the early dry season and the early wet season, but dominated by relatively less common grass species such as *I. afrum*, *S. pappophoroides* and *P. deustum* during the late dry season (Figure 9a, b, c).

Monthly patterns of diet breadth showed that during August and September of the less severe year of 2006, the diet of sable was less diverse than during the same period of the drier year of 2007. However, zebra showed the opposite trend and buffalo diet breadth appeared less affected by the severity of the drought. During times of extreme limitations in food quality (October 2006 and September 2007), sable tended to have a wider and more even diet than buffalo and zebra by seeking less abundant grass species, whereas buffalo or zebra concentrated feeding on the most abundantly available grass species and showed a relatively less diverse diet (Figure 8).

Diet overlap

The overlap in the grass species eaten was higher between sable and buffalo than between sable and zebra. With the exception of the overlap between sable and zebra during the early dry season of 2007, the overlap tended to decrease with the progress of the dry season (Figure 10) as sable increased the use of relatively less common grass species that contributed little to the diet of buffalo or zebra, such as *I. afrum*, *P. deustum* or *S. pappophoroides*. Buffalo and zebra remained supported by locally more abundant grass species that were neglected by sable when these grass species retained no green leaves, such as *U. mosambicensis* and *S. incrassata*, respectively. However, during October of the less severe dry season of 2006 sable increased the use of *S. incrassata* and showed the highest diet overlap with zebra.

Discussion

The low density sable were more narrowly selective for grass species, grass greenness and grass height than the high density grazers, buffalo and zebra, which were more broadly tolerant to grass species and grass features. The diversity of grass species making up the diet did not differ among grazers, but grass species making up the diet of sable were less abundant on feeding sites than the grass species more prevalent in the diet of buffalo and zebra. Grass greenness was the grass feature influencing the acceptability of grass species by sable during the early and late dry season, but it had relatively weak effect on the acceptance of grass by buffalo and zebra, which tolerated brown grass. Sable restricted grazing to tall grass, whereas buffalo and zebra grazed grass of a wider range of height. The three grazers overlapped in the acceptance of grass species when grass was green during the early dry season. However, as grass dried out with the progress of the dry season and the availability of commonly favoured grass species declined, the low density sable relied on less common grass species that retained green leaves while buffalo and zebra remained supported by locally more abundant grass species not favoured by sable when brown.

The narrower selection for green forage and grass species by sable than by buffalo or zebra was as expected from the niche breadth theory, which predicts that low density species use a narrow range of resources than high density species (Brown 1984). However, differences in body size (Geist 1974) and in the morphology and function of the digestive system (Gordon and Illius 1988; Illius and Gordon 1992) might also have contributed to differences in precision and tolerance in food niche. Being a smaller ruminant than buffalo, sable selected for higher quality green leaves to meet the higher energy requirement relative to body mass, whereas the larger ruminant buffalo and the non-ruminant zebra are less constrained by food quality, hence tolerated forage of a wider range of phenological stages to secure the requirement for high absolute intake of forage. Despite higher requirements for food quality by sable than by buffalo or zebra, sable also accepted tall grass with high number of stems. However, differences or similarities between grazers in tolerance for these grass features could have been affected by differences between grazers in the acceptance frequency of grass species that attained

different heights or number of stems. Sable took bites on grass stems (personal observations), but I failed to document the relative frequency of biting stems versus selectively feeding on grass leaves from stems of tall grass. Parrini (2006) also documented tolerance of stems by sable during the dry season. Heitkönig (1993) reported that the closely related roan antelope (*Hippotragus equinus,* 260 kg) consumed forage with many stems and hence of poor quality, and suggested an intermediate digestive system between ruminants and non-ruminants for roan. This could also explain the tolerance of stems by sable.

Although sable grazed a range of grass species as wide as buffalo and zebra, the acceptability of most grass species by sable was lower than by buffalo, suggesting that sable were narrowly selective for grass species. However, the tolerance of grass species by sable was influenced by the greenness that the grass species retained. This became more apparent during the late dry season when sable reduced the number of highly accepted grass species when the most widespread grass species retained no green leaves. During the late dry season, sable remained selective for tufts of grass species that retained green leaves. On the other hand, buffalo and zebra readily accepted a wider range of grass species than sable, particularly the grass species most abundant in feeding sites, even when most of the grass leaves were brown. This suggests that buffalo and zebra relied on grass species securing adequate intake of bulk forage and were generalists in grass greenness, tolerating even the most widespread brown leaves. Bell (1970) had previously documented zebra reliance on the commonest and most accessible food, whereas ruminants most selective for greener grass such as Thomson's gazelle (*Gazella thomsoni,* 16 kg) depended on sparser food resources during the dry season. Wildebeest (*Connochates taurinus*, 163 kg), which is of similar body size to sable but attain higher density (±10 animals/km^2) across their distribution range showed broad tolerance of grass species (Ben-Shahar 1991) and of grass phenological stages during the dry season (Murray and Brown 1993). This suggests that differences in tolerance to food resources among large grazers could also be explained by differences in regional density, rather than by differences in body mass alone.

Sable narrower selection for grass species than buffalo and zebra suggests that the niche breadth hypothesis (Brown 1984) could explain sable occurrence at low density

because the range of grass species favoured by sable is restricted. In addition, the grass species that most contributed to the diet of the low density sable during the critical late dry season were less common in feeding sites than the grass species that supported the high density buffalo and zebra, suggesting that the niche position or resource availability hypothesis (Gaston and Kunin 1997; Gregory and Gaston 2000) might also contribute to explaining why sable occur in low density. Sable also showed a narrower food niche than buffalo and zebra by feeding selectively on green leaves and grass species with many stems. The availability of green leaves decreased while the availability of brown leaves tolerated by buffalo and zebra increased with the progress of the dry season. Accordingly, at the plant parts level, resource breadth and resource availability hypotheses also appear to jointly determine the seasonal variability in the quality and quantity of resources supporting sable compared to resources used by high density grazers, buffalo and zebra.

The diet breadth in terms of the range of grass species upon which the grazers depended did not differ substantially among grazers. However, while buffalo and zebra depended on the most common grass species during different conditions of food availability, sable depended on the commonest grass species only during the early dry season. During times of the year of limited food quality like the late dry season sable sought for patches of less widespread grass species. This suggests that the progressive decline in the availability of food influenced the composition of the diet of sable but had little influence on the food resources supporting buffalo or zebra. During the late dry season of the less severe dry season of 2006 the diet of sable was less diverse than during the late dry season of the drier 2007. This indicates that during late dry season of years with above average rainfall sable relied on few grass species as the main components of the diet, but during the late dry season of drier years the diet of sable was made up by many grass species due to limited availability of preferred food species.

The general decrease in diet overlap with the progress of the dry season that I documented in this study suggests that competition for the commonly preferred food species resulted in resource partitioning, with different grazers relying on different food refuges as the critical late dry season approached, as previously suggested by Jarman (1971), Holbrook and Schmit (1989) and Owen-Smith (1989). However, if few options for food selection are available to allow diet divergence or if a bridging food species that

is used by different grazers remains abundant, the overlap in diet among grazers should increase during critical periods. Ego et al (2003) reported high diet overlap between wildebeest, kongoni (*Alcelaphus buselaphus*) and cattle (*Bos indicus*) during both the wet and dry season when preferred forage species were abundantly available year-round. This suggests that a high overlap does not necessarily indicate potential for competition, but rather that preferred resources are abundant to be shared. Therefore, the increase in overlap between sable and zebra at the end of the dry season of the less severe dry season could indicate that the grass species that supported both grazers during this period were not limiting, hence diet overlap did not result in competition and diet divergence. In addition, during the late dry season the home ranges used by sable and zebra were separated (Chapter 4), which reduced the potential for food competition despite similarity in diet composition.

This study showed limited partitioning of food resources among grazers, but rather overlaps in grass species grazed. Neglecting more grass species, depending on grass species occurring in lower availability and selecting for green leaves during the limiting dry season suggest that sable were more restricted by the availability of food of acceptable quality than buffalo and zebra, which accepted the readily available bulk. This suggests that low density grazers have a narrower food niche and a more precise foraging at the grass species and grass features level than high density grazers.

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Table 1a. Model comparison statistics for grass features influencing the acceptability of grass species by sable during the early and late dry season

Sable: early dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Greenness x Height x Stems x grazed/not grazed	180.3	4	172.3	3.1	0.123	0.212
Greenness x Stems x grazed/not grazed + Height x Stems x grazed/not grazed	201.4	8	185.4	16.2	0.000	0.000
Greenness x Height x grazed/not grazed + Height x Stems x grazed/not grazed	185.2	8	169.2	0	0.579	1.000
Greenness x Height x grazed/not grazed + Greenness x Stems x grazed/not grazed	184.5	7	170.53	1.33	0.298	0.514
Height x Stems x grazed/not grazed	421.9	12	397.9	228.7	0.000	0.000
Greenness x Height x grazed/not grazed	222.9	10	202.89	33.69	0.000	0.000
Greenness x Stems x grazed/not grazed	218.5	10	198.5	29.3	0.000	0.000
Greenness x grazed/not grazed	444.7	10	424.7	255.5	0.000	0.000
Height x grazed/not grazed	1281.4	12	1257.4	1088.2	0.000	0.000
Stems x grazed/not grazed	800.0	12	776	606.8	0.000	0.000

Sable: late dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Greenness x Height x Stems x grazed/not grazed	1046.4	3	1040.4	0	0.733	1.000
Greenness x Stems x grazed/not grazed + Height x Stems x grazed/not grazed	1052.9	5	1042.9	2.5	0.210	0.287
Greenness xHeight x grazed/not grazed + Height x Stems x grazed/not grazed	1169.5	5	1159.5	119.1	0.000	0.000
Greenness x Height x grazed/not grazed + Greenness x Stems x grazed/not grazed	1055.6	5	1045.6	5.2	0.054	0.074
Height x Stems x grazed/not grazed	1276.8	7	1262.8	222.4	0.000	0.000
Greenness x Height x grazed/not grazed	1245.2	7	1231.2	190.8	0.000	0.000
Greenness x Stems x grazed/not grazed	1065.4	7	1051.4	11	0.003	0.004
Greenness x grazed/not grazed	1113.0	7	1099	58.6	0.000	0.000
Height x grazed/not grazed	1234.6	7	1220.6	180.2	0.000	0.000
Stems x grazed/not grazed	1273.0	7	1259	218.6	0.000	0.000

Table 1b. Model comparison statistics for grass features influencing the acceptability of grass species by buffalo during the early and late dry season

Buffalo: early dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Greenness x Height x Stems x grazed/not grazed	111.1	4	103.1	0.4	0.266	0.819
Greenness x Stems x grazed/not grazed + Height x Stems x grazed/not grazed	120.4	8	104.4	1.7	0.139	0.427
Greenness xHeight x grazed/not grazed + Height x Stems x grazed/not grazed	119.6	8	103.6	0.9	0.207	0.638
Greenness x Height x grazed/not grazed + Greenness x Stems x grazed/not grazed	116.7	7	102.7	0	0.325	1.000
Height x Stems x grazed/not grazed	148.0	12	124	21.3	0.000	0.000
Greenness x Height x grazed/not grazed	126.0	10	106	3.3	0.062	0.192
Greenness x Stems x grazed/not grazed	158.8	10	138.8	36.1	0.000	0.000
Greenness x grazed/not grazed	382.7	10	362.7	260	0.000	0.000
Height x grazed/not grazed	231.0	12	207	104.3	0.000	0.000
Stems x grazed/not grazed	199.9	12	175.9	73.2	0.000	0.000

Buffalo: late dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Height x Stems x grazed/not grazed	39.0	2	35	0	1.000	1.000
Height x grazed/not grazed + Stems x grazed/not grazed	235.0	6	223	188	0.000	0.000
Height x grazed/not grazed	60.3	4	52.3	17.3	0.000	0.000
Stems x grazed/not grazed	71.9	4	63.9	28.9	0.000	0.000

Table 1c. Model comparison statistics for grass features influencing the acceptability of grass species by zebra during the early and late dry season

Zebra: early dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Greenness x Height x Stems x grazed/not grazed	178.8	4	170.8	1.9	0.196	0.387
Greenness x Stems x grazed/not grazed + Height x Stems x grazed/not grazed	186.0	8	170	1.1	0.292	0.577
Greenness xHeight x grazed/not grazed + Height x Stems x grazed/not grazed	198.3	8	182.3	13.4	0.001	0.001
Greenness x Height x grazed/not grazed + Greenness x Stems x grazed/not grazed	182.9	7	168.9	0	0.506	1.000
Height x Stems x grazed/not grazed	202.6	12	178.6	9.7	0.004	0.008
Greenness x Height x grazed/not grazed	201.7	10	181.7	12.8	0.001	0.002
Greenness x Stems x grazed/not grazed	207.5	10	187.5	18.6	0.000	0.000
Greenness x grazed/not grazed	227.4	10	207.4	38.5	0.000	0.000
Height x grazed/not grazed	249.0	12	225	56.1	0.000	0.000
Stems x grazed/not grazed	241.6	12	217.6	48.7	0.000	0.000

Zebra: early dry season

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Height x Stems x grazed/not grazed	357.9	2	353.9	4.2	0.048	0.122
Height x grazed/not grazed + Stems x grazed/not grazed	361.7	6	349.7	0	0.395	1.000
Height x grazed/not grazed	358.4	4	350.4	0.7	0.278	0.705
Stems x grazed/not grazed	358.4	4	350.4	0.7	0.278	0.705

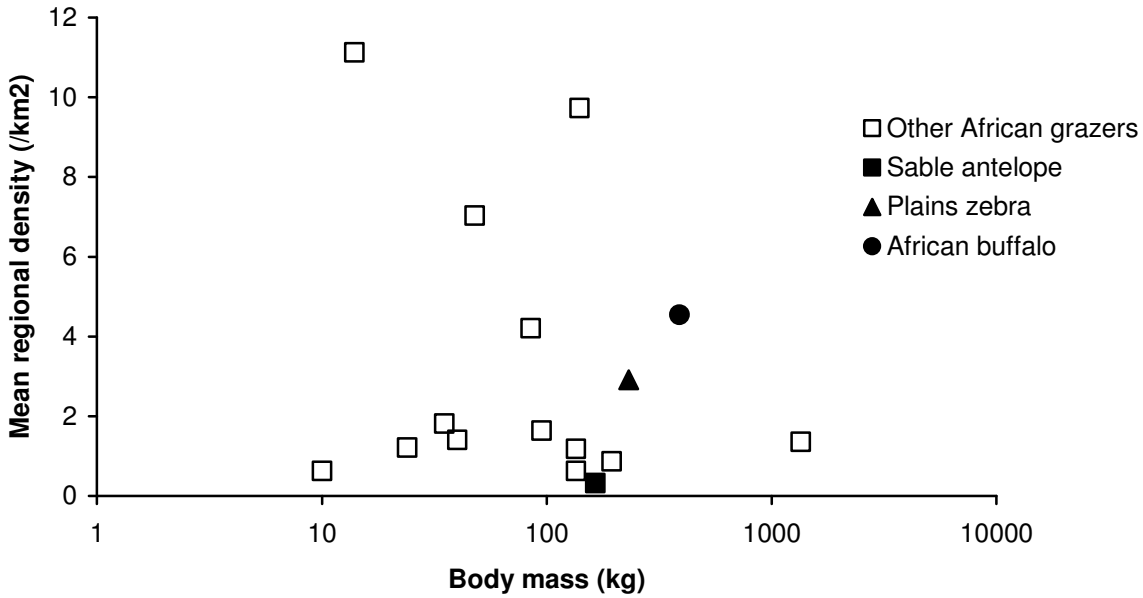


Figure 1. Mean regional density of sable, zebra, buffalo and other African grazers in protected areas

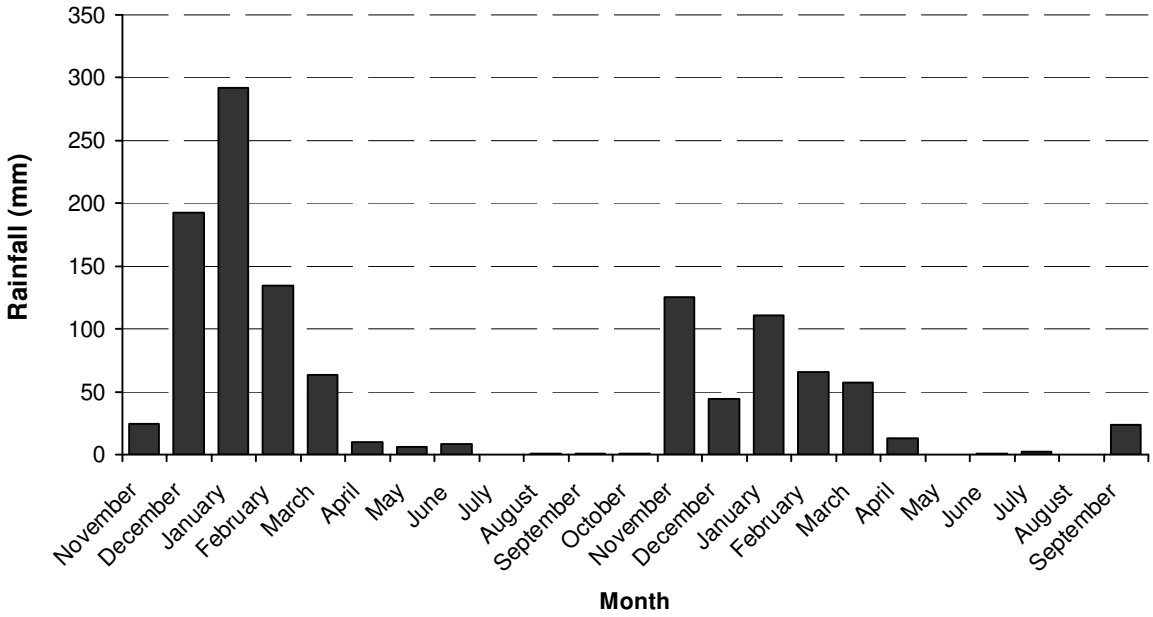


Figure 2. Total monthly rainfall in Punda Maria from November 2005 to September 2007. Source of data: South African Weather Services

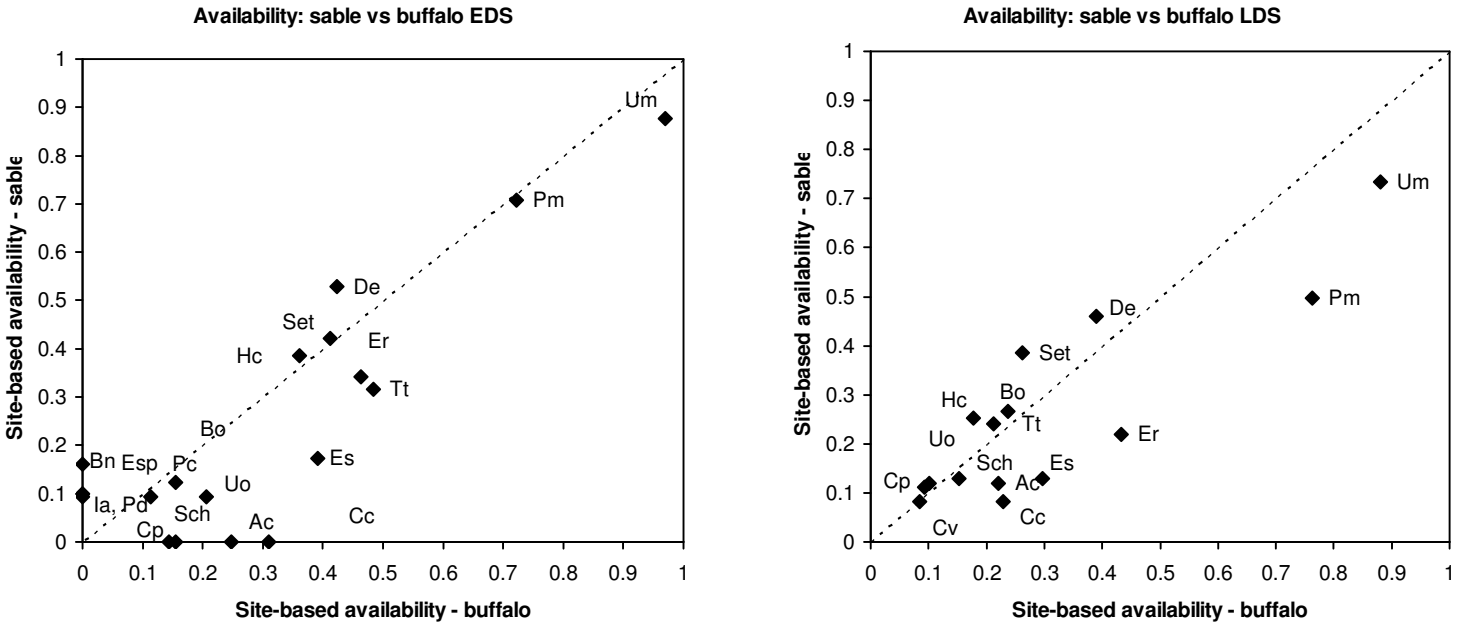


Figure 3a. Comparative availability of grass species on feeding sites used by sable and buffalo during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined. Dashed diagonal line represents the points of equal availability of grass species between grazers. Pm - *Panicum maximum*, Pd - *P. deustum*, Pc - *P. coloratum*, Um - *Urochloa mosambicensis*, Uo - *U. Oligotricha*, De - *Digitaria eriantha*, Tt - *Themeda triandra*, Set - *Setaria incrassata*, Hc - *Heteropogon contortus*, Er - *Eragrostis rigidior*, Es - *E. superba*, Esp - *Eragrostis* sp, Cc - *Cenchrus ciliaris*, Sch - *Schmidtia pappophoroides*, Bo - *Bothriochloa* spp, Bn - *Brachiaria nigropedata*, Ia - *Ischaemum afrum*, Cp - *Cymbopogon plurinodis*, Ac - *Aristida congesta*, Cv - *Chloris virgata* and Pp - *Perotis patens*.

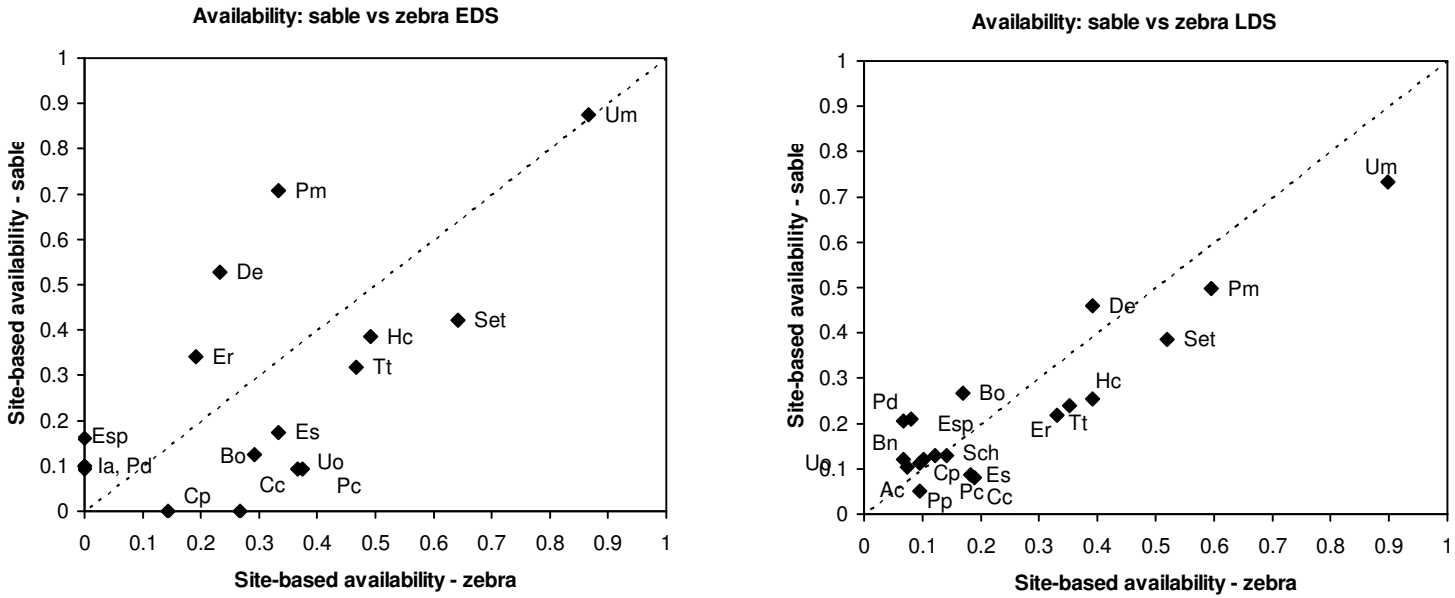


Figure 3b. Comparative availability of grass species on feeding sites used by sable and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined. Dashed diagonal line represents the points of equal availability of grass species between grazers. Acronyms are listed in Figure 3a.

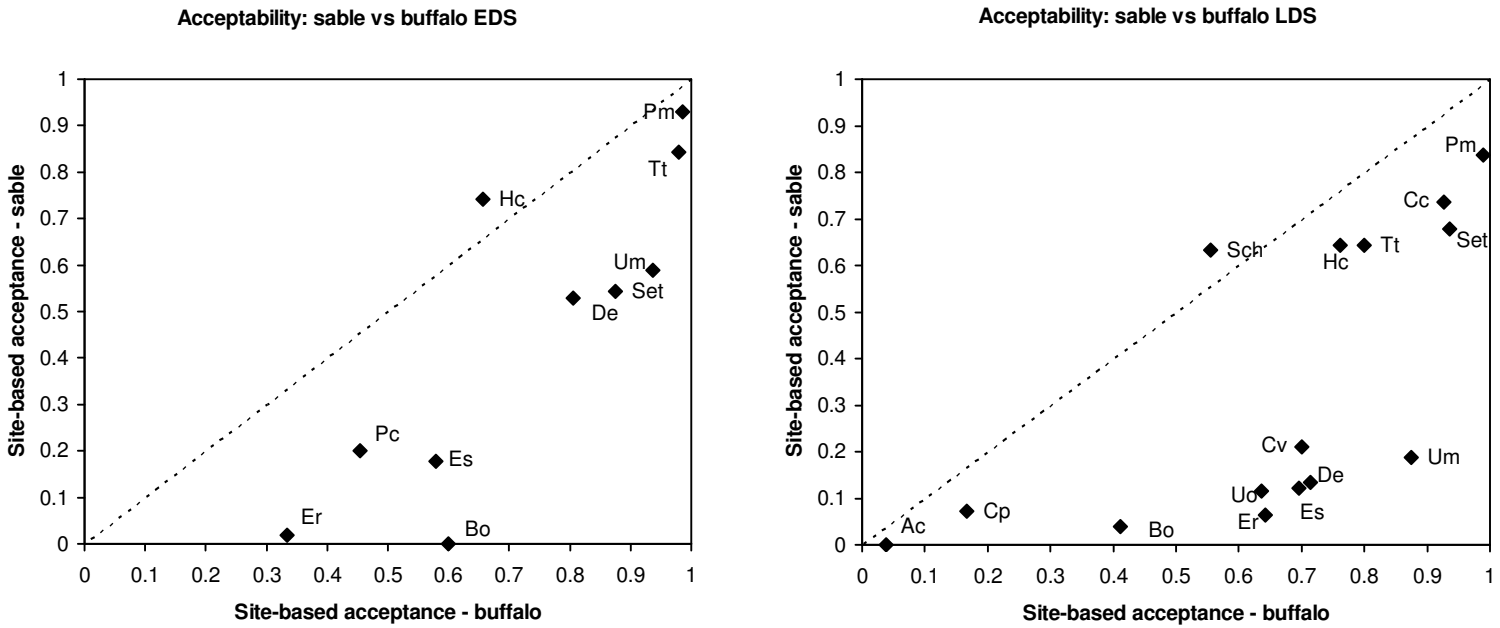


Figure 4a. Comparative acceptability of grass species by sable and buffalo during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined. Dashed diagonal line represents the points of equal acceptability of grass species between grazers. Acronyms are listed in Figure 3a.

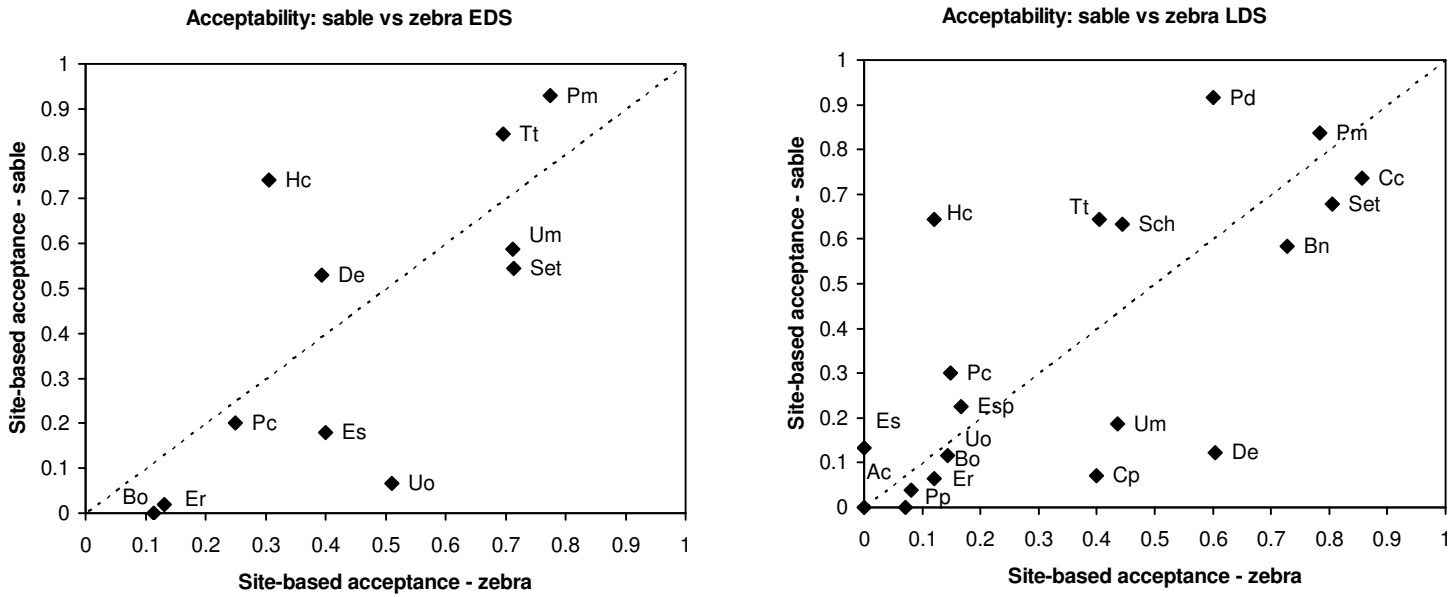
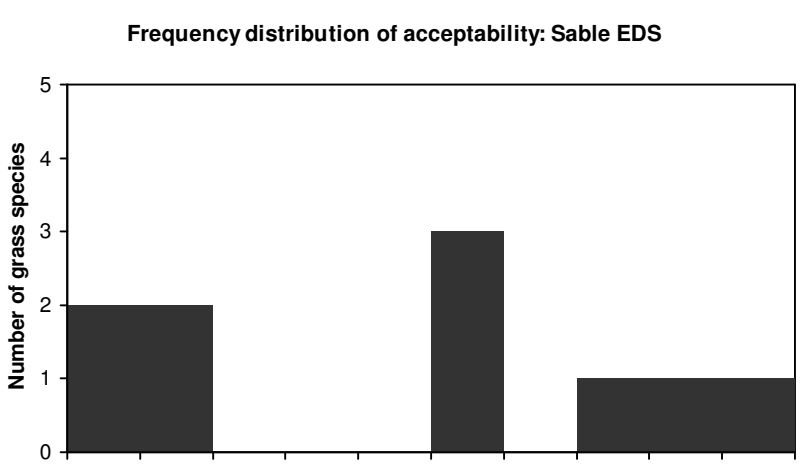
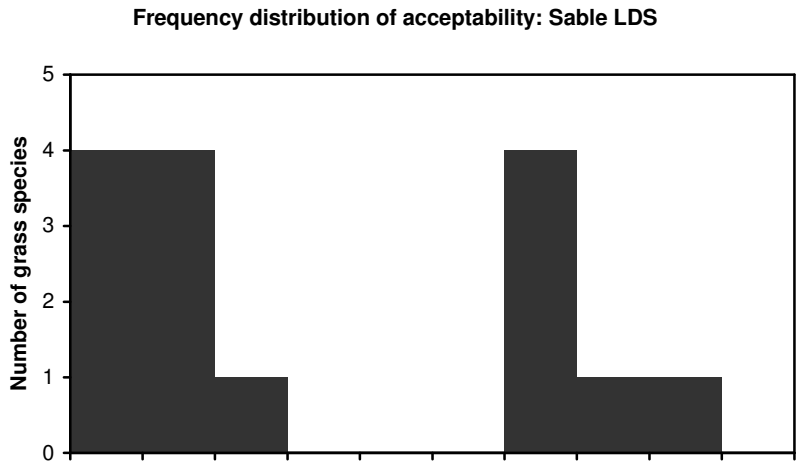
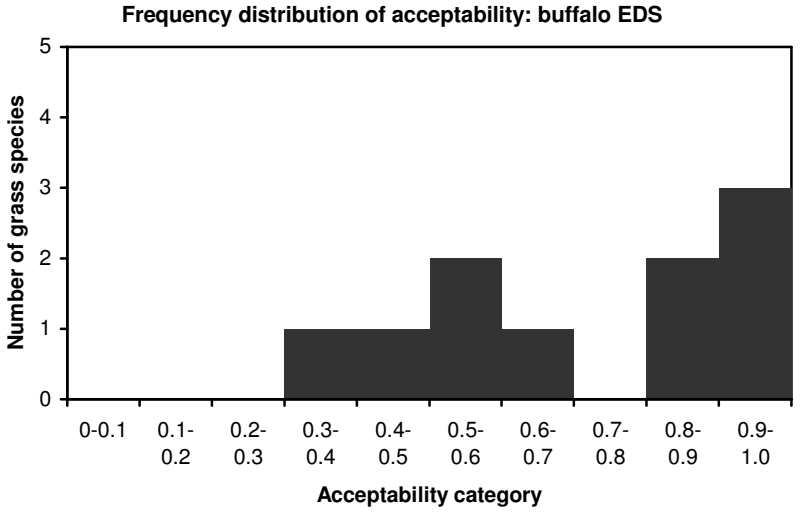
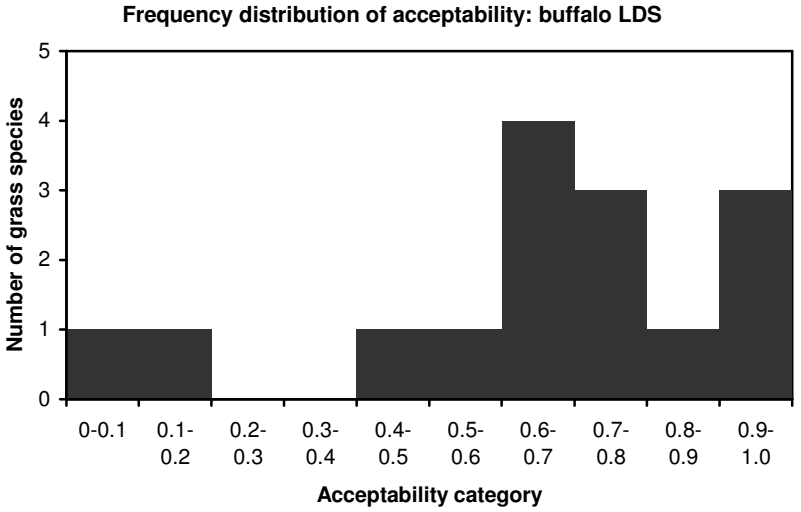


Figure 4b. Comparative acceptability of grass species by sable and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined. Dashed diagonal line represents the points of equal acceptability of grass species between grazers. Acronyms are listed in Figure 3a.


Frequency distribution of acceptability: Sable EDS
Number of grass species
0
1
2
3
4
5


Frequency distribution of acceptability: Sable LDS
Number of grass species
0
1
2
3
4
5


Frequency distribution of acceptability: buffalo EDS
Number of grass species
0
1
2
3
4
5
0-0.1
0.1-0.2
0.2-0.3
0.3-0.4
0.4-0.5
0.5-0.6
0.6-0.7
0.7-0.8
0.8-0.9
0.9-1.0
Acceptability category


Frequency distribution of acceptability: buffalo LDS
Number of grass species
0
1
2
3
4
5
0-0.1
0.1-0.2
0.2-0.3
0.3-0.4
0.4-0.5
0.5-0.6
0.6-0.7
0.7-0.8
0.8-0.9
0.9-1.0
Acceptability category

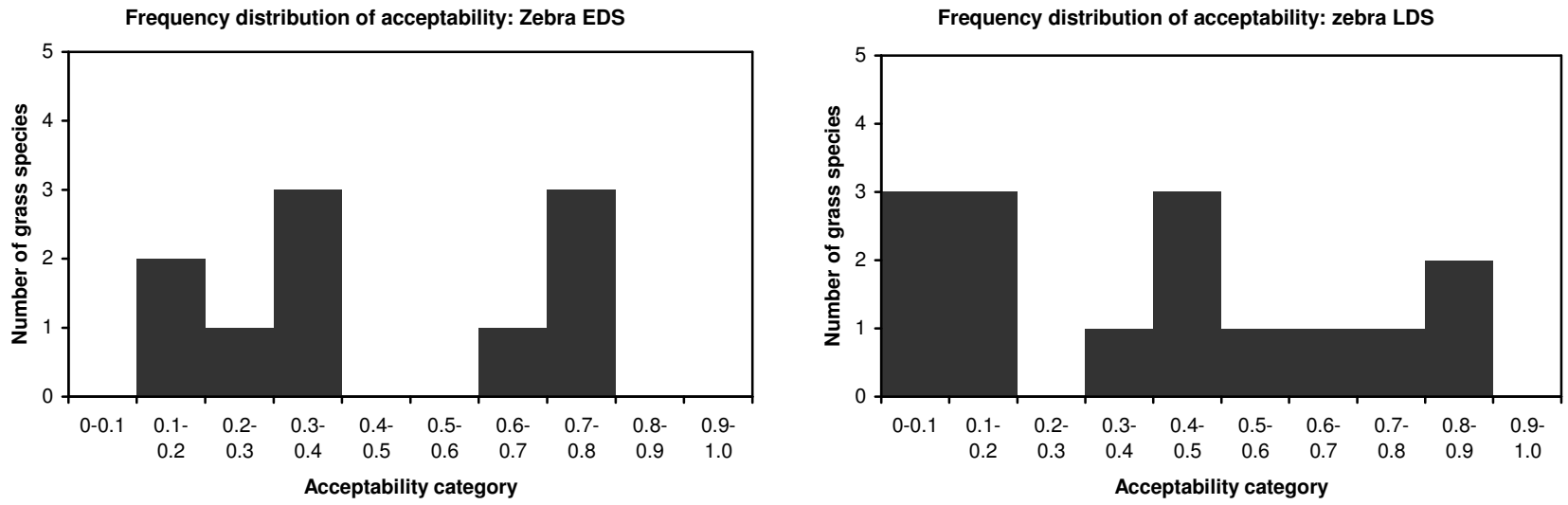
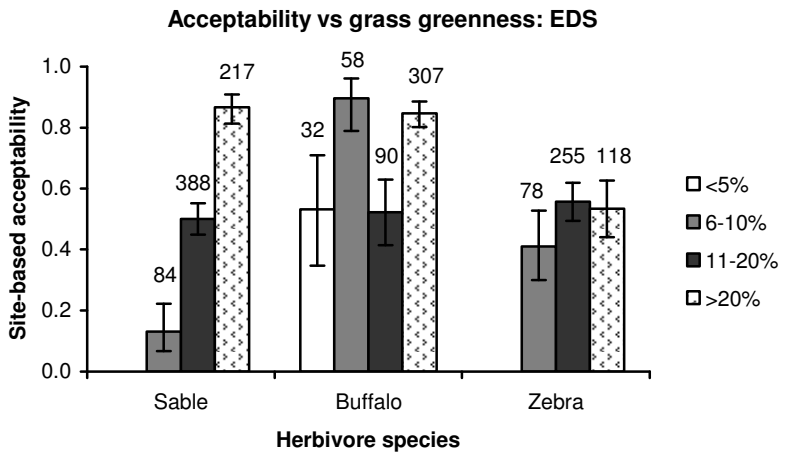
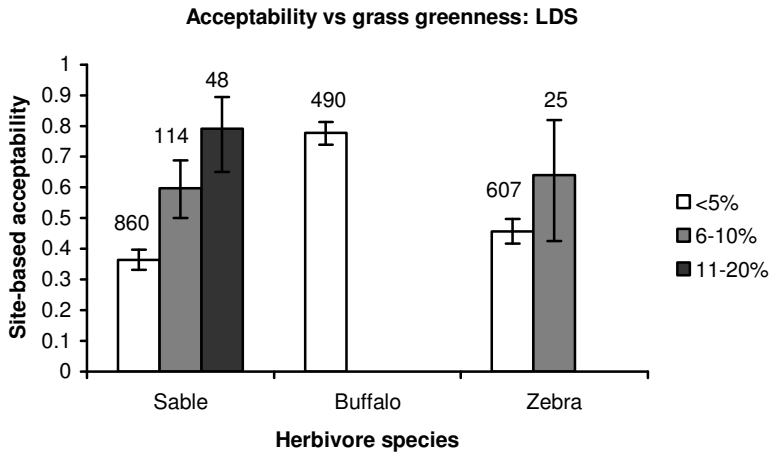
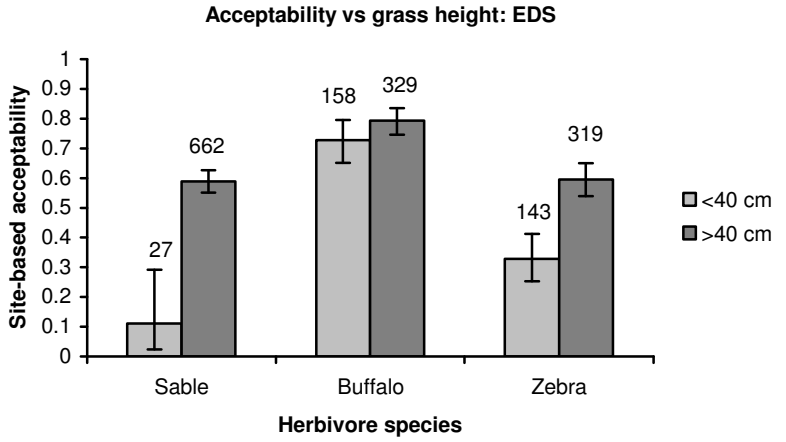
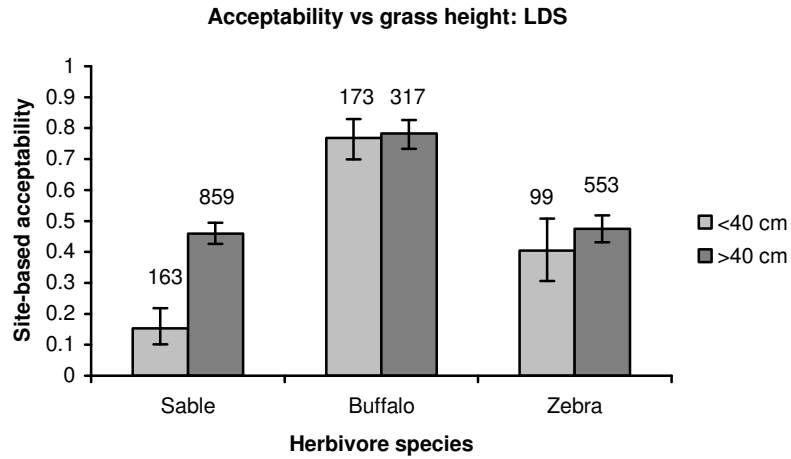


Figure 5. Frequency distribution of acceptability of grass species by sable during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined.


Acceptability vs grass greenness: EDS
Site-based acceptability
1.0
0.8
0.6
0.4
0.2
0.0
84
388
217
32
58
90
307
78
255
118
Sable
Buffalo
Zebra
Herbivore species
<5%
6-10%
11-20%
>20%


Acceptability vs grass greenness: LDS
Site-based acceptability
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
860
114
48
490
607
25
Sable
Buffalo
Zebra
Herbivore species
<5%
6-10%
11-20%


Acceptability vs grass height: EDS
Site-based acceptability
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
27
662
158
329
143
319
Sable
Buffalo
Zebra
Herbivore species
<40 cm
>40 cm


Acceptability vs grass height: LDS
Site-based acceptability
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
163
859
173
317
99
553
Sable
Buffalo
Zebra
Herbivore species
<40 cm
>40 cm

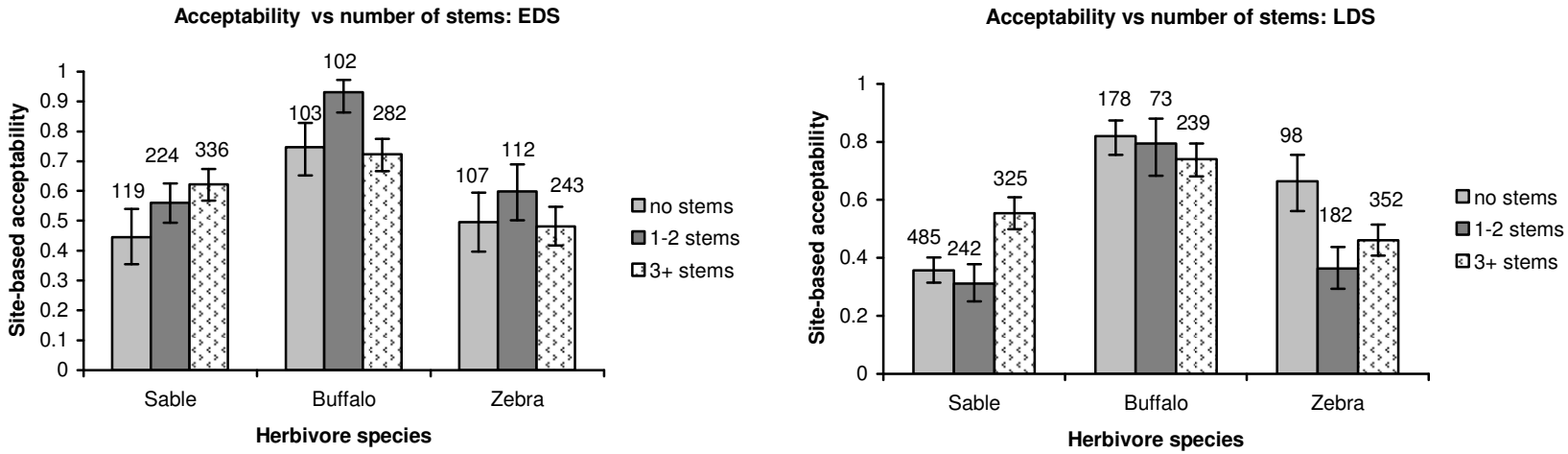
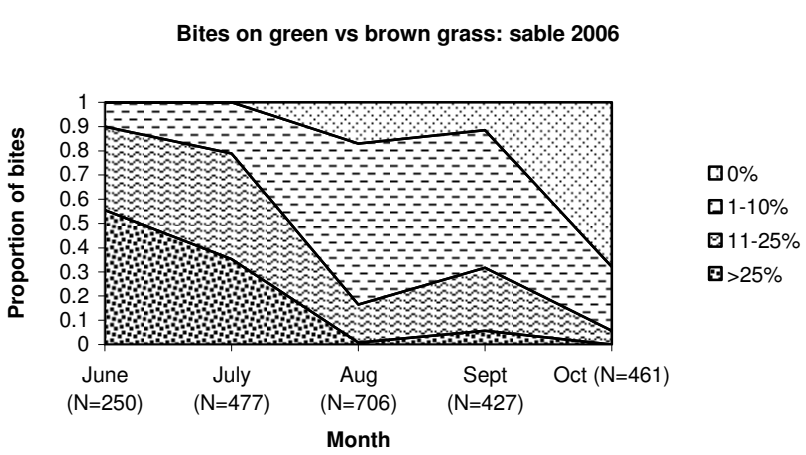
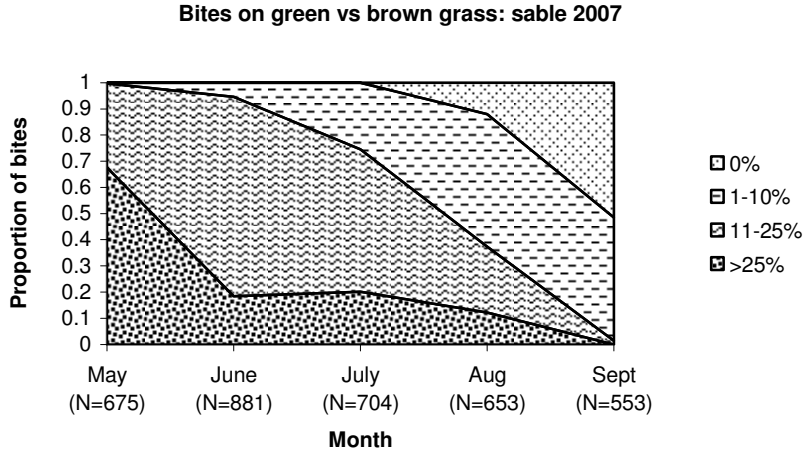
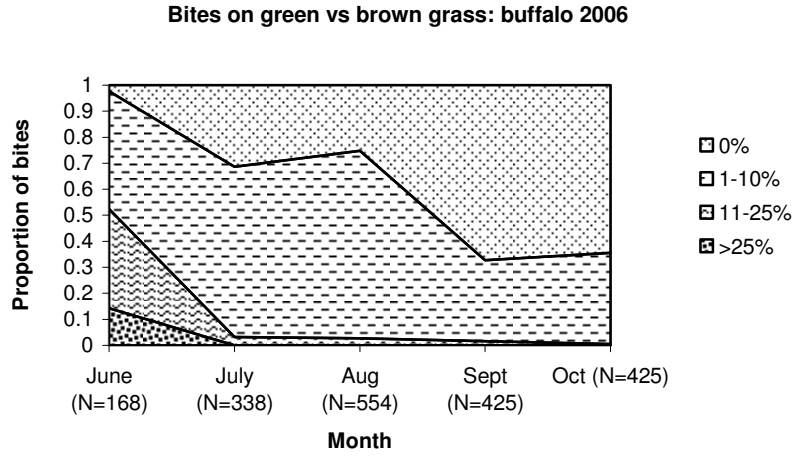
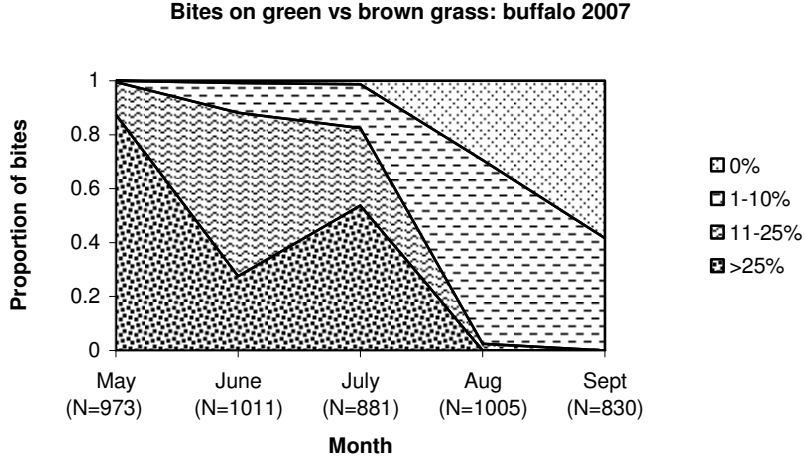


Figure 6. Comparative tolerance to grass greenness, grass height and number of stems between sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007 combined. Bars denote 95% binomial confidence intervals. Numbers on bars indicate sample size (number of feeding sites with grass species amalgamated).


Bites on green vs brown grass: sable 2006
Proportion of bites
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
June (N=250)
July (N=477)
Aug (N=706)
Sept (N=427)
Oct (N=461)
Month
0%
1-10%
11-25%
>25%


Bites on green vs brown grass: sable 2007
Proportion of bites
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
May (N=675)
June (N=881)
July (N=704)
Aug (N=653)
Sept (N=553)
Month
0%
1-10%
11-25%
>25%


Bites on green vs brown grass: buffalo 2006
Proportion of bites
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
June (N=168)
July (N=338)
Aug (N=554)
Sept (N=425)
Oct (N=425)
Month
0%
1-10%
11-25%
>25%


Bites on green vs brown grass: buffalo 2007
Proportion of bites
1
0.8
0.6
0.4
0.2
0
May (N=973)
June (N=1011)
July (N=881)
Aug (N=1005)
Sept (N=830)
Month
0%
1-10%
11-25%
>25%

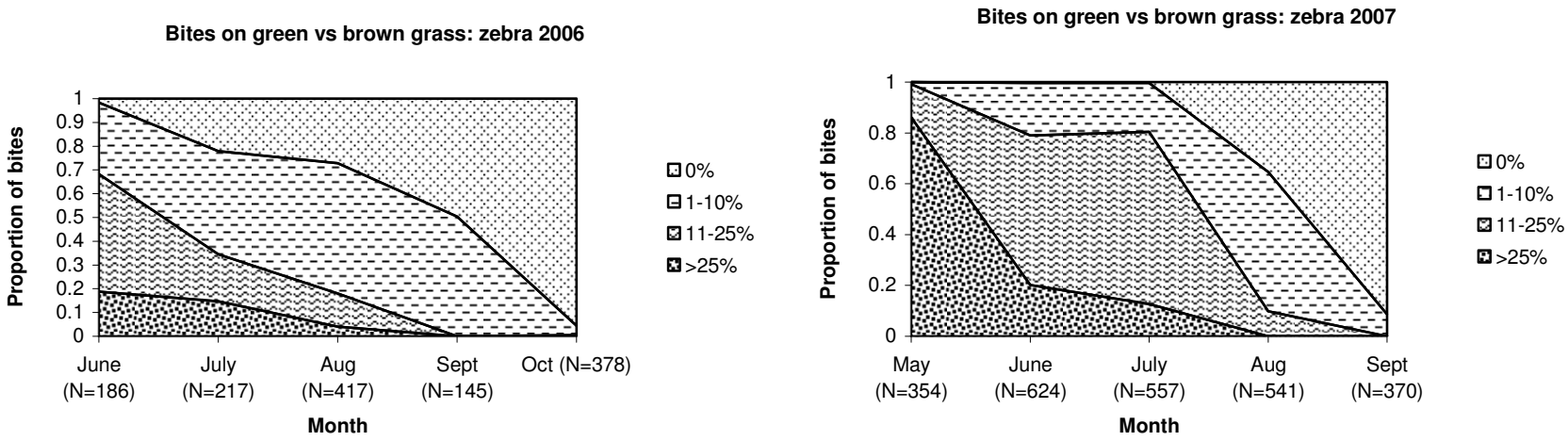


Figure 7. Monthly changes in the proportion of bites taken on grass within different categories of grass greenness during the dry season of 2006 and 2007 (N= number of bites).

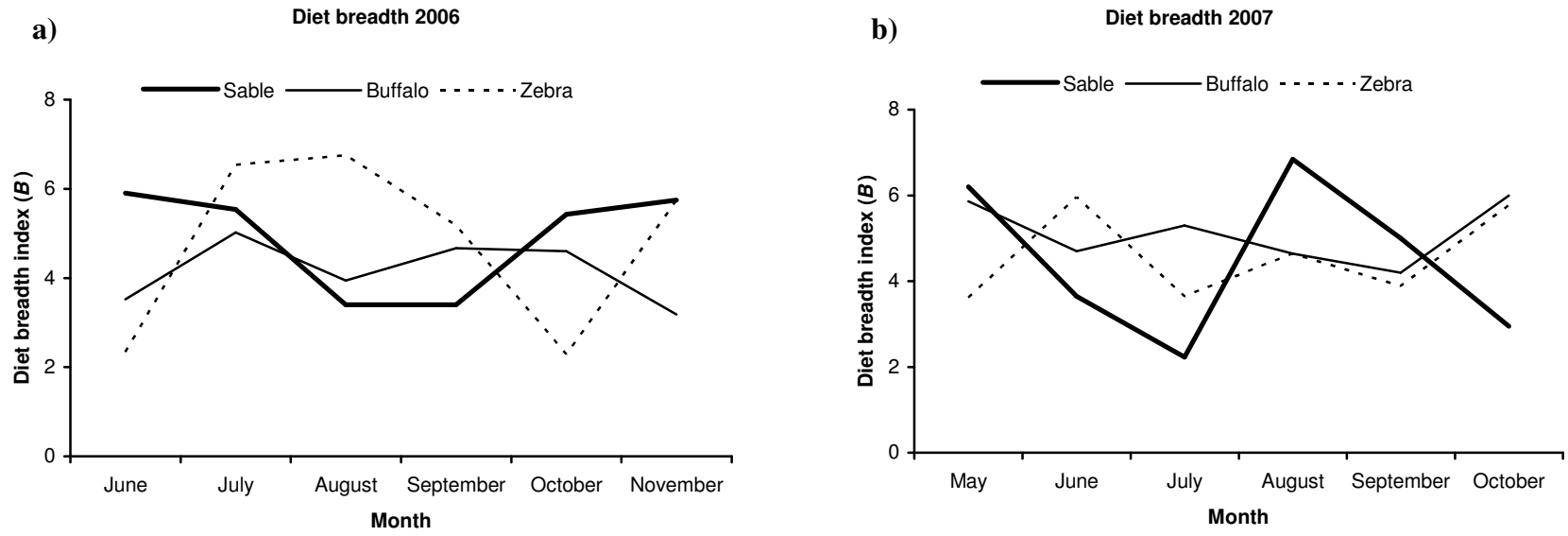


Figure 8. Monthly variations in diet breadth index (*B*) of low density sable and high density grazers, buffalo and zebra, during 2006 and 2007

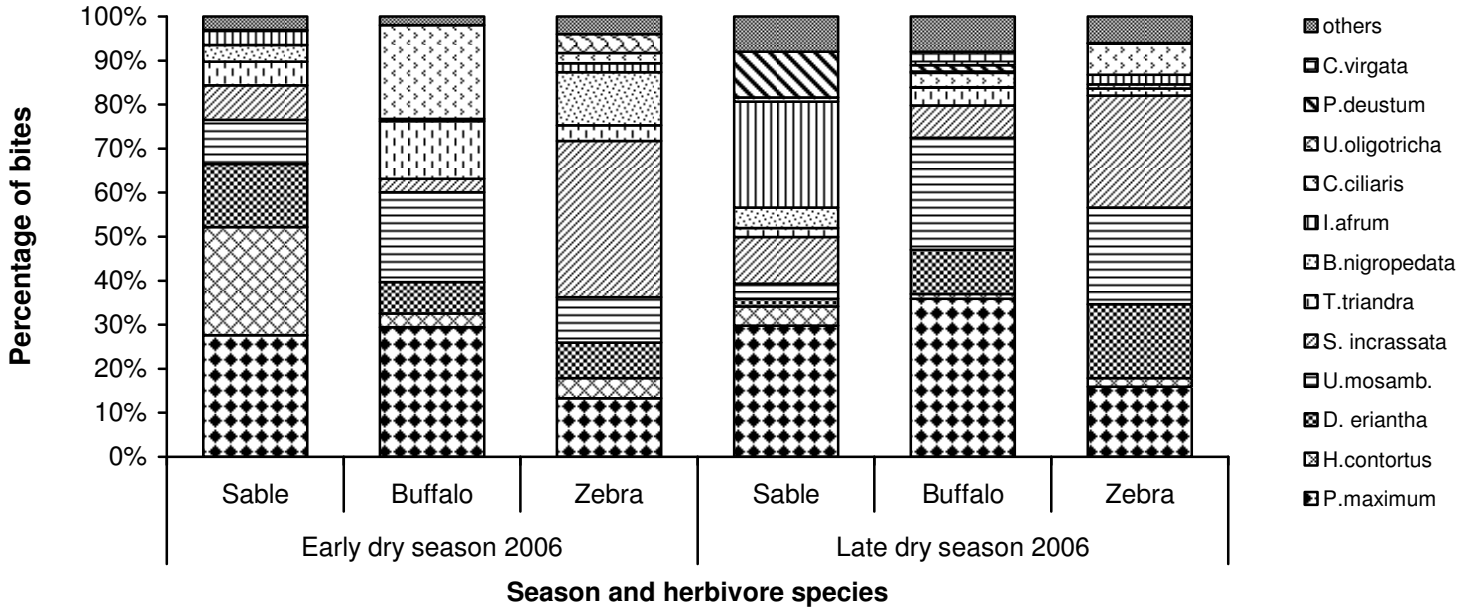


Figure 9a. Diet contribution of grass species during the early and late dry season of 2006, assessed as the percentage of bites taken on each grass species

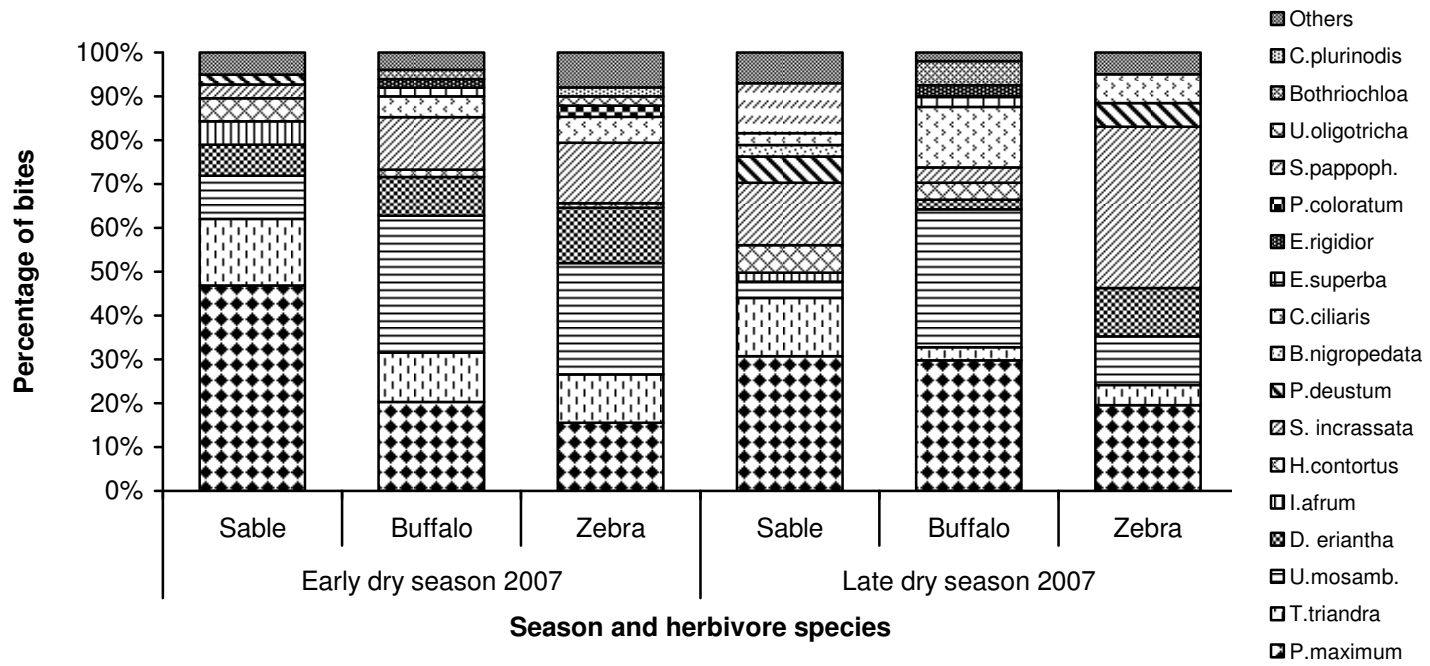


Figure 9b. Diet contribution of grass species during the early and late dry season of 2007, assessed as the percentage of bites taken on each grass species

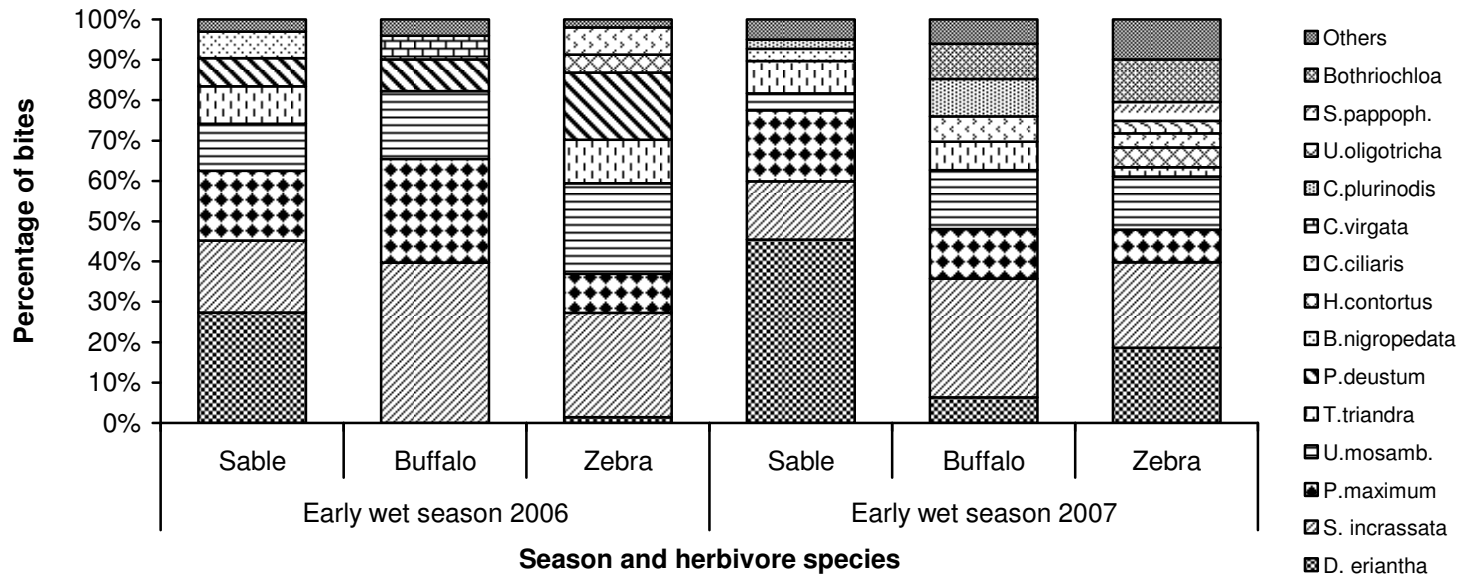


Figure 9c. Diet contribution of grass species during the transition period to the wet season of 2006 and 2007, assessed as the percentage of bites taken on each grass species

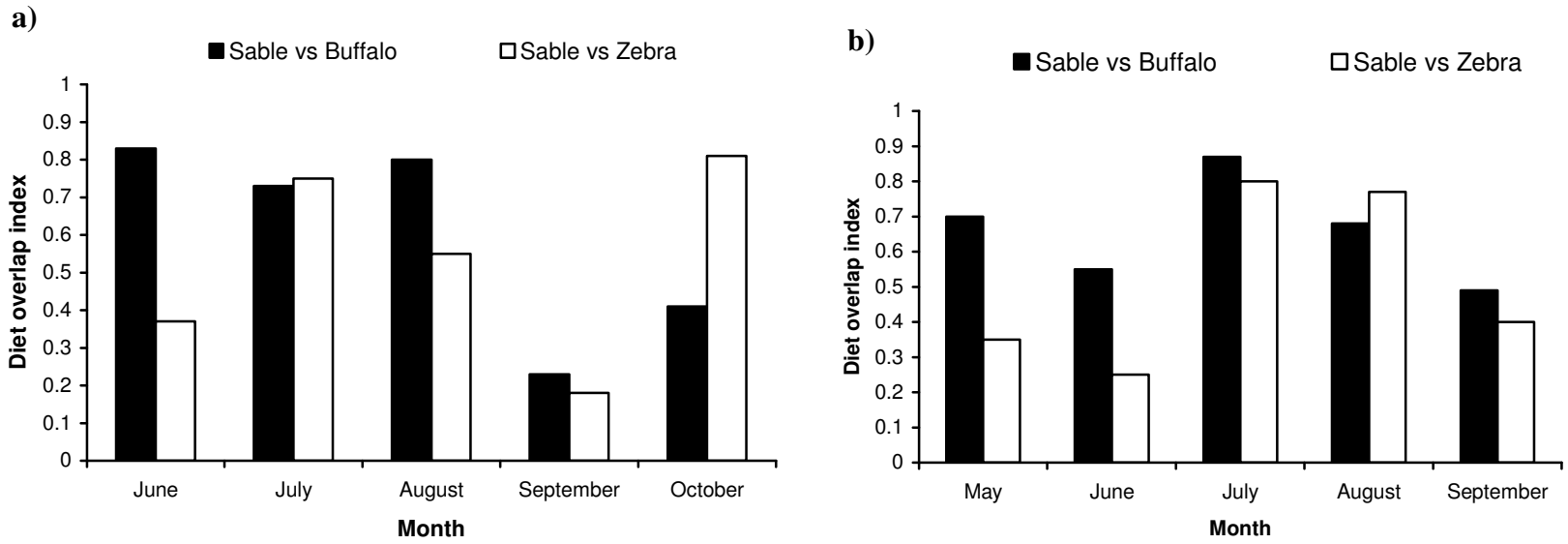


Figure 10. Monthly variations in the index of overlap on grass species eaten between sable and buffalo and between sable and zebra during the dry season of 2006 (a) and 2007 (b)

CHAPTER TWO

Comparative habitat use by low density versus high density grazers

Abstract

Distinctions in habitat use between the low density sable and the high density buffalo and zebra were investigated in northern Kruger National Park during the dry seasons of 2006 and 2007. GPS-GSM collars were deployed on females from herds of these grazers and foraging areas used by the herds were located by means of GPS tracking. Habitat features such as catena position, grass greenness, grassland height and woody vegetation cover were recorded on each foraging area. Data were pooled across herds of the same species, to make inference about habitat use at the population level. The prevalence of habitat features was compared between foraging areas used by sable and foraging areas used by buffalo or zebra using log-linear models. The habitat features or their combinations that best distinguished foraging areas used by sable from those used by buffalo or zebra were determined using Akaike's Information Criterion. Sable foraged in areas retaining greener grass than buffalo and zebra. Sable overlapped with zebra by foraging on uplands, but were distinct from buffalo which foraged mainly on bottomlands and midslopes. Sable and buffalo overlapped by foraging mainly on open woodlands, whereas zebra tolerated a wider range of woody vegetation cover, by using more evenly open woodlands and treeless grasslands. The three grazers overlapped in the use of tall grass grasslands, although zebra were more broadly tolerant of grassland height than sable and buffalo, by also foraging in areas with short grass. Results suggest that sable were narrower than buffalo and zebra in grass greenness, but were similar to buffalo and zebra in other habitat features prevailing on foraging areas. This limited ecological separation at the habitat level suggests that there is potential for competition for food during periods of limited food supply if these grazers use overlapping home ranges.

Introduction

The acquisition of resources for survival, growth and reproduction of foraging animals depends on the habitat used, i.e. on the set of physical environmental conditions and resources surrounding the animal (Johnson 1980; Hall et al. 1997; Garshelis 2000; Morrison 2001) and on the breadth of habitat conditions used (Feinsinger et al. 1981; Smith 1982). In addition, habitat breadth provides insights into the animal's potential distribution range (Brändle and Brandl 2001; Morrison 2001; Morrison et al. 2006), such that species with broad habitat tolerance are potentially more widely distributed than species using a narrower diversity of habitats.

Habitat features for large herbivores include resources such as food and water, conditions such as shelter and shade; and safety from predators (Owen-Smith 2002). The use of a narrow range of habitat features reflects specialization or marginality, which is one measure of niche breadth (Calenge et al. 2005). Habitat specialization may limit the potential of species to use spatially and temporally variable resources, conditions and security. Brown (1984) and Rosenzweig and Lomolino (1997) argued that habitat specialization leads to both local and regional rarity of species. However, Seagle and McCraken (1986) and Gaston and Kunin (1997) demonstrated that specialization on abundant resources or widely distributed habitats can result in high abundance of a species. du Toit and Owen-Smith (1989) observed differences in habitat use and in habitat breadth among African browsers, with smaller species such as steenbok (*Raphicerus campestris*, 11 kg) using a narrower range of habitats than larger browsers such as kudu (*Tragelaphus strepsiceros*, 180 kg) and giraffe (*Giraffa camelopardalis*, 800 kg), which exploited a wider range of habitats, including habitats patches neglected by the smaller browser. Following the Jarman (1968 in Jarman 1974) and Bell (1970) principle, du Toit and Owen-Smith (1989) proposed that the more even use of a broader range of habitats by kudu and giraffe was because larger animals tolerate a wide range of food items, including low quality and food items of large size neglected by the smaller animal. Among African grazers, Fritz et al. (1996) observed that the larger-sized cattle (*Bos taurus* and *B. indicus*) used a wider range of habitat types than the smaller animal, impala (*Aepyceros melampus*).

Habitat use is a hierarchical process (Senft et al. 1987), scaling spatially from the selection of geographical range (first order habitat selection), selection of broad vegetation types across the landscape when establishing home ranges (second order habitat selection), selection of habitats within the home range (third order selection), selection of feeding areas within habitats to selection of food items within feeding areas (fourth order selection) (Johnson 1980). Following the limiting similarity theory for species coexistence (MacArthur and Levins 1967), Rosenzweig (1981) stated that species using the same landscape differ in the use of one or more habitat features, because differential habitat use reduces the potential for competition. Therefore, similarities or differences in habitat selection among co-occurring ungulates, hence potential for competition or for stable coexistence through habitat partitioning should take place at those hierarchical levels of habitat selection.

Grassland height, catena position, woody canopy cover, grassland species composition (Jarman and Sinclair 1979; Sinclair 1985; Ben-Shahar 1995; Owen-Smith 2002) and grass greenness (McNaughton 1985; Sinclair 1985) influence forage resources and habitat conditions for large grazers. Therefore, distinct habitat preference (Rosenzweig 1991; Johnson et al. 2000; Owen-Smith 2002) among grazers could be through differences among species in preference for these habitat features. Green grass leaves have higher concentration of protein, minerals and soluble carbohydrates than brown leaves (Bell 1970; Owen-Smith 1982). Accordingly, during the dry season grazers should select foraging areas where the highly nutritious green grass prevails (O'Reagain 2001). Food intake rate increases with grass height because with increasing grass height, bite size increases as animals apprehend a bigger volume of herbage through increased bite depth (Illius and Gordon 1990; Laca et al. 1992; O'Reagain 2001). Thus, during the dry season when forage quantity declines due to the absence of regrowth, large grazers should concentrate foraging on patches of tall grass offering high intake rates (Wilmshurst et al. 1999).

Catena position influences soil moisture availability, so that lower levels of the catena such as bottomlands, which contain more clay than uplands (Scholes 1990; Scoones 1995), retain soil moisture sustaining the availability of green grass and higher grass biomass than upper levels of the catena (Bell 1970; McNaughton 1985; Scoones

1995). Therefore, during the dry season grazers should concentrate foraging on bottomlands potentially retaining greener grass than uplands as documented by Bell (1970) for grazers in the Serengeti, by Estes and Estes (1974), Magome (1991) and Parrini (2006) for sable antelope (*Hippotragus niger*) and by Funston et al. (1994) for African buffalo (*Syncerus caffer*).

Woody vegetation cover influences the quantity and quality of food resources, shelter and shade from extreme weather conditions and security from predation. Certain highly rated forage species such as *Panicum maximum* grow beneath trees and shrubs (van Oudtshoorn 1999). Shade also reduces the rate of soil moisture loss from evaporation (Scholes 1990). Therefore, grass growing beneath trees potentially remains green for longer than grass in the surrounding more open areas; hence grazers should prefer foraging underneath trees. Shrubs might compete with grass for soil nutrients and water, resulting in low grass biomass in areas of thick bush (Smit et al. 1999). Therefore, grazers should avoid foraging in areas of high shrub cover. In African savannas shade is an important habitat condition to reduce heat load during the hot late dry season, particularly for animals with dark coat like sable and buffalo. Therefore, the need for refuge from adverse weather is another determinant of habitat use by ungulates (Duncan 1983; Owen-Smith 1988).

Habitat use by large herbivores is partly influenced by the spatial and temporal variation in the quantity and quality of forage and by water availability (Duncan 1983; Owen-Smith 1988; Bowyer et al. 1998; Winnie et al. 2008). However, apart from differences in food preference among grazers and differences in the availability of preferred food among habitats, differences in predation risk among habitats as well as differences in anti-predator behaviour (Jarman 1974; Sinclair and Arcese 1995; Bowyer et al. 1998) and social system (Duncan 1983) might contribute in explaining differential habitat use among ungulate species. Aggregation also reduces the risk of predation through simple dilution or by increased probability of detecting predators (Fryxell 1995). Accordingly, species that occur in large herds and that are able to fight against predators through group attack such as buffalo (Prins and Iason 1989; Prins 1996) may use a wide range of habitats, including habitats with relatively higher predation risk such as thick bush (Elliot et al. 1977; van Orsdol 1984). Ungulates that run away to escape predators

such as plains zebra (*Equus burchelli*, Estes 1991) should select for open habitats with good visibility for rapid detection of predators and should avoid thick bush providing cover for stalking predators (Elliot et al. 1977; van Orsdol 1984; Owen-Smith 2002), whereas species such as sable, not documented to successfully fight against large predators, should avoid being detected by predators by using habitats providing adequate woody cover for concealment.

Ruminants require higher quality forage than non-ruminants of similar body mass (Illius and Gordon 1992). Smaller herbivores require higher quality forage than larger herbivores (Bell 1970; Jarman 1974; Owen-Smith 1988). Sharing space with conspecifics results in rapid attrition of food resources within habitat patches (Owen-Smith 1988), but the high mobility of animals in large herds allows animals to use spatially variable resources, whereas sedentary species use resources occurring in small areas (Ritchie 2002). Animals occurring in smaller groups are able to use high quality food resources occurring in small habitat patches not detected or neglected by larger herds (Fryxell 1991). Therefore, following allometric relations of body mass and group size as well as gut morphology and function, smaller ruminants occurring in smaller herds should select for the combination of habitat features that ensure the acquisition of the required higher quality food resources, whereas larger ruminants occurring in larger herds and hindgut fermenters should use habitat feature more evenly.

Sable is a low density ruminant with a mean adult female weight of about 220 kg (Wilson 1968 cited by Owen-Smith 1988), occurring in herds of 15-25 individuals (Estes 1991). Zebra is a high density non-ruminant, with a mean adult female weight of about 310 kg (Wilson 1968 cited by Owen-Smith 1988; Skinner and Chimimba 2005) occurring in social units averaging 6-7 animals. Buffalo is a high density large ruminant (520 kg; Pienaar 1969), highly mobile and gregarious, in Punda Maria occurring in herds of about 200 - 400 animals. The low density and smaller ruminant, sable, was more precise in feeding on grass species retaining green leaves into the dry season, whereas buffalo and zebra showed broader tolerance to food resources at the grass species and grass features level (Chapter 1). There was overlap in the botanical composition of the diet between the low density sable and the high density grazers, raising potential for food competition. However, differential habitat preference might reduce potential for food competition

during periods of limited food supply such as the dry season. To establish the habitat features ecologically separating these co-occurring species during the critical dry season, I investigated similarities and/or differences in habitat features prevailing on sites used by sable, zebra and buffalo during periods of the day when these herbivores were expected to be foraging. I hypothesized that:

1. Sable should be a habitat specialist and narrower in habitat use than buffalo and zebra, by precisely foraging in habitat patches with green grass during the dry season, whereas zebra and buffalo should be more tolerant to the widely available brown grass
2. Sable should restrict foraging to areas with high woody vegetation cover and bottomlands where grass potentially remains green for longer during the dry season, whereas buffalo and zebra would forage in habitats with a broader range of woody vegetation cover and catena positions

Methods

Study area

I conducted this study to the south of Punda Maria Camp (22°68'S, 31°018'E) in northern Kruger National Park (KNP), South Africa, within an area of about 600 km^2. During the seasonal cycle July 2005- June 2006 rainfall was about 20-35% above the long term average recorded in 4 neighbouring weather stations at Punda Maria, Shangoni, Woodlands and Vlakteplaas. However, between July 2006 and June 2007 rainfall was about 30-50% below the long term average (see Chapter 1 for details). Rainfall is highly seasonal, falling mainly between October and March, while the period between April and September is generally dry. However, in July of the drier year of 2007, the study area received 9 mm of rainfall (average across the 4 weather stations).

Gertenbach (1983) described four landscape types covering the study area based on woody vegetation species composition and physiognomy, namely the Punda Maria sandveld on sandstone of the Soutpansberg group (Schutte 1986; Venter 1990), characterized by mixed *Combretum* spp woodland in the north-west of the study area; *Colophospermum mopane* woodland on Ecca shale in the north-east consisting generally

of dense tall mopane trees (>10 m); *Pterocarpus rotundifolius*/*Combretum* spp woodland on basalts of the Soutpansberg group covering the south-west, dominated by sparse small trees and shrubs; and *C.mopane*/*Acacia nigrescens* woodland mostly on granitic gneiss, consisting of medium sized trees covering the south of the study area. Perennial sources of drinking water were pools along the Mphongolo River in the south and a gravel pit in the south-west of the study area, opened in 1962. Water sources available only during the wet season and early dry season (until August in 2006, but only until May in the drier 2007) included few streams and many ephemeral pans widely distributed in the study area.

Study design

In May 2006 and June 2007, Global Positioning System (GPS) - cellular phone (GSM) collars were placed on sable, zebra and buffalo located south of Punda Maria Camp (see Chapter 1 for details). I initially scheduled the collars to record the GPS coordinates of the herds every six hours, at 2:00, 8:00, 14:00 and 20:00. However, during days of observation of each herd I adjusted the schedule of the collar to record the GPS coordinates of the herd hourly to obtain detailed data on the spatial location of the herds during the main potential foraging periods for the animals in the morning (6:00 – 10:00) and late afternoon/early evening (16:00-20:00) (Chapter 1) and to ensure that foraging areas were obtained for the assessment of habitat features prevailing in these areas. I applied study design 1 (Thomas and Taylor 1990), whereby I amalgamated data from different herds of the same herbivore species and made inference about habitat use at the population level. The entire sable and buffalo regional populations were included in this study, whereas the zebra population was represented by 4-6 collared herds corresponding to about 15-20% of the population.

Field data collection

Habitat selection was assessed at two levels, namely the selection of habitats at the broad level of landscapes distinguished by Gertenbach (1983) and the selection of habitat features on foraging areas within these landscapes.

I collected field data on habitat use by sable, zebra and buffalo during the dry seasons of 2006 (June–October) and 2007 (May-September). The study was conducted during the dry season because this is the period of limited food availability for large mammalian herbivores (Scoones 1995). Therefore, in this study I identified the habitat features prevailing on areas with resources supporting the populations of the three herbivores species during the limiting period of the year. To establish differences in habitat use between sable and buffalo or zebra, I used a modification of the site attribute design (Garshelis 2000), whereby the resource conditions and characteristics of the physical environment of feeding sites used by sable were not compared with available unused sites as commonly done (Thomas and Taylor 1990), but rather contrasted with habitat attributes that prevailed on feeding sites used by buffalo or zebra. Therefore, habitat features not used by any of these three species during the sampling period were ignored. I focused on measurements of habitat attributes on sites used by each species during foraging periods, assuming that during these periods habitat use was most influenced by forage distribution than by any other factor. Habitat features used by the animals during non-foraging periods were excluded from sampling. By means of GPS tracking, I visited sites used by each species during two days each week, recording habitat variables on 1-5 foraging areas used by the herd during each morning or afternoon foraging session. While use of habitat by the sable herd represented the use of habitat by the sable population because only one sable herd occurred in the study area, effort of data collection was distributed among collared zebra and buffalo herds to ensure that the collected data represented patterns of habitat use by the populations of these species. Distributing sampling effort between buffalo and collared zebra herds consisted of weekly alternating the herd of these species to be tracked for data collection.

In the surrounding of each herd location I recorded the following data to describe the prevailing resource conditions and characteristics of the physical environment:

- Topography or catena position: the position of the herd on the catena was classified and recorded as bottomland, midslope or upland;
- Woody canopy cover: woody cover was estimated as the proportion of the foraging area shaded or covered by tree (height $\geq$2.5m) or shrub (height <2.5m). Estimates were made within a 25 m radius from the GPS location of the herd

using the procedure outlined by Walker (1976). The percentage cover was grouped into the following classes: 0; 1-10; 11-25; 26-50; 51-75. Higher values of woody cover were not represented in foraging areas.

- The height of the top canopy cover within a 25 m radius was estimated and grouped into the following height categories: short trees (height ≤5 m); medium trees (6-10 m) and tall trees (>10 m).
- Grassland height: it was determined by the predominant grass height within a 25 m radius. Grass height was estimated and grasslands were categorized as short grass grassland (≤10 cm), medium (11-20 cm), medium-tall (21-40 cm), tall (41-80 cm) and very tall grass grassland (>80 cm).
- Grass greenness of the foraging area was estimated as the proportion of green leaves available in the sward within 25 m radius and classified according to the eight-point scale proposed by (Walker 1976): 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-90%, 100%.

Data analysis

Landscape selection: for the assessment of landscape selection, following Aebischer et al. (1993), I estimated the availability of each landscape in the study area as the proportion of the study area covered by each landscape. I estimated the total and core range of each herbivore species as the 95% and 50% adaptive kernel probability isopleths (Worton 1989; Seaman and Powell 1996); respectively, using locations of herds of each herbivore species between June 2006 and September 2007 (see Chapter 3 for details about kernel home range estimations). Following Johnson (1980) I assessed the preference for landscapes as the proportion of the total and core distribution range of the population of each herbivore species that was covered by each landscape relative to the availability of each landscape in the study area. I did this analysis in ArcGIS 9.1. (Environmental Systems Research Institute Inc, USA).

Sampling unit: I considered that habitat conditions in foraging areas during successive hours were not independent. Separation distances between successive hourly foraging locations of sable and zebra were generally less than 200 m, but up to about 1

km for the larger buffalo herds. A resting period between the morning and afternoon foraging sessions might have ensured independence between the foraging sessions, such that the area chosen by the herd to forage in the afternoon was likely to be independent of where the herd foraged in the preceding morning. Accordingly, I considered each morning or afternoon foraging session as an independent sampling unit for habitat features. I calculated the midpoint of the categories of habitat features on foraging areas used by the herd during different hours of the same morning or afternoon and then I averaged the midpoints to obtain the average habitat characteristics of the area used by the herd during the foraging session for each of the habitat feature. During the dry season most of the grass was brown. Thus, I used only Walker's (1976) four lowest grass greenness categories to detect small differences in greenness that can be influential in the selection of foraging areas by grazers during the dry season. Accordingly, for the analysis of prevalence of habitat features in foraging areas, I used the following categories: 0%, 1-10%, 11-25% and >25%. For each herbivore species, I combined all feeding areas where more than 25% of grass was green because these were less represented. I categorized tree and shrub cover into three broad categories of open (0-10%), mainly open (11-25%) and mainly closed (>25%). Tree height, grassland height and catena position remained with the categories applied during field data collection.

Seasonal subdivisions: I subdivided the data into the following stages of the dry season: early dry season of 2006 (June-July), late dry season of 2006 (August – October), early dry season of 2007 (May-July), and late dry season of 2007 (August-September). I defined these periods based on rainfall patterns and on the proportion of foraging areas retaining green grass. Months when more than 50% of foraging areas used by sable had >10% of green grass were combined into the early dry season, whereas months with no rainfall and more than 50% of foraging areas retaining <10% of green grass were grouped into the late dry season period. Early dry season and late dry season of 2006 and 2007 covered different calendar months because rainfall patterns were different between the two years. For instance, while in 2006 October was a late dry season month because rainfall only began in November, in 2007 October was an early wet season month because rainfall began at the end of September. In addition, in 2006 I started field data collection in June but in 2007 I started in May.

Habitat conditions in core vs peripheral range: Differential use of space might reflect spatial differences in resources (Marzluff et al. 2004), but also in predation risk (Bowyer et al. 1998). To relate the frequency of use of a specific section of the range to spatially variable habitat features, I estimated the core area (50% kernel isopleths) and the total area (95% kernel isopleths) used by sable, buffalo and the sampled zebra herds during the period of field data collection. Using the selection function in ArcGIS 9.1, from all foraging areas that I collected data for each herbivore species, I identified and separated the foraging areas that were within the core range from the foraging areas that were in the peripheral range. This was done to compare the habitat conditions that prevailed on sable core range with those of zebra or buffalo core range, and to compare habitat features of core areas and those of peripheral range for each herbivore species. I expected resources and habitat conditions to differ between core and peripheral range because concentrated use of a core range indicates preference for resources and conditions occurring in that area. These conditions might differ from conditions prevailing on the peripheral range, which is used only occasionally or during excursions outside core range, particularly as an adaptive response of foraging animals to the shrinking abundance of resources within the core range as the dry season progresses. Out of 99 sable foraging areas that I sampled between June and October 2006, 59 (60%) were within the core area occupied during the dry season, covering 6.0 km^2 and the remaining 40 foraging areas were in the peripheral range. Only 29 (38%) of the 76 foraging areas used by zebra that I sampled were within the core section of the range (11.5 km^2), whereas 46 (79%) of the 58 sampled foraging areas used by buffalo were within the core area covering 77 km^2. Between May and September 2007, 35 (52%) of sampled sable foraging areas were within 11.9 km^2 of core area, 27 (46.5%) of zebra foraging areas and 25 (65.8%) of buffalo foraging areas were within the core area of 16.7 km^2 and 65.0 km^2, respectively. Hence samples represented core and peripheral range roughly in proportion to their relative use.

Statistical analysis and model selection

Habitat features were the predictor variables whereas the count of foraging sessions within each category of habitat feature was the response variable. Count data do not generate a normal frequency distribution, but rather a Poisson distribution (Agresti 1990; Quinn and Keough 2002). Therefore, I applied Generalized Linear Models (GLM), which do not require normality in the distribution of the data. Because both predictor and response variable were categorical, I applied log-linear models, which based on observed cell counts, model the expected cell frequencies using the log link and a Poisson error term to obtain the log-likelihood, which is a measure of the fit of the model (Agresti 1990; Quinn and Keough 2002).

Differences in habitat features between the core and the peripheral range used by each species might confound the differentiation of herbivore species in habitat use, particularly if the proportions of sightings on core vs peripheral range differ greatly between species. To account for this potential confounding factor, prior to species comparisons, for each herbivore species I assessed whether habitat features differed significantly between range sections (core and peripheral range). I did this exploratory analysis using two-way log-linear analysis for each herbivore species separately. Each model included range section (factor 1) and each of the habitat features (grass greenness, grassland height, catena position and tree cover) as the second factor.

To establish distinctions between sable and buffalo or zebra in the habitat features prevailing on foraging areas used, I performed pair-wise loglinear models, whereby sable were compared with buffalo or zebra in the prevalence of each habitat variable or combination of habitat variables in foraging areas. Differences between stages of the dry season in rainfall, hence in forage and habitat conditions might confound the differentiation of herbivore species in habitat use. Therefore, the stage of the dry season was included as an additional factor in the model. Accordingly, I started off with a saturated model including the following factors, each with two levels: herbivore (sable and buffalo or zebra), season (early and late dry season), grass greenness (<10% and >10% of grass green), catena position (upland and non-upland = midslope and bottomland), grassland height (<40 cm and >40 cm) and tree cover (<10% and >10% tree cover). I only included tree cover to represent woody vegetation structure in the final

model because using either tree cover, shrub cover or tree canopy height yielded similar results regarding the influence of woody vegetation cover in species differentiation in habitat use. Grassland height showed no influence in distinguishing foraging areas used by sable from the foraging areas used by buffalo. Therefore, I excluded grassland height in the full model for the comparison between sable and buffalo. However, for the comparison between sable and zebra, I included grassland height in the full model in place of catena position, which showed no influence in the distinction in habitat use between sable and zebra. From each pair-wise comparison, i.e. sable vs buffalo and sable vs zebra, I left out of the model the habitat feature that had the lowest influence in the overall fit of the model. This reduced the complexity of the contingency table, ensured larger cell counts and made the model simpler and easier to interpret.

From the saturated model, I removed each factor or interactions between two, three or four of the factors and noted the likelihood ratio chi-square (G^2) and the degrees of freedom of the model without the removed factor or interaction of factors (Quinn and Keough 2002), i.e. the likelihood ratio chi-square and degrees of freedom of the model with all the remaining factors and interactions. By removing individual factors and different interaction of factors I produced a set of candidate models with different combinations of factors potentially explaining the differences in habitat use between sable and buffalo or zebra. I performed log linear analysis using SYSTAT 11.0 for Windows (SYSTAT Software, Inc., USA).

I compared the relative weight of support by the data of models assessing the effect of different combinations of habitat features in distinguishing foraging areas used by sable from areas used by buffalo or zebra using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Following Agresti (1990, pg. 251) and Quinn and Keough (2002, pg. 390-396) I applied the following formula to calculate AIC from results of loglinear models:

$AIC = G^2-2df,$

where:

G^2 - deviance of each model or log likelihood ratio chi-squared

df - degrees of freedom

Results

Habitat selection at the broad landscape level

For the establishment of home range sable selected for the mixed *Combretum* woodland and for the *Colophospermum mopane* woodland. The proportion of the core range covered by *Combretum* woodland and the proportion of the total range covered by *C. mopane* woodland were more than double of their relative availability in the study area (Table 1). Zebra showed preference for the less wooded *Pterocarpus rotundifolius*/*Combretum* spp woodland, with about 50% of core and total range being covered by this landscape, which occupied only 15% of the study area. Sable and zebra appeared to avoid the *C.mopane*/*Acacia nigrescens* woodland at both total and core range. On the other hand, buffalo were broad in landscape occupation, revealing no preference for specific landscape. The proportions of buffalo total and core range covered by different landscapes approximated the relative availability of these landscapes in the study area.

Distinctions in habitat conditions between the core and the peripheral range

Grass was greener in the sable core range than in the peripheral range. Overall, about 40% of foraging areas within the core section of the range occupied during the dry season retained >10% of grass green, whereas only about 20% of foraging areas had >10% of grass green in the peripheral range. Although sable generally foraged on uplands, within core range about 15% of foraging areas were in bottomland along a drainage line, whereas outside core range only 1% of foraging areas were on bottomland. The prevalence of other habitat features did not differ between sable core range and peripheral range. For buffalo and zebra, the habitat features prevailing on foraging areas did not differ between the core and the peripheral range. Therefore, for the comparison between herbivore species in habitat use I included all the foraging area data regardless of differences in the frequency of use of different sections of the home range.

Comparative habitat use between species

Sable vs buffalo

The model assessing the effect of grass greenness alone and the model assessing the effect of grass greenness and stage of the dry season were almost equally supported by the data as the best explanatory models of differences in habitat use between sable and buffalo (ΔAIC <0.3 and relative likelihood of 0.88 – 1.0, Table 2). Owing to its simplicity, I consider the model including grass greenness alone as the best model. Sable generally foraged in areas retaining greener grass than buffalo. During the early dry season of both 2006 and 2007, about 80% of foraging areas used by sable retained >10% of green grass and during the late dry season of both years in about 15% of foraging areas used by sable grass remained with >10% of grass green (Figure 1). Less than 20% of foraging areas used by buffalo had >10% of grass green, except during the early dry season of 2007 when buffalo appeared to use areas with greener grass than sable. During this period, although for both species about 70% of foraging areas retained >10% of grass green, about 50% of foraging areas used by buffalo retained >25% of grass green whereas only about 20% of foraging areas used by sable had >25% of grass green (Figure 1).

The model incorporating catena position alone also contributed to explaining distinctions between foraging areas used by sable and by buffalo (ΔAIC < 3, Table 2), with a likelihood of 28% the effect of catena alone in distinguishing habitats used by sable and buffalo cannot be discounted. However, adding catena to greenness did not improve the fit of the model, indicating that the effect of catena was weaker than the effect of greenness in distinguishing herbivore species. Overall, about 70% of foraging areas used by sable were on uplands, whereas about 60% of foraging areas used by buffalo were on bottomlands and midslopes (Figure 2). The stage of the dry season also influenced distinctions between sable and buffalo in the catena position of habitats used (likelihood of 32%). Whereas sable remained generally on uplands during most of the dry season, buffalo shifted from uplands and midslopes used during the early dry season to bottomlands towards the end of the dry season (Figure 2).

Tree cover alone did not contribute to the fit of the model, with a likelihood of 3% the effect of tree cover can be discounted in the ecological separation between sable and

buffalo at the habitat level. The effect of tree cover in distinguishing areas used by sable and by buffalo depended on grass greenness (likelihood of 32%). Overall, about 70% of foraging areas used by both species had >10% cover of shrubs and medium-tall trees (6-10 m) (Figure 3, 4 and 5). However, while during the less severe year of 2006, for both species around 50% of foraging areas were in open areas with <10% tree and shrub cover, in the drier 2007 about 60% of foraging areas used by both species were in more wooded areas, with >10% tree and shrub cover (Figure 3, 4 and 5). Grass taller than 40 cm prevailed in about 75% of foraging areas used by both species during all seasons sampled (Figure 6).

Sable vs zebra

The full model including the effects of grass greenness, tree cover, grassland height and stage of the dry season and the model assessing the effect of the interaction between tree cover and grass greenness received similar support from the data in distinguishing foraging areas used by sable from foraging areas used by zebra (ΔAIC <1.0 and relative likelihood of 0.69 - 1.0 Table 3). The support for the full model indicates that each of these habitat features had an effect in distinguishing foraging areas used by both grazers, but also each habitat feature influenced the effect of other features. The exclusion of any of these predictors from the model reduced substantially the fit of the model. However, due to its simplicity I considered the model including only tree cover and grass greenness as the best model. Among single habitat features tree cover was the most distinct feature between foraging areas used by sable and by zebra (relative likelihood of 7%, Table 3). Overall, about 70% of foraging areas used by sable were in wooded areas with >10% cover of shrubs and medium-tall trees (6-10 m). Although zebra foraged in areas with a wider range of tree cover than sable, about 50% of foraging areas were in open areas with <10% of tree cover and a wide range of tree canopy height (Figure 3, 4 and 5). The contribution of the interaction between tree cover and grass greenness indicates that the effect of tree cover depended on grass greenness. The more wooded areas used by sable retained greener grass (>10% of grass green) than the more open habitats used by zebra. In about 60% of foraging areas used by zebra grass was predominantly brown (<10% of grass green), except during the early dry season of 2007

when about 50% of foraging areas had >10% of grass green (Figure 1). Sable used a narrow range of grassland height, with grass taller than 40 cm prevailing in about 75% of foraging areas, whereas for zebra grass taller than 40 cm prevailed in about 50% of foraging areas and in about 20% of foraging areas grass was shorter than 20 cm (Figure 6). However, the model assessing the effect of grass height alone was not supported by the data in explaining ecological separation between sable and zebra at the habitat level (Table 3). For both species approximately 70% of foraging areas were in upland regions of the landscape (Figure 2).

Discussion

In this paper I predicted that sable, being a smaller ruminant, occurring in smaller herds and attaining lower regional density, would use a narrow range of habitats by restricting foraging to areas retaining green grass. Accordingly, I expected sable to restrict foraging to areas with habitat features that might contribute to the retention of green grass, such as wooded/shaded areas and bottomlands. I predicted that buffalo, being a larger ruminant occurring in larger herds and the non-ruminant zebra would forage on the widely available brown grass and use foraging areas with a wider range of catena positions and woody vegetation cover than sable.

Results showed that sable were distinct from both buffalo and zebra by using areas retaining greener grass. Sable were also distinct from buffalo by using foraging areas on uplands whereas buffalo foraged mostly on bottomlands and midslopes. Sable were different from zebra by using areas with higher woody cover than the areas used by zebra, but overlapped with buffalo in woody vegetation cover prevailing on foraging areas. Sable and zebra overlapped on the use of foraging areas on uplands. Sable were narrower than both buffalo and zebra in grass greenness and narrower than zebra in grassland height and in woody vegetation cover prevailing in areas used for foraging. Buffalo were broader than sable and zebra in the range of landscape types occupied.

The use of woodlands with about 25% woody vegetation cover by sable had also been previously documented by Estes and Estes (1974) in the Luando Integral Nature Reserve in Angola, by Wilson and Hirst (1977) in the Hans Merensky Nature Reserve in

the lowveld of South Africa and in the Matetsi area of Zimbabwe and by Parrini (2006) in the Kgaswane Mountain Reserve, South Africa. However, Estes and Estes (1974), Sekulic (1981) and Parrini (2006) also reported use of treeless grasslands during the dry season, whereas Magome (1991) documented that sable neglected treeless grasslands. The findings of this and previous research suggest that sable use foraging areas with a wide range of woody vegetation cover and that what constitutes preferred habitat as well as the range of habitats used by sable vary between study areas that differ in the physiognomy of the vegetation. Results from this study are also similar to the findings by Funston et al. (1994) and Ryan et al. (2006) that buffalo selected for open woodlands and made relatively little use of treeless areas in the Sabi Sand Nature Reserve and Klaserie Private Nature Reserve, respectively. However, other studies (Taylor 1989; Prins 1996) showed buffalo dependency on floodplain grasslands with plentifully available green grass during the dry season and use of wooded savannas on the uplands only when the floodplains were inundated during the wet season. Therefore, findings from previous studies on habitat use by sable and buffalo, although conducted in distinct areas, show similarity in woody vegetation cover prevailing in areas used by these grazers, which I also documented using herds of these species occupying the same broad landscape during the same time. The use of a broad range of habitat types by zebra, from treeless short and tall grasslands to woodlands had also been documented by Davidson (2002) in north-eastern KNP. However, Smuts (1975) reported that zebra favoured grasslands and avoided woodlands. Tolerance of zebra for a wide range of food resources (Smuts 1975) could explain the high variability in grassland height and woody vegetation cover on foraging areas used by zebra during this study.

Contrary to findings of previous studies (Estes and Estes 1974; Magome 1991; Parrini 2006) that during the dry season sable use bottomlands due to retention of green grass in these regions of the catena,, sable remained on uplands through the dry season. Henley (2005) also in the Punda Maria area observed sable more frequently on uplands during the dry seasons of 2002 and 2003. The difference in the seasonal patterns of catena position in foraging areas used by sable between this and previous studies could be because in the Luando Integral Nature Reserve (Estes and Estes 1974), Pilannesberg National Park (Magome 1991) and Kgaswane Mountain Reserve (Parrini 2006),

bottomlands were generally vleis and swamps retaining soil moisture and green grass year-round. These habitats do not occur in Punda Maria where bottomlands are in the form of river banks and seasonal drainage lines. The banks of the single river running in the study area were used by buffalo as core range through the late dry season (Chapter 4), hence grass was probably depleted by frequent grazing by buffalo. Similar to previous studies (Jarman and Sinclair 1979; Funston et al. 1994; Macandza et al. 2004 and Bowers 2006), I documented an increasing use of midslopes and bottomlands by buffalo with the advance of the dry season. Funston et al. (1994) suggested that the retention of high biomass of favoured grass species such as *P. maximum* and proximity to water were the habitat variables influencing the concentration of buffalo on bottomlands during the dry season. Therefore, the likely depleted grass resources on bottomlands by frequent buffalo grazing, and perhaps avoidance of predation risk in areas with high concentration of buffalo could explain why sable did not concentrate foraging on bottomlands during the dry season of 2006 and 2007.

When sable and buffalo used an environment with similar resources and habitat conditions, such as between June and August of 2006, grass on foraging areas used by sable was greener than in areas used by buffalo, which tolerated the abundantly available brown grass. This finding was expected because smaller herbivores have higher energy requirements relative to body mass, hence select for higher quality forage than larger herbivores, which require higher absolute quantity but tolerate poor quality food (Bell 1970; Jarman 1974; Owen-Smith 1988). However, this difference in greenness of the grass prevailing on foraging areas does not necessarily indicate a difference between species; it could be a result of differences in group size between the two species. Fryxell (1991) suggested that animals occurring in smaller groups are able to forage on small patches of resources not used by animals occurring in larger group sizes. Sinclair (1977) and Jarman and Sinclair (1979) documented that small groups of male buffalo used small habitat patches along drainage lines retaining greener grass than areas used by larger breeding herds. During the dry season, brown grass is more widely distributed than green grass, which becomes progressively sparser and restricted to areas retaining soil moisture (Bell 1970). Therefore, although all grazing herbivores prefer to feed on green grass due to its higher nutritional value than brown grass (Bell 1970; Owen-Smith 1982), with

decrease in the availability of green grass as the dry season advances, large herbivores should broaden their tolerance to grass phenology and forage on areas with predominantly brown grass. Reliance on discrete patches of green grass by sable suggests dependency on a narrow range of resources and hence limited ability to cope with the shrinking availability of green forage with the advance of the dry season.

The greener grass recorded on foraging areas used by buffalo than by sable during the early dry season of the more severe year of 2007 could be explained by spatial separation between sable and buffalo during this period. While sable used upland regions of the landscape as did during the dry season of 2006, buffalo shifted from uplands used during the wet season to bottomlands and midslopes early in the dry season (in April). Bottomlands generally retain more green leaves into the dry season due to higher clay content on the soil and hence higher retention of soil moisture than soils on uplands. The shift in range location by buffalo from uplands to bottomlands and midslopes could be because beyond April 2007 drinking water on uplands was limited to scattered small pans, unable to sustain the drinking needs of individuals from the large buffalo herd, until the wet season rains started at the end of September. Besides differences in catena position, the Punda Maria weather station, which was the nearest to sable home range during the early dry season, received less rainfall (2.6 mm) than the nearest weather stations to buffalo range (16 mm of rainfall at Shangoni and 8.5 mm at Woodlands weather station) during the first week of July 2007. Therefore, the combination of higher clay content on the lower levels of the catena and the relatively higher rainfall received in the buffalo range might have contributed to a higher proportion of green grass within buffalo than within sable range during the early dry season of 2007. Although zebra tolerated a wider range of grassland heights than sable and buffalo by also foraging on areas with shorter grass, the three herbivore species overlapped in the use of foraging areas where tall grass prevailed. Among short grass grazers, Arsenault and Owen-Smith (2008) also documented overlap in the prevailing grassland height on foraging areas.

Overall, results showed no clear separation between sable and buffalo or zebra, but rather similarities in the habitat features prevailing on foraging areas, although buffalo used more bottomlands and zebra used more open areas than sable. Therefore,

when using overlapping ranges during periods of limited food availability such as the dry season, the three grazers might compete for food resources.

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Table 1. Proportions of different landscapes within total ranges (95%) and core ranges (50%) of sable herd, both buffalo herds and collared zebra herds combined compared to the proportional availability of the landscapes in the study area

		Sable		Zebra		Buffalo	
	Availability	95%	50%	95%	50%	95%	50%
Mixed *Combretum* spp woodland	12	26	82	26	14	13	22
C. mopane woodland	20	55	18	18	24	24	20
P.rotundifolius/*Combretum* woodland	15	12	0	48	62	22	20
C.mopane/*A. nigrescens* woodland	53	7	0	8	0	41	38

Table 1. Comparison of models incorporating different factors or interaction of factors in the distinctions in habitat use between sable and buffalo

Models	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Herbivore x season x greenness x tree cover x catena	34.78	10	14.78	7.29	0.01	0.03
Herbivore x catena x tree cover	51.1	14	23.1	15.61	0.00	0.00
Herbivore x greenness x tree cover	37.78	14	9.78	2.29	0.11	0.32
Herbivore x season x tree cover	45.16	14	17.16	9.67	0.00	0.01
Herbivore x season x catena	37.77	14	9.77	2.28	0.11	0.32
Herbivore x catena x greenness	42.24	14	14.24	6.75	0.01	0.03
Herbivore x season x greenness	35.75	14	7.75	0.26	0.30	0.88
Herbivore x greenness + Herbivore x catena + Herbivore x tree cover	56.06	18	20.06	12.57	0.00	0.00
Herbivore x catena	40.03	15	10.03	2.54	0.10	0.28
Herbivore x greenness	37.49	15	7.49	0	0.35	1.00
Herbivore x tree cover	47.33	16	15.33	7.84	0.01	0.02

Table 2. Comparison of models incorporating different factors or interaction of factors in the distinctions in habitat use between sable and zebra

	G^2	DF	AIC	Δ AIC	Akaike weight (*wi*)	Relative likelihood
Herbivore x season x greenness x tree cover x grassland height	140.9	10	120.9	0	0.44	1.00
Herbivore x grassland height x tree cover	160.44	14	132.44	11.54	0.00	0.00
Herbivore x greenness x tree cover	149.63	14	121.63	0.73	0.31	0.69
Herbivore x season x tree cover	151.71	14	123.71	2.81	0.11	0.25
Herbivore x season x grassland height	152.54	14	124.54	3.64	0.07	0.16
Herbivore x grassland height x greenness	153.67	14	125.67	4.77	0.04	0.09
Herbivore x season x greenness	164.98	14	136.98	16.08	0.00	0.00
Herb. x greenness + Herb. x grassland height + Herb. x tree cover	184.14	18	148.14	27.24	0.00	0.00
Herbivore x grassland height	161.09	15	131.09	10.19	0.00	0.01
Herbivore x greenness	174.47	15	144.47	23.57	0.00	0.00
Herbivore x tree cover	156.24	15	126.24	5.34	0.03	0.07

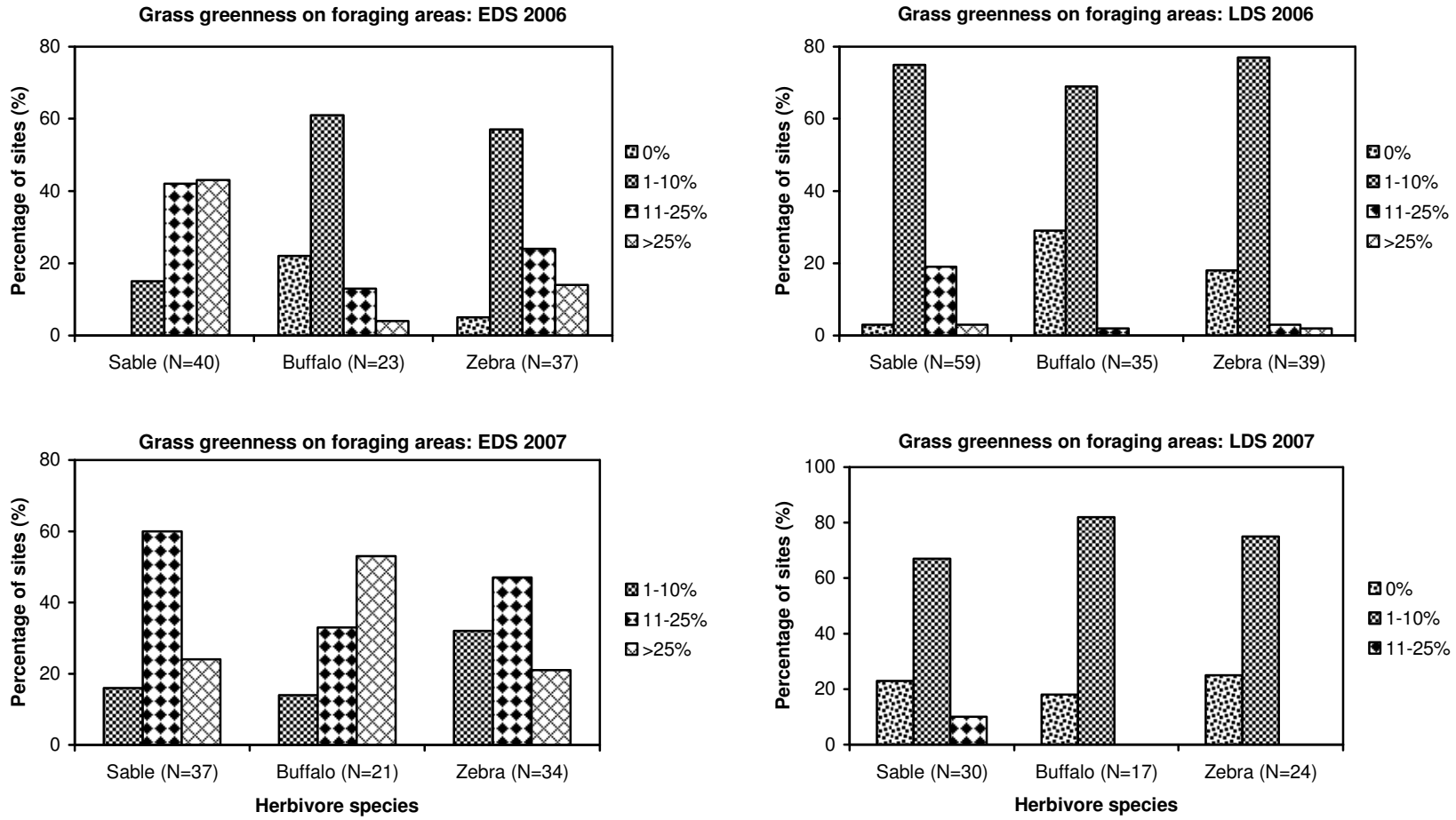


Figure 1. Comparison of herbivore species in grass greenness prevailing in foraging areas used during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007

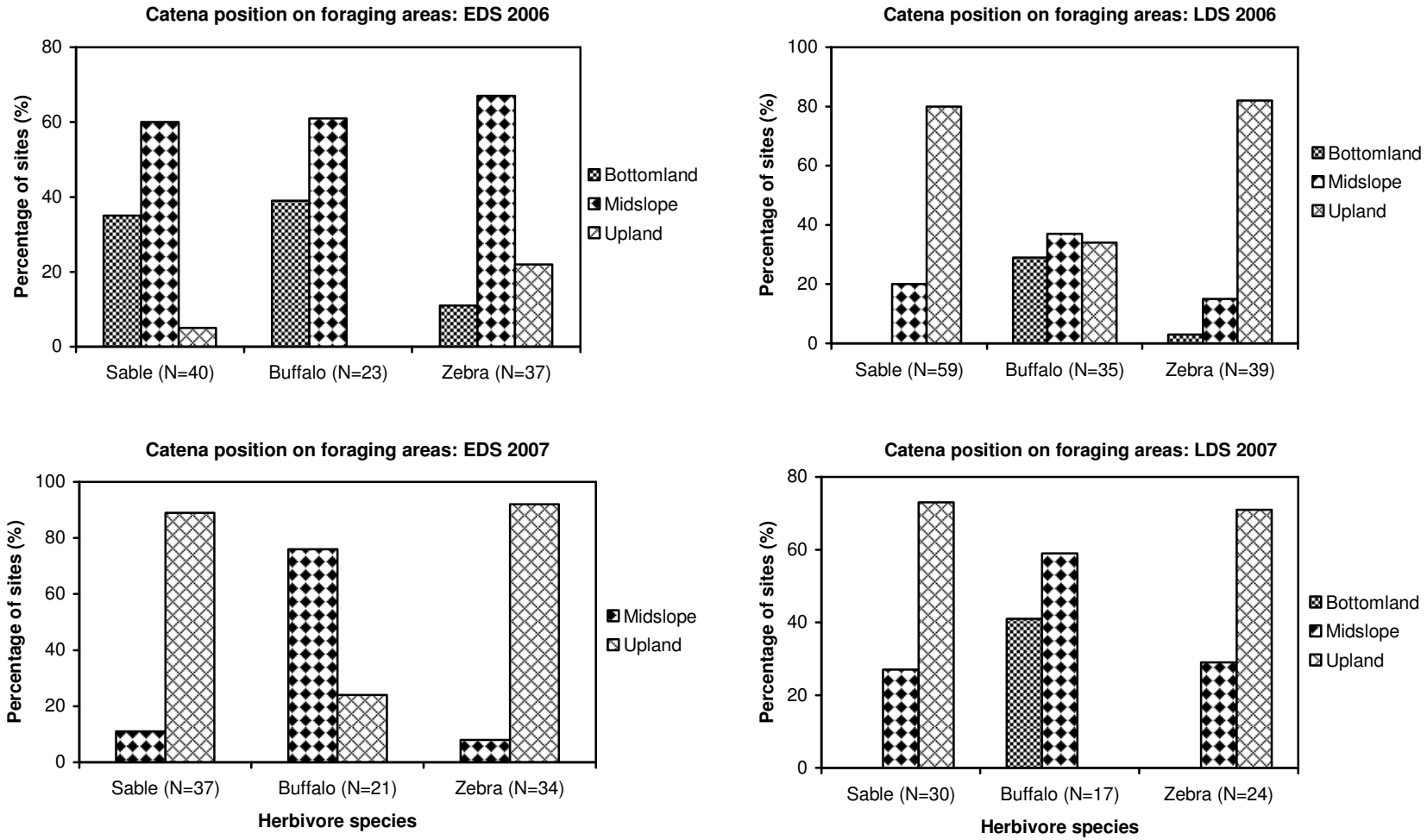


Figure 2. Comparison of catena position on foraging areas used by sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007

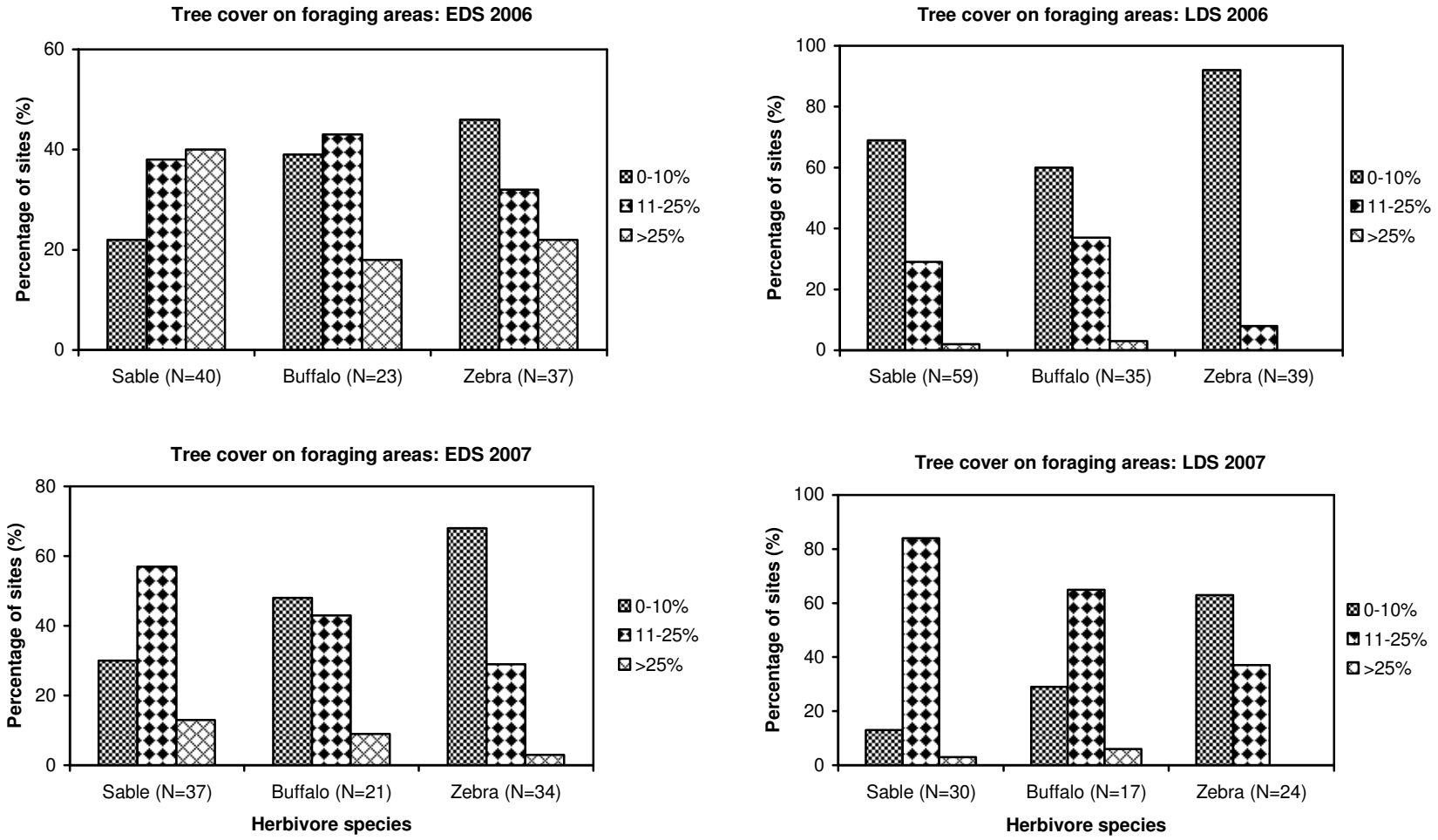


Figure 3. Comparison of tree cover prevailing in foraging areas used by sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007

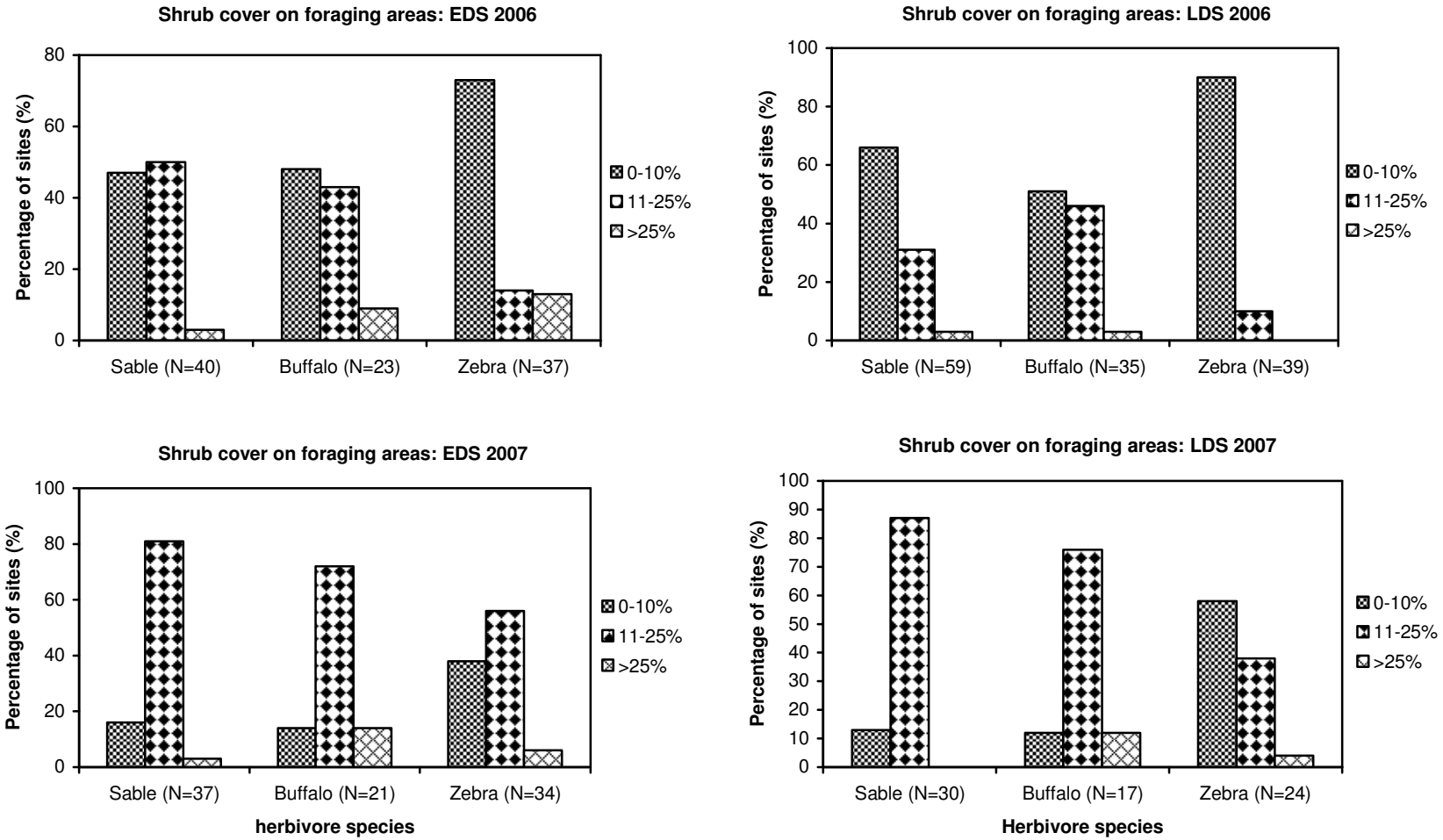


Figure 4. Comparison of shrub cover prevailing in foraging areas used by sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007

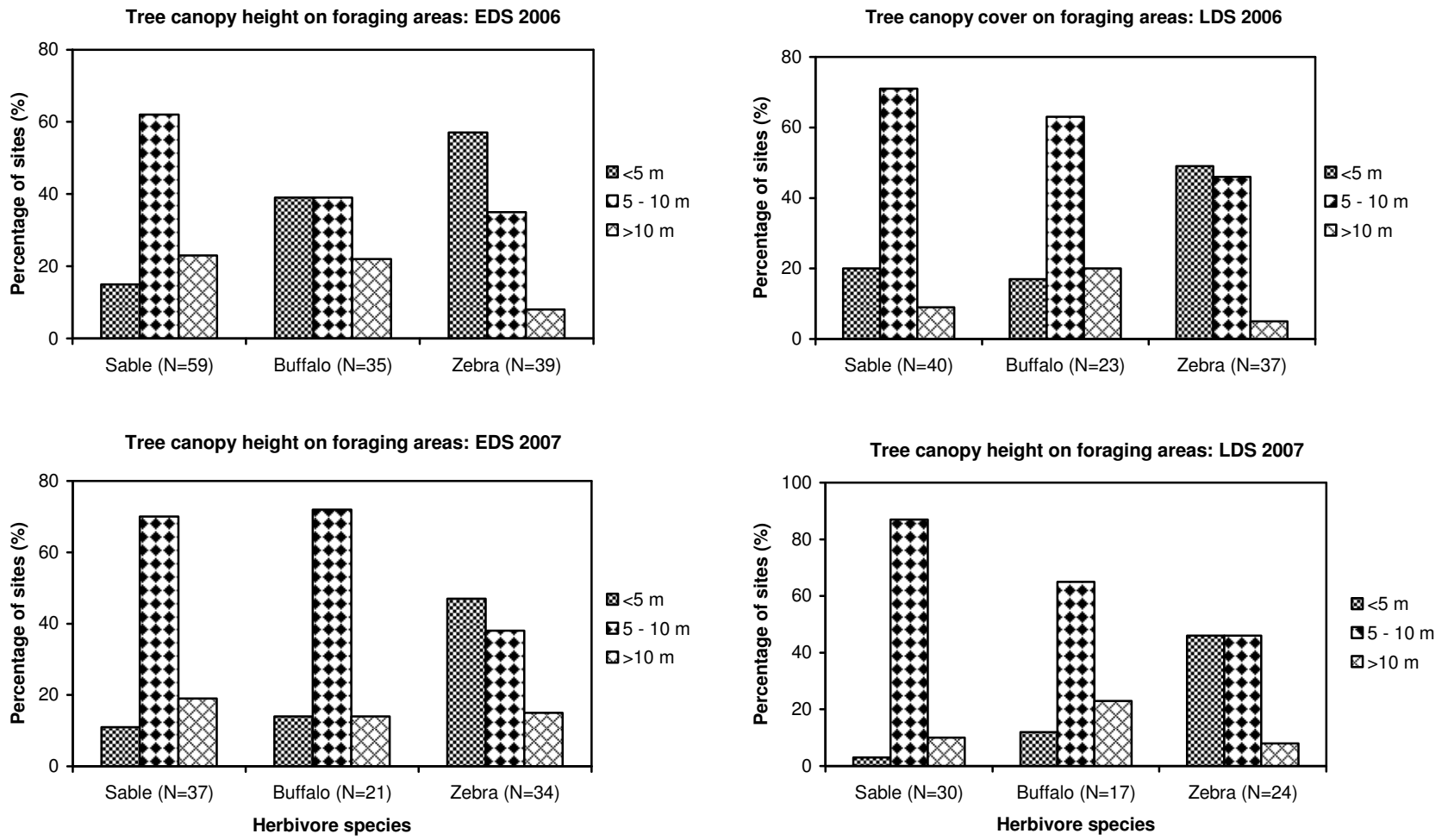


Figure 5. Comparison of tree canopy height prevailing in foraging areas used by sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007

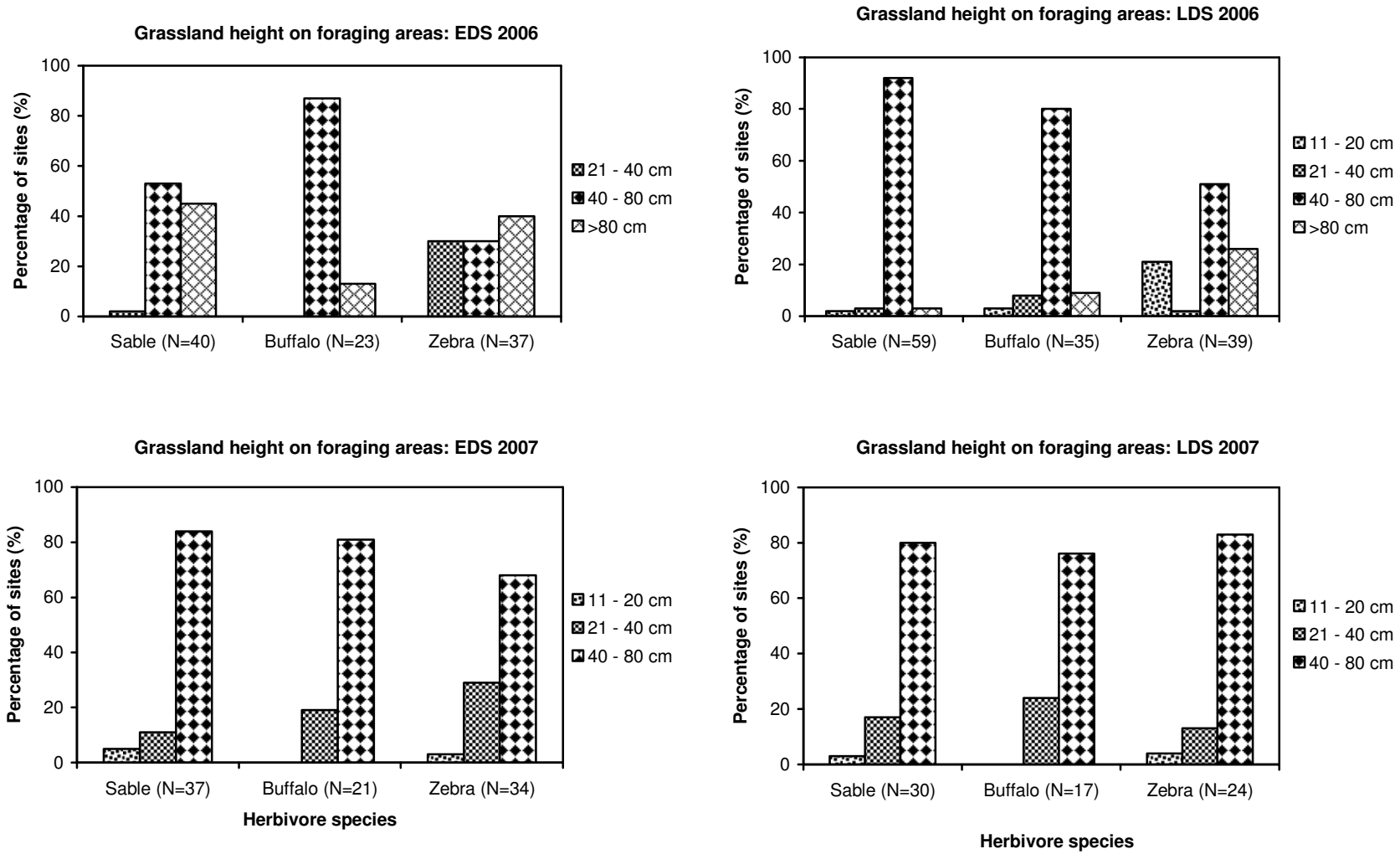
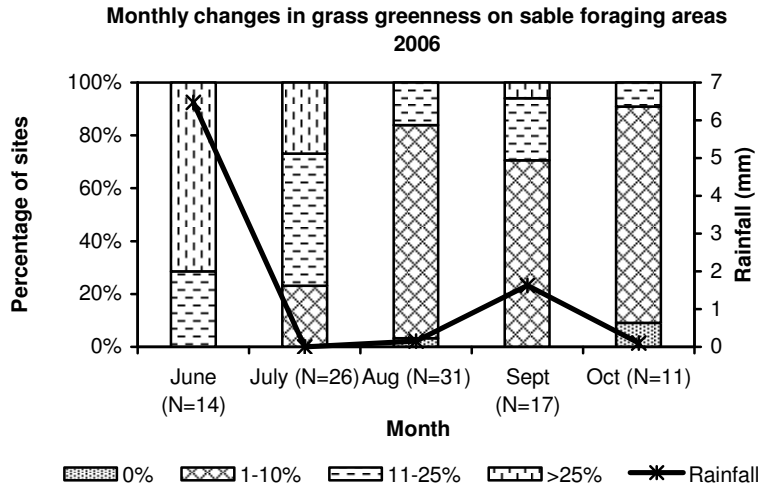
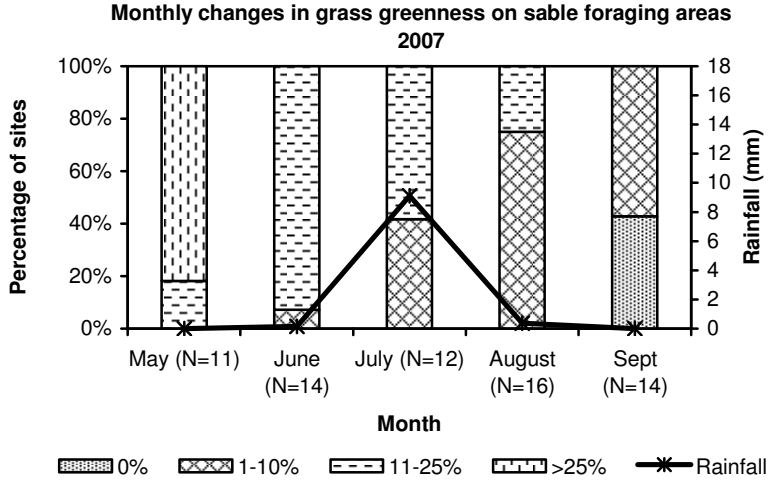
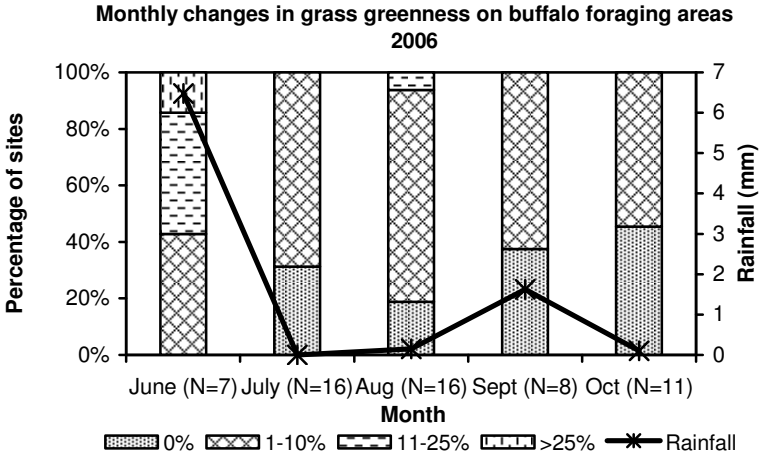
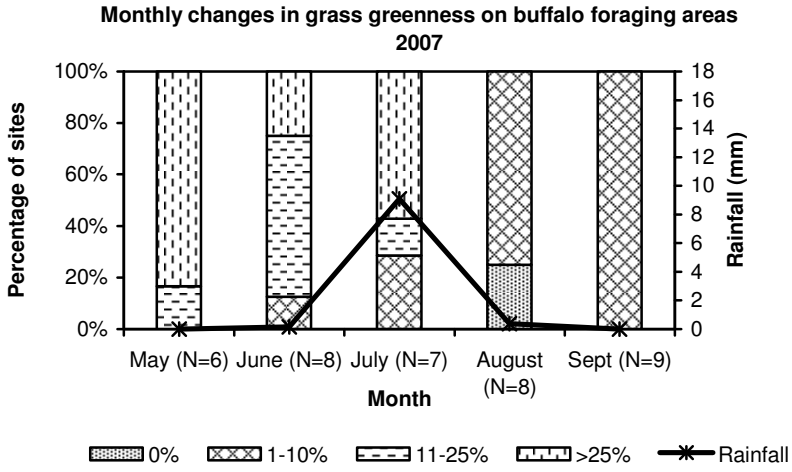


Figure 6. Comparison of grassland height prevailing in foraging areas used by sable, buffalo and zebra during the early dry season (EDS) and late dry season (LDS) of 2006 and 2007


Monthly changes in grass greenness on sable foraging areas
2006
Percentage of sites
Rainfall (mm)
100%
80%
60%
40%
20%
0%
7
6
5
4
3
2
1
0
June (N=14)
July (N=26)
Aug (N=31)
Sept (N=17)
Oct (N=11)
Month
0%
1-10%
11-25%
>25%
Rainfall


Monthly changes in grass greenness on sable foraging areas
2007
Percentage of sites
Rainfall (mm)
100%
80%
60%
40%
20%
0%
18
16
14
12
10
8
6
4
2
0
May (N=11)
June (N=14)
July (N=12)
August (N=16)
Sept (N=14)
Month
0%
1-10%
11-25%
>25%
Rainfall


Monthly changes in grass greenness on buffalo foraging areas
2006
Percentage of sites
Rainfall (mm)
100%
80%
60%
40%
20%
0%
7
6
5
4
3
2
1
0
June (N=7)
July (N=16)
Aug (N=16)
Sept (N=8)
Oct (N=11)
Month
0%
1-10%
11-25%
>25%
Rainfall


Monthly changes in grass greenness on buffalo foraging areas
2007
Percentage of sites
Rainfall (mm)
100%
80%
60%
40%
20%
0%
18
16
14
12
10
8
6
4
2
0
May (N=6)
June (N=8)
July (N=7)
August (N=8)
Sept (N=9)
Month
0%
1-10%
11-25%
>25%
Rainfall

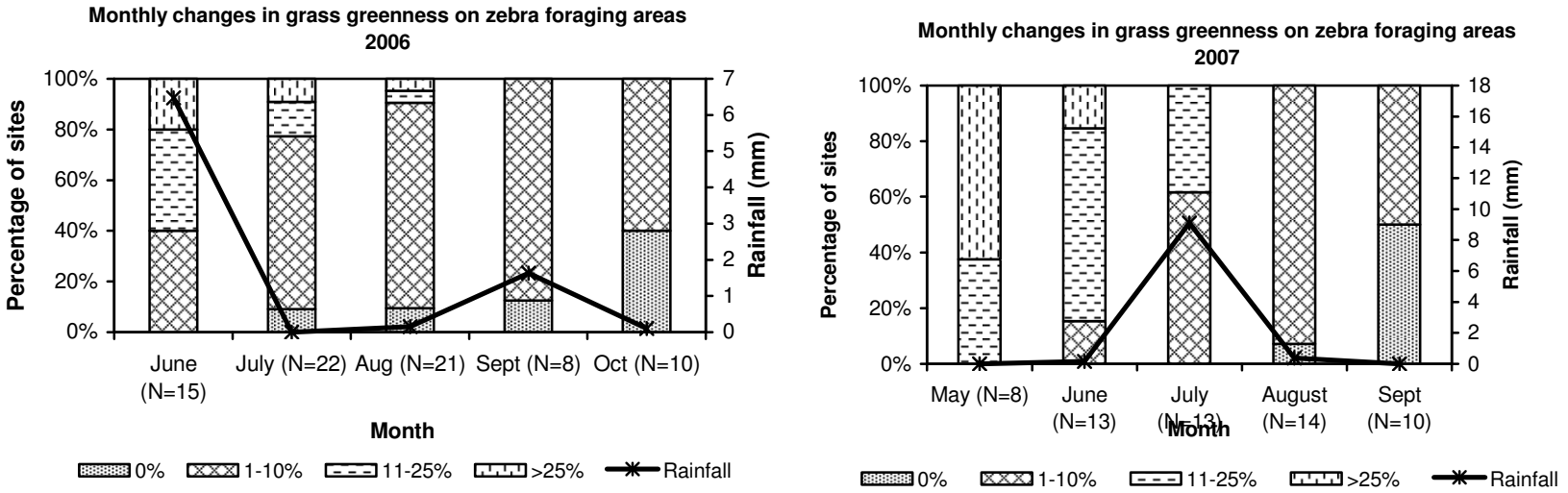


Figure 7. Monthly rainfall and changes in the percentage of foraging areas retaining green grass for sable, buffalo and zebra during the dry season of 2006 and 2007

CHAPTER THREE

Precision in home range use by low density versus high density grazers

Abstract

This investigation aimed at establishing distinctions in patterns of home range use between grazers that differ in regional density, body size, group size and feeding specialization. GPS-GSM collars were fitted on females within a sable herd, representing a low density, smaller and specialist grazer, and on females within buffalo and zebra herds, representing high density and generalist grazers, in northern Kruger National Park. Home ranges were estimated for different herds of these grazers during distinct periods of food availability using kernel methods. The relationship between the metabolic use intensity and the home range increments for successive kernel contours was assessed as a measure of the flow of energy from forage to herbivore biomass. During the wet season when food and water were abundant the sable herd showed intense use of a small section of the range, whereas zebra and buffalo used home ranges more evenly. However, when resources were limiting during a severe dry season, the sable herd became less precise in the use of the range, moved more widely and the intensity of metabolic use of space became lower than by buffalo and most zebra herds. Sable and buffalo herds increased range size from the wet to the dry season, but the magnitude of the increase was greater for sable than for buffalo, while zebra herds reduced range sizes as the dry season progressed. Results show that during the wet season forage resources from smaller areas provided the necessary energy for the specialist grazer. However, the dry season was a stressful period for sable, with wider movements reflecting search for specific resources that became sparser with the advance of the season. Generalist grazers appeared less stressed by the seasonal changes in forage availability, suggesting that they were supported by abundant and widely distributed resources.

Introduction

The distinction of rare from common species has been based on local population size, resource selectivity and geographical distribution of the species (Gaston 1997). Patterns of home range use by mobile animals have been neglected in the concept of rarity and commonness. The seasonal availability and spatial distribution of resources supporting the population should determine how precisely or evenly a species use space to satisfy resource requirements. However, the seasonal changes in the availability of food resources for grazers are influenced by the breadth of tolerance to these resources, which differs among grazers attaining different regional densities (Chapter 1). In heterogeneous landscapes, grazers that depend on resources that occur in specific sections of the landscape or those that require less quantity of food should show a narrow distribution of utilization of space suggestive of a more precise use of space for foraging, whereas grazers that depend on widely distributed resources or those that have higher absolute intake requirements should reveal an even distribution of density of animal locations across the landscape.

In general, the determinants of home range size vary with the level of biological organization (McLoughlin and Ferguson 2000). Body size determines differences between species in range size; habitat productivity determines differences in range size between populations of the same species; whereas food availability, patchiness in the environment and predation are the factors influencing home range size and patterns of its utilization by individuals within a population (McLoughlin and Ferguson 2000). Home range size increases with increasing body mass because larger animals require higher food quantity than smaller animals (McNab 1963; Owen-Smith 1988) and tend to be generalist feeders (Bell 1970). Within populations of the same species, home range sizes should increase with decrease in food density towards the end of the dry season. However, if sections of the landscape retain key resources for the population during the critical late dry season, such as drainage lines retaining green forage (Scoones 1995; Knoop and Owen-Smith 2006), foraging animals might concentrate use of space on these smaller areas during the dry season than during periods when food is widely distributed.

Herbivore aggregation patterns also influence the spatial scale of patch use (Fryxell 1991), because the energetic requirements of the herd are dependent on group

size due to its direct influence on the metabolic biomass (Owen-Smith 1988). Therefore, herbivore species occurring in larger group sizes should use larger home ranges than similarly sized species occurring in smaller social groups. Harestad and Bunnell (1979), Jetz et al. (2004) and Anderson et al. (2005) maintained that animals use the smallest area that contains the resources required by the animals during the specified time period. Therefore, during periods of abundance of the favoured food, low density, smaller resource specialist herbivores such as sable antelope (*Hippotragus niger*, 220 kg) should use relatively smaller home ranges than the larger generalist grazers like African buffalo (*Syncerus caffer*, 520 kg). This is because when the density of food is high selective feeding allows energetic requirements to be met in a small area. However, during periods of food limitation, resources for specialist herbivores become sparser (Chapter 1) prompting these species to move over relatively wider home ranges than the generalist consumers that can exploit the readily available food of low quality.

According to Owen-Smith (1988), from the allometry of home range size and metabolic requirements, the extent of an individual home range is equal to $1.07M^{0.83}$. The population mean mass per individual (M) is 165 kg for sable, which is three-quarters of adult female body mass (Owen-Smith 2008). Based on the above allometric relationship, the home range of a sable of 165 kg (0.74 km^2) should be about half a buffalo (M=390 kg) range (1.5 km^2) and 75% of a plains zebra (*Equus burchelli*) (M=232 kg) home range (0.98 km^2). However, the extent of the total area covered by the herd will be a function of herd size. Thus, multiplying the range extent per individual by herd sizes in my study area, the home range of the sable herd (20 animals) should be about 15 km^2, approximately 5% of the home range of the buffalo herd (200 animals, 300 km^2) and about double of the home range of zebra herds (7 animals, 7 km^2).

In this paper I investigated how narrow selection of forage resources by the smaller and low density sable influenced seasonal space use patterns, compared with buffalo and zebra, which were much more abundant and showed broader tolerance to food resources. I tested the following hypotheses:

1. Sable should depend on resources that occur in more restricted areas, hence be more precise at locating resource-rich patches and their core range should consist of smaller discrete patches than zebra or buffalo core ranges;

2. Sable, being a low density and specialist consumer should be more precise in foraging during periods of food abundance, i.e. resource requirements of the herd should be met in a smaller area than buffalo and zebra. However, during periods of resource limitation sable specialization on resources that become sparser with the progress of the dry season should result in wider movements and spread use over a larger home range than zebra, a similar sized generalist feeder;
3. Being larger and occurring in larger herd size, buffalo should use a larger home range than sable and zebra
4. Feeding selectively on plant parts of high quality, sable should be more efficient in obtaining the energy from the forage in the places selectively utilized than zebra or buffalo. Therefore, the intensity of metabolic use of space by sable within core range should be higher than by zebra and buffalo, i.e. core areas should support more sable biomass than buffalo or zebra.

Methods

Study area

I conducted this study to the south of Punda Maria Camp (22°68'S, 31°018'E) in northern KNP, South Africa, within an area of about 600 km^2. Between July 2005 and June 2006 rainfall (743 mm) was above the long term average of 600 mm, but during the seasonal cycle July 2006 – June 2007 rainfall (419 mm) was lower than the long term average (see Chapter 1 for details). Geologically the study area is underlaid largely by sandstone substrates, but also by basalts of the Soutpansberg group, Ecca shale of the Karoo system and granitic gneiss (Schutte 1986; Venter 1990; Joubert 2007). Broadly, two main woodland types can be distinguished in the study area based on the dominant tree species, namely the mixed *Combretum* spp woodland on the sections of the study area underlaid by sandstone and granitic formations, and *Colophospermum mopane* woodland or shrubland on basalt of the Soutpansberg group and Ecca shale (Gertenbach 1983; Venter 1990) (see Chapter 1 and 2 for details).

Perennial sources of drinking water were pools along the Mphongolo River in the south and a gravel pit in the south-west of the study area, opened in 1962. Five boreholes

were established in the study area between 1963 and 1970 to supply drinking troughs for animals. Two of these boreholes were closed around 1992. Two boreholes remained open until July 2006, one in the north-west and one around the center of the study area. The fifth borehole in the south-west supplied water to animals until February 2007. Water sources available only during the wet season and early dry season (until August in 2006, but only until May in the drier 2007) included few streams and many ephemeral pans widely distributed in the study area.

Study design and data collection

Three adult females from two sable herds, four adult females from four herds of zebra and two females in one buffalo breeding herd were fitted with GPS-GSM collars. Additional collars were placed on animals within herds of these species in June 2007, being one on sable, two on zebra and one on buffalo (see Chapter 1 for details). Using the GPS tracking technology I remotely collected herd location data without influencing animal movements by human presence. I scheduled the collars to record and send the GPS coordinates of the herds every six hours. GPS herd locations were obtained for 8:00 AM and 8:00 PM assumed to represent the feeding periods, and for 2:00 AM and 2:00 PM assumed to represent the resting periods. To confirm the activity of the animals during these periods, I visited the sites used by the animals during the 8:00 AM and 8:00 PM and observed signs of fresh feeding on most of these sites (Chapter 1), which means that animals were commonly feeding during these times, or that the animals had been feeding on these sites during earlier hours. Therefore, I considered the 8:00 AM and 8:00 PM herd locations as representing the areas used by the animals during the morning and evening foraging spells. To save the power of the battery and extend the period of collar functionality, I set the schedule of collars AM142 and AM147 fitted on zebra and collar AM150 fitted on buffalo to record one GPS herd location per day during September and October 2006. Unfortunately these collars did not deliver data for longer periods than the collars delivering data every six hours, but rather there was a loss of opportunity to obtain detailed location data from these collars during that period.

Using this schedule collars representing the three herbivore species delivered data for more than one annual cycle. Of the nine collars placed on animals in May 2006, collar AM143 placed on sable, collars AM141 and AM142 fitted on zebra and collar AM152 fitted on buffalo delivered data beyond September 2007, collar AM147 fitted on zebra provided data up to July 2007, collar AM145 also on zebra worked only until September 2006 and collar AM150 fitted on buffalo stopped sending data in March 2007 (Appendix 4). All collars fitted in June 2007 provided data through the late dry season of 2007. All sable females bearing collars were in the same herd during the study duration, except a few weeks during the early wet season when the herd had split. Therefore, only data from the collar that lasted longest (AM143) were used to assess space use by the sable herd, whereas data obtained from five collars fitted on zebra and two collars fitted on buffalo were used for the analysis. For the estimation of precision in foraging I included in the analysis only herd locations during the prime foraging periods of morning (8:00 AM) and early evening (8:00 PM). Geographical coordinates of herd locations were projected into WGS 1984 UTM zone 36S datum before home range analysis.

Sable movements at the end of the dry season of 2006 and 2007 were influenced by the availability of water resources, which were restricted to pools along the Mphongolo River. Sable journeys to water occurred generally every 2-3 days in the early morning and occasionally in the late afternoon. Distance to water was about 7–8 km from the normal range. When journeys to water started in the morning (around 5:00AM) the sable herd could be back to normal range in the afternoon (around 5:00PM) and when journey started around 4:00PM the herd was back to normal range around 10:00PM. Journeys to water sources were also observed for zebra AM141 during the late dry season of 2007. During the late dry season of 2006, zebra AM141 did not depend on the water from the river because a borehole was open within the normal range of this zebra herd. For the estimation of precision in foraging, I excluded all herd locations that fell in a narrow strip of herd locations revealing a corridor normally used by the animals during southwards movements from the main range to the river, for the months of October 2006 for sable and August-September 2007 for both sable and zebra AM141, because these movements were influenced by water rather than by forage requirements. No herd locations were excluded in the analysis of precision of foraging within the home range by

buffalo and the other zebra herds because at the end of the dry season the home ranges of these herds were close to water sources. Therefore, no distinctions could be readily made between the movements to water and those during foraging activity.

Data analysis

Home range estimates

The relative frequency of use of space by animals can be evaluated using utilization distribution contours, which indicate an animal's probability of occurrence at each point in space during a specified time period (van Winkler 1975; White and Garrott 1990; Powell 2000; Marzluff et al. 2001). To estimate utilization distributions I used adaptive kernel density estimates (Worton 1989) using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcGIS 9.1. (Environmental Systems Research Institute Inc, USA). Kernel methods estimate different intensities of space use by creating isopleths containing a certain probability of animal occurrence based on the distribution of density of animal observations suggestive of the frequency of use of an area, and identify multiple areas of intense use (centers of activity) within the home range (Worton 1989; Seaman and Powell 1996).

In kernel analysis, the smoothing parameter h controls the search radius or the distance over which a data point influences the grid intersections and therefore the density estimate at that point (Silverman 1986; Worton 1995; Gitzen et al. 2005). Small smoothing parameters reveal more detailed patterns of home range use, but leave out locations that are far apart from the others, particularly the outermost locations. This could result in a type II error in home range estimates. Large smoothing parameters tend to connect all local patches into a single surface, give a coarse estimate, and reveal the general shape of the utilization distribution but obscure fine details of the utilization of space (Silverman 1986; Worton 1995; Seaman and Powell 1996; Powell 2000). Large smoothing values tend to produce a type I error in range estimates by extending home ranges to include areas not used by the animals. I selected h using least-squares-cross validation (lscv) because this method selects h that results in the minimum type I and type II error in the estimation of utilization distribution, thus it is the recommended

bandwidth selection method to analyze ecological data (Seaman and Powell 1996; Seaman et al. 1999).

In fixed kernel *h* remains constant for all data points, whereas adaptive kernel estimates local *h* values that depend on the local density of data points (Silverman 1986; Gitzen et al. 2005). I selected adaptive kernel as the smoothing application for the data because it performs well in estimating probability density plots for partially clumped data (Silverman 1986). Buffalo showed more even distribution of location data, which suggest that fixed kernel would also be appropriate to smooth the data (Silverman 1986). However, to make the results comparable, I used adaptive kernel to analyze data obtained from the three herbivore species. An alternative to the adaptive kernel method could be the use of the nearest-neighbor convex hull method (Getz and Wilmer 2004). However, Chirima (in prep.) found similar results in the extent and boundaries of utilization distributions estimated by both methods, when the distribution of herd locations did not show large gaps of non-use between clumps of location data. Within the seasonal subdivisions that I defined for data analysis, locations data of sable, zebra and buffalo showed no gaps of non-use between clumps of location data; hence I expected similar results from the two methods. In addition, the nearest-neighbor convex hull method is computationally tedious because it lacks an objective way of selecting the parameters for home range estimation.

To reveal differences in the intensity of use of different parts of the home range, I estimated 2-dimensional utilization distribution by plotting adaptive kernel probability contours enclosing 25%, 50%, 75% and 95% of the home range estimate. The scale of the maps showing the contours was kept constant across temporal scales and across species to allow a visual comparison of the size and location of the home range. The 25% isopleths represent the centre of activity, the 50% isopleths represented the core range and the 95% probability isopleths represented the total home range, excluding the excursions and exploratory movements outside home range (White and Garrott 1990; Powell 2000). To reveal details in area increments for successive kernel probability isopleths, I further plotted the isopleths covering 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 100% of the utilization distribution. Areas covered by the contours were estimated using Hawth's Tools in ArcGIS 9.1.

Seasonal subdivisions

I conducted this study for a period of 16 months, from June 2006 to September 2007. To identify distinctions in home range location and movement lengths over the course of the study period, I estimated overlap between monthly sable ranges and calculated animal movement lengths (diel displacement) between successive 8:00AM locations for all the collared animals. This was done to guide the delineation of temporal scales for the analysis of precision in home range use. Overlapping monthly home ranges were amalgamated within the same period. In October 2006, and in August 2007 sable shifted home range location during the month, which resulted in sable using two distinct home ranges in the same month. For these cases, during the analysis of home range anatomy, data from dates of the month before range shift were analyzed with data from the previous months and data from dates after range shift were analyzed with data from the following month.

To evaluate the effect of resource surfeit or limitation on the precision of foraging, I focused the seasonal comparisons on distinct periods along the seasonal gradient of declining rainfall and associated decline in food availability from the wet season to the end of the dry season. Accordingly, the benign period was defined to span from January to April 2007 because during this period, the sable herd and buffalo herds showed overlapping monthly home ranges and the shortest diel movements of the year, suggesting that water and food resources were plentiful. April is the beginning of the dry season in the lowveld of South Africa, however this month was grouped with the late wet season months due to the carry-over effect of rain on food availability. The second period for analysis spanned from May to July 2007, this period was considered as a transitional period of intermediate food availability. During this early dry season period, the focal species of this study, sable, remained within the late wet season range but increased diel movements lengths, meaning that although water and food conditions were not bad to prompt sable to shift home range location, to drink water, sable needed to increase movements lengths as water became progressively restricted in distribution. Another period of intermediate food availability was the early dry season of 2006 (June-August), but this period could not be compared to earlier periods of 2006 in terms of sable movements and home range location because this was the initial period of the study. The

third period was the late dry season, generally the time of the year when water, food quantity and quality are limiting factors. This was restricted to the period from 5 October – 8 November 2006 and from 19 August - September 2007 because during these periods sable shifted to a range separated from the range used during earlier periods. Time periods for the three species were defined on the basis of sable movements and range shifts, to ensure a comparison of ranging patterns among species under similar environmental conditions. Defining time periods on the basis of distinctions between short and long movements as well as shifts in home range location was biologically justifiable as it reflected behavioral responses of animals to the seasonally changing environment.

Assessing precision in home range use

Precision in home range use was assessed by plotting the incremental change in kernel probability against area. The number of animal locations per unit area is an indication of the frequency of use of the area (Worton 1989; Seaman and Powell 1996). Therefore, high kernel probability densities for small areas of the range indicates precision in home range use, i.e. that the herd satisfied resource needs in a small home range during the specified period, whereas animal locations evenly distributed suggest an imprecise use of the home range.

Precision in foraging was also assessed by the relationship between the metabolic use intensity and successive increments in the home range used. The metabolic use intensity is a measure of the flow of energy from forage resources to herbivore biomass. To account for differences in individual body mass due to differences in age classes among individuals within the herds, following Owen-Smith (2008) I estimated the mean body mass for each herbivore species as three-quarters of adult female body mass. Therefore, I used the following mean body masses: 165 kg, 232 kg and 390 kg for sable, zebra and buffalo, respectively. I transformed the individual biomass to metabolic biomass by raising mean body mass to the power 0.75 (Owen-Smith 1988). To obtain the herd metabolic biomass, I multiplied the individual metabolic mass by mean herd sizes, which were 20, 7 and 200 individuals for sable, zebra and buffalo, respectively. Area increments were estimated as the difference between the areas covered by successive

10% kernel isopleths. Metabolic use intensity was estimated by dividing 10% of the metabolic biomass by the home range increment between successive 10% kernel isopleths. The metabolic use intensity was plotted against each increment in home range size, such that high metabolic use intensity indicate high number of grazing days in small areas, which reflects precision in foraging.

As a further indication of precision in space use, I calculated the number and size of discrete patches contributing to 50% kernel contour, such that smaller and more numerous distinct patches indicate precision at locating and exploiting patches with the required resources for the herd, whereas a small number of large patches reveal even use of space for foraging. I overlaid the monthly 50% core range with the shapefile of the study area using ET Geowizards in ArcGIS 9.1. This allowed me to count and estimate the size of individual patches contributing to the core range. Each discrete patch used by each collared herd was considered as an independent observation for statistical analysis. Data for collared herds of the three herbivore species revealed a low number of distinct patches used for foraging during the late dry season period ($\leq$ 3 patches). Therefore, I restricted the statistical comparison of the size of patches contributing to core range to the wet season period (January – April). Buffalo used 2-3 large patches as core range during both the wet and the dry season, a sample which is too small for statistical comparisons. Therefore, I excluded buffalo in the statistical testing of differences in the size of used patches. I performed the Kruskal-Wallis test to compare the median size of patches used by sable and zebra.

Results

Comparative seasonal range extent among species

The annual home ranges of sable and zebra were larger than the expected from the allometric scaling of home range size with body mass ($1.07M^{0.83}$) and herd size (15 km^2 for sable and 7.0 km^2 for zebra), whereas buffalo annual range extent was similar to the range extent expected from empirical patterns based on allometry (302 km^2) (Table 1). During the late wet season period of food abundance (January – April 2007), both the total and core ranges used by the sable herd were about half of the ranges used by two out

of three zebra herds that provided data during that period and about 65% of the total and core range of the third zebra herd (Table 1). The total and core ranges of the sable herd were about 8% of buffalo total and core ranges, respectively, which is higher than 5% predicted from empirical patterns based on allometric scaling considering body mass and group size. The total and core ranges of zebra herds during the late wet season corresponded to approximately 12 – 20% of buffalo ranges, which is also above the 2% expected from allometry (Table 1). During the early dry season (May – July 2007) and the late dry season period (August – September 2007) of the more severe year, the sable herd moved over a wider total and core ranges than did zebra herds AM141, AM142 and AM280. For example, the total and core ranges of the sable herd more than doubled those of zebra AM141 and AM280 during the late dry season. Sable used smaller total and core ranges than zebra AM147 and AM277 during the early and late dry season of 2007, respectively (Table 1).

On a monthly basis, sable core range (Figure 2) and total range (Figure 3) remained smaller than the home ranges of all zebra herds during the late wet season months from January to April 2007. During the early wet season months of November and December 2006 and early dry season months from May to July 2007, sable used smaller home ranges than zebra AM142 and AM147 but larger home ranges than zebra AM141, whereas during the late dry season months from August to October 2006 and August to September 2007, the monthly range used by the sable herd was larger than the range used by zebra herds, except zebra AM147.

Sable and buffalo herds increased the extent of the total and core ranges from the wet to the late dry season, whereas zebra herds AM141 and AM142 reduced range sizes (Table 1). However, the magnitude of the dry-wet-dry season change in home range extent was greater for the sable herd than for buffalo and zebra herds. For instance, the sable herd increased home range size to more than double from the late wet season to the late dry season of 2007, buffalo increased range by about 20%, zebra AM141 reduced home range to almost half and zebra AM142 reduced range size by about 17% during the same period. Zebra AM147 expanded the wet season range by about three times during the early dry season period (Table 1).

Although both sable and buffalo herds moved more widely during the late dry season than during the wet season period, distinctions in the seasonal spatial behavior were observed between the two species. The sable herd expanded the wet season range during the early dry season and used a separate late dry season range, whereas the buffalo herd used separate wet and early dry season ranges, but expanded the early dry season range towards the end of the dry season. Contrary to sable and buffalo that revealed seasonal range shifts, the zebra herds used the same range year-round (Figure 1a,b,c,d,e).

Patchiness of home range use

The sable herd used 9 distinct patches and the zebra herds used 6-8 patches as part of the core range during the wet season. During the late dry season sable used 1-2 patches and zebra used 1-3 patches in the core area (Figure 1a,b,c,d,e). The median patch size contributing to sable core range during the wet season was smaller (0.08 km^2, N=9), but not statistically different from the median patch size contributing to the core range of zebra AM141 (0.15 km^2, N=8) and zebra AM142 (0.51 km^2, N=8) (Kruskal-Wallis test statistic, H =3.5, df=2, p=0.17). For both species the patches used as core range were smaller but more numerous during the late wet season than during the late dry season. Patches contributing to sable late dry season core range were larger (3.3 km^2) than the patches used by zebra AM141 (1.45 km^2), but of similar size to the mean patch size contributing to the core range of zebra AM142 (2.9 km^2). There was no influence of the seasonal fluctuations in food availability in the patchiness of buffalo range, with the number of patches contributing to buffalo core range varying between one and three during both the wet and dry season (Figure 1a,b,c,d,e).

Concentration of use within the home range

During the late wet season of 2007 and during the early dry season of the less severe 2006 the area covered by each kernel probability contour was smaller for sable than for zebra and buffalo. This resulted in a steeper curve of the relationship between range extent and kernel probability isopleths (Figure 4). The smaller increments in range

size for successive kernel increments for sable than for zebra and buffalo show concentrated use of space by sable and that forage resources from smaller areas provided the necessary energy for the sable herd, as revealed by the higher metabolic use intensity of space by sable than by buffalo and zebra (Figure 5). This also shows that the sable herd spent more days grazing in smaller areas than the zebra and buffalo herds. The lower metabolic use intensity for buffalo and zebra indicates that the energy flow from forage to buffalo and zebra herd biomass was lower, which suggests that buffalo and zebra tolerated forage of low quality; hence the herds required forage from larger areas to satisfy their energy needs (Figure 5).

During the mild early dry season of 2007, the metabolic use intensity was similar between herds of different grazers. However, during the more severe late dry season of 2007, the area covered by each kernel probability contour was larger for the sable herd than for the zebra herds. This resulted in a less steep curve of the relationship between kernel probability contour and range extent for sable than for most zebra herds (Figure 4). Larger area increments by sable show that during the late dry season the available forage provided little energy to sable, therefore the herd needed to increase the area used for foraging to satisfy energy requirements. Buffalo and zebra herd AM141 showed higher concentration of space use than the sable herd during this time of the year as indicated by the more intense metabolic use of space. However, during the late dry season of 2006, although sable used a larger total home range than zebra AM141, within the core range the energy flow from the available forage to the sable herd was higher than to the zebra herd (Figure 5). The metabolic use intensity by the buffalo herd was higher than by the zebra herds during all periods defined for data analysis, but higher than by sable only during the dry season of 2007.

Discussion

This paper addressed the relationship between patterns of species abundance and the patterns of home range use between ecologically similar species that attain different regional densities, within the large grazer assemblage. The overall prediction was that sable, representing the low density species would be more precise in using intensively smaller patches for foraging than the high density species buffalo and zebra.

Using the extent of the core range as the indicator of precision of foraging, the findings of this study suggest that the sable herd used smaller core range than the zebra herds during the late wet season, which is a period of forage abundance. The sable herd satisfied their metabolic requirements in a smaller proportion of the landscape than the area supporting each zebra herd. However, towards the end of the dry season, a period when food was in short supply, the sable herd spread its use of space over a wider core and total range than the zebra herds, indicating a progressively less precise foraging by sable with the advance of the dry season.

The second indicator of precision in foraging was the number and size of distinct patches contributing to the core range. This measure revealed a similar number of discrete patches for sable and the zebra herds. However, owing to smaller range size used by sable, the patches were also smaller for sable than for zebra during periods of resource abundance. Therefore, the patterns of patchiness in home range use revealed by the herds of these species do not necessarily suggest differences in precision. However, considering that zebra occur in smaller group sizes and hence are of lower herd biomass than the sable herd, this result might indicate that the sable herd was more precise at exploiting resources occurring in smaller patches.

Buffalo covered a much larger core and total home range than both zebra and sable. However, the comparison of range area among species is confounded by differences in body size and herd size, such that buffalo was expected to use a larger home range than zebra and sable because home range size scales allometrically with body size and also with herd size (McNab 1963; Owen-Smith 1988). Therefore, large and gregarious species like buffalo tend to use evenly large areas for foraging due to the combined effect of higher absolute intake requirements for large animals and the sharing

of space with companions (Owen-Smith 1988). Buffalo used larger and less numerous patches than sable and zebra, suggesting that buffalo were more even in patch use than sable and zebra.

There is limited research literature relating patterns of home range use to patterns of species abundance and niche relations within species assemblages. This prevents comparison between this and previous studies. In this study, I related home range use patterns to resource availability by delineating the temporal scales for data analysis on the basis of rainfall, the primary driver of primary productivity (Walker 1993) and on animal movements and shifts in home range location, which reveal changes in forage conditions over the seasonal cycle (Owen-Smith and Cain 2007). Differences in the methodological approach between this study and previous research on home range use also prevent direct comparison of results. However, over the annual cycle the sable herd used a larger total home range (39.1 km^2) than previously documented elsewhere (10-24 km^2 in the Shimba Hills, Sekulic 1981; 27.3 km^2 in the Pilannesberg National Park, Magome 1991; 19.1 km^2 in Kgaswane Mountain Reserve, Parrini 2006), but about 60% of the total range and 45% of the core range of a similarly sized sable herd (AM1) in the central KNP also estimated using kernel methods (Owen-Smith and Cain 2007). The annual buffalo home range from this study (298 km^2 for 200 individuals) was similar to the estimations by Ryan et al. (2006) in the Klaserie Private Nature Reserve, South Africa (240 km^2 for 224 individuals), to estimations by Bowers et al. (2007) in the granite landscape of central KNP (292 km^2 for 244 individuals), but larger than the home range in the basalt landscape of central KNP (152 km^2 for 643 animals, Bowers et al. 2007) and than the year-round buffalo home range in the Sabi Sand Nature Reserve (120 km^2 for 248 individuals, Funston et al.1994). My findings suggest smaller home ranges (32-51 km^2) for the zebra herds than previous studies conducted in northern KNP, reporting a mean annual home range size of about 130 km^2 (Smuts 1975). However, the merit of this comparison is constrained by differences in methods used because Smuts (1975) used Minimum Convex Polygon (MCP), which tends to produce larger home ranges than the kernel probability estimates, by simply joining the outer herd locations (Kernohan et al., 2001).

Following the resource availability hypotheses (Gaston and Kunin 1997; Gregory and Gaston 2000), low density species depend on resources that occur in restricted areas. In agreement with this theory and confirming my expectations, the sable herd was more precise in using smaller home ranges and smaller patches of resources during the wet season than the herds of high density grazers. However, due to seasonal variations in resource availability, this pattern was not consistently observed throughout the year. According to Harestad and Bunnell (1979), animals use smaller home ranges when resources are abundant and larger home ranges when the density of resources is low. Therefore, home ranges should be large enough to contain the resources required by the animals (Harestad and Bunnell 1979; McLoughlin and Ferguson 2000), but small enough to allow familiarity with the area and reduction of travel and predation costs associated with movements over a large and non-familiar area (McLoughlin and Ferguson 2000; Borger et al. 2008). According to Kjellander et al. (2004), resource attrition results in range expansion to satisfy resource requirements of the individuals in the herd. When resources were plentifully available, such as during the late wet season, sable restricted their movements to a small area of concentrated use, suggesting that the sable herd obtained the required resources in a more restricted area than the zebra and buffalo herds. However, during the late dry season, the sable herd became less precise in home range use than zebra, as indicated by the spread of use over a larger area and lower metabolic use intensity than the zebra herds. This switch in precision from higher to lower precision in home range use by sable than by zebra suggests that resource limitations became more severe for sable than for zebra as the dry season progressed. From this differential impact of shrinking resource conditions on the spatial behavioral response of sable and zebra, I suggest that specializations on resources that became rarer and more discretely distributed in the landscape (Chapter 1), prompted sable to move widely in search for these specific resources, whereas the broad tolerance to food resources allowed zebra to consume the readily available food resources during the late dry season, as also previously documented by Bell (1970). This shows that differences in the breadth of food niche influence distinctions in patterns of space use among large grazers.

The higher metabolic use intensity of space shown by sable during the wet season indicates higher local flow of energy from forage to sable than to zebra and buffalo

within the patches exploited, which means that sable were more efficient in selectively feeding on plant parts with high concentration of energy. On the other hand, generalist grazers obtain diets of relatively high fibre and low energy content than specialist grazers prompting herds of these species to move over wider areas to satisfy their energy requirements. However, during the late dry season, sable specialization on progressively sparser energy-rich plant parts such as green leaves, resulted in less concentrated use of space as sable needed to move widely to find suitable patches, whereas generalists feeders able to digest the poor quality brown grass leaves and stems, obtained the energy from the readily available forage and showed more concentrated use of space than the specialist sable. Results on the intensity of metabolic use of space might have been affected by overlaps between home ranges of zebra and buffalo herds or by short term congregations between herds of these species.

The home range extent of sable and buffalo increased with the decline in the availability of food from the wet to the end of the dry season. Increasing home range size as a response to increasing sparseness in the distribution of food resources has also been reported for sable (Parrini 2006; Owen-Smith and Cain 2007), buffalo (Funston et al.1994; Ryan et al. 2006) and white rhinoceros (*Ceratotherium simum*, Owen-Smith 1988). However, although the sable and buffalo herds used larger ranges during the dry season than during the wet season, the extent of the seasonal changes in range extent was greater for sable than for buffalo. This means that the energy flow from the forage resources prevailing in the core area of sable during the late dry season was lower than the energy flowing from forage to buffalo. Conversely, most zebra herds contracted the wet season range during the late dry season. If during periods of food limitations the energy gains obtained from increasing home range in search for food are less than the costs of range expansion, home range size may decrease with decreases in food availability. Contraction of range size with the advance of periods of limited resource supply has also been documented for kudu (*Tragelaphus strepsiceros*, Owen-Smith 1979) and for roe deer (*Capreolus capreolus*; Tufto et al. 1996; Said et al. 2005; Borger et al. 2006).

Sable use of space was concentrated in smaller distinct patches than zebra and buffalo core ranges during the late wet season. Generally, during the wet season forage is

abundant and of high quality. Thus, the distribution of adequate food for grazers is continuous, which should result in a continuum use of space by grazing herbivores (Johnson et al. 2002). Results from this study revealed continuity in the use of space for foraging by buffalo but not by sable and zebra. During the dry season localized resource depletion due to grazing make the environment more heterogeneous in terms of the distribution of food resources. Therefore, during this limiting period foraging activity might become restricted to key resource areas (Scoones 1995; Knoop and Owen-Smith 2006) that were less exploited when food was abundant and widely available. Alternatively, foraging animals might move more widely procuring for sparser resources. I observed that the sable herd used separate wet and the late dry season ranges, and that during the wet season sable used more numerous and smaller patches than during the late dry season when the sable herd foraged on fewer but larger patches not used during the preceding period of food abundance. Diet assessments revealed that sable were more selective for green grass leaves than zebra and buffalo (Chapter 1), thus wider movements by sable during the late dry season might be associated with increasing sparseness of these dietary components and to a lack of key resource areas. On the other hand, the zebra herds did not show separation between the wet and the late dry season range, suggesting that resource levels for the more generalist consumer zebra remained satisfactory at the end of the dry season.

Although depletion of preferred food might have contributed to range shift by the sable herd, water restrictions appeared to be the primary factor that determined the location of the late dry season sable range, which was towards the south-east of the study area, about 7 km to the existing water source at that time of the year. The influence of water source on the location of the late dry season buffalo and zebra range was more evident than for sable, with both buffalo and zebra herds establishing home ranges closer to water than the sable herd. Therefore, for water dependent species in environments where water is a limiting resource, the use of space by foraging animals is also influenced by water needs, such that range extent depends by both the availability and distribution of food and water (McLoughlin and Ferguson 2000), particularly during the late dry season when water distribution is most limiting than forage.

The two sable herds that existed in the study area from 2001 to 2003 (Henley 2005) joined to form one sable herd in the study area; hence there could be no competition for space between sable herds. This means more available choices of the landscape region for home range location, expansion and/or seasonal shifts by the sable herd, because home ranges of different sable herds rarely overlap (Sekulic 1981), whereas a high number of zebra herds resulted in overlapping seasonal ranges.

The seasonal patterns of space use for foraging presented in this paper reveal that the low density sable met their resource requirements in restricted areas of the landscape during periods of resource abundance. The resources required by low density species became of low local abundance and more dispersed towards the end of the critical dry season. On the other hand, the populations of high density, zebra and buffalo, appeared to be supported by readily available forage resources.

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Table 1. Adaptive kernel total (95%) and core (50%) home range estimates (km^2) for the sable herd, different buffalo and zebra herds during different seasons.

	Sable AM143						Buffalo AM152					
	Annual	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07	Annual	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07
95% kernel	39.1	14.3	38.3	15.2	28.0	40.0	298.0	173.6	298.8	185.2	189.7	219.7
50% kernel	6.0	1.96	4.7	2.4	4.7	5.4	65.5	34.8	60.9	29.2	36.5	30.2
Proportion of core range	0.15	0.14	0.12	0.16	0.17	0.14	0.21	0.20	0.20	0.16	0.19	0.14

	Zebra AM141						Zebra AM142				
	Annual	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07	Annual	EDS06	LWS 07	EDS 07	LDS 07
95% kernel	32.1	26.9	18.4	23.2	18.6	13.3	74.4	31.5	41.3	33.1	34.3
50% kernel	4.5	3.1	3.2	3.6	3.1	2.6	11.2	5.9	5.4	4.2	5.8
Proportion of core range	0.14	0.12	0.17	0.16	0.17	0.20	0.15	0.19	0.13	0.13	0.17

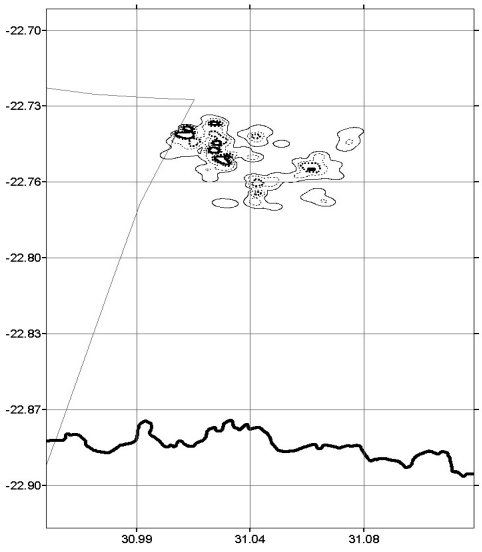
	Zebra AM147				Buffalo AM150		Buffalo AM278	Zebra AM277	Zebra AM280
	Annual	EDS 06	LWS 07	EDS 07	EDS 06	LWS 07	LDS 07	LDS 07	LDS 07
95% kernel	51.4	49.8	32.8	95.3	336.3	125.8	137.0	122.8	15.1
50% kernel	7.8	7.0	3.6	15.2	82.2	22.4	21.3	17.2	2.4
Prop. of core range	0.15	0.14	0.11	0.16	0.24	0.18	0.16	0.14	0.16

EDS 06 – Early dry season (June – August 2006); LDS 06 – late dry season (5th October – 8th November 2006); LWS 07 – late wet season (January – April 2007); EDS 07 – early dry season (May – July 2007); LDS 07 – late dry season 2007 (19th August – September 2007)

SABLE AM143

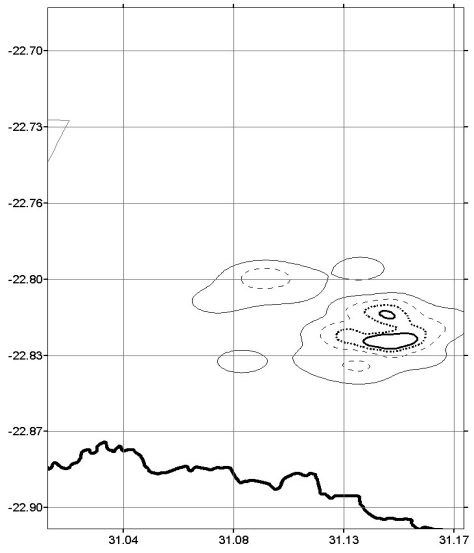
Early dry season 2006

(h_{lscv}=0.08, N=178 locations)



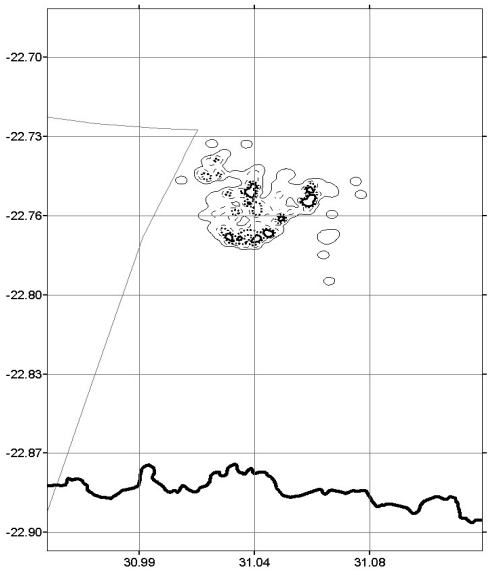
Late dry season 2006

(h_{lscv}=0.25, N=57 locations)



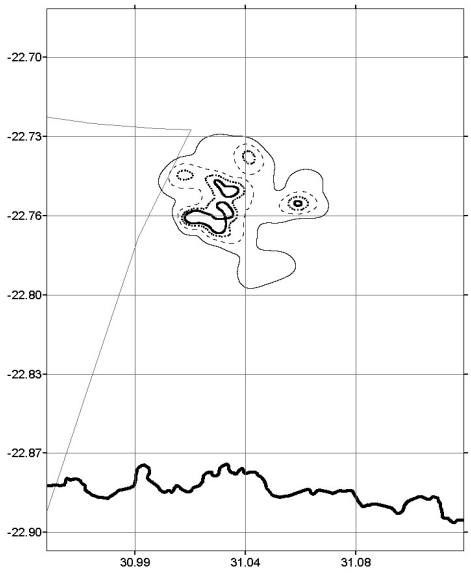
Late wet season 2007

(h_{lscv}=0.08, N=220 locations)



Early dry season 2007

(h_{lscv}=0.2, N=164 locations)



Late dry season 2007

(h_{lscv}=0.19, N=62 locations)

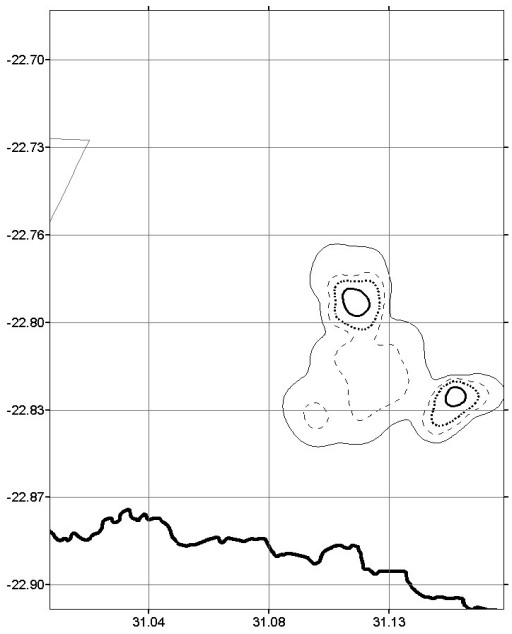
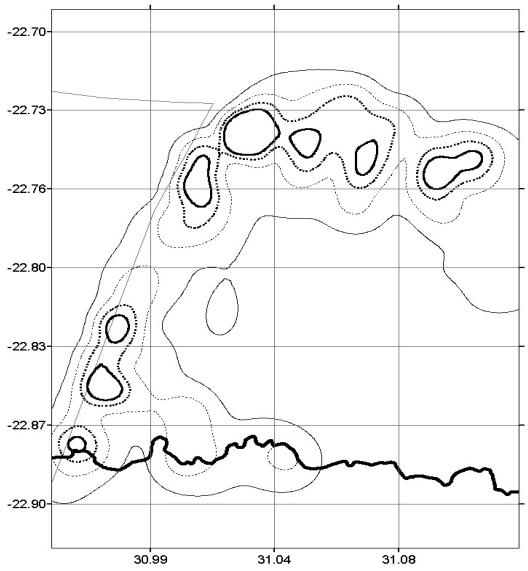


Figure 1a. Distribution of the intensity of space use for foraging by the sable antelope herd AM143 during different seasons. Contours indicate adaptive kernel probability density estimates: 25% (dark full line), 50% (dark dashed line), 75% (narrow dashed line) and 95% (narrow full line).

BUFFALO AM152

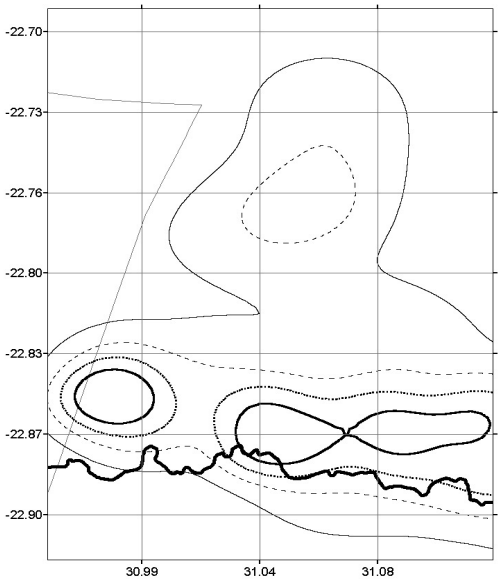
Early dry season 2006

(h_{lscv}=0.12, N=174 locations)



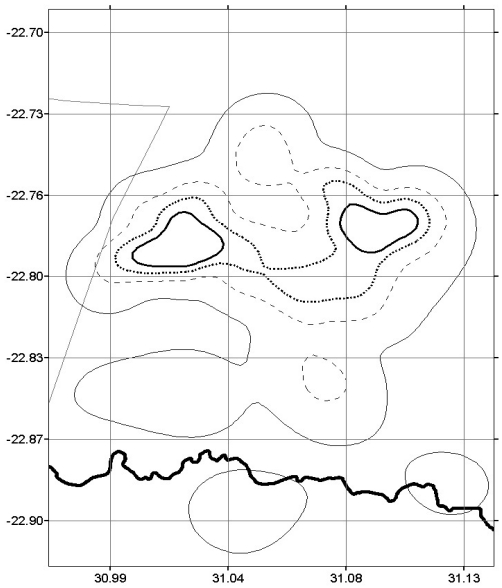
Late dry season 2006

(h_{lscv}=0.25, N=69 locations)



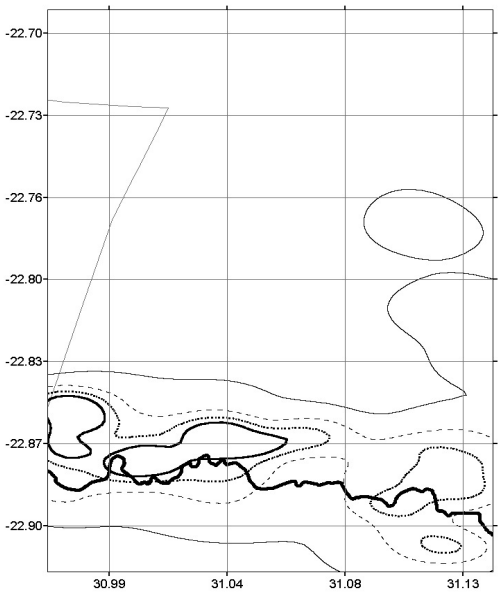
Late wet season 2007

(h_{lscv}=0.2, N=200 locations)



Early dry season 2007

(h_{lscv}=0.19, N=180 locations)



Late dry season 2007

(h_{lscv}=0.26, N=82 locations)

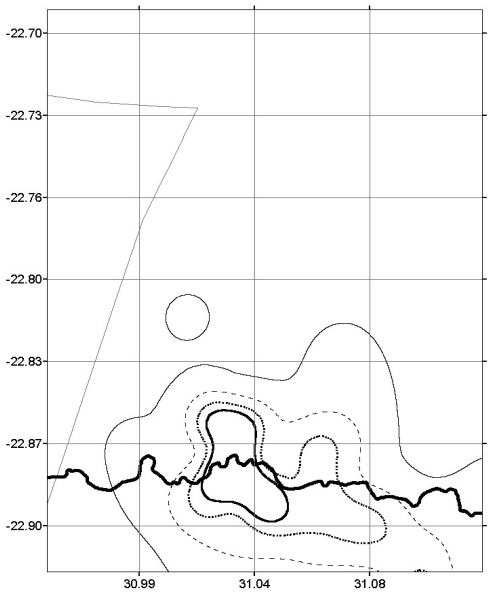
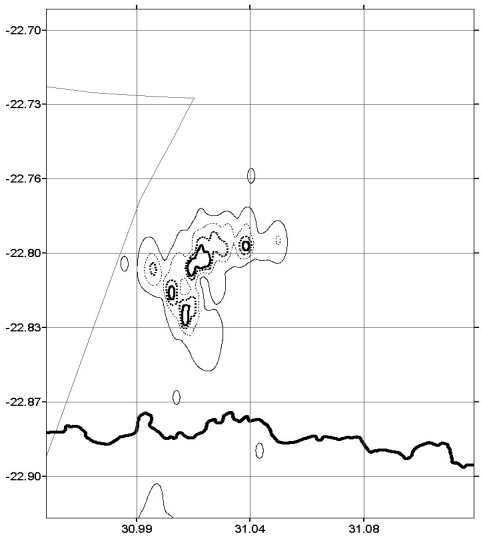


Figure 1b. Distribution of the intensity of space use for foraging by the buffalo herd AM152 during different seasons. Contours indicate adaptive kernel probability density estimates: 25% (dark full line), 50% (dark dashed line), 75% (narrow dashed line) and 95% (narrow full line).

ZEBRA AM141

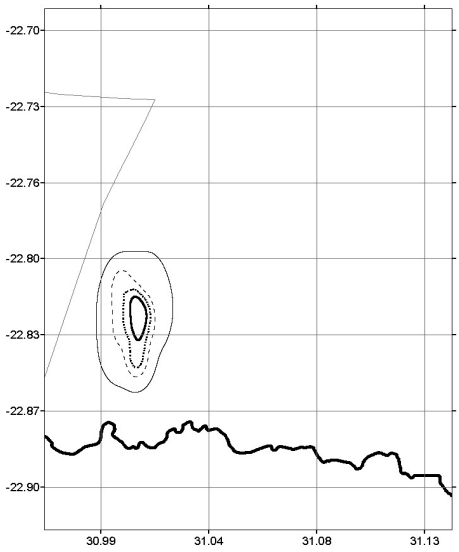
Early dry season 2006

(h_{lscv}=0.11, N=179 locations)



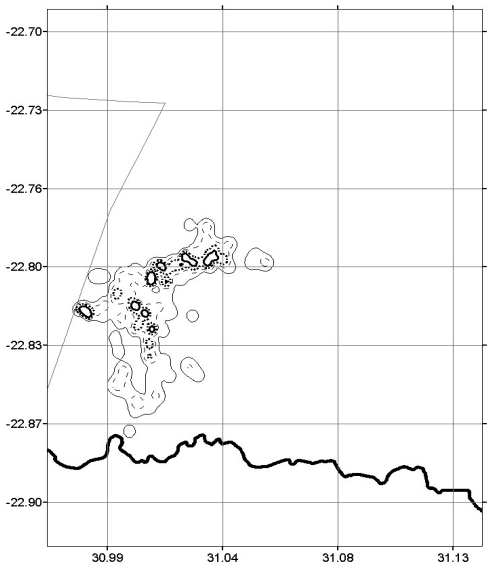
Late dry season 2006

(h_{lscv}=0.48, N=66 locations)



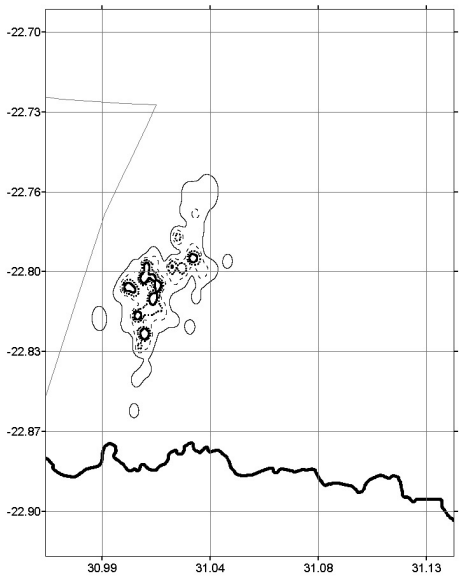
Late wet season 2007

(h_{lscv}=0.08, N=203 locations)



Early dry season 2007

(h_{lscv}=0.12, N=164 locations)



Late dry season of 2007

(h_{lscv}=0.26, N=63 locations)

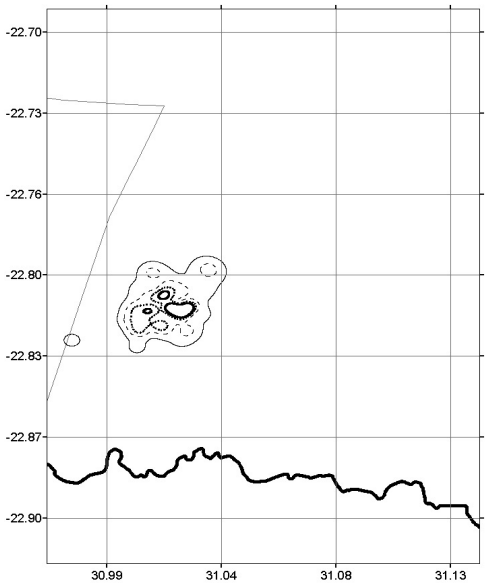
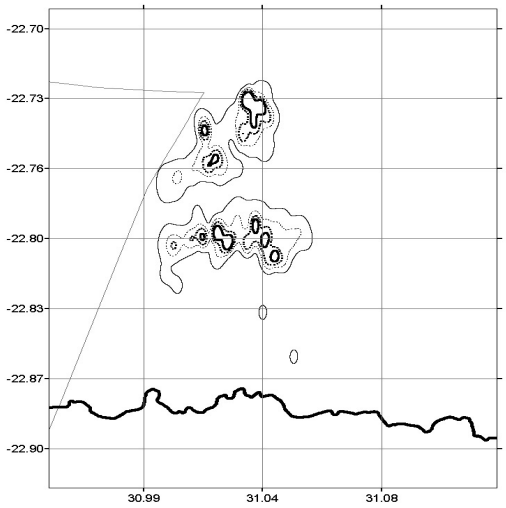


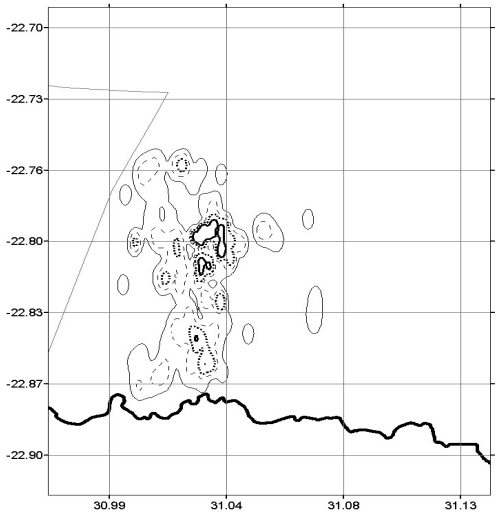
Figure 1c. Distribution of the intensity of space use for foraging by the zebra herd AM141 during different seasons. Contours indicate adaptive kernel probability density estimates: 25% (dark full line), 50% (dark dashed line), 75% (narrow dashed line) and 95% (narrow full line).

ZEBRA AM142

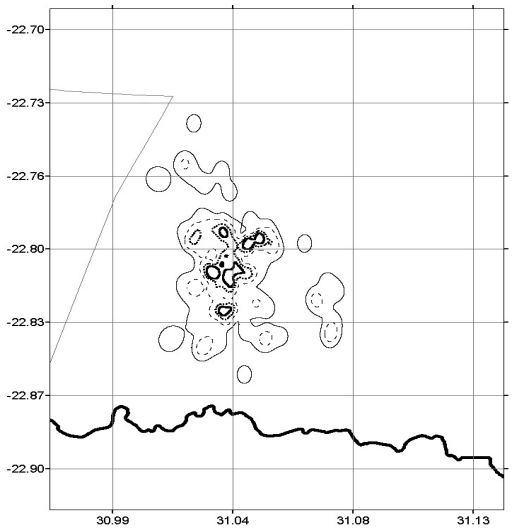
Early dry season 2006 (h_{lscv}=0.11, N=178 locations)



Late wet season 2007 (h_{lscv}=0.1, N=211 locations)



Early dry season 2007 (h_{lscv}=0.12, N=180 locations)



Late dry season 2007 (h_{lscv}=0.29, N=82 locations)

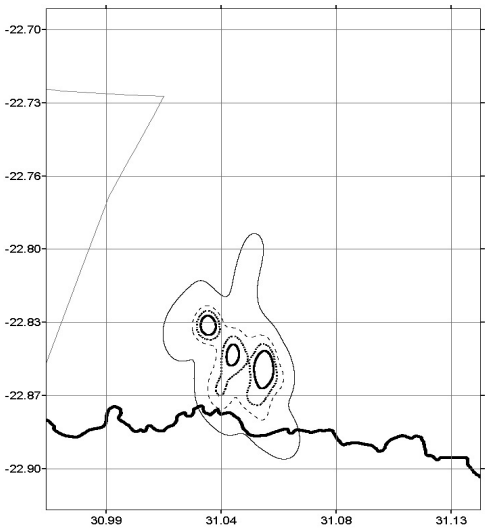
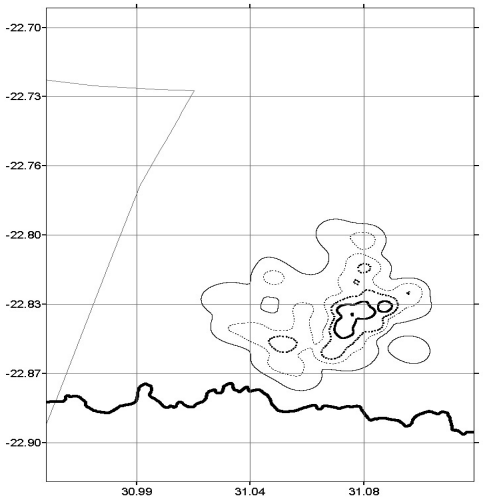


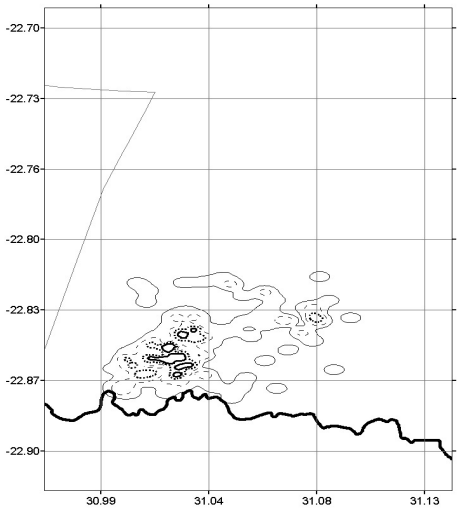
Figure 1d. Distribution of the intensity of space use for foraging by the zebra herd AM142 during different seasons. Contours indicate adaptive kernel probability density estimates: 25% (dark full line), 50% (dark dashed line), 75% (narrow dashed line) and 95% (narrow full line).

ZEBRA AM 147

Early dry season 2006 (h_{lscv}=0.17, N=180 locations)



Late wet season 2007 (h_{lscv}=0.24, N=131 locations)



Early dry season 2007 (h_{lscv}=0.24, N=131 locations)

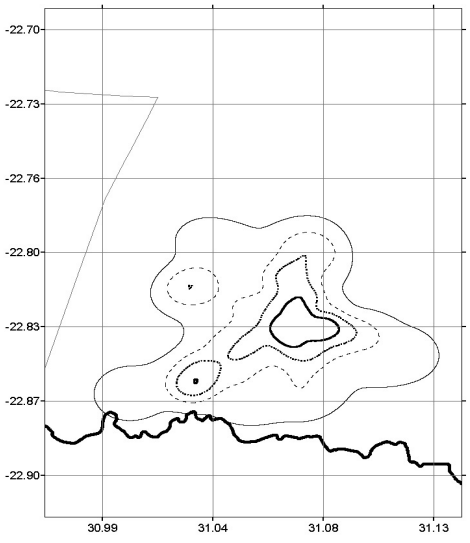


Figure 1e. Distribution of the intensity of space use for foraging by the zebra herd AM147 during the wet season and early dry season. Contours indicate adaptive kernel probability density estimates: 25% (dark full line), 50% (dark dashed line), 75% (narrow dashed line) and 95% (narrow full line).

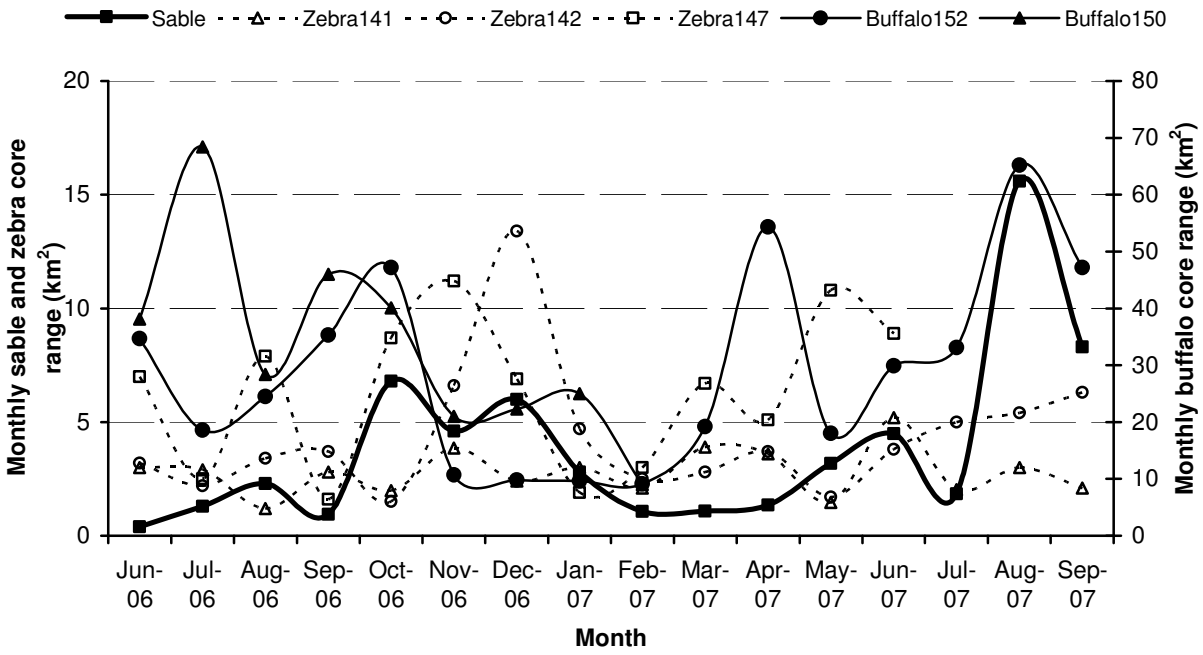


Figure 2. Monthly variations in the extent of the core range for the sable, buffalo and zebra herds.

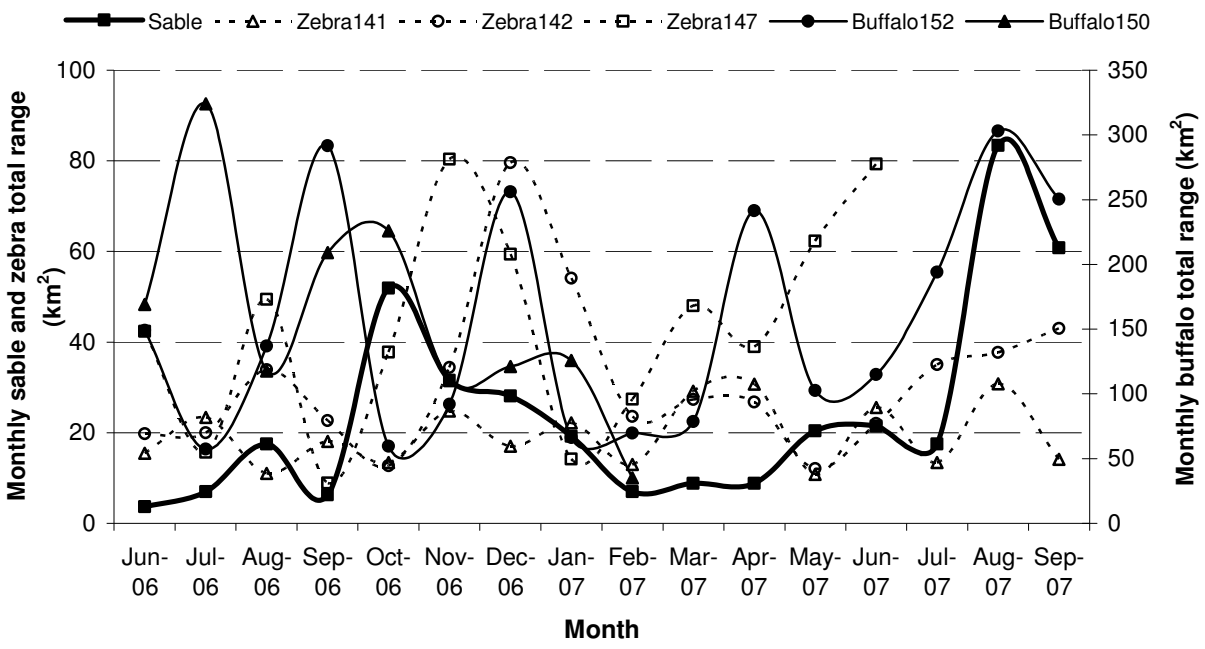
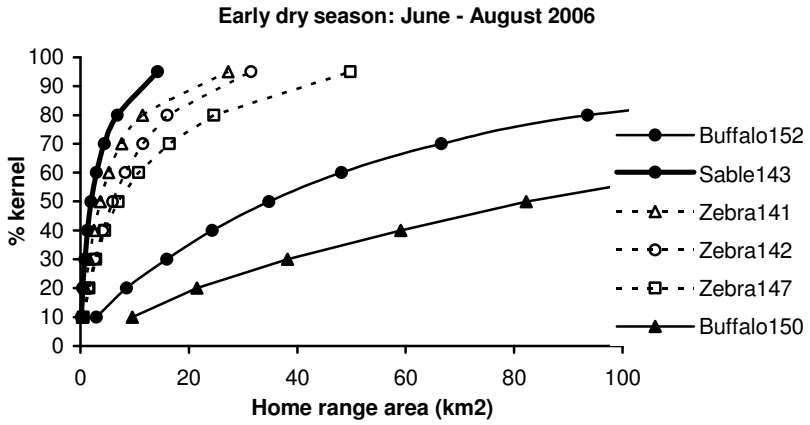
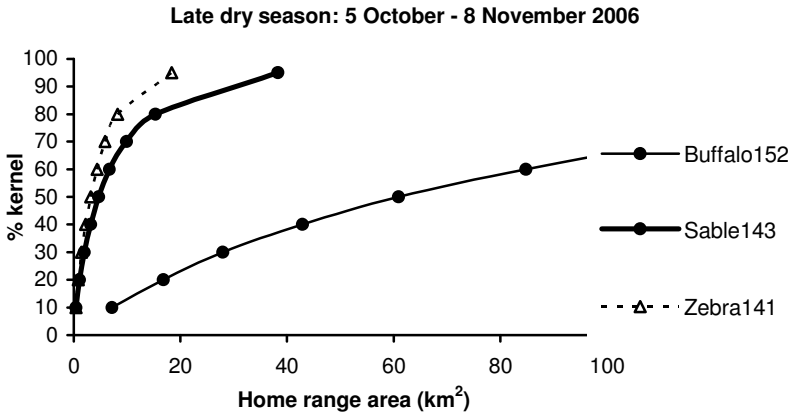
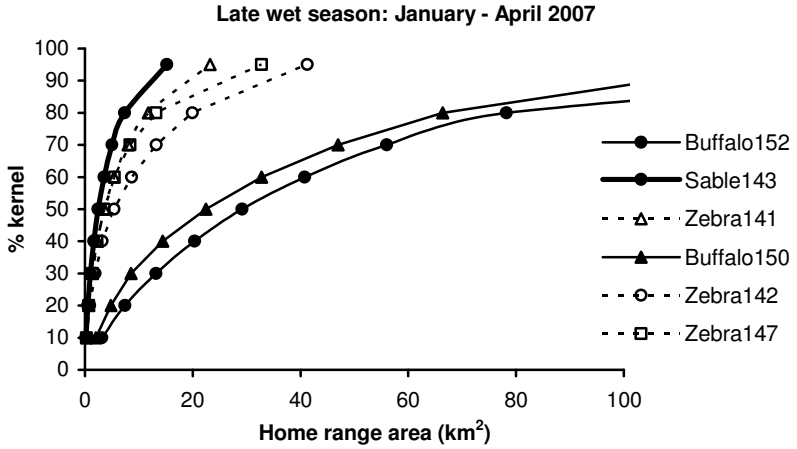
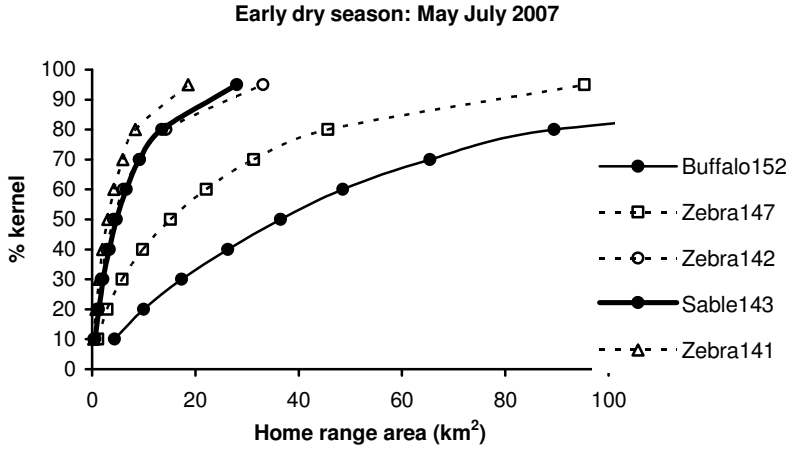


Figure 3. Monthly variations in extent of the total home range of sable, buffalo and zebra herds.


Early dry season: June - August 2006
% kernel
Home range area (km2)
Buffalo152
Sable143
Zebra141
Zebra142
Zebra147
Buffalo150


Late dry season: 5 October - 8 November 2006
% kernel
Home range area (km2)
Buffalo152
Sable143
Zebra141


Late wet season: January - April 2007
% kernel
Home range area (km2)
Buffalo152
Sable143
Zebra141
Buffalo150
Zebra142
Zebra147


Early dry season: May July 2007
% kernel
Home range area (km2)
Buffalo152
Zebra147
Zebra142
Sable143
Zebra141

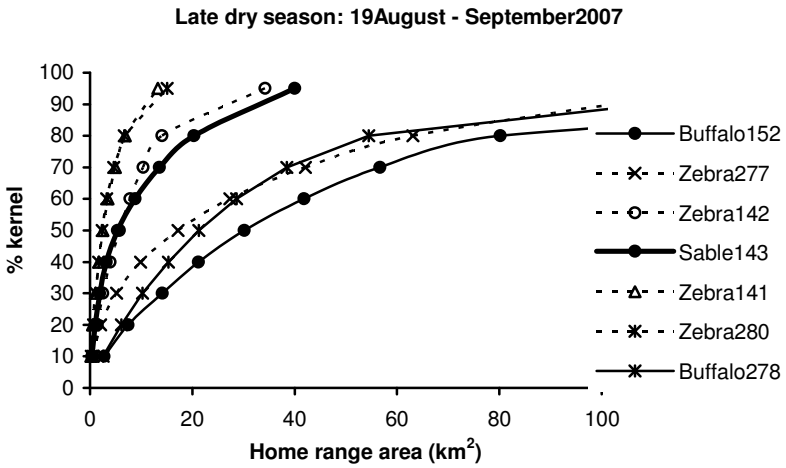
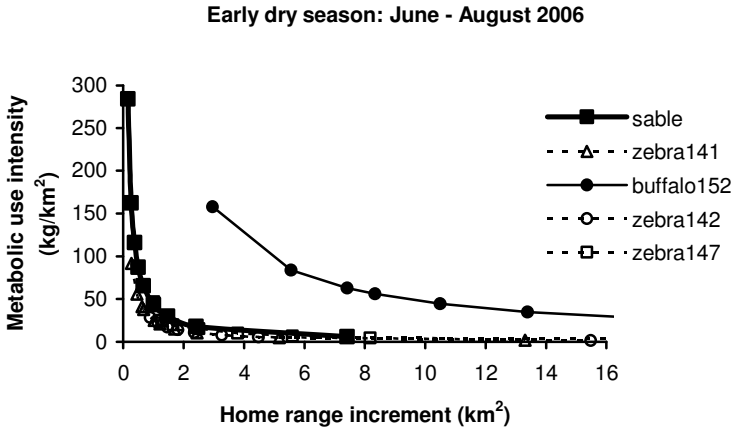
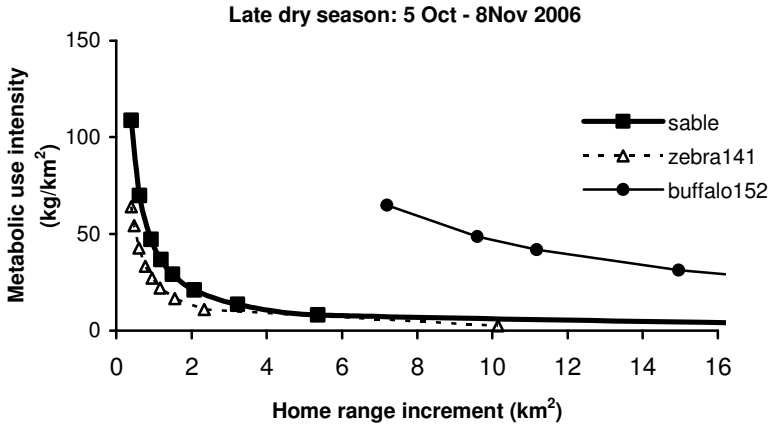
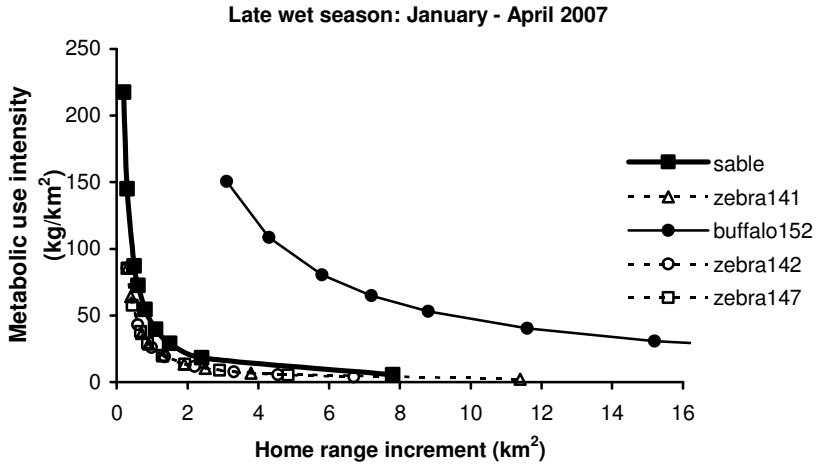
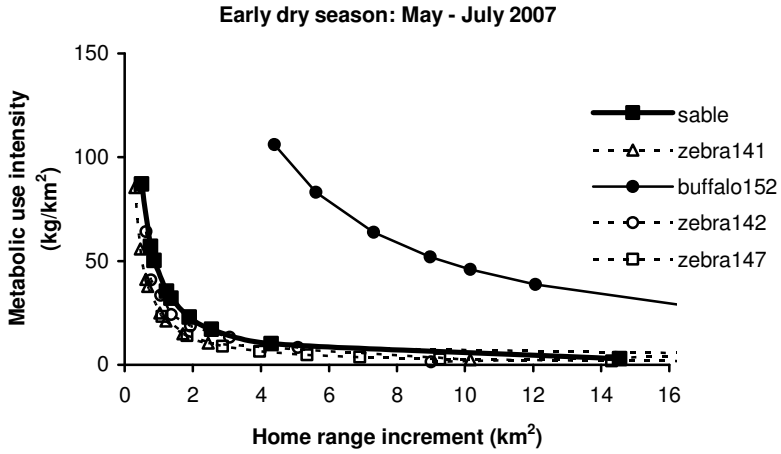


Figure 4. Comparative precision of foraging among herds of the three herbivore species during different periods of the year.


Early dry season: June - August 2006
Metabolic use intensity (kg/km2)
Home range increment (km2)
sable
zebra141
buffalo152
zebra142
zebra147


Late dry season: 5 Oct - 8Nov 2006
Metabolic use intensity (kg/km2)
Home range increment (km2)
sable
zebra141
buffalo152


Late wet season: January - April 2007
Metabolic use intensity (kg/km2)
Home range increment (km2)
sable
zebra141
buffalo152
zebra142
zebra147


Early dry season: May - July 2007
Metabolic use intensity (kg/km2)
Home range increment (km2)
sable
zebra141
buffalo152
zebra142
zebra147

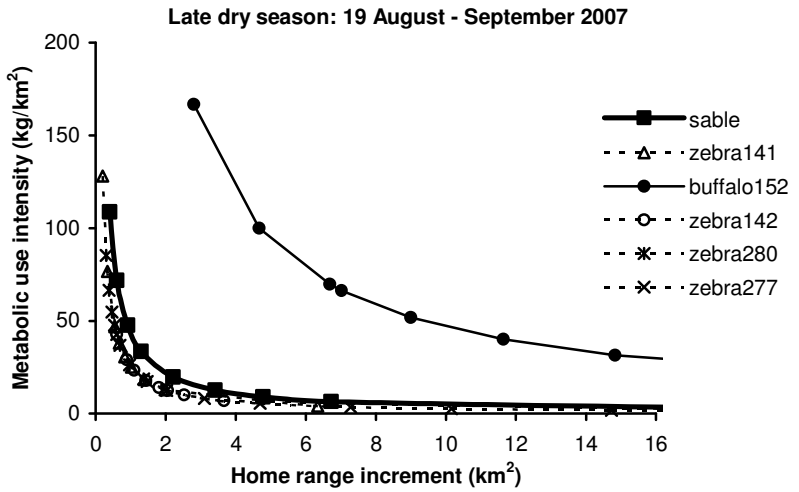


Figure 5. Metabolic use intensity within areas associated with each 10% increment in probability of use.

CHAPTER FOUR

Competitive relationships and the decline of a low density grazer in the Kruger National Park

Abstract

The aim of this study was to establish whether competitive interactions in the use of space between sable and ecologically similar but more abundant grazers might have contributed to the sable decline in the Kruger National Park. GPS-GSM collars were fitted on females from sable, buffalo and zebra herds occupying the same region during the same time. I amalgamated herd location data from collars placed on different herds to estimate the distribution range of the population of each species during distinct periods of food and water availability. Distribution ranges were computed using kernel methods and proportional area overlap between ranges was estimated. Spatial displacement was assessed as a shift in the location of sable core range following an influx of buffalo into the core range. Grazing facilitation was assessed as the grazing by sable on areas grazed by buffalo 15 and 30 days before. Movement responses of sable to buffalo or zebra proximity were assessed by comparing the diel displacement of sable following close encounters (<1 km) with buffalo or zebra with the median sable diel displacement for each month. During the wet season of food abundance the total sable range was almost completely included within buffalo range, but the core ranges were largely distinct and during the dry season the total and core range of both grazers were completely separated. Range overlap between sable and zebra was partial during both seasons. Sable moved away from areas that were being heavily grazed by buffalo and did not return to graze on these areas within 15 to 30 days, which shows that buffalo created no grazing facilitation of sable. Sable were frequently more than 1 km from buffalo and zebra, but appeared not to move away when buffalo and zebra were closer. This study showed that buffalo potentially limited the use of space and resources therein by sable and that when water and food resources were limiting during the dry season sable and buffalo occupied distinct section of the landscape.

Introduction

While there is detailed theory about the genetic, demographic and environmental factors likely to result in the extinction of small populations, there is lack of generalizations about the causes of decline of populations (Caughley 1994). The challenge is to distinguish climatic influences affecting habitat suitability from biotic interactions restricting populations. More specifically, resource limitations due to competition might contribute to the decline in the abundance of a species. Mac Nally (1983) and de Boer and Prins (1990) stated that for competition to occur there must be a combination of overlap in resource use and limited resource supply.

Potential competitors can coexist if resources supporting the populations of these species vary spatially and temporally (Atkinson and Shorrocks 1981; Hanski 1981; Hanski 1983; Wang et al. 2002) because environmental fluctuations and disturbance create spatial and temporal niche opportunities (Chesson and Huntly 1997). Aggregation by superior competitors on discrete patches of resources enhances coexistence between species with different competitive abilities (Atkinson and Shorrocks 1981; Inouye 1999), because it leaves out unoccupied patches that are exploited by inferior competitors as competition refuges (Inouye 1999). Hanski (1981) suggested that inferior competitors survive if across the landscape there are areas of concentrated use and areas of infrequent use by superior competitors. In addition, change in resource conditions over time and space alters the competitive advantage among species (Atkinson and Shorrocks 1981), such that no species is consistently a superior competitor across time and space.

Gaston and Kunin (1997) argued that low density species are fugitive species with lower competitive abilities than abundant species. Hanski (1983) and Wang et al. (2002) added that competitively superior locally abundant species can exclude locally rare species from patches of resources. Therefore, when low density and high density species overlap in their utilization of space, resource gains by low density species could be reduced due to competitive exploitation and exclusion by high density species. Rosenzweig and Lomolino (1997) proposed that competitive inferiority is a potential cause of species rarity. Accordingly, low density species should avoid sharing space with trophically similar much more abundant and competitively superior species, particularly during seasons of limited food availability.

Smaller herbivores are expected to be superior competitors than larger herbivores on high quality but sparse resources (Prins and Olff 1998; Owen-Smith 2002), but should be out-competed by larger herbivores when food is abundant but of poor quality (Owen-Smith 2002). The potential for competition among large mammalian grazers is greatest during the dry season, when food quantity and quality decline (Owen-Smith 1989; Prins 2000). It could also be reduced if potentially competing species rely on different resources during this time (Jarman 1971; Holbrook and Schmit 1989; Owen-Smith 1989).

Sinclair (1985) reported that along with interspecific competition, predation contributed to the spatial separation between wildebeest (*Connochates taurinus*) and plains zebra (*Equus burchelli*) in the Serengeti-Mara ecosystem. According to Hanski (1981) and Sinclair (1985), predators congregate in areas of the landscape where prey abundance is highest. James et al. (2004) reported that spatial separation of caribou (*Rangifer tarandus caribou*) from an alternative prey for wolves (*Canis lupus*), the moose (*Alces alces*), reduced predation pressure on caribou because elevated moose density caused a numerical response in wolves, which would increase the incidental predation on caribou and contribute to its decline.

Within the Kruger National Park (KNP) a progressive decline of low density grazers such as sable antelope (*Hippotragus niger*), roan antelope (*Hippotragus equinnus*) and tsessebe (*Damaliscus lunatus*) has occurred since 1987 (Grant and van der Walt 2000; Owen-Smith and Ogutu 2003). The decline of roan was preceded by an influx of zebra into the roan range in the northern basalt plains of the KNP following the 1982/3 El Niño-related drought, raising competition for grazing as a potential cause of the roan decline. However, Harrington et al. (1999) identified increased adult mortality due to predation by lion (*Panthera leo*) as the most likely cause of the decline of roan. Apparent competition (Holt 1977) mediated by an increase in the abundance of principal prey species for lion was implicated as prime cause of population decline by other ungulate populations including sable (Owen-Smith and Mills 2006; Owen-Smith and Mills 2008).

Sable, buffalo and zebra are all medium-tall grass grazers (Skinner and Chimimba 2005), raising the potential for exploitative competition. Sable and buffalo are both ruminants, thus the outcome of exploitative competition between these species should depend on population density (Holbrook 1973; Hanski 1983; Gaston and Kunin 1997)

and body mass ratio (Prins and Olff 1998). However, larger grazers such as buffalo (520 kg, Pienaar 1969) might provide grazing facilitation to smaller grazers like sable (220 kg, Wilson 1968 cited by Owen-Smith 1988), through a grazing succession. The larger grazer, tolerating poorer quality food could graze the tall and fibrous grass facilitating access to short and tender grass for grazing by the smaller grazer requiring higher concentration of protein and energy in the forage (Vesey-FitzGerald 1960; Bell 1970). Zebra are non-ruminants and hence should theoretically be out-competed by ruminants, which are more efficient in using sparse food (Illius and Gordon 1992), but high local densities of non-ruminants could potentially exclude low density ruminants from specific habitats. In addition to similarity in resource requirements, sable, zebra and buffalo share a common predator, the lion. Therefore, in areas of high abundance of buffalo and zebra, apparent competition (Holt 1977; Holt et al. 1994) caused by a numerical response of lions to high availability of principal prey species as well as competition for food, could jointly contribute to the decline of sable.

To establish whether competitive interactions between sable and buffalo or zebra over long time scales might have contributed to sable decline, I investigated seasonal, monthly and daily patterns of species interactions in the use of space. I hypothesized that:

1. Sable, being a low density and declining species, should concentrate use of space on the sections of the landscape infrequently used by buffalo and zebra to reduce competition for resources and/or the predation risk associated with high concentration of buffalo and zebra
2. Sable should exhibit short term avoidance by moving away from buffalo and zebra proximity to reduce predation risk
3. There should be grazing succession, whereby the smaller grazer sable will benefit by grazing in areas previously grazed by buffalo

Methods

Study area

I conducted this study to the south of Punda Maria Camp (22°68'S, 31°018'E) in northern Kruger National Park (KNP), South Africa, within an area of about 600 km^2. This area was selected for the study because the decline of sable was more severe in Punda Maria than further south in the park (Henley 2005). During the 2005-2006 rainfall year the study area received higher rainfall (743 mm) than the long term mean rainfall of 600 mm, but 2006-2007 was a drier rainfall year (419 mm). The wet season spans normally from October to March and more than 80% of the annual rainfall falls during this period, whereas the dry season spans from April to September, generally with little or with no rainfall (see Chapter 1 for details).

The vegetation is mainly characterized by mixed *Combretum* spp woodland on sandstone and granite substrates and *Colophospermum mopane* woodland or shrubland on basalt of the Soutpansberg group and Ecca shale (Gertenbach 1983; Venter 1990). Drinking water for animals was abundant and widely distributed in the study area during the wet season and early dry season in the form of streams and many ephemeral pans. However, between August 2006 and the first wet season rains in early November 2006 and between May 2007 and the first wet season rains at the end of September 2007, drinking water was restricted to pools along the Mphongolo River in the south and to a gravel pit in the south-west of the study area.

Study design and data collection

I conducted this study between June 2006 and September 2007, a period that covered two dry seasons and one wet season. Three adult females from two groups of sable, four adult females from four herds of zebra and two females from one buffalo herd located south of Punda Maria Camp were fitted with GPS-GSM collars in May 2006. In July 2006, the two sable herds joined to form one single herd, whereas the buffalo herd split to form two herds. In June 2007 additional collars were fitted, being one on sable, two on zebra and one on buffalo. Collars were fitted on female sable and buffalo from the

same herd that had the collars fitted in May 2006, and on two female zebra from additional herds within sable range. Except during the calving period of sable (Estes and Estes 1974; Skinner and Chimimba 2005), females remain within the breeding herds. Therefore, the movements of the collared females are regarded as representing the movements of the herds.

The single sable herd and the two buffalo herds included in this study represented the entire populations of 20 and 400 animals of these species in the study area, respectively, whereas 4-6 collared zebra herds included in this study corresponded to about 15-20% of the total zebra population of 200-300 animals. The last total area Ecological Aerial Survey (EAS) in Punda Maria was conducted in 1993 and indicated that there were 19 sable antelope, 140 buffalos and about 570 zebra (KNP census data). This indicates that there was an increase in buffalo numbers and a decrease in zebra numbers between 1993 and 2006, while the sable population remained stable.

I scheduled the collars to record the GPS coordinates of the herds routinely every six hours, at 2:00, 8:00, 14:00 and 20:00. However, during days of observation of each herd I adjusted the schedule of the collar to record the GPS coordinates of the herd hourly. I visited the sites used by the herds of each herbivore species during the morning (6:00 – 10:00) and late afternoon/early evening (16:00-20:00) foraging period (Chapter 1). At each site used by each species I recorded the presence or absence of dung of the other two species, as an indication of previous use of the site by potential competitors or facilitators. Based on feeding observations (Chapter 1), I considered the 8:00 and 20:00 herd locations as representing the areas used by the herds during the morning and evening foraging sessions, respectively.

Data analysis

Estimation of seasonal distribution ranges

To estimate seasonal utilization distributions of herds making up populations I used adaptive kernel density estimates (Worton 1989) using the Animal Movement Extension (Hooge and Eichenlaub 1997) in ArcGIS 9.1. (Environmental Systems

Research Institute Inc, USA). I selected the smoothing parameter *h* using least-squares-cross validation (lscv) (see Chapter 3 for details).

For the estimation of distribution range of sable, zebra and buffalo populations between June 2006 and September 2007, for each species I amalgamated data obtained from all the collars that delivered data during the specified period in analysis, except during times when collared females of the same species were in the same herd. The two buffalo females stayed apart during the duration of this study, except during the first two weeks of June and December 2006 when the two herds had joined. All collared zebra herds stayed consistently separated. GPS coordinates were projected into WGS 1984 UTM zone 36S datum before the analysis of distribution ranges. I estimated the total range and the core range of the population as the kernel probability isopleths enclosing 95% and 50% of the locations of herds, respectively (White and Garrott 1990). Areas covered by the contours were estimated using Hawth's Tools in ArcGIS 9.1.

Overlap in the utilization distribution

Due to the difficulty of measuring the intensity of inter-specific competition in observational studies (Putman 1996; Stewart et al. 2002), the extent of spatial overlap in habitat occupation has been suggested as a measure of the potential for competition (Schoener 1983; Putman 1996; Arlettaz et al. 1997). The proportional overlap between distribution ranges of populations and/or home ranges of two individuals is a measure of spatial interaction between populations or between animals, respectively (Doncaster 1990; White and Garrot 1990; Kernohan et al. 2001). Doncaster (1990), Kernohan et al. (2001), Millspaugh et al. (2004) and Fieberg and Kochanny (2005), suggested that differential use of space within range boundaries should be taken into account in the analysis of space use sharing because animals might use largely overlapping ranges but the core areas might be distinct.

To identify distinctions in distribution range over the course of the study period, I estimated overlap between monthly sable ranges. Overlapping monthly ranges indicated that sable used the same range during that period, whereas non-overlapping monthly ranges indicated that sable shifted range between months. In October 2006 and in August 2007 sable moved into a distinct range during the month. For these cases, data from dates

of the month before range shift were analyzed with data of the previous months and data from dates after range shift were analyzed with data of the following months. Using this procedure, I identified five distinct periods of sable distribution, namely the early dry season of 2006 spanning from June to August 2006, the late dry season of 2006 from 5th October to 8th November, the late wet season period spanning from January to April 2007, the early dry season period covering the period from May to July 2007 and the late dry season period of 2007 extending from 19th August to 30th September. The indicated dates such as 5th October and 8th November 2006 and 19th August 2007 were the dates when sable moved from one range to another, separating ranges used by the herd during the same month, i.e. during the first week of November 2006 sable used a separate range from the range used after the 8th of November. The period between 1st and 18th August 2007 was excluded from the analysis because during this period the sable herd had moved from the range used in July, but the range used during this period was separated from the range used from 19th August. Therefore, I considered 1st-18th August as a transition period between the early dry season range (May - July) and the late dry season (19th August - 30th September). The range used by sable in September 2006 was also a transitional range between the early dry season and the late dry season range. Therefore, September 2006 was also omitted from the analysis.

While sable and buffalo data represented the distribution of the total populations during the periods in analysis, zebra data represented a sample of the population and there was variation in the number of zebra herds that provided data during different periods. For instance, data were obtained from four collared zebra herds between June and August 2006, from three zebra herds during the periods 5th October - 8th November 2006 and January - April 2007, from five zebra herds between May and July 2007 and from four collared zebra herds between 19th August and 30th September 2007. I estimated total ranges and core areas of sable, buffalo and sampled zebra populations and measured percentage overlap between the total ranges and between the core areas of these local populations during these periods. Core areas represent the areas of the landscape most frequently used by the animals within populations. Therefore, overlap on these areas could provide an indication of the potential for competition for space and harvestable resources therein, whereas distinct core areas might reveal sections of the landscape that

most contribute in resources supporting the populations of each species. However, competitive exclusion from specific habitats might also result in distinct ranges (Rosenzweig 1981), which makes it not clear whether spatial separation between potential competitors is caused by competitive exclusion or simply by distinct habitat preference, unless a removal experiment is undertaken (Holbrook 1973; Holbrook and Schmitt 1989). To obtain a more detailed temporal variation in the partitioning of space among species I estimated monthly core ranges of each population and assessed monthly proportional core area overlap.

To measure spatial separation or overlap on total and core ranges I overlaid the total range and core ranges of sable with those of buffalo and the sampled zebra populations during different periods and during different months using ET Geowizards in ArcGIS 9.1. The shared area was defined as the intercept between two ranges. Areas covered by the two ranges as well as the extent of the shared range were estimated using Hawth's Tools in ArcGIS 9.1. Following White and Garrot (1990) and Kernohan et al. (2001), I measured space use sharing as the percentage overlap between two ranges. This was calculated by dividing the extent of the shared range between sable and buffalo or between sable and zebra by the extent of sable range, either the total or the core range, using the following formula:

$$HR_{\text{sable, buffalo}} = \frac{Asable, buffalo}{Asable} X100$$

where;

$HR_{sable,\ buffalo}$ is the percentage of sable range shared with buffalo; $A_{sable,\ buffalo}$ is the extent of the range shared between sable and buffalo and A_{sable} is the extent of sable range.

Spatial displacement of sable

I assessed spatial displacement of sable by buffalo or zebra as a shift in the location of sable monthly core range following an overlap of sable core range with buffalo and zebra monthly core range. To establish that sable core range in a previous month was occupied by buffalo or zebra during the present month, I estimated the percentage overlap between sable core range the previous month and buffalo or zebra core range during the month that followed.

Assessing grazing facilitation

To assess the potential benefit to sable by buffalo grazing the tall, low quality grass and opening space for the regrowth of high quality grass (Vesey-FitzGerald 1960; Bell 1970), I examined whether sable grazed on areas previously grazed by buffalo. This was done by calculating the distances between sable locations during the morning foraging spell (8:00) to the locations grazed by buffalo 15 days and 30 days before. I did the analysis for these two time scales because 3 weeks is a lag long enough for the grass to respond to rainfall (Bell 1970) and hence recover from grazing. Therefore, this analysis would reveal whether there is a grazing succession whereby sable graze in areas previously grazed by buffalo. This analysis was restricted to the wet season when both sable and buffalo used largely overlapping ranges and grazed grass was renewing in response to rainfall. I also calculated the proportion of sable, buffalo or zebra feeding sites that had been or had not been previously used by the other two species, as indicated by the presence or absence of their dung.

Separation distances between grazers

To establish patterns of separation distances between sable and potential competitors as well as between buffalo herds and among zebra herds, I calculated the distance between the locations of the sable herd at 8:00 and the locations of each buffalo and zebra herds also collected at 8:00 of the same day. The distance between herd locations were estimated using Hawth's Tools in ArcGIS 9.1. To assess the effect of seasonal contrasts in rainfall and hence on food and water availability on the spacing between herds, I divided the separation distances into the dry season covering the periods June - October 2006 and May – September 2007 and the wet season spanning from November 2006 to April 2007. I grouped the separation distances between herds in distance categories of 1 km and estimated the proportion of simultaneous locations between herds that were within each distance category for each season. To compare the relative proximity of sable to zebra and to buffalo, I calculated the frequency distribution of separation distance during months of high overlap on core ranges between sable and buffalo or zebra and computed binomial confidence intervals for the proportion of simultaneous herd locations within each category of separation distance.

Sable short term movement responses to buffalo and zebra

To establish sable short term movement responses to buffalo or zebra proximity, I restricted the analysis to the buffalo and zebra herds with ranges that overlapped with sable range and to the months when such range overlap was observed, because only herds with overlapping ranges can get close to each other and cause sable short term movement response. The exploratory analysis indicated monthly core range overlap between the sable herd and buffalo herds AM150 and AM152 in July 2006, December 2006 and March 2007 and between sable and zebra herds AM277 and AM280 in July 2007. In July 2006, the total home range of the sable herd was nearly enclosed within the total range of zebra herd AM142 and these two herds used adjoining core ranges, thus sable could potentially get close in proximity to this zebra herd. For these months, I estimated separation distances between sable herd locations and buffalo or zebra herd locations collected simultaneously at 8:00. I estimated sable diel AM displacement as the distance between the 8:00 herd locations of successive days. To establish whether sable move away or did not respond to buffalo or zebra proximity, I compared sable diel displacement when sable were less than 1 km from buffalo or zebra a day before with the median sable diel displacement recorded for the month.

Results

Seasonal total and core range location and overlap

The sable herd, representing the sable population, concentrated its use of space in the north-west of the study area during the early dry season of both 2006 and 2007 and during the wet season of 2007, but shifted to the south-east from late August to the end of the dry season of both years (Figure 1). The two buffalo herds constituting the buffalo population covered a more extensive area than that occupied by sable or collared zebra herds (Table 1) but concentrated use of space on the upland regions of the landscape in the north of the study area during the wet season and shifted range to concentrate along the Mphongolo River from April to the end of the dry season of 2007. However, in 2006 the buffalo herds only moved from uplands to River banks in August. The sample of six

zebra herds concentrated their use of space in the western half of the study area year-round (Figure 1).

During the wet season the total range of the sable population was almost completely included within buffalo range, but only overlapped partially with the range of the zebra herds that were collared. However, only 11% of the small sable core range overlapped with the larger buffalo core range (Table 2). The range of the sampled zebra population was likewise almost enclosed within the range of buffalo, but only about 8% of the core area of the collared zebra herds overlapped with buffalo core range. Thus, during the late wet season, despite the generally shared range, the areas most intensively used by the herds of the three species were largely distinct. During the early dry season in 2007 there was no overlap between sable and buffalo core range, but there was an increase in overlap between sable range and the range of collared zebra herds (Table 2). Towards the end of the dry season in 2007, sable and some collared zebra herds shifted range southwards closer to pools along the Mphongolo River. However, despite the common dependency on the water from the river, sable dry season core range was about 6-8 km from the core range of the two buffalo herds, and only a partial overlap in total range was observed (Figure 1). Some collared zebra established core ranges close to the River and hence overlapped with buffalo, whereas other remained on the upland regions of the landscape, drinking water in a drainage line in the proximity of the Punda Maria camp.

Monthly core area overlap

The core area of the sable herd overlapped with buffalo core areas used during certain early dry season and wet season months. For instance, in July 2006 sable core range was completely enclosed within buffalo core range when buffalo were still on uplands in the north of the study area, but the proportional overlap on core areas declined later, such that herds constituting the populations of the two species used completely distinct core ranges after August 2006. Following the early rains in November 2006, buffalo shifted range from the river banks used during the late dry season to the uplands, increasing the overlap with sable core range during certain wet season months. In

December 2006 and March 2007, about 20% and 40% of monthly core ranges of sable were also used as core range by the buffalo herds, respectively (Figure 2). When water became a limiting resource in the upland regions during the early dry season of 2007, buffalo shifted range southwards close to the Mphongolo River, the overlap on sable core area declined to zero and remained so during the rest of the dry season (Figure 2). The sable herd used a separate core range from the core range of the zebra herds that were collared in May 2006. However, when two additional collars were fitted on zebra herds found within the sable range, about 60% of the sable core range in July 2007 was part of the core range of the sampled zebra herds, particularly of the two zebra herds that were collared in June 2007 (Figure 2).

Spatial displacement of sable

The sable herd shifted the location of its monthly core range to a distinct core range when the area used as core range the preceding month was occupied by buffalo as monthly core area. For instance, in August 2006 when buffalo used as core range about 65% of the area that had been used by sable as core range in July 2006, the sable population moved to a different core range that was about 3.5 km from their core area used in July. Shift of sable core range following an influx of buffalo was also observed in November 2006 and February 2007. More than 50% of the area used by sable as core area in November 2006 and February 2007 was used by buffalo as core area in December 2006 and March 2007, respectively. In December and March sable moved to core ranges that overlapped less than 40% with core ranges used in November and February, respectively. I found no evidence of displacement of sable by zebra from the monthly core area used.

Grazing facilitation

Only 2% of sable locations during the wet season were close (<1 km) to areas grazed by buffalo 15 and 30 days before (Figure 3). About 35% of sable range in January 2007 had been used as core grazing area by buffalo in December 2006, but the proportion

of sable grazing locations <1 km from areas previously grazed by buffalo remained at around 2%. The three grazers used feeding areas that were spatially separated. Only about 10% of feeding sites used by sable (N=427) during the dry season of 2006 and 2007 had been previously used by buffalo or zebra. About 5% of feeding sites used by buffalo (N=263) and zebra (N=314) had old zebra and buffalo dung, respectively. Less than 1% of feeding sites used by each of the three grazers had been recently used by the other two grazers, as indicated by the presence of fresh dung (still moist).

Separation distance between grazers

The sable herd was rarely within less than 1 km from a buffalo or collared zebra herd both during the wet and dry seasons. Zebra herds were also generally more than 1 km from each other (Figure 4 and 5). Buffalo herds were more often <1 km to each other than to sable or zebra herds. During months of high overlap on core ranges with buffalo, the sable herd remained distant from buffalo, with only 5% and 13% of simultaneous herd locations within 1 km and 2 km separation distance, respectively. But when overlapping core range with zebra, about 15% and 50% of simultaneous locations between sable and collared zebra herds were within 1 km and 2 km separation distance, respectively. Therefore, sable were more often closer to collared zebra herds than to buffalo herds (Figure 6).

Short term movement responses

Sable were generally more than 3 km away from buffalo and more than 1.5 km away from zebra, even during months of high overlap on core ranges (Table 3). From June 2006 to September 2007, the closest separation distance between sable and buffalo was about 330 m. Separation distances shorter than 1 km were only recorded in 10 simultaneous locations, i.e. 10 days. Of these 10 occasions, in three (30%) sable diel displacement a day later was greater than the monthly median sable diel displacement (Table 3) but on the remaining seven close encounters, nor sable or buffalo moved away. Separation distances of less than 1 km between sable and zebra herds were found in 24

simultaneous locations (days) during this study. In three of these occasions, sable and zebra were foraging together (separation distance of less than 100 m). During months of high overlap on core ranges such as July 2007, sable stayed within 1 km from zebra for four consecutive days. In addition to the findings revealed by the GPS collar data, I observed sable foraging alongside zebra but did not observe sable and buffalo foraging together.

Discussion

Sable range was almost completely encompassed within buffalo range during periods of water and food abundance such as the late wet season, but both grazers used completely distinct ranges when these resources were most limiting in the late the dry season. Although during the late wet season sable and buffalo overlapped in their total range, their core ranges were largely distinct. Results also showed that sable shifted the location of their monthly core range after a high proportion of this core range overlapped with buffalo, which suggests spatial displacement of sable by buffalo. Sable did not graze on areas heavily grazed by buffalo 15 to 30 days before, which shows that buffalo created no grazing facilitation of sable. Daily simultaneous herd locations showed that herds of these grazers remained spatially separated, rarely within 1 km separation distance, even collared herds of the same species. This is unusual for zebra because zebra family groups have been reported to occasionally aggregate during the dry season to form larger groups (Smuts 1975). Sable were most of the times well separated from buffalo and/or zebra even during months of high core area overlap, but showed weak evidence of short term avoidance of close encounters with buffalo and no avoidance of zebra.

Previous studies of spatial and temporal interactions among sympatric African ungulates at the level of detail covered in this study are not available because the GPS tracking technology allowing the collection of simultaneous locations of animals in time and space is a new tool in wildlife research in Africa. However, Sinclair (1985) using direct observations of grazers in the Serengeti-Mara ecosystem, documented that during the dry season zebra avoided close proximity of wildebeest, but during periods of food abundance when competition was unlikely, zebra stayed close to wildebeest to reduce

predation risk. When both prey species were available on woodlands, lions switched predation pressure from zebra to wildebeest. In North America, Johnson et al. (2000) and Stewart et al. (2002) using VHF telemetry reported movements by mule deer (*Odocoileus hemionus*) to avoid areas frequently used by elk (*Cervus elaphus*). They suggested that it could be a mechanism to reduce interspecific competition. Stewart et al. (2002) also documented shifts in the habitat used by mule deer and elk following the introduction or removal of cattle (*Bos taurus*) in the study area, suggesting that cattle competitively displaced mule deer and elk from preferred habitats. Cooper et al. (in press) used GPS collars and calculated separation distances between simultaneous herd locations between white-tailed deer (*Odocoileus virginianus*) and cattle and found that white-tailed deer moved away from close proximity to cattle and avoided grazing in areas of concentrated grazing by cattle.

Exploitative competition might occur among grazers overlapping in the utilization of space during any time of the year, but it is more pronounced during the dry season (Owen-Smith 1989). The overall wet season core areas of sable and buffalo were largely distinct. The overlap between sable and buffalo core areas during certain wet season months and the displacement of sable by buffalo from the monthly core areas indicates that distinct habitat preference does not explain spatial separation of the overall wet season core range. Sable used monthly core ranges of about 1-6 km^2 (average 2.8 km^2) during the wet season (Figure 2). If a great proportion of this small core range was used by buffalo herds as core grazing area during the same month, grass depletion could have occurred which might have prompted sable to shift range to areas temporarily not exploited by buffalo. Even during the months when sable core range was completely within buffalo core range such as July 2006, at small temporal scales like a day sable were generally more than 3 km away from buffalo. Close encounters, i.e. separation distance less than 1km, occurred only on 3% of all simultaneous observations of collared herds and lasted only 1-2 days. Heavy grazing combined with trampling grass by buffalo herds could have resulted in reduced forage availability to sable, which might have caused departure of sable from areas that were being used by buffalo. However, close encounters between sable and buffalo had short duration (1-2 days), which might also suggest that in addition to the likely localized resource depletion, other mechanisms

might have contributed in explaining the large separation distances. Holt et al. (1994) pointed out that over short timescales predator aggregate on patches with abundant prey. Owen-Smith and Mills (2008) documented that shifting from principal to alternative prey species by lions was the prime cause of decline of some ungulate populations in the KNP. James et al. (2004) also reported that spatial separation from abundant prey species for wolves, such as the moose, was an antipredator strategy of a low density and declining species, the caribou, and reduced their mortality from predation. Accordingly, sable might have avoided grazing in areas of concentrated use by buffalo to reduce predation risk. However, abundant prey over long time periods result in increased predator population (Holt et al. 1994), which has long term negative impact on the populations of alternative prey species.

Sable moved away in response to the influx of buffalo into their monthly core range and did not return within 15 to 30 days to graze the grass that regenerated following heavy grazing by buffalo. Prins and Olff (1998) suggested that for facilitation to occur there must be some "optimal" difference in body mass between grazers; otherwise there will be no grazing facilitation. In the Serengeti, Bell (1970) documented a grazing succession in order of decreasing body mass along a catena gradient, with zebra (219 kg) grazing first the coarse tall grass on the bottomlands and providing grazing facilitation to wildebeest (163 kg), which in turn benefited Thomson's gazelle (*Gazella thomsoni,* 16 kg) that grazed later in the succession. The body mass ratio (Prins and Olff 1998; Owen-Smith 2002) between the two ruminants where the smaller (Thomson's gazelle) benefited from grazing by the larger (wildebeest) is about 10.2. In Uganda, Eltringham (1974) reported facilitation between hippopotamus (*Hippopotamus amphibius*, 2330 kg) and buffalo, body mass ratio of 4.48, but buffalo were out-competed at high hippopotamus density. Therefore, the difference in body mass between buffalo (520 kg, Pienaar 1969) and sable (220 kg, Wilson 1968 cited by Owen-Smith 1988) in the KNP, yielding a body mass ratio of 2.3, although adequate for species co-occurrence (Prins and Olff 1998), it is perhaps too small for sable to benefit from buffalo grazing. Thus, buffalo had a negative impact on sable by competitively displacing sable from core grazing areas and not creating grazing conditions beneficial to sable.

Large separation distances between herds, including between herds of the same species, indicate an absence of nutrient hotspots in the study area that would attract the congregation of animals to graze high quality grass, during both the wet season when grass resources renew from grazing in response to rains and during the dry season when concentration of animals might occur in bottomlands retaining soil moisture that sustains grass regrowth (McNaughton 1985). While during the wet season green grass was widely available, there were no areas notably retaining green grass during the dry season. This could explain why animals did not congregate during grazing periods, except when grass regrowth was available on burnt areas during the early wet season.

During the early dry season of the wetter 2006 and during the late wet season of 2007 when water was widely distributed in the landscape, sable total range was enclosed within buffalo total range. However, during the early dry season of 2007 when water on the uplands became restricted to small pans and streams, buffalo herds shifted range to the bottomland regions near large and several pools along the Mphongolo River to satisfy their drinking needs, whereas sable and zebra remained in the uplands until late August when herds of these species also moved southwards closer to the River. Smaller herbivores are expected to be superior competitors than larger herbivores due to their ability to survive on sparse food of high quality (Prins and Olff 1998). However, under severe dry season conditions that prevailed when I conducted this study most of the available food was of low quality in the form of completely brown grass. Therefore, the larger grazer, buffalo, tolerating the widely abundant brown grass were likely to out-compete sable, which were more selective for sparse green leaves (Chapter 1). Accordingly, range shifts by buffalo from uplands to bottomlands might have created a relief for sable from potential competition with buffalo for the scarce water and for the progressively diminishing favoured grass species and green grass.

During the late dry season sable range was largely separated from the range of buffalo and collared zebra herds, though the three grazers used ranges closer to the water restricted to pools along the Mphongolo River during this time of the year. Aggregation of buffalo and zebra near water in the south-west of the study area left other parts of the landscape temporarily unused by these abundant species. This might have created a seasonal variation in the spatial predation risk, and sable might have reduced risk of

predation by establishing the late dry season core area in areas less used by these staple preys for lions. The cost of avoiding concentrations of buffalo and zebra included undertaking journeys of more than 7 km to and from drinking water every 2-4 days, which reduced foraging time, increased energy expenditures and the risk of encountering an ambush predator on the way to and from water.

Results also show little overlap between sable and zebra core ranges during all seasons. However, this could be because in May 2006 I only sampled 4 zebra herds (15-20% of the population). When additional collars were fitted on zebra in June 2007, there was an increase in proportional core area overlap between sable and zebra in July 2007. I found no range shift by sable following high overlap on core range with zebra. This could be because zebra occur in small family groups and are widely distributed in the study area, which creates no opportunity for the sable herd to shift home range to areas temporarily not used by zebra. The collared zebra herds concentrated use of space in the south-west of the study area, an area which is out of the current sable distribution range. This spatial separation could be explained by distinct habitat preference, because this is an open area with about 10% of woody vegetation cover, while sable used more wooded habitats (Chapter 2). In addition, the south-west of the study area have a gravel pit which is a permanent water source where both buffalo and zebra drunk frequently. Thus, the lack of use of this section by sable may also indicate avoidance of the concentrations of these species.

The seasonal, monthly and daily interactions showed that the low density sable consistently avoided areas of frequent use by buffalo, which indicates that buffalo had negative impacts on the use of space and resources therein by sable as well as by potentially increasing predation pressure. This finding supports the theory that low density species avoid competition by ecologically similar more abundant species (Gaston and Kunin 1997). However, the confirmation of resource competition or apparent competition can only be achieved by reducing the density of buffalo and zebra to the population densities prior to sable decline and subsequently monitor patterns of space use and population dynamics of sable antelope. The closure of artificial boreholes will likely contribute to the decline of the local abundance of buffalo and zebra.

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Table 1. Extent (km^2) of total ranges (95%) and core ranges (50%) of sable herd, both buffalo herds and collared zebra herds combined during different seasons

	Sable					Zebra					Buffalo				
	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07
Total range	14.3	38.3	15.2	28.0	40.0	94.5	58.0	58.4	78.5	138.7	269.0	254.0	175.0	235.0	247.3
Core range	1.96	4.7	2.4	4.7	5.4	14.9	9.4	8.1	12.8	16.2	63.4	48.1	38.3	42.0	45.6

EDS 06 – Early dry season (June – August 2006)

LDS 06 – late dry season (5^{th} October – 8^{th} November 2006)

LWS 07 – late wet season (January – April 2007)

EDS 07 – early dry season (May – July 2007)

LDS 07 – late dry season 2007 (19^{th} August – September 2007)

Table 2. Proportional (%) overlap of total and core ranges of sable herd with the total and core ranges of buffalo and zebra herds

	Zebra					Buffalo				
	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07	EDS 06	LDS 06	LWS 07	EDS 07	LDS 07
Total range	47	6.7	10.9	59.3	54.3	99.8	22.7	85.9	24.3	2.4
Core range	24	0.0	0.0	17.9	0.0	46	0.0	10.8	0.0	0.0

Table 3. Median separation distance (km) between sable, buffalo and collared zebra herds during months of high overlap on core ranges

Month	Separation distance (km) from sable	
	buffalo	collared zebra
July 2006	3.3	1.4
December 2006	3.5	
March 2007	3.7	
July 2007		2.5

Early dry season 2006 Late dry season 2006 Late wet season 2007 Early dry season 2007 Late dry season 2007

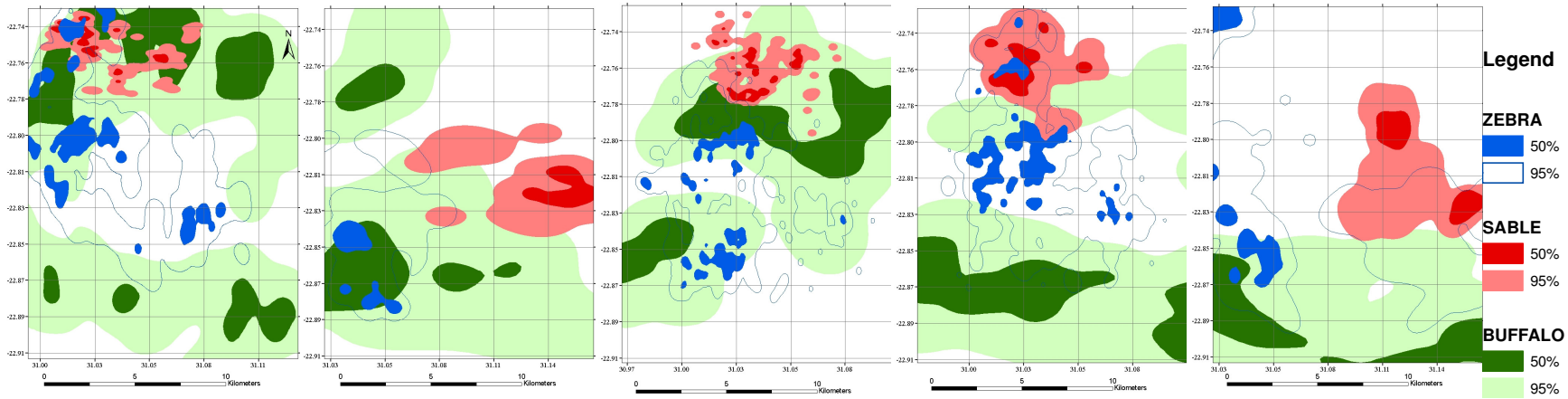


Figure 1. Seasonal total (95%) and core (50%) distribution ranges of the sable herd, both buffalo herds and sampled zebra herds in the study area.

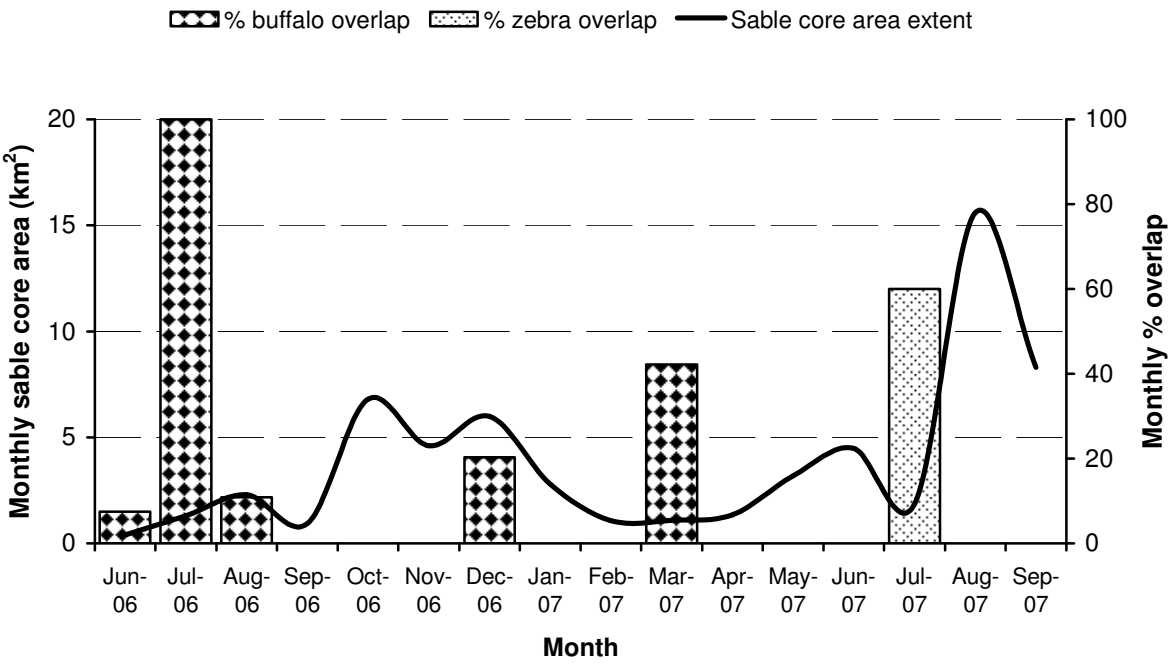


Figure 2. Changes in proportional overlap between monthly core range of sable and the core range of buffalo and collared sample of zebra herds

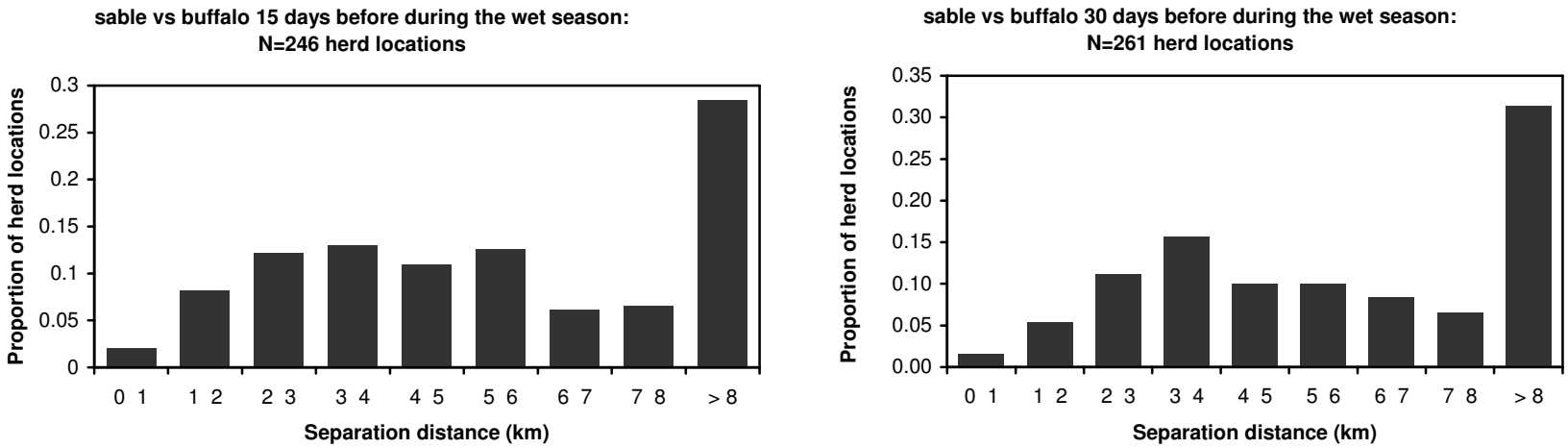


Figure 3. Frequency distribution of separation distances between sable foraging areas and buffalo foraging areas 15 and 30 days before during the wet season (November 2006 – April 2007)

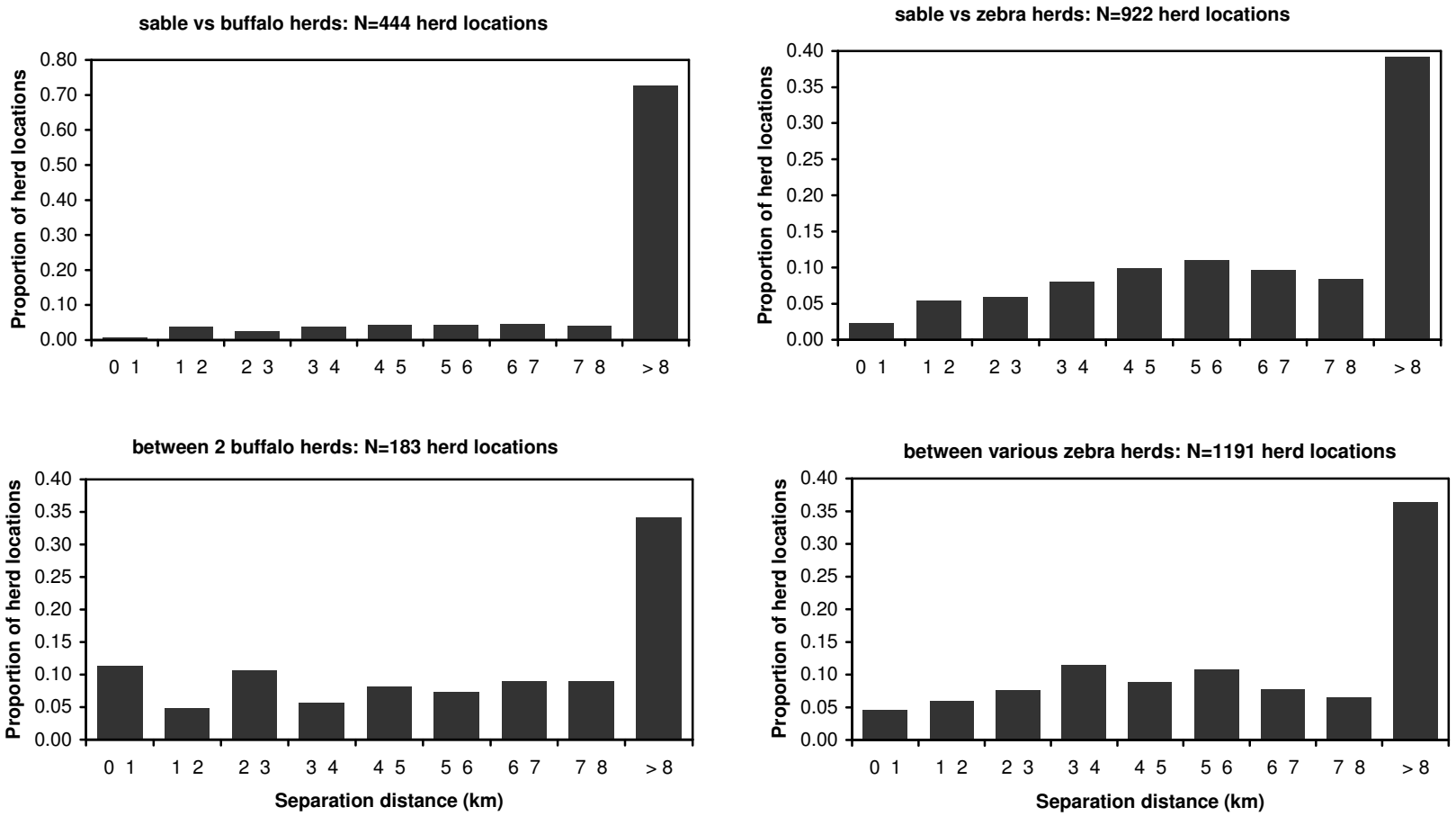


Figure 4. Frequency distribution of separation distances between sable and buffalo or collared zebra herds during the dry seasons of 2006 and 2007

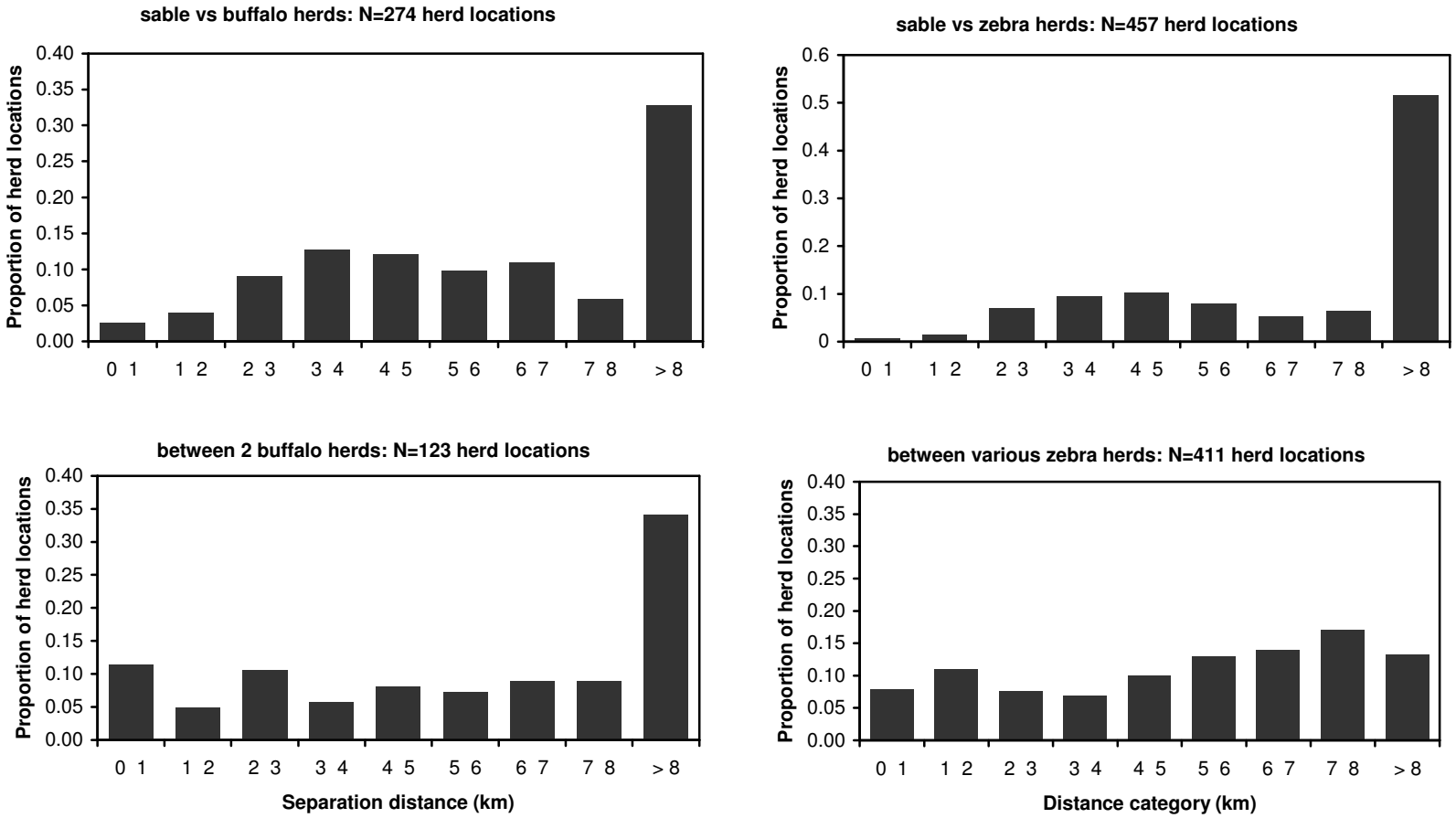


Figure 5. Frequency distribution of separation distances between sable and buffalo or collared zebra herds during the wet season of 2006/7

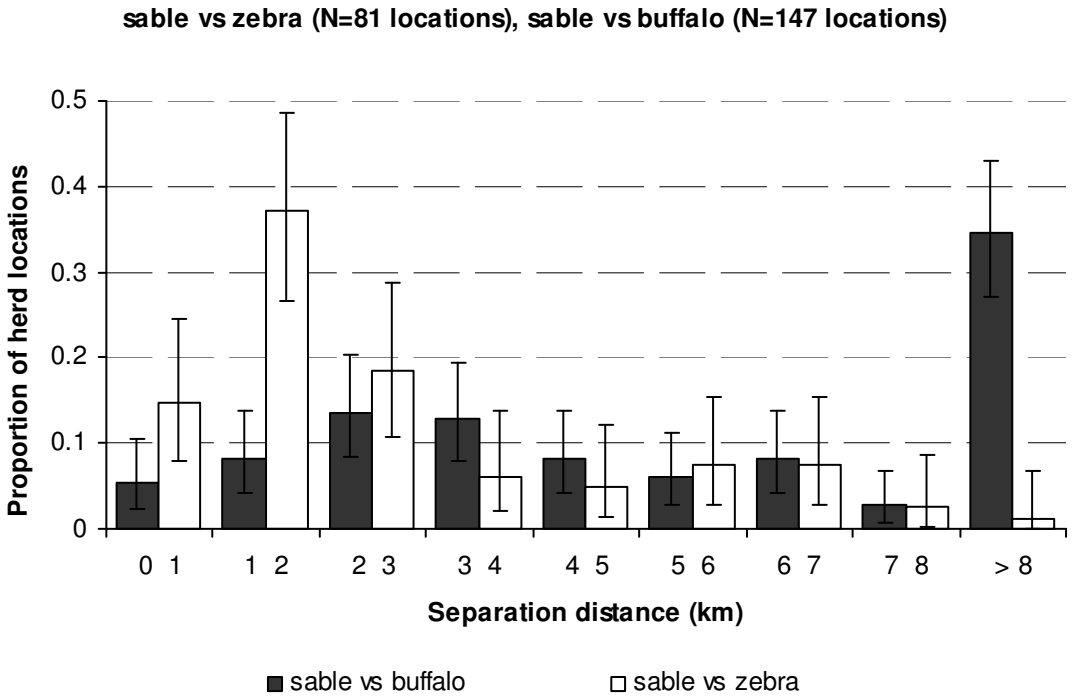


Figure 6. Frequency distribution of separation distances during months of overlap on core range between sable and collared zebra herds (July 2006 and July 2007) and between sable and buffalo (July 2006, December 2006 and March 2007). Vertical lines indicate 95% binomial confidence intervals.

CHAPTER FIVE

Faecal nutritional indicators and the population trend of sable antelope

V.A. Macandza and E. Le Roux

Abstract

In the Kruger National Park (KNP), sable antelope have failed to recover from their drastic decline experienced after 1987. This investigation aimed at establishing whether forage quality is limiting the recovery of sable. We collected fresh faecal samples of sable from Punda Maria (annual rainfall of 600 mm) and Pretoriuskop (annual rainfall of 730 mm), and compared with buffalo and zebra, which have maintained high abundance at Punda Maria. The samples were collected during the dry season of 2006 and 2007. Faecal samples were analyzed for nitrogen, phosphorus, sodium and crude fibre. Faecal crude protein and phosphorus levels for sable were similar to buffalo but were higher than the recorded for the non-ruminant zebra. Faecal crude protein for sable through the dry season months varied around the approximation of minimum faecal concentrations for maintenance (7%), and was lower than faecal crude protein recorded for sable populations elsewhere. Nevertheless, it was not that different from faecal crude protein levels recorded for wildebeest, which are thriving in the KNP. This suggests that nutritional limitations might indirectly be restricting sable recovery, through reduction in areas occupied by sable that retain high forage quality.

Introduction

Populations of large herbivores may be limited by top-down processes such as predation as well as by bottom-up processes such as nutrient availability (Sinclair 2002; Sinclair and Krebs 2003). While predation by large carnivores such as lion (*Panthera leo*) limits populations by causing mortality of adult individuals (Owen-Smith and Mills 2006, 2008), nutritional limitations due to poor supply of protein, energy or minerals from the forage may restrict recruitment by reducing the birth rates and/or the survival of offspring (Gaillard et al. 1998; Mduma et al. 1999). Malnutrition may increase the vulnerability of adult individuals to predation because when food is limited in safer habitats herbivores might forage in habitats with higher predation risk and be killed by predators before they actually die from starvation (Sinclair and Arcese 1995). In addition, malnourished animals are weaker and easier to catch by predators than well nourished animals (Owen-Smith and Ogutu 2003). Sinclair and Arcese (1995) and Mduma et al. (1999) documented that in the Serengeti-Mara ecosystem wildebeest (*Connochaetes taurinus*) dying from predation were in better body condition (measured using bone marrow fat) than individuals dying from non-predation causes, including starvation. This suggests that if predation limits populations, the remaining individuals should not reveal nutritional deficiencies, whereas animals remaining from a population that is limited by food shortages should reveal malnutrition.

The quality of the forage is determined by the proportion of cell wall fibre relative to cell contents and by the concentrations of protein, soluble carbohydrates and minerals in the cell content (Bell 1970; Owen-Smith 1982, 2002). The soluble carbohydrates and the digestible fraction of the cell wall determine the potential nutritional yield in the form of metabolizable energy to be obtained from the forage, but fibre also reduces the rate of the digestion process, which restricts the rate at which energy and nutrients become available to the animal, particularly to ruminants (Owen-Smith 2002; Murray and Baird 2008). Free-ranging herbivores are confronted by the nutritional bottleneck during the dry season when the proportion of the nutritious green leaves decreases and most of the remaining forage is of low digestibility due to high fibre content (Owen-Smith 1982). Fryxell (1987) suggested that losses in body condition and increase in mortality rates in

white-eared kob (*Kobus kob leucotis*) during the dry season of drier years were caused by low quality of the forage available. Mduma et al. (1999) documented that density dependent food limitations during periods of drought regulated the population of the migratory wildebeest by increasing adult and calf mortality. Mduma et al. (1999) and Owen-Smith (2008) suggested that apart from poor forage quality during the dry season, food limitations for large herbivores could also be through limited quantity of standing biomass due to depletion of grass biomass by heavy grazing, particularly during dry seasons of years with below average rainfall.

Faecal nitrogen (N) in grazers is positively correlated with dietary protein (Mould and Robbins 1981; Irwin et al. 1993; Wrench at al. 1997), dietary dry matter digestibility (Leslie and Starkey 1985, Irwin et al. 1993; Grant et al. 1995), dry matter intake (Irwin et al. 1993) and animal body condition (Grant et al. 1995). Therefore, faecal N is a useful measure of cell contents to monitor diet quality and establish critical times of the year for herbivore nutrition (Hodgman et al. 1996). Leslie and Starkey (1985) and Irwin et al. (1993) suggested that the faecal nutritional indicators of free-ranging herbivores reveal the quality of resources provided by the habitats to the animals, and hence could also be used to monitor forage quality in relation to animal requirements.

Sinclair (1977) calibrated the following regression equation derived from trials with zebu cattle by Bredon at el. (1963) cited by Sinclair (1977), to estimate dietary crude protein from faecal crude protein for buffalo: $DP\% = 1.677\ FP\% - 6.93$, where *DP* is dietary crude protein and *FP* is faecal crude protein and suggested that the minimum dietary protein for body maintenance is 5% because buffalo lost body weight when consuming diets with lower levels of protein. Minson (1971) cited by Grant et al. (1995), Kinyamario and Macharia (1992) and van Hooven (2002) also proposed a minimum dietary crude protein concentration of 5% for ruminants to maintain body weight, but Prins (1996) proposed a higher value of 6.2%. Following the above equation, 5% dietary crude protein corresponds to 7% faecal crude protein as the minimum for maintenance. However, the actual requirements of crude protein should differ among ungulate species that differ in body size and/or in the physiology of the digestive system.

Smaller ungulates require higher concentrations of nutrients in their food than larger ungulates (Bell 1970; Jarman 1974; Geist 1974). Accordingly, faecal crude protein

of smaller ungulates should be higher than faecal crude protein of larger ungulates. Ruminants have higher digestive efficiency but are less tolerant of fibre than non-ruminants of similar body size, which due to their hindgut fermentation tolerate plant parts with high fibre content (Bell 1970, 1971; Illius and Gordon 1992). According to Duncan el al. (1990), Illius and Gordon (1992) and Menard et al. (2002), hindgut fermenters extract more nutrients from forage with high fibre content than ruminants. This is because hindgut fermenters digest protein in the stomach before the passage of the forage for fermentation in the hindgut (Bell 1971). Therefore, faecal crude protein should be higher for ruminants than for non-ruminants.

Apart from N, minerals such as phosphorus (P) and sodium (Na) are also critical for herbivore nutrition (Robbins 1993). These are the two most deficient minerals in natural pasture, with concentrations generally below the requirements of herbivores (Belovsky and Jordan 1981; van Soest 1994; McDowell 1985; McNaughton 1990). McNaughton (1988, 1990) suggested that the concentration of limiting minerals may indicate the habitats most preferred by grazing animals. In the Serengeti National Park, Tanzania, P and Na concentrations in the grass were higher in grazing hotspots than in less frequently grazed areas (McNaughton 1988). Estes and Estes (1974), McNaughton (1988) and Eksteen and Bornman (1990) reported that termite mounds have higher concentrations of minerals such as Na, P, Calcium (Ca), Potassium (K) and Magnesium (Mg) than the surrounding areas. Therefore, grazers tend to favour grass growing in the proximity of termite mounds in order to increase the intake of these minerals (McNaughton 1988). In northern Angola, Estes and Estes (1974) observed sable antelope (*Hippotragus niger*) eating mineral-rich soil at the base of termite mounds. Wilson and Hirst (1977) also reported geophagia and osteophagia by sable in the Loskop Dam Nature Reserve, South Africa, reflecting deficiencies in Ca and P. Faecal Na concentration is a potential indicator of the concentration of Na in the diet (Belovsky and Jordan 1981). van Soest (1994) and McDowell (1985) indicated that the minimum required concentration of Na in the diet is 0.05% - 0.18% (0.5 – 1.8 kg^{-1}DM). However, the relationship between faecal and dietary Na concentration has not been quantitatively established. Dietary P is positively correlated with faecal P (Leslie and Starkey 1985; Wrench at al. 1997) and

Wrench et al. (1997) suggested that the minimum faecal P for maintenance of grazers is 0.2% (2 g kg^{-1}DM).

The sable population of the KNP declined after 1987 (Grant and van der Walt 2000; Owen-Smith and Ogutu 2003), but at the time of this study the population had stabilized. Predation by lions was apparently the primary cause of the decline of sable in the park (Owen-Smith and Mills 2006, 2008). However, changes in habitat conditions associated with prolonged or more severe droughts might also have contributed to the sable decline and currently restrict recovery by limiting the quality or abundance of the forage available to sable. Therefore, the aim of this study was to establish critical periods of the year for the nutrition of sable, comparing faecal indices of diet quality between sable and a larger ruminant buffalo and a non-ruminant of similar size zebra, which were numerically more abundant than sable. Faecal indices of diet quality for sable were also compared with sable and similarly-sized ruminants from elsewhere, relative to the population status of these species. We predicted that:

1. if the KNP sable population was limited by food quality, during the dry season faecal crude protein should be lower than faecal crude protein concentrations for populations of sable from elsewhere and for similarly-sized grazers that are thriving in the KNP
2. Sable should forage in proximities of termite mounds more often than buffalo and zebra, to compensate for the negative mineral balance by feeding on mineral-rich grass
3. Sable, being a smaller ruminant and more narrowly selective for green grass should show higher faecal crude protein concentration than the larger ruminant buffalo and the non-ruminant zebra, which require higher absolute quantity of food and tolerate brown grass and diet with high fibre content

Methods

Study area

We conducted this study to the south of Punda Maria Camp (22°68'S, 31°018'E) in northern Kruger National Park (KNP) and in the vicinity of Pretoriuskop (25°09'S, 31°16'E) in the south of the park. During the seasonal cycle July 2005 – June 2006 rainfall at Punda Maria was 24% above long term (1960-2007) average of 600 mm, whereas between July 2006 and June 2007 rainfall was 34% below the long term average (Chapter 1). The long term mean rainfall at Pretoriuskop (737 mm) is higher than at Punda Maria. During the seasonal cycle July 2005 – June 2006 the total rainfall at Pretoriuskop was 934 mm and during July 2006 – June 2007 rainfall was about 600 mm, which was 27% above and 18% below the long term average, respectively. About 80% of the rain falls during the wet season that spans from October to March. The dry season extends from April or May to September or October. In 2006 wet season rains began in early November, whereas in 2007 wet season rains began at the end of September.

At Punda Maria the woody vegetation is dominated by *Combretum* spp woodland on sandstone and granite formations and *Colophospermum mopane* woodland or shrubland on basalts of the Soutpansberg group and Ecca shale. At Pretoriuskop the vegetation is predominantly *Combretum* spp – *Terminalia sericea* woodland on granite substrate (Gertenbach 1983; Venter 1990). In mid July 2006 a prescribed fire burnt 28% of the Punda Maria study area, but no grass regrowth was available until the first wet season rains in early November. In mid September 2007, an accidental fire burnt the south east of Punda Maria and grass regrowth became available three weeks later, following rains at the end of September. However, when grass regrowth was available on burnt areas, green grass was also available in unburnt areas. Therefore, during the early wet season of 2007 (October 2007) sable, zebra and buffalo grazed both in unburnt and in burnt areas. About 90% of the Pretoriuskop study area was accidentally burnt in early August 2007 and remained with no grass regrowth until the end of September.

Study design and data collection

We fitted GPS-GSM collars on sable, zebra and buffalo located south of Punda Maria (see Chapter 1 for details). In Pretoriuskop only sable herds were collared. Data collection covered the dry seasons of 2006 (June – October) and 2007 (May – September) and the early wet season of 2007 (October 2007). Sable faecal indices of diet quality were compared between two regions of the park that differ in rainfall. Faecal indicators of nutritional status of zebra and buffalo were compared only with the sable foraging under the same conditions at Punda Maria. We conducted the study during the dry season because this is the period of lowest food quality and hence is the period when nutritional deficiencies are likely to be more pronounced, whereas we included the early wet season in the study because the new growth of the grass following the early wet season rains has the highest concentrations of crude protein, although the quantity is still limiting. Therefore, result will reveal the quality of the diet obtained by the three grazers during distinct periods of food quantity and quality.

Using GPS tracking we visited sites used by herds of each herbivore species two days each week during their potential feeding periods in the morning (6:00 – 10:00) and late afternoon/early evening (16:00-20:00) (Sinclair 1977; Beekman and Prins 1989; Prins 1996; Parrini 2006; Magome et al. 2008). At each site we recorded the presence or absence of termite mounds within a 25 m radius. We visited sites used by the herds within the last 24 hours to ensure that we obtained fresh faecal samples, which were still moist. We collected one composite fresh faecal sample per day and considered a day as the independent sampling unit. We also collected faecal samples encountered occasionally, dropped by animals from herds that were not collared, provided that the samples were fresh. We made faecal samples composite by mixing dung from different dung piles per day, assuming that distinct dung piles were dropped by different animals within the herd or by animals from different herds. Amalgamating faecal samples obtained from different herds of the same herbivore species allow inference about diet quality to be made at population level. We neglected faecal samples with signs of dung beetle activity or faecal samples that received heavy rain, because dung beetles increase faecal N and rains decrease both faecal N and P (Wrench et al. 1996). We air-dried the faecal samples in the field during two-three days in shade and stored the samples in paper

bags. We further oven-dried the faecal samples at 60^{o}C during 24 h prior to nutritional analysis in March 2007 (for the faecal samples collected between June and October 2006) and in March 2008 (for the faecal samples collected between May and October 2007).

We divided the faecal samples into months and seasons to describe monthly and seasonal patterns in indices of diet quality. For data collected at Punda Maria, we used the following seasons: early dry season (June – July 2006 and May – July 2007), late dry season (August-October 2006 and August-September 2007) and first month of the early wet season (October 2007), whereas we used the following season for data collected at Pretoriuskop: early dry season (May-June 2007), late dry season of 2006 (August-September 2006), late dry season of 2007 (July 2007), burnt period without grass regrowth (August-September 2007), early wet season of 2006 (October-November) and early wet season when grass regrowth was available to sable (October 2007). No data were collected at Pretoriuskop during the early dry season of 2006. These seasonal subdivisions were based on seasonal changes in the proportion of grass that retained green leaves (Chapter 1 and 2). Therefore, these seasons potentially reflect distinct periods of food quality for grazers, as evaluated by the prevalence of green grass. We used different seasons for the Punda Maria and the Pretoriuskop study area because grass greenness and the seasonal changes in the prevailing grass greenness were different between the two study areas. Late dry seasons of 2006 and 2007 could not be combined for Pretoriuskop because years were different in terms of factors influencing grass greenness such as rainfall and occurrence of fire.

Nutrient analysis

The faecal samples were analyzed for nitrogen using a nitrogen analyzer and expressed as a percentage of the dry matter (DM). Faecal concentrations of phosphorus and sodium were determined using the Inductively Coupled Plasma-Optical Emission Spectroscopy (ICP-OES) method (Jarvis et al. 1992) and expressed as % of DM and mg kg $^{-1}$ DM, respectively. Faecal nitrogen, phosphorus and sodium were analyzed by the BEMLAB (Pty) Ltd. in Cape Town, South Africa. Crude fibre was analyzed using the standard digestion method (AOAC 1984) by the Agricultural Research Council – Irene,

Pretoria and also expressed as % of DM. Following van Soest (1994) we calculated faecal crude protein (CP) by multiplying the nitrogen content of the faeces by a factor of 6.25. Faecal samples collected in 2006 were only analyzed for N and P, whereas samples collected in 2007 were analyzed for N, P, Na and crude fibre. The samples collected during the dry season of 2006 and 2007 were analyzed for N, P and Na by the BEMLAB as two separate batches, i.e. batch of 2006 and batch of 2007, whereas samples collected in 2007 were analyzed for fibre as one batch. Grouping samples in few batches for chemical analysis reduced bias in comparisons of nutrient concentrations that might be caused by likely differences between batches in chemical results.

We collected sable and zebra faecal samples by hand but directly to paper bags, hence with minimal handling to avoid contamination of samples by Na from the fingers. Due to the soft texture of buffalo faecal samples, we used a wood stick to collect the samples from the dung pies to paper bags. This eliminated the risk of Na contamination.

Statistical analysis

Each day was the replicate for the statistical analysis. We applied two-factor analysis of variance (factor 1: herbivore species and factor 2: season) to establish distinctions between herbivores and the influence of the stage of the dry season on differences between herbivores in the faecal concentrations of each nutrient and crude fibre. We also used two-factor analysis of variance to compare nutrient concentrations on sable faecal samples between regions (Punda Maria and Pretoriuskop) and seasons. Prior to statistical analysis, concentrations of nitrogen, phosphorus and crude fibre were arcsine transformed to approximate the data to normal distribution (Quinn and Keough 2002). We used Tukey post-hoc test for multiple comparisons to identify significant differences at 95% significance level ($p<0.05$). We did not analyze statistically data collected during the early wet season because the sample size was small (N = 8 faecal samples for each herbivore species). We applied a pairwise chi-squared test to test for differences in the proportion of feeding sites that had termite mounds between sable and buffalo or zebra. The statistical analysis was done using STATISTICA 6.0 software.

Results

At Punda Maria faecal crude protein was significantly higher for the ruminants sable and buffalo than for the non-ruminant zebra throughout the dry season (Figure 1; Table 1a; $F=4.22$, $df=2$, $p=0.015$), but sable and buffalo did not differ significantly in faecal crude protein levels (Tukey post-hoc test: $p>0.05$). The mean faecal crude protein for sable of Punda Maria (8.12±0.14%) was significantly higher than the mean faecal crude protein for sable of Pretoriuskop during the early dry season of 2007 (7.1±0.59%). During the late dry season faecal crude protein levels for sable from Punda Maria (7.2±0.09%) were lower than for sable from Pretoriuskop in 2006 (8.4±0.28%), but higher than for sable from Pretoriuskop in 2007 (6.3±0.32%). For the three grazers faecal crude protein levels dropped between the early and the late dry season months when grass became predominantly brown, but the seasonal decrease was significant only for sable, dropping from 8.12±0.14% to 7.2±0.09% (Tukey post-hoc test: $p<0.001$) (Figure 1, Table 1a). At Punda Maria during the sampled first month of the early wet season (October 2007), when the three grazers grazed on burnt as well as on unburnt areas after the rains, the faecal crude protein increased sharply to reach 10.7±0.85% for sable, 9.3±0.63% for buffalo and 11.2±0.52% for zebra, reflecting the availability of green and young grass leaves. At Pretoriuskop during October 2007, when sable grazed only on grass regrowth post-burn, faecal crude protein increased to 15.5±0.51%, which was more than double of the levels of faecal crude protein recorded during the late dry season.

Faecal phosphorus (P) was higher for sable and buffalo than for zebra ($F=71.1$, $df=2$, $p<0.001$), but sable and buffalo did not differ significantly in the levels of faecal P (Figure 2; Table 1a). Faecal P did not differ significantly between sable at Punda Maria and Pretoriuskop ($F=2.47$, $df=1$, $p=0.118$). At Punda Maria, for the three grazers faecal P increased by more than 50% between the late dry season when grass was completely brown and the early wet season when grass regrowth post rains was widely available. The increase in faecal P from late dry season to early wet season was more pronounced at Pretoriuskop when sable fed on grass regrowth post burns (Table 1a, b).

Sodium (Na) concentrations in the faeces were significantly lower for sable than for buffalo and zebra ($F=39.8$, $df=2$, $p<0.001$, Table 1a), suggesting that Na concentration in the diet consumed or water drunk by sable were lower than the intake of

Na by buffalo or zebra. Unlike faecal crude protein and faecal phosphorus, faecal sodium levels appeared not influenced by the seasonal variation in grass phenology (Figure 3).

The percentage of crude fibre in the faecal samples of sable (22.01±0.48%) and buffalo (21.78±0.49%) showed no significant difference during the early dry season (Tukey post-hoc test: p=0.999) and late dry season (sable: 21.82±0.45% and buffalo: 23.88±0.57%; Tukey post-hoc test: p= 0.206). The non-ruminant zebra showed higher faecal crude fibre (27.55±0.69%) than the ruminants buffalo and sable ($F=43.91$, df=2, $p<0.001$), suggesting that zebra consumed forage with higher fibre content than sable and buffalo (Figure 4, Table 1a). During the late dry season the crude fibre was lower on faecal samples of sable from Punda Maria than from Pretoriuskop (Table 1a, b, $F=5.7$, df=1, p=0.02), but during the early dry season faecal crude fibre did not differ significantly between sable populations of the two regions.

The overall prevalence of termite mounds in feeding sites used by sable was significantly lower than in feeding sites used by zebra ($\chi^2=16.0$, df=1, $p<0.001$) and buffalo ($\chi^2=8.39$, df=1, $p<0.001$) (Figure 5).

Discussion

The limitation of this study is that requirements for nutrients for each of the grazers studied are not specifically established. This limits, at some extent, the understanding of the implications of the faecal indices of diet quality reported here for animal nutrition. However, during the dry season and early wet season sable and buffalo showed levels of faecal crude protein marginally higher than the coarse approximations of minimum levels for ungulates to maintain body mass, but zebra showed lower concentrations that these estimates except during the early wet season. While for sable faecal P remained above the minimum level for maintenance, the concentrations of P on the faeces of buffalo and zebra dropped during the late dry season. Faeces of sable were poorer in sodium than the faeces of both buffalo and zebra.

The faecal crude protein concentrations for sable during the dry season documented in this study were generally higher than the average faecal CP of 7% for sable during the dry season reported by Codron et al. (2007) in the Pretoriuskop area of

the KNP. In the Punda Maria area, Henley (2005) reported faecal CP of as low as 5.4% during a severe dry season of 2002. The faecal CP of the KNP sable population appeared lower than the faecal CP of sable populations that did not decline in other regions of South Africa (Figure 6). For example, Magome et al. (2008) in the Pilanesberg Game Reserve (PGR) reported dry season faecal crude protein generally above 8%. In the Kgaswane Mountain Reserve (KMR), Parrini and Owen-Smith (submitted) also reported faecal CP >8% when sable grazed on burnt areas, but dropping to 7.4% when re-growth post-burns was not available. Differences in nutritional status between the KNP sable population with that of the KMR seem to be in part due to differences in the time of the year when burns are implemented. In the KMR fire is applied as a management tool during the early dry season, which makes the more nutritious green flush available to sable during periods of the year that would otherwise be of nutritional stress. On the other hand in Punda Maria and Pretoriuskop in 2006 and 2007, burns occurred during the late dry season when there was not enough soil moisture to support grass regrowth. However, when regrowth post-burns became available to sable after the rains, diet quality improved considerably, with faecal crude protein levels increasing to more than double of the levels recorded during the most limiting late dry season.

The dry season levels of faecal crude protein documented for sable in this study were similar to the 7.5% documented for the similarly-sized wildebeest (Grant et al. 2000), which were thriving in the KNP as well as with wildebeest of the Mkuzi Game Reserve (Edwards 1991). They were higher than the results obtained by Knoop (2004) and Codron et al. (2007, 2009) for roan antelope (*Hippotragus equinus*) (5.1 – 6.25% CP), which declined severely in the northern basalt plains of the KNP and fail to recover and also higher than the roan population of the Nylsvley Nature Reserve (6.9% CP) (Dörgeloh et al. (1998), which was thriving (Figure 6).

Contrary to the expectation of a negative relationship between body mass and crude protein concentration (Bell 1970; Jarman 1974; Geist 1974), during the dry season faecal crude protein levels did not differ significantly between sable and buffalo. Codron et al. (2007) had previously reported higher faecal crude protein for buffalo (8.8%) than for sable in the KNP (7%). Heitkönig (1993) observed that roan have shorter retention time of forage in the gut and higher tolerance to dietary fibre than cattle and suggested

that the mechanism of forage digestion in roan could be intermediate between ruminants and non-ruminants. If this is also true for the closely related sable, it could explain the lack of significant differences in faecal crude protein between sable and buffalo, despite sable being smaller. Faecal nitrogen includes metabolic faecal nitrogen, i.e. microbial cells, mucus and eroded cells of the gastrointestinal tract, particularly if the diet has high content of the costly digestible fibre (Robbins 1993). According to Arman et al. (1975 cited in Leslie and Starkey 1985) smaller ruminants produce relatively more metabolic faecal nitrogen than larger ruminants. Faecal crude protein concentrations obtained in this study did not support this theory, unless sable consumed a diet with lower nitrogen concentration than the diet consumed by buffalo.

That ruminants have higher faecal crude protein levels than non-ruminants had been previously found (Edwards 1991; Grant et al. 2000; Codron et al. 2007). Codron et al. (2007) reported lower faecal CP for zebra (7.5%) than for buffalo during the dry season. In the Mkuzi Game Reserve, Edwards (1991) reported dry season faecal crude protein of 7% for zebra, which was lower than 8.2% recorded for wildebeest under the same grazing conditions. Lower faecal crude protein levels for zebra (5%) than for wildebeest (7.5%) during the dry season were also obtained by Grant et al. (2000). In the Timbavati region of South Africa, Bodenstein et al. (1990) documented that zebra and wildebeest grazing in the same fenced area consumed diets that did not differ significantly in crude protein content. On the other hand, faecal crude fibre was higher for zebra than for the ruminants. Edwards (1991) also documented faecal crude fibre higher for zebra (33.26%) than for wildebeest (24.34%). These findings show that free ranging zebra consumed diet poorer in crude protein and richer in crude fibre than similarly sized ruminants.

Faecal crude protein levels documented for buffalo in this study were lower than the findings by Codron et al. (2007) who reported average faecal CP levels of as high as 8.8% in the northern basalt plains of the KNP during the dry season, but did not differ from the results obtained by Sinclair (1977) and Grant et al. (2000) who reported dry season levels of faecal CP ranging between 5.6 and 7.5%, despite potential differences in the severity of drought during the periods of data collection. The mean faecal CP obtained for zebra in this study was lower than the findings by Codron et al. (2007) in the

northern basalt plains of the KNP (7.5%) and by Edwards (1991) in the Mkuzi Game Reserve (7%). However, results of this study were not different from the results obtained for zebra by Grant et al. (2000).

Faecal concentrations of P for sable did not differ from results obtained for sable of the KMR (Parrini and Owen-Smith, submitted) or for roan of the Nylsvley Nature Reserve (Dörgeloh et al. (1998). Faecal P for zebra and buffalo also did not differ significantly between this study and the findings by Grant et al. (2000), with both studies documenting faecal levels of P varying between 1.2 and 1.96 g kg^{-1} DM for zebra and between 1.5 – 2.8 g kg^{-1} DM for buffalo throughout the dry season. Higher faecal P for ruminants than for non-ruminants reported in this study had also been previously documented by Grant et al. (2000), comparing buffalo, wildebeest and zebra. The lower faecal P for zebra could be because in non-ruminants faecal P is more diluted by the high content of fibre. There is paucity of data on faecal Na concentrations for African ungulates, but the levels of faecal Na documented for sable appeared higher than Na concentrations in faecal samples of roan from different regions of South Africa (Dörgeloh et al. (1998). The more frequent use of feeding areas with termite mounds by zebra and buffalo than by sable indicates that zebra and buffalo use parts of the landscape with high concentrations of soil nutrients, particularly minerals. This might explain the higher levels of faecal Na for buffalo and zebra than for sable.

Sable faecal crude protein levels were similar to those found for populations of species that are thriving in the KNP such as the similarly-sized wildebeest and the larger buffalo. However, were lower than faecal crude protein concentrations on sable populations that are thriving elsewhere. This suggests that nutritional limitations might indirectly be restricting sable recovery, through reduction in areas occupied by sable that retain high forage quality.

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Table 1a. Seasonal changes in the mean concentrations of faecal indicators of diet quality for sable, buffalo and zebra in Punda Maria

	Sable			Buffalo			Zebra		
Nutrient/Season	E.D.S.	L.D.S.	E.W.S.	E.D.S.	L.D.S.	E.W.S.	E.D.S.	L.D.S.	E.W.S.
Crude protein (%DM)	8.12±0.14 N=50	7.2±0.09 N=53	10.65±0.85 N=8	7.84±0.31 N=28	7.70±0.08 N=41	9.27±0.63 N=8	6.20±0.19 N=49	5.83±0.07 N=45	11.23±0.52 N=9
Phosphorus (g kg^{-1} DM)	2.54±0.07 N=50	2.27±0.06 N=53	3.53±0.35 N=8	2.27±0.08 N=28	2.1±0.06 N=41	3.14±0.38 N=8	1.85±0.08 N=49	1.45±0.05 N=45	4.58±0.45 N=9
Sodium (g kg^{-1} DM)	0.78±0.07 N=27	0.76±0.14 N=19	0.64±0.13 N=8	1.94±0.16 N=16	2.26±0.21 N=15	2.54±0.43 N=8	1.55±0.16 N=27	1.57±0.14 N=23	1.70±0.27 N=9
Crude fibre (%DM)	22.0±0.48 N=27	21.82±0.45 N=19	18.47±0.93 N=8	21.78±0.49 N=16	23.88±0.57 N=15	19.30±1.04 N=8	25.89±0.57 N=27	27.55±0.69 N=23	20.19±0.89 N=9

E.D.S. – early dry season (June-July 2006 and May-July 2007)

L.D.S. – late dry season (August-October 2006 and August – September 2007)

E.W.S. – early wet season (October 2007)

Table 1b. Seasonal changes in the mean concentrations of faecal indicators of diet quality for sable in Pretoriuskop

Nutrient/Season	E.D.S. 2007	L.D.S. 2006	L.D.S. 2007	Burns without regrowth 2007	E.W.S. 2006	Burns with regrowth 2007
Crude protein (%DM)	7.1±0.59 (N=23)	8.4±0.28 (N=34)	6.3±0.32 (N=16)	6.08±0.14 (N=24)	9.5±0.56 (N=12)	15.50±0.51 (N=9)
Phosphorus (g kg^{-1} DM)	2.4±0.07 (N=23)	2.3±0.07 (N=34)	2.1±0.07 (N=16)	2.20±0.04 (N=24)	2.9±0.34 (N=12)	6.54±0.44 (N=9)
Crude fibre (%DM)	22.7±0.27 (N=33)	-------	23.42±0.27 (N=16)	24.36±0.30 (N=34)	-----	19.15±1.76 (N=9)

E.D.S. – early dry season 2007 (May-June)

L.D.S. – late dry season (August-September 2006 and July 2007)

Burns without regrowth – August-September 2007)

E.W.S. – early wet season 2006 (October-November)

Burns with regrowth – October 2007

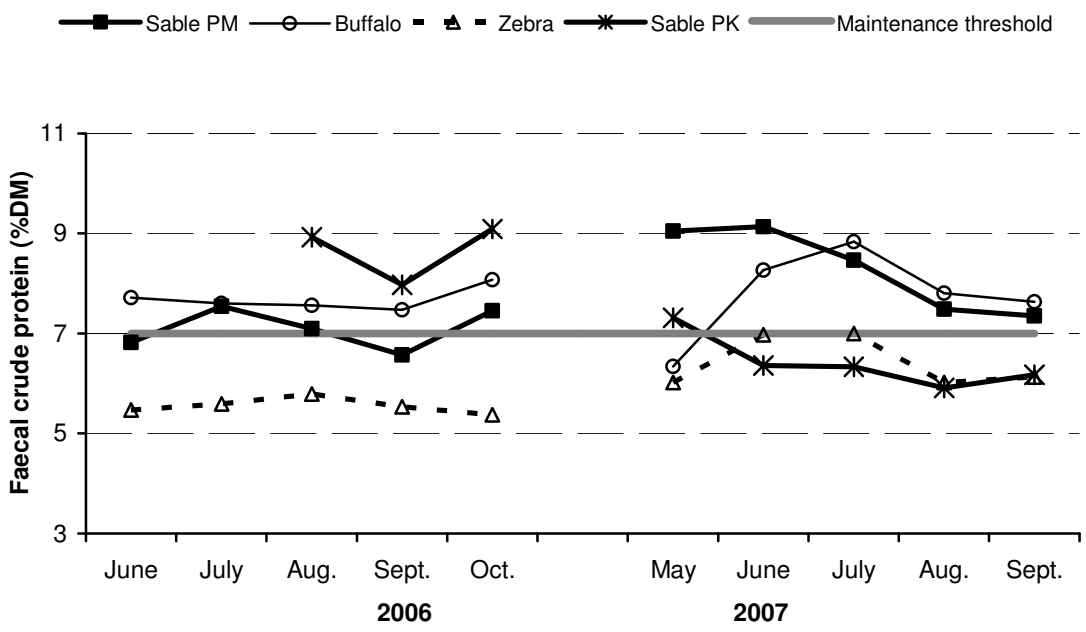


Figure 1. Monthly changes in faecal crude protein concentration for sable from Punda Maria (PM) and Pretoriuskop (PK), buffalo and zebra during the dry season of 2006 and 2007

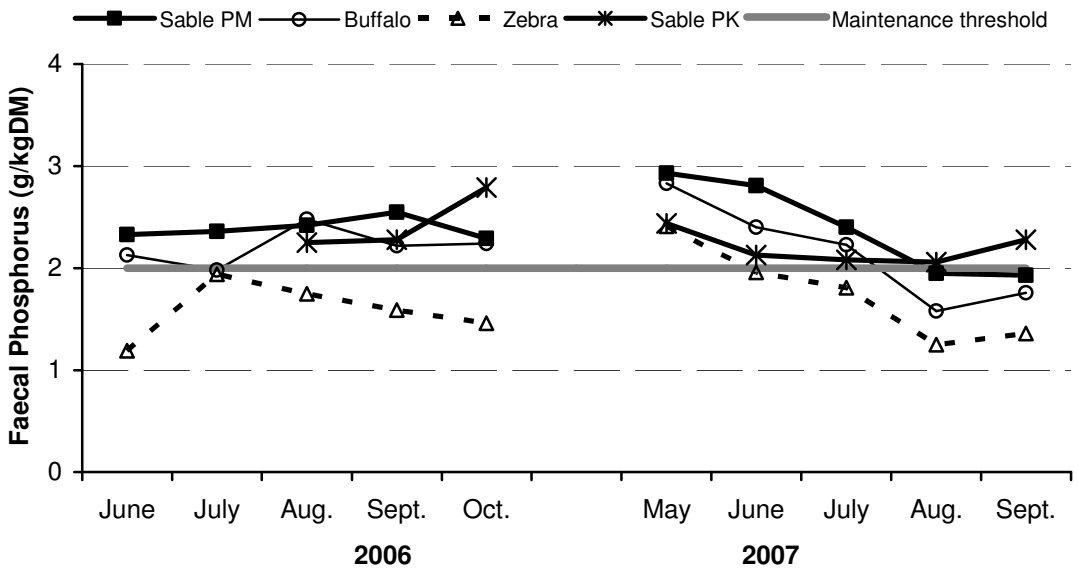


Figure 2. Monthly changes in faecal phosphorus concentrations for sable from Punda Maria (PM) and Pretoriuskop (PK), buffalo and zebra during the dry season of 2006 and 2007

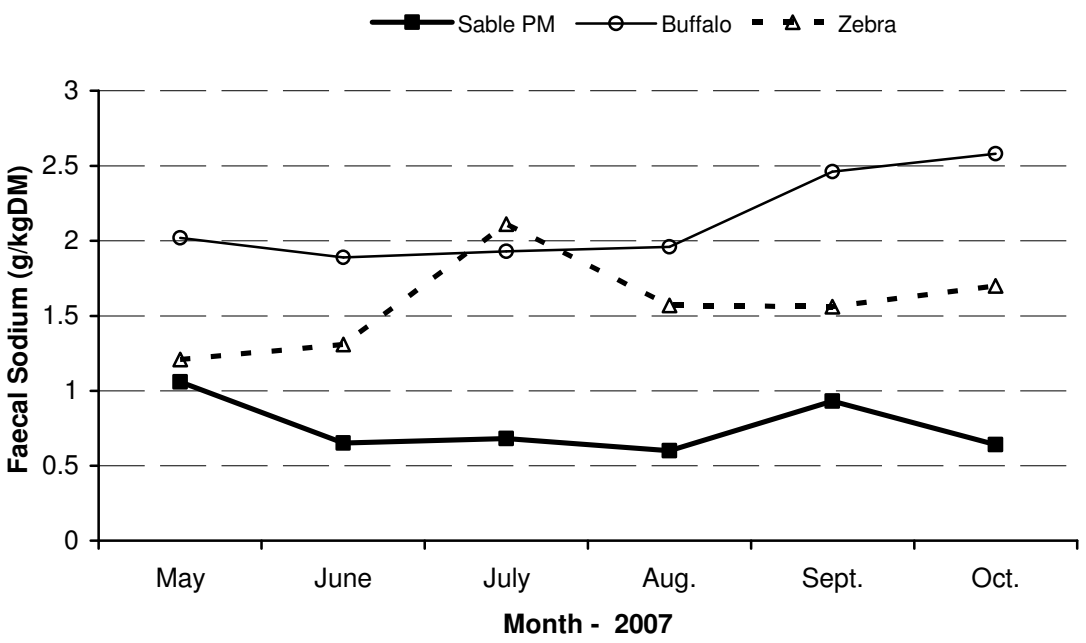


Figure 3. Monthly changes in faecal sodium for sable from Punda Maria (PM), buffalo and zebra during the dry season and early wet season

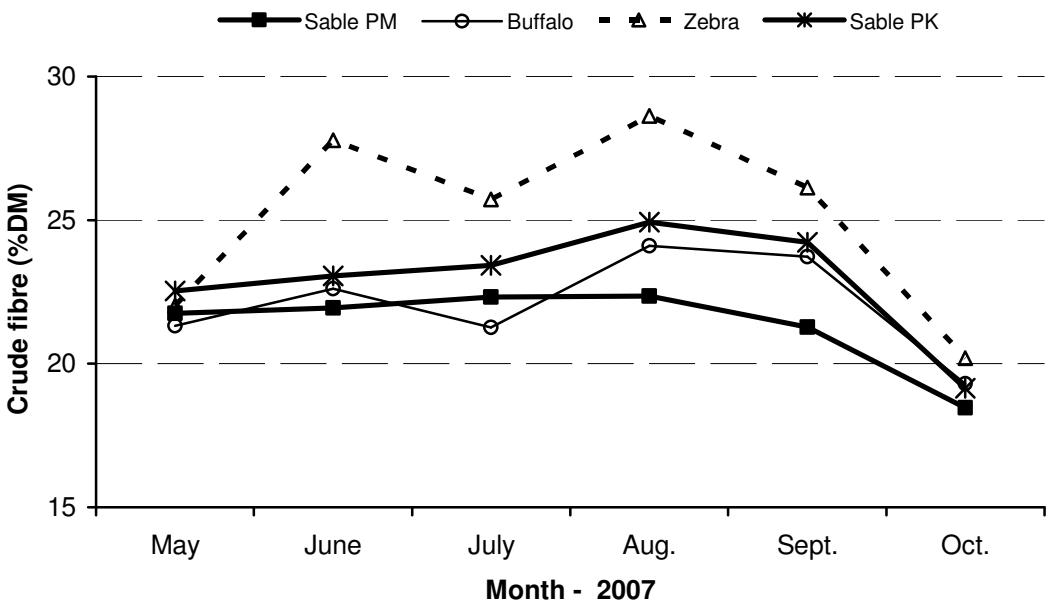


Figure 4. Monthly changes in faecal crude fibre for sable from Punda Maria (PM) and Pretoriuskop (PK), buffalo and zebra during the dry season and early wet season

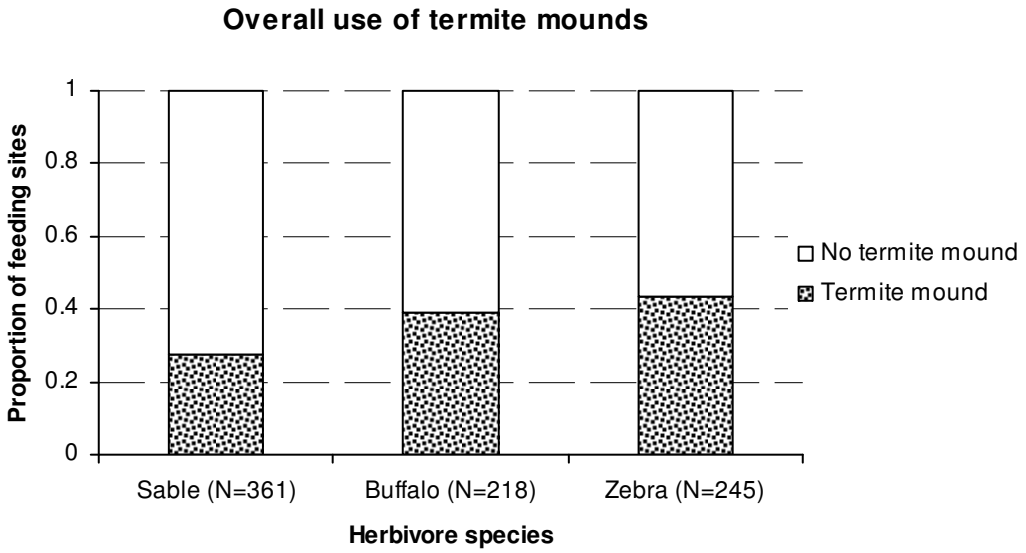


Figure 5. Comparative use of feeding sites with termite mounds nearby (<25 m) between sable, buffalo and zebra during the dry season

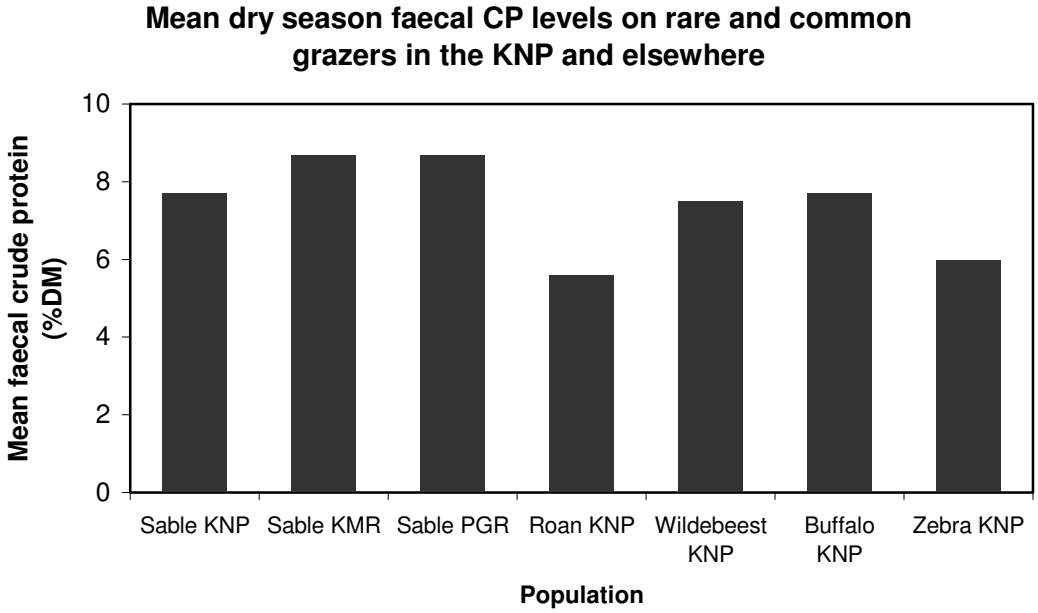


Figure 6. Mean dry season faecal crude protein levels recorded for sable antelope and other grazers in different regions of South Africa (this study, Grant et al. 2000; Parrini and Owen-Smith, submitted; Codron et al. 2007; Magome et al. 2008 and Codron et al. 2009)

CONCLUSION AND MANAGEMENT IMPLICATIONS

Conclusion

In the context of contributing to the identification of factors responsible for the decline or for the lack of recovery by the sable population in the KNP, this research project was designed with the broad aim of improving the understanding of resource partitioning between low and high density grazers at different hierarchical levels of resource selection. The specific objectives included: 1) to assess diet separation between low density and high density grazers and assess diet breadth at the grass species and plant parts levels, 2) to establish a comparative analysis of habitat use between sable, zebra and buffalo, 3) to establish distinctions in space use patterns between the low density grazer, sable and the high density grazers, buffalo and zebra, 4) to investigate competitive interactions between sable, buffalo and zebra in the use of space and 5) to identify critical periods of the year for sable nutrition.

The key questions addressed in this study are: 1) what do sable do differently in terms of resource use at different hierarchical levels that could contribute to their occurrence at lower abundance than other grazers occupying the same broad landscape? and 2) at what hierarchical level resource partitioning occurs to explain the coexistence among grazers or at what level of resource use sable might be limited by competition to remain at low density while ecologically similar grazers attain higher densities?

Sympatric grazers are likely to compete for food resource if not separated at the grass species and grass features level. Previous studies showed that grazing herbivores differ in preferred grass height for grazing (Bell 1970), but overlap on grass species eaten (Jarman and Sinclair 1979). However, sable, buffalo and zebra are all regarded as grazers that prefer to graze medium-tall grass (Skinner and Chimimba 2005). Arsenault and Owen-Smith (2008) found overlap on grazed grass height among short grass grazers. This suggests that differences in grass height alone should not be adequate to ecologically separate grazers with similar preferences in grass height for grazing. Based on the niche breadth theory (Brown 1984) and resource availability theory (Gaston and Kunin 1997; Gregory and Gaston 2000) as explanatory mechanism of rarity and commonness within

species assemblages and on the suggestion that competition among grazers decreases during the dry season through the use of different alternative resources (Jarman 1971; Holbrook and Schmit 1989 and Owen-Smith 1989), in Chapter 1 I investigated the degree of diet overlap among herbivore species and assessed the breadth of the food niche of each herbivore species at the grass species and grass features levels.

The key findings of Chapter 1 were:

1. The low density grazer showed narrow tolerance to grass species and grass features, grazing frequently a few grass species that were tall and retained green grass during the dry season, whereas high density grazers were generalists feeders, grazing more grass species and tolerating a wide range of grass phenological stages, including completely brown grass. Accordingly, the breadth in acceptance to grass resources could explain the differences in density attained by different grazers occupying the same landscape.
2. The overlap in acceptance of grass species as well as in diet composition decreased from early to late dry season. During the late dry season of severe food limitations the diet of low density grazer sable became more diverse and dominated by grass species that occurred in lower availability than the grass species that supported the populations of high density grazers. This suggests that the density attained by each grazer is at some extent determined by the abundance of the grass species most contributing to the diet during critical periods.
3. Results showed high overlap between low density and high density grazers at the grass species and grass features levels. However, the narrower food niche of sable than buffalo and zebra at both levels indicates that sable are vulnerable to competition from more common grazers. Sable are also more vulnerable to the shrinking availability of food resources as the dry season advances than abundant grazers with broader tolerances to grass resources.

In Chapter 2 I investigated whether resource partitioning and coexistence occurred because the grazers were ecologically separated by using different habitat types as previously suggested (Lamprey 1963; Jarman and Sinclair 1979). It has been suggested that low density species use a narrow range of habitats than abundant species

(Brown 1984; Rosenzweig and Lomolino 1997) or use habitats of limited availability (Seagle and McCraken 1986; Gaston and Kunin 1997), whereas body size theory suggests that smaller herbivores require higher quality food than larger herbivores (Bell 1970; Jarman 1974). Based on these foundations, I hypothesized that the low density and smaller sable will be a habitat specialist and be more precise in habitat use than buffalo and zebra, by restricting foraging to habitat patches retaining green grass during the dry season such as bottomlands and areas with high woody vegetation cover, whereas zebra and buffalo will be more tolerant of the widely available brown grass, hence forage in habitats with a broader range of woody vegetation cover and catena positions.

The habitats used by each grazer reported in this study had been reported previously (Estes and Estes 1974; Smuts 1975; Magome 1991; Funston et al. 1994; Davidson 2002; Ryan et al. 2006; Parrini 2006). However, the novel contribution of this study is that low density and high density grazers do not differ in the range of habitat features prevailing on areas used. Sable showed similarities with buffalo or zebra in the range of woody vegetation cover, catena position and grassland height prevailing on foraging areas. This finding suggests that differences between grazers in regional density are not explained by differences in habitat breadth on foraging areas. At the broader landscape, sable and zebra appeared more narrowly selective than buffalo, which showed no preference for specific landscape type. The limitation of this Chapter was the lack of data on relative availability of different habitat structures in the study area. This prevented an assessment of potential differences in habitat selection between low density and high density grazers.

In Chapter 3 I assessed distinctions in patterns of home range use between low density and high density grazers. The use of space by large herbivores is partly influenced by the quantity and quality of food. However, how much food is perceived and used is determined by feeding specialization (Bell 1970), body size (Bell 1970; Prins and Olff 1998; Ritchie and Olff 1999), group size (Fryxell 1995) and digestive system (Illius and Gordon 1992). Based on the relationships between resource specialization and patterns of species abundance (Brown 1984; Rosenzweig and Lomolino 1997) and on the influence of body size and group size on the metabolic requirements of the herd (Owen-Smith 1988), hence on resources needed to meet the needs of animals in herds, I

hypothesized that: 1) the core grazing areas for the low density sable should consist of smaller discrete patches than the core areas used by buffalo or zebra; 2) during the wet season of food abundance the resource requirements of the herd of the specialist herbivore sable will be met in a smaller area than buffalo and zebra. However, during the critical dry season resources for sable will become sparser; hence sable will move widely and spread use over a larger home range than the similarly sized generalist feeder zebra; 3) feeding selectively on plant parts of high quality, sable are more efficient in obtaining the energy from the forage than the generalist grazers zebra and buffalo. Therefore, the intensity of metabolic use of space by sable will be higher than by zebra and buffalo.

The results of Chapter 3 showed the following previously undocumented information:

1. During the wet season when food and water were abundant, the sable herd showed intense use of a small section of the range and higher flow of energy from forage to herbivore biomass than buffalo and zebra, which used home range more evenly. However, when resources required by sable were limiting during a severe dry season, the sable herd became less precise in the use of the range and the intensity of metabolic use of space by sable became lower than by buffalo and zebra herds.
2. Although sable and buffalo herds increased range size from the wet to the dry season as expected from previous studies (Funston et al. 1994; Ryan et al. 2006; Owen-Smith and Cain 2007), the magnitude of the increase in range size was greater for sable than for buffalo, while space use by zebra appeared not influenced by seasonal variations in resources and habitat conditions. This shows that the dry season was a more stressful period for sable than for other grazers, with wider movements reflecting search for specific resources that became sparser with the advance of the season. The generalist grazers, buffalo and zebra, appeared less stressed by the seasonal changes in resources, suggesting that they were supported by resources that were abundant and widespread during different stages of the dry season.

In Chapter 4 I investigated competitive interactions between low density and high density grazers in the use of space. Because low density species have lower competitive ability than high density species (Hanski 1983; Gaston and Kunin 1997), less common prey species are proportionally more affected by apparent competition than abundant species (Owen-Smith and Mills 2008) and differences in body size influence the degree of competition or facilitation among co-existing grazers (Vesey-FitzGerald 1960; Bell 1970; Prins and Olff 1998), I predicted that: 1) the low density and declining species sable, will concentrate use of space on the sections of the landscape infrequently used by buffalo and zebra to reduce competition for resources and/or predation risk, and 2) being smaller, sable will benefit from grazing by the larger grazer buffalo.

In this chapter the main finding is that:

1. Core grazing areas for the low density sable were separated from areas of concentrated grazing by high density grazers. The low density sable vacated areas that were being heavily grazed by buffalo. Sable did not benefit from grazing by buffalo, suggesting that difference in body size between the two grazers is too small for facilitation to occur. The avoidance by sable of areas grazed by buffalo and the absence of facilitation, suggest that over the long term buffalo might have contributed to the sable decline. What remained unclear is whether the mechanism that governed spatial separation was avoidance of competition, predation or both.

The failure of the sable population to recover from the decline despite superabundance of food resources for a small population suggests that the quality of the diet obtained during critical periods of the year could be low; otherwise the factors limiting population recovery are not related to food resources. In Chapter 5, using faecal indicators of diet quality, I investigated whether nutritional limitations might be restricting population recovery. Based on findings from previous studies addressing factors regulating populations of free ranging herbivores (eg. Sinclair and Arcese 1995; Mduma et al. 1999), I hypothesized that if the KNP sable population was limited by food quality, during the dry season faecal crude protein should be below the levels of faecal crude protein for sable populations that are thriving elsewhere and than faecal protein

levels for grazers that are numerically more abundant in the KNP, including buffalo and zebra.

Results showed that faecal crude protein levels on sable of the KNP varied around the crudely estimated minimum levels for maintenance, but were lower than levels for sable populations that are thriving elsewhere, and similar to levels for the larger ruminant buffalo and to faecal protein levels for the similarly-sized wildebeest population, which is numerically more abundant in the KNP. This suggests that nutritional limitations might indirectly be restricting sable recovery, through reduction in areas occupied by sable that retain high forage quality.

Overall, this study showed that the dry season was a more stressful period to sable than to the more common grazers. Sable showed larger seasonal variation in home range, more drastic changes in diet composition between seasons and more severe decline in faecal indices of diet quality than buffalo and zebra as the dry season progressed. These findings on sable spatial, foraging and nutritional ecology indicate that sable are potentially more restricted than other grazers in number and distribution by the seasonal and spatial variations in the prevalence of critical resources. Results showed overlap and potential for competition between grazers at small spatial scales of resource use such as habitat types, grass species and grass features, particularly between sable and buffalo. Resource partitioning was apparent through use of distinct sections of the landscape as core grazing areas. Nevertheless, the spatial separation documented in this study appears to be a result of avoidance of competition and/or predation risk. Home ranges used by sable did not differ from those used by buffalo in the prevailing habitat features, which suggests that the spatial separation reported in this study was not a result of distinct habitat preference. However, extensive areas that were occupied by sable, buffalo and zebra prior to the sable decline currently represent gaps of non-use by sable, but remain with high concentrations of buffalo and zebra. This might suggest that apart from potential avoidance of competitors and predators by sable, some fundamental elements of the habitat might have changed over time, probably due to the persistent dry conditions, reducing the suitability of the habitats for sable while remaining suitable for grazers with broader tolerances to food resources.

Management implications

According to the KNP hierarchy objectives, the management for system integrity and maintenance of biodiversity should take precedence over species management (Braack 1997). However, according do the threatened biota objective (Braack 1997), the extinction of species should be prevented by allocating resources to particular species that are under some threat category globally or regionally. The factors limiting the sable population in the KNP appear to be the deterioration of habitat conditions and forage resources associated with the persistence of annual rainfall below long term average and decrease in dry season rainfall (Ogutu and Owen-Smith 2003; Owen-Smith and Ogutu 2003). These climatic conditions reduce the availability of green forage during the dry season and potentially the biomass of food species favoured by sable such as *P.maximum*, *T. triandra* and *H.contortus*. The resulting poor nutrition weakens herbivores and increases their vulnerability to predation (Owen-Smith and Ogutu 2003). The high degree of food specialization at the grass features and grass species level documented in this study limits at a great extent the range of interventions that can be taken to improve conditions for sable and ensure long-term conservation of this species under high variability in rainfall associated with climate change. However, sable have survived through many droughts in the past and recovering during years with above average rainfall (Owen-Smith and Ogutu 2003). Therefore, the current lack of recovery suggests that some fundamental element of the habitat might have changed, preventing sable population size from increasing during years with high rainfall. Inter-specific interactions through competition or apparent competition could also be playing a role in the lack of recovery. Sable appeared to occupy areas of the landscape that were less frequently used by buffalo or zebra. Accordingly, I suggest that management should be directed at reducing the overlap in core distribution range between sable and the more common grazers. Therefore:

- The closure of artificial water points, including dams, within the core sable range is a management action that will reduce the local abundance of water dependent grazers, thereby reduce potential for competition for resources and predation pressure to sable through apparent competition. Besides creating regions with low

predation risk where sable could survive, this strategic closure of water points will reduce grazing pressure and prevent further habitat deterioration during periods of drought. Sable will cope with limited water availability resulting from the closure of artificial water points because they are less water dependent than other grazers like buffalo, remaining without drinking for about 3 days when water is not available within the core range during the late dry season (Owen-Smith and Cain 2007), although not very different from zebra, which appear to potentially remain about 2 days without drinking (Cain and Owen-Smith, in prep.).

- Burning of the vegetation during the late dry season generally increases the severity of food limitations for grazers by removing most of the grass biomass during a period without rainfall and with the remaining soil moisture not enough to sustain grass regrowth. As a consequence of lack of grass regrowth, sable, buffalo and zebra did not use burnt areas before the first wet season rains promoted grass regrowth. Accordingly, burns of sable core range should be avoided during the late dry season. Grass regrowth on areas burnt during the early dry season has been reported to reduce nutritional deficiencies in sable during critical periods (Parrini and Owen-Smith, submitted). However, when I conducted this study (2006 and 2007), in Punda Maria there were no areas burnt during the early dry season to assess the availability of grass regrowth as well as the relative use of these areas by grazers.
- Information on calf production and survival need to be collected from sable herds across the park. This data will indicate the availability of forage resources of adequate quality for reproduction and survival of offspring.

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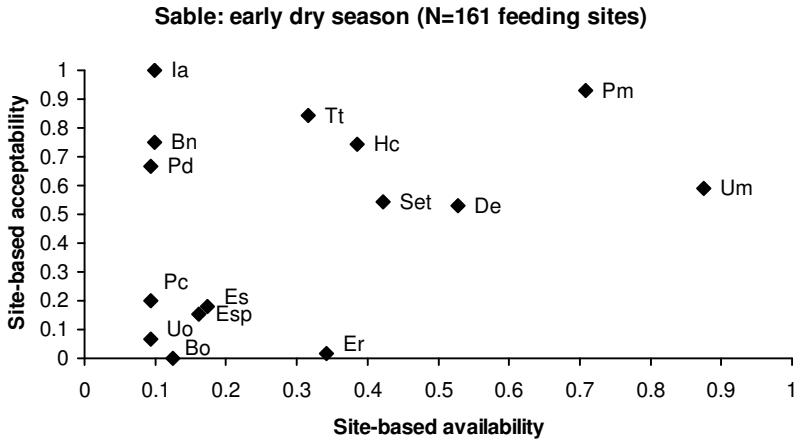
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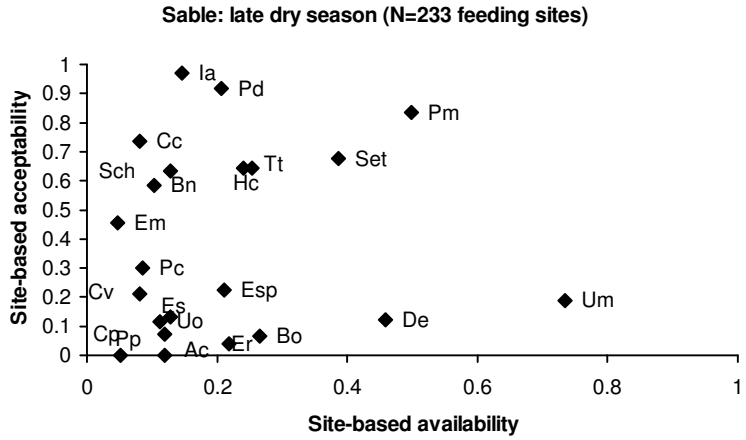
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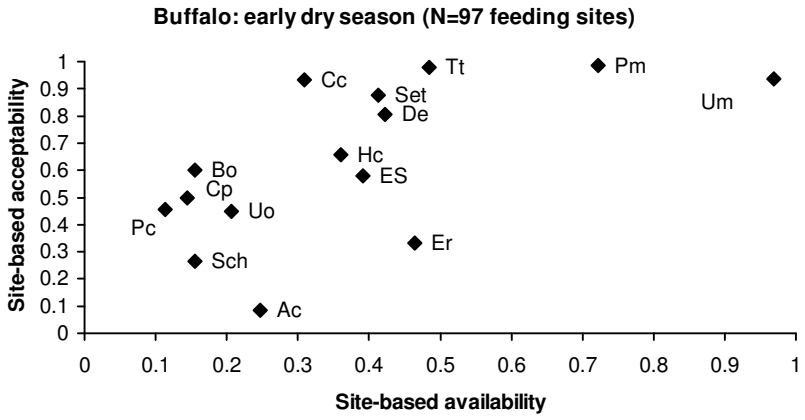
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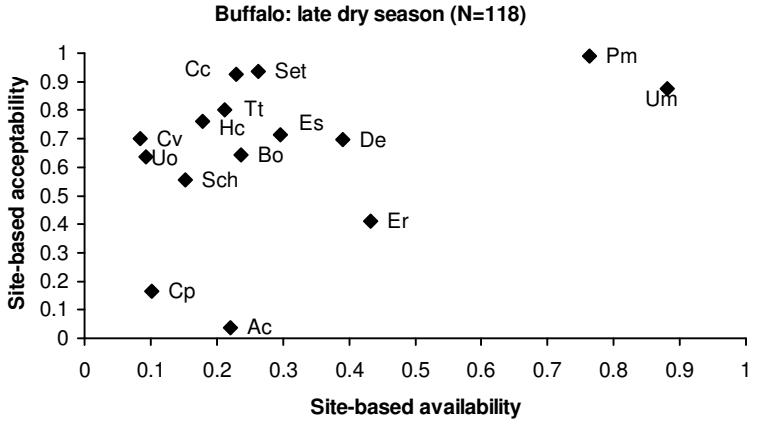
APPENDICES

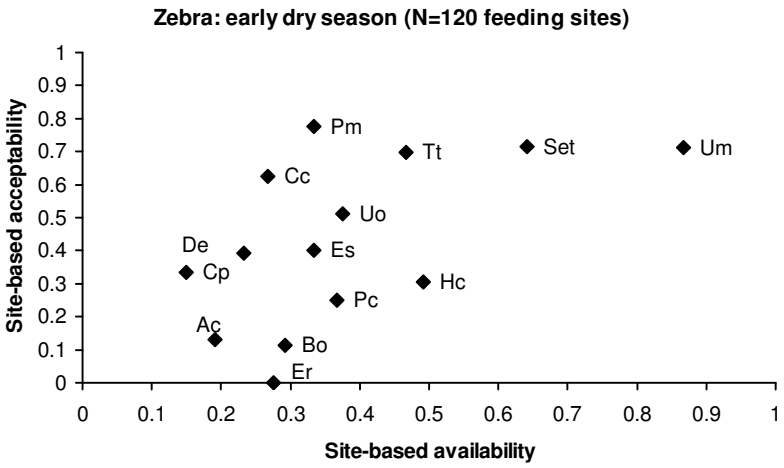
Appendix 1. Availability and acceptability of grass species on feeding sites during different seasons

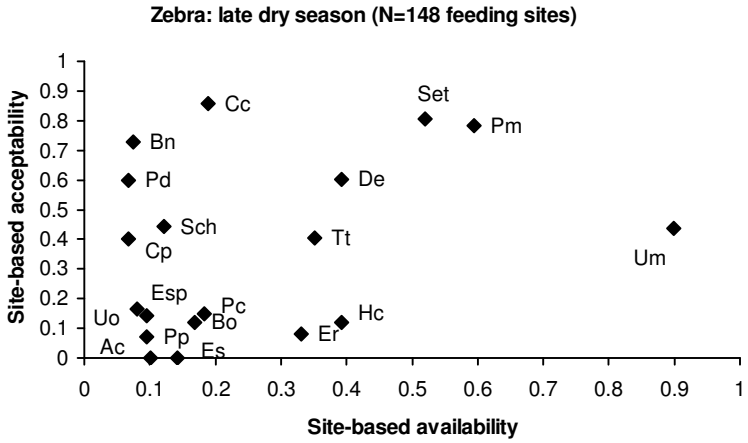




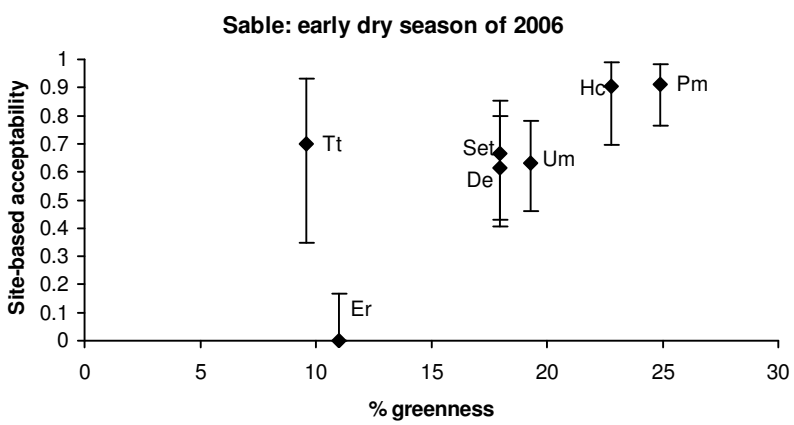


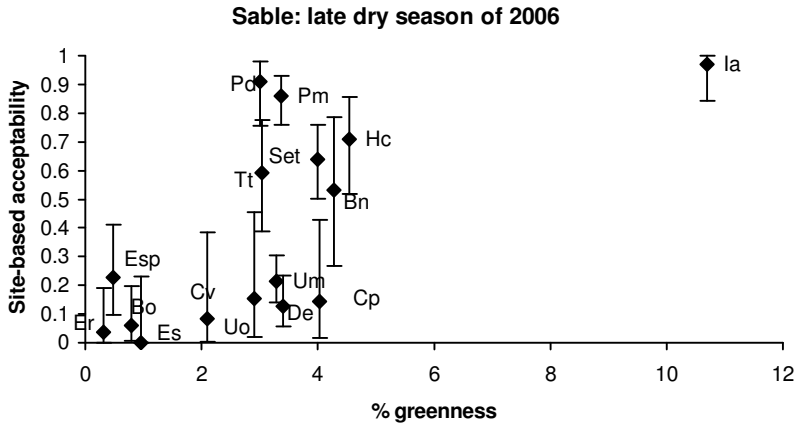


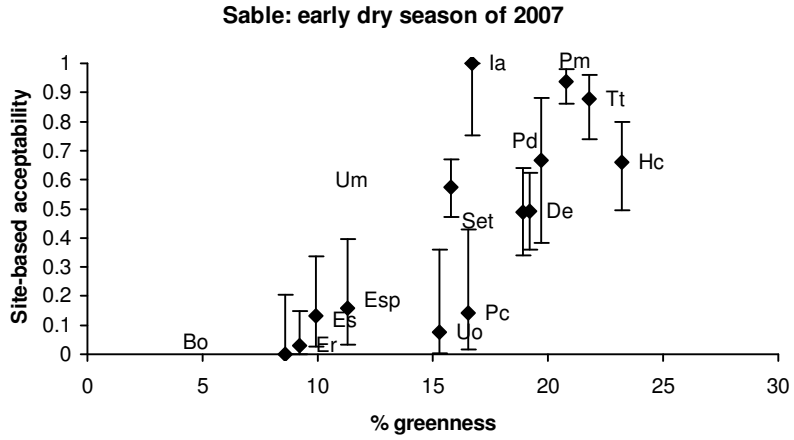

Zebra: early dry season (N=120 feeding sites)
Site-based acceptability
Site-based availability
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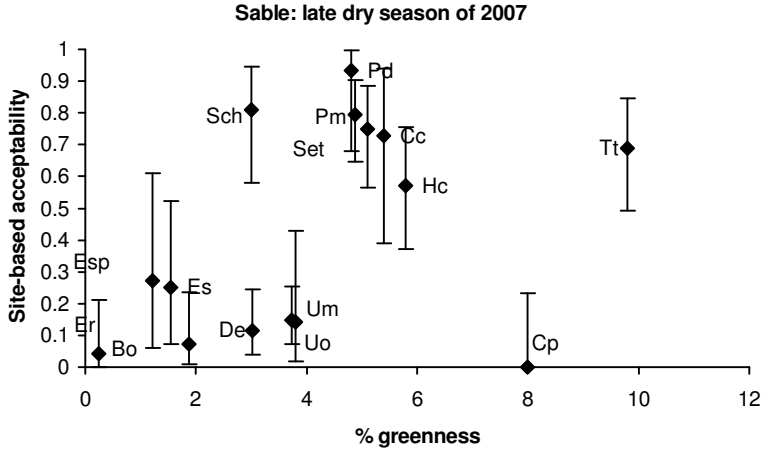

Zebra: late dry season (N=148 feeding sites)
Site-based acceptability
Site-based availability
Cc
Set
Pm
Bn
Pd
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Esp
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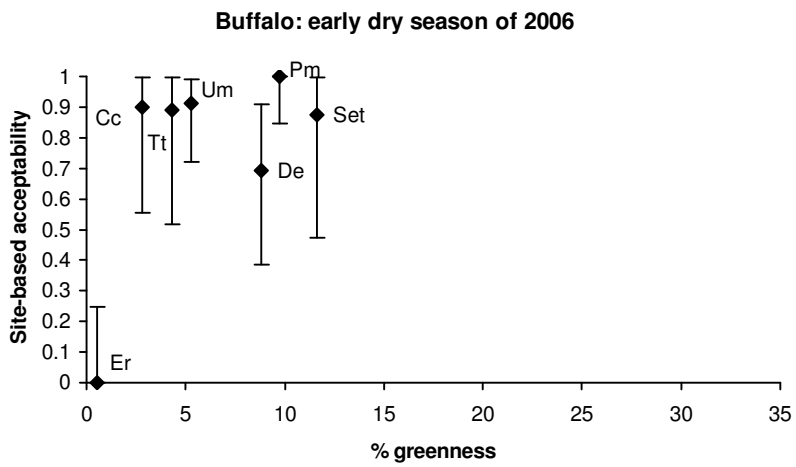
Appendix 2. Acceptability of grass species by sable, buffalo and zebra in relation to the proportion of green leaves retained by each grass species during the early and late dry season of 2006 and 2007. Vertical lines indicate 95% binomial confidence intervals.

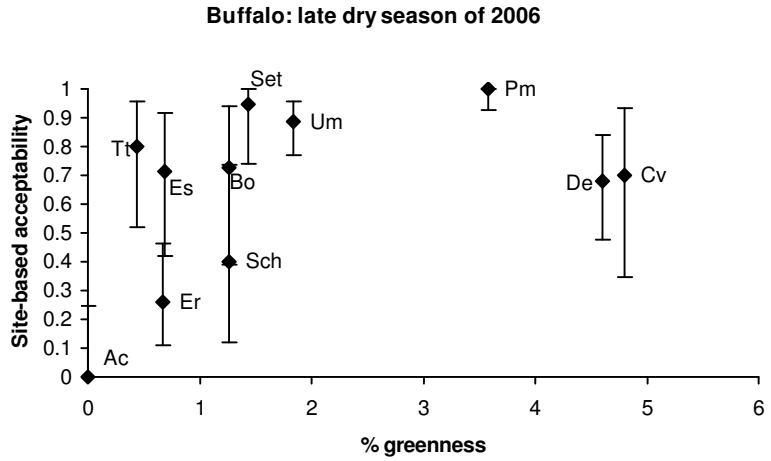


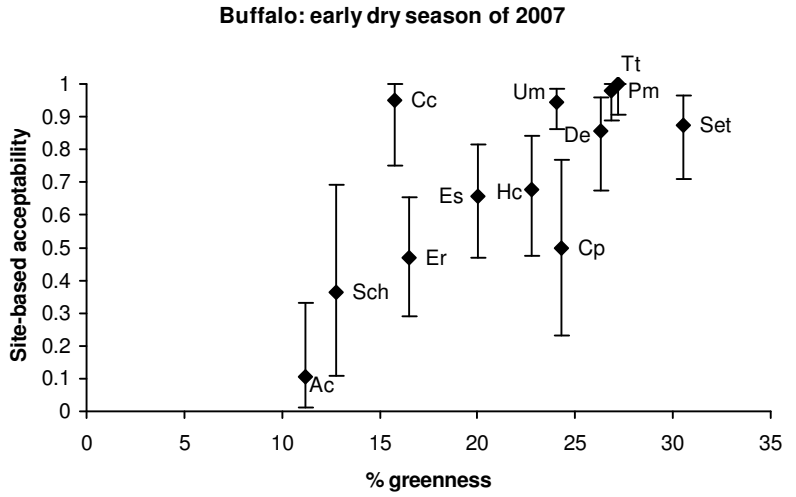


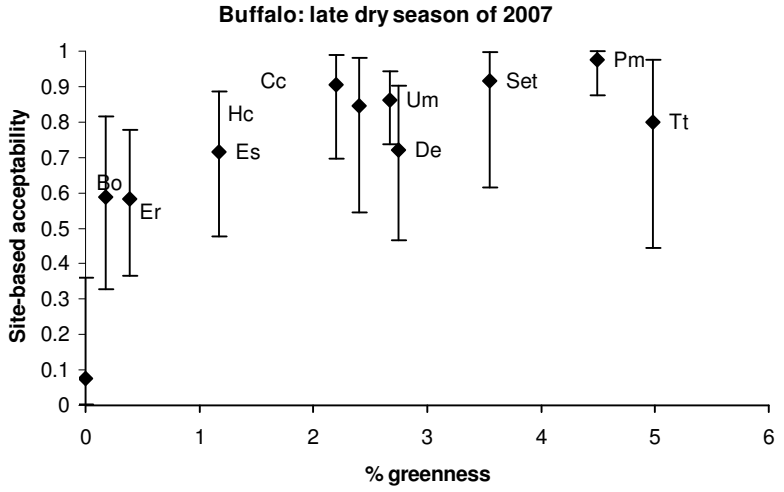


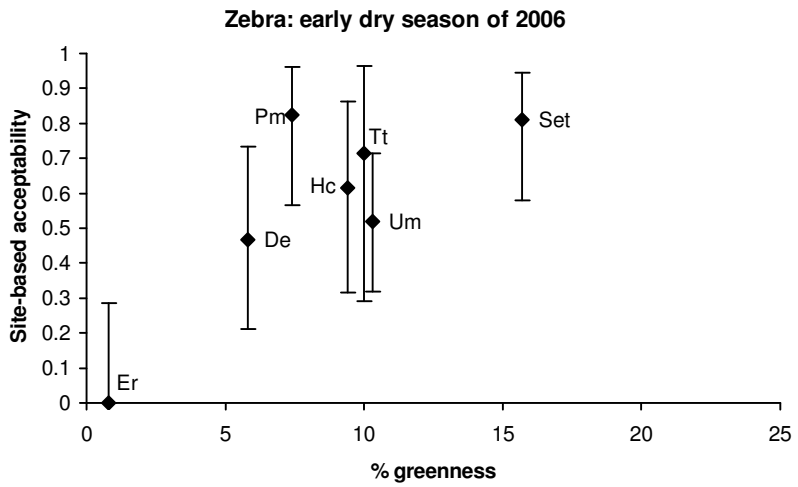


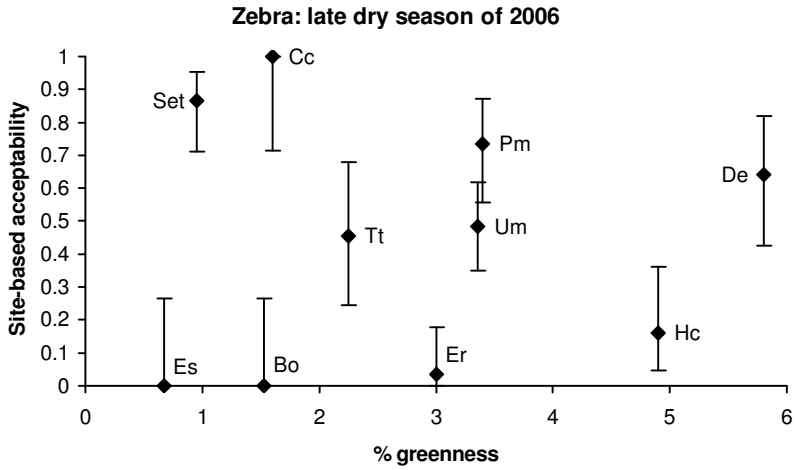

Buffalo: early dry season of 2006
Site-based acceptability
% greenness
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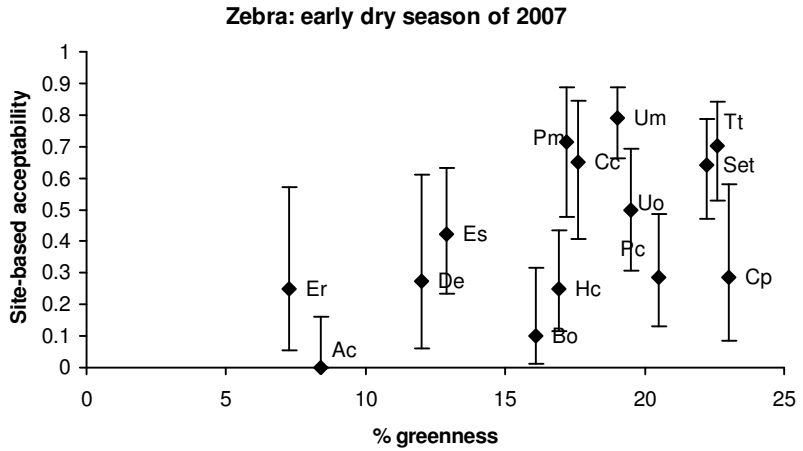

Buffalo: late dry season of 2006
Site-based acceptability
% greenness
Set
Pm
Tt
Um
Es
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Cv
Sch
Er
Ac

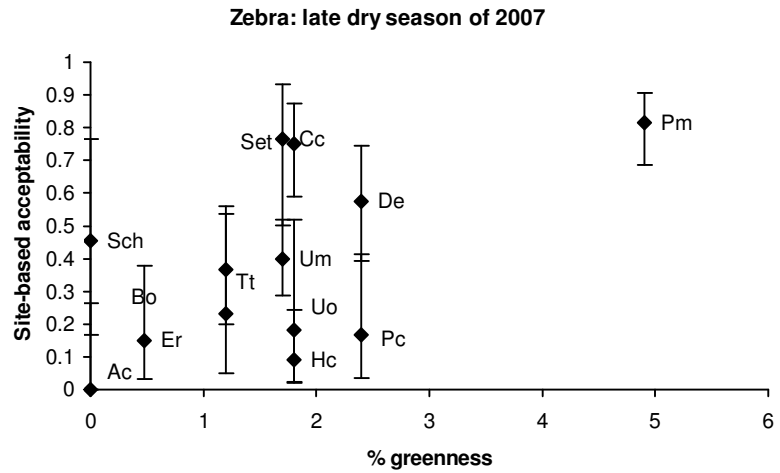

Buffalo: early dry season of 2007
Site-based acceptability
% greenness
Tt
Cc
Um
Pm
De
Set
Es
Hc
Er
Cp
Sch
Ac


Buffalo: late dry season of 2007
Site-based acceptability
% greenness
Pm
Cc
Set
Hc
Um
Tt
Es
De
Bo
Er


Zebra: early dry season of 2006
Site-based acceptability
% greenness
Er
De
Pm
Hc
Tt
Um
Set


Zebra: late dry season of 2006
Site-based acceptability
% greenness
Es
Set
Bo
Cc
Tt
Er
Pm
Um
Hc
De


Zebra: early dry season of 2007
Site-based acceptability
% greenness
Er
Ac
De
Es
Pm
Cc
Hc
Bo
Um
Uo
Pc
Tt
Set
Cp


Zebra: late dry season of 2007
Site-based acceptability
% greenness
Ac
Sch
Bo
Er
Tt
Set
Cc
Um
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Hc
De
Pc
Pm

Appendix 3a. Diet contribution of grass species to the diet (mean ± SE) during dry season of 2006, estimated as the proportion of epidermis fragments of each grass species on faecal samples

Early dry season - 2006				Late dry season - 2006		
	Sable (N=20)	Buffalo (N=13)	Zebra (N=19)	Sable (N=29)	Buffalo (N=23)	Zebra (N=24)
Panicum maximum	0.22±0.03	0.24±0.03	0.14±0.02	0.24±0.03	0.28±0.03	0.14±0.02
Heteropogon contortus	0.25±0.03	0.03±0.008	0.03±0.01	0.03±0.007	0.004±0.002	0.02±0.004
Digitaria eriantha	0.10±0.01	0.09±0.01	0.09±0.03	0.02±0.004	0.11±0.01	0.16±0.02
Urochloa mosambicensis	0.10±0.006	0.18±0.03	0.08±0.02	0.004±0.002	0.20±0.03	0.18±0.02
Setaria incrassata	0.14 ±0.01	0.14±0.03	0.46±0.04	0.26±0.03	0.17±0.03	0.37±0.05
Themeda triandra	0.10±0.01	0.11±0.02	0.09±0.02	0.02±0.005	0.06±0.009	0.06±0.008
Brachiaria nigropedata	0.03±0.007	0.009±0.004	0.05±0.02	0.006±0.002	0.02±0.004	0.02±0.006
Ischaemum afrum	0.02±0.007	0.00	0.01±0.004	0.20±0.03	0.00	0.00
Cenchrus ciliaris	0.01±0.003	0.16±0.03	0.02±0.006	0.00	0.04±0.006	0.03±0.008
Schmidtia pappophoroides	-		0.00	0.00	0.00	0.00
Panicum deustum	-		0.01±0.004	0.15±0.02	0.02±0.006	0.00
Chloris virgata				0.01±0.002	0.04±0.008	0.00
Dicots	0.01±0.005	0.02±0.004	0.01±0.007	0.03±0.006	0.04±0.006	0.02±0.003

Appendix 3b. Diet contribution of grass species to the diet (mean ± SE) during dry season of 2007, estimated as the proportion of epidermis fragments of each grass species on faecal samples

	Early dry season - 2007			Late dry season - 2007		
	Sable (N=27)	Buffalo (N=26)	Zebra (N=26)	Sable (N=14)	Buffalo (N=17)	Zebra (N=17)
Panicum maximum	0.30±0.02	0.17±0.02	0.14±0.01	0.19±0.02	0.24±0.03	0.14±0.02
Themeda triandra	0.19±0.02	0.14±0.02	0.09±0.02	0.18±0.04	0.07±0.02	0.06±0.009
Urochloa mosambicensis	0.11±0.01	0.24±0.03	0.08±0.02	0.03±0.01	0.26±0.04	0.18±0.02
Digitaria eriantha	0.06±0.005	0.09±0.01	0.09±0.03	0.03±0.01	0.08±0.02	0.16±0.02
Ischaemum afrum	0.08±0.02	0.00	0.01±0.004	0.007±0.004	0.00	0.00
Heteropogon contortus	0.05±0.007	0.05±0.01	0.03±0.01	0.02±0.008	0.02±0.004	0.02±0.004
Setaria incrassata	0.16±0.01	0.22±0.03	0.46±0.04	0.32±0.03	0.14±0.03	0.38±0.05
Panicum deustum	0.005±0.003	0.00	0.01±0.01	0.03±0.01	0.00	0.00
Brachiaria nigropedata	0.002±0.002	0.007±0.002	0.05±0.02	0.01±0.006	0.003±0.002	0.02±0.006
Cenchrus ciliaris	0.003±0.001	0.07±0.02	0.02±0.006	0.003±0.003	0.16±0.03	0.03±0.008
Schmidtia pappophoroides	0.002±0.001	0.00	0.00	0.16±0.03	0.00	0.00
Dicots	0.03±0.004	0.006±0.003	0.01±0.001	0.03±0.008	0.04±0.007	0.02±0.003

Appendix 4. Performance of GPS-GSM collars fitted on animals in Punda Maria in 2006 and 2007

Species	Collar ID	Placement	Status	Duration (months)
Sable	AM 143	22/05/2006	Last signal 18/12/07	19 months
Sable	AM 146	23/05/2006	Animal died on the 11/02/07	8 months
Sable	AM 149	23/05/2006	Last signal 15/07/07	14 months
Sable	AM 279	18/06/2007	Last signal 09/01/08	6 months
Buffalo	AM 150	23/05/2006	Last signal 11/03/07	9 months
Buffalo	AM 152	23/05/2006	Still functioning 08/04/09	> 34 months
Buffalo	AM278	18/06/2007	Last signal 14/11/07	5 months
Zebra	AM 141	23/05/2006	Last signal 29/09/07	16 months
Zebra	AM 142	23/05/2006	Last signal 6/11/08	17 months
Zebra	AM 145	22/05/2006	Last signal 16/09/06	3 months
Zebra	AM 147	22/05/2006	Last signal 07/07/07	14 months
Zebra	AM 277	18/06/2007	Still functioning 08/04/09	> 21 months
Zebra	AM 280	18/06/2007	Last signal 15/03/08	9 months