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2011-02-25
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HABITAT AND FORAGE DEPENDENCY OF SABLE ANTELOPE (*HIPPOTRAGUS NIGER*) IN THE PRETORIUS KOP REGION OF THE KRUGER NATIONAL PARK

Elizabeth le Roux

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Masters in Science

Johannesburg, 2010

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Masters in Science 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)

Date 26/08/2010

ABSTRACT

The distribution of animals across landscapes is driven by processes operating across a multitude of spatial scales. In essence, the spatial and temporal variability in nutrient availability characteristic of savanna ecosystems, superimposed on the spatial pattern of the distribution of predator risky areas, govern the herbivore foraging response. Thus studying the foraging behaviour of individual herds is a fundamental link in ultimately understanding demographic responses of entire populations. This study formed part of a broader research programme managed by the Centre for African Ecology (CAE) specifically focusing on the decline of rare antelope species in the Kruger National Park (KNP). Ultimately the aim was to contribute towards identifying the causal factors of a recent decline in sable antelope (*Hippotragus niger*) in the KNP. Specifically, this research was designed to span two levels of selection. Firstly to identify the forage resources that sable depend on by investigating the acceptability and dietary contribution of grass species and by examining the way in which the selection of particular species is influenced by changes in grass phenology and structure. In addition, with this study I attempted to describe the characteristics of sable foraging habitat and to identify the landscape features that distinguish areas suitable for feeding from those areas that remain unaccepted for feeding. I predicted at the level of the grass species that factors influencing the distribution and concentrations of nutrients between species and between tufts of the same species should influence the relative acceptance of a species by sable. Similarly, I expected sable's use of foraging areas and feeding sites to be governed largely by nutrient distributions across the landscape, but to be restricted within safe areas

with high visibility where the probability of the timely detection of predators is high. Four herds of sable were fitted with GPS/GSM collars and tracked from the early dry season to the start of the wet season for a total of two years during which characteristics of the foraging area and forage selection were recorded. The dietary contribution and the attributes of the foraging area remained largely descriptive and only involved analysis of seasonal and herd differences. Grass species and phenological and structural features influencing species acceptance were analysed using generalised linear models (GLM). A similar analysis technique was employed to identify the landscape attributes that played an important role in the distinction between feeding and non-feeding sites. The grass species that were consistently highly accepted by all four herds and contributed considerable proportions to the diet of each herd, included *Panicum maximum*, *Heteropogon contortus*, *Hyperthelia dissoluta* and *Setaria sphacelata*. Sable increased the dietary contribution of *P. maximum* and *H. dissoluta* during the dry season by feeding more frequently in areas where it was abundantly available. Regardless of the identity of the grass species, sable were more likely to feed from tufts that were green relative to the greenness available in that season. Sable also adjusted their acceptance of grass species based on the height of the tuft and were more likely to feed from tufts greater than 20 cm in height. The foraging area was mostly located on upper catena positions and a lack of a dry season increase in the use of bottomlands suggested that nutrients were either not accumulating in bottomlands as expected, or that sable were not responding to an accumulation of nutrients. Sable foraged and fed readily in low to high shrub cover and showed no response to the increased predation risk that would be expected to be associated with increased shrub cover. Sable were more likely to feed in areas with a

relatively high tree canopy cover and more likely to feed in areas with a relatively green sward. However, sable still fed fairly frequently in open areas or areas with a predominantly brown sward. Overall, sable seemed unexpectedly tolerant of landscapes that would be predicted to range widely in nutrient distributions and forage quality as well as relative predation risk.

ACKNOWLEDGEMENTS

I am indebted to Prof Norman Owen-Smith. Thank you firstly for giving me the opportunity to have the time of my life. Thank you for sharing your knowledge and experience. I will value your influence throughout the rest of my career.

Big thanks go to all the office staff at Wits. Thank you for your help and support. I would like to thank the National Research Foundation for providing the funding that made this study possible.

Many people contributed to the success of this project. I am grateful to South African National Parks (SanParks) for the financial contribution to the study. To the many people at Scientific Services who provided logistical support and intellectual input. Thanks go to the veterinary team in Kruger National Park. Particular thanks goes to Dr Markus Hofmeyr, for always demonstrating a sincere involvement in the project and showing a keen interest in the progress.

To Mr Khutani Bulunga, your efforts extended beyond your duty of field ranger. My thanks are for your hard work but most of all for being my friend and my teacher. I will always strive to know the signs of the veld as you do.

To Michelle Hofmeyr for being my soundboard during trying times and to the entire Hofmeyr family for always making me feel welcome in their home.

To my colleagues at Wits, Jo Chirima, Valerio Machandza, Francesca Parrini, Jo Shaw, Tracy-Lee Robinson and Gaby Teren among others. Everything is easier if you don't have to go through it alone. Thank you for your encouragement, your constructive comments and your pep talks. Thanks to Francesca for proofreading some of my work.

My heartfelt thanks go to Rob Guldemond. You have been my strength and my inspiration. Thank you for your insights, advice and encouragement but most of all your constant interest. Your part in my success is immeasurable.

I am in infinite debt to my parents for their continual love and encouragement. To my mother who always believed in me. A special thanks go to my father who has supported me financially throughout. And lastly, my sincerest thanks go to numerous family and friends, especially my brothers, who were always willing to listen to my frustrations and ready to provide some diversions when needed.

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CHAPTER 1

GENERAL INTRODUCTION

THE NEED FOR THE STUDY

Facets of animal behaviour ranging from individual foraging responses to predator avoidance strategies affect habitat selection across many levels of ecological resolution, creating a complex ecological pattern which ultimately influences how animals distribute themselves across the landscape. In this way the behaviour of individual animals are linked to the performance of the population as a whole.

My research was aimed at gaining a better understanding of the dependence of sable antelope (*Hippotragus niger*) on forage resources and habitat in the Kruger National Park, South Africa. Sable antelope have declined considerably in numbers in the Kruger National Park (hereafter KNP), falling from in excess of 2000 individuals in 1986 to a recent estimate of slightly more than 300 animals (I.J. Whyte, KNP Scientific Services Report, 2006). The decline was not limited to sable but occurred across populations of several other rare antelope species in the park. As such my research forms part of a broader research programme initiated by the Centre for African Ecology (CAE) of the University of the Witwatersrand ultimately aimed at determining the potential causes of the decline in low density antelope species in the KNP.

The last complete census of the KNP was conducted in 1993 during which 221 sable antelope were counted in breeding herds in the southern section of the KNP, of

which 198 where found in the four census blocks across which the study area stretches (Numbi; Nwaswitshaka; Sithungwane; and Dabidabi) (KNP census records). Subsequently these censuses did not achieve total coverage of the KNP but during 1997 the count was again completed in the southern section of the park only and of the 139 breeding herd individuals located, 131 were found in the four census blocks of the study area. From 1998 the census technique was changed to sample counts during which only 22% coverage of the southern section was achieved with transect lines placed approximately 3.7 km apart (KNP census records). The sample sizes obtained with the sample counts technique proved inadequate and did not provide a reliable population size estimate for sable antelope. As a result the only recent estimate of sable population size is from ranger's records of 2006 within which only 45 individuals in breeding herds were recorded for the study area (I.J. Whyte, KNP Scientific Services Report, 2006). However, the inconsistency in the census methods followed prevents direct comparison and severely complicates interpretation and as such it is unclear how many sable remain.

The causal factors implicated in the changes in abundance of KNP ungulate species have been diverse. The drastic population crash experienced by roan antelope (*Hippotragus equinus*) in the north of KNP has been attributed to increased predation caused by an increase in predator numbers. The movement of predators into roan range was believed to be in response to an influx of other prey species which was in turn prompted by the provision of artificial water points (Harrington *et al.* 1999). This cause was unlikely to be the main reason behind the declines in sable populations occurring in

the south of the park as this is a relatively high rainfall area compared to the rest of the park and relatively few water points were added in this region (Gaylard *et al.* 2003).

The rare antelope decline has also been linked to rainfall deficits, possibly leading to habitat deterioration (Harrington *et al.* 1999). Sable are viewed as being very susceptible to drought conditions (Grant *et al.* 2002). Severe droughts were recorded during 1982-83 and 1991-92. Yet the decline in sable abundance only commenced four to five years after the first drought. Owen-Smith & Ogutu (2003) reported that during the period between 1988 and 1994, very little dry season rainfall was received. The sable decline coincided more closely with these years (Owen-Smith & Ogutu 2003), albeit later than the roan decline. Owen-Smith & Mills (2006) implicated an increase in vulnerability to predation brought about by the effects that such variability in dry season rainfall would have on the availability of food resources and the suitability of the habitat.

Although the conservation status of sable antelope is categorised as of least concern globally (IUCN 2009), the local decline in the KNP is of serious concern to park management. The Kruger National Park adopts a strategic adaptive management approach through which they adjust management practices in accordance with an improved understanding of system function, which can only be achieved through continued research. Consequently, such observable changes in species abundance should be investigated. As such this study is aimed at contributing towards discovering the drivers behind the decline of sable antelope in the KNP by characterising the forage resources that sable rely on for survival and identifying the habitat characteristics that renders an area suitable for feeding.

MAIN OBJECTIVES

- To identify the grass species that sable depend on and the changes in use associated with the progression of the dry season.
- To discover the structural and phenological characteristics associated with grass species that render them acceptable to sable.
- To describe the variation in the structural and phenological characteristics within grass species that would influence the' acceptability of the species to sable.
- To describe the characteristics of the habitats used by sable during times when they are likely to be foraging.
- To recognise the features of the landscape that deter sable from feeding in a particular area and the change in the effect of these features as conditions turn drier.
- To determine the influence of the structural and phenological characteristics of the grass layer and the composition of the sward on the suitability of a feeding patch to sable.

LITERATURE REVIEW

Studies on food selection are confounded by the hierarchical ordering of selection processes (Senft *et al.* 1987). Patterns of selection are driven by different sets of selection criteria at different spatial scales all of which are influenced by both ecological and physiological factors. A further complication lies in the complex nature of savanna

systems where the quality and quantity of food resources vary spatially and change temporally. High quality forage is distributed sparsely and requires substantial amounts of time and energy to obtain, whereas low quality forage is in abundance yet requires substantial amounts of time and energy to digest. Diet selection is also constrained by non-foraging decisions operating at larger scales. The need to acquire sufficient forage yet simultaneously avoid predation ultimately determines the distribution of animals across landscapes (Seagle & McNaughton 1992).

Essentially selection should be based on the balance between the nutritional and structural content of the forage. The slowly digestible fibrous material dilutes the nutritious cell content and prolongs retention time which delays further ingestion. The foraging herbivore is thus faced with the dual objectives of needing to augment its nutrient acquisition while simultaneously reducing fibre intake. The particular tactic an animal can adopt in order to achieve this depends on three main factors, namely body size, the animal's digestive constraints and its relative selective capacity (Owen-Smith 1982).

Larger animals require less food per unit body mass and are therefore able to tolerate slowly digestible foods (Bell 1970, Jarman 1974, Owen-Smith 1988). Ruminants have a greater capacity for fibre digestion compared to non-ruminants, yet are limited by gut retention time and thus require food of greater quality than similar sized non-ruminants (Illius & Gordon 1992).

However, the intake of sufficient forage quality may be mediated through selective consumption of particular plants and/or plant parts. The extent to which animals are capable of such selective foraging is likely to depend on their muzzle

structure (Owen-Smith 1982). Narrow mouth dimensions may promote selection of discrete plant components from amongst nutritionally inferior material.

Stems contain considerably higher levels of structural carbohydrates compared to leaves and animals would therefore be expected to feed from stems only when the absence of leaves compels them to do so. The preference of leaves above stems has been demonstrated convincingly (Bell 1970, Duncan 1975, O'Reagain & Schwartz 1995). An herbivore would additionally be able to maintain a higher intake rate when foraging in swards where stem density is low (Drescher *et al.* 2006).

At a broader scale, selection may operate across the landscape where aspects such as soil composition, topography and vegetation structure may influence nutrient distributions. The geological template determines the characteristics of the soil which in turn determine the vegetation pattern (Venter *et al.* 2003). Granitic rock gives rise to soils with a high sand content which are prone to leaching and therefore considered to be generally deficient in nutrients, especially in areas with high rainfall (Bell 1984). Conversely, basaltic areas give rise to nutrient rich, fertile soils (Venter *et al.* 2003). Topography also affects grass quality through its influence on the distribution of nutrients. Nutrients together with water move down a slope gradient and accumulate in bottomland areas. This promotes the retention of green foliage, yet also stimulates a build up of structural carbohydrates which ultimately dilute the higher nutrient density found there (Bell 1970, McNaughton 1985, Scoones 1995, Scholes *et al.* 2003). Finally, woody vegetation contributes to the heterogeneous arrangement of nutrients across the landscape through a process referred to as the nutrient pump mechanism. Nutrient stocks occurring outside the tree canopy and in soil strata too deep for grass roots to access are

brought to the surface through absorption by tree roots. These nutrients are subsequently concentrated underneath the tree canopy through litterfall and in this manner made available for absorption by grass roots (Scholes 1990).

Forage digestibility is also expected to depend on plant phenology (Heady 1964, Fryxell 1991, Owen-Smith 1982, Georgiadis & McNaughton 1990) and an animal should adjust its foraging behaviour in accordance with the temporal changes in food quality. As a plant matures, it gradually accumulates structural tissue which would impose digestion constraints on the foraging herbivore (Van Soest 1987). As such, the herbivore is expected to focus its foraging activities on young fresh growth and avoid senescent material when fresh growth is available. Similarly, the herbivore should therefore also benefit from foraging in areas where a prevalence of fresh green grass is available. However, fresh growth is often short and thus offers limited amounts of forage which may force the animal to consume more established tufts and therefore forage in areas with a tall grass sward.

Nutritional variation between grass species has also been demonstrated (Georgiadis & McNaughton 1990) and subsequent preference for particular species above others has similarly been confirmed (Bodenstein *et al.* 2000, Macandza *et al.* 2004). Ben-Shahar & Coe (1992) found that the variation in nutrient content between ten different grass species was less influenced by soil nutrient levels and more by the intrinsic differences between species.

Nevertheless, factors influencing the composition of the herbaceous layer may play a role in determining grazing distributions at a larger scale. *Panicum maximum*, a grass species shown to be highly palatable to cattle, has been shown to grow

preferentially in shady conditions (Van Oudtshoorn 1999) and is thus expected to closely follow tree distribution. *P. maximum* maintain high levels of crude protein whether growing on relatively fertile or infertile soils and this has been attributed to the nutrient enhancing effect of the trees under which they grow (Downing 1979).

Morphological and structural differences between grass species may additionally influence the rate of ingestion and nutrient assimilation and ultimately determine species specific preferences (O'Reagain 1993).

Grazing distribution patterns are further shaped by grazers' response to the risk of predation. In risky habitats, animals are expected to reduce their foraging behaviour and increase their vigilance behaviour despite high food availability and/or quality (Sih 1980). The distribution of such risky environments is likely to be influenced by aspects such as topography and vegetation cover. Vegetation cover and topographical barriers that interfere with visibility would be expected to prevent timely predator detection and increase predation risk (Elliot *et al.* 1977). An animal's reluctance to utilise risky areas is also expected to have a seasonal component. During the limiting season when food resources become scarce elsewhere, animals may be forced to forage in areas with high predation risk (Sinclair & Arcese 1995).

According to the results of a quantitative analysis on muzzle shape in ungulates performed by Gordon & Illius (1988), sable have relatively narrow mouth dimensions compared to other ruminants of similar body size. Consequently, sable are likely to display high levels of selectivity and this has indeed been demonstrated by several authors at levels ranging from the forage species, the tuft and the plant part (Wilson &

Hirst 1977; Grobler 1981; Skinner & Smithers 1990; Magome 1991). Sable have been found to feed preferentially on fresh growth (Estes & Estes 1974, Sekulic 1981) spanning a height range of 4 – 40 cm (Grobler 1981, Gureja & Owen-Smith 2002, Parrini 2006). Previous studies on sable foraging behaviour have also indicated a preference for green leaves and an avoidance of stems (Grobler 1981, Parrini 2006) with the avoidance of stems being more pronounced during dry season months (Parrini 2006). Sable have also been shown to move into bottomland areas during the dry season to make use of the higher greenness retention associated with these areas (Jarman 1972, Estes & Estes 1974, Grobler 1981, Magome 1991). Furthermore, sable have been reported to utilise open savanna woodlands for foraging (Jarman 1972, Wilson & Hirst 1977, Grobler 1981, Sekulic 1981, Magome 1991, Parrini 2006), yet giant sable have been documented to leave the woodlands for the lowland grasslands during the dry season (Estes &Estes 1974).

STUDY AREA DESCRIPTION

The study was carried out in the Kruger National Park (KNP), a roughly 20 000 km^2 national park situated in the savanna biome in the lowveld region of north-eastern South Africa. The KNP is an elongated park (approximately 350 km from north to south) situated in a low-lying area (average elevation of 300 m above sea level) bordered by the Drakensberg Great Escarpment in the west and the Mozambique coastal plain in the east (Venter *et al.* 2003).

The study area was located in the south western section of the park (31°12′-31°24′E, 25°02′-25°13′S) in a region surrounding Pretorius Kop camp. This area was chosen based on an initial assumption that despite substantial declines of sable antelope throughout the entire KNP, the southern area represented more favourable conditions for the species compared to the rest of the park. The area is approximately 400 km^2 in extent and is bordered by the western boundary fence (Figure 1.1) which was erected in 1961 (Mabunda *et al.* 2003). The region is moderately undulating with elevations ranging from 450 m to 780 m above sea level (Venter 1990).

The study area is underlain predominantly by granitic parent material characterised by sandy soils (Venter *et al.* 2003). These soils are generally regarded as infertile, especially in high rainfall areas where these soils are prone to leaching (Bell 1984). A gabbro intrusion cuts through the granite and transverses the study area (Venter *et al.* 2003).

The woody vegetation is comprised of broad-leaved savanna tree species such as *Combretum* spp and *Sclerocarya birrea* with *Terminalia sericea* occurring frequently (Venter *et al.* 2003). The section underlain by the gabbro intrusive rock supports more extensive grasslands with a fairly sparsely distributed woody component comprised of relatively few trees and a somewhat dense shrub component.

The KNP falls within a summer rainfall region with the majority of rainfall received during October to April. The annual long-term mean rainfall calculated across the entire park is 533 mm (Venter *et al.* 2003). The Pretorius Kop region annually receives 737mm of rain, calculated as a 60 year running average (South African Weather Service). During the study period the rainfall totals for the hydrological year (July to

June) were 934 mm during 2005/06 and 600 mm during 2006/07. The rain received during the first year were 25% more than the average long-term rainfall estimate for the area, whereas the rain received during the second year of the study represented 20% less than the average long-term estimate (Appendix I; South African Weather Service).

The fire management protocol applied in the KNP entails annual burns of an area of predetermined extent which previously ranged between 12 – 24% of the total park area. The actual extent is determined on an ongoing basis based on the annual rainfall patterns and the fuel accumulation loads. This practice, adopted in 2002, tolerates unplanned and natural lightning ignited fires up until the set target area has been burnt after which these fires are suppressed. If natural fires do not occur frequently enough, management fires are deliberately set in order to achieve the stipulated target (Van Wilgen *et al.* 2008).

STUDY DESIGN AND DATA COLLECTION PROTOCOL

Foraging and habitat use observations were made on four breeding herds of sable antelope, consisting of between seven to eleven animals per herd. In June 2006 a GPS/GSM collar was fitted to one adult female from each of these four herds. These units utilise the Global Positioning System and the Global System for Mobile Communications to locate the animals. Data was collected over the dry seasons and the transition into the wet seasons across two years between May to November during 2006 and 2007. The time frame for data collection was chosen so as to reflect the foraging response of sable during the nutritionally critical seasons. These seasons represent

crucial periods in the seasonal cycle, with forage being of limited quality during the dry season and of limited quantity during the first months of the wet season. Throughout the two years of data collection there were no signs of any breeding herds other than the four collared herds. It was therefore assumed that the study animals represented the entire subpopulation of sable present in the study area during the time of the study.

Direct observations of a particular herd were performed sequentially and each herd's feeding patterns and habitat use were observed for a period of three days. The collar of the herd under observation was scheduled to transmit locations on an hourly basis, whereas the collar schedule of the herds not under direct observation in that week were set to transmit a location every six hours.

The feeding behaviour of sable has been described by Grobler (1981) and the peak of their feeding activity was found to be between 06:00 – 09:00 in the mornings and between 14:00 – 17:00 in the afternoons. He also observed that sable were active before sunrise and after sunset. As such, in an attempt to ensure that the data collected reflected the characteristics of sable foraging areas, data was collected by visiting sites where sable were recorded in the mornings (roughly between 05:00 – 10:00) and the afternoons (roughly between 15:00 – 19:00) (see Appendix II). The daily number of feeding sites recorded ranged from one to six with an average of three feeding sites per day. I visited the areas where sable were recorded approximately 24 hours after the presence of sable in order to avoid disturbing their feeding patterns.

At each site, a radius of 10 m surrounding the GPS location was searched for fresh bites, the presence of which classified the site as either a feeding site or a non-

feeding site. The distance between the recorded GPS location and the nearest fresh sable spoor was measured in an attempt to verify sable presence and quantify the location accuracy. The presence of fresh sable dung as well as any fresh signs of other grazers was also recorded to establish whether the foraging activity visible in the area could be attributable to animals other than the sable (see Appendix III for results).

Herbaceous layer measurements were done within 0.7 × 0.7 m quadrats. A central quadrat was placed on the recorded GPS coordinate or on the first fresh signs of feeding located within a 10 m radius from the GPS coordinate. In the case of a feeding site, a further two quadrats were placed in each of the cardinal directions, spaced two meters apart, totalling nine quadrats overall. In the case of a non-feeding site, only one quadrat was placed in each of the cardinal directions, spaced two meters from the central quadrat, totalling five quadrats overall (Figure 1.2).

In an attempt to identify characteristics defining a foraging area, landscape features in terms of vegetation structure, topography and the general phenological characteristics and composition of the sward were recorded in a 25 m radius from the GPS given location.

Furthermore, I collected dung samples which was analysed for nitrogen and phosphorus to obtain an estimate of the nutritional quality of the diet. These faecal measurements of nutrition are reported in appendix VIII.

THESIS STRUCTURE

Each chapter is written up in article format each with a separate introduction, methods, results and discussion section. A detailed description of the study design is given in the general introduction chapter and I elaborate on the methods pertaining to each particular chapter in the text of that chapter. The references relevant to the particular chapter are reported at the end of each chapter. Supplementary information and results that aren't directly relevant to the chapters yet are necessary background information are reported as appendices.

Grazing distribution patterns are influenced by processes that operate across multiple spatial scales and as such I attempted to incorporate this spatial variability in the study design. The study is structured to reflect two spatial scales at which selection could operate, one pertaining to the feeding station and the other pertaining to the feeding patch (as defined by Bailey *et al.* 1996). I also attempted to distinguish between bottom-up considerations driven by nutrient requirements and top-down constraints driven by the need to avoid predation.

Firstly, I examined diet selection at the level of the feeding station (Chapter 2). This analysis is based on the feeding data collected at the level of the grass species. I only included the locations in which evidence of fresh feeding was found. This was done in an attempt to limit the behavioural responses to those concerning foraging decisions and try to minimise the constraints imposed on diet selection as a result of non-foraging decisions such as predator avoidance.

Subsequently I examined selection at the level of the feeding patch (Chapter 3) by comparing feeding areas with similar sized areas where sable did not feed. The comparison involved grass layer characteristics as well as landscape features. In this section I attempted to differentiate between bottom-up and top-down effects by partitioning cover into tree cover, believed to influence forage quality and availability and shrub cover believed to influence visibility and hence predation risk. Although selection for less risky areas would be expected to occur at a broader scale (i.e. selection of habitat used from within the broader landscape) one would expect an additional element of predator avoidance during foraging sessions (i.e. animals are expected to be less vigilant during feeding bouts and thus should select less risky feeding areas from within the broader foraging area).

The study of diet selection and habitat use requires location estimates that are highly representative of the animal's actual location. As such it was deemed necessary to report the discrepancy in the telemetry points in order to justify the scale of resolution in the study. As this assessment did not form part of the original objectives, I used what little data we had to assess the accuracy and precision of the location estimate provided by the GPS/GSM collars used in the sable study. The data used in this assessment was insufficient to allow for a critical appraisal of collar function. As such this section does not form part of the main thesis body and is only included as an appendix. The results are reported in Appendix IV.

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FIGURES



Figure 1.1: The location of the study area within the greater Kruger National Park and the home range estimates of the four herds included in the study area (Numbi, Phabeni, Shitlave and Nhape) The home ranges were calculated from 6-hourly locations recorded between June 2006 to March 2007 using the adaptive kernel method and display the 50% and the 90% density contours.

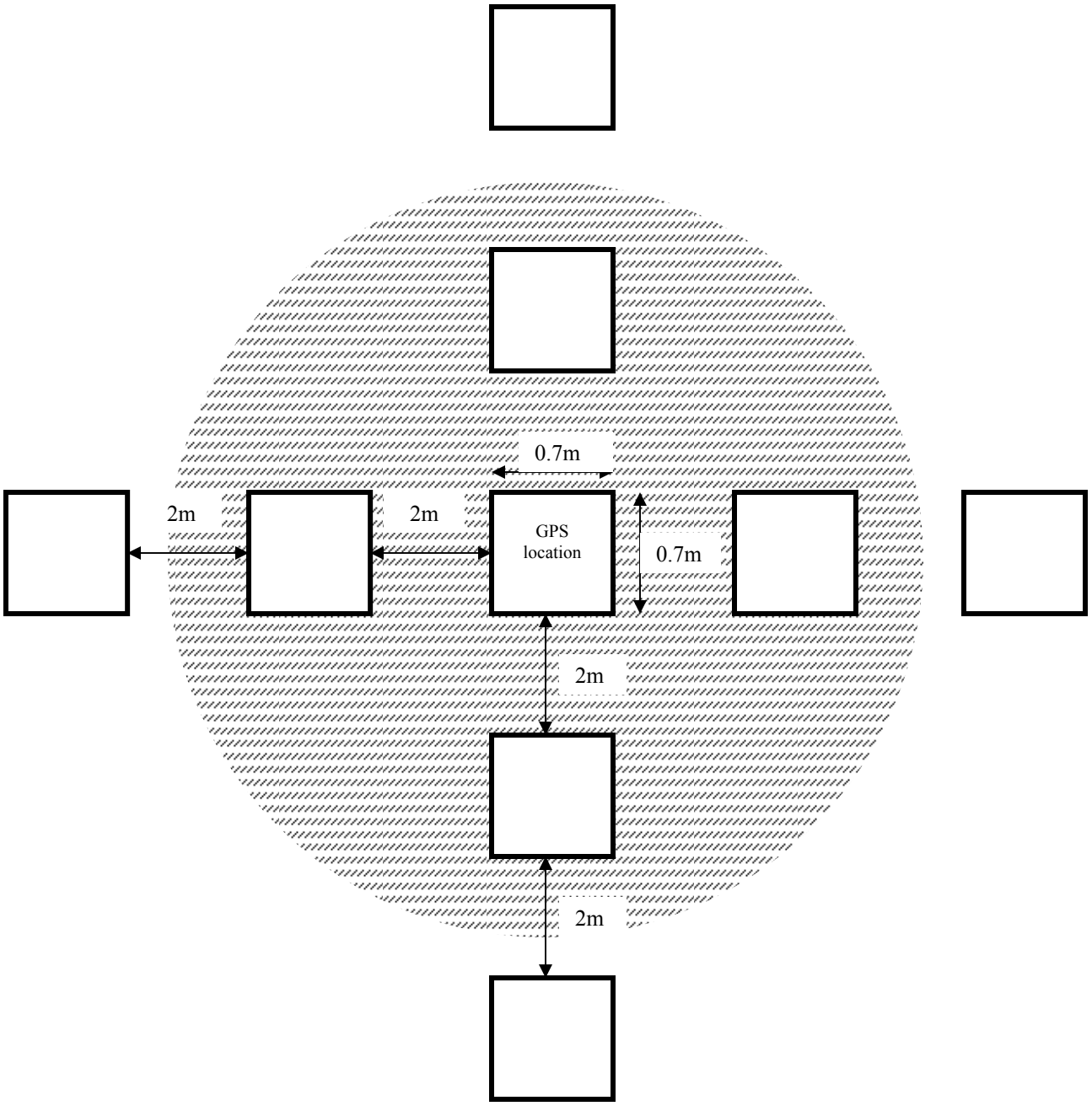

Figure 1.2: A schematical representation of the quadrat layout at a feeding site. Each square represents a 0.7 m × 0.7 m quadrat, with the central quadrat placed on the GPS location. A further two quadrats, spaced two meters apart, were placed in each cardinal direction. The shaded area represents the area surrounding the GPS location within which I searched for fresh bites. Thus the central quadrat could be placed anywhere within this area, depending on where the fresh bites were located.

CHAPTER 2

RESOURCE DEPENDENCE BY SABLE ANTELOPE IN THE KRUGER NATIONAL PARK: DETERMINANTS OF DRY SEASON FOOD SELECTION.

ABSTRACT

Digestibility of individual grass species and therefore their value as forage for grazers is influenced by species identity as well as by the phenological stage of the species through its effect on the relative proportions of crude protein and fibrous material. The food selection pattern of sable antelope (*Hippotragus niger*) and the contribution of grass species to their diet was studied in the Pretorius Kop region of the Kruger National Park. Movements of four herds were tracked through the use of GPS-GSM collars and grazing was recorded at the level of the grass species. The study spanned the dry season of two years varying considerably in rainfall and grass greenness. The four different herds demonstrated similar acceptabilities for the majority of grass species, with species such as *Panicum maximum*, *Heteropogon contortus*, *Hyperthelia dissoluta* and *Setaria sphacelata* shown to be important forage species in terms of acceptability as well as dietary contribution. Sable increased the dietary contribution of the species on which it depended during the dry season by feeding more frequently in areas where it was prevalent. The probability of feeding was found to depend not only on the identity of the grass species but also on the greenness, height and stemminess of the species independently of species identity. Sable infrequently accepted species that were typically

less than 20 cm in height, regardless of its grazing value to cattle or preference by other wild grazers. The effect of the degree of stemminess on species selection however, was found to be opposite to what was predicted. In general, sable were found to depend on grass species that have also been shown to be valuable dietary species to other grazers and adjust their acceptance of tufts within these species by grazing selectively based on its greenness, stemminess and height.

INTRODUCTION

Animals are faced with a spatially complex and temporally varying environment within which they must obtain a steady food supply. To maximise nutrient acquisition, forage selection should depend on the relative proportions of the easily digestible components and the slowly digestible, structural components, which increase retention time and delay digestion (Owen-Smith 1982, Bell 1984, Illius & Gordon 1993).

The grass layer, however, is characterised by an abundance of fibrous material and scantily distributed, good quality forage resulting in a large amount of time and energy being spent in its acquisition. Accordingly, grazers must find a balance between quantity and quality, which is largely determined by the animal's size, digestive capacity and its ability to be selective when feeding, which in turn is mainly controlled by mouth morphology (Owen-Smith 1982). Larger animals need less food per unit body mass and are therefore more tolerant of lower quality forage than smaller animals (Bell 1970, Jarman 1974, Owen-Smith 1988). Ruminants, through facilitation by micro-organisms, are capable of digesting fibre more efficiently than non-ruminants. On low quality forage

however, non-ruminants benefit by having a shorter gut retention time which outweighs the cost of a less efficient digestive system. Ruminants would therefore be more efficient at extracting nutrients only when feeding on relatively high quality forage (Illius & Gordon 1992).

A narrow muzzle structure would allow grazers to be selective at the level of the plant part (Owen-Smith 1982) by picking the high quality portions out from among the low quality portions. Conversely, animals with a broad muzzle are forced to consume the low quality parts along with the high quality bits but benefit when feeding on short swards where larger bites would allow for an increased intake rate. Nutrient concentrations vary across different spatial scales and the herbivore can be selective at some or all of these scales, depending on its ability to be selective (Senft *et al.* 1987, Bailey *et al.* 1996).

Young, fresh plant material is expected to be favoured by herbivores as mature leaves are associated with a build up of structural carbohydrates (Van Soest 1987). Following from this, herbivores are expected to prefer green grass and reject senescent material. O'Reagain & Owen Smith (1996) noted a positive correlation between sward greenness and the selection of higher quality diets. Similarly, animals are expected to feed from young short growth preferentially as it should contain less structural tissue. However, depending on the density of leaves, tall tufts may offer the alternative benefit of providing larger quantities of forage. Thus, the dependence of a particular grazer on certain grass heights should largely follow from its strategy in balancing nutritional benefits and costs.

Differences in digestibility are also expected at the level of the plant part, with stems containing substantially more structural carbohydrates and offering fewer nutritive rewards compared to leaves. A variety of studies have pointed out the preference of grazers for green leaves (Duncan 1975, Bell 1984) and the avoidance of stems (Bell 1970, Wallis de Vries & Daleboudt 1994, O'Reagain & Schwartz 1995).

Seasonal changes in protein concentrations and fibre content associated with gradual senescence (Fryxell 1991, Owen-Smith 1982) could lead to seasonal changes in acceptability for a species. Georgiadis & McNaughton (1990) indicated a seasonal decline in nutritional value associated with fibre build-up. Similarly, seasonal variations in grass height and the degree of stemminess (i.e. the density of stems) could also potentially influence grass species acceptability as both factors affect the balance of soluble and structural carbohydrates (Heady 1964).

Differences in nutritional quality are also expected to occur between different grass species. Species-specific forage preferences have been reported for domestic grazers (O'Reagain & Mentis 1989, O'Reagain & Grau 1995), and wild grazers under penned conditions (Bodenstein *et al.* 2000) and free ranging conditions (Macandza *et al.* 2004). Georgiadis & McNaughton (1990), while investigating the nutritional content of savanna grasses in eastern Africa, were able to show that each of the grass species revealed a characteristic elemental profile. However, very few studies have attempted to relate the preference for particular species and the seasonal and spatial changes in species-specific preference to the physical features characteristic of a particular species. As such, few studies attempt to answer the question of why particular species are chosen above others. Rather than emphasising the dynamic nature of selectivity, identification of

the underlying principles governing selection could instead illustrate the constancy of the process.

To accommodate the depletion of the forage supply during the dormant season, animals are expected to increase their dietary tolerances as resources become increasingly limited (Casebeer & Koss 1970). This is in accordance with optimal foraging theory, whereby dietary width should broaden in response to dry season shortages (Emlen 1966) as animals progressively include species of lower nutritive value.

In accordance with a strategy expected from an animal with a ruminant digestive system, sable have been described as selective feeders demonstrating a narrow diet breadth with regards to the forage species selected as well as the tuft or plant part consumed (Wilson & Hirst 1977; Grobler 1981; Skinner & Smithers 1990; Magome 1991). Relative to body size, sable have a fairly narrow incisor arcade which would enable them to exhibit a greater degree of selectivity compared to other ruminant grazers of similar body size (Gordon & Illius 1988). Such a dental structure may permit sable to maintain a selective diet, which would ultimately enable a sufficiently high intake rate of adequate quality required by a fairly large-bodied ruminant. Conversely, the narrow muzzle structure may limit the bite size attainable on short swards and thereby reduce intake rate when feeding on short grass. Nevertheless, previous studies have described the preferred feeding height of sable antelope as broadly ranging from 4 – 40 cm (Grobler 1981, Gureja & Owen-Smith 2002, Parrini 2006). Moreover, Grobler (1981) recorded no sable bites below 4 cm height throughout his study, despite there being seemingly suitable tufts available at that height. Additionally, sable have been shown to select fresh growth preferentially (Estes & Estes 1974, Sekulic 1981) and to favour green leaves

while avoiding stems (Grobler 1981, Parrini 2006) with the avoidance of stems being greater during the dry season (Parrini 2006).

The aim of this study was therefore to identify the grass species that sable depend on and the characteristics associated with these species that make them acceptable to sable. In addition, I wanted to ascertain whether differences in tuft characteristics within species would further influence the probability that sable will feed on a particular tuft. Particular hypotheses put forward included:

- The diet of sable would be comprised of relatively few grass species.
- Sable would depend on species known to be of high nutritional value to cattle.
- Throughout all seasons, the grass species that sable feed from frequently when encountered will be greener than the grass species that sable feed from infrequently when encountered.
- The seasonal changes in the acceptability of a particular grass species to sable will be related to the seasonal changes in greenness of that species relative to the greenness of the forage available in that season.
- The probability that sable will feed from a tuft would be greatest for species with a characteristically short to medium tuft height (4 – 40 cm) and species typically shorter than 4 cm will be rejected by sable.
- Sable will show a relatively low acceptability for species with a growth form characterised by relatively many stems.

METHODS

Study area

The study was carried out in the south-western section of the Kruger National Park (hereafter KNP) (31°12′-31°24′E, 25°02′-25°13′S) in a roughly 400 km^2 area surrounding the Pretorius Kop camp. The Pretorius Kop area is situated in a summer rainfall region and receives a relatively high mean annual rainfall of 737 mm, calculated as a 60-year running average (South African Weather Service). During the first year of the study 25% above average rainfall was recorded, while during the second year, rainfall was 20% less than the long term-mean (South African Weather Service). For detailed descriptions of rainfall patterns, refer to the general introduction in Chapter 1 and Appendix I.

The majority of the area consists of granite derived sandy soils, while a subsection is underlain by a gabbro intrusion. The soils are generally considered to be relatively infertile as a result of extensive leaching. The vegetation consists of broad-leaved savanna tree species such as *Combretum* spp and *Sclerocarya birrea* with *Terminalia sericea* occurring in the highest numbers (Venter *et al.* 2003). The gabbro sill gives rise to more open areas with relatively few trees.

Study design

The detailed study design is given in the general introduction in Chapter 1. Briefly, four female sable from four different breeding herds were fitted with GPS-GSM collars in June 2006. These units use the Global Positioning System and the Global System for Mobile Communications to locate the animal.

Foraging data were collected from May to November during 2006 and 2007. During the periods of data collection the collar of the herd being observed was set to transmit locations hourly. The sites visited were generally restricted to the locations recorded in the mornings (05:00 - 10:00) and afternoons (15:00 – 19:00) (see Appendix II) as these times were assumed to coincide with the foraging periods of sable (Grobler 1981). An average of 3 feeding sites was recorded per day, ranging between 1 to 6 feeding sites.

To avoid disturbing the animals, locations were visited at least 24 hours after the presence of sable. The presence of fresh bites within a radius of 10 m from the recorded GPS location was used to classify an area as a feeding site. For this part of the study, only those locations in which evidence of fresh feeding were found were included for analysis. This was done in an attempt to retain the focus on species and tuft selection and avoid factors associated with feeding area selection (e.g. predator avoidance) which is the topic of Chapter 3.

Data collection

At each feeding site, a 0.7 × 0.7 m quadrat was placed on the recorded coordinates or on the nearest point that showed evidence of fresh feeding provided that it occurred within a 10 m radius of the original GPS location. A further 8 quadrats were placed systematically, two in each cardinal direction and spaced two meters apart. All of the grass species within each quadrat were identified and both fresh and recent grazing were noted. For every tuft of each species in the quadrat, the following information was recorded:

- The proportion of leaves that were green on each tuft estimated using the Walker's 8 point scale (Walker 1976).
- The height under which approximately 95% of leaf biomass of the tuft occurred. The measurement was done on the ungrazed leaves of the same tuft or ungrazed tufts in the vicinity to estimate tuft height prior to grazing. The estimate of 95% of the biomass was crudely obtained through a visual assessment after which the measurements were done using a measuring tape. The measurements were taken in increments of 5 cm unless the tuft was shorter than 10 cm in which case it was measured to the nearest centimetre.
- An estimate of the degree of stemminess of the tuft, categorised as none, few (≤ 2) or many (> 2) stems per tuft.

Statistical analysis

The quadrats were not considered to constitute independent samples and consequently I calculated a single value of the above mentioned measurements across all tufts of a particular species occurring within a feeding site. This was achieved for tuft height by merely averaging for each species the measured tuft height across all tufts of that species occurring in the site. To obtain a single value for the greenness of each species at a feeding site, I allocated the midpoint value of the Walker's greenness category to each tuft occurring in the feeding site and subsequently averaged across all the tufts of a particular species to obtain a site-based greenness value for each of the species present. A site-based value for the degree of stemminess of each species present within the feeding site was obtained by calculating the proportion of tufts of a particular species that was recorded to have many stems. At each feeding site a species was considered to have been encountered by the sable if it occurred in at least one of the nine quadrats comprising the feeding site. Similarly, a grass species was considered to have been eaten if at least one fresh bite was found on at least one tuft of that species.

To ensure an accurate estimate of grass species acceptability, only species that occurred in at least ten sites in at least one season were considered for analysis. Under these criteria only eighteen of the 47 identified grass species were included in the analysis.

As very few feeding sites contained grasses below 4 cm in height, I formulated categories other than those initially postulated. By using data percentiles, the site-based species height values were subsequently divided into three categories based on their

relative position within the range of heights encountered over the data collection period. The categories were defined as short (20 cm or less); medium (21 – 40 cm) or tall (more than 40 cm).

Again using data percentiles, the site-based greenness of each species was categorised as mostly brown, intermediately green or mostly green. The greenness categories were assigned for each season separately such that the greenness values reflect the relative greenness of a species compared to the greenness of all the other species available during that particular season. The degree of stemminess of a species was categorised as none (0% of the species' tufts with many stems), few (less than 75% of the species' tufts with many stems) and many (75% or more of the species' tufts with many stems).

The seasons were demarcated based on the monthly changes in grass greenness of the sites, measured during the data collection period (Appendix V). Substantial differences in the amount of rainfall received during the two years resulted in different greenness estimates in corresponding months i.e. the early dry season of 2006 was noticeably greener than the early dry season of 2007 and similarly, the late dry season of 2006 was much greener than the late dry season of 2007. Furthermore, during August 2007 almost the entire study area was burnt and sufficient regrowth was only evident after September 2007. Due to these large differences in greenness as well as the fire and the flush events, corresponding seasons could not be viewed as replicates, leading to the identification of seven distinct seasons: The period May to July 2006 was considered to represent the early dry season of 2006 (EDS_06); August to September 2006 formed the late dry season of 2006 (LDS_06); and October to November 2006 signified the start of

the wet season of 2006 (EWS_06). During 2007, May and June were regarded as the early dry season of 2007 (EDS_07) and July represented the late dry season of 2007 (LDS_07). August and September were analysed as the burn period (hereafter Burn). October was considered to be the start of the regrowth period, but species identification during this time was unreliable and consequently the regrowth period was excluded from the analysis.

A site-based dietary contribution was calculated for each grass species as the number of bites taken from a species at a feeding site, expressed as a proportion of the total number of recorded bites across all species at that feeding site. A bite was defined as the area of cropped grass that could be covered by my closed fist. These proportions were then averaged across sites to obtain a seasonal contribution per grass species.

A site-based acceptability was calculated for every season per grass species as the number of feeding sites in which the species was eaten by sable expressed as a proportion of the total number of feeding sites in which the species was present (Owen-Smith & Cooper 1987). Similarly, the seasonal availability of each grass species in the feeding sites of each herd was calculated as the number of feeding sites in which the species was present expressed as a proportion of the total number of feeding sites at which data were collected in that season. Such proportions follow a binomial distribution and as such 95% binomial confidence limits were calculated for each acceptability value and reported as well.

The site-based greenness, height and stemminess of each species served as predictor variables, with the binary value of whether a species was eaten at a particular site or not considered as the response. Analysis was performed in R (R Development

Core Team 2008), using generalised linear models (GLMs) with a binomial error structure and a logit link function. In GLMs, the explanatory variables are used collectively to produce a linear predictor which is related to the expected value, *E(Y),* of the response variable *Y* through a link function *g()*, such that $g[E(Y)] = \alpha + \beta X$ where α is the intercept, X is a vector of the predictor variables, and β is the vector of the coefficients. (Agresti 1996). Models with a logit link calculate the likelihood of a particular response at each setting of the suite of predictor variables (Agresti 1996).

The statistical modelling procedure involves the development of a set of candidate models. These candidate models should be specifically formulated to address the particular hypotheses one wishes to explore which in turn should be based on previous knowledge of the system under investigation.

The model generates a statistic termed the residual deviance calculated as:

-2*log likelihood,

which is a measure of the goodness of fit of a particular model (Agresti 1996; Quinn & Keough 2002). The residual deviance can then be used in the calculation of an information theory statistic such as Akaike Information Criterion (AIC) defined as:

AIC = -2 × log-likelihood +2(p+1),

where p is the number of parameters in the model (Crawley 2007). AIC is a model selection technique that evaluates competing models while penalising for the number of predictor variables used (Quinn & Keough 2002). Using AIC, the competing models can then be ranked according to the relative support for each through the calculation of a delta AIC statistic (Δ AIC) which represents the difference in AIC of each model relative to the most supported model in the candidate set. Models with small Δ AIC values of

two or less can be considered as more or less equivalent to the best supported model and thus for the benefit of parsimony those with the least number of parameters are preferable (Burnham & Anderson 1998).

Furthermore, a value equivalent to the R^2 statistic used in linear modelling can be calculated for the best supported model to quantify the overall measure of fit as measured by the model deviance. Using the residual deviance (the deviance of the fitted model) and the null deviance (the deviance of a model including an intercept only) through the following calculation: (null deviance – residual deviance)/null deviance, the proportion of deviance explained can be obtained (Wood 2006), which can serve a similar purpose to the more familiar R^2.

GLMs have the capacity to handle categorical predictor variables. The number of parameters represents the number of categorical variables as well as the number of levels within each variable through the calculation $\sum_j(n-1)+1$, where n represents the number of levels within each of j number of variables. Each category within the qualitative explanatory variable acts as a "dummy variable" such that an effect can be calculated for every level within the categorical variable. Therefore a categorical variable with three levels will be expressed as $y = \alpha + \beta_1 c_1 + \beta_2 c_2$, where each term relates to a particular category with the intercept (α) corresponding to the third category ($c_1 = c_2 = 0$) (Agresti 1996).

Apart from season, the following explanatory variables were considered in the modelling process: (1) The relative greenness of each species at a feeding site; (2) The average tuft height of each species at a feeding site; (3) The proportion of tufts of each species with many stems and (4) The identity of the grass species.

Two separate sets of models were constructed of which the first set tested the contribution of each factor to species acceptability individually. The second set incorporated all factors to ascertain which of these characteristics played an important role in species selection. Combining all explanatory factors (i.e. greenness, height or stemminess) enables one to assess whether the features identified as important were characteristic of the species chosen and whether within species differences in tuft characteristics had any additional influence in tuft selection.

The data on dietary contribution was not normally distributed and violated the assumptions of parametric statistical tests. As such, seasonal changes in dietary contribution were assessed separately for each herd using the Wilcoxon rank-sum test at significance level $P < 0.1$. A chi-square analysis at significance level $P < 0.1$ was carried out to assess the seasonal differences in the availability of grass species between the feeding sites of the different herds as well as to ascertain whether the four herds showed any differences in their acceptance of particular grass species. As this involved several non-independent tests, the type I error is likely to be inflated and results should be interpreted with caution.

RESULTS

A total of 47 grass species was recorded of which 32 were eaten at least once. Only 18 of these were encountered frequently enough to warrant inclusion in the analysis (i.e. were found to occur in ten or more sites in at least one season across all herds). As some sites contained only species other than these 18 grass species, the effective sample

size represented 251 feeding sites. These sites were fairly evenly spread across seasons with approximately 20% of sites falling within the EDS_06, 24% within the LDS_06, 10% in the EWS_06, 15% fell within the EDS_07, 8% within the LDS_07 and 22% recorded during the burn period.

Grass species availability

During 2006, *Panicum maximum* was significantly more available in the feeding sites of the Phabeni herd (60%) than in the feeding sites of the Numbi herd (32%; χ^2 = 6.056; d.f. = 1; P = 0.014). During 2007 *P. maximum* became significantly more available in the feeding sites of the Numbi herd (84%) than it was during 2006 (χ^2 = 27.63; d.f. = 1; P < 0.0001), whereas its availability in the feeding sites of the Phabeni herd remained unchanged. Subsequently *P. maximum* was significantly more available in the Numbi herd feeding sites than in the Phabeni herd feeding sites during 2007 (58%; χ^2 = 6.16; d.f. = 1; P = 0.013). The availability of *P. maximum* in the feeding sites of the Shitlave herd also increased significantly from an average of 35% in 2006 to approximately 70% in 2007 (χ^2 = 3.9, d.f. = 1, P = 0.048).

The availability of *Hyperthelia dissoluta* in feeding sites during 2006 did not differ significantly between herds and ranged from 25 – 35%. *H. dissoluta* was significantly more available in the feeding sites of the Numbi (χ^2 = 22.04; d.f. = 1; P < 0.0001) and Phabeni (χ^2 = 4.98; d.f. = 1; P = 0.026) herds during 2007 than in 2006, increasing from 35% to 82% and from 34% to 63% respectively. During 2007, *H. dissoluta* was significantly more available in the feeding sites of the Numbi herd than in

the feeding sites of the Phabeni herd ($\chi^2 = 3.05$; d.f. = 1; P = 0.08) and the Shitlave herd ($\chi^2 = 8.04$; d.f. = 1; P = 0.005).

During 2006, *Heteropogon contortus* was significantly more available in the feeding sites of the Shitlave herd (79%) than in the feeding sites of the Nhape herd (48%; $\chi^2 = 3.15$; d.f. = 1; P = 0.076) and the Numbi herd (51%; $\chi^2 = 3.53$; d.f. = 1; P = 0.06). The availability of *H. contortus* did not differ significantly between 2006 and 2007 in the feeding sites of either of the herds.

Setaria sphacelata occurred in the feeding sites of the Nhape herd significantly less frequently in 2006 (20%) compared to the feeding sites of the other three herds ($\chi^2 = 27.77$, d.f. = 1, P < 0.0001). The availability of *S. sphacelata* in the feeding sites of the Numbi herd (67%) differed significantly from its availability in the feeding sites of the Phabeni herd (100%; $\chi^2 = 7.5336$, d.f. = 1, P = 0.006), yet its availability in the feeding sites of the Shitlave herd (89%) was not significantly different from either the Numbi ($\chi^2 = 2.65$, d.f. = 1, P = 0.1) or the Phabeni ($\chi^2 = 0.64$, d.f. = 1, P = 0.42) herds. *S. sphacelata* occurred significantly less frequently in the feeding sites of all three herds during 2007, declining from 67% in 2006 to 37% in 2007 for the Numbi herd ($\chi^2 = 6.93$, d.f. = 1,P = 0.008), from 100% to 58% for the Phabeni herd ($\chi^2 = 9.61$, d.f. = 1, P = 0.002) and from 89% to 48% for the Shitlave herd ($\chi^2 = 6.36$, d.f. = 1, P = 0.01). During 2007 neither herd differed significantly in terms of the feeding site availability of *S. sphacelata* ($\chi^2 = 2.98$, d.f. = 2, P = 0.23).

The availability of *Themeda triandra* in feeding sites of the Phabeni and Shitlave herds differed significantly. *T. triandra* was only found in the feeding sites of the Shitlave herd during the early dry season of 2006 and 2007 and in the late dry season of

2007. Yet its availability in the early dry season of 2006 was significantly less (3%) than the early dry season of 2007 (8%; $\chi^2 = 3.61$; d.f. = 1; P = 0.057) and the late dry season of 2007 (19%; $\chi^2 = 8.21$; d.f. = 1; P = 0.004). There was no significant difference in the availability of *T. triandra* in the feeding sites of the Shitlave herd between the early and the late dry season of 2007 ($\chi^2 = 0.82$; d.f. = 1; P = 0.37). In the feeding sites of the Phabeni herd, *T. triandra* was significantly more available in the early dry season of 2006 (79%) than in the late dry season of 2006 (6%; $\chi^2 = 12.61$; d.f. = 1, P = 0.00038) whereas it wasn't found in feeding sites during the early wet season of 2006. Similarly, *T. triandra* was more available during the early dry season of 2007 (75%) than in the late dry season of 2007 (14%; $\chi^2 = 3.36$; d.f. = 1; P = 0.067).

Brachiaria nigropedata was significantly more available in the feeding sites of the Nhape herd (10%) compared to the feeding sites of the other three herds which ranged from 3% to 4% availability ($\chi^2 = 16.2$, d.f. = 1, $P < 0.0001$). There was no significant seasonal differences in the availability of *B. nigropedata* in the feeding sites of the Nhape herd ($\chi^2 = 3.04$, d.f. = 1, P = 0.22).

Trachypogon spicatus was found frequently only in the feeding sites of the Numbi herd. Its availability in feeding sites did not differ significantly between the seasons of 2006 ($\chi^2 = 3.3$; d.f. = 2; P = 0.19) and ranged from 5% to 12%. During 2007, *T. spicatus* was only available in feeding sites during the early dry season and its availability during this season did not differ significantly from its availability during 2006 ($\chi^2 = 4.17$, d.f. = 3, P = 0.24).

Grass species acceptability

Testing for seasonal differences in acceptance of herds for particular grass species, using only the species that occurred in more than ten feeding sites per season per herd yielded only the acceptance of *P. maximum* by the Numbi herd during the burn period (acceptability = 0.95) as significantly greater than its acceptance during the early dry season of 2007 (acceptability = 0.58; $\chi^2 = 4.43$; d.f. = 1; P = 0.035) and the late dry season of 2007 (acceptability = 0.6; $\chi^2 = 3.63$; d.f. = 1; P = 0.057).

Only the acceptability of *S. sphacelata* in the late dry season of 2006 differed between herds. The Shitlave herd showed a significantly higher acceptance of *S. sphacelata* (acceptability = 0.9) than the Numbi herd (acceptability = 0.48; $\chi^2 = 3.5$; d.f. = 1; P = 0.061) and the Phabeni herd (acceptability = 0.33; $\chi^2 = 5.69$; d.f. = 1; P = 0.017).

In figure 2.1 the site based acceptability of each grass species is amalgamated across seasons to highlight the differences in acceptability amongst herds. The acceptability of *P. maximum* and *H. contortus* was consistently above 0.5 for all four herds, while the acceptability of *H. dissoluta* remained above 0.5 to all three herds in whose feeding sites it was available. *S. sphacelata* had an acceptability of above 0.5 to two of the three herds for which it was available. The acceptability of *S. sphacelata* by the Numbi herd, however, was slightly lower at 0.4. *T. spicatus*, only found in the feeding sites of the Numbi herd, was the most accepted species to this herd. Similarly, *B. nigropedata* that was most available in the feeding sites of the Nhape herd was the most accepted species for this herd (Figure 2.1). Despite these differences, data from all herds

were combined for subsequent analysis of the effect of species and the characteristics associated with these species on acceptability.

The effect of grass features on grass species acceptance

Grass greenness

See table 2.1 for a description of the relative greenness categories. The greenness of a grass species had a positive influence on species acceptance, with sable showing a higher probability of feeding from tufts when the tuft was green (Table 2.2; Figure 2.2). Sable were 16% more likely to feed from an intermediately green species and 21% more likely to feed from a mostly green species compared to a mostly brown species. However, sable still fed from approximately 35% of the mostly brown tufts encountered.

The preference for intermediate to mostly green species was found to be consistent across all seasons except in the early dry season of 2007 and the burn period (Figure 2.2). Thus, with the exception of these two periods, sable consistently favoured the greenest grass available. However, the selection for green tufts seem to operate under a threshold effect and sable differentiated less between the two upper most categories (intermediately green and mostly green) and only showed a lower acceptance of the mostly brown category. During the burn period, approximately 65% of the grass encountered in feeding sites retained no green leaves and only 20% were considered to be mostly green relative to the grass encountered in this period. Entirely brown grass was

only eaten in the burn period, during which 62% of all the tufts eaten were completely brown.

Grass height

Species shorter than 4 cm were present in only eight feeding sites and were eaten in only one. These included mostly *Perotis patens* and *Pogonarthria squarrosa* but also one record of *Urochloa mossambiciensis* and one record of *H. dissoluta* encountered during the burn period. Tuft height influenced species acceptance (Table 2.2) and sable tended to favour grass taller than 20 cm. Sable were 21% more likely to feed from species of medium height and 31% more likely to feed from tall species compared to species less than 20 cm. This pattern was evident in all but the early wet season of 2006 and during the burn period (Figure 2.2). During the burn period, 55% of all grass tufts recorded in feeding sites were above 20 cm tall and sable ate 72% of the tall grass encountered compared to 60% of the short grass encountered.

Grass stemminess

Contrary to my prediction, the degree of stemminess of a species showed no consistent relationship with species acceptability (Table 2.2; Figure 2.2). Sable seemed to favour grasses with many stems during the late dry season of 2007 and the burn period (Figure 2.2). When the effect of stems are considered separately, sable were 12% more

likely to feed from intermediately stemmy species and 18% more likely to feed from highly stemmy species compared to species with no stems.

Species identity

When comparing models incorporating species identity and greenness, the best model retained both the greenness of the species as well as the identity of the species (Table 2.3). The retention of both factors suggests that greenness had an additional influence on acceptance independent of the identity of the species. During most of the year, however, mean greenness remained above 40% (Figure 2.3). During the late dry season of 2006, the mean greenness of some species fell to a low of 30%, whereas during the late dry season of 2007, every species was below 30% in mean greenness. Only during these latter two periods were the most highly accepted grass species the greenest species available. During the burn period, when forage availability was severely diminished, species acceptance varied irrespective of species greenness (Figure 2.3), although only 14% of the tufts encountered during the burn period were above 10% green of which only 42% were above 20 cm in height.

The models in which the effects of species height and the degree of stemminess of a species were included received much stronger support with a delta AIC difference of 25.4 (Table 2.3) affirming the additional influence of these parameters on species acceptance. As with the consideration of greenness, the inclusion of species height in addition to species identity indicated that the height of the species influenced acceptance of a species above and beyond the effect of species identity. The influence of height on

species acceptance rather displayed a threshold effect where sable demonstrated increased acceptance for species above 20 cm. Short species of low acceptance included *Cynodon dactylon* (average height of 20 cm), *P. patens* (17 cm), *P. squarrosa* (16 cm) and to a lesser extent *Digitaria eriantha* (18 cm).

Although the effect of the degree of stemminess played a role in species acceptance, the effect was opposite to what was predicted i.e. a greater probability of feeding associated with a greater degree of stemminess. Highly stemmy species that were favoured included *T. triandra*, *P. maximum* and *H. dissoluta.*

Dietary contribution

The bulk of the diet of each herd was made up of approximately five grass species which comprised 70 - 80% of their diet. Of these, *P. maximum* and *H. contortus* contributed a relatively large proportion to the diet of all four herds, and *H. dissoluta* and *S. sphacelata* were present in relatively high proportions in the diets of three of the four herds considered (Figure 2.4).

During 2006, *P. maximum* contributed significantly more to the diet of the Phabeni herd (25%) than that of the Numbi herd (10%; $W = 760.5$, $P = 0.014$). However, during the drier year of 2007 the contribution of *P. maximum* to the diet of the Numbi herd was significantly higher than it was during the more benign year of 2006 ($W = 763$; $P < 0.0001$) whereas there was no significant seasonal change in the dietary contribution of *P. maximum* to the diet of the Phabeni herd which averaged 23% across all seasons. Thus, during 2007, the contribution of *P. maximum* to the diet of the Numbi herd (35%),

was significantly more than its contribution to the Phabeni herd (21%; W = 1166.5; P = 0.057). Similar to the seasonal pattern observed in the Numbi herd, the Shitlave herd also significantly increased the contribution of *P. maximum* to their diet from 3% during 2006 to 32% in 2007 (W = 148.5; P = 0.006). There was no seasonal change in the contribution of *P. maximum* to the diet of the Nhape herd with an average of 30% of their diet consisting of this species throughout 2006 (Figure 2.4).

The dietary contribution of *H. dissoluta* was consistently low throughout 2006 with no significant differences between herds, contributing on average 4% to sable diet during this year. All three herds significantly increased the contribution of *H. dissoluta* to their diet during the drier year of 2007 compared to 2006 with *H. dissoluta* contributing on average 50% to the diet of the Numbi herd (W = 475; P < 0.0001), 27% to the diet of the Phabeni herd (W = 410.5; P = 0.001) and 19% to the diet of the Shitlave herd (W = 187; P = 0.059). During 2007, the proportion of the Numbi herd diet comprised of *H. dissoluta* was significantly more than that of the Phabeni (W = 1267; P = 0.006) and Shitlave (W = 993; P = 0.0005) herds.

In 2006, the dietary contribution of *H. contortus* did not differ significantly between herds. The contribution of *H. contortus* significantly declined only in the diet of the Numbi herd from 14% in 2006 to 2% in 2007 (W = 1681; P = 0.034). Thus during 2007, the proportional contribution of *H. contortus* to the diet of the Numbi herd was significantly less than that of the Phabeni herd (W = 67.6; P = 0.003) and that of the Shitlave herd (W = 508; P = 0.017).

During 2006, there were significant differences between herds in the contribution of *S. sphacelata* to the diet. The diet of the Nhape herd contained significantly less (2%)

of this species compared to the diets of the Numbi (12%; W = 514; P = 0.023) and Phabeni (10%; W = 333; P = 0.058) herds. There were no significant differences between the Numbi and Phabeni herds in terms of the dietary contribution of *S. sphacelata* (W = 1033.5, P = 0.73) during 2006. However, the diet off the Shitlave herd contained significantly more *S. sphacelata* (33%) than that of the Numbi (W = 318; P = 0.003) and Phabeni (W = 185; P = 0.003) herds. Only the contributions of *S. sphacelata* to the diet of the Numbi and Shitlave herds were significantly less in 2007 than in 2006 declining from 12% to 2% for the Numbi herd (W = 1766; P = 0.004) and from 33% to 8% for the Shitlave herd (W = 386; P = 0.001). There were no significant seasonal differences in the contribution of *S. sphacelata* to the diet of the Phabeni herd. During 2007 the Phabeni herd included a significantly greater proportion of *S. sphacelata* in their diet than the Numbi herd (W = 662; P = 0.001).

Other grass species, including *B. nigropedata* and *T. triandra*, made up a considerable fraction of the diet of only a single herd, despite occurring within the home range of the other herds. The Shitlave herd was only recorded to feed on *T. triandra* during the early to late dry season of 2007. There was no significant difference in the contribution of *T. triandra* to the diet of the Shitlave herd between these two seasons contributing on averaged 16% (W = 16.5; P = 0.3). Compared to the Shitlave herd, a significantly greater proportion of the diet of the Phabeni herd consisted of *T. triandra* (W = 2076.5; P = 0.004). In both years, *T. triandra* contributed considerably to the diet of the Phabeni herd only during the early dry seasons (Figure 2.4). During the early dry season of 2006, 20% of the Phabeni diet consisted of *T. triandra* and this decreased significantly to 1% in the late dry season (W = 169; P = 0.001). Similarly, the diet of the

Phabeni herd during the early dry season of 2007 was comprised of approximately 14% *T. triandra*. This differed significantly from the 2% contribution during the late dry season 2007 (W = 45; P = 0.038) and from the 8% contribution during the burn period (W = 142; P = 0.014; Figure 2.4).

The dietary contribution of *B. nigropedata* to the Nhape herd was significantly greater during the early dry season of 2006 (25%) than the late dry season of 2006 (13%; W = 71.5; P = 0.045).

In 2006, *T. spicatus* contributed significantly more to the diet of the Numbi herd during the late dry season (41%;W = 162.5; P = 0.06) and during the early wet season (40%; W = 69; P = 0.016) compared to the early dry season (17%). In the early dry season of 2007, the only season in 2007 in which it was available, *T spicatus* made up approximately 21% of the Numbi herd diet, which was not significantly different to its dietary contribution during 2006 (W = 570; P = 0.43; Figure 2.4).

DISCUSSION

Several of the species on which sable depended, specifically *H. dissoluta*, *H. contortus* and *T. spicatus,* have been described as of low to medium grazing value to cattle. Similarly, many of the grass species that were relatively abundantly available within sable feeding sites, yet remained low in acceptability, specifically *U. mossambiciensis* and *D. eriantha*, are species known to be of high grazing value to cattle. *C. dactylon*, although of moderate grazing value to cattle due to its short growth form, have been shown to be highly acceptable to short grass grazers such as wildebeest

(Andere 1981), yet also remained low in acceptability to the sable. Regardless of the species identity, sable were found to be more likely to feed from tufts of intermediate to high greenness compared to tufts of low greenness, yet still accepted predominantly brown tufts relatively frequently. In addition, sable frequently accepted grass tufts above 20 cm and were less likely to feed on tufts less than 20 cm in height.

Many of the grass species important to sable in terms of acceptability and dietary contribution have previously been documented as important forage species for sable elsewhere e.g. *P. maximum*, *H. contortus*, *H. dissoluta*, *T. triandra*, and *B. nigropedata* (Wilson & Hirst 1977, Grobler 1981; Parrini 2006, Magome *et al.* 2008). The high acceptance of *T. spicatus* and *S. sphacelata* was previously undocumented.

Species such as *P. maximum*, *T. triandra*, *S. sphacelata,* and *B. nigropedata* have been described as nutritious species with high leaf production and are considered to be of high grazing value to cattle (Van Oudtshoorn 1999). Many of these species have been shown to be highly acceptable to other wild grazers such as *P. maximum* and *T. triandra* to roan (*Hippotragus equinus*; Knoop & Owen-Smith 2006) and *P. maximum* and *H. contortus* to buffalo (*Syncerus caffer*; Macandza *et al.* 2004). In addition, many grazers depend on these grass species for the bulk of their dietary intake e.g. *P. maximum* constitute a large proportion of the diet of buffalo (Macandza *et al.* 2004) and species such as *P. maximum*, *H. contortus* and *T. triandra* have been shown to contribute a large fraction to the dietary proportions of blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*; Bodenstein *et al.* 2000). Although many of the grass species that occurred in high proportions in the sable diet are also favoured by many other species, Macandza (2009) found that sable were more narrowly selective for certain grass features

such as greenness and height than buffalo and zebra, which may possibly reduce the potential for competition between these species.

However, certain grass species favoured by sable are regarded as of low to intermediate grazing value, particularly species such as *H. contortus*, and *H. dissoluta*, whereas others have been described as unpalatable to cattle, specifically *T. spicatus*. During the relatively benign year of 2006 and the early dry season of 2007, the Numbi herd accepted *T. spicatus* on every occasion it was encountered. Consequently, *T. spicatus* contributed greatly to the diet of the Numbi herd during these seasons (up to 41%), despite a relatively low availability ranging from between 5 – 12%. During the dry season of 2007 and the burn period, the Numbi herd did not forage in areas where this species was available. According to Van Oudtshoorn (1999), although *T. spicatus* is generally considered to be unpalatable to cattle, it will be grazed when in a young growth form. Perhaps during the relatively benign year of 2006, sable were still able to locate young tufts of *T. spicatus*. Unfortunately, as no *T. spicatus* tufts were found in sable feeding sites during the dry year of 2007, tuft characteristics could not be compared between years.

Owen-Smith (1994) while studying the foraging behaviour of kudus (*Tragelaphus strepsiceros*), demonstrated how kudus respond to the forage shortages associated with the dry season by accepting a higher proportion of preferred species during the dry season and foraging more often in areas where the preferred species was abundant. During the dry year of 2007, *P. maximum* was more available in feeding sites, suggesting that these herds foraged more often in areas where this species was abundant. The dietary contribution of *P. maximum* also increased significantly in the dry year of 2007 compared

to the relatively wet year of 2006. Similarly, the Numbi and the Phabeni herds foraged more frequently in areas where *H. dissoluta* was prevalent and all three herds increased their proportional intake of *H. dissoluta* during the dry year. This suggests that sable increased their dependence on these preferred species during dry periods by including a greater proportion of these species in their diet. This was achieved, not by increasing their acceptance for the species, but by focusing their foraging effort in areas where these species were most available, as demonstrated by Owen-Smith (1994).

Sable fed from approximately 35% of the mostly brown tufts they encountered. Unfortunately, I did not attempt to record selection at the level of the plant part, which would have provided valuable information in explaining their fairly high use of such mostly brown tufts. However, following the burn, sable were faced with a severely diminished food supply with the remaining forage likely to have been of low quality, as is to be expected towards the end of the dry season. During this time, approximately 65% of the grass encountered was entirely brown, and roughly 62% of all the tufts fed from, had no green leaves remaining. Notwithstanding, sable seemed to retain a healthy body condition throughout the two months of scarcity (personal observation), which possibly suggests a high tolerance of brown, fibrous forage. In all other seasons, however, sable were never recorded to feed from tufts that were entirely brown. An alternative hypothesis that remains to be tested in future research is therefore the extent to which sable can feed selectively at the level of the plant part. According to Gordon & Illius (1988), the width of the incisor arcade of sable antelope is 56.6 mm, which is rather narrow compared to other grazers of similar body size such as wildebeest which have an

incisor arcade width of 73.1 mm. Such a narrow muzzle structure may facilitate plant part selection (Jarman 1974), allowing an animal to demonstrate a greater degree of selectivity by singling out only the green leaves from amongst those comprising a generally brown tuft. Such selection at the level of the plant part have been documented previously for topi, a fairly narrow muzzled antelope (Murray & Illius 2000), yet remains to be tested for sable.

While previous studies on sable feeding height have found sable to accept grass ranging from 4 – 40 cm, the Pretorius Kop sable were less likely to feed from short growth species less than 20 cm in height. Parrini (2006) also observed that the sable occurring in the Kgaswane Mountain Reserve were less likely to feed from very short species. Short swards limit the possible bite depth attainable. Therefore, among grazing animals, incisor width will influence intake rate on short swards where a broad muzzle would allow for larger bites. Narrow mouth dimensions may therefore limit the acquisition of sufficient amounts of forage on very short swards, and sable may benefit from feeding on taller swards where a greater bite depth may be obtained. The scarcity of grasses shorter than 4 cm in feeding sites, particularly *C. dactylon*, despite its availability in the surrounding areas (personal observation), may be a further indication of sable's avoidance of short growth species, suggesting that sable may also be avoiding the foraging patches where short growth species predominate. Species that were mostly avoided by sable, in particular *C. dactylon* that have been shown to be highly acceptable to short grass grazers such as wildebeest (Andere 1981) and to a lesser extent *D. eriantha,* were generally below the 20 cm threshold, with average heights of 20 cm and

19 cm respectively. However, sable still fed occasionally on tufts of *D. eriantha*, *H. contortus*, *H. dissoluta* and *S. sphacelata* when less than 20 cm in height.

Contrary to the initial prediction, there was a tendency for sable to feed from stemmy species preferentially. In particular, sable favoured species such as *P. maximum* and *H. dissoluta*, while *T. triandra* was favoured by one herd. Although these species are considered to be of intermediate to high grazing value to cattle, all tended to have many stems. Additionally, the growth form of *P. maximum,* and especially *T. triandra*, were such that they often offered relatively few basal leaves and supported a considerable amount of leaves along the length of the stem (personal observation). Although I made no attempt to record the actual plant part consumed, fresh bites were often observed on stems. Macandza (2009) also noted sable feeding directly on stems and attributed this to a possible high tolerance of grass with high stem densities, as documented by Heitkönig & Owen-Smith (1998) for roan antelope. A high tolerance of stems may allow sable to feed on leaf-bearing stems when sufficient amounts of basal leaves are unavailable. Again, this study would have greatly benefited from the inclusion of selection at the level of the plant part. I suggest that future investigations on sable foraging focus on this fine level of selection.

This study showed that the grass species that sable depended on consisted of species that have been shown to be very acceptable to cattle and other wild grazers as well as species of low grazing value to cattle. Although greenness positively influenced tuft acceptance, the effect was small, suggesting that further selection for greenness may be operating at different scales. Sable only selected for the species of the highest greenness available below a threshold of approximately 30% greenness. Sable showed a

preference for species taller than 20 cm, and species generally considered to be of high grazing value to cattle, that were less likely to be fed on by sable included mostly short species typically less than 20 cm in height. Sable's high tolerance of stemmy grass suggested a greater than expected digestive efficiency. Sable increased their dependence on certain preferred species during drier periods by increasing their dietary contribution through feeding more frequently in areas where these species predominated.

Notwithstanding the ruminant digestive system of sable that would suggest that they should display a high level of selectivity and consume high quality forage, the diet breadth of sable was not much narrower than that of other grazers and contained several grass species considered to be of low grazing value. Additionally, by frequently feeding from predominantly brown tufts and highly stemmy species, sable showed a surprisingly high tolerance of grass features that would be expected to be associated with lower forage quality.

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TABLES

Table 2.1: The greenness categories calculated relative to the greenness available in each season.

	Mostly brown	Intermediately green	Mostly green
Early dry season 2006	< 40%	40 – 60%	> 60%
Late dry season 2006	< 30%	30 – 50%	> 50%
Early wet season 2006	< 50%	50 – 70%	> 70%
Early dry season 2007	< 40%	40 – 50%	> 50%
Late dry season 2007	< 10%	10 – 20%	> 20%
Burn period	0%	1 – 10%	> 10%

Table 2.2: Single factor contributions and seasonal differences. The statistics reported include the residual deviance or -2 log-likelihood (-2LL), the AIC, the delta AIC value and the "proportion of deviance explained" (the value equivalent to R^2).

Model	-2LL	AIC	delta AIC	R^2
Eaten/Not ~ Season + Species + Season:Species	1002.10	1112.10	0.00	0.307
Eaten/Not ~ Season + Species	1075.70	1121.70	9.60	0.256
Eaten/Not ~ Season		1420.40	308.30	0.026
Eaten/Not ~ Season + Height + Season:Height	1273.70	1309.70	0.00	0.119
Eaten/Not ~ Season + Height	1317.30	1333.30	23.60	0.089
Eaten/Not ~ Season		1420.40	110.70	0.026
Eaten/Not ~ Season + Greenness + Season:Greenness	1318.50	1354.50	0.00	0.088
Eaten/Not ~ Season + Greenness	1344.90	1360.90	6.40	0.070
Eaten/Not ~ Season		1420.40	65.90	0.026
Eaten/Not ~ Season + Stem	1391.30	1407.30	0.00	0.038
Eaten/Not ~ Season + Stem + Season:Stem	1371.90	1407.90	0.60	0.051
Eaten/Not ~ Season		1420.40	13.10	0.026

Table 2.3: Model selection statistics for multiple models of the site based acceptability of grass species as influenced by species identity and species greenness, height and stemminess. The highlighted model is the best model from the candidate set. The statistics reported include the residual deviance calculated as -2×log-likelihood (-2LL), the AIC, the delta AIC value and the value equivalent to the R^2.

Model	-2LL	AIC	delta AIC	R^2
Eaten/Not ~ Season + Species + Greenness + Height + Stem + Season:Greenness	970.28	1048.30	0.00	0.329
Eaten/Not ~ Season + Species + Greenness + Height + Stem + Season:Greenness + Season:Height	950.95	1049.00	0.70	0.343
Eaten/Not ~ Season + Species + Greenness + Height + Season:Greenness + Season:Height	959.80	1053.80	5.50	
Eaten/Not ~ Season + Species + Greenness + Height + Season:Greenness	981.55	1055.50	7.20	
Eaten/Not ~ Season + Species + Greenness + Stem + Season:Greenness	985.07	1059.10	10.80	
Eaten/Not ~ Season + Species + Greenness + Stem + Season:Greenness + Season:Stem	973.89	1067.90	19.60	
Eaten/Not ~ Season + Species + Greenness + Season:Greenness	1003.70	1073.70	25.40	
Eaten/Not ~ Season + Species + Greenness + Season:Greenness	1003.70	1073.70	25.40	
Eaten/Not ~ Season + Species + Greenness + Season:Greenness + Season:Species	940.70	1074.70	26.40	
Eaten/Not ~ Season + Species + Greenness + Season:Species	965.76	1079.80	31.50	
Eaten/Not ~ Season + Species + Greenness	1030.20	1080.20	31.90	
Eaten/Not ~ Season + Species + Season:Species	1002.10	1112.10	63.80	
Eaten/Not ~ Species + Greenness	1075.60	1115.60	67.30	
Eaten/Not ~ Season + Greenness + Season:Greenness	1318.50	1354.50	306.20	

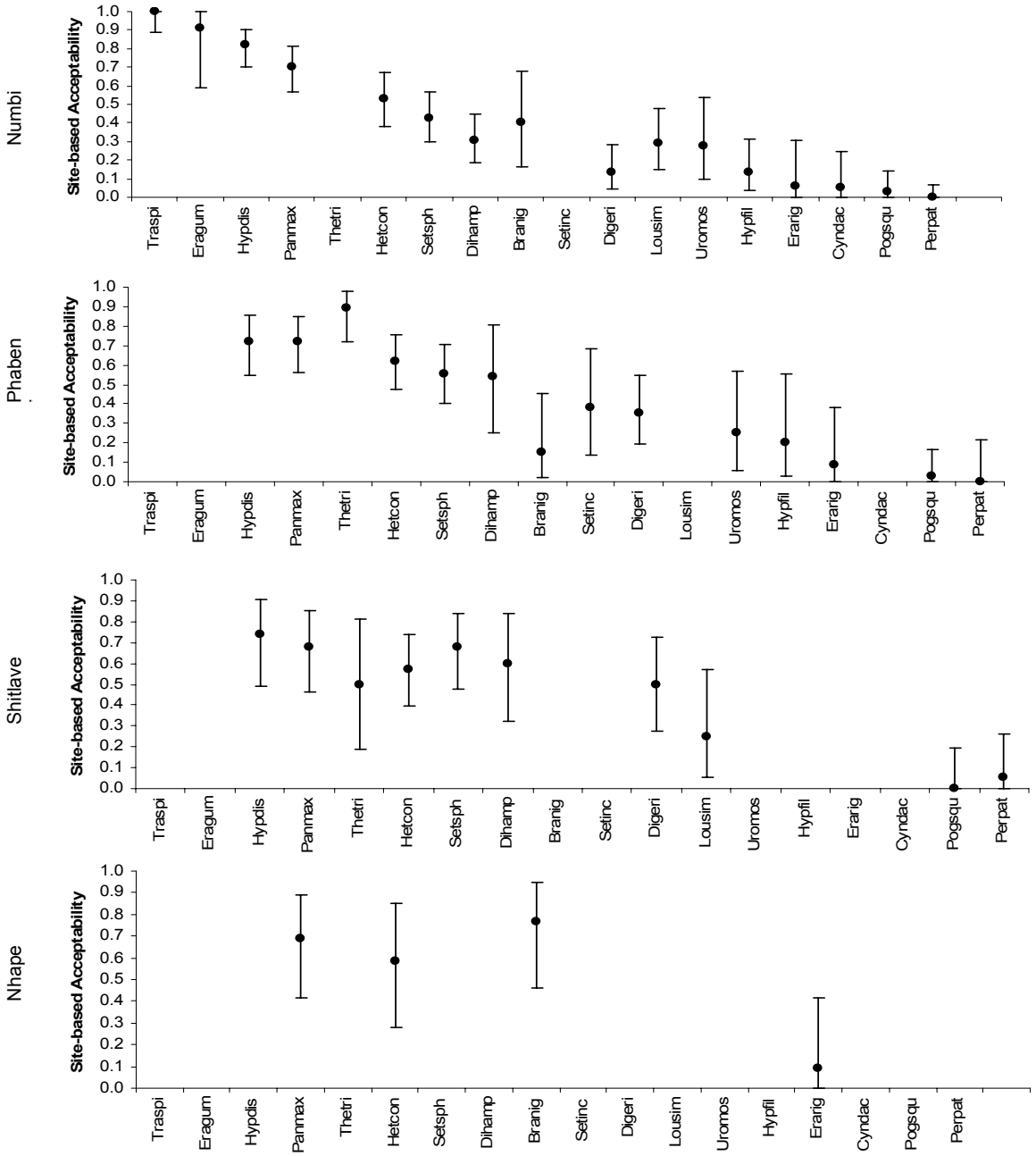

Figure 2.1: Comparison of site-based grass species acceptance by the four sable herds studied, amalgamated over all seasons considered. Based on their acceptability to the Numbi herd, the grass species are ranked from the most acceptable to the least acceptable. This sequence is retained for the remaining herds to highlight the changes in acceptability of each grass species to the other herds. Only species available in ten or more sites for each herd are represented. Vertical bars represent 95% binomial confidence limits. Traspi – *Trachypogon spicatus*; Eragum – *Eragrostis gummiflua;* Hypdis – *Hyperthelia dissoluta*; Panmax – *Panicum maximum*; Thetri – *Themeda triandra*; Hetcon – *Heteropogon contortus*; Setsph – *Setaria sphacelata*; Dihamp – *Diheteropogon amplectans*; Branig – *Brachiaria nigropedata*; Setinc – *Setaria incrassata*; Digeri – *Digitaria eriantha*; Lousim – *Loudetia simplex*; Uromos – *Urochloa mossambiciensis*; Hypfil – *Hyparrhenia fillipendula*; Erarig – *Eragrostis rigidior*; Cyndac – *Cynodon dactylon*; Pogsqu – *Pogonarthria squarosa*; Perpat – *Perotis patens.*

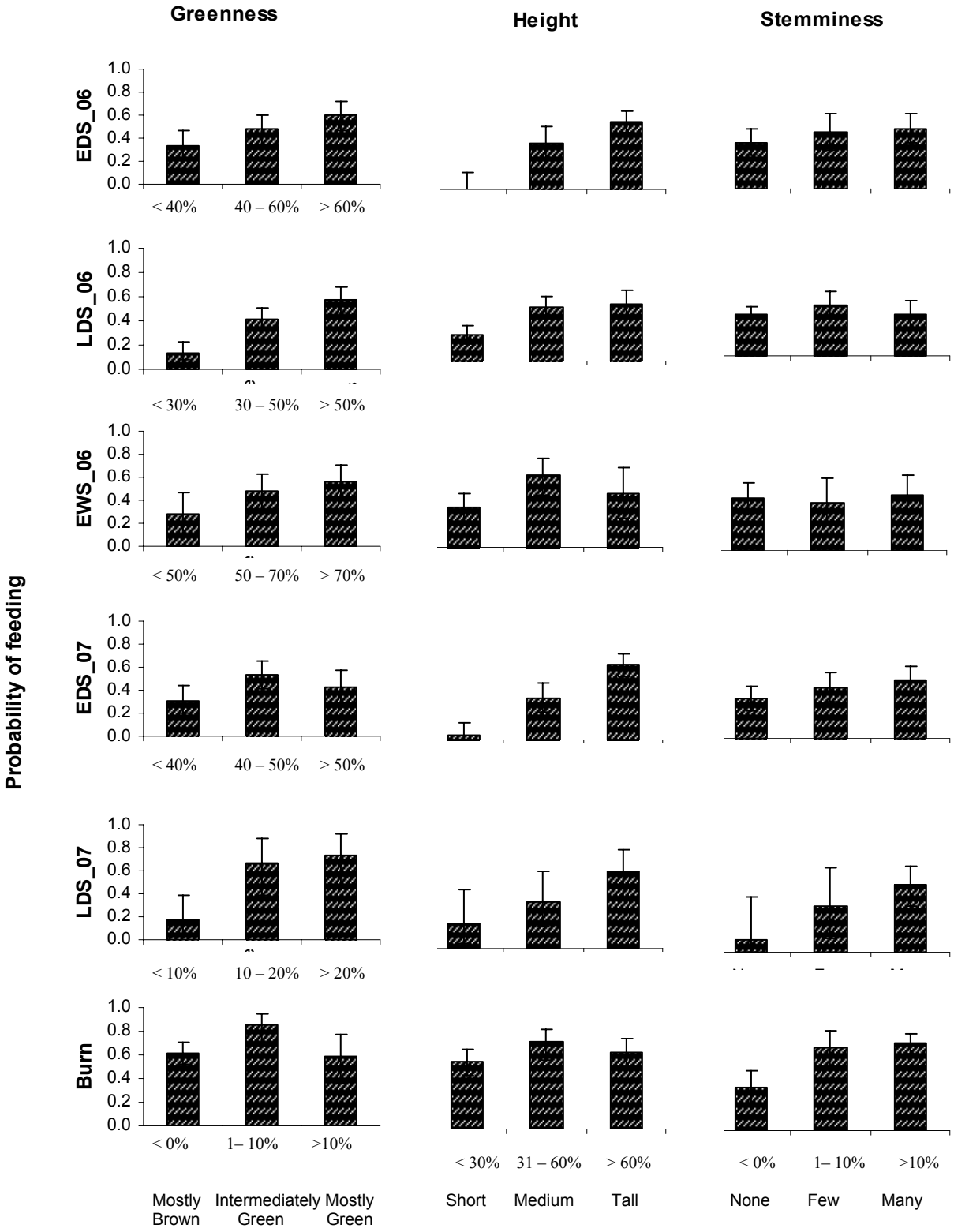

Figure 2.2: The probability of feeding within each category of greenness, height and stemminess irrespective of species identity. The stemminess categories refer to the proportion of tufts with many stems: None (0% of tufts with many stems); Few (less than 75% of tufts with many stems) and Many (75% or more of tufts with many stems). The vertical bars represent 95% binomial confidence intervals.

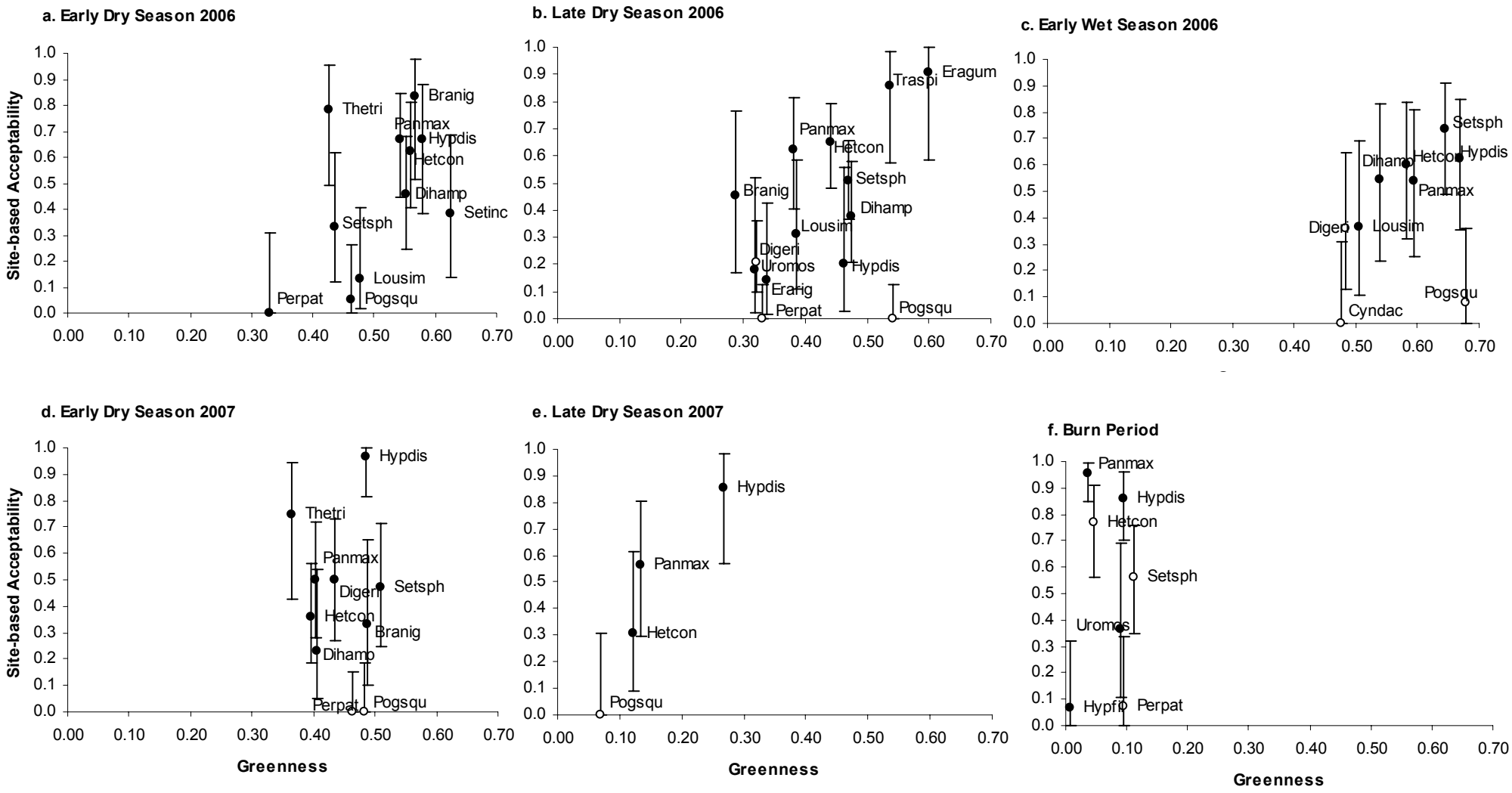

Figure 2.3: Seasonal acceptability of grass species in relation to the average seasonal greenness of the species. Closed circles represent species with an average seasonal height of more than 20 cm, whereas open circles represent species with an average seasonal height of less than 20 cm. The vertical bars represent 95% binomial confidence intervals.

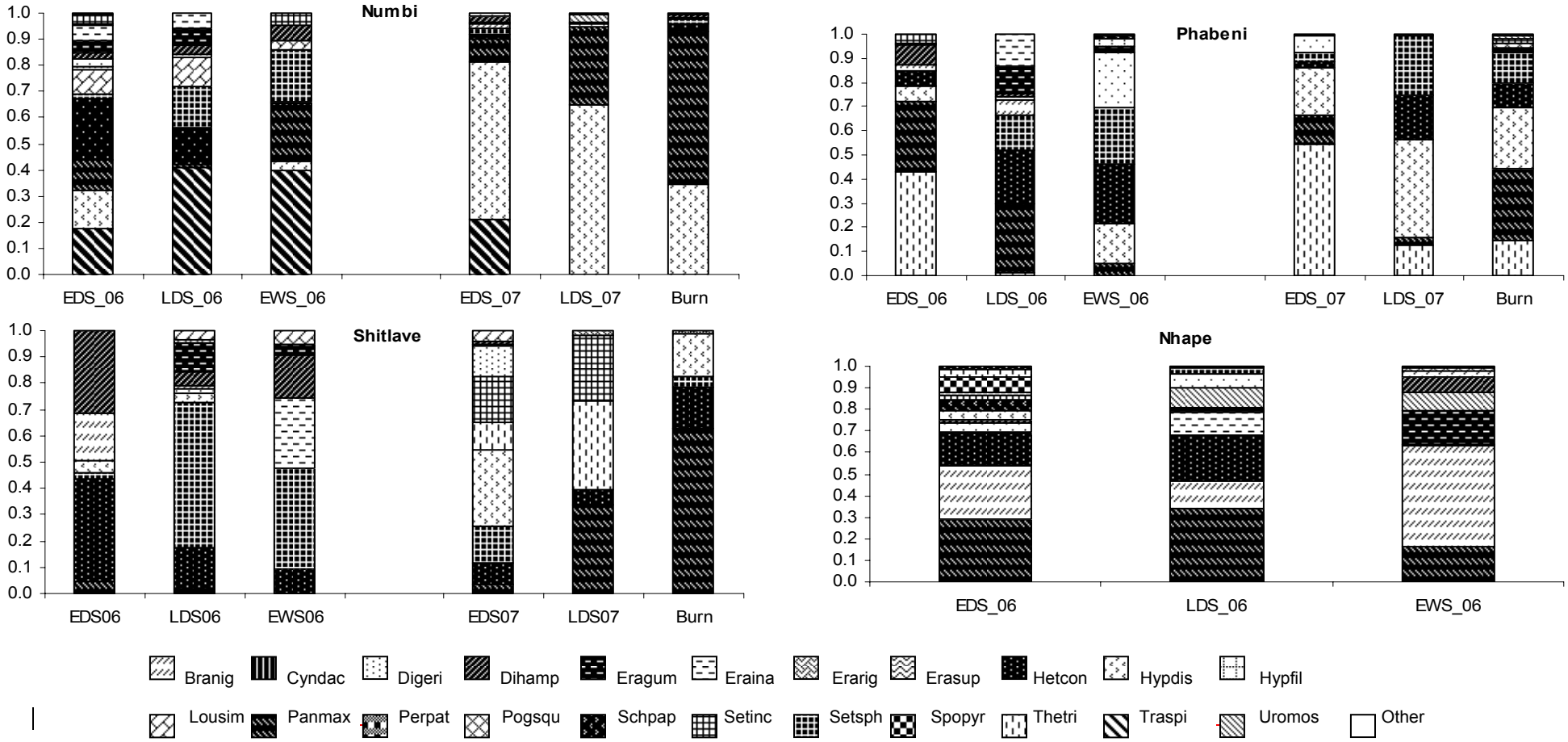

Figure 2.4: The seasonal change in contribution of different grass species to the dietary proportions of the four herds. Species with a dietary contribution of less than 10 % throughout all seasons are categorised as "Other". Branig – *Brachiaria nigropedata* Cyndac – *Cynodon dactylon*; Digeri – *Digitaria eriantha*; Dihamp – *Diheteropogon amplectans*; Eragum – *Eragrostis gummiflua*; Eraina - *Eragrostis inamoena*; Erarig – *Eragrostis rigidior*; Erasup – *Eragrostis superba*; Hetcon – *Heteropogon contortus*; Hypdis – *Hyperthelia dissoluta*; Hypfil – *Hyparrhenia filipendula*; Lousim – *Loudetia simplex*; Panmax – *Panicum maximum*; Perpat – *Perotis patens*; Pogsqu – *Pogonarthria squarrosa*; Schpap - *Schmidtia pappophoroides*; Setinc – *Setaria incrassata*; Setsph – *Setaria sphacelata*; Spopyr – *Sporobolus pyramidalis*; Thetri – *Themeda triandra*; Traspi – *Trachypogon spicatus*; Uromos – *Urochloa mossambiciencis*.

CHAPTER THREE

HABITAT FEATURES DISTINGUISHING FEEDING SITES FROM NON-FEEDING SITES OF SABLE ANTELOPE

ABSTRACT

The characteristics of the foraging habitat and the selection of feeding sites of sable antelope (*Hippotragus niger*) were investigated in the Kruger National Park. A detailed description of the areas used for foraging are given in terms of the presence of certain landscape attributes, in particular the catena position, tree and shrub cover and the presence of termitaria. Phenological characteristics of the sward, including the predominant greenness and height are also reported. Using generalised linear models, distinctions between feeding and non -feeding sites are investigated. Sable made very little use of bottomland areas while foraging. The foraging areas of the four herds included in the study differed widely in terms of tree cover, the greenness and height of the sward and the density of termitaria. In the distinction between feeding and non-feeding sites, the four herds responded similarly to all the habitat parameters considered. Through a process of model selection, area attributes that emerged as important explanatory factors in the distinction between feeding and non-feeding sites included tree canopy cover and the greenness of the sward. Although areas with greater tree cover and a relatively green sward were more likely to be utilised as feeding sites, the effect was

marginal and sable demonstrated an unexpectedly large acceptance of areas void of tree cover and areas with a predominantly brown sward.

INTRODUCTION

The landscape acts as a platform that provides food and water resources and shelter from the elements. Consequently, it plays an undeniably crucial role in the distribution, abundance and performance of animals and influences survival by enabling predator avoidance and nutrient acquisition. As a result, animals are expected to be selective in the areas that they occupy (Duncan & Gordon 1999).

The environment within which an animal occurs is characterised by a heterogeneous arrangement of forage quality (Mutanga *et al.* 2004). This variability is one of the major drivers determining the distribution of animals across landscapes (Seagle & McNaughton 1992).

In an undulating landscape, the effects of water runoff and its effect on soil nutrient concentrations is largely responsible for the spatially heterogeneous distribution of grass quality (Anderson & Talbot 1965, McNaughton 1983, McNaughton 1985, Seagle & McNaughton 1992, Mutanga *et al.* 2004). Nutrients and water moving down the catena collect in bottomlands maintaining green forage for longer during the dry season. However, the high water content also promotes the build up of structural carbohydrates (Bell 1970, McNaughton 1985, Scoones 1995, Scholes *et al.* 2003). Thus, bottomlands may provide a nutritional benefit during the dry season when green forage is scarce elsewhere. Conversely, due to the high fibre associated with bottomland foliage, grazers

may benefit from foraging further up the catena when green forage again becomes more widely available (Bell 1984).

Soil enrichment underneath tree canopies occurs as a result of the nutrient pump mechanism whereby tree roots take up nutrients from deeper soil layers, inaccessible to grass roots, and from outside the canopy reach, concentrating these nutrients in the topsoil underneath the canopy through litterfall (Scholes 1990). Treydte *et al.* (2007) showed significant increases in leaf nitrogen and phosphorus levels and lower stem:leaf ratios and dead:living leaf material associated with sub-canopy grass. In addition, the highly palatable grazing grass, *Panicum maximum* grows best under shady growing conditions and is therefore frequently found under tree canopies (Van Oudtshoorn 1999). Georgiadis & McNaughton (1990) demonstrated how *P. maximum* maintains high levels of crude protein despite growing on relatively infertile soils and attributed this to the localised enrichment of soils underneath tree canopies where this species is often found.

At a finer scale, the quality of an area is governed by variation in sward composition and phenology and animals are expected to selectively utilise patches of high quality (O'Reagain 2001). Grazers are expected to focus their foraging activities in areas that retain green grass as the consumption of green grass would be nutritionally advantageous (O'Reagain & Owen-Smith 1996). Similarly, tall grass swards are often in later growth stages and due to the structural build up of carbohydrates in individual plants (Van Soest 1987), such swards would contain high densities of grass characterised with high fibre content.

The heterogeneous arrangement of forage quality may also be brought about by structures such as termite mounds which have long been associated with elevated mineral

nutrients (Lee & Wood 1971). The richer chemical content linked to termite mounds has frequently been implicated in studies examining herbivore preferences for the vegetation growing on termite mounds (Loveridge & Moe 2004).

Fire improves the quality of grassland forage through the removal of dead biomass and by stimulating resprouting. Grazers have been repeatedly shown to utilise the fresh growth following a fire event (Heitkönig & Owen-Smith 1998, Gureja & Owen-Smith 2002, Tomor & Owen-Smith 2002, Traill 2004).

Concepts of habitat selection cannot be considered in isolation and must be melded with the constraints of predation risk. In a predator rich environment, animals are expected to modify their foraging behaviour by opting to feed in areas offering less preferred food, but facilitating predator detection (Sih 1980). Shrub cover would be expected to reduce visibility more than tree cover and is likely to prevent timely predator detection (Elliot *et al.* 1977). According to the "predation-sensitive food" hypothesis, herbivores would be more willing to forage in areas of higher predation risk during dry seasons, when food resources become scarce (Sinclair & Arcese 1995).

Prior studies particularly focused on aspects of sable foraging have found sable to forage in a medium to tall sward, ranging from 4 to 40 cm in height (Grobler 1981, Parrini 2006). Several studies have shown that sable concentrate their dry season foraging activities in edaphic grasslands on floodplains or drainage lines (Jarman 1972, Estes &Estes 1974, Grobler 1981, Magome 1991), attributing this to greenness retention. In addition, the majority of studies have found sable to forage in open savanna woodlands (Sekulic 1981) particularly during the wet season (Jarman 1972, Magome 1991, Parrini 2006). Estes & Estes (1974) have described giant sable (*H. n. variani*) as foraging in

woodlands during the wet season and only moving onto open drainage line grasslands during the dry season. Comparing dry season habitat preferred by sable between five different reserves, Wilson & Hirst (1977) report that the sable occurring in parks where historical records show that they have naturally occurred in the past, utilise areas with a significantly higher lateral visibility.

In the present study, I describe the characteristics of the habitat used by sable during the times when they are likely to be foraging. Within sable foraging areas, I also attempted to identify the differences between locations used by sable for feeding and those visited in which no signs of feeding were evident. As herbivore distribution is determined by multiple drivers including nutritional considerations and constraints imposed by predation, I chose to focus on selection within areas already likely to be foraging areas in an attempt to eliminate some of the broader scale influences on habitat selection. As such, the aim of this study was to focus only on recognising those habitat characteristics specifically distinguishing locations in which sable chose not to feed. The predictions made included:

- The grass sward in locations where sable feed in would be greener than the sward in non-feeding areas.
- Locations where sable fed in would be in the vicinity of termitaria more often than non-feeding sites.
- During the dry season sable would be foraging in areas that are likely to retain green grass. Consequently,

    - During the times that sable are likely to be foraging, they would be located in bottomland areas more often in the late dry season than during seasons of abundant water and green forage elsewhere.
    - During the late dry season, sable would occur more frequently in areas with high levels of canopy cover when foraging, relative to the more benign seasons.
- Similarly, during the dry season sable would feed more frequently from areas characterised by the retention of green grass. As such,
    - Visited locations with signs of feeding would be located in bottomland areas more frequently in the late dry season than during the seasons when water and green grass would be expected to be more readily available elsewhere.
    - During the dry season, feeding locations would have a greater degree of tree canopy cover than locations in which sable chose not to feed.
- The grass sward in locations with signs of feeding would be taller than the sward in non-foraging locations.
- Feeding locations would be expected to have a lower shrub cover compared to non-feeding locations.

METHODS

Study area

The study was carried out in the south-western section of the Kruger National Park (hereafter KNP) (31°12′-31°24′E, 25°02′-25°13′S) in an approximately 400 km^2 area surrounding Pretorius Kop camp. The study area receives an average annual rainfall of approximately 737 mm (calculated as a running average over a 60 year period; South African Weather Service). Approximately 80% of the annual rainfall is received between October to April. During the two years within which the study was conducted, the first year was a relatively wet year, receiving approximately 25% more rain than the long term mean while the second year was relatively dry, receiving 20% less than the long term average (see Appendix I; South African Weather Service).

The study area is mostly characterised by sandy soils of granitic origin. Due to the relatively high rainfall received in this area, these soils are prone to leaching and are considered to be less fertile (Bell 1984). Additionally a gabbro sill transverses the study area Broad-leaved species such as *Combretum* spp, *Sclerocarya birrea* and *Terminalia sericea* occur on the granite derived soils (Venter *et al.* 2003), whereas the gabbro support areas characterised by relatively low levels of woody cover with few trees and moderately dense shrub cover (Venter 1990). A more detailed description of the study area is given in the general introduction chapter (Chapter 1).

Study design

A detailed description of the study design is given in the introduction chapter (Chapter 1). In June 2006 four adult females each belonging to a different breeding herd were fitted with GPS-GSM collars. These collars used the Global Positioning System and the Global System for Mobile Communications to record the location of each animal.

Features characteristic to the habitat were recorded from May to November during 2006 and 2007. Observations on particular herds were performed sequentially by switching to the next herd after every three days of data collection. During periods of direct observation, the collar interval were set at hourly and changed to a six-hourly interval in between observation periods. Studying feeding activity of sable antelope during the months August to October, Grobler (1981) noticed a peak in feeding activity between 06:00 – 09:00 and another peak at 14:00 – 17:00. Although he did not attempt to record night time feeding, he mentions that sable were often active before sunrise and after sunset. As such, to incorporate sites during which sable were likely to be feeding, the locations where sable were recorded in the mornings (more or less between 05:00 - 10:00) and in the afternoons (more or less between 15:00 – 19:00) (see Appendix II) were used to collect habitat data.

Herd locations were examined at least a day after the presence of sable so as not to disturb their normal feeding patterns. At each location, a 10 m radius adjoining the recorded GPS location was searched for fresh bites, the presence or absence of which defined the area as a feeding site or a non-feeding site. At each site, I recorded the distance of the nearest sable spoor from the GPS location as well as the presence of fresh

dung piles to serve as an indication of the accuracy of the location. The presence of spoor and/or dung of any other grazer were noted and classified as fresh or old, to be able to substantiate the claim that any foraging activity in the area can be assumed to be indicative of sable foraging (see Appendix III for detailed results). In only 30% of non-feeding sites was neither sable spoor nor fresh dung found.

Subsequent hourly locations were not considered independent and consequently locations were pooled based on whether it was a feeding or a non feeding location and whether the sable visited the location in the morning or the afternoon. Thus all the morning feeding locations on the same day were amalgamated and formed a separate sample from the morning non-feeding locations, and also from the afternoon feeding locations and the afternoon non-feeding locations. Consequently each day yielded a maximum of four samples i.e. morning feeding sites amalgamated, afternoon feeding sites amalgamated and similarly for non-feeding sites, each sample consisting of one or more hourly locations.

Data collection

Data collected included structural features of the vegetation, topographical information and more detailed information concerning the phenological stage of the grass layer. At both feeding and non-feeding sites, I recorded the position of the site on the catena, classified into five categories: 1) bottomland, defined as the flat section at the base of the catena; 2) footslope, defined as the start of the incline at the base of the slope; 3) midslope, defined as the middle area of the catena with the maximum gradient; 4)

topslope, represented by a reduction in slope gradient towards the top of the catena and; 5) upland, defined as the flat section at the top of the catena. For analysis the bottomland and footslope were subsequently combined into a single category as well as the topslope and crest, yielding three categories, namely lower slope, midslope and upper slope. The catena position of the morning or afternoon sample, each of which consisted of several hourly locations, was classified based on the catena position represented in the majority of the locations comprising the sample. If a sample did not contain a majority of a particular catena position, the value for catena position was treated as a missing data point. A catena position could not be allocated to approximately 16% of the samples, leaving 285 samples for which catena position could be described.

Woody canopy cover was categorised, based on a crude height estimation, as trees (> 2.5 m in height) and shrubs (< 2.5 m in height). The canopy cover of trees and shrubs were then separately assessed within a 25 m radius and recorded using Walker's 8-point scale (Walker 1976). To combine site cover values into the morning or afternoon samples, the midpoint value of the recorded cover category was allocated to each site and then averaged across all the sites comprising the sample. The shrub and tree canopy cover of the samples was then reclassified based on data percentiles as low, medium or high. For shrub and tree cover, 0 - 10% represented a low percentage cover, 11 – 20% represented the medium cover category and > 20% represented the high cover category.

Characteristics of the sward, specifically sward height and the greenness of the leaves, were estimated in a 25 m radius. Sward greenness was estimated again using Walker's 8-point scale and combined into a morning or afternoon sample by similarly allocating the midpoint value to the relevant site and subsequently averaging across sites

to obtain a greenness value particular to the sample. Two techniques were used in the allocation of greenness categories. Firstly, using data percentiles of the available greenness across all seasons and in the foraging areas of all herds, sample greenness was reclassified as mostly brown (≤ 30% of the leaves were green), intermediately green (more than 30% but less than 60% of the leaves were green) or mostly green (≥ 60% of the leaves were green). This set of greenness categories was used in the description of the greenness available in the foraging areas i.e. feeding and non-feeding sites combined, of the different herds and throughout the various seasons. Throughout the remaining text this set of greenness categories will be referred to as the absolute greenness categories. Secondly, again using data percentiles, a separate set of greenness categories were assigned for each season separately, so that the greenness categories do not represent absolute values but rather reflect relative greenness in that season. This second set of greenness categories were used to establish the effect of greenness on the probability of feeding during times of different greenness availability. Throughout the remainder of the text, this set of greenness categories will be referred to as the relative greenness categories. An approximation of the leaf height of the sward was obtained by estimating the predominant sward height of the leaves within a 25 m radius and again averaging across sites to obtain a sample value, which was reclassified based on data percentiles as short (< 20 cm); medium (21 - 35 cm) or tall (> 35 cm). Furthermore, the presence of a termitarium within a 25 m radius was recorded.

Statistical analysis

To describe the characteristics of the foraging area i.e. the areas in which they were located during the times when they were expected to be foraging regardless of whether the sable fed or not, the relative proportions of each of the habitat features in foraging areas were estimated. The absolute greenness categories were used to describe the foraging areas. Differences between herds and across seasons in the prevalence of these habitat features in foraging areas were tested using Pearson's χ^2 with significance level $P < 0.1$. Differences in the greenness of the swards across catena positions were tested using a one-way analysis of variance with significance level once again set fairly conservatively at $P < 0.1$.

Analysis was performed in R (R Development Core Team 2008). Generalized Linear Models (GLMs) were employed as analysis technique, considering the feeding or non-feeding distinction between samples as the response. The binary nature of the response necessitated a binomial error structure and a logit link (Crawley 2007). In GLM's all the predictor variables are combined to form a single linear predicted that is related to the response through the link function. By using a logit link, the odds ratios are computed from which the probability of a particular response can be calculated for each combination of predictor variables.

Akaike Information Criterion (AIC) is a model selection technique that emphasizes parsimony by penalizing models for having large numbers of parameters and is calculated as AIC = -2 × log-likelihood + 2(p+1) where p represents the number of parameters in the fitted model. Because the explanatory variables are categorical the

number of levels within each category is taken into account when computing the number of parameters. The parameters are calculated as $\sum_t(n-1)+1$ where t represents the number of categorical variables and n represents the number of levels within each variable. The levels within each categorical explanatory variable are treated as "dummy variables", where each term in the model estimates relates to a particular level within each category (Agresti 1996).

The generation of a suite of candidate models needs to be focused on the particular questions considered and the inclusion of a category should be justified based on a clear theoretical understanding of its role in the system under investigation (Johnson & Omland 2004). The use of AIC enables the comparison of the candidate models, which can be ranked in order of their relative explanatory power. Moreover, these models can then be scaled to reflect the relative strength of evidence for each model (Burnham & Anderson 2001). This is achieved through the calculation of the AIC differences (Δ AIC) which allows for the comparison of each model relative to the model with the lowest AIC value within the candidate set (Johnson & Omland 2004). Burnham & Anderson (1998) suggests a rough guideline whereby models with a Δ AIC of 2 or less may be viewed as having a comparable level of support to the model with the lowest AIC value. The selection of the best model is then based on the comparison of such AIC differences and the overall complexity of each model.

The proportion deviance explained, calculated as (null deviance – residual deviance)/null deviance can be used to estimate model fit (Wood 2006). This value may be viewed as equivalent to the more familiar R^2 value used in linear modelling and could elucidate on the adequacy of a specific model. However, as this "adjusted R^2 value does

not take into account the number of parameters and thus the complexity of the model, it is unsuitable for model selection.

Differences between herds in the effect of each landscape variable on the probability of feeding were tested using likelihood ratio tests with significance level $P < 0.1$. Although model selection was performed through the examination of AIC differences, likelihood ratio significance testing was employed prior to the formulation of a set of candidate models. This was done in an attempt to reduce the number of factors and avoid the problems associated with incomplete contingency tables. Ultimately to justify the amalgamation of the data on different herds and to make inferences regarding all sable included in the study.

The likelihood ratio test provides a means of assessing the change in deviance by estimating the change in likelihood caused by the removal of a term, approximated by a χ^2 statistic. The process involves the systematic removal of terms, starting with the highest order terms and subsequently examining the resultant change in deviance. Large differences in deviance indicates a relatively poor fit of the simplified model compared to the more complex model and therefore signify the substantial contribution of the removed term to the goodness of fit (Agresti 1996, Ramsey & Schafer 1997, Quinn & Keough 2002).

The seasonal divisions were based on available greenness measured as the average monthly greenness of the sites (Appendix V). Considerable differences in rainfall between the two years during which the study was conducted (Appendix I) resulted in substantial variation in the available greenness in corresponding seasons. Furthermore a fire burnt through the entire study area during August of 2007 and

sufficient regrowth was only evident after September. This prompted the partitioning of both years into seven separate seasons i.e.:

- early dry season of 2006 (May to July 2006; hereafter EDS_06);
- late dry season of 2006 (August to September 2006; hereafter LDS_06);
- early wet season 2006 (October to November 2006; hereafter EWS_06);
- early dry season of 2007 (May and June 2007; hereafter EDS_07);
- late dry season of 2007 (July 2007; hereafter LDS_07);
- the burnt period (August and September 2007; hereafter Burn); and
- the period following the flush of regrowth (October and November 2007; hereafter Flush).

Apart from season as a model factor, the following explanatory variables were considered in the distinction between feeding and non-feeding sites: Catena position, tree canopy cover, shrub cover, the presence of termitaria, relative greenness and approximate sward height.

RESULTS

Habitat attributes were recorded at a total of 571 GPS locations of which 320 (56%) were feeding sites (see Appendix VI for full description of sample sizes). Combining the total number of sites into morning and afternoon foraging sessions, a total of 338 samples were obtained of which 182 (53.8%) were feeding site records.

Foraging area features

Catena position

In only five samples (approximately 1%) were the majority of sites located in a bottomland. However, in cases where the GPS location was situated on the lower section of the slope i.e. downslope areas, the 25 m radius over which data were collected often included bottomland areas. Thus, the broad 25 m radius resolution of data collection often made the distinction between bottomlands and lower slope areas somewhat ambiguous and prompted the amalgamation of catena categories into lower slope, midslope and upper slope as explained previously.

There were no significant differences between the four herds in their use of catena positions ($\chi^2 = 7.79$, d.f. = 6, P = 0.25). Sable generally foraged in midslope and upper catena areas (Figure 3.1). In 2006, an average of 15% of foraging samples was located in the lower slope areas. During the drier year of 2007, sable appeared to reduce their usage of bottomland areas, with only 8% of foraging samples located in bottomlands. This difference however, was not statistically significant ($\chi^2 = 1.81$, d.f. = 1, P = 0.18).

Tree canopy cover

The use of the range of tree cover during foraging bouts differed significantly between herds ($\chi^2 = 13.47$, d.f. = 6, P = 0.036; Figure 3.2). The Numbi herd foraged fairly frequently in areas with high tree cover (on average approximately 30% across all

seasons), whereas the other three herds foraged in high tree cover less often (average use of high canopy cover across all seasons were 18% for Phabeni, 22% for Shitlave and 15% for Nhape). The Numbi herd foraged in areas with high tree canopy cover more frequently during the late dry seasons of 2006 and 2007 compared to the relatively benign early wet season of 2006 and the flush period ($\chi^2 = 9.55$, d.f. = 1, P = 0.002). Although the Phabeni herd appeared to forage more often in high canopy cover during the late dry season of 2006 the differences was not statistically supported ($\chi^2 = 0.4$, d.f. = 1, P = 0.53). The late dry season of 2007 and the burn period were distinct in that none of the Phabeni herd's foraging areas were located in high tree cover during this time ($\chi^2 = 7.11$, d.f. = 1, P = 0.008). A similar pattern was seen in the Shitlave herd's use of foraging areas. During the early to late dry season of 2006, more than 50% of foraging sites were located in areas with above 20% canopy cover and the Shitlave herd moved into more open areas with tree cover below 20% during the early growing season. However, the Shitlave herd's use of high tree cover differed significantly between 2006 and 2007 ($\chi^2 = 6.56$, d.f. = 1, P = 0.01), where during the relatively drier year of 2007, very few of the Shitlave herd's foraging areas were located in areas with high canopy cover. The Nhape herd showed no significant seasonal difference in their use of high tree cover ($\chi^2 = 0.71$, d.f. = 2, P = 0.7; Figure 3.2).

Shrub cover

There were no significant differences between the herds in their use of foraging areas ranging in shrub cover ($\chi^2 = 7.79$, d.f. = 6, P = 0.25). Approximately 28% of the

sable foraging areas were located in areas with low shrub cover. In the early dry season of 2006 sable foraged more frequently in areas with less than 10% shrub cover than areas of more than 10% shrub cover ($\chi^2 = 4.44$, d.f. = 1, P = 0.035). Throughout the remainder of the study period sable did not significantly alter their use of foraging areas of low shrub cover (Figure 3.3).

Sward greenness

The available greenness within the foraging areas of the four herds differed significantly ($\chi^2 = 15.15$, d.f. = 6, P = 0.019). During 2006, the Nhape herd foraged more often in swards of less than 30% greenness compared to the other herds. On average Nhape foraged in swards of low greenness in almost half (46%) of the foraging locations recorded, compared to 11% for Numbi, 26% for Phabeni and 17% for Shitlave. Throughout 2006, there were no significant seasonal differences in the relative proportion of foraging sites that contained swards of low greenness (Numbi: $\chi^2 = 2.58$, d.f. = 2, P = 0.28; Phabeni: $\chi^2 = 1.87$, d.f. = 2, P = 0.39; Shitlave: $\chi^2 = 2.4$, d.f. = 2, P = 0.30; Nhape: $\chi^2 = 0.53$, d.f. = 2, P = 0.77).

The three herds for which data were collected during 2007 all significantly increased the frequency with which they foraged in predominantly brown grass swards during the late dry season and during the burn period (Numbi: $\chi^2 = 7.54$, d.f. = 1, P = 0.006; Phabeni: $\chi^2 = 21.74$, d.f. = 1, P < 0.0001; Shitlave: $\chi^2 = 21.4962$, d.f. = 1, P < 0.0001). As expected, all herds foraged in predominantly green swards (more than 30% green) during the growing seasons (Figure 3.4).

Sward height

Sward height differed significantly between the foraging areas of all four herds (χ^2 = 28.43, d.f. = 6, P = 0.0001) yet there were no consistent trends across herds (Figure 3.5). The four herds tended to forage in swards taller than 20 cm in the two dry seasons and feed in swards shorter than 20 cm more frequently during the early wet season, although this pattern was also not consistent for every herd. During the burn all the grass in the medium to tall category i.e. grass taller than 20 cm were patches of unburnt grass. Burnt remains made up 76% of the short swards while only 13% of the short swards were located in unburnt patches and only 11% were regrowth (Figure 3.5).

Presence of termitaria

Foraging areas of the various herds differed in terms of the presence of termitaria (χ^2 = 9.18, d.f. = 3, P = 0.03). Again there seemed to be no consistent pattern in the differences between herds (Figure 3.6). The Nhape, Numbi and Shitlave herds did not differ significantly between seasons in their use of foraging areas where termitaria were present and foraged in the vicinity of termitaria on average in 61%, 33% and 46% of the locations respectively. Only the foraging areas of the Phabeni herd changed significantly seasonally although the pattern appeared ambiguous. The Phabeni herd foraged significantly more often in the vicinity of termitaria during the early wet season of 2006 compared to the early dry season of 2006 (χ^2 = 4.39, d.f. = 1, P = 0.04). Similarly, they

foraged significantly less often close to termitaria during the early dry season of 2007 compared to the rest of 2007 ($\chi^2 = 18.39$, d.f. = 1, $P < 0.0001$; Figure 3.6).

Distinction between feeding and non-feeding areas

Herd differences

The removal of the interaction term between herd and each of the landscape features each time yielded an insignificant loss of fit, indicating that the effect that each of the habitat features had on the probability that sable would feed in an area was not significantly different between herds (Catena: $\chi^2 = 359.2$, d.f. = 257, $P = 0.11$; Tree cover: $\chi^2 = 354.34$, d.f. = 257, $P = 0.35$; Shrub cover: $\chi^2 = 354.39$, d.f. = 257, $P = 0.7$; Sward greenness: $\chi^2 = 347.08$, d.f. = 257, $P = 0.45$; Sward height: $\chi^2 = 361.16$, d.f. = 257, $P = 0.21$; Termitaria presence: $\chi^2 = 359.85$, d.f. = 258, $P = 0.69$). Thus, the data for the four herds were combined for all remaining analysis on the distinction between feeding and non-feeding areas.

Multiple model comparisons

The best supported yet most parsimonious model amongst the candidate set was the model including the additive effects of season, tree cover and sward greenness with an adjusted R^2 value amounting to 0.094 (Table 3.1).

Areas with a medium to high canopy cover were more likely to be used for feeding whereas sable were approximately 20% less likely to feed in areas with a low canopy cover compared to areas with a high tree cover. However, approximately 30% of sable feeding sites were located in areas of low tree cover (Figure 3.7). There was no significant interaction between season and tree cover, indicating that the preference of sable for greater tree cover was not restricted to the late dry season, as predicted, but was apparent throughout the year.

Models omitting greenness received much weaker support that the models in which it was retained (Table 3.1). Sable were more likely to feed in an area if the sward was relatively green compared to the greenness encountered in that season. Sable were approximately 30% more likely to feed in areas of the highest greenness than in areas of the lowest greenness available. Nevertheless, despite the increased probability of sable to disregard areas with a sward of relatively low greenness for feeding sites, approximately 30% of feeding areas were within swards of the lowest greenness available in the season (Figure 3.7).

DISCUSSION

Sable did not forage more often in bottomland areas during the dry season, nor were they more likely to feed in bottomland areas. The Numbi herd foraged more often in areas with high tree cover during drier times, while the other three herds foraged more often in low tree cover during the drier year of 2007. All herds, however, were less likely to feed in areas of low tree canopy cover compared to areas of medium to high tree cover.

During the good rainfall year the majority of foraging areas were above 30% green, yet during the bad rainfall year the greenness within foraging areas fell below 30% greenness. Nevertheless, all four herds were more likely to feed in swards of the highest greenness. Despite this preference, sable still often fed in swards with little greenness. There were no consistent patterns among herds and across seasons in sable's use of shrub cover, the height of the sward or the presence of termitaria while foraging and each of these three variables had a negligible effect on whether sable would feed in an area.

The relatively low R^2 value obtained for the best supported model signifies a weak influence of the factors specified. Alternatively, non-feeding sites may have been misidentified as a result of inaccurate GPS location estimates. However, fresh signs of sable presence i.e. fresh dung or spoor, were found at 73% of all non-feeding sites despite the grass layer at many sites often concealing spoor (Appendix III). Fresh sable spoor were found in 65% of all non-feeding sites and the average distance of the spoor from the central quadrat at non-feeding sites in particular was 69 cm. This does not imply that the GPS locations were precise within 69 cm, as the closest spoor was not necessarily from the collared animal and could have been from any of the individuals in the herd. As such, I argue that the effect of miss-specified non-feeding sites should be minimal.

Previous studies on sable habitat use had indicated how sable utilise valley bottomlands such as floodplains during the late dry season to exploit the characteristic retention of green grass associated with such areas (Jarman 1972, Estes & Estes 1974, Magome 1991, Parrini 2006). However, differences in geology and climate result in many variations on bottomland structure. The Pretorius Kop area falls mainly in the Skukuza land system which is characterised by very distinct hillslope profiles (Venter

1990). According to Venter *et al.* (2003), many of the drainage lines in the Skukuza land system are still actively eroding. This results in a hillslope type with incised bottomlands and little accumulation of alluvium. However, during the late dry season of 2006 and the burn period, the swards in bottomland foraging areas were significantly greener than the swards further up the catena. Macandza (2009) and Henley (2005) both investigating aspects of sable habitat use in the Punda Maria section of the KNP, also observed sable to forage in upland regions more frequently and Macandza (2009), similarly attributed it to bottomland structure, but also to enhanced competition with buffalo herds that utilise the bottomlands.

The greater tree cover in the foraging areas of the Numbi herd may have been due to a greater availability of high tree cover in the Numbi range, yet the broader availability of landscape features was beyond the scope of this study. Although sable foraging areas occurred across the entire range of tree canopy cover recorded, sable were slightly less likely to feed in areas of low tree canopy cover than in areas of medium to high tree canopy cover. *Panicum maximum* has been described as a palatable, shade loving species, often found under tree canopies (Van Oudtshoorn 1999). In this study sable have been shown to exhibit a high acceptability for *P. maximum* (Chapter 2). Conceivably, the abundance of *P. maximum* underneath tree canopies may influence sable's dependence on areas with elevated tree cover. Apart from the effect of tree cover on grass layer composition, tree canopies may also enhance soil nutrient levels through the effects of litterfall and the nutrient pump mechanism (Scholes 1990) which may augment nutrient levels and thereby the attractiveness of grass tufts growing underneath.

Nevertheless, sable foraged readily in swards occurring in areas with low tree cover and also often fed in areas of low tree cover. However, *Heteropogon contortus* and *Hyperthelia dissoluta*, both of which have been shown to be highly acceptable to sable and make up a considerable fraction of sable diet (Chapter 2) are more commonly associated with open grassland (Van Oudtshoorn 1999; personal observation). This may explain sable's use of areas with low tree cover, despite their preference for areas of intermediate to high tree cover.

During the growing seasons when green grass were abundant, sable foraged in areas with swards above 30% green. During the more limiting times however, the swards of almost all of the foraging areas used by sable were below 30% green. Although sable were less likely to feed in predominantly brown swards, an unexpectedly large proportion of feeding sites (approximately 30%) were still located in mostly brown swards. However, within the foraging patch, sable are also more likely to feed from green species and more likely to feed from a species when it is green (Chapter 2). Although sable still foraged in predominantly brown swards, they may be selective for green growth at a finer level.

The tendency of sable to forage in areas with a shorter sward during the early wet season and the flush period merely reflects the increased abundance of nutritious fresh growth during the growing seasons. As young plant material contain fewer structural carbohydrates (Van Soest 1987), sable would benefit from foraging in areas where abundant young growth is available. During the nutritionally limiting seasons however, sable foraged more readily on taller swards. Wilmshurst *et al.* (2000) suggest that during

the dormant season, large grazers should feed in tall, high biomass swards that offer greater intake rate.

Only one herd differed seasonally in the frequency with which they foraged in the vicinity of termite mounds, yet the pattern was inconsistent. The presence of termitaria did not influence whether sable would feed in an area. However, according to Arshad (1982) the soil nutrient enrichment effects of termite mounds are far reaching and have been shown to affect areas within a radius of up to 25 m of the actual mound. Therefore, sable may nutritionally benefit merely by foraging in areas with a high density of termite mounds.

Use is often compared to general availability within the home range. Johnson (1980) warns against defining a resource as available simply because it is present. As food selection is but one of multiple considerations influencing animal movement, presence of the food resource within the home range does not necessarily equate to the resource being available to the animal itself. By attempting to describe the distinction between feeding and non feeding areas within what is already believed to be foraging areas, hopefully partly eliminated at least some of the influences that operate at higher levels of selection.

However, this work would have been greatly improved through the inclusion of the broader level of selection i.e. selection of foraging areas. Regrettably, without data on the availability of landscape features within the broader home range, no inferences could be made regarding selection of the landscape attributes in foraging areas which greatly complicates interpretation. Although the investigation of selection at this level

was beyond the scope of this study, it would be advisable for future research on sable habitat use.

In general, sable seem to be more tolerant than expected of a wide range of factors that would influence forage quality and relative predation risk. Although tree cover and the relative greenness of the sward influenced the probability that sable would feed in an area, the effect was generally small and many feeding areas were located in open areas or areas with a predominantly brown sward. Sable did not respond in terms of their likelihood to feed to aspects such as catena position, sward height or the presence of termitaria, all of which would be expected to influence the distribution and availability of nutrients. Similarly, sable foraged and fed in areas ranging from open to shrubby and did not respond to possible changes in predation risk normally associated with higher shrub densities.

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TABLES

Table 3.1: Multiple models concerning the distinction between feeding and non-feeding sites, as influenced by the attributes of an area. The highlighted model is the best model from the candidate set. The statistics reported include the residual deviance, the AIC, the delta AIC value and the value equivalent to the R^2

Model	Res Dev	Res df	AIC	Δ AIC	R^2
F.N ~ Season + Catena + Tree + Green + Height + Season:Catena + Season:Height	269.76	224	347.76	0	0.256
F.N ~ Season + Catena + Tree + Shrub + Green + Height + Season:Catena + Season:Height	266.97	222	348.97	1.21	0.264
F.N ~ Season + Tree + Shrub + Green	323.81	250	349.81	2.05	0.107
F.N ~ Season + Tree + Green	328.63	252	350.63	2.87	0.094
F.N ~ Season + Tree + Green + Termitaria	327.73	251	351.73	3.97	
F.N ~ Tree + Green	342.19	258	352.19	4.43	
F.N ~ Tree + Shrub + Green	338.66	256	352.66	4.9	
F.N ~ Season + Green + Height	332.62	252	354.62	6.86	
F.N ~ Green	348.84	260	354.84	7.08	
F.N ~ Season + Catena + Tree + Shrub + Green + Height + Termitaria + Season:Catena	295.93	233	355.93	8.17	
F.N ~ Season + Tree + Shrub + Green + Season:Tree	313.99	238	363.99	16.23	
F.N ~ Season + Tree + Season:Tree	338.21	242	380.21	32.45	
F.N ~ Season + Catena + Season:Catena	340.87	242	382.87	35.11	

FIGURES

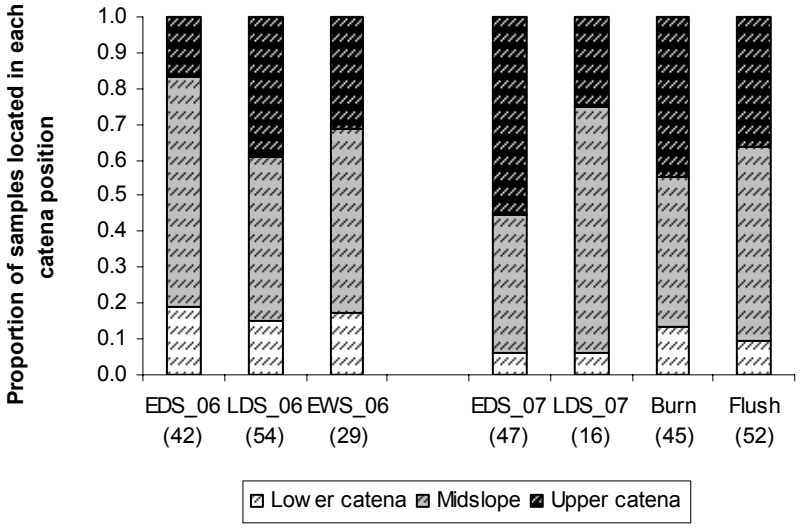

Figure 3.1: The proportion of foraging samples that were located in each catena position. There were no significant differences between herds in their use of catena positions thus all herds are amalgamated. The numbers in brackets following each season is the number of samples included in the seasonal estimate.

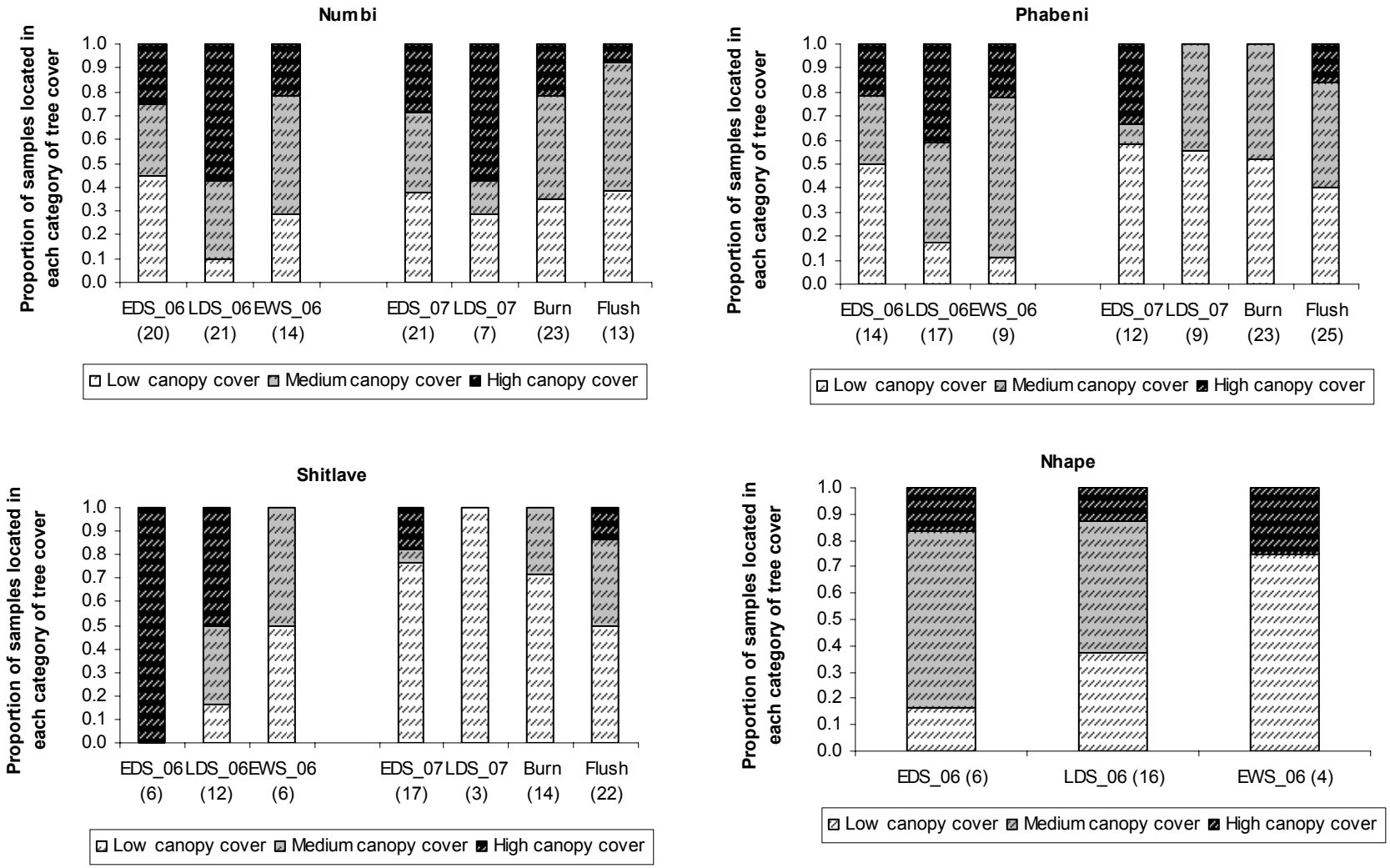

Figure 3.2: The proportion of foraging samples within low, medium and high tree cover. The numbers in brackets following each season is the number of foraging area samples included in the seasonal estimate of that herd.

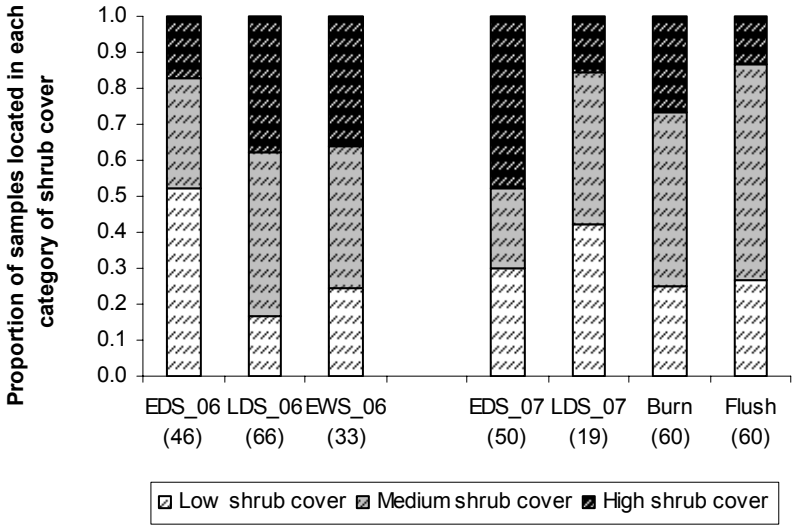

Figure 3.3: The proportion of foraging samples within low, medium and high shrub cover. The herds did not differ significantly in their use of shrub cover and were therefore amalgamated. The numbers in brackets following each season is the number of samples included in the seasonal estimate.

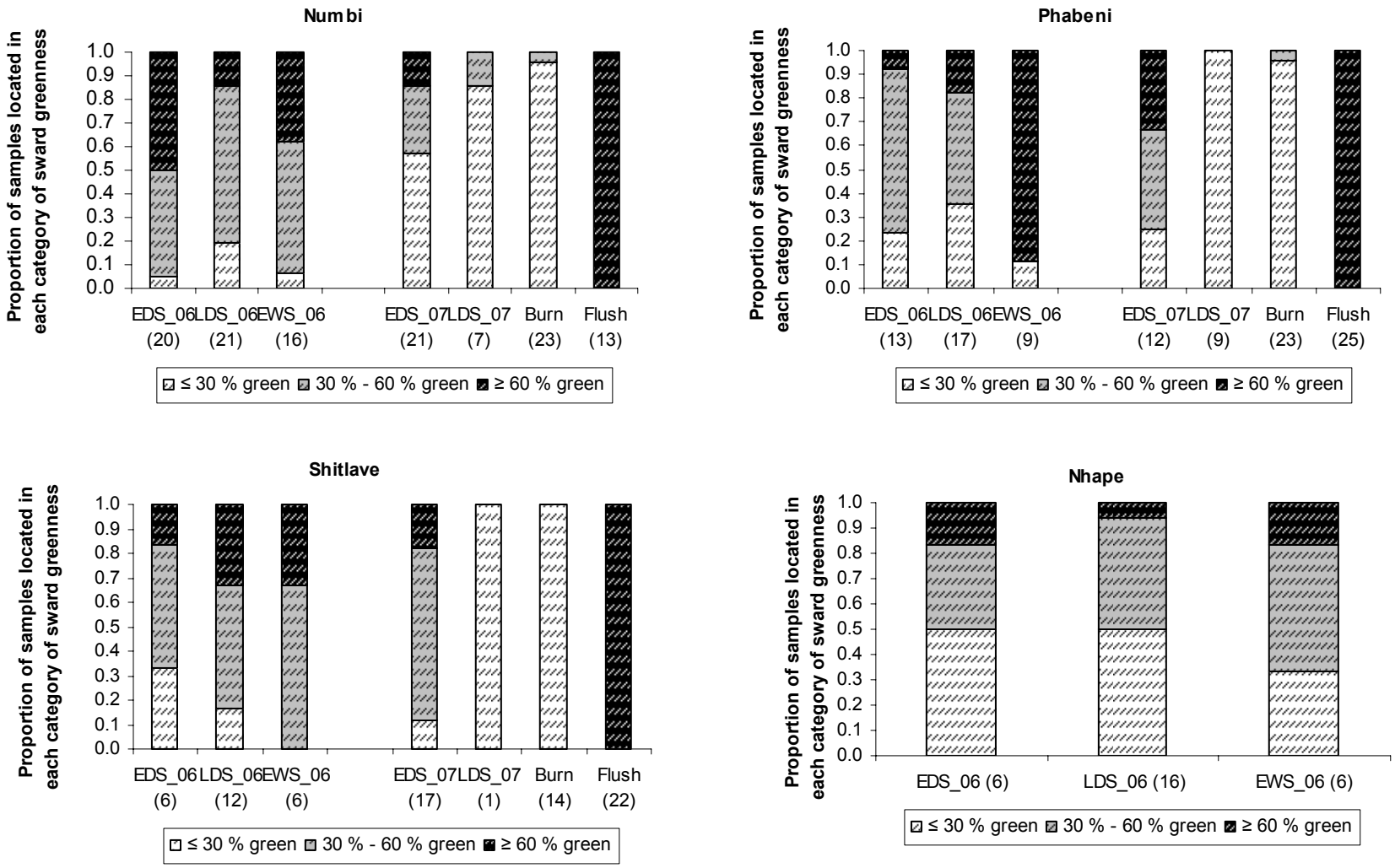

Figure 3.4: The proportion of foraging areas with swards of different absolute greenness used by sable. The numbers in brackets following each season is the number of samples included in the seasonal estimate of that herd.

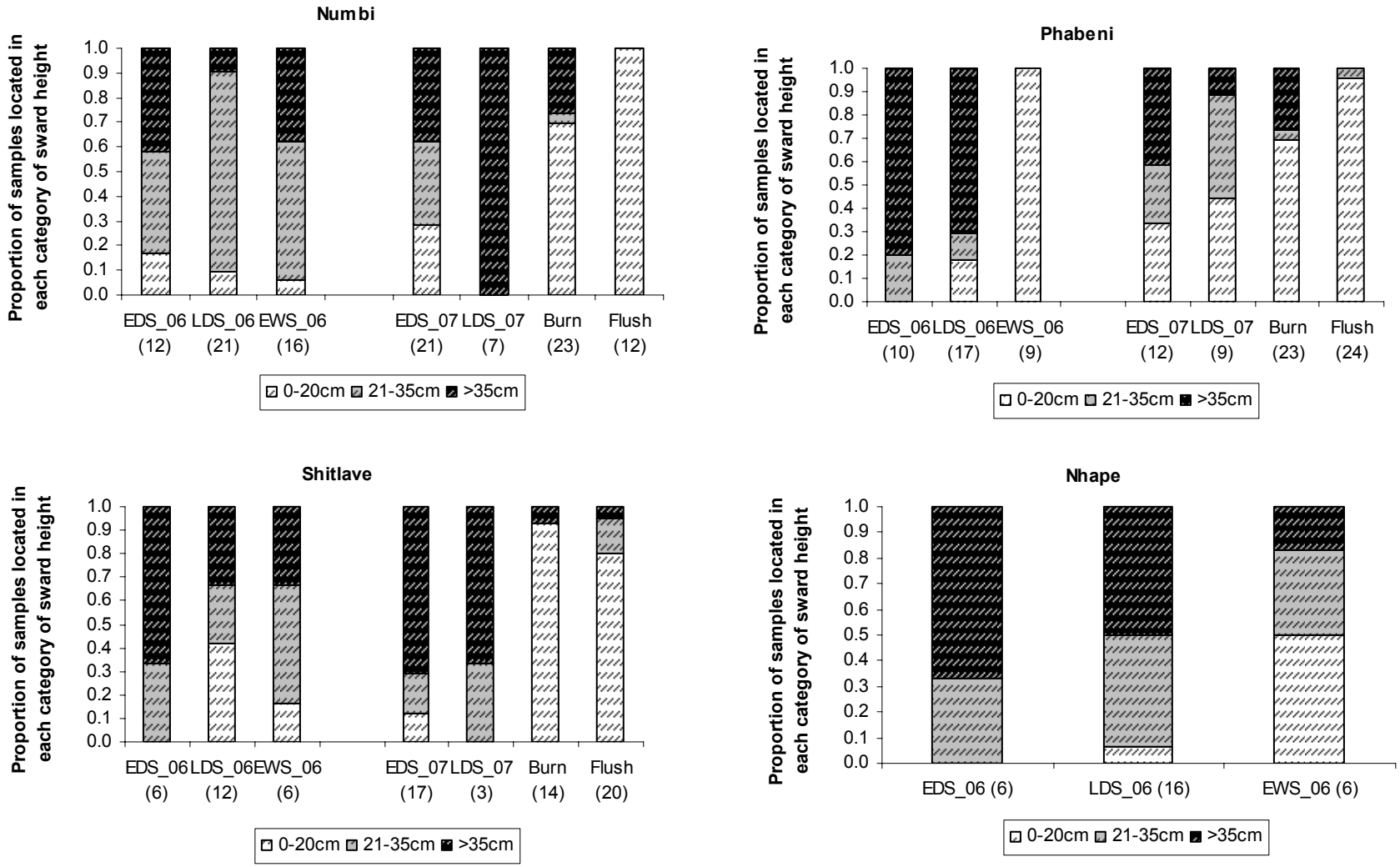

Figure 3.5: The proportion of foraging areas with swards of different heights used by the four herds. The numbers in brackets following each season is the number of samples included in the seasonal estimate of that herd.

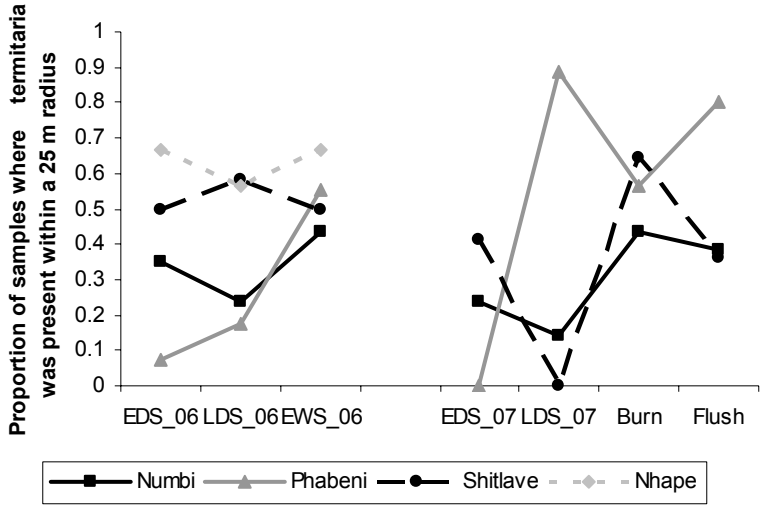

Figure 3.6: The proportion of foraging areas where termitaria were present within a 25 m radius of the GPS location.

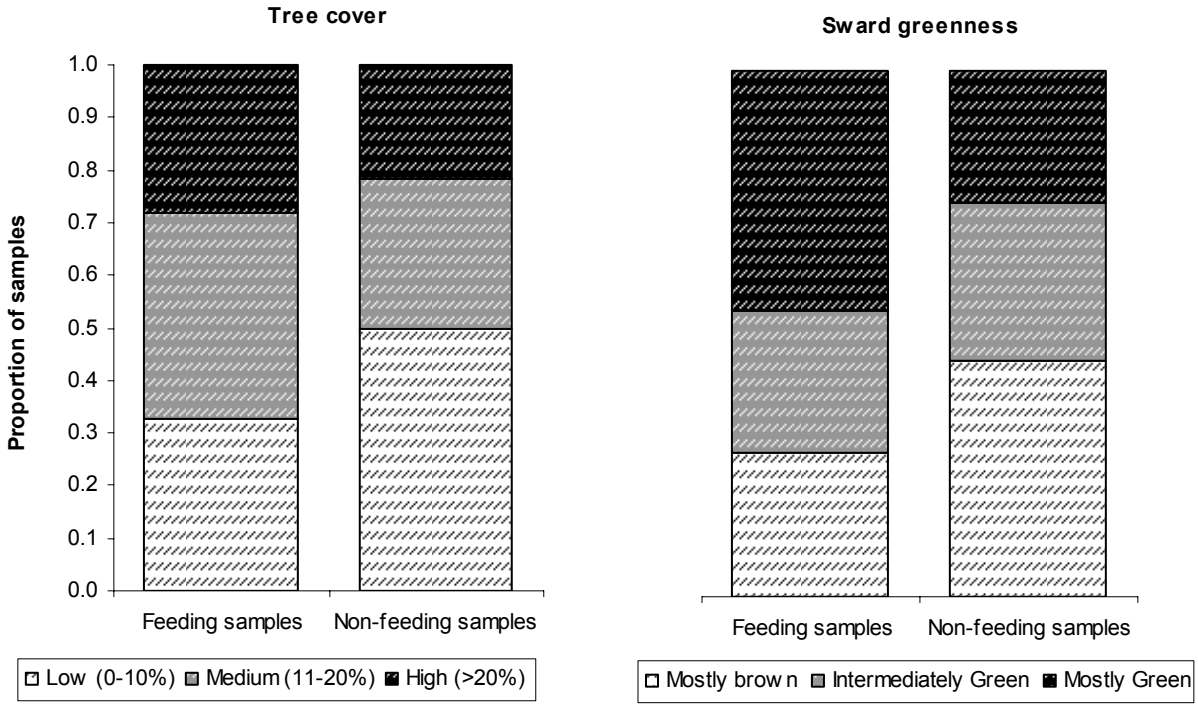

Figure 3.7: The proportion of feeding and non-feeding samples within low, medium and high tree canopy cover and in each category of sward greenness. The tree canopy cover classes include low (0-10%); medium (11-20%) and high (>20%) and the greenness categories represent relative greenness.

CHAPTER FOUR

SYNTHESIS

Discovering the cause of the decline in numbers of sable antelope in the Kruger National Park has been problematic for three main reasons. Firstly, population dynamics is controlled by multiple mechanisms of a dietary and a non-dietary nature. Top-down regulating mechanisms of predation interact with bottom-up constraints associated with dietary requirements and operate jointly to limit populations. Identifying one of these drivers as the primary cause of an observed decline, or at least determining the relative contribution of each, is difficult as a change in one of these factors alters the influence of the other and the animal's response to both. Consequently the ultimate cause of population decline is often overshadowed by a proximate cause immediately visible.

A further complication lies in the fact that these interactive processes operate across different ecological scales (Senft *et al.* 1987, Bailey *et al.* 1996). An animal's foraging behaviour may be determined primarily by biotic factors and the need to acquire forage of sufficient quantity and quality. However, diet selection operates within the constraints imposed by larger scale factors such as landscape elements which would determine broader animal distribution patterns through its effect on the distribution of nutrients and predators. Therefore, a response pattern observed at one spatial scale may be as a result of a limitation imposed at an entirely different scale.

The third complication deals with the temporal gradient over which the decline occurred. Sable have declined from in excess of 2000 individuals to slightly more than

300 individuals over the last two decades with the population apparently stabilising in recent years (I.J. Whyte, KNP Scientific Services Report, 2006). Thus current patterns are observed to understand processes that occurred more than 20 years ago.

To address these constraints my study adopted a hierarchical framework, spanning two spatial scales designed to incorporate multiple possible drivers of population regulation. I investigated foraging patterns ranging from diet selection at the level of the feeding station, driven by nutrient requirements and physical constraints on digestion, to the selection of a grazing location at the level of the foraging patch, driven by nutrient distributions and predation risk.

While assessing diet choice at the level of the feeding station (Chapter 2) I focused on the identity of the species as well as the characteristics of the species in terms of phenological stage and general growth form. Several of these species have previously been described as of low grazing value to cattle. However, sable seemed to feed on some of these low grazing value species only in the high rainfall year when they are likely to still locate tufts in a young, palatable growth form possibly taking advantage of a fairly narrow window of opportunity before these species become unpalatable through desiccation.

During the dry season, when forage resources are typically depleted and food quality limiting, sable compensated by expanding their intake of certain preferred forage species, most noticeably *Panicum maximum* and *Hyperthelia dissoluta*. The documented increase of their dietary intake of such favoured forage species occurred not by increasing their acceptance of the species and eating it more frequently upon encounter, but rather by adjusting their choice of feeding area and feeding more frequently in areas where

these species predominated, thereby increasing the rate of encounter. The same foraging response has previously been documented by Owen-Smith (1994) for kudus (*Tragelaphus strepsiceros*).

Sable responded positively to the greenness of a species and was more likely to feed from a species when it was green. Macandza (2009) while comparing the feeding habits and habitat use of sable to that of buffalo (*Syncerus caffer*) and zebra (*Equus quagga*) in the north of the KNP around the same time as this study, also found sable to be much more narrowly selective for green grass than either buffalo or zebra who tolerated dry grass. Yet, in this study, only species below a 30% greenness threshold were less likely to be grazed. Regardless, sable still showed a surprisingly high tolerance of mostly brown species. In addition, during the burn period, at a time when the available food supply was severely diminished, sable maintained a seemingly healthy body condition despite the bulk of their dietary intake being void of any green leaf material and almost certainly highly fibrous, perhaps indicating a degree of fibre tolerance.

In this study sable were also found to avoid short growth species and hence the prediction that sable would focus their foraging activities on species with a tuft height as short as 4 cm was refuted. In general, sable were less likely to feed from species if they were below 20 cm in height. The relatively narrow width of the incisor arcade of sable antelope (56.6 mm; Gordon & Illius 1988), may inhibit the bite depth obtainable on short species and a faster intake rate may be achieved when feeding from species taller than 20 cm.

The initial prediction postulating that sable would reject species with characteristically stemmy growth forms was contradicted as sable fed frequently from highly stemmy species. Fresh bites were often observed directly on stems, particularly on species such as *Themeda triandra* and *P. maximum* where the majority of accessible leaves grows along the length of the stem. A possible implication of this foraging behaviour may be that, by feeding on leaf-bearing stem and thus tolerating high quantities of stem material in the diet, sable may meet their energy requirements in situations where sufficient amounts of basal leaves are unavailable. A high tolerance of stemmy forage has recently been documented for sable antelope by Parrini 2006 and Macandza 2009, and for the closely related roan antelope (*Hippotragus equinus*) by Heitkönig & Owen-Smith (1998).

At the level of the foraging patch (Chapter 3) I described the areas used by sable when they were likely to be foraging in terms of certain landscape features and characteristics of the grass layer. I also compared these features in areas in which sable fed with those from areas in which sable did not feed. Sable foraging areas were mostly located in midslope and upper catena levels. As conditions turned drier, sable were expected to move to lower levels of the catena during foraging bouts as these areas are often associated with higher greenness retention. Although previous studies have found sable to utilise bottomland areas (Jarman 1972, Estes & Estes 1974, Grobler 1981, Magome 1991, Parrini 2006), sable at Pretorius Kop foraged infrequently in low lying areas and did not increase their use of bottomlands during drier periods. However, the incised bottomland structure characteristic of the Skukuza land system within which Pretorius Kop falls (Venter *et al.* 2003) are unlike the vlei type bottomlands often

characterised by extensive accumulation of alluvium, to which previous studies on sable's use of the catena refer to. Macandza (2009) also demonstrated an avoidance of bottomlands by sable antelope and similarly attributed this to the specific types of bottomlands available within his study area. However, during the late dry season of 2006 and the burn period, the greenness of the swards recorded in bottomland foraging areas remained significantly greener than the swards recorded in midslope and upland positions.

As predicted, sable were more likely to feed in areas characterised by high levels of tree cover and a relatively green sward. The prevalence of *P. maximum* under tree canopies most likely contributed to sable's preference for woody areas. Additionally, the enhanced soil nutrient levels associated with sub-canopy areas may have further enhanced the appeal of woody areas to sable.

Despite sable's preference for feeding in high tree densities, they still fed frequently in open areas. Grass species such as *Hyperthelia dissoluta* and *Heteropogon contortus*, that were shown not only to contribute a large proportion to sable diet but also to be highly acceptable to sable (Chapter 2), often grow in areas with little tree cover (Van Oudtshoorn 1999), which may explain sable's use of such relatively open foraging areas. *H. dissoluta* contributed relatively little to sable diet during 2006 and a dependence on this species was only documented during the dry year of 2007, perhaps indicating that sable were forced to use this species in order to meet their nutritional requirements. Despite the increase in the use of areas where *H. dissoluta* were present, sable also increased their use of areas where *P. maximum* was present, which may explain the lack of a seasonal difference in the use of tree cover.

Sable fed preferentially in the greenest swards available, yet still readily utilised predominantly brown swards. However, sable were also shown to select for greenness at a finer level i.e. the level of the feeding station, where sable preferentially fed from green species and were more likely to feed from a species when it was green. As such, within a foraging patch, sable may have been capable of locating individual tufts that were greener than the average greenness of the sward.

The regional distribution of sable antelope across the KNP has been linked to areas of low predation risk (Chirima 2009). Consequently sable may be responding to predation risk at smaller scales as well. During times when food resources are in abundance, animals are expected to seek out low risk areas for foraging (Lima & Bednekoff 1999). Using shrub cover as a proxy for predation risk, I expected feeding sites to be distinguished from non-feeding sites by its lower levels of shrub cover. However, shrub cover did not represent a significant difference between feeding and non-feeding sites.

Recommendations for future research

This work would have benefitted greatly through the inclusion of a further two levels of selection i.e. at a finer scale, investigating selection at the level of the plant part and at a broader scale, investigating forage area selection from within the broader landscape. The overall tolerance of specifically brown swards and brown tufts as well as highly stemmy species was unexpected. Future research should be aimed at identifying the mechanisms with which sable achieve such tolerance including the extent to which

sable can forage selectively within tufts and their physiological capacity of fibre digestion.

Similarly, sable's willingness to forage across such a broad range of landscape features should be examined more closely. Specifically, future studies should focus on the broader availability of these landscape features so that inference could be made regarding the selection of such features for foraging. Specifically pertaining to the decline of sable antelope in the KNP, the information gained in terms of the selection of foraging areas together with the knowledge of sable's forage and habitat dependency gained during this study, could then be used as the basis for a comparison between the areas in which sable have persisted and the areas from which they have disappeared. This comparison should incorporate vegetation structure differences as well as differences within the grass layer, so that bottom-up effects of food acquisition could be effectively separated from the top-down considerations such as predator avoidance.

Conclusions and management implications

Being a medium-sized ruminant, sable would be expected to be highly selective while feeding and indeed, Macandza (2009) demonstrated a comparatively narrow tolerance of sable to grass species and grass features when compared to buffalo and zebra. However, in this study, sable were found to tolerate a broad range of foraging area and grass layer features that are known to influence the distribution of nutrients and overall forage quality. The relatively small effect that nutritional considerations had on the foraging response of sable suggests that the inability of the sable population at

Pretorius Kop to recover from the decline is not related to a nutritionally deficient grass layer. The possibility remains that the grass layer in the areas from which sable disappeared underwent some fundamental change in suitability, preventing recolonisation of these areas, and should form the next research focus.

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APPENDIX I

RAINFALL AT PRETORIUS KOP

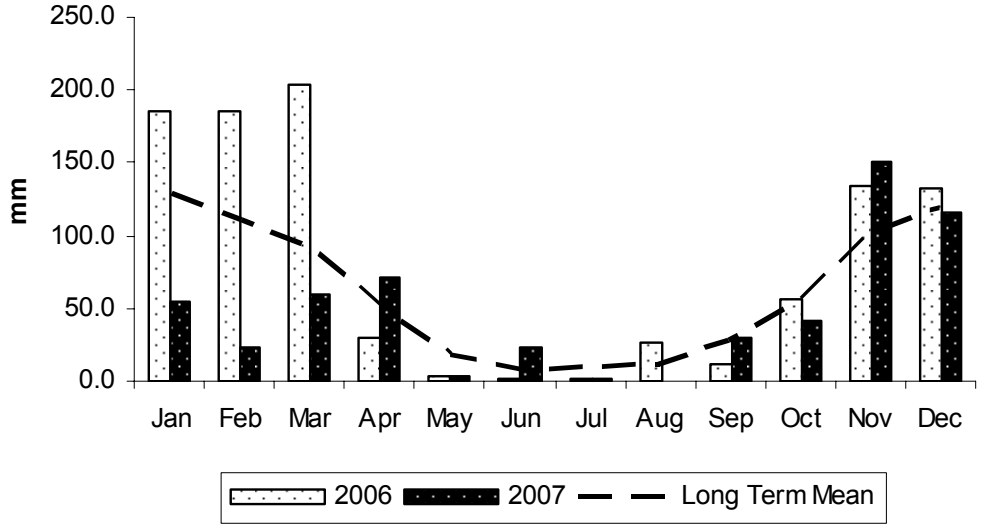

Figure I.I: Average monthly rainfall recorded at Pretorius Kop over the two year study period (2006-2007) including the long term mean. Data obtained from the South African Weather Service.

APPENDIX II

DISTRIBUTION OF SITES VISITED

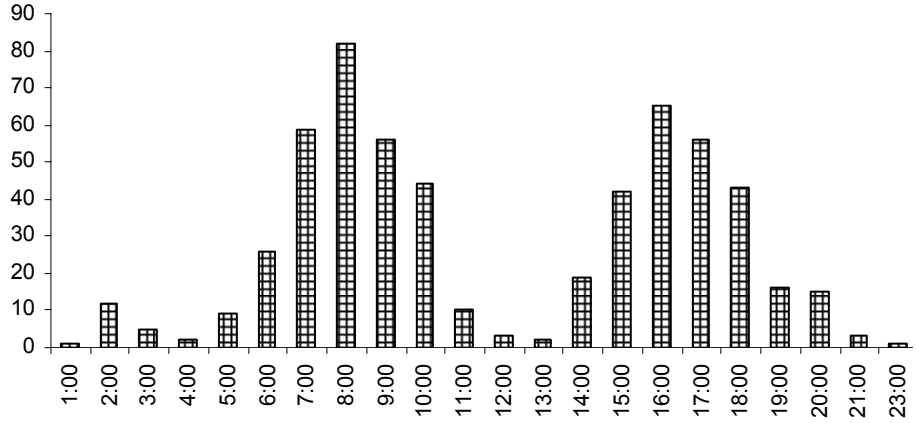

Figure II.I: Distribution of sites visited across the time of day sable were recorded there.

APPENDIX III

SABLE DUNG AND SPOOR AND SIGNS OF OTHER SPECIES

At each site, I recorded the distance of the nearest sable spoor from the GPS location as an indication of the accuracy of the location. Signs of any other herbivore species were noted and classified as fresh or recent, to be able to substantiate the claim that any foraging activity in the area can be assumed to be indicative of sable foraging.

A total of 571 sites were visited across the two year field season of which 320 were classified as feeding sites. Of all the sites visited, 80% of sites had fresh signs of sable's presence (Figure III.I). Fresh dung pellets were found in 38% of all sites and fresh sable spoor in 69% of all sites. The average distance of the nearest sable spoor from the central quadrat was 69 cm in non-feeding sites and 53 cm in feeding sites (Figure III.II). Only 27.5% of sites had any fresh signs (i.e. fresh spoor or dung) of other grazers (Figure III.III).

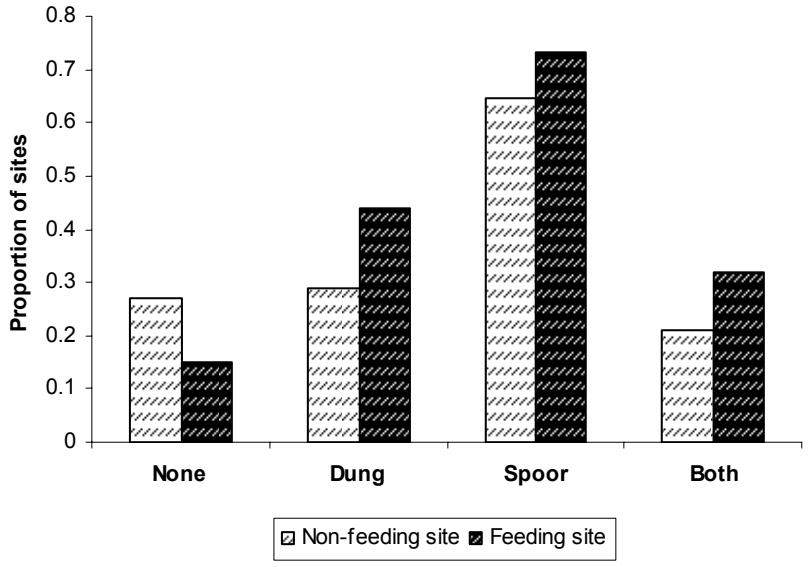

Figure III.I: The proportion of feeding or non-feeding sites in which fresh sable dung or spoor was encountered.

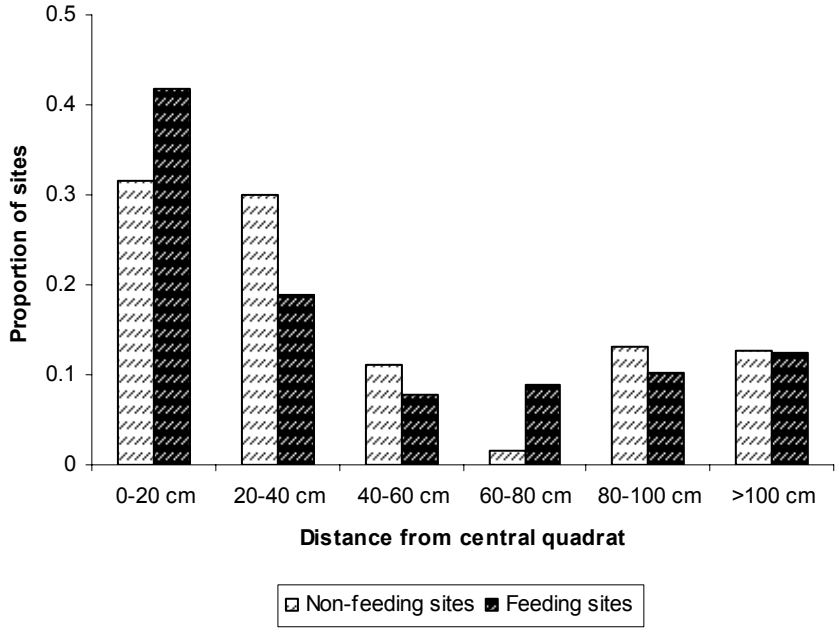

Figure III.II: Frequency distribution of the distance of the nearest sable spoor from the central quadrat in feeding and non-feeding sites.

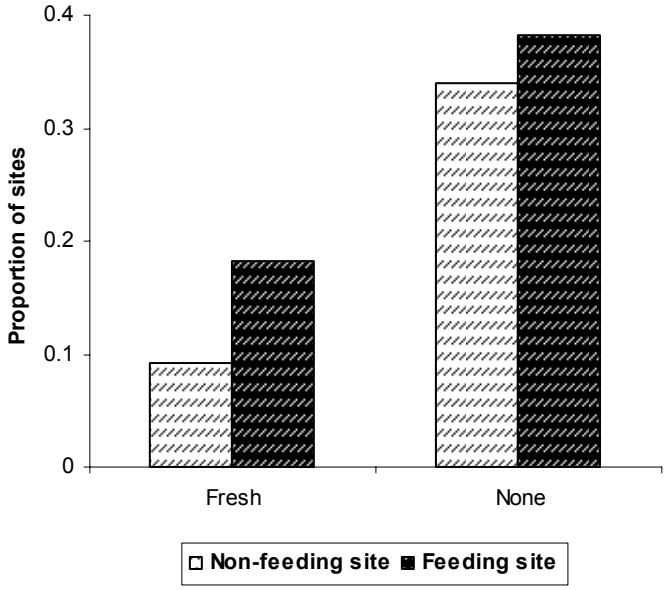

Figure III.III: The proportion of feeding or non-feeding sites in which signs of other grazers (fresh dung or spoor) was encountered.

APPENDIX IV

EVALUATION OF GPS/GSM COLLAR PERFORMANCE: ESTIMATING LOCATION PRECISION

ABSTRACT

The scale at which a telemetry based study can be conducted is dependent upon the location accuracy obtainable from the Global Positioning System (GPS). As such, the discrepancy between location and estimate must be addressed. I used non-differentially corrected GPS data obtained from stationary GPS/GSM collars to assess location error in terms of the precision and accuracy of the location estimate. I tested three different collars at 6 reference points. The reference points used were locations within buildings and vehicles in which the collars were stored and as such were characterised by maximum cover. The estimates seemed to display some directional bias, yet without a differentially corrected true location, interpretation of accuracy estimates remained tentative. The average precision error for each collar ranged from 10.44 m to 43.49 m and the locations were within 10 m of the average estimate 50% of the time and within 40 m 95% of the time.

INTRODUCTION

Global positioning system (GPS) technology presents a major advancement for use in applied ecological research as it is a relatively easy to use technique that provides instantaneous location data and automatic data collection. It enables the researcher to maintain interference levels at a minimum and remain unobtrusive during tracking which remains a crucial element in any study involving the collection of behavioural data. Additionally, the development of progressively more accurate instruments enables the researcher to investigate habitat use and foraging at increasingly finer scales such as the foraging patch.

Despite the advancements in GPS systems, discrepancies still exist and the evaluation of collar performance remains a necessity for every study making use of telemetry data. Especially with fine scale foraging and habitat use studies even slight location errors may be erroneously interpreted as biologically meaningful. The problem with the performance of GPS systems, specifically when used in habitat assessment studies, lies perhaps not so much in the inaccuracy itself but more so in the inconsistency of the inaccuracy, brought about by patchy environments. If the probability of missed fixes is consistently higher within particular habitats for example, the conclusions of the study may underestimate the importance of this habitat type to the animal in question Visscher (2006).

An animal's location is determined by calculating the time it took for the signal to travel, between the satellite and the animal borne receiver (O'Neil *et al.* 2005). Typically

three satellites are necessary to obtain triangulation, while 3D fixes requires four satellites to obtain a location estimate. While the first three satellites are necessary to locate a point in three dimensional space, the fourth satellite is required to correct for differences in timing between the satellite and the receiver. The discrepancy in timing is created because the satellites are fitted with atomic clocks whereas the receivers are not and as the location estimation is based on the timing of the signal transfer, the fourth satellite is an essential component in obtaining a 3D fix (O'Neil *et al.* 2005). When only three satellites are available, a 2D fix is generated where the location altitude is calculated by averaging the altitude estimates of the last five 3D fixes (Bowman *et al.* 2000).

The calculations most often used in describing collar performance are precision, bias and accuracy (O'Neil *et al.* 2005). Precision is a measure of the proximity of repeated readings of the same location (Zar 1999). Precision can be measured through the calculation of the variance which is the average of the squared deviations between the multiple location estimates and the expected location, which can be described as the midpoint of the estimates. Bias refers to the distance of the average value of repeated readings from the true location. Accuracy can be seen as a combination of the two previously described measures i.e. precision and bias, where a location estimate which is both precise and unbiased can be considered accurate and thus representative of the location of interest (O'Neil *et al.* 2005).

In assessing collar function, researchers routinely use not only measures of accuracy and precision, but also indicators such as the time required to acquire a location fix (Hansen & Riggs 2008), the number of satellites in range (Hansen & Riggs 2008) or

alternatively the proportion of 3D fixes obtained (Obbard *et al.* 1998), the positional dilution of precision (PDOP) (Obbard *et al.* 1998, Hansen & Riggs 2008) and observation rates or fix success rate i.e the proportion of attempted fixes that were successful (Obbard *et al.* 1998). PDOP is a measure of satellite geometry which may serve as an indication of the quality to be expected from the GPS location obtained. It indexes the precision of an estimate based on the locations of the satellites relative to each other and to the animal-borne receiver (O'Neil *et al.* 2005). Satellites clustered close together will provide location estimates of low precision and the PDOP values reported will be high (Obbard *et al.* 1998).

The accuracy of a GPS signal is a function of environmental factors. As the location estimate is based on the time a signal travels from the receiver to the satellite, a delay in the timing of the signal caused by an obstruction would result in inaccuracies (De'Eon *et al.* 2002, O'Neil *et al.* 2005). Vegetation cover or topography obstructing the signal path may therefore cause either reflection or refraction which can result in some silent regions in the study area (Dussault *et al.* 1999, Cain *et al.* 2005).

Vegetation structure has previously been shown to influence signal transmission negatively, where greater canopy cover is associated with greater GPS errors (Dussault *et al.* 1999, DeCesare *et al.* 2005, Hansen & Riggs 2008). Additionally, the frequency of failure of GPS location attempts has previously been directly linked to tree density (Rumble & Lindzey 1997, De'Eon *et al.* 2002). Obbard *et al.* (1998) have found the fix success rate to be lowest for collared black bears in habitat characterised by dense cover and greatest in open habitat home ranges.

Reception of GPS signals may be further hampered by undulating terrain where the obstruction of the GPS receiver by topographical features has been found to decrease the fix success rate (Cain *et al.* 2005). De'Eon *et al.* (2002) identified topographical features as a factor in influencing fix success rate, yet only in combination with canopy cover.

Researchers are often concerned with how behaviour affects collar performance. Studies focusing on the effect of animal behaviour, and in particular movement and collar orientation, on collar function, have delivered mixed results. Moen *et al.* (1996), by placing collars on moose while simultaneously monitoring them visually, found that movement of the moose did not affect collar success in any way. However, the collars deployed on the moose showed a slight yet significant decrease in fix success rate when the collar orientation changed from vertical to horizontal (Moen *et al.* 1996). In a study directly aimed at investigating the effects of collar orientation on collar function, De'Eon & Delparte (2005) similarly showed a positive relationship between the angle of the collar from a vertical orientation and both location error and fix success rate, yet suggested that the effect may only become meaningful at a threshold of 90º from the vertical. Conversely, Bowman *et al.* (2000) found no significant differences in the accuracy of an estimate or the fix success rate between fix attempts with white-tailed deer holding their head at different angles. An effect of collar orientation on collar performance, may introduce a bias in favour of animal activities that maintain collar orientation close to the vertical i.e. walking, whereas activities such as foraging, where collar orientation is tilted towards the horizontal, run the risk of being underrepresented.

Here I evaluate the performance of GPS/GSM collars used as part of a study investigating foraging and habitat use of sable antelope (*Hippotragus niger*). In attempting to quantify the error associated with the animal locations that formed the bases of the two preceding chapters, I hope to attest to the validity of the study. The performance of the collars was tested in artificial environments under maximum cover and as such represent the upper limit of error expected under field conditions.

METHODS

Study design

The GPS Units used were provided by African Wildlife Tracking (AWT; http://www.awt.co.za) and the electronics were designed by YRLESS Tracking Solutions (YRLESS International (PTY) Ltd). The GPS and antenna were housed in a unit on top of the collar with the battery at the bottom. Data recorded included the date, time of day, longitudinal and latitudinal coordinates and temperature. If the satellite were unable to obtain an estimate within a period of three minutes the fix was classified as a failed fix and the receiver was switched off until the next scheduled fix (personal communication AWT). It is necessary to limit the time allowed per fix attempt as the GPS unit expends a considerable amount of battery power (Moen *et al.* 1996).

I evaluated GPS performance using non-differentially corrected GPS data obtained from stationary collars. As this assessment did not form part of the original objectives stipulated in the sable study, the data collected were not specifically aimed at

assessing collar function. However, data were collected inadvertently while the collars were in storage. As these artificial environments represent highly exaggerated cover conditions, much greater cover than would be expected in a natural environment, I aimed with this assessment to establish an estimate of maximum possible collar error. The estimates used for the evaluation were obtained from three different collars periodically stored in six different locations. At four of these test locations, the collars were stored in the back of a canopied truck and at the remaining locations the collars were kept inside a closed caravan and inside a brick building. The structures in which each collar was enclosed in, i.e. a vehicle, caravan or building, were expected to obstructed signal transfer and assumed to symbolized near total cover. However, in all but site 2 and site 6, the collars were situated close to a window with at least some access to open sky. At site 2 on the other hand, the collar was located in the vehicle which was parked in a walled parking area with little access to open sky. The collar placed inside the building, similarly had no access to open sky. Data points were obtained sporadically during a total of 113 days between 20/08/2007 and 02/12/2007. An hourly fix interval was maintained throughout. The collars that remained in the caravan and the building provided fixes of the same location 24 hours a day, whereas the collars placed in the vehicle only provided estimates of the same location during the night. Each test site was in a particular parking area to which the vehicle and therefore the collars were returned every night. Consequently, only estimates obtained between 20:00 in the evening and 04:00 in the morning from the collars located in the vehicle were used to assess precision and accuracy (Refer to Table IV.I for further details).

PDOP values were not available for download and the collar recorded only 3D fixes (AWT). As such I was unable to consider the effect of satellite configuration. Regrettably no true location could be obtained as I did not have a differential GPS available. However, all of the locations had reference points that could be visually recognised on a Google Earth image, enabling me to use the coordinates provided by Google Earth (Version 5.1) as the assumed true location. Although this method is not ideal as it introduces a second source of error, I believe that the bias is acceptable as it provides a reference point from a source other than the locations given by the collars.

All latitude and longitude coordinates recorded by the stationary collars were transformed to the universal transverse Mercator (UTM) coordinate system using Arcmap software (Version 9.1). All projections used the WGS 1984 spheroid. I calculated three measures of collar performance, i.e. precision and bias of the estimates and the fix success rate. To obtain a measure of precision per collar at each location, I calculated the distances between each of the multiple estimates and the average estimate. A measure of bias was obtained by calculating the average distance between the multiple estimates and the assumed true location visually obtained from Google earth software.

RESULTS

Fix success rate

At every site where the collar was located close to a window and had some access to the skyline, the fix success rate consistently remained above 80% (Table IV.I). The

collars located in the fenced parking structure (Site 2) and the building (Site 6), that had limited view of the sky, had a fix success rate of 20% or less (Table IV.I).

Location precision and bias

The two collars placed at site 1 were fairly evenly distributed around the "true" location obtained from the Google Earth image (Figure IV.I). However, at all other sites the collar estimates were not uniformly scattered around the "true" location. Instead, the cluster of estimates was misaligned with the "true" location and was shifted towards one side (95% CI 18.24 ± 0.93; Figure IV.I). On the whole, the estimates were within 15 m of the Google Earth location 50% of the time and within 44 m 95% of the time (Figure IV.II). Average precision errors ranged from 10.44 m to 43.49 m and were within 10 m of the average estimate 50% of the time and within 40 m 95% of the time (Figure IV.III).

DISCUSSION

Despite the high degree of cover at every site brought about by the artificial structures in which the collars were housed, a fairly high fix success rate was obtained as long as the skyline was accessible to the GPS receiver, even if to a limited extent. The collars located in the sites with no available sky, had severely reduced fix success rates. The influence of canopy cover on collar performance was not directly investigated during this study. However, as the error estimates were measured using collars enclosed in

either a building or a vehicle, I argue that the error associated with these estimates must represent the error expected under near maximum natural cover.

The accuracy estimates obtained were within 15 m of the visually located Google Earth "true" location 50% of the time and within 44 m 95% of the time. However, at all sites, apart from site 1, the estimates demonstrated directional bias, where the cluster of location estimates was misaligned with the "true" location. The Google Earth image would also be expected to have a certain degree of error associated with it whether inherent in the software or related to the rather vague visual selection of the site on the image. Consequently the location used as the "true" location, is also an estimate itself, and would introduce a second source of error. The fact that at each site where two collars were placed i.e. sites 2, 5 and 6, the discrepancy away from the "true" location was in the same direction for both collars would perhaps suggest that the error lies in the estimation of the Google Earth location. Nonetheless, without the benefit of a differentially corrected GPS point, the interpretation of such differences remains tentative.

Management implications

In a heterogeneous environment, location error may vary across landscape types. For that reason I would recommend that in future studies, an assessment of collar function should be carried out in each of the habitat types present within the study area, prior to the placement of the collars on the study animal. This would enable the researcher to statistically correct for any potential biases in each landscape type after the data has been collected. If the lack of precision in greater cover areas are known and

could be quantified, Obbard *et al.* (1998) suggest to adjust the interval between fix attempts to obtain similar quantities of fix successes. Alternatively, sample weighing or iterative simulation may also reduce the misclassification of habitat used (Frair *et al.* 2004). Such preventative measures can only be achieved through a preliminary study on collar performance and the consequence of the environmental conditions and vegetation structure specific to the area.

For measurement of accuracy to be possible, putting in place a reference station in the proximity of the majority of the park's telemetry studies may be useful. Alternatively, access to a differential GPS is advisable. However, if it is impossible to calculate true accuracy for lack of a differential GPS, one may strive to rely on an appropriately considered experimental design in an attempt to minimise the effects associated with measurement error.

In such a complex heterogeneous system, such as African savannas, where study objectives and data requirements are often focused on a fine spatial scale, correcting for, or at the very least reporting telemetry error, is essential. The consequence of such measurement error will depend on the specifics of the study area in terms of vegetation structure and topographical variation as well as on the specific study objectives.

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TABLES

Table IV.I: Details regarding the hourly location estimates of each stationary collar at each site, including the structure in which each collar was stored and the date range during which the estimates were obtained. The collars were removed from these sites at times and thus not all fixes recorded during this date range were used. As such the actual number of days and the time period during which fixes were obtained are also reported. The number of fix attempts and the fix success rate of each collar at each location are also reported.

Location	Structure Stored	Collar ID	Dates	Number of days	Time period	Number of fix attemts	Number of fix successess	Fix success rate
		AM140	23/10/2007 - 14/11/2007	18	20:00 - 04:00	162	143	0.8827
Site1	Vehicle	AM151	03/09/2007 - 14/11/2007	71	20:00 - 04:00	639	512	0.8013
		AM140	15/11/2007 - 01/12/2007	16	20:00 - 04:00	144	29	0.2014
Site2	Vehicle	AM151	20/11/2007 - 29/11/2007	9	20:00 - 04:00	81	10	0.1235
Site3	Vehicle	AM151	26/08/2007 - 28/08/2007; 01/09/2007 - 02/09/2007	3	20:00 - 04:00	27	26	0.9630
Site4	Vehicle	AM151	28/08/2007 - 01/09/2007	4	20:00 - 04:00	36	36	1.0000
		AM140	21/08/2007 - 23/08/2007	2	24 hours	63	62	0.9841
Site5	Caravan	AM148	20/08/2007 - 23/08/2007	3	24 hours	86	84	0.9767
		AM140	23/08/2007 - 21/10/2007	59	24 hours	1416	45	0.0318
Site6	Building	AM148	23/08/2007 - 02/12/2007	101	24 hours	909	97	0.1067

FIGURES

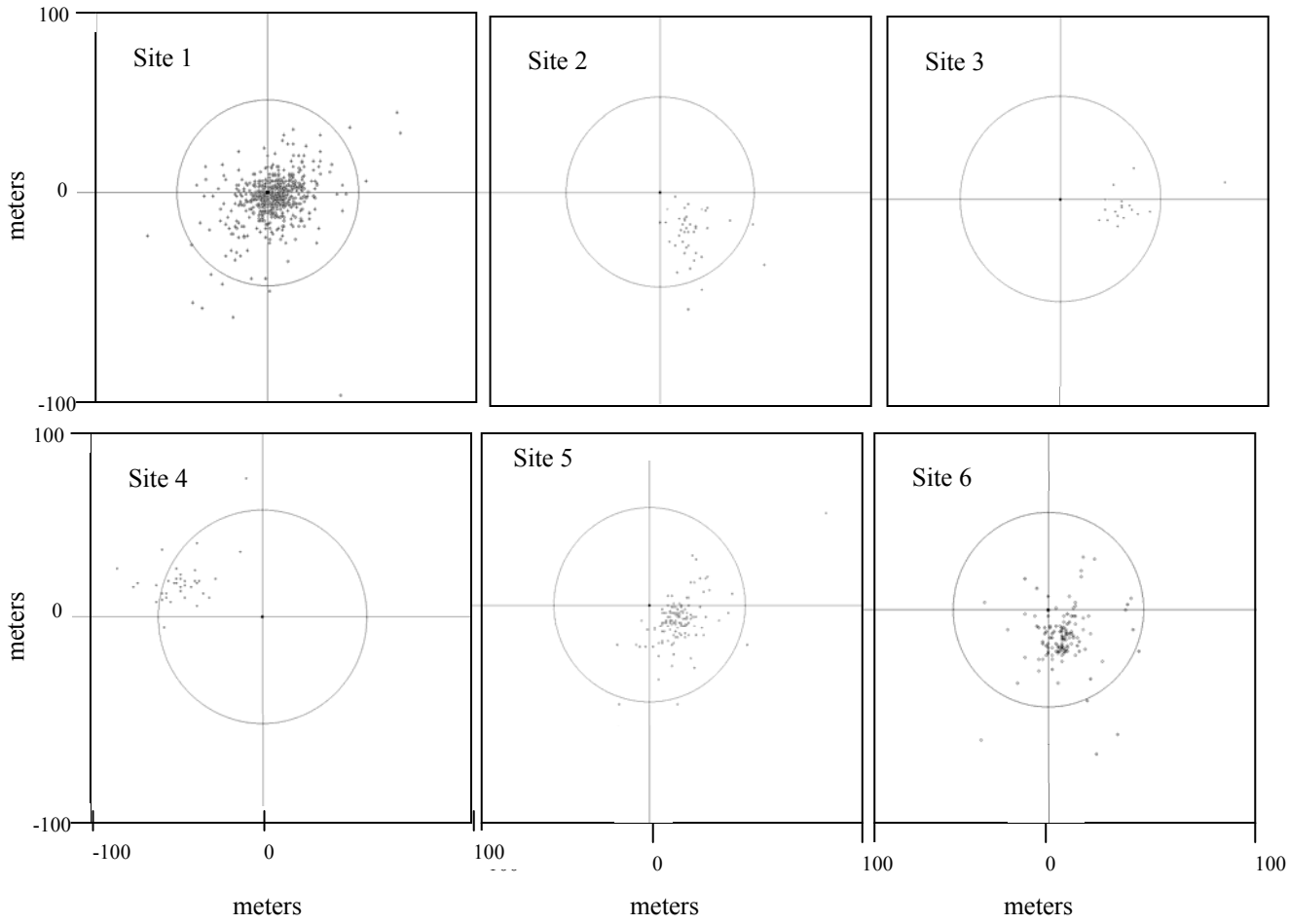

Figure IV.I: Location estimates recorded by the stationary collars compared to the assumed true location recorded in google earth software for sites representing maximum cover. The circles have a radius of 50 m from the Google earth location. The different symbols represent the different collars used (AM140 – full circle; AM148 – open circle; AM151 – cross).

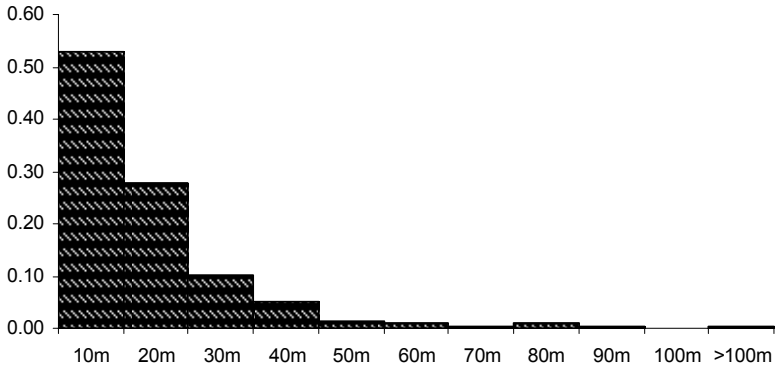

Figure IV.II: Frequency distribution of precision i.e. the distances from the average estimate.

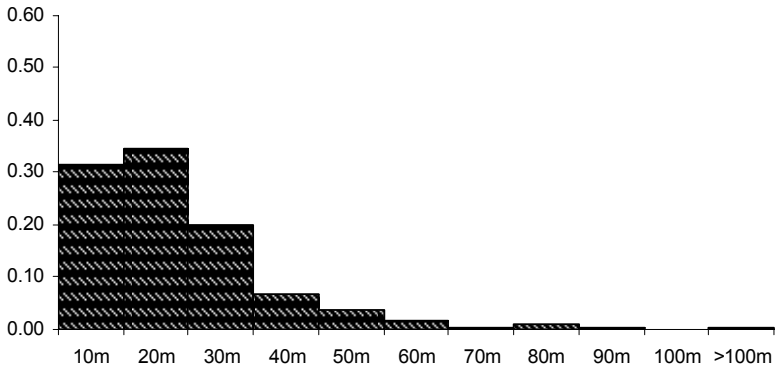

Figure IV.III: Frequency distribution of accuracy i.e. the distances from the google earth "true" location.

APPENDIX V

SEASONAL DIVISION BASED ON MONTHLY GREENNESS VALUES

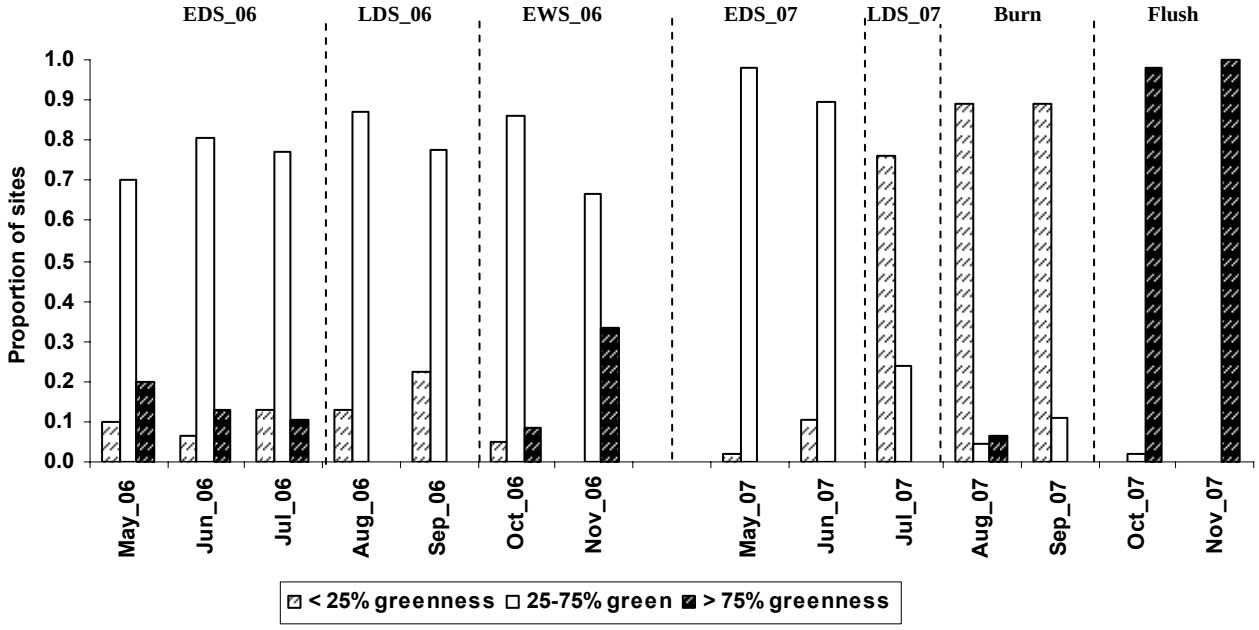

Figure V.I: Monthly site greenness averages on which the seasonal divisions were based.

APPENDIX VI

SAMPLE SIZES

Table VI.I: Sample sizes for sites separated seasonally and per herd.

		All sites	Feeding sites	Non-feeding sites
All seasons (06-07)	**All herds**	571	320	251
	Numbi	214	121	93
	Phabeni	167	102	65
	Shitlave	140	71	69
All seasons (06)	**All herds**	264	137	127
	Numbi	96	57	39
	Nhape	50	26	24
	Phabeni	65	35	30
	Shitlave	53	19	34
All seasons (07)	**All herds**	307	183	124
	Numbi	118	64	54
	Phabeni	102	67	35
	Shitlave	87	52	35
EDS_06: May-July (06)	**All herds**	80	51	29

	Numbi	31	21	10
	Nhape	11	9	2
	Phabeni	24	14	10
	Shitlave	14	7	7
EDS_07: **May-June (07)**	**All herds**	74	38	36
	Numbi	35	18	17
	Phabeni	15	8	7
	Shitlave	24	12	12
LDS_06: **Aug-Sept (06)**	**All herds**	123	60	63
	Numbi	36	22	14
	Nhape	33	13	20
	Phabeni	28	15	13
	Shitlave	26	10	16
LDS_07: **July (07)**	**All herds**	28	21	7
	Numbi	12	10	2
	Phabeni	12	7	5
	Shitlave	4	4	0
Burn period: **Aug-Sept (07)**	**All herds**	106	58	48
	Numbi	47	22	25

	Phabeni	33	23	10
	Shitlave	26	13	13
EWS_06: **Oct-Nov (06)**	**All herds**	61	26	35
	Numbi	29	14	15
	Nhape	6	4	2
	Phabeni	13	6	7
	Shitlave	13	2	11
Flush period: **Oct-Nov (07)**	**All herds**	99	67	32
	Numbi	24	14	10
	Phabeni	42	29	13
	Shitlave	33	24	9

APPENDIX VII

SPECIES LIST

Table VII.I: Grass species recorded in the Pretorius Kop region of the Kruger National Park between May 2006 and November 2007.

Grass species	**Grass Codes**	**Grass species**	**Grass Codes**
Aristida adscensionis	Ariads	*Heteropogon contortus*	Hetcon
Aristida congesta	Aricon	*Hyperthelia dissoluta*	Hypdis
Aristida transvaalensis	Aritra	*Hyparrhenia filipendula*	Hypfil
Bothriochloa insculpta	Botins	*Loudetia simplex*	Lousim
Brachiaria brizantha	Brabri	*Melinis repens*	Melrep
Brachiaria nigropedata	Branig	*Microchloa caffra*	Miccaf
Brachiaria serrata	Braser	*Panicum maximum*	Panmax
Chloris gayana	Chlgay	*Panicum natalense*	Pannat
Chloris virgata	Chlvir	*Panicum schinzii*	Pansch
Cymbopogon nardus	Cymnar	*Perotis patens*	Perpat
Cynodon dactylon	Cyndac	*Pogonarthria squarrosa*	Pogsqu
Digitaria eriantha	Digeri	*Schmidtia pappophoroides*	Schpap
Digitaria monodactyla	Digmon	*Setaria incrassate*	Setinc
Diheteropogon amplectens	Dihamp	*Setaria sphacelata*	Setsph

Eragrostis chapelieri	Eracha	*Sporobolus nitens*	Sponit
Eragrostis chloromelas	Erachl	*Sporobolus pyramidalis*	Spopyr
Eragrostis curvula	Eracur	*Sporobolus sanguineus*	Sposan
Eragrostid gummiflua	Eragum	*Themeda triandra*	Thetri
Eragrostis heteromera	Erahet	*Trachypogon spicatus*	Traspi
Eragrostis inamoena	Eraina	*Trichoneura grandiglumis*	Trigra
Eragrostis rigidior	Erarig	*Tricholaena monachne*	Trimon
Eragrostis superba	Erasup	*Urochloa mosambicensis*	Uromos
Eriochloa meyeriana	Erimey		

APPENDIX VIII

SEASONAL CHANGES IN FAECAL NUTRIENTS

Faecal samples were analysed for nitrogen and phosphorus in an attempt to estimate the quality of the forage consumed by sable antelope in the Pretorius Kop area. A positive correlation has been shown between dietary quality and faecal indicators of nutrition such as nitrogen and phosphorus (Leslie & Starkey 1985).

I collected fresh faecal samples from deposits with no signs of dung beetle activity. Faecal deposits located within the same day were combined to form a single composite sample. Each sample was air-dried in paper bags and subsequently oven-dried at 60ºC in preparation for the nutritional analysis.

Faecal nitrogen were analysed using a nitrogen analyser and faecal phosphorus were estimated through the Inductively Coupled Plasma-Optical Emission Spectroscopy (ICP-OES) method (Jarvis *et al.* 1992). The samples were analysed by BEMLAB (Pty) Ltd. in Cape Town, South Africa. Both indices were expressed as percentage dry matter. Faecal nitrogen content was used to calculate the percentage crude protein by multiplying the value with 6.25 (Van Soest 1994).

The percentage crude protein and the percentage phosphorus were separately analysed for differences among sable herds and variation across seasons. Despite

attempts at transformation, the data remained non-normally distributed and was thus analysed with a non-parametric Kruskal –Wallis Ranks Sum Test. All analyses were performed in R (R Development Core Team 2008) at 95% significance level ($p<0.05$).

RESULTS

There were no significant differences between the faecal samples from the four herds in the percentage crude protein ($K = 1.12$; d.f. = 3; P = 0.77) nor in the percentage faecal phosphorus ($K = 1.28$; d.f. = 3; P = 0.73). The percentage crude protein in the faecal samples and the percentage faecal phosphorus differed significantly seasonally (CP: $K = 59.26$; d.f. = 5; $P < 0.0001$;P: $K = 35.81$; d.f. = 5; $P < 0.0001$).

Crude protein levels were generally higher during the relatively wet year of 2006 compared to 2007 during which relatively little rainfall was received (Table VIII.I; Figure VIII.I). The faecal indicators of nutrition did not drop during the burn period despite the low availability of green foliage with crude protein increasing from 6.03 ± 0.35% in the late dry season of 2007 to 6.17 ± 0.14% during the burn period (Table VIII.I; Figure VIII.I) and phosphorus levels increasing from 0.20 ± 0.01% during the late dry season to 0.22 ± 0.00% during the burn period (Table VIII.I; Figure VIII.II).

Both the percentage crude protein and the percentage phosphorus increased considerably during the flush period when fresh regrowth was again abundantly available. During the flush period faecal crude protein averaged 15.21 ± 0.54% and faecal phosphorus averaged 0.63 ± 0.05% (Table VIII.I).

During the relatively dry year of 2007, sable faecal crude protein levels averaged just below the minimum maintenance level of 7% suggested by Sinclair (1977).

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TABLES

Table VIII.I: Seasonal changes in the percentage of faecal crude protein and phosphorus. The bracketed value following each season represents the number of samples within that season.

	LDS 06 (19)	**EWS 06 (8)**	**EDS 07 (18)**	**LDS 07 (9)**	**Burn (22)**	**Flush (10)**
CP (%)	8.76 ± 0.37	9.79 ± 0.73	6.89 ± 0.36	6.03 ± 0.35	6.17 ± 0.14	15.21 ± 0.54
P (%)	0.24 ± 0.01	0.32 ± 0.05	0.23 ± 0.01	0.20 ± 0.01	0.22 ± 0.00	0.63 ± 0.05

LDS 06 – Late dry season 2006 (August – September)

EWS 06 – Early wet season 2006 (October – November)

EDS 07 – Early dry season 2007 (May – June)

LDS 07 – Late dry season 2007 (July)

Burn period 2007 (August – September)

Flush period 2007 (October – November)

FIGURES

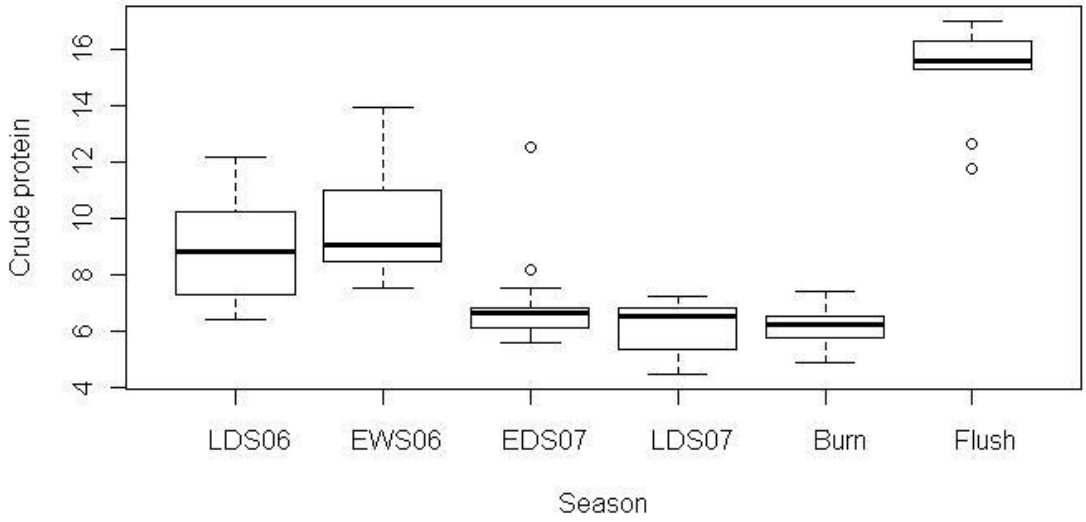

Figure VIII.I: Seasonal changes in percentage faecal crude protein.

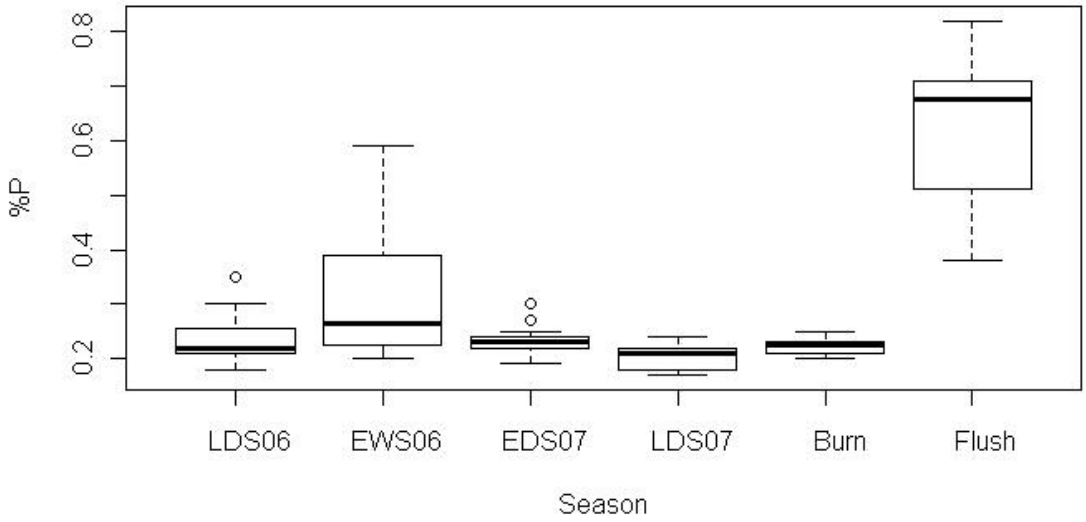

Figure VIII.II: Seasonal changes in percentage faecal phosphorus.