HOME RANGE AND RESOURCE USE OF SABLE ANTELOPE IN THE OKAVANGO DELTA

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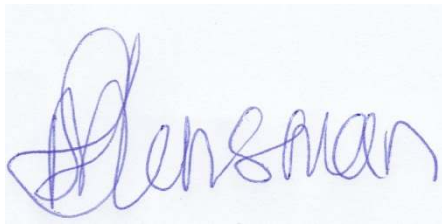
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<u>DECLARATION</u>

I declare that this dissertation is my own, unaided work and does not involve plagiarism or collusion unless otherwise acknowledged (Chapter 4). It is being submitted to the University of the Witwatersrand, Johannesburg for the degree of Masters in Science. It has not been submitted before for any degree or examination in any other University.

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ABSTRACT

Habitat selection occurs across a range of different spatial scales and is influenced by a variety of factors, ultimately determining how animals distribute themselves across the landscape. Studying the decisions that an individual animal makes across different levels of selection, from its choice in dietary item to predator avoidance strategies, is a fundamental link in understanding the response of groups of animals and ultimately entire populations that may provide insight into population performance. The study formed part of a broader study focused on the decline of rare antelope species. Specifically this study was aimed at establishing the home range and resource use of sable antelope in a region where they were initially expected to be thriving.

The levels of selection covered in this study are: the location of home ranges of an individual or social group within the landscape; the use of various habitat components within the home range; and the procurement of food items within those habitats. At the highest level, the broad objectives were (1) to determine where sable occupied home ranges within the landscape, indicating the suitability of various landscape units to sustain sable populations and (2) to determine the relative use of habitat types within those home ranges that may enable sable to avoid predation and acquire resources required to survive and reproduce. At the lowest level of selection the characteristics of forage selection and how the grass quality in the different vegetation types during different seasons affects the success of sable herds was explored. The broad objectives were (1) to determine the effect of seasonal flooding and rainfall on grass greenness in the floodplains and upland vegetation types and the consequent use of those vegetation types by sable antelope and (2) to determine how exploitation of resources in the floodplains and in the uplands contributed to the nutritional status of sable. I additionally quantified the time spent browsing and determined the composition of the browse component of the diet of sable.

Adult female sable from each of three adjacent sable herds were fitted with GPS collars providing hourly GPS co-ordinates. Adaptive LoCoH was used to determine home range location and annual, seasonal and core home range extents. A vegetation map was created and the number of GPS locations within each vegetation type was counted to determine their relative use in relation to availability within the home ranges. GPS collars were used to locate herds daily so that foraging observations of browsing and characteristics of the grasses grazed could be attained. Acceptability and dietary contributions of grass species and browse were determined for each sable herd during different seasons. The availability of grass species on the floodplain grasslands and in the upland grasslands and woodlands was estimated.

Water and the availability of key resources posed a constraint on where sable home ranges were established. Sable simply did not occupy the region in the north of the study area further than 7 km from permanent water and floodplain grasslands. Herds generally avoided open savanna, mopane woodlands and Kalahari apple-leaf woodlands characterised by sparse grass cover, particularly during the dry season. Home ranges were relatively small compared

to the range estimates from herds in Kruger National Park. There was no obvious seasonal difference in home range extent nor were there large areas of overlap between home ranges of adjacent herds. Observations during the study indicated that competitor species, including zebra and wildebeest, concentrated on the floodplain grasslands. Throughout the year *H. dissoluta* was the most strongly favoured grass species and contributed most to the diet of the sable herds in both the wet and dry season. During the dry season sable herds expanded their diet to include *Aristida stipitata* and *Aristida meridionalis* which are generally considered poor forage value species for cattle but that retained some greenness. Additionally, the contribution of browse, especially the leaves of *Croton megalobotrys, Philenoptera nelsii* and *Combretum mossambicense* and the flowers of *Kigelia africana*, constituted an important bridging resource during the extended dry season. Crude faecal protein levels remained above the suggested maintenance levels throughout the annual cycle. Crude faecal protein levels were elevated prior to calving when sable spent more time foraging on the floodplain grasslands where high value forage species such as *Paspalum scrobiculatum*, *Panicum repens* and *Urochloa mossambicense* and sedges were eaten. Indications are that the constraint posed by the distribution of water within the landscape, rather than resource limitations within occupied home ranges, are the primary limitation to population performance in the Kwedi concession.

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CHAPTER 1 – GENERAL INTRODUCTION

Project background and motivation

In the southern African sub-region sable formerly had a wide distribution but have been eliminated from large areas due to cattle ranching, agriculture and other development (Skinner *et al.* 2005) restricting their spatial distribution to protected reserves covering a small portion of their former range (Skinner *et al.* 2005). Recently, sable have even shown alarming population declines in South Africa's Kruger National Park (KNP), (Harrington *et al.,* 1999; Grant & van der Walt, 2000; Ogutu & Owen-Smith, 2005) where indications are that fewer than 400 sable antelope remain (Whyte, 2006). The population decline and lack of recovery of sable antelope has become a major conservation concern in other parts of southern Africa (Skinner *et al.* 2005) and it is still unclear whether the declines are related to the effects of climatic extremes on habitat conditions, competition from other grazers, or heightened predation following excessive water provision. Fortunately, sable have been afforded some protection on private land (Skinner *et al.* 2005) and the species is thus not threatened.

The Okavango is a unique wetland ecosystem in that primary productivity there is linked to both rainfall and the seasonal, long and short term flooding fluctuations that occur in the region. Most of the previous studies conducted in the Okavango have focused predominantly on the hydrological, vegetation and socio-economic issues with very little attention being directed towards wildlife despite the high diversity of wildlife in the area. It is only since about 2000 that herbivore studies have been conducted. Hence my study was a baseline study for the region to determine the factors governing habitat suitability for sable.

This study was also designed to contribute towards the rare antelope research programme undertaken by the Centre of African Ecology (CAE) at the University of the Witwatersrand. This broad project was aimed at identifying why sable and other rare antelope species have experienced substantial population declines in KNP and at understanding the ecology of these rare antelope species (Henley, 2005; Parrini, 2006; Owen-Smith & Cain, 2007; Rahimi & Owen-Smith, 2007; Parrini & Owen-Smith, 2009; Macandza, 2009; Chirima, 2009; LeRoux, 2010; Owen-Smith *et al.,* in press).

Broad project aim

This study was aimed at establishing the home range and resource use of sable antelope in the Kwedi Concession.

Study area

The opportunity to conduct the study in Botswana was made possible by Wilderness Safaris who manage Kwedi Concession (NG22) situated in the northeast of the Okavango Delta (S $18^0 55'37.46''$, E $22^0 48'19.43''$). The region is semi-arid and is characterised by a

prolonged dry season (April/May to October/November) where temperatures become hot before the rains break. Rain normally occurs in thundershowers towards the end of November and the Okavango region receives about 500 mm of rainfall per year (McCarthy, Bloem and Larkin, 1998). The soils are mainly composed of deep, well-drained, nutrient deficient Aeolian sands with some alluvial clay soils characteristically occurring along the edge of permanent water. The quality of forage offered is especially poor due to the sandy, infertile soils (Bell, 1984) that are predominant in the region. The delta is unique in that its dynamics are also partly driven by flooding which occurs during the dry season when the water arrives from the Angolan highlands. The floodplain grasslands are typically inundated during the floods, limiting the area available for foraging, but regrowth of green grass is induced and surface water gets trapped in depressions after the water recedes (Butchard, 2000).

Study species

Sable antelope fall within the Bovide family. They are medium-sized grazing ruminants, with adult females attaining masses of about 220 kg and males 235 kg (Estes, 1991). There are four subspecies of sable antelope (*Hippotragus niger,* Harris 1938) in Africa: *H. n. niger, H. n. roosevelti, H. n. kirkii* and *H. n. variani*. All the subspecies exhibit some degree of sexual dimorphism. Although there are slight variations between subspecies, males have black coats while females and young are generally sorrel to rich chestnut in colour (Estes, 1991). The subspecies in this study, *H. n. niger*, can be distinguished from the other sub-species by the near black colour of the females (Estes, 1991) and is the sub-species with the least dimorphic characteristics. *H. n. niger* exhibits the largest distribution of the sub-species and occurs in Zimbabwe, Botswana, South Africa, Zambia, Mozambique, and Malawi (Skinner & Chimimba, 2005). Historically, the western limit to the distribution of sable extended from Botswana into regions of Angola (Wilson & Hirst, 1977). Sable herds typically number between 15-25 individuals, though herds of up to 75 females and young are not uncommon (Estes, 1991; Estes 1997). The reduced sexual dimorphism of *H. n. niger* may enable young males to remain in the herd for longer and thus facilitate the formation of larger, mixed sex herds (Estes, 1991). Sable antelope occupy fixed, spatially discrete home ranges in dry savanna (Estes, 1991) where they typically occur in low densities. Sable may undertake seasonal movements between open grasslands and woodlands to burnt areas or drainage sump grasslands where green grass is found in the dry season (Estes, 1991). Sable have been described as being a water-dependant species implying that they need to drink daily (Skinner, Smithers & Chimimba, 2005). However, recent studies have shown that sable herds in Kruger National Park (KNP) only travelled to water at 2-4 day intervals during the dry season (Rahimi & Owen-Smith, 2007; Cain, Owen-Smith & Macandza, 2011).

Literature review

<u>Spatial scales and resource selection hierarchies</u>

The distribution of large herbivores across the landscape is influenced by aspects of animal behaviour ranging from an individual's choice in dietary items to predator avoidance strategies that affect habitat selection across many levels of ecological resolution (Senft *et al*., 1987; Shaefer & Messier, 1995; O'Reagain & Schwartz, 1995). In this way the use of resources across different scales by individual and groups of animals can be linked to population performance as a whole. In this thesis, resource use at different scales was explored to establish how conditions in the Kwedi Concession, northern Botswana influenced whether sable are thriving there or not. I used a concept of selection order described by Johnson (1980) in which a selection process was of higher order than another if it was conditional upon the latter. The natural ordering of selection processes described by Johnson (1980), is such that: first order selection involves the selection of the physical or geographic range of an organism; second order refers to the home range of an individual or social group; third order pertains to the use made of various habitat components within the home range; and fourth order pertains to the procurement of food items. The higher levels controlled and constrained the lower levels and the lower levels provided a mechanism or details required to explain the response of the focal level (Bailey, 1996; Turner *et al.,* 2001).

<u>Landscape selection</u>

Landscape-scale determinants of the distribution of large herbivores are important for wildlife managers (Bailey *et al.,* 1996; Redfern *et al.,* 2003). A landscape refers to a mosaic of heterogeneous land forms, vegetation types, and land uses (Urban *et al*., 1987) and can be divided into several relevant units for large herbivores. Bailey *et al.* (1996) suggested that abiotic factors, such as distance to water and slope, are the primary determinants of large-scale distribution patterns for herbivores and act as constraints within which biotic factors operate.

At a landscape level, the mosaic created by water sources poses a constraint on where herbivores can establish home ranges (Western, 1975; Redfern, 1993; Gaylard *et al.* 2003) and distance to water can be used as a criterion for understanding landscape selection. Grazers tend to be more dependent on drinking water than browsers because tree foliage and succulents tend to retain more moisture than grasses (Owen-Smith, 2002). In arid and semi-arid areas, water-dependent animals normally confine their utilization of food to areas within 6 to 10 kilometres of water points (O'Reagain & Schwartz, 1995). Western (1975) found that 99% of herbivore biomass in the Amboseli (Kenya) occurred within 15 km of surface water in the dry season. This area comprised 52% of the total ecosystem area. However, the mosaic created by water sources changes seasonally through rainfall events and evaporation (Gaylard *et al.,* 2003). For example, in the wet season surface water is distributed widely over the landscape in rivers, springs, pans, and vleis (Gaylard *et al.,* 2003). The changes in the

distribution and availability of surface water can explain why herbivores move between distinct regions in different seasons. Western (1975) showed that herbivores responded strongly to seasonal availability of water and green vegetation. It is clear that water poses a constraint on where home ranges can be established in landscapes with sparsely distributed water.

Sable antelope are a water-dependent species and Grobler (1981) and Martin (1983) suggested that they remain within 3 kilometres and 1 kilometre of water respectively. A more recent study recorded movements of over 7 km to water when water was not available within the core home range (Owen-Smith & Cain, 2007). It has also recently been documented that sable only have to drink at 2-4 day intervals when water became restricted to a few perennial sources during the dry season (Owen-Smith & Cain, 2007; Cain, Owen-Smith & Macandza, 2012). The longer interval between trips to water may enable sable to occupy regions of the landscape further from water where more common herbivores are less abundant (Cain, Owen-Smith & Macandza, 2012). It is clear that home ranges of sable must be able to satisfy the nutritional requirements of an animal within the constraints set by the location of water sources.

Home range selection

Burt (1943) defined a home range as the area normally traversed by an animal over a period (i.e.: month, season, year or lifetime) while it meets its needs for food, shelter, security and reproduction; but what is meant by the term 'normally' remains vague. The estimation of an animal's home range is at the core of many space use analyses (Kernohan *et al*., 2001; Borger *et al.,* 2006). Hayne (1949) recognised that the biological significance of an animal's home range must include knowledge of the intensity of use in different areas and that this knowledge changes where the limit of a home range is drawn. He therefore suggested a method to determine the 'centre of activity' based on the number of times an animal was located at a point. The concept of a 'core area' used to describe the intensity of use of habitats has replaced Hayne's (1949) 'centre of activity' terminology (Hodder *et al.,*1998).

Since the concept of home range was introduced, the extent has been calculated using a number of different methods (e.g., minimum convex polygons; Local Convex Hull, adaptive Kernels and fixed Kernels) (Kernohan *et al*., 2001). The minimum convex polygon which connects the outer points to define the overall area of use is the oldest and was the most common home range estimator (Kernohan *et al.,* 2001). For this reason, it is still used to make comparisons of home range size between different studies (Kernohan *et al.,* 2001).

The Kernel and Local Convex Hull (LoCoH) are methods that are able to determine core areas of use using utilization distributions (UDs). Van Winkle (1975) defined a UD as 'the two-dimensional relative frequency distribution for the points of location of an animal over a period of time'. A UD is important in home range studies because it assesses the probability of an animal or group of animals occurring at any point (Van Winkle, 1975;

Worton, 1989; Kernohan *et al.,* 2001) and allows habitats used by animals to be identified with increasing clarity (Marzluff *et al.,* 2001).

Kernel methods estimate a probability function corresponding to the UD (Millspaugh *et al*., 2006) and are generally reported as the minimum area that includes a fixed percentage of the UD area (Kernohan *et al*., 2001). Fifty percent isopleths are normally used to determine 'core areas' of use and 95% isopleths are used to define the outer limits of a home range (e.g.: Owen-Smith & Cain, 2007) although 50 and 95% are arbitrary numbers (Powell, 2000). Fixed kernel methods use the same smoothing parameter over the entire evaluation area, whereas the adaptive kernel method uses different smoothing parameters such that the data points are covered with kernels of different widths ranging from low, broad kernels for widely spaced points to sharply peaked, narrow kernels for tightly packed points (Worton, 1989; Powell, 2000; Kernohan *et al.,* 2001). A weakness of kernel methods is that they are unable to define hard boundaries and discontinuities (Millspaugh *et al*., 2006) although home ranges do not inherently have hard boundaries (Powell, 2000). However, LoCoH, which is a relatively new method, is able to represent hard boundaries and gaps within the home ranges (Getz & Wilmers, 2004) and tends not to include areas where a species was not recorded. It is also useful for determining boundaries between home ranges of different herds (Getz *et al.* 2007) and quantifying resource use by linking areas of high use with satellite imagery with matching resolution (Millspaugh *et al.* 2006; Getz *et al.* 2007).

Home range extent

The home range extent of different groups of the same species shows considerable variation (Owen-Smith, 1988). In a recent review on modelling home range behaviour, Borger *et al.* (2008) suggested that this occurs because interactions among individual characteristics, individual state, and the external environment vary between populations (Borger *et al.,* 2006; Borger *et al.,* 2008). Borger *et al.* (2008) also explains how memory, focal point attraction, habitat and resource distribution, territoriality and other social interactions affect the shape and size of home ranges. Social factors and interactions between neighbours also need to be considered in order to understand animal space use patters (Borger *et al*., 2006). For example, some animals defend territories, which influence the shape and size of a neighbour's home range. Territoriality arises when individuals exhibit spatially orientated aggressive behaviour, i.e. aggressive defence of a space containing limiting resources (Burt, 1943) and may be limited to a circumscribed area within the home range, where specific activities are performed (e.g. mating), or may extend to the whole home range (Borger *et al.,* 2008).

Body size, sex, herd size and season also influence the extent of an animal's home range (Burt, 1943; Anderson *et al.,* 2005) because these factors influence energetic and nutritional requirements. The total extent of the home ranges of African herbivores increased steeply with body size (power co-efficient of 1.25± 0.32; Owen-Smith, 1988). Species that form large herds (e.g. impala, *Aepyceros melampus*; African buffalo, *Syncerus caffer*; and

Thomson's gazelle, *Gazella thomsoni*) tend to fall above the regression line while solitary species such as white rhino (*Ceratotherium simum*) fall below it (Owen-Smith, 1988). The larger home ranges in herding herbivores can be viewed as a cost of sharing a home range with companions.

The seasonal change in the quality and quantity of resources also influences the home range size of herbivores and many lead to distinct dry and wet season (or favourable and adverse season) home ranges (Burt, 1943). Owen-Smith (1988) and Ryan *et al.* (2006) showed that white rhino and African buffalo respectively, all had larger home ranges in dry season (when food was scarce) than in the wet season (when food was more abundant). By definition migratory herbivores have distinct wet and dry season home ranges, though what constitutes a distinct range remains somewhat vague. In the Serengeti-Mara ecosystem species such as wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) migrate between the Masai-Mara and the southern Serengeti where the availability of green forage is a major criterion for movement (Musiega & Kazadi, 2004; Boone *et al.,* 2006). The movements of non-migratory herbivore species occur on a localized landscape scale (i.e.: down slopes to dry season grazing areas or drainage sinks in transition zones; Scoones, 1995).

Within their home ranges, animals often have more than one core area due to the heterogeneous environment in terms of food availability, resting sites, and density of competitors and predators (Hodder *et al.,* 1998). Grazing distribution by large herbivores is dependent on biotic factors such as species composition, plant morphology, productivity and forage quality (Bailey *et al.,* 1996) and herbivores will 'match' time spent in the different areas based on the resource levels found there (Senft *et al.,*1987).

Using minimum convex polygons, a wide range of annual home range sizes for sable antelope have been reported in different areas (Wilson & Hirst, 1977; Grobler, 1981; Parrini, 2006; Magome, 1991; Cain & Owen-Smith, 2007; Magome *et al.,* 2008). They vary between 2.4 km^2 (Rhodes Matopos National Park, Zimbabwe; Grobler, 1981) and 196 km^2 (KNP; Henley, 2005). Sable antelope are not a migratory species but have been reported to make seasonal movements of up to 50 kilometres (Estes, 1997). Several sable herds occupied somewhat larger home ranges (using 95% isopleths kernel home range estimates) in the dry season than the wet season (Henley, 2005; Parrini, 2006; Rahimi & Owen-Smith 2007; Owen-Smith & Cain 2007). In many of these cases, the expansion of the home ranges occurred during the dry season to take advantage of green grass growth following burns or that retained greenness in drainage sump grasslands.

Habitat and resource use

A habitat is defined as 'the resources and conditions presented in an area that produce occupancy, including survival and reproduction by a given organism' and is organism specific. It relates the presence of a species, population, or individual (animal or plant) to an area's physical and biological characteristics (Hall *et al*., 1997). Usage or use takes place over

several different scales and is defined as 'the quantity of the resource or habitat used by a consumer in a fixed period of time' (Johnson, 1980). The usage an animal makes of its environment, specifically the kinds of food it consumes and the variety of habitats it occupies within its home range is central to the study of animal ecology (Johnson, 1980). Habitat and resource use within home ranges is a complex process involving trade-offs between forage intake and risks such as predation (Mysterud & Ims, 1998). A suitable home range must contain a mixture of habitats that provide opportunities for all activities essential for reproduction and survival (i.e.: food resources and protective cover) (Mysterud & Ims, 1998). Habitat distinctions are not often clear-cut and a researcher might visually distinguish between a large number of different habitat types (e.g. Scoones, 1995; Ryan *et al.,* 2006) whereas the study animals might distinguish fewer broad habitat types (Garshelis, 2000).

For large herbivores the structure and species composition of the vegetation define not only the habitat but also distinct characteristics such as food resources available (Owen-Smith, 2002). Over different periods of time, herbivores may shift between different habitats to obtain these resources (Owen-Smith, 2002). The grazing succession in the Serengeti region is a good example because grazing ungulates there move from the short upland grasslands during the wet season to the tall bottomland grasslands offering higher biomass in the dry season, in a sequence governed largely by body size (Bell, 1970). Larger-bodied herbivores (zebra, *Equus quagga* and wildebeest, *Connochaetes taurinus*) have a greater absolute food requirement than smaller species (Thomsons gazelle, *Gazella thomsoni*) but because of their lower metabolic rate per unit of body, they are able to tolerate lower quality diets (Bell, 1971). Therefore, during the dry season as larger grazers progressively become unable to maintain themselves on the short grass they move down the catena to areas with higher biomass, which they open up allowing the smaller grazers to select the lower levels of the herb layer that are more nutritious (Bell, 1970; Bell, 1971). Grass features, such as grass height, stemminess and greenness affect grass quality (Bell, 1970; Owen-Smith, 1982). Short grasses tend to be more nutritious to herbivores than taller grasses because they contain less structural tissue – crude protein is negatively correlated with fibre content (Owen-Smith, 1982). Stems have a lower digestibility compared to the green fraction of the plant since they have a higher content of fibre than green leaves (Owen-Smith, 2002). Grass greenness is an indicator of grass quality because crude protein levels decline and the concentration of fibre increases as grasses become senescent (and turn brown) during the dry season (Owen-Smith, 1982).

In African savannas, vegetation varies in woody cover from open areas with very few trees to dense, almost closed woodlands, which affects the distribution of food resources for herbivores (Riginos & Grace, 2008). For example, areas with high tree density may have less grass because the trees occupy a larger percentage of the habitat (Riginos & Grace, 2008) but better grass quality due to elevated nutrient concentrations attributed to the influence of litter fall beneath tree canopies (Sutton *et al.,* 2002). Tree density and canopy cover results in alterations to grass species composition and forage abundance (Angassa & Baars, 2000).

Aside from affecting habitat use through the distribution of forage, tree density and canopy cover provide shade and wind protection. Heat stress arises from high ambient temperature and direct solar radiation (Owen-Smith, 2002). Animals differ in their heat tolerance depending on the colour and thickness of their coats as well their capacity to allow body temperature to rise while maintaining constant body temperature (Owen-Smith, 1982). For animals that are not very heat tolerant, feeding locations can be constrained by woody cover (Owen-Smith, 2002). Habitats with woody cover are likely to be used more during the hottest time of day and in the hottest months by animals responding to heat stress.

In addition, because not all landscapes are uniform, herbivores perception of safe or unsafe areas may change over very short distances as they forage around dangerous features (Shrader *et al.,* 2008). In the presence of predators, herbivores choose feeding sites away from obstacles that can impede escape, decrease visibility or provide predators with ambush sites (Ripple & Beschta, 2003). Ungulates that depend on running speed to avoid predation are disadvantaged in thick bush whereas species dependent on jumping ability for evasion are more at risk in open vegetation (Owen-Smith, 2002). To avoid predation risk, prey species may alter their selection of habitats by spending more time in open ground where predators can be detected from a long way off and where the prospect of escape is high (Shrader *et al.,* 2008). Among African grazing ungulates, open savannas are preferred by species such as wildebeest (*Connochaetes gnou*), zebra (*Equus quagga*) and warthog (*Phacochoerus aethiopicus*) (Hirst, 1975). Animals engage in a number of daily activities including, feeding, travelling and resting as well as maintenance activities such as drinking wallowing and grooming (Owen-Smith 1988) and different habitats offering different attributes are needed to perform different activities.

Fluctuations in rainfall and temperature during different seasons largely control vegetation growth (O'Reagain & Schwartz, 1995; Redfern *et al.,* 2003) and therefore, food production for herbivores. Plants regenerate much of their aboveground biomass at the beginning of the wet season (Owen-Smith, 2002). As temperature and rainfall changes during the year, the leaf to stem ratio, greenness and growth stage of grasses change with consequent seasonal variation in grass quantity and quality (Owen-Smith, 2002). Changes in rainfall and temperature affect the distribution of key resource areas (KRAs) that in turn influence the distribution of herbivores (Scoones, 1995). Key resource areas are defined as dry season foraging zones for herbivores (Ngugi & Conant, 2008) and are areas that contain reserves that sustain herbivores through dry season (e.g. *Themeda triandra*) and buffer resources that help alleviate starvation during critical periods (e.g. browse components for grazers and unpalatable grasses) (Owen-Smith, 2002). Ngugi and Conant (2008) indicated that KRAs in Kenyan landscapes were accessed by herbivores during the dry season when all other easily accessible rangeland was depleted. They also identified a number of factors that characterize KRAs and affect their distribution such as water availability, catena position, steepness of slopes, soil type, altitude, temperature, human habitation and rainfall. For example, some people regarded absence of water as a major factor in whether an area was a KRA because such areas are never used for forage until very severe droughts occur and they are then used

at the considerable cost of long distance walks to far water sources (Ngugi & Conant, 2008). Similarly, soils were cited as an important contributor to dry season forage production because fertile soils and soils with good moisture retention support growth well into dry seasons (Ngugi & Conant, 2008). Cattle in the Zimbabwean dryland used key resource areas by increasingly concentrating on the lower catena, riverine strips and dambos during the dry season as upland resources decreased in quality and quantity (Scoones, 1995).

There are apparent conflicting opinions on what constitutes preferred habitat for sable because substantial variation exists in descriptions of the broad scale habitats selected by them (Henley, 2005). There is no doubt that drinking water represents a critical habitat component (Grobler, 1981; Wilson & Hirst, 1977; Henley, 2005; Rahimi & Owen-Smith, 2007; Cain *et al.* 2012). Sable antelope seem to prefer a mosaic arrangement of open woodlands and grasslands (Wilson & Hirst, 1977; Magome, 1991; Estes, 1991; Skinner & Chimimba, 2005) and have been reported using areas ranging from vleis with no canopy cover (Parrini 2006) to areas with woody canopy cover as high as 25% in the Matetsi area (Grober, 1981). Sable are not adept to crop short grass and prefer foraging in habitats containing medium to tall grass swards (Grobler, 1981; Parrini, 2006, Le Roux, 2009) though occasionally forage on short grass in burnt areas (Parrini & Owen-Smith, 2009). During the dry season sable seek moist areas where grass greenness is retained such as on floodplains, vleis, drainage lines and valley bottoms (Grober, 1981; Magome, 1991; Parrini, 2006) or where new grass emerges following burns (Wilson & Hirst 1977; Magome, 1991; Parrini & Owen-Smith, 2009).

In the Kgaswane Mountain Reserve, Parrini (2006) also showed that sable always chose the greenest grasses available at feeding patch and grass tuft levels. Other studies have also reported preference for green grass by sable antelope (Grobler, 1981; Magome, 1991).

Nutritional status and faecal analysis

Whether an animal survives, grows and later reproduces is dependent on the quality and quantity of resources it can obtain from the environment (Owen-Smith, 2002). Free ranging herbivores exert choice in consuming different plant species and parts from the available vegetation. Since the concentration of nutrients in the different plant species and plant parts selected varies, it can have a marked effect on herbivores nutrient intake (Owen-Smith, 1982). Crude protein, soluble carbohydrates, mineral elements and the digestible energy content of the plant determine its nutritional value (Owen-Smith, 2002). Nutrient intake is important for determining the production performance of animals and is an indicator of the well-being of herbivore populations (Meyes & Dove, 2000). Resource deficiencies can eventually deplete body reserves of herbivores to critical levels of malnutrition that weakens them and makes them susceptible to predators, parasite and disease infestations that can lead to their death (Owen-Smith 2002). Mortality losses for herbivores through malnutrition, even if mediated by predation, generally intensify towards the dry season when food diminishes

and energy expenditure increases as herbivores range wider in search of food (Owen-Smith, 2002).

Measuring nutritional gains through faecal analyses provides an alternative to direct field observations or rumen content analysis and is a useful research tool (Holecheck *et al.,* 1982; Parrini & Owen-Smith, 2009) to predict dietary quality of free-ranging grazers (Verheyden *et al.,* 2011) because faecal nitrogen is positively correlated to dietary protein (Holecheck, Vavra & Pieper, 1982). Multiplying faecal nitrogen content as a proportion of dry matter by 6.25 gives an estimate of crude protein level..Faecal analysis has several advantages: 1) it is a non-invasive method for investigating diet quality; 2) it allows repeated sampling and; 3) it does not interfere with normal animal behaviour (Holechek *et al.,* 1982; Meyes & Dove, 2000). However, it is important to note that faecal analysis has a limitation in that browse can have a significant effect on faecal N since browse contains significant amounts of tannins, which bind with proteins in the diet leading to decreased protein digestibility and inflation of nitrogen in the faeces (Robbins, 1996; Verheyden *et al.,* 2011). Therefore if there is an appreciable amount of condensed tannins in the diet (>2%; Verheyden *et al.,* 2011) one could expect higher N values in faeces that does not necessarily reflect higher N gains. Very little information is available on the nutrient requirements of wild herbivores (Grant & Scholes, 2006) although the dietary crude protein requirement for maintenance of wild ruminants is estimated to be between 5 and 8% of dry matter (Robbins, 1996). The faecal nitrogen concentration threshold is approximately 13 g kg^{-1} below which dietary deficiency that may precipitate in nutritional stress in animals while faecal phosphorous concentrations of between 1.9 and 2.0 g kg^{-1} over a long period of time would indicate a deficiency that may lead to low reproductive rates (Grant, *et al.,* 2000). Apart from protein, other macro-minerals such as phosphorus, potassium and sodium are important for grazing ruminants and may even restrict animal distributions (Robbins, 1996).

A number of studies on sable have used faecal crude protein to measure the nutritional status of sable (Henley, 2005; Codron *et al.* 2007; Magome *et al.,* 2008; LeRoux, 2009; Parrini & Owen-Smith, 2009). Most studies report seasonal differences in crude protein levels where the wet season levels are much higher than dry season levels (Henley, 2005; Codron *et al.* 2007; Magome *et al.* 2008). Crude faecal protein levels below 6 – 8% in sable suggest that the diet is potentially nitrogen limited and indicates nutritional deficiency. Crude protein levels below maintenance levels were recorded for sable in Kruger National Park (5.4 % during the dry season and 7.5 % during the wet season; Codron *et al.,* 2007). High faecal protein levels were recorded when sable were feeding on burnt areas during the early wet season in the Pilanesberg Game Reserve and in the Kgaswane Mountain Reserve (14.2 %; Magome *et al.*, 2008; Parrini & Owen-Smith, 2009).

Thesis structure

The original study design was based on the following objectives:

1. to determine home range extent and utilization distribution of sable herds during different seasons;
2. to determine the regional landscape units available but not occupied by sable antelope and how the conditions in the units change seasonally in the study area;

3. to identify use of habitats by sable antelope within home ranges and how the habitat conditions presented change seasonally;
4. to determine how the nutritional status of sable antelope change seasonally.

The three sable herds that we managed to locate in the study area were small (12, 14 and 19 individuals) suggesting that sable may not have been doing as well in the study area as initially suspected. An area where the population was performing well would be expected to have a larger number of herds and more individuals within each herd (+/- 25 individuals). Thus, the entire study was adapted to determine why sable may or may not have been thriving. This study was structured to incorporate the second, third and fourth orders of resource selection as defined by Johnson (1980). The second and third orders are reported in Chapter 2 where various top-down constraints such as the limitations posed by availability and distribution of drinking water were explored. I also explored factors governing habitat suitability for sable within their home ranges that may prevent sable from being more widely distributed or more abundant. The new study objectives for Chapter 2 are:

1. to determine where sable occupy home ranges and which landscape units occur where sable home ranges are absent within the broad landscape and;
2. to determine the extent of home ranges and the relative use of habitat types within the home ranges during different seasons.

The fourth order of resource selection (the procurement of food items from different vegetation types) was explored and reported in Chapter 3. The original objectives of Chapter 3 changed shortly after I arrived in the Kwedi concession to take advantage of opportunities that I had not anticipated to have been possible before I arrived in the study area. For example, all three sable herds in the study area allowed vehicles to approach to within a few meters of them allowing direct feeding observations that had not been possible for sable studies in Kruger National Park. The objectives of Chapter 3 were redirected to address the opportunity. The specific objectives of the chapter were changed to:

1. determine the effect of seasonal flooding and rainfall on grass greenness in the floodplains and upland vegetation types and the consequent use of those vegetation types by sable antelope and;
2. determine how exploitation of resources on the floodplains and in the uplands contributes to the nutritional status of sable.

Through being able to observe the sable herds from so close, it became apparent that the sable were spending a considerable amount of time browsing. Following the initial observations I began recording the amount of time the herds spent performing different foraging activities during the wet and the late dry season in 2010. The objectives of chapter 4 were:

1. to quantify the contribution of browse to the diet of sable
2. to determine the composition of the browse component of the diet of sable in our study area.

The thesis has been written so that each chapter represents a potential paper to be submitted to peer reviewed journals for publication. Chapter 4, co-authored with my supervisors, Prof. Norman Owen-Smith, Dr. Francesca Parrini and Dr. Barend Erasmus, has been submitted to the African Journal of Ecology. Each chapter lists references relevant to that particular chapter and each chapter also has its own introduction, methods, results, and discussion sections. The final chapter (Chapter 5) serves as an overview of the findings. It also links the other chapters together and highlights areas that still need further research. It considers and reports what the study has accomplished towards achieving the aim of this and the broad CAE study as well as what it has achieved in terms of sable ecology, management and conservation.

References

ANDERSON, D.P., FORESTERM, J.D., TURNER, M.G., FRAIR, J.L., MERRILL, E.H., FORTIN, D., MAO, J.S., & BOYCE, M.S. (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*. 20, 257-271.

ANGASSA, A., & BAARS, R.M.T., (2000) Ecological condition of encroached and non-encroached rangelands in Borana, Ethiopia. *African Journal of Ecology*. 38, 321-328.

ARCHIBALD, S & SCHOLES, R.J. (2007) Leaf green-up in a semi-arid African savanna—separating tree and grass responses to environmental cues. *Journal of Vegetation Science.* 18, 583–594.

BAILEY, D.W., GROSS, H.E., LACA, E.A., RITTENHOUSE, L.R., COUGHENOUR, M.B., SWIFT, D.M., & SIMS, P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management.* 49 (5), 386-400.

BELL, R.H.V. (1970) The use of the herb layer by grazing ungulates in the Serengeti. In: *Animal Populations in Relation to Their Food Resources* (Eds. Watson, A.). Blackwell Scientific Publications, Oxford. 112-124

BELL, R.H.V. (1971) A grazing ecosystem in the Serengeti. *Scientific American.* 225, 86-93.

BELL, R.H.V. (1984) Soil–plant–herbivore interactions. In: *Conservation and Wildlife Management in Africa* (Eds. R.H.V. Bell & E. McShane-Caluzi). US Peace Corps, Washington D.C.

BOONE, B. R., THIRGOOD, S.J. & HOPCRAFT, J.G.C. (2006) Serengeti wildebeest migratory patterns modelled from rainfall and new vegetation growth. *Ecology.* 87 (8), 1987-1994.

BORGER, L., DALZIEL, B.D & FRYXELL, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters.* 11, 637–650.

BORGER, L., FRANCONI, N., FERRETTI, F., MESCHI, F., MICHELE, G., GANTZ, A., & COULSON, T. (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist.* 168 (4), 471-485.

BOX, E.O., HOLBEN, B.N., & KALB, V. (1989) Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO2 flux. *Plant Ecology.* 80 (2), 71–89.

BURT, W.H. (1943) Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy.* 24 (3), 346-352.

BUTCHARD, D. (2000) *Wildlife of the Okovango – common animals and plants*. Struik Publishers. Cape Town.

CAIN, J.W., OWEN-SMITH, N., & MACANDZA, V.A. (2012) The costs of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology.* 286, 58-67.

CHIRIMA, J.G. (2009) *Habitat suitability assessments for sable antelope.* PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

CODRON, D., CODRON, J., LEE-THORP, J.A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R., & FOURIE, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology.* 273, 21-29.

ESTES, R.D. (1991) *The Behavior Guide to African Mammals: including hoofed mammals, carnivores, primates.* The University of California Press, California.

ESTES, R.D. & ESTES, R.K. (1974) The biology and conservation of the giant sable antelope, *Hippotragus niger variani* (Thomas 1961). *Proceedings of the Academy of Natural Sciences of Philadelphia.* 126, 73-104.

GARSHELIS, D.L. (2000) Delusions in Habitat Evaluation: Measuring Use, Selection, and Importance, In: *Research Techniques in Animal Ecology* (Eds: L. Boitani & T.K. Fuller), Columbia University Press. 111-164.

GAYLARD, A., OWEN-SMITH, N. & REDFERN, J. (2003) Surface water availability: implications for heterogeneity and ecosystem processes. In: *The Kruger experience; ecology and management of savanna heterogeneity* (Eds: J.T. du Toit, K.H. Rogers & H.C. Biggs), Island Press. Washington.

GETZ, W.M., FROTMANN-ROE, S., CROSS, P.C., LYONS, A.J., RYAN, S.J., & WILMERS, C.C. (2007) LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE.* 2, 1-11.

GETZ, W.M. & WILMERS, C.C. (2004) A local nearest-neighbour convex-hull construction of home ranges and utilization distributions. *Ecography.* 27, 489-505.

GRANT, C.C. & VAN DER WALT. (2000) Towards an adaptive management approach for the conservation of rare antelope in the Kruger National Park – outcome of a workshop held in May 2000. *Koedoe.* 43, 103-111.

GRANT, C.C., PEEL, M.J.S., ZAMBATIS, N., & VAN RYSSEN, J.B.J. (2000) Nitrogen and phosphorus concentration in faeces: an indicator of range quality as a practical adjunct to existing range evaluation methods. *African Journal of Range& Forage Science.* 17, 81-92.

GROBLER, J.H. (1981) Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. *South African Journal of Zoology.* 16 (1), 50-58.

HALL, L.S., KRAUSMAN, P.R., & MORRISON, M.L. (1997) The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin.* 25 (1), 173-182.

HARRINGTON, R., OWEN-SMITH, N., VILJOEN, P., & BIGGS-MASON, D. (1999) Establishing the causes of the roan antelope decline in the Kruger National Park. *South African Biological Conservation.* 90, 69–78.

HAYNE, D.W. (1949) Calculation of size of home range. *Journal of Mammology.* 30 (1), 1-18.

HEITKONIG, I.M.A. (1993) *Feeding strategy of roan antelope in a low nutrient savanna.* PhD thesis. University of Witwatersrand, Johannesburg.

HENLEY, S. (2005) Habitat dependency and nutritional ecology of sable antelope in two regions of the Kruger National Park. *Report to South African National Parks.* Centre for African Ecology. University of the Witwatersrand, Johannesburg.

HIRST, S.M. (1975) Ungulate-habitat relationships in a South African woodland/savanna ecosystem. *Wildlife Monographs.* 44, 1–60.

HODDER, K.H., KENWOOD, R.E., WALLS, S.S. & CLARKE, R.T. (1998) Estimating core ranges: a comparison of techniques using the common buzzard (*Buteo buteo*). *Journal of Raptor Research.* 32(2), 82-29.

HOLECHECK, J.L., VAVRA, M. & PIEPER, R.D. (1982) Botanical composition determination of range herbivore diets: A review. *Journal of Range Management.* 35, 309 – 315.

HUETE, A., DIDAN, K., MIURA, T., RODRIGUEZ, E.P., GAO, X., & FERREIRA, L.G., (2002) Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment.* 83, 195–213.

ILLIUS, A.W. & O'CONNOR, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos.* 89 (2), 283-294.

JOHNSON, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology.* 61 (1), 65-71.

JUSTICE, O., TOWNSEND, J.R.G., HOLBEN, B.N., & TUCKER, C.J. (1985) Analysis of the phenology of global vegetation using meteorological satellite data. *International Journal of Remote Sensing.* 6, 1271-1378.

KERNOHAN, B.J., GITZEN, R.A., & MILLSPAUGH, J.J. (2001) Analysis of space use and movements. In: *Radio tracking and animal populations*. (Eds. MILLSPAUGH, J.J. & MARZLUFF, J.M.) Academic Press, USA.

KNOOP, M. & OWEN-SMITH, N. (2006) Foraging ecology of roan antelope: key resources during critical periods. *African Journal of Ecology.* 44, 228-236.

LE ROUX, E. (2010) *Habitat and forage dependency of sable antelope (Hippotragus niger) in the Pretoriuskop region of the Kruger National Park.* MSc Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A. (2009) *Resource partitioning between low-density and high-density grazers: sable antelope, zebra and buffalo.* PhD Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A., OWEN-SMITH, N., & CROSS, P.C. (2004) Forage selection by buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research.* 34 (2), 113-121.

MAGOME, D.T. (1991) *Habitat selection and the feeding ecology of the sable antelope (Hippotragus niger niger) (Harris 1838), in Pilanesberg National Park, Bophuthatswana.* MSc Thesis, University of the Witwatersrand, Johannesburg.

MAGOME, H., CAIN, J.W., OWEN-SMITH, N., & HENLEY, S.R. (2008) Forage selection of sable antelope in Pilansberg Game Reserve, South Africa. *South African Journal of Wildlife Research.* 38 (1), 35–41.

MARTIN, R. B. (1983) Transboundary species project: roan, sable and tsessebe – background study. *Report for roan sable and tsessebe in support of the Transboundary mammal project.* University of Pretoria, Pretoria.

MARZLUFF, J.M., KNICK, S.T., & MILLSPAUGH, J.J. (2001) High-tech behavioural ecology: modelling the distribution of animal activities to better understand wildlife space use and resource selection. In: *Radio tracking and animal populations*. (Eds. J.J. Millspaugh & J.M. Marzluff) Academic Press, USA.

McCARTHY, T. S., BLOEM, A. & LARKIN, P. A. (1998) Observations on the hydrology and geohydrology of the Okavango Delta. *South African Journal of Geology*. 101 (2), 101–117.

MEYES, R.W. & DOVE, H. (2000) Measurement of the dietary nutrient intake in free-ranging mammalian herbivores. *Nutrition Research Reviews*. 13, 107-138.

MILLSPAUGH, J.J., NIELSON, R.M., McDONALD, L., MARZLUFF, J.M., GITZEN, R.A., RITTENHOUSE, C.D., HUBBARD, M.W., & SHERRIF, S.L. (2006) Analysis of resource selection using utilization distributions. *The Journal of Wildlife Management*. 70(2), 384-395.

MUSIEGA, D.E. & KAZADI, S. (2004) Simulating the East African wildebeest migration patterns using GIS and remote sensing. *African Journal of Ecology*. 42, 355–362.

MYSETRUD, A. & IMS, R.A. (1998) Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*. 79 (4), 1435-1441.

NGUGI, M.K., & CONANT, R.T. (2008) Ecological and social characterization of key resource areas in Kenyan rangelands. *Journal of Arid Environments*. 72, 820–835.

O'REAGAIN, P.J. & SCHWARTZ, J. (1995) Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. In: *Recent developments in the nutrition of herbivores. Proceedings of the IVth International Symposium on the Nutrition of Herbivores* (Eds. M. Journet, E. Grenet, M-H. Farce, M. Theriez & C. Demarquilly). 407 – 423. INRA Editions, Paris.

OGUTU, J.O. & OWEN-SMITH, N. (2005) Oscillations in large mammal populations: are they related to predation or rainfall? *African Journal of Ecology*. 43, 332–339.

OWEN-SMITH, N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of Tropical Savannas* (Eds. B.J. Huntley & B. H. Walker) Springer-Verlag, Berlin, 359-404.

OWEN-SMITH, N. (1988) *Megaherbivores – The influence of a very large body size on ecology*. Cambridge University Press. Cambridge, UK.

OWEN-SMITH, N. (2002) *Adaptive Herbivore Ecology (Student Edition).* Wits University Press, Johannesburg.

OWEN-SMITH, N. & CAIN, J.W. (2007) Indicators of adaptive response in home range utilization and movement patterns by a large mammalian herbivore. *Israel Journal of Ecology and Evolution.* 53, 423-428.

OWEN-SMITH, N. & COOPER, S.M. (1987) Assessing the food preferences of ungulates by acceptability indices. *Journal of Wildlife Management.* 51, 372-378.

OWEN-SMITH, N., CHIRIMA, G.J., MACANDZA, V.A. & LE ROUX, L. (in press) Shrinking sable antelope numbers in Kruger National Park: what is supressing population recovery? *Animal conservation.*

PARRINI. F. (2006) *Nutritional and social ecology of the sable antelope in the Magaliesberg Nature Reserve.* PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

PARRINI, F. & OWEN-SMITH, N. (2010) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology.* 48 (2), 526-534.

RAHMINI, S. & OWEN-SMITH, N. (2007) Movement patterns of sable antelope in the Kruger National Park from GPS/GSM collars: a preliminary assessment. *South African Journal of Wildlife Research.* 37 (2), 143–151.

REDFERN, J.V., GRANT, R., BIGGS, H., & GETZ, W.M. (2003) Surface-Water Constraints on Herbivore Foraging in the Kruger National Park, South Africa. *Ecology.* 84 (8), 2092-2107.

RIGINOS, C. & GRACE, B.J. (2008) Savanna tree density, herbivores and the herbaceous community: bottom-up vs.top down effects. *Ecology.* 89 (8), 2228–2238.

RIPPLE, W.J., & BESCHTA, R.L. (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management.* 184, 299–313.

ROBBINS C.T. (1996) *Wildlife feeding and nutrition*. Academic Press, San Diego, California, USA.

RYAN, S.J., KNECHTEL, C.U., & GETZ, W.M. (2006) Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management.* 70, 764-776.

SCOONES, I. (1995) Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments.* 29, 221 – 237.

SENFT, R.L., COUGHENOUR, M.B., BAILEY, D.W., RITTENHOUSE, L.R., SALA, O.E. & SWIFT, D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience.* 37, 789 – 799.

SHAEFER, J.A. & MESSIER, F. (1995) Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography.* 18, 333-344.

SHRADER, A.M., BROWN, J.S., KERLEY, G.I.H., & KOTLER, B.P. (2008) Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *Journal of Arid Environments.* 72, 1811– 1819.

SKINNER, J.D., SMITHERS, R.H.N. & CHIMIMBA, C.T. (2005) *The mammals of the Southern African Subregion*. 3rd edn. Cambridge University Press, Cambridge, UK.

SOUTH, A. (1999) Extrapolating from individual movement behaviour to population spacing patterns in a ranging mammal. *Ecological Modelling*. 117, 343–360.

SUTTON, P., MASKALL, J. & THORNTON, I. (2002) Concentrations of major and trace elements in soil and grass at Shimba Hills National Reserve, Kenya. *Applied Geochemistry.* 17, 1003 – 1016.

TUCKER, C. J. (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*. 8, 127 – 150.

TUCKER, C. J., TOWNSHEND, J. R. G., & GOFF, T. E. (1985) African land-cover classification using satellite data. *Science*. 227, 369 – 375.

TURNER, M.G., GARDNER, R.H., & O'NIEL, R.V. (2001) *Landscape ecology in theory and practice: pattern and process.* Springer publishers.

URBAN, D.L., O'NIEL, R.V., & SHUGART, H.H. (1987) Landscape ecology. *Bioscience.* 37(2), 119-127.

VAN WINKLE, W. (1975) Comparison of several probabilistic home range models. *Journal of Wildlife Management.* 39, 118-123.

VERHEYDEN, H., AUBRY, L., MARLET, J., PETIBON, P., CHAUVEAU-DURIOT, B., GUILLON, N., & DUNCAN, P. (2011) Faecal nitrogen, an index of diet quality in roe deer *Capeolus capreolus*? *Wildlife Biology.* 17, 166-175.

WESTERN, D. (1975) Water availability and its influence on the structure and dynamics of a savannah large mammal community. *East African Wildlife Journal.* 13, 265-286.

WHYTE, I.J. (2006) *Rare antelope in the Kruger National Park: Trends, current status, and options for future management.* Scientific Report, South African National Parks.

WILSON, D.E. & HIRST, S.M. (1977) Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife Monographs.* 54, 3-111.

WORTON, B.J. (1989) Kernel methods for estimating utilization distributions in home range studies. *Ecology.* 70 (1), 146-148.

CHAPTER 2 – HOME RANGE OCCUPATION AND HABITAT USE BY SABLE ANTELOPE IN THE OKAVANGO DELTA

Abstract

I investigated where home ranges were established by sable within the landscape and their use of various habitat types within their home ranges in the Okavango delta region of northern Botswana. GPS collars fitted to three adjacent sable herds recorded hourly GPS locations over two years. A vegetation map of the study area was created and a basic assessment of the locations and availability of drinking water in temporary pans as well as the location of potential competitors was made. The seasonal and annual extents of the home ranges of each herd were determined using MCPs and a-LoCoH at the 95% and 50% isopleth levels. The home ranges were overlaid on the vegetation map and the availability vs. utilization of different vegetation types was determined to give an indication of which vegetation types were selected. In comparison to other regions sable herds occupied relatively small home ranges, there was no obvious seasonal difference in home range extent and nor were there large areas of overlap between home ranges of adjacent herds. All these indications suggest that sable could thrive there. However, the sable herds simply did not occupy the region in the north of the study area further than 7 km from permanent water and floodplain grasslands vegetation types. Herds also generally avoided open savanna, mopane woodlands and Kalahari apple-leaf woodlands characterised by sparse grass cover, particularly during the dry season. These unsuitable habitats may pose the greatest constraint on sable abundance in the region.

Introduction

Resource selection requires consideration of a multitude of different levels because of resource selection criteria at different scales ranging from the procurement of food items to predator avoidance strategies (Senft *et al*., 1987; Shaefer & Messier, 1995; O'Reagain & Schwartz, 1995). Individuals or groups of animals integrate behaviours from lower levels with constraints posed by higher levels, ultimately influencing how they distribute themselves across the landscape. Johnson (1980) defined a hierarchical ordering framework in which selection could occur from a geographic range (1st order); the home range (2nd order); habitat use within a home range (3rd order); to the procurement of food items (4th order). This study was designed to explore the 2nd and 3rd orders of resource selection and the extent of home ranges to determine why sable may or may not be thriving in the Okavango Delta. Central to both these orders of selection and the estimation of home range extent is the concept of a home range which was first described as the area normally traversed by an animal over a period (i.e.: day, month, season, year or lifetime) as it meets its food, shelter, security and reproductive requirements (Burt, 1943).

Specifically, the 2nd order of selection relates to how herbivores select where to establish home ranges within the landscape (Johnson, 1980). Suitable areas for home range occupation within the landscape are those that have conditions necessary to maintain a viable population. Interactions between abiotic and biotic factors may influence the suitability of areas where home ranges can be established (Soberón and Peterson, 2005).Abiotic factors, such as geology, slope, distance to water, temperature and precipitation may pose physiological constraints within which animals can operate and are the primary determinants of large-scale distribution patterns for animals (Bailey *et al.,* 1996; Soberón & Peterson, 2005; Chirima, 2009). The mosaic created by the distribution of water in the landscape poses a restriction on where the home ranges of some herbivores (particularly grazers) can be established (Western, 1975; Redfern, 1993; Gaylard *et al.*, 2003) such that water-dependent species in arid and semi-arid areas are confined to within 6 to 10 km of surface water (O'Reagain & Schwartz 1995).

The 2nd order of resource selection can be related to population performance because it reveals which areas of the landscape are suitable or unsuitable for the establishment of home ranges (Gaston, 1991). If an animal population is thriving, a broad tolerance to conditions presented within the landscape is expected such that all landscape units will be suitable and occupied by an abundance of animals. If a population is becoming depressed, one would expect the lowest quality landscape units not to be occupied at all or to be occupied by low-status animals and juvenile herds (Senft *et al.*, 1987) leaving large unsuitable areas unoccupied within or between the annual home ranges.

The 3rd order of resource selection described by Johnson (1980) pertains to the usage of those various habitat components within home ranges. Habitat use is defined as 'the environmental and resource conditions surrounding the animal and the way it consumes them' (Johnson, 1980; Hall *et al.*, 1997). In order for an animal to survive, its home range must contain a mixture of habitats providing the requisites for life, namely: food of sufficient quality and quantity to survive and reproduce; the opportunity to lower the risk of predation, competition and thermal stress (Mysterud & Ims, 1998; Hall *et al.*, 1999; Henley, 2005). The relative abundance of vegetation types (a useful measure of forage availability because they are defined by plant assemblages) within the known home ranges provide a simple index of the foraging opportunities and food resources available to herbivores (Henley, 2005). In order for herbivores to thrive, they are dependent on the availability of particular vegetation components to offer food resources within their home ranges throughout the year. During the critical dry season when resources are most limiting, animals will need to survive on areas retaining plant species of high quality and quantity until the next period of food abundance (Owen-Smith & Cooper, 1989; Owen-Smith, 2002; Henley, 2005; Shaw, 2011). The risk of predation may also vary between habitats influencing the impact of predation on the population (Owen-Smith, 2002). To lower predation risk, prey species may alter space use by selecting habitats where the prospect of escape is high (Shrader *et al.,* 2008) or by avoiding habitats where predators concentrate. Perceived negative effects of predation and competition in habitats may exclude large herbivores from those habitats that would

otherwise have supported them (Grobler, 1981; Sinclair, 1985, (Soberón & Peterson, 2005). Extreme weather conditions and discomforts (i.e. floodplain grasslands that are inundated by water during part of the year) can restrict foraging activities and increase metabolic costs that reduce body reserves to critical levels of malnutrition and eventually cause mortality that ultimately affects population performance (Owen-Smith, 2002). So, animals may also select habitat types providing shelter from extreme weather conditions (Owen-Smith, 1988; Macandza, 2009) and to avoid discomforts in otherwise attractive areas. Social factors and interactions between neighbours is an important consideration when trying to understand animal space use patters (Borger *et al*., 2006). Large areas of range overlap between ranges of adjacent animals that occupy fixed ranges might indicate stressful conditions prompting trespassing as herds search for resources in neighbours' ranges.

The estimation of an animal's home range has been at the core of many space use analyses (Kernohan *et al*., 2001; Borger *et al.,* 2006) and in itself can provide insight into population performance because space use translates to population density as the inverse of area per animal is the number of animals per unit area (Owen-Smith & Cain, 2007). However, one needs also consider the number of individuals sharing the range as well as the overlap occurring between individuals occupying adjacent ranges (Owen-Smith 1988). Harestad & Bunnell (1979) suggest that animals will occupy smaller home ranges when resources are abundant or locally concentrated (i.e. during the wet season) and larger home ranges when resources are scarce, thinly distributed or widely scattered (i.e. during the late dry season). Unusually large home range extents for a species may indicate poor habitats conditions requiring the animal to occupy larger home ranges to meet their survival requirements (Reid *et al.,* 2007). Increased predation risk and energy expenditure associated with movements over large unfamiliar areas in search of resources to meet their survival requirements may push populations into decline. Due to seasonal variations in resource availability, an animal might also occupy more contracted home ranges in habitats providing quality resources during the wet season when conditions are favourable and much larger home ranges during the harsh dry season when further ranging in search of green grass and water is necessary (Owen-Smith, 1988 & Ryan *et al.,* 2006).

The Okavango Delta region is unique in that the distribution of both water and food are not only influenced by local seasonal precipitation but also by the seasonal, long and short term flooding fluctuations that occur in the region when rainwater arrives from the catchment area in the Angolan highlands (Ellery & Ellery, 1997). Flooding limits the area available for foraging but also induces grass regrowth when the floodwaters recede offering a valuable key resource (van Bommel *et al*., 2006; Bonyongo, 2009) that may be extremely important in maintaining an animal population there through the dry season (Chapter 3). Sable (*Hippotragus niger*) are of particular interest because there is evidence that sable populations have declined to unprecedented levels in South Africa's Kruger National Park (Whyte, 2006). The status of sable in Botswana is hence of concern for wildlife managers and conservationists in Botswana,

The objectives of this study were:

1. to determine where sables occupied annual home ranges in the landscape and which landscape units occurred where sables annual home ranges were absent. If sable in the Kwedi are thriving, I expected that:

   a. annual home ranges would occur in all landscape units providing high quality resources within the study area;

   b. landscape units that were within 7 km(based on previous studies; Cain *et al.* 2012) of water and did not include part of the home range would represent landscape units least suitable for occupation by sable.

2. to determine the extent of home ranges and the relative use of habitat types within annual and seasonal home ranges. If sable in the Kwedi were thriving, I expected:

   a. sable herds would have occupied floodplain grasslands after floodwaters had receded due to the availability of food and water there, but to avoid the floodplains when they were inundated, and mopane and teak during the late dry season when they offered very little green grass or nearby water.

   b. sable herds would not trespass into habitats occupied by adjacent herds (i.e. very little overlap between different herds home ranges) in search of food and water

   c. sable herds would not occupy habitats with high concentrations of competitors or predators

   d. sable herds to occupy relatively smaller seasonal home ranges than sable in areas where they were not thriving, such as Kruger National Park.

   e. sable herds would not increase the size of their home ranges as the dry season progressed in wider search of resources.

Methods

Study site

The study area comprised the Kwedi (NG22), Duba Plains (NG23) and Mapula (NG12) concessions (Fig. 1) in the north east of the Okavango Delta (S $18^0$55'37.46", E 22048'19.43"). The Okavango is a large (approximately 22000 km^2) alluvial fan within the Kalahari basin (Butchart, 2000; Gumbricht et al., 2004; McCarthy, 2006). The soils are mainly composed of deep, well-drained, nutrient deficient Aeolian sands with some alluvial clay soils characteristically occurring along the edge of permanent water. The region is relatively flat with elevations around 980 m above sea level.

A buffalo fence that was completed in 2002 and that bisects the Mapula concession was used to define the northern boundary of the study area and also marks the northern boundary of the sable range (Fig 1). I defined the other borders of the 252 km^2 study area arbitrarily at the end of the study to encompass an area about 1 km beyond the furthest GPS location in each directional axis. Permanent open water occurs in the southern part of both the Kwedi and Duba concessions.

The study area consisted of a mosaic of vegetation types that run more or less parallel with the edge of the Permanent water and changing with soil type. I broadly classified the vegetation types in the study areas as: Open water, Floodplain grasslands, Dryland grasslands and savanna woodland types (e.g. Mixed woodland, Open savanna, Mopane woodland and Kalahari apple-leaf woodland that are described in table 2).

Common tree species found in the woodland vegetation types include mopane (*Colophospermum mopane*), Kalahari apple-leaf (*Philenaptera nelsii*), jackalberry (*Diospyros mespiliformis*), sausage tree (*Kigelia africana*), knob thorn (*Acacia nigrescens*) and leadwood (*Combretum imberbe*). Common grass species include giant three-awn (*Aristida meridionalis*), long-awned grass (*Aristida stipitata*), couch grass (*Cynodon dactylon*), curly leaf love (*Eragrostis rigidior*), yellow thatching grass (*Hyperthelia dissoluta*) and sand quick (*Schmidtia pappophoroides*).

All three concessions contain a variety of predators including cheetah (*Acinonyx jubatus*), hyena (*Crocuta crocuta*), lion (*Panthera leo)*, leopard (*Panthera pardus*), wild dog (*Lycaon pictus*), black-backed jackal (*Canis mesomelas)* and side-striped jackal (*Canis adustus*). Herbivore species that could potentially compete with sable in the study area include buffalo (*Syncerus caffer*), elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), impala (*Aepyceros melampus*), red lechwe (*Kobus leche*), tsessebe (*Damaliscus lunatus*), waterbuck (*Kobus ellipsiprymnus*), blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga***).** Some of these competitors could attract and support lion and contribute to the sable decline through apparent competition (Holt 1977). Zebra and buffalo also have similar resource requirements to sable and could contribute to sable decline through depletion of food resources during the critical dry season (Skinner and Chimimba, 2005; Macandza, 2009).

Seasons

The climate is semi-arid with summer rainfall mainly between November and April. Records from Shakawe and Maun between 1964 and 1994 revealed highly variable rainfall with annual amounts ranging between 288 mm and 1145 mm with an annual mean of 513 mm (McCarthy *et al.* 1998).

I used rainfall recorded by a weather station situated in the study area between January 2009 and December 2010 to define different seasons. April was the first month in both 2009 and 2010 that recorded nil rainfall (Fig. 2) and was therefore used to define the onset of the dry season. The dry season (April to November) was divided into the early dry season (1st April to 31st July) and late dry season (1st August to 31st October). The first rainfall in the dry season was recorded at the end of October in 2009 and the beginning of November in 2010 (Fig. 2). Soon after these rainfall events, grass became visibly greener but no specific date could be used to indicate a change from the dry to the wet season because convective rainfall was patchy across the landscape. Therefore, I defined the entire month of November as a 'transition period' (Fig. 2) between the late dry and wet season. During the

wet season (1st December 2009 to 31st March 2010) between 10 mm and 140 mm of rain was recorded monthly (Fig. 2). In 2009 and 2010, the Kwedi received 500 mm and 436 mm of rain during the calendar year, respectively.

Flooding, another major driver of the dynamics of the Okavango, affects habitat conditions and drinking water availability. Shallow water typically covers the Floodplain grasslands during the floods, limiting the area available for foraging, but also induces regrowth of grasses and traps water in depressions on the floodplains after the water recedes (van Bommel *et al*., 2006).Variation in the timing and intensity of the floods in the study area depends on the timing and intensity of rainfall in the catchment area and the amount of water remaining in the delta from the previous season. Flooding in the region normally begins between February and May when floodwaters arrive from the Angolan highlands through the Okavango River. The peak of the floods usually occurs in August (McCarthy, 2006; van Bommel *et al*., 2006) and lasts until October (Gumbricht *et al.,* 2004). In both 2009 and 2010, the Okavango recorded exceptionally high floods due to above average inflows from Angola in 2008 and 2009. At the beginning of September 2009, the majority of the floodwater had receded and most of the Floodplain grasslands were dry. The flood water reached its peak in the Kwedi in mid-May 2010 after which water levels remained high until the beginning of July when water gradually began to recede again. By the beginning of September 2010, most of the Floodplain grasslands were completely exposed. July was the coldest month of the year with a mean monthly temperature of 16^{0}C. October was the hottest month of the year with a mean monthly temperature of 26^{0}C.

Data collection

GPS locations

Africa Wildlife Tracking (AWT; http://www.awt.co.za) provided collars containing a Global Positioning System (GPS) unit; Ultra High Frequency (UHF) and Very High Frequency (VHF) transmitters; and batteries that were designed to last an entire year. Each collar recorded the date, time of day, latitude and longitude co-ordinates, temperature, altitude, speed and direction of the animal. Hourly GPS locations and associated data were collected from the collars by using a VHF R-1000 Telemetry Receiver and antenna to locate and get within 500m of the herd in order to download the data using a UHF downloading console consisting of an EeePC viewer console and USB UHF modem.

Due to the gregarious and cohesive nature of sable, I represented the movements of entire sable herds by collaring a single adult female sable from each herd. Two sable (Eastern Herd and Western Herd) were fitted with collars in August 2009 and a third female (Central Herd) was fitted with a collar in October 2009. The collar batteries fitted on the Eastern and Western herds unexpectedly failed at the beginning of December 2009 and were replaced at the beginning of March 2010. The female fitted with the collar from the Central herd was killed by lion in August 2010 and when I recovered the collar, found that the battery had failed and data had only been recorded until the end of March 2010. The collar on the Central

herd was not replaced because the end of the fieldwork period was so near. The collars fitted onto the females from the Eastern and Central herds were removed at the end of November 2010. Table 1 provides a summary of when different collars were functioning. The period over which the collars successfully transmitted GPS locations and the number of GPS locations collected by each collar is provided in tables 3 and 4.

Water points and competitors

At the beginning of the study, I used information provided by the Kwedi guides to record the location of all pans in the study area using a GPS. I then used Google earth (CNES/SPOT imagery dated 31/05/2008) to locate pans in remote areas that the guides did not know about. There is a possibility that some small pans were overlooked. If there were two or more pans less than 500 m apart, I only recorded the largest of them and if the pans were less than 500 m from permanent water I did not record their location separately. Towards the end of each month, I visited each pan and noted if drinking water was available in them.

If I saw tsessebe, impala, zebra, buffalo, and wildebeest while driving between the camp and various sable herds, I recorded the species and the vegetation type I saw them in. No observations were made in the Flooded *Terminalia* vegetation type as it is not on the route between the camps and the herds.

Data Analysis

Home range extent and location

The GPS locations of three adult females (one per herd- three replicate herds) were projected with Universal Transverse Mercator (UTM) zone 34S and the WGS 1984 spheroid and loaded into the a-LoCoH toolbox (http://locoh.cnr.berkeley.edu/arctutorial; Getz & Wilmers, 2004) in Arc GIS 9.3.1. I used a-LoCoH (adaptive-Local Convex Hull) to calculate annual and seasonal home range areas. All collected GPS positions and associated data from each herd were used to create the annual Minimum Convex Polygons (MCPs) and *a*-LoCoH home ranges. All GPS locations collected between 1st August 2009 and 31st October 2009; 1st December 2009 and 31st March 2010; 1st April 2010 and 31st July 2010; 1st August 2010 and 31st October 2010 were used to create seasonal home ranges for the Late Dry Season 2009, Wet Season, Early Dry Season and Late Dry Season 2010 respectively (see table 1).

The LoCoH family of algorithms generally use a user-specified number of nearest neighbour points to each location in a dataset to construct polygons that delineate the outer boundaries of location records and construct isopleths around areas that exhibit the same probability of use by the collared animal (Getz *et al*., 2007; Chirima, 2009). Specifically, *a*-LoCoH (adaptive-LoCoH) constructs polygons from the nearest points such that the sum of their distances from the root point is equal to or less than *a* (Getz *et al*., 2007). The *a*-LoCoH is particularly good at identifying shifts, disruptions, gaps and sharp boundaries within a

home range (Getz *et al*., 2007 & Chirima, 2009). The *a*-LoCoH method is better able to reveal gaps in the occurrence and is influenced less by outliers than Kernel methods (Getz & Wilmers, 2004).

A limitation of *a*-LoCoH is that selecting the appropriate *a* and *k* values is somewhat subjective and requires experience with the method (Getz & Wilmers, 2004; Getz *et al*., 2007; Chirima, 2009) or knowledge of where gaps and sharp boundaries occur in the range beforehand. Values that are too small lead to gaps in the distribution where they should not exist whilst values that are too large lead to the distribution including areas that are not actually used.

To determine appropriate *a* and *k* values, I adopted Getz & Wilmers' (2004) "minimum spurious hole covering" (MSHC) rule. The rule requires plotting the area of the 100% isopleths against varying values of *a* and *k*. The estimated area covered by the distribution should level off once all spurious holes are covered (Getz & Wilmers, 2004; Ryan *et al*., 2006), but should increase again when real gaps in the distribution become totally or partially covered (Getz & Wilmers, 2004). I initially fixed the value of *k* at three and plotted increasing values of *a* against the range area until it began to level off. With *a* fixed at that value, I then varied *k* and plotted the *k* value against range area until the MSHC was again determined. I finally used the joint values of *a* and *k* to determine the final home range.

I used different isopleths to determine areas of core and marginal use. The *a*-LoCoH uses the union of the hulls from smallest to largest to construct the isopleths, which encompass a determined proportion of the distribution of locations. Core and marginal areas of use can be determined at different isopleth levels using the principal that smaller hulls include heavily used areas and that larger hulls include areas of marginal use (Chirima, 2009). In this study 100% isopleths were used to define Minimum Convex Polygons for total home ranges (area encompassing all GPS locations from each herd – including occasional excursions). 95% isopleths were used to represent the annual and seasonal home ranges (thereby omitting occasional excursions beyond this area); and 50% probability isopleths were used to identify seasonal core home ranges.

The MCPs delineate outer limits to occurrence, creating a range extent that includes gaps and occasional excursions beyond the limits of the range normally traversed. Before Kernel and LoCoH home range analysis were developed many sable studies measured home range extent using MCPs (e.g.: Sekulic, 1981; Magome, 1991). Therefore MCPs are useful for comparisons with studies completed before LoCoH and kernel methods were developed but are subject to distortion by outlying points and do not provide information on patterns of use within the home range. Although Kernel home range estimates produces similar range extents to *a*- LoCoH, comparisons of home range extents using different methods should be interpreted with caution.

Habitat use/non use

Google earth (CNES/SPOT imagery dated 31/05/2008) was used to create a vegetation map by drawing polygons around nine previously identified vegetation types within the study area. The limits to each polygon were determined visually and with prior knowledge of the area. Seventy ground control points were randomly created and visited to verify the different vegetation types by visually determining the predominant tree species (defining woodland vegetation types) and whether inundation had occurred from open grassland within 200m radius of the GPS location. The digitized vegetation polygons were then converted to shapefiles. Digitizing errors were fixed using standard topology generation procedures implemented within ArcMap 10.0. Areas of each vegetation type within the study area were determined using Hawths Analysis Tools (http://www.spatialecology.com) in ArcGIS 9.3.1.

The proportion of available vegetation types within the study area was then calculated (available vegetation types = area of each vegetation type within study area / total area of study area). Permanent water was not included in available area. The home ranges were overlaid on the vegetation map and the area of each vegetation type within the home ranges was also determined using Hawths Analysis Tools in ArcGIS. Third order selection was then calculated (third order selection = area of vegetation types within home range / area of vegetation type within study area).

Results

Landscape selection

The three herds occupied adjacent home ranges along the edge of the Permanent water. The home range of the Central herd was located between the ranges of the other two herds (Fig. 5). The areas south of the annual MCP ranges of all three herds and west of the range of the Western herd where there was Permanent water were not occupied (Fig. 5). The western herd was prevented from ranging further north by the buffalo fence (Fig. 5). A large area between the annual MCP home range of the Eastern and Central herds and the northern boundary of the study area was also not occupied by sable (Fig. 5). This area was predominantly made up of large expanses of Kalahari apple-leaf and Mopane woodland vegetation but was also far (+/- 8km) from permanent water (Fig. 3). Permanent water and rain filled pans occurred within the annual MCPs of all three herds. By mid-October in both years, particularly during 2010 surface water became restricted to the Permanent swamp and a few perennial rain-filled pans. The water remaining in the few perennial pans in 2009 (Fig. 4) was likely attributed to the high rainfall in March and the unusually late rainfall recorded in June 2009 (Fig. 2) and was very muddy. None of the annual MCP's extended further than 7 km from permanent water and no other sable herds were sighted more than 7 km from permanent water despite occasional game drives in the area. None of the herds occupied the area in the south east of the study area where the seasonally Flooded *Terminalia* woodland

vegetation type and the camps were located (Fig. 5). The unoccupied area on the eastern side of the annual MCP range of the Eastern herd consisted of Kalahari apple-leaf and mopane woodland. Apart from seasonally Flooded *Terminalia* woodland, all other vegetation types occurred within the home ranges of at least one of the three sable herds (Fig. 10).

An area was not occupied between the annual 95% *a*-LoCoH home ranges of the Western and Central herds where large expanses of Floodplain grassland and open savanna occurred (Fig. 5). The annual ranges of the Eastern and Central herds were separated into two parts and the unoccupied area between the parts consisted of Kalahari apple-leaf and Mixed Woodland vegetation types (Fig. 5). An area south of the airstrip consisting of permanent water and large expanses of floodplain grasslands was avoided by the Central herd.

Habitat use

Dryland grassland, Open savannah, Teak woodland and Mixed woodland occurred in greater proportion within the annual home ranges than their availability in the study area (Fig. 10). Teak woodland occurred in greater proportion within the combined annual home ranges of all three herds than its availability within the study area despite being available only to the Eastern herds (Fig. 11). Mopane and Kalahari apple-leaf (KAL) occurred in a smaller proportion within the combined annual home ranges than their proportional availability within the study area (Fig. 10). Mopane woodland made-up 14 % of the study area and Kalahari apple-leaf together made up 11 % of the study area (Fig. 10). Mopane woodland did not occur within the annual home range of the Western herd (Fig. 11). Kalahari apple-leaf made up a larger proportion of the 95% annual home range of the Eastern herd than the other two herds; Floodplain grassland made up a larger proportion of home range of the Western herd than the other two herds; and Floodplain grassland and Mixed woodlands made up a smaller proportion of the annual 95 % home range of the Eastern herd than the ranges of the other two herds (Fig. 11) despite the wet season home range of the Eastern herd being made up entirely of these two vegetation types (Fig. 12).

All three herds moved southwards during the transition (November) between the late dry and wet season (compare Fig. 6 with Fig. 8). The wet season ranges of the Central and Western herds remained overlapped with their dry season ranges while there was a greater degree of separation between the wet and dry season ranges of the Eastern herd. The shift made by the Eastern herds was the most pronounced - shifting from a late dry season home range (Fig. 8) to a completely distinct wet season home range (Fig. 6). After the southward range shift that occurred during November 2009, the wet season range all three herds contained larger proportions of Floodplain grasslands and Mixed woodlands than during the late dry seasons in 2009 and 2010 (Fig. 12,13, 14). The dry season ranges of all three herds contained larger proportions of Open grassland than were available in the annual home ranges (Fig. 12, 13 & 14). The wet season 95% ranges of the Eastern herd did not contain Mopane woodland, Dryland grassland or Teak woodland (Fig. 12 b) which had all occurred

in dry season range of the herd. The late dry season 95% home range of the Eastern herd contained a large proportion of Teak woodland (Fig. 12).

Core home ranges

During the late dry season the intensely utilized areas (core ranges) of all three herds were larger and closer together (Fig. 8 & 9) than they had been during the early dry season. The core home range of the Western herd was made of areas widely separated during the wet season. The Central herd occupied a single large core home range while the Eastern herd occupied several smaller core ranges that were within close proximity of each other. Dryland Grasslands made up a large proportion of the dry season core home ranges of all three herds. Floodplain grasslands and Mixed woodlands both made up large proportions of the wet season core home ranges of all three herds (Fig. 12, 13 & 14). During the late dry seasons the core home ranges of all three herds contained proportionally less floodplain grassland than was available within the late dry 95% home ranges (Fig. 12, 13 & 14). Open savanna also occurred in the 95% late dry season ranges of all three herds but made up a considerably smaller proportion of their seasonal core ranges (Fig. 12, 13 & 14). During the wet season, however open savanna occurred proportionally more in the core home ranges than the 95% wet season ranges (Fig. 12, 13 & 14).

Home range extent and overlap

The annual MCP of the Central herd overlapped with that of the Eastern herd by 2.3 km^2 (2.3 % of the combined MCP area of the Central and Eastern herd). The Central herds MCP range also overlapped with the MCP range of the Western herd by 12.5 km^2 (11.2 % of the combined MCP area of the Central and Western herds). The a-LoCoH annual home range extents were between 50% and 53% of those suggested by MCPs. The Central herd occupied the largest annual home range (31 km^2; table 3) whilst the Eastern herd occupied the smallest annual home range (20.7 km^2; table 3) despite the two herds being very similar in size (table 3). The annual kernel 95% home ranges sizes of sable herds in KNP varied between 35.6 km^2 and 181.4 km^2 (mean = 80 km^2, n = 9; Henley, 2005; Owen-Smith & Cain, 2007; Macandza, 2009). Seasonal home range overlap occurred during the wet season when the range of the Central herd overlapped with the ranges of the Eastern and Western herds by 0.39 km^2 (2%) and 1.80 km^2 (6%) respectively (Fig. 6). During all the other seasons, no overlap occurred between the three herds.

There appeared to be more influence of herd identity on seasonal home range size than that of seasons. Seasonal home range extents followed a similar pattern to the annual *a-*LoCoH home range extents. The Central herd occupied the largest seasonal home ranges (19. 8 km^2 and 17.2 km^2; table 4) and the Eastern herd occupied the smallest seasonal home ranges (3.4 km^2 to 11.3 km^2: table 4). The smallest and largest home ranges were recorded during the wet season by the Eastern and Central herds respectively and the smallest and

largest home ranges of the Western herd were both occurred during the late dry season (table 4).

Competitors

Impala, zebra and wildebeest concentrated in Mixed woodland and open savanna but zebra concentrated in open savanna more than the other species (table 5). All competitor species concentrated on Floodplain grasslands (table 5).

Discussion

Landscape selection

The buffalo fence represented the northern limit of occurrence for the Western herd. Permanent water represented the southern limit of occurrence for all three herds. A narrow strip of permanent water represented the western limit of the home range of the Western herd but the habitat on the western side of that strip of water may have been suitable for sable to occupy because an un-collared sable herd was sighted there. None of the annual MCP's extended further than 7 km from Permanent water but the occupied annual MCPs of all three herds contained rain filled water-points most of which were dry by mid-October in both years. The availability of Permanent water and the adjacent Floodplain grassland vegetation seems to pose a general limitation on where home ranges are established. There is agreement in the literature that sable depend on regular access to drinking water (Estes, 1997, Skinner & Chimimba, 2005; Cain, Owen-Smith & Macandza, 2012). Some literature suggests that sable remain less than 4 km from water (Wilson & Hirst, 1977; Grobler, 1981; Magome, 1991) while more recently movements of over 7 km to water at 3-4 day intervals have been recorded (Owen-Smith & Cain, 2007). Sable in the Kwedi depend on the Floodplain grasslands as key resource areas during the dry season and foraged intensely on the Floodplain grasslands during the wet season (Chapter 3). Areas more than 7 km from Permanent water and Floodplain grasslands, which constitutes the majority of the Kwedi concession, were not occupied and represent unsuitable habitat for sable herds that likely limits the abundance of sable there.

Large expanses of homogenous Mopane, Kalahari apple-leaf and Floodplain grasslands in the Kwedi were avoided by sable herds within the study area. In KNP, sable herds also established fewer home ranges in areas predominated by mopane shrubveld than other bushveld types (Chirima, 2009). In homogenous Mopane and Kalahari apple-leaf, my monthly observations of temporary pans suggest that the availability of drinking water (in temporary pans) and green grass may have been a general limitation, particularly during the late dry season when it is extremely hot. The idea is supported by the southward shift that occurred during the transition period towards Mixed woodland and Floodplain grassland vegetation types where green grass and water were still abundant. The sable herds in the Kwedi included Floodplain grasslands that were interspersed with patches of Mixed

woodland within their annual ranges, but large expanses of homogenous Floodplain grasslands without mixed woodland patches were unoccupied by sable herds throughout the study period. Occasionally the sable herds were observed foraging along the ecotone between large expanses of homogenous Floodplain grassland and adjacent vegetation types. In previous studies, sable have been described as favouring ecotones (Child & Wilson, 1964 cited in Henely, 2005; Sekulic, 1981; Henley, 2005) and areas interspersed with thickets (Stevenson-Hamilton, 1947) where the interface between different vegetation types provides diverse opportunity for foraging, shelter and predator avoidance. Sable differ from most other African ungulates by the dark colour of their coats which may make them susceptible to a high heat load at the skin surface (Hofmeyer, 1985; Henley, 2005) and could even result in the death of an animal (Moen, 1973). The thermal environment may exert a strong influence on the habitat selection by sable (Henley, 2005) and may explain why sable herds avoided homogenous expanses of Floodplain grassland that have sparse tree cover and offer little protection from direct sunlight and high temperatures. Sable are also not particularly fast runners and are likely to have been more vulnerable to predation on the open Floodplain grasslands where very little cover was available for concealment and where other prey species concentrated attracting predators.

The Eastern herd noticeably avoided the area where Camps were situated as well as the area directly east of them. Avoidance of the area surrounding the camps is likely attributed to a combination of focused human activity and the characteristics of the vegetation types that occur there. However, human activity seems to be less influential than vegetation characteristics because the sable herds allowed vehicles to approach to within a few meters of them without showing signs of agitation. The area surrounding the camp is characterised by deep Kalahari sand which may have been dissuasive for sable because greater energy expenditure is required for locomotion in deep sand as well as the increased predation risk associated with not being able to run as fast in deep sand. The area east of the camps consists of large expanses of Kalahari apple-leaf and Mopane (the same type of vegetation that was not occupied in the north), but also a large area of seasonally Flooded *Terminalia* woodland that is also characterised by deep sand and where sparse, unpalatable *A. meridionalis* is the predominant grass species.

Habitat use

Open savanna, Dryland grassland, Mixed woodland, and Teak woodland were favoured (occurred proportionally more in annual home ranges than was available within the study area) while Mopane, Flooded *Terminalia* woodland and Kalahari apple-leaf were avoided (occurred proportionally less within home ranges than was available in the study area) by sable herds in the Kwedi. Sable utilized the Open savanna intensively (occurred within core home range) during the wet season when palatable grass species were abundant there. By the late dry season none of the herds utilized the Open savanna because the grass there had already been grazed very short by the other herbivores. Dryland grasslands may

have been attractive to sable because they are characterized by tall grass species, such as *H. dissoluta* that were highly favoured by the sable herds (Chapter 3). Dryland grassland grasses also retained a high proportion of green leaves within the tufts long into the dry season (Chapter 3). As such, Dryland grasslands were intensely utilized for foraging by all three herds during the late dry season (Chapter 3) and made up a large proportion of the core home ranges then. Mixed woodlands, also predominantly contained palatable grass species such as *Panicum maximum* that may have attracted sable herds. Other studies have also reported that sable preferentially forage in woodlands (Sekulic, 1981) especially during the wet season (Magome, 1991; Parrini, 2006). Mixed woodlands may also provide shade that sable use as refuge during the heat of the day. As mentioned, Mopane and Kalahari apple-leaf were generally avoided by the sable herds within the study area where the availability of drinking water and green grass may have been a general limitation during the late dry season. The home range occupied by the Western herd likely represented the most suitable habitat for sable within the study area as indicated by the high number of sable per unit area (0.9 sable/km^2). This is attributed to the habitat features within the home range including easy access to drinking water throughout the range, large areas of favoured vegetation types (i.e.: Floodplain grassland interspersed with Mixed woodland and Open grassland) and little or none of the avoided vegetation types (i.e.: Mopane, Teak woodland and Kalahari apple-leaf).

In the Kwedi during November, sable herds shifted from the upland vegetation types towards the Floodplain grasslands and Mixed woodlands. In previous sable studies excursions and range shifts have been documented for sable to take advantage of green flushes of grass following burns (Sekulic, 1981; Magome, 1991; Parrini, 2006). Floodplain grasslands became exposed mid-way through the late dry season (September; Chapter 3) where competitor species concentrated for the green grass. Shortly after the first rainfall in mid – October/early-November, broad leaf grasses (such as *Panicum maximum*) also emerged in Mixed woodland vegetation types, offering a valuable food resource during a period when grass in most other vegetation types is still brown and sparse. Sable herds only shifted towards the Floodplain grasslands during the transition period (November 2009) despite the floodwater there having receded as early as September. The herds may have been dissuaded from utilizing the Floodplain grasslands more intensely during the late dry season by the other herbivores concentrated there and the increased predation risk due to the prey species attracting lion. In KNP, both predation risks and competition had negative influences on the distribution of sable, with predation being more influential than competition (Chirima, 2009). During the wet season, Floodplain grasslands were utilized intensively and large areas of Floodplain grasslands were part of the core home ranges of all three herds which had made-up very little of the core home ranges during the late dry season.

Drinking water represents a critical habitat component, particularly during the dry season. Very few temporary pans in the upland vegetation types still contained water at the end of the late dry season in 2009 and may have been a contributing factor for the southward range shifts. The lack of available drinking water was particularly influential on the Eastern herd that was dependent on the perennial pans for drinking water during the dry season since

it did not contain Permanent water protruding into its dry season home range. The southward shift occurred towards the end of the late dry season when those perennial pans also began to dry and could explain the greater degree of separation between the wet and dry season ranges of the Eastern herd than the other two herds.

In the Kwedi very little home range overlap occurred between adjacent herds. The small overlap that was evident occurred between the Central herd and the other two herds during the wet season when resources were judged to be plentiful (Chapter 3). The area where adjacent ranges overlapped were used by the different herds at different times: the Central herd occupied the overlapped range during February 2010 and had already moved north-west before the Eastern herd occupied it during March; the Western herd used the overlapped area at the beginning of March and the Central herd used the area at the end of March. No home range overlap occurred during the critical dry season. Large areas of range overlap between herds might indicate stressful conditions prompting trespassing as herds search for resources in neighbours' ranges. Sable in the Kwedi maintained crude faecal protein levels above the levels recommended for maintenance of an animal of this size (Chapter 3). In the Kwedi, the non-overlapping home ranges, particularly during the dry season when conditions were judged to be most stressful could indicate that resources within the home ranges of the three herds did not deplete to the extent that trespassing was necessary.

Home range extent and overlap

There appeared to be some influence of herd identity on home range size because the Central herd consistently occupied the largest seasonal annual and core ranges while the Eastern herd occupied the smallest. Owen-Smith & Cain (2007) suggested that the size of the herd may influence home range size due to greater local resource depletion when the grass resources became non-renewing. In the Kwedi, however, herd size also did not seem to have an influence on home range size. The Eastern herd (14 individuals) and Western herd (19 individuals) occupied similarly sized annual home ranges even though the Western herd contained more individuals(Table 3). The Western herds' range was also much smaller than the range of the Central herd (12 individuals) that had fewer individuals (Table 3). The difference in home range extent seems to be more closely linked to the availability and distribution of resources within areas where the home ranges were established. Harestad & Bunnell (1979) suggested that animals will occupy larger home ranges when resources are scarce, thinly distributed or widely scattered and smaller home ranges when resources are abundant or locally concentrated. The annual kernel 95% home ranges sizes of sable herds in KNP were more than double the size of the home range estimates for the herds in the Kwedi concession. In KNP crude faecal protein levels often fell below levels required for maintenance (<6%; Codron *et al*., 2007; Henley, 2005), herd sizes were generally small and the sable population has experienced a dramatic decline (Henley, 2005) whereas sable herds in the Kwedi were generally larger and faecal nitrogen levels did not drop below the levels

required for maintenance (> 8%; Chapter 3). Although the conclusions drawn should be interpreted with caution due to the differences in methodology (*a*-LoCoH vs. Kernel) between studies and because generalizations were drawn from the small number of samples available, the comparison suggests that sable in the Kwedi concession were able to meet all their nutritional requirements within a much smaller area than KNP herds. Small home ranges where adequate resources are available provide opportunity for additional herds to occupy space within the landscape. In the Kwedi concession during 2007 records from the sightings book indicates that an additional sable herd did once occupy an area south east of the airstrips, part of which is now occupied by the Central herd. Current occupation of that area by the Central herd suggests that the habitat there is suitable for sable and may also explain the large range size of the Central herd – it simply incorporated part of the range that the 'missing' herd used to occupy within its own home range. The sightings book records indicate that the 'missing' herd disappeared by the end of 2007 and that more than 7 adult individuals from that herd were killed by lion in the months leading up to the disappearance of the herd.

There did not appear to be any influence of season on home range size for sable herds in the Kwedi. The herds did not reflect distinctly larger occupied home ranges during the late dry season than the wet season. The larger dry season than wet season home range of the Eastern herd is misleading because of shifts between separate wet and late dry season extents during that period. This is contrary to our initial expectations because we expected resources to be scarcer and scattered more widely during the dry than the wet season and that sable would consequently range further in order to acquire them. Previous studies on sable (Henley, 2005; Parrini, 2006; Owen-Smith & Cain, 2007; Macandza, 2009) documented larger home range sizes during the dry than the wet season attributed to expansions of wet season ranges in response to the scarcity and wide distribution of resources during the dry season. During the late dry season in the Kwedi, however, sable may have been restricted from ranging wider by the localized distribution of food (Chapter 3) and water available close to the Floodplain grasslands. It is likely due to the concentration of resources in those vegetation types that it was not necessary for the sable herds in the Kwedi to range more widely or expand their ranges in search of food during the dry season.

Summary

Within 7 km of Floodplain grasslands and surface drinking water, sable herds occupied reasonably small home ranges. There was very little overlap between adjacent home ranges. The dry season home ranges are not distinctly larger than the wet season home ranges. All these indications suggest that sable are doing well. However, the greatest limitation to sable abundance in the Kwedi concession appears to be the unsuitable habitat occurring more than 7 km from the Floodplain grasslands and the constraints posed by the available surface drinking water, particularly during the dry season. Herd sizes of sable in the

Kwedi were also rather small. Although supporting evidence is weak, the sightings book records show a high level of adult sable mortality due to predation by lion since 2007.

Tables

Table 1: A summary of seasons based on rainfall; flooding events based on field experience; and periods when collars were fitted, working or failed. T= transition period.

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov
Season	Late Dry 09			T	Wet				Early Dry				Late Dry 10			T
Floodwater conditions	Receding			Exposed						Flooded			Receding		Exposed	
Western herd	Working					Failed		Working								
Central herd	Not fitted		Working					Failed								
Eastern herd	Working				Failed		Working									

Table 2: Characteristics of different vegetation types found in the study area at Kwedi (adapted from Butchart, 2000).

Vegetation Type	Defining Characteristics
Mopane woodland	Dominated by Mopane (*Colophospermum mopane*) on compacted clay soils. Depressions in the clay soils capture and hold rain water until late in the dry season. Grass cover is sparse (particularly during the late dry season) and grass species are generally unpalatable.
Open savanna	Open savanna with widely spaced trees in compact silt and loose sand. Tall trees include Knobthorn (*Acacia nigrescens*) and Umbrellathorn (*Acacia tortilis*). Very few understory trees and shrubs present. Large herbivores are abundant in this habitat (particularly during the wet season) due to abundance of palatable grass species there. The grass is normally grazed very short before the dry season commences.
Mixed woodland	Typified by tall trees such as Jackalberry (*Diospyros mespiliformis*), Sausage tree (*Kigelia africana*) and Rain tree (*Philenoptera capassa*) with an understorey typically containing Confetti bush (*Gymnosporia senegalensis*), Red star-apple (*Diospyros lycioides*) and Magic guarri (*Euclea divinorum*). In the wet season, broad-leafed palatable grass species are abundant but quickly disappear as the dry season progresses.
Kalahari-apple leaf woodland (KAL)	In deep soft Kalahari sand, with predominantly Kalahari Apple leaf (*Philenoptera nelsii*) trees. Predominantly contains tall grass species such as Giant three-awn (*Aristida meridionalis*) and Long-three awn (*Aristida stipitata*) and Sand quick (*Schmidtia pappophoroides*).
Floodplain grassland	Normally adjacent to permanent water. Seasonally inundated giving rise to medium height green, grasslands when floodwaters recede and shallow wetlands during the floods. Grasses preferring moist habitats (e.g. *Cynodon dactylon* and *Panicum repens*) and sedges are common. Islands appear and disappear as flood water fluctuates trapping water in depressions. Trees and shrubs are scarce but occur on the refuge of termite mounds.
Dryland grassland	In deep sand. Predominantly contains tall grass species such as Giant three-awn (*Aristida meridionalis*) and Long-three awn (*Aristida stipitata*), Sand quick (*Schmidtia pappophoroides*) and Yellow thatching grass (*Hyperthelia dissolute*). Occasionally Silver Terminalia (*Terminalia sericea*) shrubs are scattered through the grassland.
Teak woodland	Dominated by Rhodesian Teak (*Baikiaea plurijuga*) in deep and soft Kalahari sand. Contains small patches of tall grass species such as those common in Dryland Grasslands as well as Common finger grass (*Digitaria eriantha*).
Permanent water	Inundated by water all year round. Typified by beds of papyrus, islands rimmed with forests, lagoons and deep water channels.
Flooded *Terminalia* woodland	Occurs adjacent to Floodplain grassland, is seasonally inundated, is interspersed with *Terminalia sericea* shrubs, is characterised by deep Kalahari sand and sparse grass cover.

Table 3: Annual home range sizes (95% isopleths) and annual core home range sizes (50% isopleths) estimated using a-LoCoH. The number of GPS locations used in the a-LoCoH estimates of three sable herds is also reported as well as the number of days over which the GPS positions were recorded.

Herd ID	Herd size on 30/12/2009	No. of Days	No. of hourly GPS positions	Annual MCP Home Range (km^2)	Annual a-LoCoH Home Range	Sable Density (Animals/km^2) using a-LoCoH annual range extent
Eastern	14	378	8978	38.5	20.7	0.7
Western	19	375	8984	40.5	21.5	0.9
Central	12	161	3856	61.6	31.0	0.4

Table 4: Seasonal home range sizes (95% isopleths) and seasonal core home range sizes (50% isopleths) estimated using a-LoCoH. The number of seasonal GPS locations used for the a-LoCoH estimates of three sable herds is also reported as well as the number of days over which the GPS locations were recorded.

Herd ID	Season	Period of GPS functioning (dd/mm)	No. of Days	No. of hourly GPS locations	Seasonal overall home range size (km^2)	Seasonal core home range size (km^2)
Eastern	Wet Season	07/03 to 31/03	24	587	3.4	0.8
	Late Dry 2010	01/08 to 31/10	92	2204	9.3	2.0
	Late Dry 2009	16/08 to 31/10	77	1833	10.6	2.2
	Early Dry	01/04 to 31/07	122	2922	11.3	1.7
Western	Late Dry 2009	16/08 to 31/10	76	1823	11.8	1.5
	Wet Season	1/12 to 31/03	44	1047	12.0	2.0
	Early Dry	01/04 to 31/07	122	2926	12.5	2.6
	Late Dry 2010	01/08 to 31/10	92	2206	15.9	3.9
Central	Late Dry 2009	12/10 to 31/10	20	470	17.2	3.8
	Wet Season	1/12 to 25/03	112	2668	19.8	3.2

Table 5: Number of sightings of competitor species in different habitat types. Observations were made between 27th November 2009 and 27th November 2010, omitting March, April, May and June 2010.

Vegetation Type	Number of competitor species sightings				
	Impala	Wildebeest	Zebra	Buffalo	Tsessebe
Floodplain Grassland	11	10	32	3	29
Kalahari-apple leaf (KAL)	7	0	1	1	1
Mixed Woodland	64	5	16	3	18
Open savanna	30	8	30	0	9
Mopane	7	0	2	1	1
Dryland Grassland	3	0	4	0	6
Teak Woodland	1	0	0	0	0

Figures
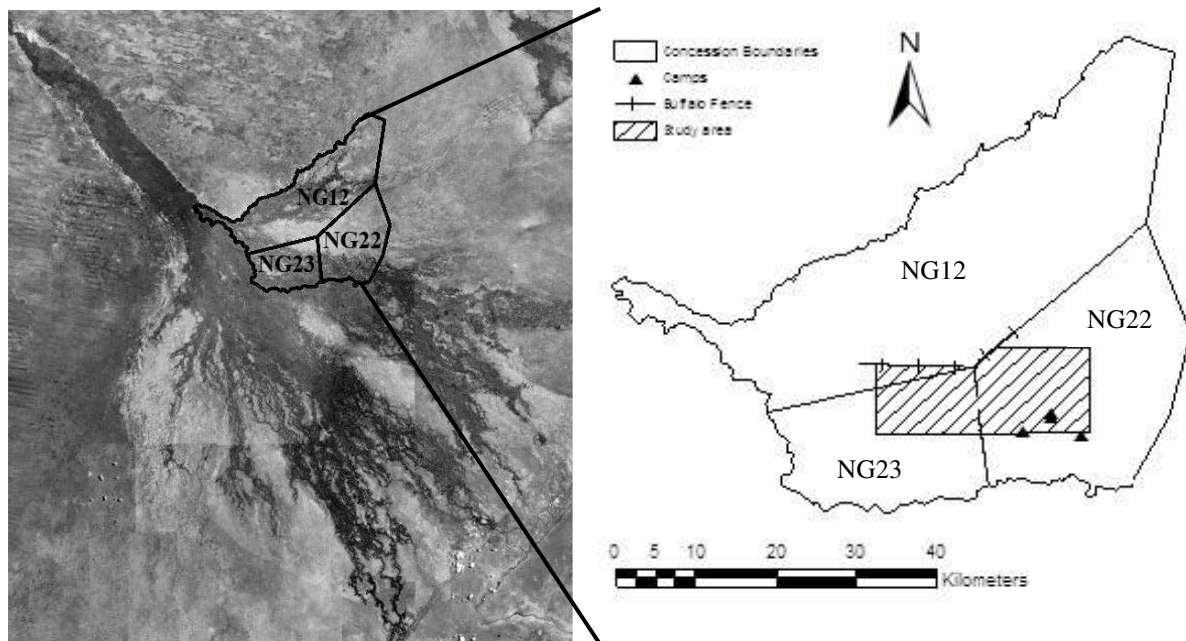
Figure 1: The location of the Kwedi (NG22), Duba Plains (NG23) and Mapula (NG12) concessions, the buffalo fence, camps and the study area within the Okavango Delta.
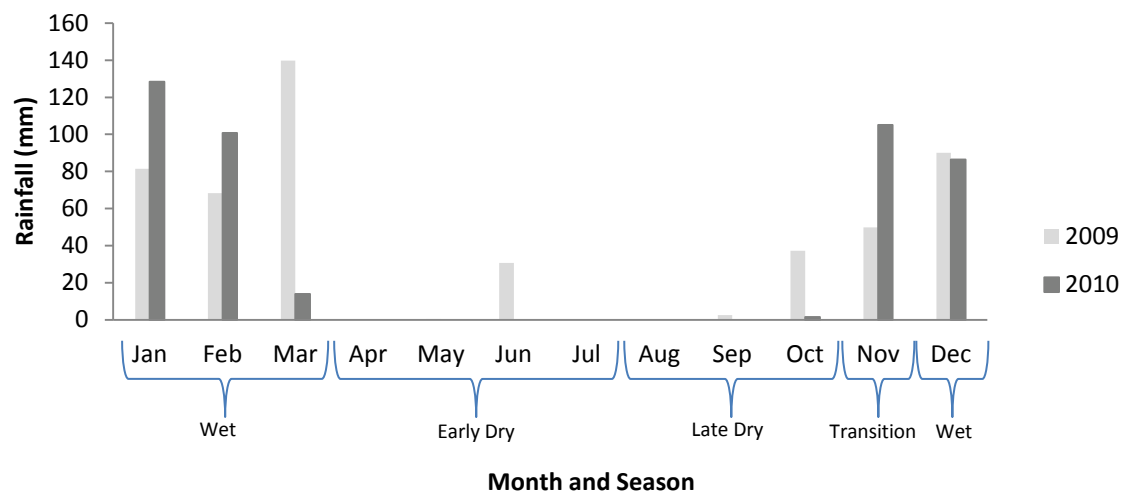
Figure 2: Precipitation recorded by the weather station at Kwedi in 2009 and 2010 showing how different seasons were defined.
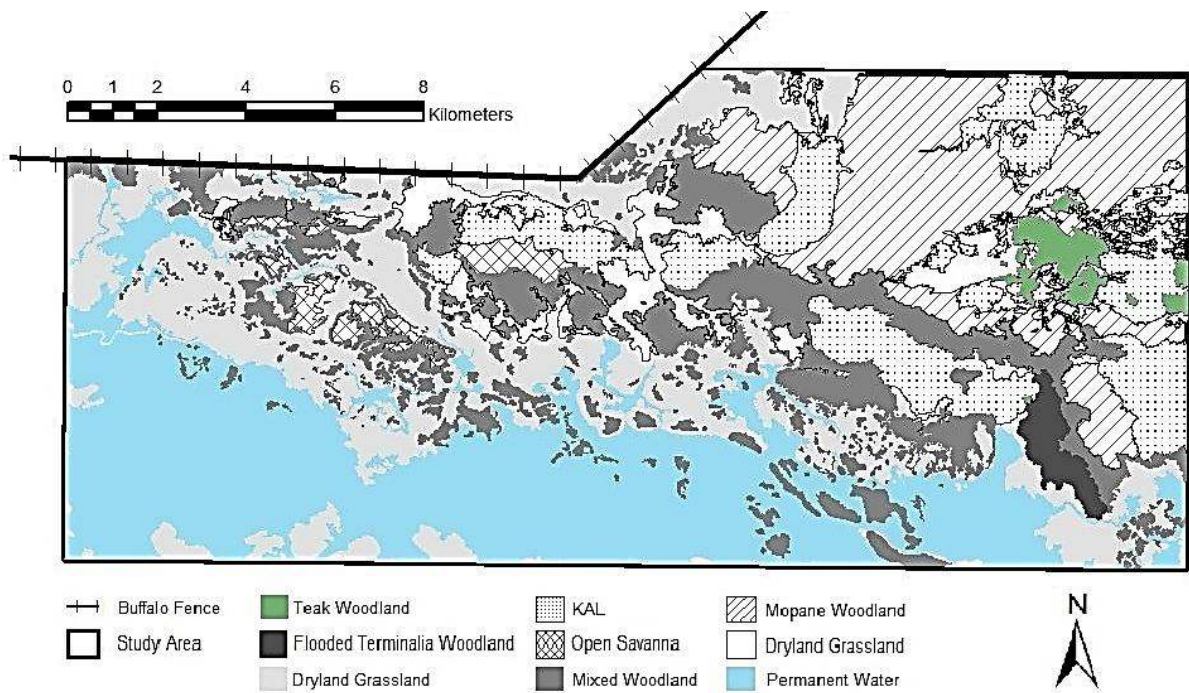
Figure 3: Vegetation map of the study site in the Okavango Delta. Kalahari apple-leaf =KAL.
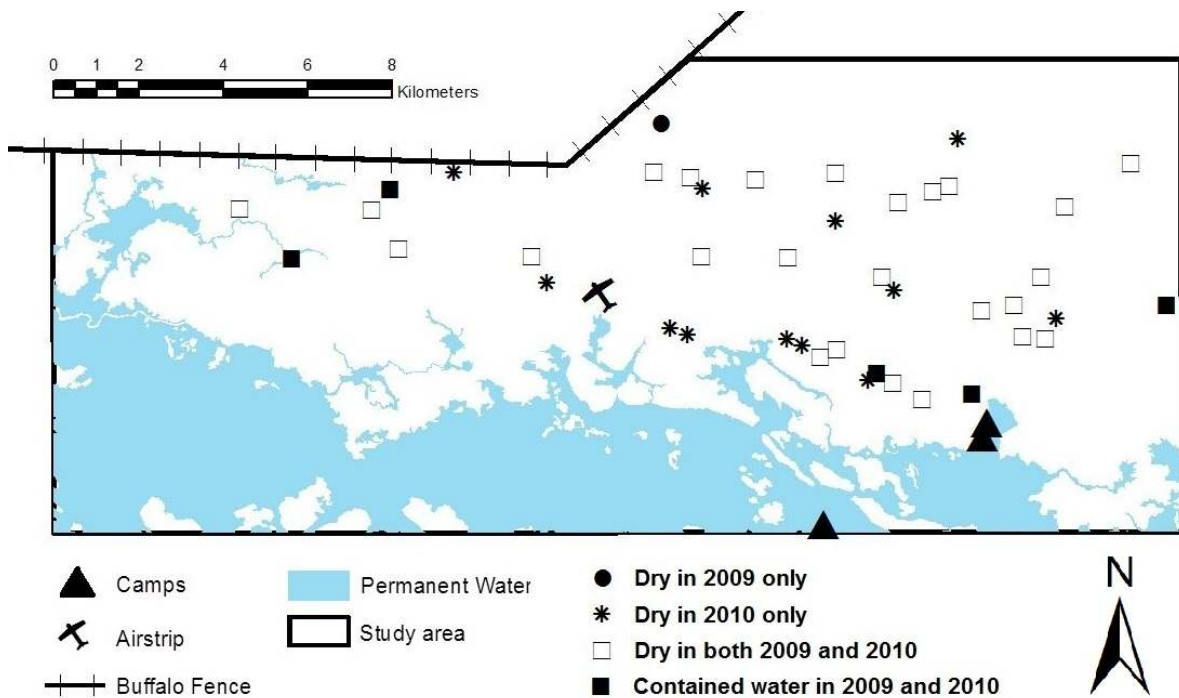
Figure 4: The location of pans within the study area indicating the availability of drinking water in them at the beginning of October 2009 and 2010.
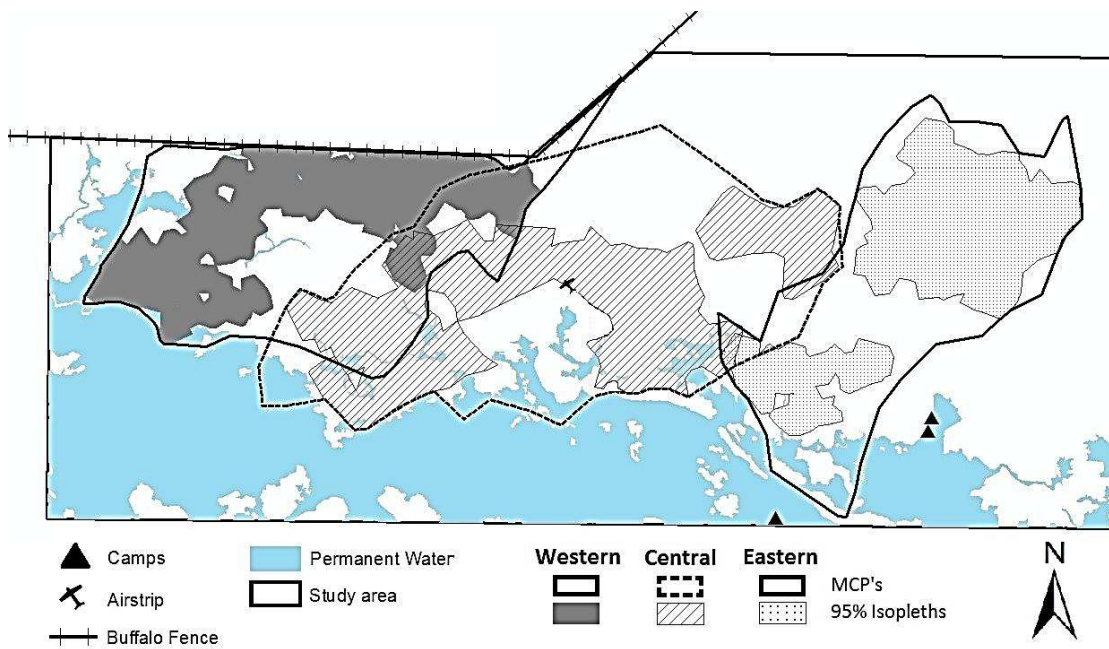
Figure 5: Annual Minimum Convex Polygons (MCPs) of three collared herds on the Kwedi Concession and the annual LoCoH (95% isopleths) that exclude occasional excursions. *a*-LoCoH and MCP analysis used 9000 GPS locations collected over 380 days for western and eastern herds and 3856 GPS locations collected over 161 days for the central herd.
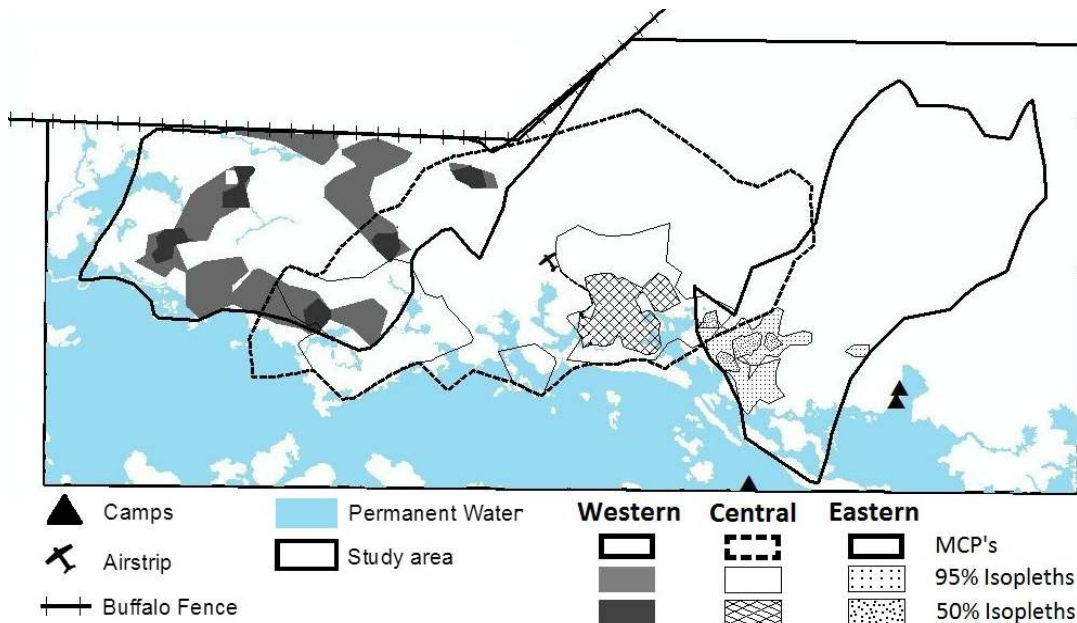
Figure 6: Annual MCPs and wet season overall (a-LoCoH 95% isopleths) and core (a-LoCoH 50% isopleths) of three collared sable herds on the Kwedi Concession. *a*-LoCoH analysis used 587 GPS locations collected between 07/03/2010 and 31/03/2010 for Eastern herd; 1047 GPS locations collected between 01/12/2009 and 19/12/2009 and from 06/03/2010 to 31/03/2010 for the Western herd; and 2668 GPS locations collected between 1/12/2009 to 25/03/2010. Some GPS locations are missing for the Eastern and Western herds due to collar failure.
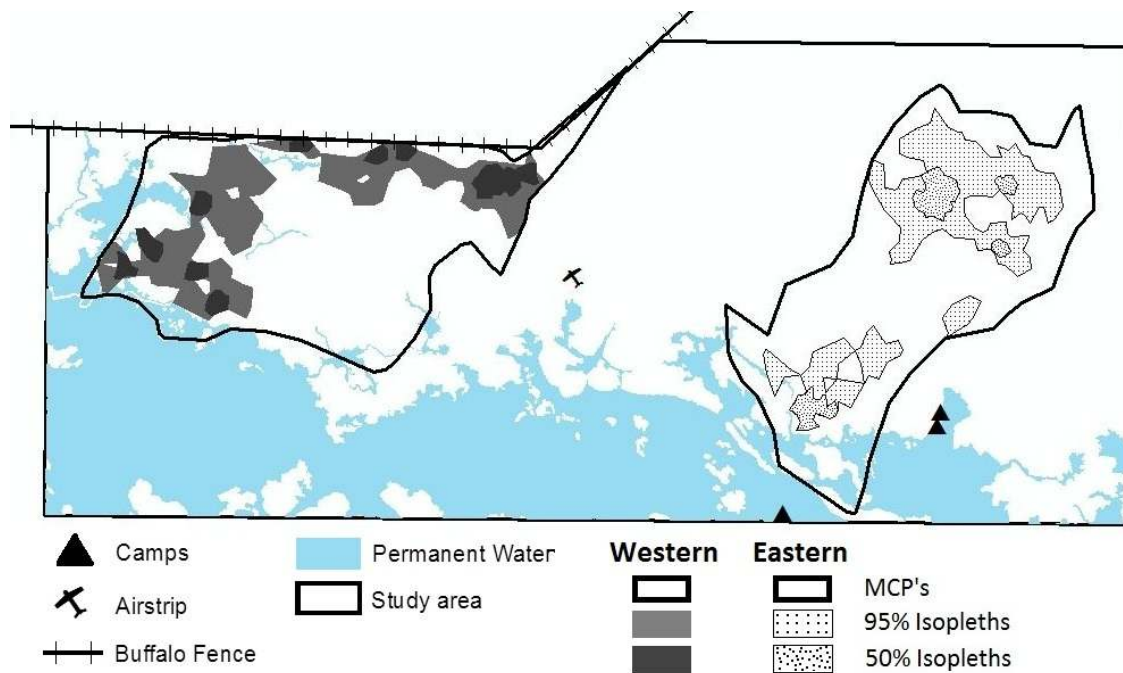
Figure 7: Annual MCPs and early dry season overall (a-LoCoH 95% isopleths) and core (a-LoCoH 50% isopleths) home ranges of the Western and Eastern sable herds on the Kwedi Concession. A-LoCoH analysis used 3000 GPS locations collected between 01/04/2010 – 31/07/2010 for both herds.
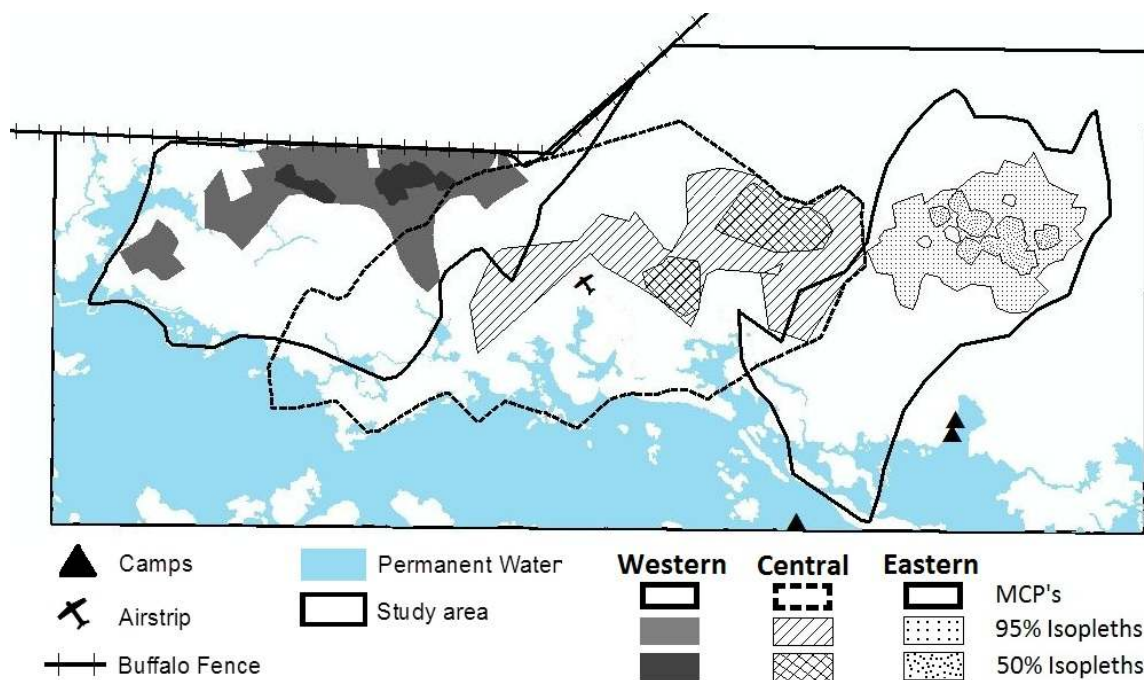
Figure 8: Annual MCPs and late dry season 2009 overall (a-LoCoH 95% isopleths) and core (a-LoCoH 50% isopleths) of three collared sable herds on the Kwedi Concession. *a*-LoCoH analysis used 1840 GPS locations collected between 16/08/2009 and 31/10/2009 for Eastern and Western herds; and 470 GPS locations collected between 12/10/2009 and 31/10/20009 for the Central herd.

Figure 9: Annual MCPs and late dry season 2010 overall (a-LoCoH 95% isopleths) and core (a-LoCoH 50% isopleths) of the Western and Eastern sable herds on the Kwedi Concession. – the Central herds home ranges are not displayed due to collar failure. *a*-LoCoH analysis used 2200 GPS locations collected between 01/08/2010 and 31/10/2010 for Eastern and Western herds. No GPS locations were collected for Central herd due to collar failure.

Figure 10: The availability of different vegetation types within the study area and the total proportion of vegetation types occurring within the annual *a*-LoCoH home range of all three herds. Kalahari apple-leaf = KAL
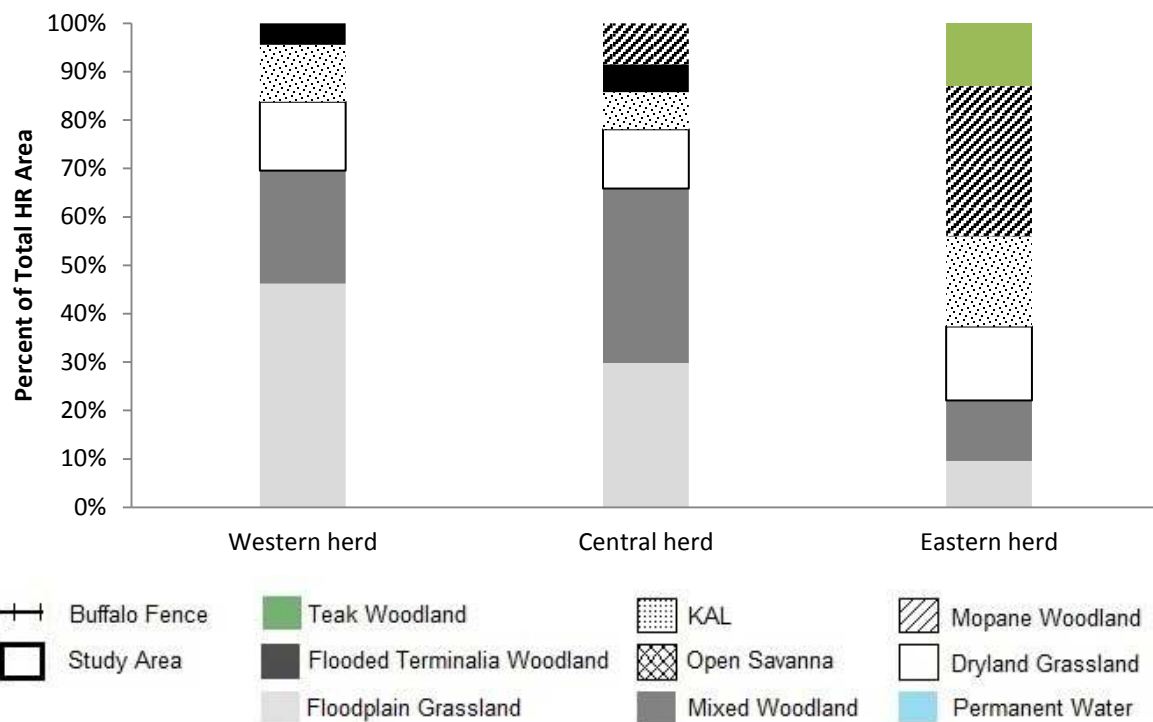
Figure 11: The vegetation composition of the annual overall (95 % isopleth) home ranges of the three study herds. Kalahari apple-leaf = KAL

a. Late Dry 2009

b. Wet

c. Early Dry

d. Late Dry 2010

Legend: Floodplain Grassland, Open Grassland, Mixed Without, Teak Woodland, Mopane, KAL, Permanent Water, Mixed Woodland, Flooded Terminalia Woodland
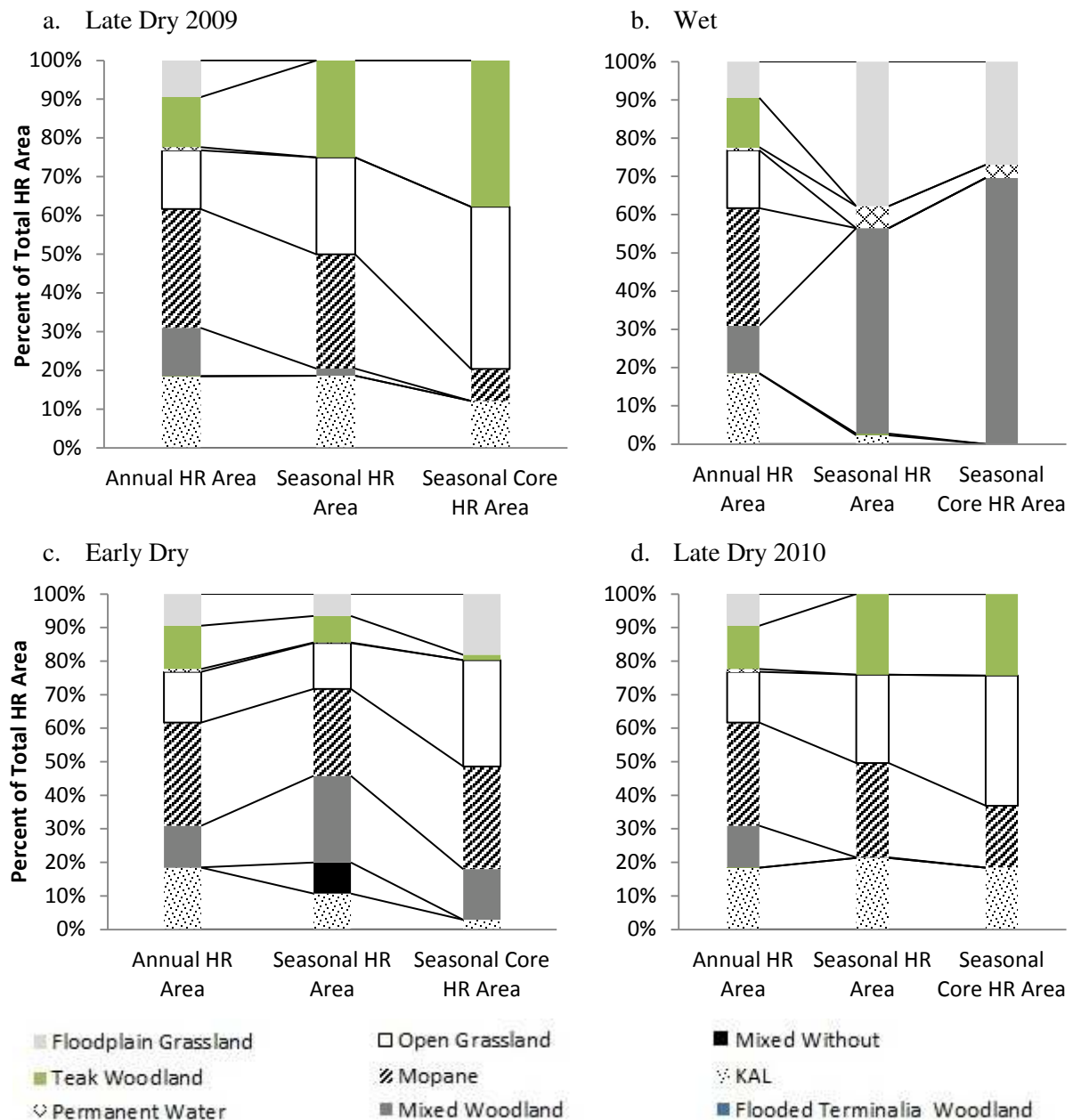
Figure 12: The proportion of vegetation types making up the annual, seasonal, core seasonal and foraging time utilization distribution of the Eastern sable herd on the Kwedi concession in the Okavango Delta. Kalahari apple-leaf = KAL
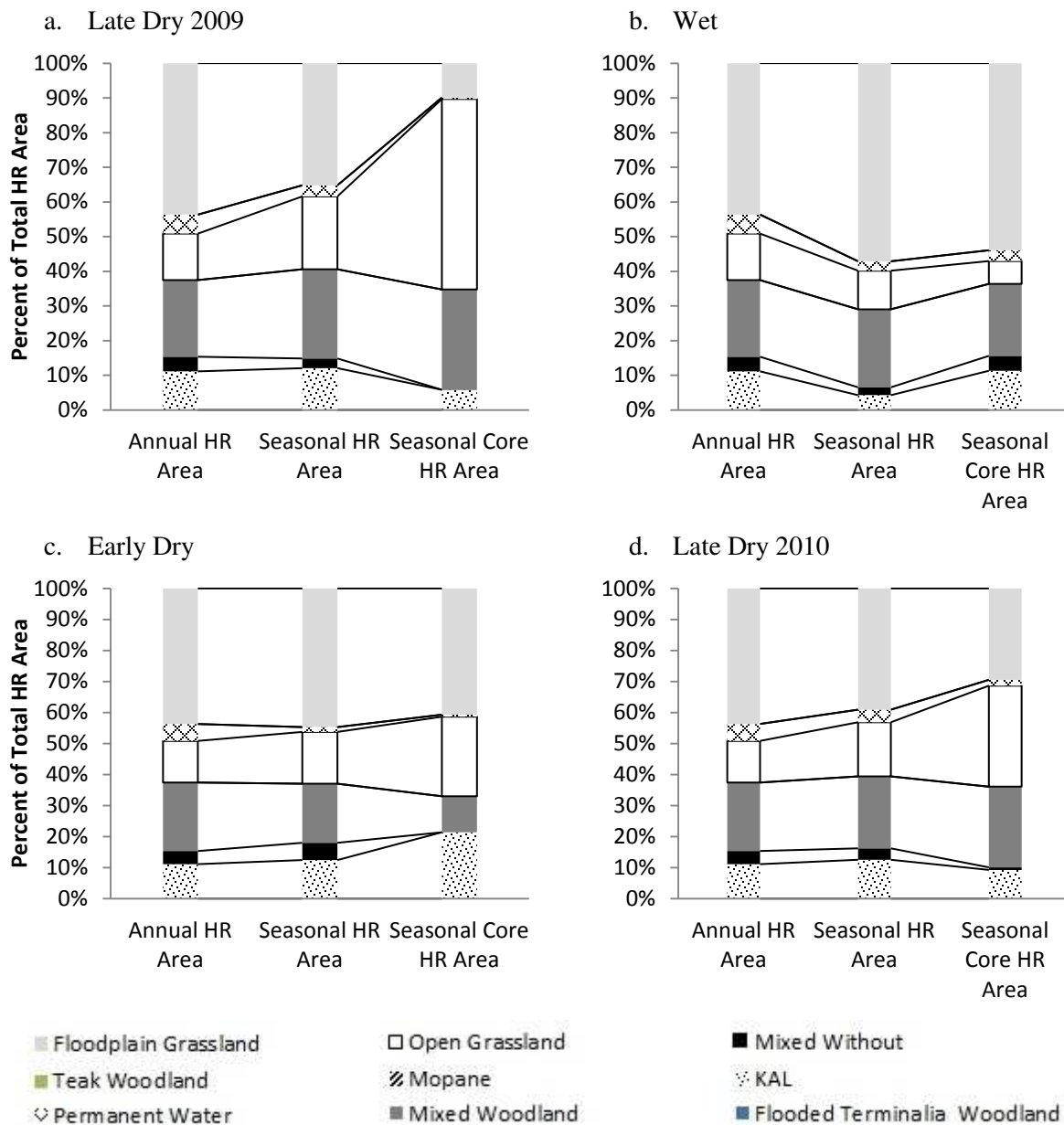
Figure 13: The proportion of vegetation types making up the annual, seasonal, core seasonal and foraging time utilization distribution of the Western sable herd on the Kwedi concession in the Okavango Delta. Kalahari apple-leaf = KAL

a. Late Dry 2009

b. Wet
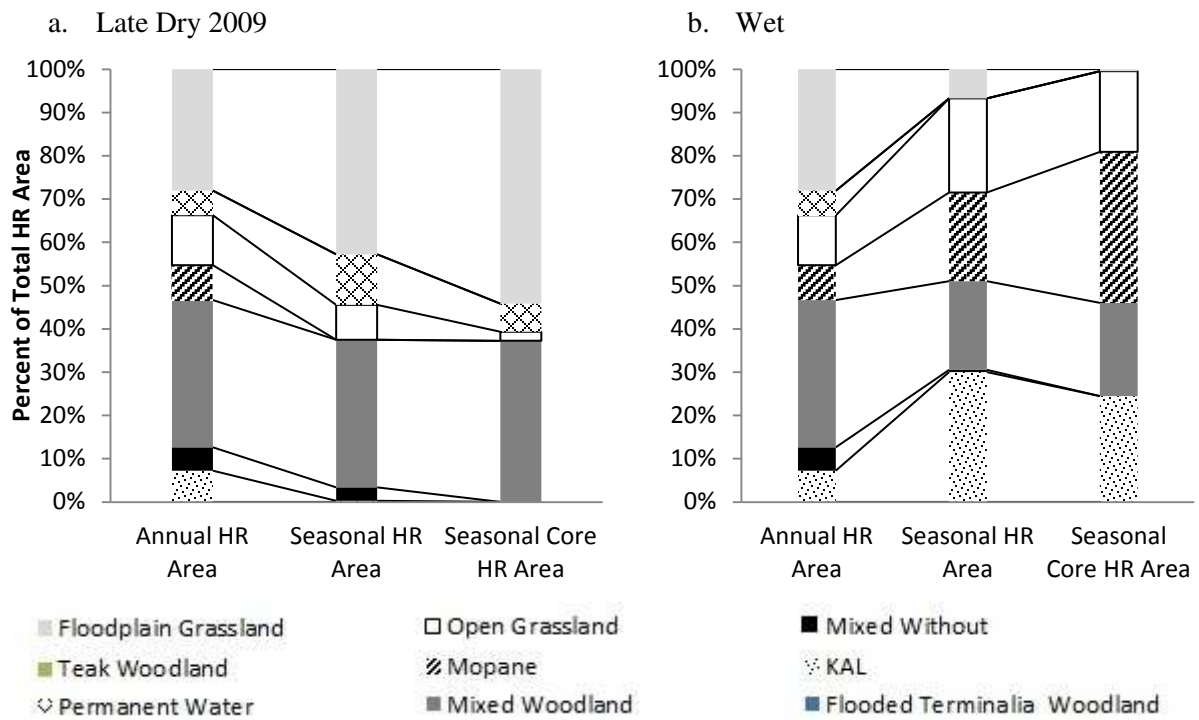
Figure 14: The proportion of vegetation types making up the annual, seasonal, core seasonal and foraging time utilization distribution of Central herd on the Kwedi concession in the Okavango Delta. Kalahari apple-leaf = KAL

References

Anderson, D.P., Foresterm J.D., Turner, M.G., Frair, J.L., Merrill, E.H., Fortin, D., Mao, J.S., and Boyce, M.S., 2005: Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecology*. **20**: 257-271.

Bailey, D.W., Gross, H.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., and Sims, P.L. 1996: Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management.* **49** (5): 386-400.

Borger, L., Franconi, N., Ferretti, F., Meschi, F., Michele, G., Gantz, A., and Coulson, T. 2006: An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *American Naturalist*. **168** (4): 471-485.

Borger, L., Dalziel, B.D and Fryxell, J.M. 2008: Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*. **11**: 637-650.

Boone, B. R., Thirgood, S.J. and Hopcraft, J.G.C. 2006: Serengeti wildebeest migratory patterns modelled from rainfall and new vegetation growth. *Ecology*. **87** (8): 1987-1994.

Burt, W.H. 1943: Territoriality and Home Range Concepts as Applied to Mammals. *Journal of Mammalogy*. **24** (3): 346-352

Butchart, D. 2000: *Wildlife of the Okavango*. Struik Publishers. Cape Town.

Cain, J.W. Owen-Smith, N. and Macandza, V.A., 2012: The cost of drinking: comparative water dependency of sable antelope and zebra. *Journal of Zoology*. **286**: 58-67.

Chirima, J.G. 2009: *Habitat suitability assessments for sable antelope.* PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R., & Fourie, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology.* **273**: 21-29.

Ellery, K. and Ellery, W. 1997: *Plants of the Okavango Delta: a field guide.* Tsaro Publishers, Durban.

Estes, R.D. and Estes, R.K. 1974: The biology and conservation of the giant sable antelope, *Hippotragus niger variani* (Thomas, 1916). *Proceedings of the Academy of Natural Sciences of Philadelphia.* **126**: 73-104..

Estes, R.D. 1997. *Behaviour Guide to African Mammals: including hoofed mammals, carnivores, primates.* Russel Friedman Books CC, South Africa.

Gaston, K.J. 1991: How large is a species' geographic range? *Oikos*. **61** (3): 434-438.

Gaylard, A., Owen-Smith, N. and Redfern, J. 2003: Surface water availability: implications for heterogeneity and ecosystem processes. In: *The Kruger experience; ecology and management of savanna heterogeneity* (Eds: du Toit, J.T., Rogers K.H. and Biggs, H.C.) Island Press. Washington.

Getz, W.M. and Wilmers, C.C. 2004: A local nearest-neighbour convex-hull construction of home ranges and utilization distributions. *Ecography*. **27**: 489-505.

Getz, W.M., Frotmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. 2007: LoCoH: nonparametric kernel methods for constructiong home ranges and utilization distributions. *PLoS ONE.* **2**: 1-11.

Grant, C.C. and van der Walt. 2000: Towards an adaptive management approach for the conservation of rare antelope in the Kruger National Park – outcome of a workshop held in May 2000. *Koedoe.* **43**: 103-111.

Grobler, J.H. 1981: Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. *South African Journal of Zoology*. **16**: 50-58.

Gumbricht, T.; McCarthy, J., and McCarthy, T.S. 2004: Channels, wetlands and islands in the Okovango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surface Processes and Landforms.* **29**: 15–29.

Hall, LS; Krausman, P.R., and Morrison, M.L. 1997: The habitat concept and a plea for standard terminology, *Wildlife Society Bulletin.* **25** (1): 173-182.

Harestad, A.S. and Bunnell, F.L. 1979: Home range and body weight – a reevaluation. *Ecology.* **60**: 389-402.

Harrington, R., Owen-Smith, N., Viljoen, P., and Biggs-Mason, D. 1999: Establishing the causes of the roan antelope decline in the Kruger National Park. *South African Biological Conservation*. **90**: 69–78.

Henley, S. 2005: Habitat dependency and nutritional ecology of sable antelope in two regions of the Kruger National Park. *Unpublished Report for SANparks*.

Hofmeyr, M.D. 1985: Thermal properties of the pelages of selected African ungulates. *South African Journal of Zoology.* 20: 179-189.

Holt, R.D.1977: Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology.* 12: 197-229

Illius, A.W. and O'Connor, T.G. 2000: Resource heterogeneity and ungulate population dynamics. *Oikos.* **89**: 283-294.

Jewell, P.J. 1966: The concept of home range in mammals. *Symposia of the Zoological Society of London*. **18**: 85-109.

Johnson, D.H. 1980: The comparison of usage and availability measurements for evaluating resource preference. *Ecology*. **61** (1): 65-71.

Kelt, D.A. and Van Vuren, D.H. 2001: The ecology and macroecology of mammalian home range area. *The American Naturalist*. **157** (6): 637-645.

Kernohan, B.J., Gitzen, R.A., and Millspaugh, J.J. 2001: Analysis of space use and movements. In: *Radio tracking and animal populations*. (Eds. Millspaugh, J.J. and Marzluff, J.M.) Academic Press, USA.

Macandza, V.A. 2009: *Resource partitioning between low-density and high-density grazers: sable antelope, zebra and buffalo*. PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

Macandza, V.A., Owen-Smith, N., and Cross, P.C. 2004: Forage selection by buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research*. **34** (2): 113-121.

McCarthy, T. S., Bloem, A. and Larkin, P. A. 1998: Observations on the hydrology and geohydrology of the Okavango Delta. *South African Journal of Geology*. **101** (2): 101–117.

McCarthy, T.S. 2006: Groundwater in the wetlands of the Okavango Delta, Botswana, and its contribution to the structure and function of the ecosystem. *Journal of Hydrology*. **320**: 264–282.

McLoughlin, P.D. and Ferguson, S.H. 2000: A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience*. **7** (2): 123-130.

Magome, D.T. 1991. Habitat selection and the feeding ecology of the sable antelope (*Hippotragus niger niger*) (Harris 1838), in Pilanesberg National Park, Bophuthatswana. M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Magome, H., Cain, J.W., Owen-Smith, N., and Henley, S.R., 2008: Forage selection of sable antelope in Pilanesberg Game Reserve, South Africa. *South African Journal of Wildlife Research*. **38** (1): 35–41.

Moen, A.N. 1973: *Wildlife ecology*. W.H. Freeman& Co., San Fransisco.

Musiega, D.E. and Kazadi, S. 2004: Simulating the East African wildebeest migration patterns using GIS and remote sensing. *African Journal of Ecology*. **42**: 355–362.

Mysterud, A. and Ims, R.A., 1998: Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*. **79** (4): 1435-1441.

Ogutu, J.O., and Owen-Smith, N. 2005: Oscillations in large mammal populations: are they related to predation or rainfall? *African Journal of Ecology* **43**: 332–339.

O'Reagain, P.J. and Schwartz, J. 1995: Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. In: *Recent developments in the nutrition of herbivores. Proceedings of the IVth International Symposium on the Nutrition of Herbivores*, ed. M. Journet, E. Grenet, M-H. Farce, M. Theriez and C. Demarquilly, pp 407 – 423. INRA Editions, Paris.

Owen-Smith, N. 1988: *Megaherbivores: The influence of very large body size on ecology*. Cambridge University Press. Cambridge, pp. 369

Owen-Smith, N. 1994: Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*. **75**: 1050 – 1062.

Owen-Smith, N. 2002: *Adaptive Herbivore Ecology (Student Edition)*. Wits University Press, Johannesburg.

Owen-Smith, N. and Cain, J.W. 2007: Indicators of adaptive response in home range utilization and movement patterns by a large mammalian herbivore. *Israel Journal of Ecology and Evolution*. **53**: 423-428.

Owen-Smith, N. and Cooper, S. M., 1989: Nutritional ecology of a browsing ruminant, the kudu (*Tragelaphus strepsiceros*) through the seasonal cycle. *Journal of Zoology*, **219**: 29-43.

Owen-Smith, N and Ogutu, J. 2003: Rainfall influences on ungulate population dynamics. In: The Kruger Experience: ecology and management of savanna heterogeneity. Eds. J.T. Du Toit, K.H. Rogers and H.C. Biggs, pp. 310 – 331. Island Press, Washington.

Parrini. F, 2006: *Nutritional and social ecology of the sable antelope in the Magaliesberg Nature Reserve*. PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

Rahmini, S. and Owen-Smith, N. 2007: Movement patterns of sable antelope in the Kruger National Park from GPS/GSM collars: a preliminary assessment. *South African Journal of Wildlife Research*. **37** (2): 143–151.

Redfern, J.V., Grant, R., Biggs, H., and Getz, W.M. 2003: Surface-Water Constraints on Herbivore Foraging in the Kruger National Park, South Africa. *Ecology*. **84** (8): 2092-2107.

Ripple, W.J., and Beschta, R.L. 2003: Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management*. **184**: 299–313.

Ryan, S.J., Knechtel, C.U., and Getz, W.M. 2006: Range and habitat selection of African buffalo in South Africa. *Journal of Wildlife Management*. **70**: 764-776.

Scoones, I. 1995: Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments.* **29**: 221 – 237.

Sekulic, R. 1981: Conservation of the sable *Hippotragus niger roosevelti* in the Shimba Hills, Kenya. *African Journal of Ecology* **19**: 153 – 165.

Senft, R.L. Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M., 1987: Large herbivore foraging and ecological hierarchies. *BioScience.* **37**: 789 – 799.

Shrader, A.M., Brown, J.S., Kerley, G.I.H., and Kotler, B.P. 2008: Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *Journal of Arid Environments.* **72**: 1811– 1819.

Sinclair, A.R.E. 1977: The African buffalo: a study of resource limitations in populations. University of Chicago Press, Chicago, Illinois, USA.

Sinclair, A. R. E. 1985: Does interspecific competition or predation shape the African ungulate community? *Journal of Animal Ecology.* **54**: 899-918.

Skinner, J.D. and Chimimba, C.T., 2005: *The mammals of the Southern African Subregion (3rd Edition).* Cambridge University Press Cape Town.

Soberón, J. and Peterson, A.T. 2005: Interpretation of models of fundamental ecological niches and species' distribution areas. *Biodiversity Informatics.* **2**: 1-10.

Urban, D.L., O'Niel, R.V., and Shugart, H.H. 1987: Landscape ecology. *Bioscience.* **37** (2): 119-127.

Western, D. 1975: Water availability and its influence on the structure and dynamics of a savanna large mammal community. *East African Wildlife Journal.* **13**: 265-286.

Whyte, I.J. 2006: *Rare antelope in the Kruger National Park: Trends, current status, and options for future management.* Scientific Report, South African National Parks.

Winnie, J.A., Cross, P. and Getz, W. 2008: Habitat quality and heterogeneity influence distribution and behaviour in African buffalo (*Syncerus caffer*). *Ecology.* **89** (5): 1457-1468.

Van Beest, F.M., Rivrud, I.M., Loe, L.E., Milner, J.S., and Mysterud, A. 2011: What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology.* **80:** 771-785.

Van Bommel, F.P.J., Heitkonig, I.M.A., Epema, G.F., Ringrose, S., Bonyongo., C., and Veenendaal, E.M. 2006: Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana. *Journal of Tropical Ecology.* **22**: 101–110.

CHAPTER 3 – RESOURCE USE AND THE NUTRITIONAL STATUS OF SABLE ANTELOPE IN THE OKAVANGO DELTA.

Abstract

I investigated the use of vegetation types and forage resources of sable antelope in the Okavango delta region of northern Botswana where they were expected to be thriving. GPS collars were fitted to three adjacent herds to record use of different vegetation types during foraging times. Direct plant based observations of grazing were made during the wet season (December and January) when floodplains were also available, and the dry season (between August and November) when the floodplains became exposed mid-way through September. The resource conditions were assessed in the different vegetation types during the different periods using NDVI. Availability of grass species in the different vegetation types was determined and the dietary contribution and acceptance of grass species were calculated for during the different periods. During the adverse dry period sable spent very little time foraging on the floodplains where green grass was available and much more time foraging in the upland vegetation types where grass was much browner. Sable maintained faecal nutrition above the levels required for maintenance throughout the critical dry season and showed elevated nutritional status prior to calving. Sable consumed poor forage value plants more frequently during the dry season than in the wet season and frequently accepted grass species that retained green leaves within the tufts. Tall, fibrous grasses that are considered low forage value to cattle were amongst the most highly accepted species and made the greatest contribution to the diet of sable. Sable seemed to be able to cope with the high fibre content of such grasses. Indications are that predation, rather than resource limitations, are the primary reason for the small herd sizes of sable occurring in the Kwedi concession.

Introduction

An animal's choice, form dietry items to predator avoidance strategies affect habitat selection that ultimately influences how large herbivores distribute themselves across the landscape (Senft *et al.*, 1987; Shaefer & Messier, 1995; O'Reagain & Schwartz, 1995). This study is structured around the lower levels of resource selection, especially the selection of habitat types within the home ranges and the selection of forage resources within those habitats. The use individuals and groups of animals make of their environment, specifically the resources they consume within their home ranges, is central to the study of animal ecology (Johnson, 1980). Vegetation components utilized must provide adequate energy, protein and other essential nutrients throughout the year for herbivores to be able to survive in a region (Owen-Smith & Novellie, 1982). Animals subjected to resource deficiencies attributed to poor use or a shortage of resources can eventually deplete body reserves to critical levels of malnutrition. Although starvation is rarely the sole cause of mortality in wild herbivores, malnourished animals are susceptible to increased levels of predation because they forage for longer (raising energy expenditure) and in more risky habitats to try and obtain the resources they need to survive (Owen-Smith, 2002). The vulnerability of malnourished animals to parasite and disease infestations also increases as animals become weakened by food shortfalls and the mortality of such animals is further amplified through the effects of predation (Sinclair, 1977). In this way, the availability of resources is essentially linked to population performance.

In African savannas, seasons are largely governed by variation in rainfall that affects the availability and quality of food resources encountered by herbivores through imposing cycles of grass growth (Illius & O'Conner, 2000). The late dry season is an especially crucial period for grazing ungulates because the nutritional value of the remaining brown grass is lowest then and levels of crude protein and digestible organic matter in grass may fall below levels required for maintenance in animals (Owen-Smith, 1982). As the dry season progresses, available surface water becomes depleted and some herbivores are forced to abandon foraging areas that are simply too far from permanent water (Illius & O'Conner 2000; Chapter 2). At this time, the population size that can be supported is dependent on animals being able to find sufficiently high quality vegetation components to meet nutritional requirements (Illius & O'Connor, 2000) or at least retard starvation. Key resource areas are normally small foraging areas within the landscape that make a disproportionate contribution to supporting herbivore populations through the dry season (Scoones, 1995; Illius & O'Conner, 1999, 2000) and are normally typified by wetter conditions (i.e.: bottomlands, dambos, vleis, and drainage line grasslands) that enable retention of green grass or contain more forage biomass (Scoones, 1995; Knoop & Owen-Smith, 2006). So, it follows that the redistribution of water within a landscape might influence the availability and distribution of key resources. The Okavango region is unusual because over and above the seasonal and annual variation in local precipitation, the region also experiences seasonal fluctuations in flood water levels when rainwater from the catchment area in the central Angolan highlands

arrives at Mohembo (McCarthy, 1992; McCarthy, Bloem & Larkin, 1998). The seasonal flood fluctuations have been linked to primary productivity (Ellery & Ellery, 1997) because shallow water typically covers the floodplain grasslands downstream of the panhandle between February and August, limiting the area available for foraging and grass regrowth is induced soon after when the floodwaters begin to recede in about August (van Bommel *et al.*, 2006; Bonyongo, 2009). The green grass regrowth occurring shortly after the floodwaters recede could provide a key dry season resource that could potentially alleviate nutritional stress and reduce mortality of herbivores in the region. In the upland vegetation types, the use of productive perennial grasses (some of which may be unpalatable species) or occasionally even browse that retains adequate nutritional value through the dry season could also help alleviate starvation and sustain herbivores through the dry season (Owen-Smith, 2002).

Among the grazers present in the Okavango Delta is sable antelope (*Hippotragus niger*) which is highly valued there due to its aesthetic appeal for tourism. There are concerns about the conservation status of sable which now have a restricted distribution throughout southern African savannas due to cattle ranching, agriculture and other development (Skinner & Chimimba, 2005). During the critical dry season bottleneck, sable elsewhere depend on green grass that persists in drainage sump grasslands (dambos or vleis) or that is available in grasslands that have been burned prior to the dry season (Estes & Estes, 1974; Magome *et al.,* 2008; Parrini & Owen-Smith, 2009). Since neither burnt areas nor drainage sump grasslands were available in our study area, I expected sable to depend on the grass that became exposed on the floodplains between August and November if green grass was available there. The study aim was to determine if sable were thriving or not in the Okavango Delta depending on the availability of green forage affected by flooding and rainfall. In particular, I was interested in how exploitation of the floodplains and how the quality of grass eaten contributed to the success or failure of sable measured by the concentration of nutrients in the faecal samples. I used NDVI; the relatively new technology of GPS collars; supporting plant based foraging observations (made possible because the herds were so tame); and faecal nutrient concentration in faeces and the resources exploited by the sable herds to indicate why sable were or were not thriving.

The first study objective was to determine the effect of seasonal flooding and rainfall on grass greenness (measured using NDIV) in the floodplains and upland vegetation types and the consequent use of those vegetation types by sable antelope. I expected that:

1) During December and January grass would be green on the floodplains and the uplands due to rainfall initiating grass regrowth in both vegetation types; between August and November floodplains would be greener than the uplands due to grass regrowth in the floodplains being initiated after floodwaters had receded while uplands would become progressively browner due to lack of rainfall and increased temperature.

2) Sable would concentrate foraging where grass is greenest, i.e. in both the uplands and floodplains during December and January and on the floodplains between August and November.

The second study objective was to determine how exploitation of resources in the floodplains and in the uplands contributed to the nutritional status of sable. I expected that:

1) During December and January when all grass is green, grass species that are considered to be of high forage value to cattle would be highly accepted by sable antelope on the Kwedi concession.
2) Between August and November, grass species that retain a large proportion of green leaves within the tuft would contribute most to the diet of sable on the Kwedi concession.
3) Faecal nitrogen and phosphorus levels of sable in the Kwedi would remain high through the dry season while sable made use of the floodplains between August and November when green grass is available there.

Methods

<u>Study site</u>

The study area comprised the Kwedi (NG22), Duba Plains (NG23) and Mapula (NG12) concessions (Fig. 1) in the north east of the Okavango Delta (S $18^0$55'37.46", E $22^0$48'19.43"). The Okavango is a large (approximately 22000 km^2) alluvial fan within the Kalahari basin (Butchart, 2000; Gumbricht *et al.,* 2004) with soils mainly composed of Aeolian sand that has a relatively high hydraulic conductivity and porosity (Gieske & Obakeng, 1997) and is hence nutrient deficient. The nutrient status of soil is generally highest in the floodplain vegetation areas close to the permanent water (Bonyongo & Mubyana, 2004). The region is relatively flat with elevations about 980 m above sea level. The concession hosts a variety of both predators and competitors (Chapter 2).

The study area consists of a mosaic of vegetation types that run more or less parallel with the edge of the permanent water and with changing soil type (Chapter 2). Vegetation types were broadly classified as: open water, floodplains grasslands, upland grasslands and upland woodland vegetation (e.g. mixed woodland, open savanna, mopane woodland and Kalahari apple-leaf woodland). Common grass species include giant three-awn (*Aristida meridionalis),* long-awned grass (*Aristida stipitata),* couch grass (*Cynodon dactylon*), curly leaf love (*Eragrostis rigidior),* yellow thatching grass (*Hyperthelia dissoluta*) and sand quick (*Schmidtia pappophoroides*).

The climate is semi-arid with summer rainfall mainly between November and April. Annual rainfall in the region is highly variable and records from Shakawe and Maun between 1964 and 1994 ranged from between 288 mm and 1145 mm with a long term annual mean of 513 mm (McCarthy *et al.* 1998). I used rainfall recorded by a weather station situated at

Vumbura Camp on the Kwedi concession between January 2009 and December 2010 to define different seasons. In the Okavango region, the dry season is typically prolonged (April-May to October-November). April was the first month in both 2009 and 2010 that recorded nil rainfall (Fig. 2) and was therefore used to define the onset of the dry season. The first rainfall in the dry season was recorded at the end of October in 2009 and during mid-November in 2010 (Fig. 2). During the wet season (1st December to 31st March) between 10 mm and 140 mm of rain was recorded monthly (Fig. 2), maintaining green grass throughout the season. In 2009 and 2010, the Kwedi received 500 mm and 436 mm of rain respectively.

Flooding in the region is usually characterized by an annual single-peak event and is highly variable. Water levels at Mohembo normally begin to rise in November when floodwaters arrive from the Angolan highlands through the Okavango river (McCarthy *et al.* 1998). The flood normally reaches its peak at Mohembo between February and April before falling to the season low by the following October (McCarthy *et al.* 2006). The floodwater moves downstream from Mohembo and spreads outwards expanding the area of inundation and flooding throughout the seasonal swamps and eventually reaches the Thamalakane River some four months later (McCarthy *et al.* 2006). In both 2009 and 2010, the Okavango recorded exceptionally high floods due to above average inflows from Angola in 2008 followed by above average inflow and rainfall in 2009 and 2010. Green grass flushed on the floodplains soon after the floodwaters began to recede. The flood water reached its peak at the Kwedi concession in mid-May 2010 after which water levels remained high until the beginning of July when they began to subside and were completely subsided by mid-September 2010.

July is the coldest month of the year with a mean monthly temperature of 16^0C, a minimum temperature of 3^0C and a maximum temperature of 30^0C. Temperatures typically become very hot before the rains begin and October was the hottest month of the year with a mean monthly temperature of 26^0C, a minimum temperature of 13^0C and a maximum temperature of 41^0C.

Study design

The use of vegetation types and forage resources within various vegetation types were explored using GPS locations and direct foraging observations of three adjacent breeding herds of sable antelope that occupied home ranges in the Kwedi concession. One adult female sable from each of the three herds was fitted with a GPS collar, provided by Africa Wildlife Tracking (AWT; http://www.awt.co.za), that was scheduled to record a GPS location every hour on the hour. The first two GPS collars were fitted in August 2009 and all three collars were removed by December 2010. However, due to collar failure at different stages in the study, GPS locations were not recorded simultaneously by all thee collars throughout that period. Collection of GPS data and foraging data was restricted to five months so a comparison could be made between benign conditions presented during December 2009 and January 2010 and adverse conditions presented between August 2010 and November 2010.

From direct observations in the Kwedi concession, sable herds typically foraged for three to four hours after sunrise and for three to four hours before sunset. I only used one GPS location recorded at 08h00 every morning when sable herds were most likely foraging to determine vegetation type selection during foraging times. I judged a single GPS location recorded daily to represent reasonably independent samples without losing too much data. I amalgamated the GPS locations recorded from all three herds and made inferences about vegetation type selection for all three herds together because collars failed and some did not provide GPS locations throughout the study period. Between morning and afternoon foraging bouts (during the midday heat), sable either travelled to water or rested in shade. As such, the area chosen for foraging in the afternoon was considered to be independent of the area where the same herd foraged in the morning of the same day and the morning of the following day. Direct foraging observations were obtained for each herd and all observations from the same day were grouped into morning or afternoon samples. Foraging observations were performed sequentially by switching to a different herd at least every third day of collecting data.

Data collection

Vegetation map and NDVI images.

In order to assess conditions in different vegetation types and use of different vegetation types within the study area, a vegetation map was created. Google Earth (CNES/SPOT imagery dated 31/05/2008) was used to create a vegetation map by drawing polygons around upland grassland, upland woodland, and floodplain vegetation types within the study area (Chapter 2). The limits to each polygon were determined visually and with prior knowledge of the area. The digitized vegetation polygons were then converted to shapefiles. Digitizing errors were fixed using standard topology generation procedures implemented within ArcMap 10.0.

Imagery was obtained from the Moderate-Resolution Imaging Spectroradiometer version five (MODISv5). The Normalized Difference Vegetation Index (NDVI) data was supplied by the Agricultural Research Councils Institute for Soil Climate and Water, South Africa. The MODISv5 NDVI data are 16-day composite images with a spatial resolution of 250 m. The images are corrected for atmospheric interference and nadir BRDF reflectance (Schaepman-Strub *et al.*, 2006). Images corresponding to dates when foraging areas were sampled (January 2009, December 2010 and August 2010 to November 2010) were collected for the entire study area. Using ArcGIS 10.0 I extracted NDVI vegetation indices for each vegetation type for each composite image.

Vegetation type selection

A single GPS location recorded at 08h00 was downloaded from functioning collars fitted to an individual from each herd to provide an exact location for each herd during

foraging time. The GPS locations were overlaid on a habitat map so that vegetation type selection during foraging times could be determined. Only one collar recorded locations throughout December 2009 and January 2010. One of the collars failed before December 2010 and the other recorded locations for the first 11 days of December before it failed too. Both failed collars were replaced and successfully recorded locations from August 2010 until the end of November 2010. However, the collar that had functioned throughout December and January failed in March 2010 and consequently it did not record further GPS locations for the rest of the study. In total, 322 GPS locations were recorded at 08h00 during the study period (49 in December, 31 in January, 62 in August, 59 in September, 62 in October and 59 in November).

Resource use

The herds were located by VHF telemetry using VHF transmitters attached to the collars and a VHF R-1000 Telemetry receiver and antenna to obtain foraging observations to address the second objective. All three herds could be approached to within 20 m which allowed close range observations. When the herd I was observing was foraging, I defined foraging sites as areas where the majority of a herd had foraged on the 15th minute of the hour. Once the herds had moved off, the location of the foraging site was confirmed using fresh hoof prints and signs of fresh grazing. I noted the vegetation type (floodplain, upland grassland, or upland woodland) and the predominant grass species in each foraging site. I recorded the grass species within a 1x1 m quadrat placed every 3 m along the foraging path of a sable. If there were no bite marks within the quadrat, I placed another quadrat a meter further along the path until there were bite marks within it. In each quadrat, I noted those grass species that had been grazed and counted the number of bites taken from each tuft. A grass species was considered to have been grazed if at least one fresh bite was found on any of the tufts within any of the quadrats in the foraging site. A bite was defined as an area of cropped grass that could be covered by my closed fist. All sedges were grouped together as 'sedges'. The commonly encountered sedges included: *Cyperus denudatus, Cyperus haspan, Cyperus longus, Fimbristylis longiculmus and Schoenoplectus corymbosus*. Tuft greenness was estimated as the proportion of leaves in the tuft that were green. Estimated greenness was then classified into eight greenness categories (0 %; 0-10 %, 11-25 %, 26-50 %, 51-75 %, 76-90 %, 90-99 %, 100%) according to Walker's eight point greenness scale (Walker, 1976). All the foraging sites visited during each day were grouped separately into independent morning and afternoon foraging site samples. In total, 158 independent samples were collected. During December 2009 and January 2010 (wet season) foraging observations were recorded from 83 foraging sites and in August 2010 to November 2010 (dry season) foraging observations were recorded from 75 foraging sites.

Faecal samples

During foraging observations, the location where any adult female sable defecated was noted. Once the herd had moved away, dung pellets were collected from the top of the dung pile to prevent contamination of the samples by soil. The faecal samples were then stored in marked brown paper bags in a cool, dry place until they could be sent to BemLab in Stellenbosch (http://www.bemlab.co.za) where faecal nitrogen (N) was determined using a Leco instrument and phosphorus (P) was determined using Bray II extraction and then analysed on the inductively coupled plasma spectrometer. Results were expressed as a percentage of dry matter. Six samples per month (two from each herd) from December 2009 – January 2010 and from September 2010 – November 2010 were analysed. Only four samples were collected during August 2010 as the central herd could not be located then.

Data analysis

Vegetation conditions as indicated by satellite imagery

The use of a kriging technique and semiveriograms was assessed to deal with spatio-autocorrelation. However, for the purpose of this study, NDVI was used descriptively rather than to test a hypothesis about greenness variation in different vegetation types so, statistical support was deemed unnecessary and beyond the scope of the study. Global Morans I spatial statistic toolbox in ArcMAP 10.0 was used to measure and report the spatial auto-correlation of clusters of NDVI values.

Vegetation type selection

The GPS locations recorded by each collar at 08h00 each day, when sable herds were expected to be foraging, were used to represent independent locations. Use of upland grassland, upland woodland and floodplains was determined by counting the number of independent GPS locations in each vegetation type each month as a proportion of the total number of independent GPS locations recorded in all vegetation types each month.

Resource use

The availability of each grass species in each vegetation type was estimated as the number of samples (grouped morning and afternoon foraging sites) where a species was present divided by the total number of samples for all vegetation types. Grass species that did not occur in ten or more samples in at least one vegetation type were excluded from the analysis. Following Owen-Smith and Cooper (1987), the seasonal acceptability of each grass species was estimated as the number samples where a grass species was eaten divided by the number of samples where the grass species was present in each season. The seasonal dietary contribution of each grass species was assessed as the number of bites recorded from each

species divided by the total number of bites recorded across all species in each season. To ensure an accurate estimate of grass acceptance, forage species that did not occur in ten or more foraging sites in at least one of the seasons were excluded from the analysis. Chi-square analysis at a significance level of $p < 0.05$ was used to determine if there were seasonal differences in the availability and dietary contribution of grass species during December and January and between August and November. A greenness value for each species was obtained by averaging the midpoint greenness values for each species across all quadrats containing that species in each foraging site.

Faecal samples

A 2-way ANOVA with herd identity, season and their interaction as factors was used to compare faecal N and P content between seasons while accounting for variation between herds.

Results

Vegetation conditions as indicated by satellite imagery

The NDVI values that were assessed were significantly auto-correlated (floodplains: Morans index =0.6; z-score = 82; $p < 0.01$ & upland grassland: Morans index =0.1; z-score = 5.2; $p < 0.01$) so results should be interpreted with caution. Between August and November the floodplains (mean NDVI value = 3921) were much greener than the upland grasslands (mean NDVI value = 3159; fig. 4), but both the uplands and the floodplains were browner than they had been during December and January (fig. 4). Greenness values for the floodplains remained reasonably constant between August and November (Fig. 4). I was not able to determine how much of the floodplains were inundated from the available satellite imagery, so depended on personal observations. Floodplains were partially inundated during August and the beginning part of September after which they remained completely exposed for the remainder of the dry season through December and January. Rainfall was recorded earlier in 2009 than in 2010 (fig. 2) and in the uplands during November 2009 greenness, was considerably higher than during November 2010 (fig 4).

Vegetation type selection.

The sable herds varied their use of the floodplains and upland grasslands between seasons (Fig. 3). Sable herds spent about twice as much time on the floodplains during December and January (35% of GPS locations) than between August and November (19% of GPS locations) but even less during August (13 % of GPS locations) when the floodplains were still partially flooded (Fig. 3).

Availability, acceptability and dietary contribution

Forty six different grass species were encountered in foraging sites. Seventeen grass species plus sedges occurred in more than ten foraging sites in at least one of the two seasons and were included in the analysis (table 1). *Urochloa mosambicensis, Paspalum scrobiculatum, Panicum repens,* and sedges had high availability values (> 0.23) on the floodplains but very low availability values (< 0.07) in upland grasslands and upland woodlands (table. 1). *Brachiaria brizantha, Schmidtia pappophoroides* had greater availability values (> 0.22) in the upland grasslands than in other vegetation types (table. 1) and *Panicum maximum* had greater availability values (= 0.27) in upland woodlands than other vegetation types (table. 1). *Eragrostis rigidior* and *Hyperthelia dissoluta* had high availability values (> 0.18) in all three vegetation types (table. 1).

During December and January there was a large proportion of green leaves within the tufts of all grass species encountered in foraging sites, though they were not entirely green (Fig. 5). Most of the highly accepted grass species (acceptance values between 0.58 and 0.82) between December and January were those also considered to be of high grazing value to cattle (i.e.: *P. repens, P. maximum, Digitaria eriantha, S. pappophoroides, U. mossambicense*). Poor forage value species (i.e.: *Aristida junciformis, Aristida meridionalis, Aristida canescens, Pogonarthria squarrosa* and *Aristida stipitata*) had low acceptance values (0 - 0.27; fig. 5). *Cynodon dactylon* which is a short creeping grass is also considered to be a high value forage species but was not commonly accepted (acceptance value = 0.25) by sable herds during December and January despite it also being very green (Fig. 5). Between August and November the grass encountered in foraging sites was much browner than during December and January but even in the brownest species about ten percent of the leaves in the tufts were green. Greener grasses (i.e. sedges, *A. stipitata, A. meridionalis,* and *Eragrostis pallens*) were generally more highly accepted by sable than browner grasses despite the greener species being considered of poor forage value (fig. 6). Some high value forage species that were not especially green between August and November (i.e.: *D. eriantha* and *S. pappophoroides*) were also reasonably highly accepted then (fig. 6).

Grass species that did not occur in more than 10 foraging sites in at least one season were grouped together as 'other' and contributed about 10% of the diet in both seasons. The combined contribution of the top-six ranked grass species amounted to 70 % and 60% of the diet of the sable herds during the dry and wet seasons respectively. Throughout the year *H. dissoluta* was the most strongly favoured grass species and was almost always grazed (dry season acceptance = 0.94; wet season acceptance =1) when encountered in foraging sites (fig. 5 & 6). As such, *H. dissoluta* contributed most (25 % and 15 %) to the diet of the sable herds during the wet and dry seasons respectively (Table. 2). *A. junciformis, A. canescens, P. squarrosa* and *Eragrostis lehmanniana* were very seldom eaten despite occurring in many of the foraging sites sampled (Table. 2).

P. scrobiculatum, *P. repens* and *U. mossambicense* combined contributed 24 % of the diet of sable between December and January (Table. 2) when herds spent more time on the

floodplains where those grass species were available. When the floodplains were used less, *P. scrobiculatum*, *P. repens* and *U. mossambicense* were rarely encountered and no bites were recorded on them between August and November (Table. 2). Three grass species considered poor value species to cattle showed a significant increase in acceptability from the wet to the dry season (*A. stipitata* (0.27 to 0.81; $\chi^2 = 9.43$; df = 1; P < 0.01), *A. meridionalis* (0.06 to 0.75; $\chi^2 = 33.04$; df = 1; P <0.01) and sedges (0.36 - 0.88; $\chi^2 = 5.44$; df = 1; P = 0.02). The dietary contribution of *C. dactylon* (0.08 to 0.12; $\chi^2 = 4.98$; df = 1; P = 0.026), *A. meridionalis* (0.01 to 0.17; $\chi^2 = 4.98$; df = 1; P = 0.026), sedges (0.02 to 0.10; $\chi^2 = 4.98$; df = 1; P = 0.026) and *A. stipitata* (0.01 to 0.06; $\chi^2 = 4.98$; df = 1; P = 0.026) also increased significantly between the wet and dry season. Although *P. squarrosa* had reasonably high site based acceptability, very few bites occurred on the species because it offered very little leaf material.

Faecal samples

Results should be interpreted with caution as the sable were observed browsing during the dry season (Chapter 4) which may have elevated faecal N value. Diet quality as indicated by faecal N and P levels was substantially higher in December and January than August to November (N: ANOVA, $F_{1, 37}=4.24$, p<0.001; P: ANOVA, $F_{1, 37}=8.71$, p<0.001) and there was not a significant influence of herd identity on the seasonal difference in faecal N and P (N: ANOVA, $F_{2, 37} = 0.33$, p = 0.7; P: ANOVA, $F_{2,37} = 0.43$, p = 0.65). Faecal N monthly means were lowest in August (1.1 +/- 0.04 %) and highest during December (1.7 +/- 0.05 %; Fig. 7). Faecal P monthly means were lowest in October (0.23 +/- 0.01 %) and highest in January (0.32 +/- 0.03 %; Fig. 7). The minimums for both P and N were recorded in months when floodplains were not used extensively (fig. 7), However, without an increase in precipitation or grass greenness on either the floodplain or the upland grassland, the concentration of faecal N and P gradually increased from the minimum in August until October.The maximums were recorded in months when floodplains were used much more (fig. 7).

Discussion

Vegetation conditions and vegetation type use

The floodplains and the upland grasslands were both very green during the rainy months (December and January) but during that period sable concentrated their foraging on the floodplains. The forage on the floodplains is likely to be more nutritious as the moisture and sediment associated with flooding is higher in nutrients than the sandy soils of the uplands (Butchard, 2000).During the dry season (August to November) neither the floodplains nor the upland grasslands were as green as they had been in January and December. However, likely due to grass regrowth being supported by high soil moisture and

nutrients remaining in the soil after the floodwater had receded, the floodplains remained much greener than the upland grasslands from August to November. Between August and November, the sable herds foraged more on the browner upland grasslands than on the greener floodplains where other competitors concentrated (Chapter 2). In November, sable shifted south to where Floodplain grasslands were more abundant (Chapter 2).

The slight increase in greenness in the upland grassland recorded during mid-late October could be attributed to green-up of some of the trees and shrubs within the upland grasslands prior to the rains. The use sable in the Kwedi made of drier upland vegetation types as opposed to exposed floodplains grasslands during the dry season differs from reports from other studies. Roan antelope (*Hippotragus equinus*; Knoop & Owen-Smith, 2006) and buffalo (Macandza *et al.,* 2004) preferentially made use of bottomlands and vleis in the basaltic regions of Kruger National Park where high soil moisture enabled green grass to be retained longer during the dry season. The extent of grazing by roan antelope in the uplands only exceeded that in the bottomlands during especially dry years when grass in the vlei became depleted (Knoop & Owen-Smith, 2006). Sable herds in Mana Pools National Park (Jarman, 1972), Luando Integral Nature Reserve (Estes and Estes, 1974), Rhodes Matopos National Park (Grobler, 1981), Pilanesberg National Park (Magome, 1991) and Kgaswane Mountain Reserve (Parrini, 2006) sought moist bottomlands where green grass was retained longest during the rain-free months in the late dry season. The use of the uplands is more consistent with reports of sable in Punda Maria also in Kruger National Park where sable herds remained in the uplands during the dry season because the bottomlands were characterized by riverbanks and seasonal drainage lines where buffalo occupied core ranges, depleted food resources and attracted predators during the dry season (Macandza, 2009). The green grass in the bottomlands at Punda Maria during the dry season may have also been too short for sable to crop (Macandza, 2009).

The sable herds on the Kwedi concession seemed to be faced with the problem of how much time to spend on the floodplains during the dry season. Other grazers such as buffalo, zebra, wildebeest, impala and tsessebe were regularly observed foraging on the floodplains between August and November (Chapter 2) which is likely to have increased competition for resources there but also likely to have attracted an abundance of predators with a consequential increase in predation risk on the floodplains. Records of predator sightings in the Kwedi concession between August and November in 2007 revealed that nine sable were killed on the floodplains (7 by lion, 1 by leopard and 1 by cheetah). One of the females fitted with a GPS collar, another adult female and adult male were also killed by lion on the floodplains in August 2010. However, if the herds forage entirely in the uplands, they increase the risk of starvation, particularly towards the end of the late dry season when grass there is especially brown. The Kwedi sable herds were expected to forage more on the floodplains during August to November where an abundance of green palatable grass was accessible, but instead, sable herds seemingly utilized the floodplains just enough to retard starvation risk as indicated by faecal nitrogen and phosphorus levels. Sable utilized the uplands for the remainder of the August to November period. There are two possible

explanations for why sable used the floodplain so much during December and January. The first is that after the rains when green grass and water became available across the landscape, competitors may have dispersed into the uplands thereby reducing the risk of predation on the floodplains by drawing the predators away from there. Sable were then provided with an opportunity to use the floodplain with reduced predation risk. The second is that sable on the Kwedi calved between late-January and mid-March and their demand for high quality resources a few weeks prior to calving may have drawn the sable to the floodplains despite the higher predation risk there.

Nutritional indicators showed a seasonal contrast where levels of faecal N and P were higher during the wet season (December and January) than during the dry seasons (August to November) even though N and P concentrations may have been slightly elevated during the dry season months when sable were observed browsing (Chapter 4). If the sable had not partially utilized the floodplains during the dry season, faecal protein might have dropped below the 6-8% (faecal N multiplied by 6.25) suggested food crude dietary and faecal protein level required for maintenance in a herbivore of this size (Robbins, 1996; Grant, *et al.* 2000). The lowest faecal N level, was recorded during August (1.1 % of dry matter) when only 13 % of GPS locations were recorded on the floodplains. Between August and November the sable herds used progressively more of the floodplains as the water receded which also reflected in faecal N levels that gradually increased during the same period. The faecal N levels recorded during August were still higher than the levels documented during the dry season for thriving sable herds in Pilanesberg Game Reserve (1.05 %, Magome *et al.,* 2008) and for herds in Kruger National Park (0.68 %, Codron *et al.*, 2007; 0.8% Henley, 2005) where sable were experiencing a decline (Ogutu & Owen-Smith, 2005).

Availability, acceptability and dietary contribution

The composition of forage species encountered in foraging sites varied between seasons due to range shifts that occurred and the seasonal dietary differences seem to be largely driven by the occupation of different vegetation types. High value forage species such as *P. scrobiculatum*, *P. repens* and *U. mossambicense* had greater availability and contributed more to the diet of sable during December and January when sable foraged more on the floodplains. Faecal N and P during that time were considerably higher than during the August to November period (Fig. 7). Between August and November, *D. eriantha*, *A. stipitata*, and *B. brizantha* were highly available due to sable foraging more in the uplands where those species had high availability. During the wet season when sable foraged more on the floodplains, high quality, green grass species were abundant and made up a large portion of the diet. But during the dry season, when herds foraged in the uplands, many of their favoured high forage value species were absent or less available and the herds adjusted by expanding their consumption and acceptance of poor value grass species such as *A. stipitata* and *A. meridionalis* and short grasses such as *C. dactylon* which all had greater availability then.

During the December and January period, the grasses the herds encountered in foraging sites in the uplands and on the floodplains and uplands were all very green due to rainfall. During that period, high value forage species were most accepted. Surprisingly, sable herds still found and ate grasses that retained some greenness between August and November. Some of the green grass encountered in upland foraging sites and could be attributed to the sandy soils predominant there holding subsoil moisture reasonably well. Between August and November, greener grasses were generally more highly accepted than browner grass but greenness had little influence on acceptance of highly palatable grass species such as *D. eriantha, S. pappophoroides,* that remained highly accepted despite being brown. Grass species such as *H. dissoluta, A. meridionalis,* and *A. stipitata* which are generally considered to be of low grazing value to cattle (van Oudtshoorn, 1999) were amongst the greatest contributors to the diet of sable especially during the dry season. *H. dissoluta* was one of the greenest grass species encountered in foraging sites while *A. meridionalis* and *A. stipitata* also remained very green during the dry season. All three species increased in acceptability during the dry season when high forage value floodplain grassland species such as *P. repens, P. scrobiculatum* and *U. mossambicense* were rarely available. Previous studies have also noted that sable show a marked preference for green grass and although they do tolerate some brown grass (Grobler, 1981; Magome, 1991; Le Roux, 2010) they are more narrowly selective for green grass than bulk grazers like buffalo and zebra (Macandza, 2009). Sable are therefore largely dependent on green grass regrowth after fires (Magome *et al.,* 2008; Parrini & Owen-Smith, 2009) or found in dambos and vleis (Parrini, 2006) during the dry season which both contribute to elevating faecal nutrient levels.

A. meridionalis, *A. stipitata* and sedges have not previously been documented in the diet of sable yet they constituted a large portion of the diet of the sable in the Kwedi concession especially between August and November. *H. dissoluta* has been documented in the diet of sable in the Rhodes Matopos National Park (Grobler, 1981) and the Pilanesberg Game Reserve (Magome, 1991), but was generally not highly accepted and did not contribute much to the diet of sable there. In the Pretorius kop region of Kruger National Park *H. dissoluta* was highly accepted by four separate herds and made up a large portion of their diet particularly during the dry season (Le Roux, 2010). Throughout the year in the Kwedi concession, *H. dissoluta* was almost always eaten when encountered in foraging sites and made the largest contribution to the diet of sable in the Kwedi concession during both seasons. The consumption of tall fibrous grass species is not largely different to reports from other sable studies where, tall, stemmy grass species like *Themeda triandra*, *P. maximum, Heteropogon contortus* and *H. dissoluta* also made up the bulk of the diet of sable herds (Wilson & Hirst, 1977; Grobler, 1981; Gureja & Owen-Smith, 2002; Parrini, 2006; Le Roux, 2010). This suggests that sable, like the closely related roan antelope, which have also been documented to utilize tall, fibrous grass (Knoop & Owen-Smith, 2006) may be able to cope with high indigestible fibre content in their diet. Roan may be able to cope with fibrous grasses through the unusually rapid digestive system documented for them (Heitkonig, 1993).

In the Pilanesberg Game Reserve (Magome *et al.,* 2008) and Kruger National Park (Le Roux, 2010) *C. dactylon* also remained low in acceptability to sable herds. Despite being relatively green during both seasons and considered to be a highly accepted forage species for short grass grazers like wildebeest (Andere, 1981), *C. dactylon* also had relatively low site-based acceptance values to sable in the Kwedi concession (perhaps due to its short, creeping growth form which sable are not adept to crop; Grobler, 1981). However, it made a large contribution to the diet of sable in the Kwedi in both seasons because when it was encountered on termite mounds where it formed thick green mats, many bites were recorded.

Summary and Conclusions

Indications are that sable should spend most their time foraging on the floodplains where green, high quality grass species that have been shown to be acceptable to cattle and other wild grazers are found. Due to pressure from other grazers and predators that concentrate on the floodplains during the dry season, sable are more at risk when foraging there so spend more time in the upland grasslands. Sable herds continued to use the floodplains to a limited extent during the dry season. During the dry season sable also seemed to tolerate tall, stemmy, grasses considered to be poor forage value to cattle which may contribute to their success by enabling them to forage in areas where competitors and predators are less abundant. Grass greenness did have a positive influence on the acceptance of grass tufts but the effect was not strong and some brown grass species that are considered high value forage to cattle were still highly accepted. *C. dactylon* that had a short creeping growth form was also not highly accepted but contributed a lot to the diet of sable because large quantities of it were eaten when it was found on termite mounds. Faecal N and P levels indicate that the sable benefit nutritionally by foraging on the floodplains, but that despite generally avoiding the floodplains during the dry season they still maintain reasonably high level of faecal N and P. This suggests that if the sable population on the Kwedi is not performing well, it is likely related to other factors separated from poor use of resources. The small herd sizes, casual observations and indications from the sightings book records indicate that poor population performance of sable could be more closely related to excessive predation than poor resource use.

Tables

Table 1: The availability of grass species encountered in more than ten foraging sites in at least one vegetation type by three sable herds in the Okavango delta, northern Botswana.

Grass Species	Grazing value to cattle based on van Oudtshroorn (1999)	Availability		
		Floodplain	Upland Grassland	Upland Woodland
Eragrostis rigidior	Average	0.95	0.54	0.46
Sedges	N/A	0.75	0.02	0.06
Cynodon dactylon	High	0.45	0.17	0.44
Aristida junciformis	Low	0.43	0.07	0.02
Aristida meridionalis	Low	0.40	0.63	0.39
Panicum repens	High	0.35	0.02	0.07
Hyperthelia dissoluta	Average	0.33	0.39	0.18
Pogonarthria squarrosa	Poor	0.28	0.15	0.10
Aristida canescens	Poor	0.25	0.00	0.07
Stipagrostis uniplumis	Average	0.25	0.20	0.23
Schmidtia pappophoroides	High	0.23	0.46	0.29
Paspalum scrobiculatum	Average	0.23	0.00	0.01
Urochloa mosambicensis	High	0.23	0.00	0.00
Aristida stipitata	Poor	0.20	0.48	0.41
Panicum maximum	High	0.15	0.17	0.27
Digitaria eriantha	High	0.13	0.33	0.20
Eragrostis lehmanniana	Average	0.10	0.17	0.11
Brachiaria brizantha	Average	0.08	0.22	0.07

Availability = the number of samples (grouped morning and afternoon foraging sites) where a species was present divided by the total number of samples for all vegetation types.

Table 2: The availability and dietary contribution of forage species encountered by three sable herds in more than ten foraging sites in one of the two seasons in the Okavango Delta, northern Botswana. Chi-squared tests (p<0.05) were used to compare differences dietary contribution in grass species between season. *'s indicate a significant difference.

	Availability			Dietary Contribution		
	Dec-Jan	Aug-Nov	Sig .	Dec-Jan	Aug-Nov	Sig .
Hyperthelia dissoluta	0.41	0.16	*	0.25	0.15	*
Panicum repens	0.20	0.05	*	0.10	0.00	*
Digitaria eriantha	0.17	0.37	*	0.09	0.08	
Schmidtia pappophoroides	0.04	0.35	*	0.09	0.04	*
Paspalum scrobiculatum	0.12	0.03	*	0.08	0.00	*
Cynodon dactylon	0.47	0.31		0.08	0.12	
Urochloa mossambicense	0.14	0.00	*	0.06	0.00	*
Eragrostis rigidior	0.58	0.67		0.05	0.05	
Panicum maximum	0.13	0.19		0.03	0.03	
Sedges	0.30	0.12	*	0.02	0.10	*
Stipagrostis uniplumis	0.17	0.25		0.01	0.01	
Aristida stipitata	0.13	0.51	*	0.01	0.06	*
Aristida meridionalis	0.40	0.55		0.01	0.17	*
Eragrostis pallens	0.02	0.20		0.01	0.03	
Pogonarthria squarrosa	0.18	0.17		0.00	0.00	
Brachiaria brizantha	0.02	0.17	*	0.00	0.05	*
Aristida junciformis	0.22	0.09	*	0.00	0.00	
Aristida canescens	0.12	0.11		0.00	0.01	
Eragrostis lehmanniana	0.06	0.13		0.00	0.00	
Other	0.16	0.08		0.10	0.07	

Availability = the number of samples (grouped morning and afternoon foraging sites) where a species was present divided by the total number of samples for all vegetation types.
Dietary contribution = the number of bites recorded from each species divided by the total number of bites recorded across all species in each season

Figures
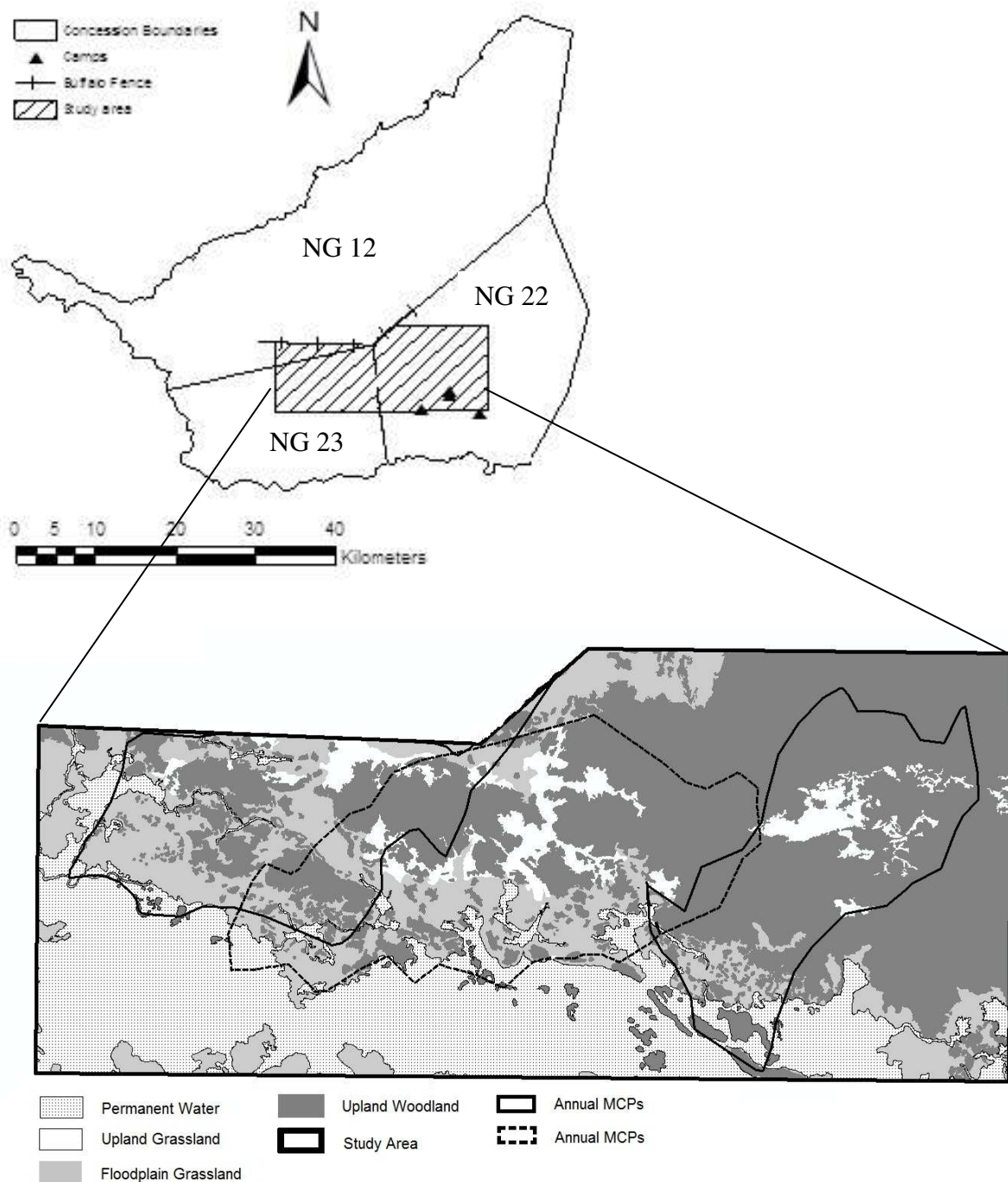
Figure 1: The location of the study area within the Kwedi (NG22), Duba Plains (NG23) and Mapula (NG12) concessions and the different vegetation types within the study area. Annual MCPs of the three collared herds are also illustrated.
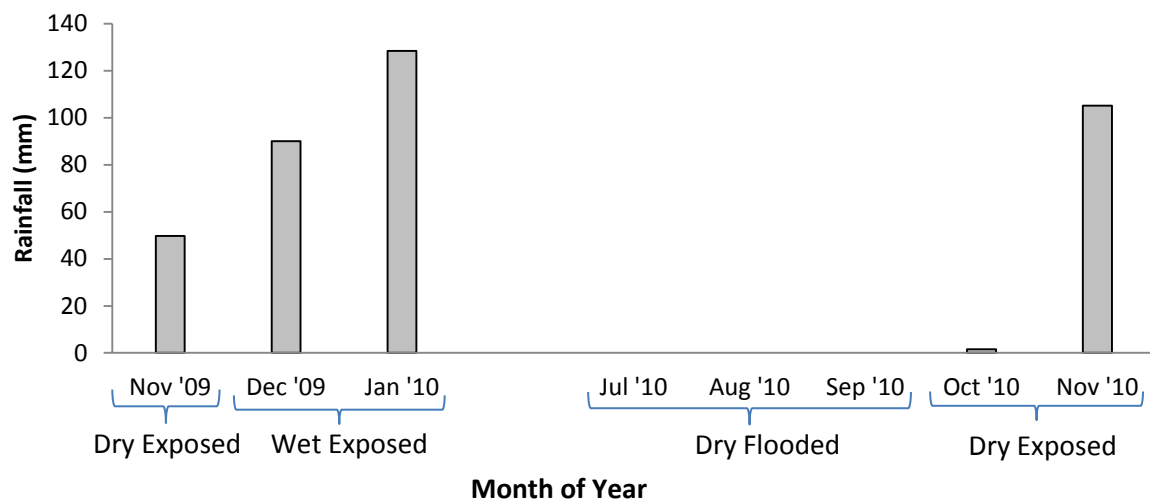
Figure 2: Precipitation recorded by the weather station at Kwedi during the study period in 2009 and 2010 showing the periods when floodplains were inundated or exposed.
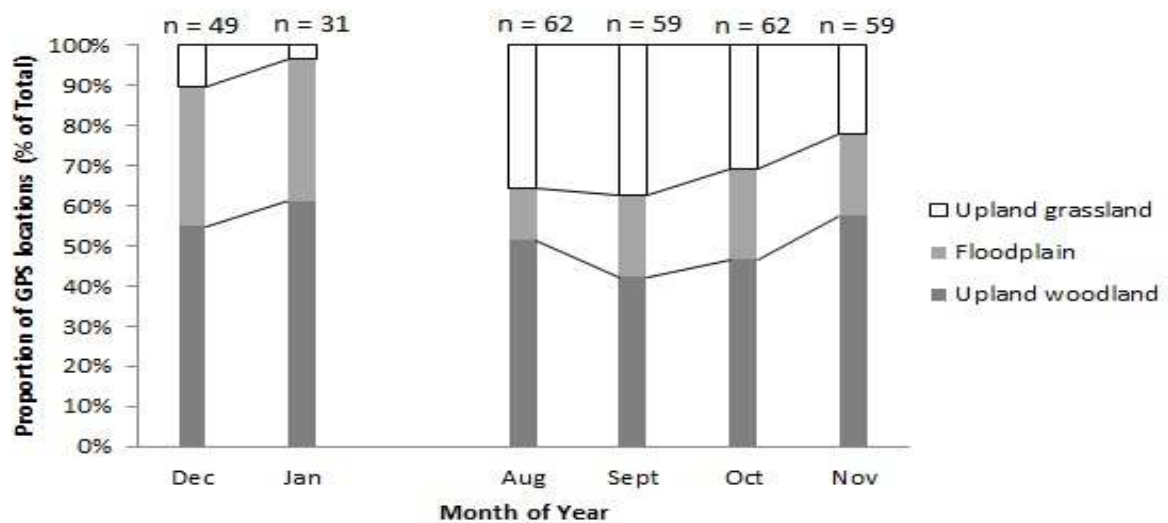
Figure 3: The proportion of GPS locations from three collared sable herds recorded within floodplains, upland grasslands and upland woodlands between December 2009 to January 2010 and August 2010 to November 2010.
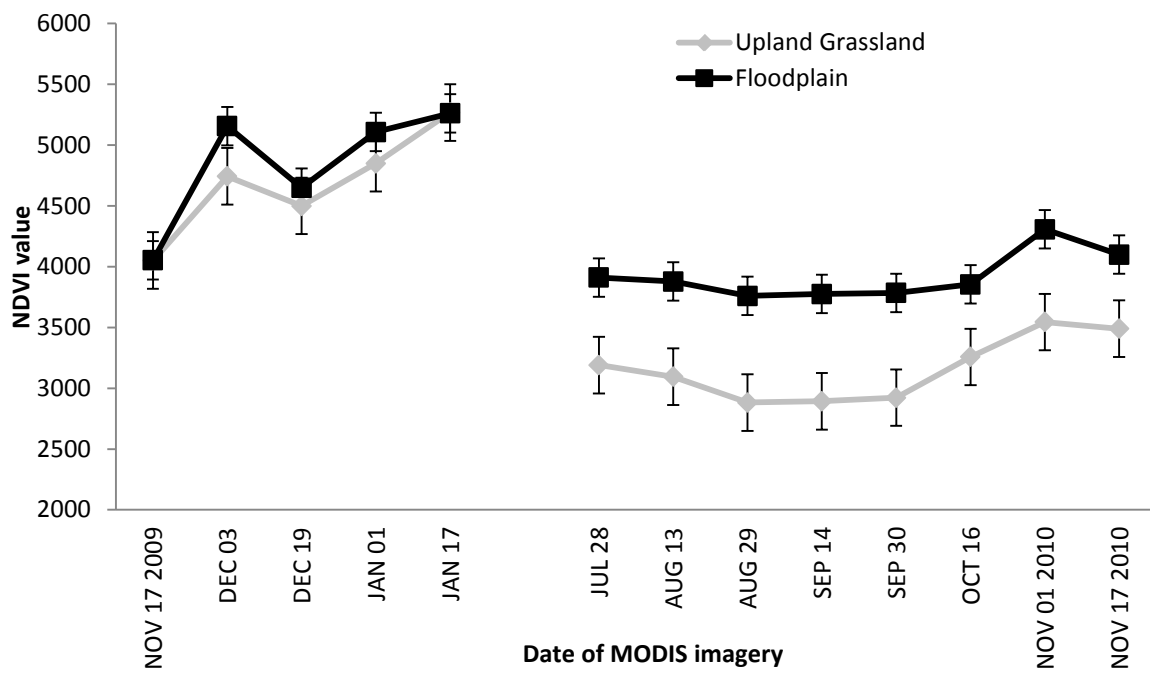
Figure 4: NDVI values for the floodplain (FPG) and the upland grassland (OPG) during the study period (November 2009 – January 2010 and August 2010 – November 2010).
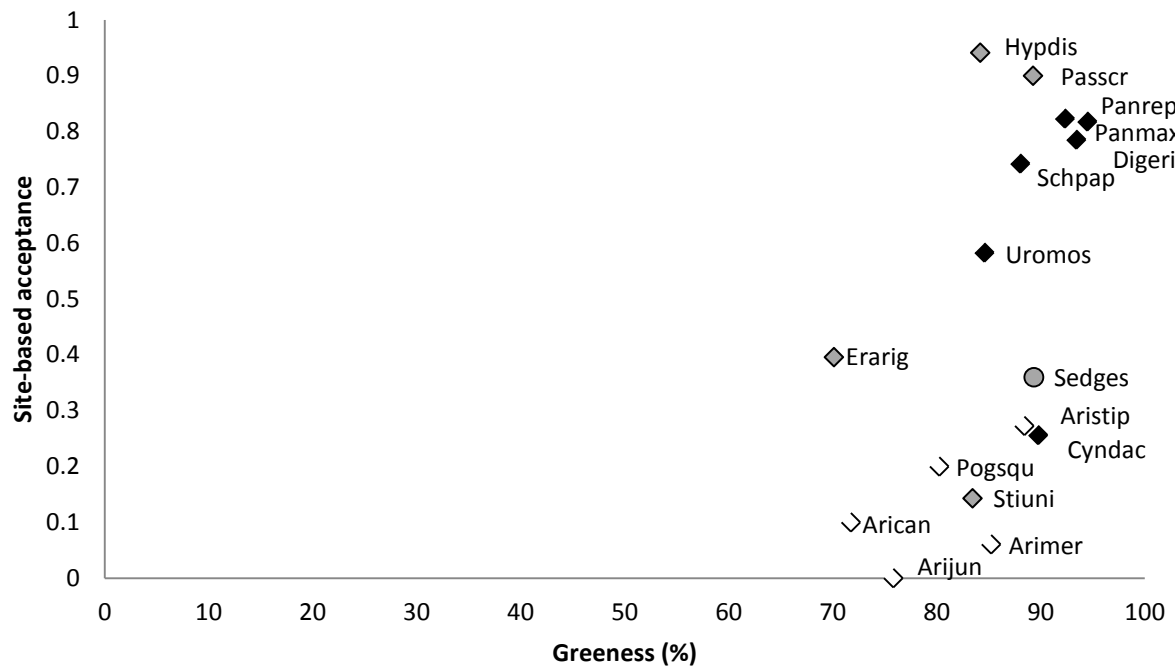
Figure 5: The greenness and acceptance of forage species encountered in more than ten foraging sites during the wet season. ◆ = high value forage species; ◇ = poor forage value species; ◆ = average forage value and; ● = unlisted forage value based on van Oudtshroorn (1999). Acceptance = as the number samples where a grass species was eaten divided by the number of samples where the grass species was present in each season. Arican - *Aristida canescens*; Arijun - *Aristida junciformis*; Arimer - *Aristida meridionalis*; Aristip - *Aristida stipitata*; Cyndac - *Cynodon dactylon*; Digeri - *Digitaria eriantha*; Erarig - *Eragrostis rigidior*; Hdis - *Hyperthelia dissoluta*; Panmax - *Panicum maximum*; Panrep - *Panicum repens*; Passcr - *Paspalum scrobiculatum*; Pogsqu - *Pogonarthria squarrosa*; Stiuni - *Stipagrostis uniplumis*; Schpap - *Schmidtia pappophoroides*; and Uromos - *Urochloa mossambicense*.
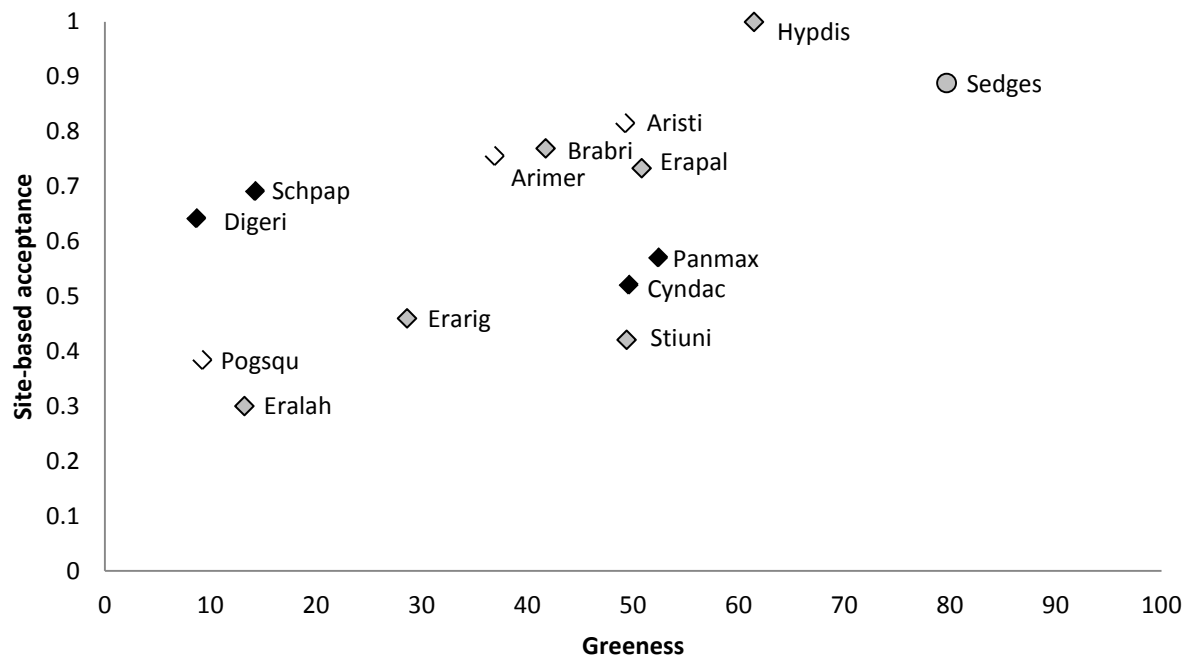
Figure 6: Greenness and acceptance of forage species encountered in more than ten foraging sites during the dry season. ◆ = high value forage species; ◇ = poor forage value species; ◆ = average forage value and; ◉ = unlisted forage value based on van Oudtshroorn (1999). Acceptance = as the number samples where a grass species was eaten divided by the number of samples where the grass species was present in each season. Arimer - *Aristida meridionalis*; Aristip - *Aristida stipitata*; Brabri - *Brachiaria* brizantha; Cyndac - *Cynodon dactylon*; Digeri - *Digitaria eriantha*; Erarig - *Eragrostis rigidior*; Eralah - *Eragrostis lehmanniana;* Erapal –*Eragrostis pallens;* Hdis - *Hyperthelia dissoluta*; Panmax - *Panicum maximum*; Pogsqu - *Pogonarthria squarrosa*; Stiuni - *Stipagrostis uniplumis*; and Schpap - *Schmidtia pappophoroides*.

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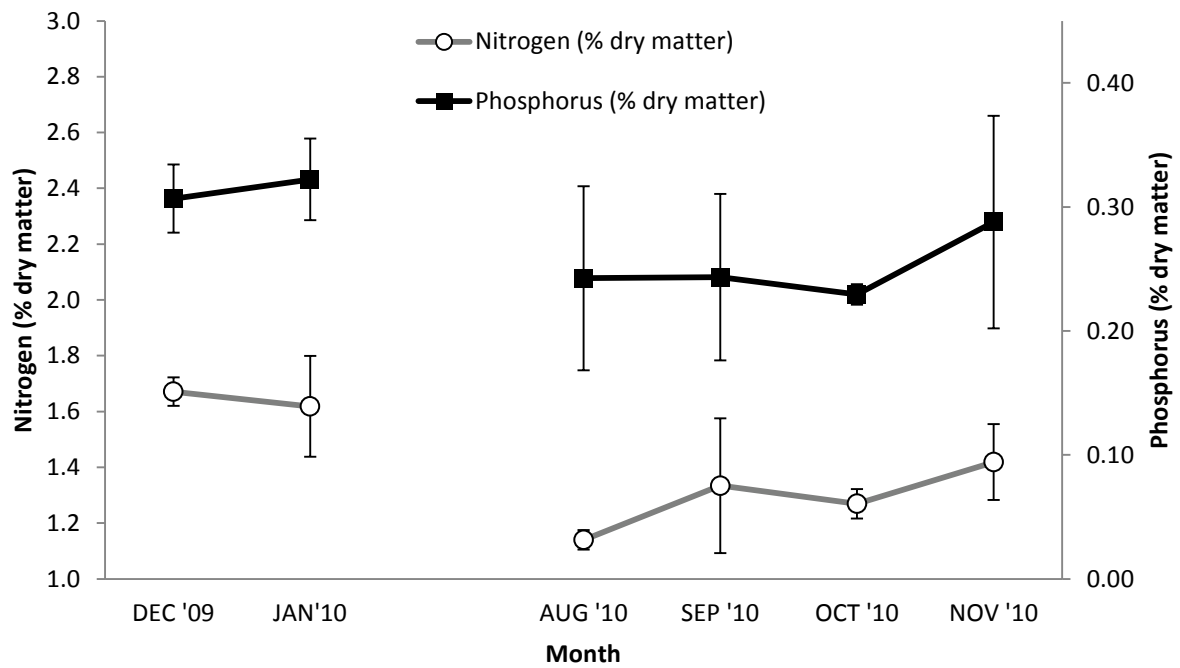
Figure 7: Monthly faecal nitrogen as a percentage of dry matter in sable antelope in the Kwedi Concession in northern Botswana. December 2009 to January 2010 and August 2010 to November 2010.

References

ARCHIBALD, S & SCHOLES, R.J. (2007) Leaf green-up in a semi-arid African savanna—separating tree and grass responses to environmental cues. *J. Veg. Sci.,* 18, 583–594.

ARNOLD G.V., (1960) Selective grazing by sheep of two forage species at different stages of growth. *Aust. J. agric. Res.*, 11, 1026-1033.

ANDERE, D.K. (1981) Wildebeest *Connocaetus taurinus* (Burchell) and its food supply in Amboseli Basin. *Afr. J. Ecol.,* 19, 239 – 250.

BELL, R.H.V. (1984) Soil–plant–herbivore interactions. In: *Conservation and Wildlife Management in Africa* (Eds. R.H.V. Bell and E. McShane-Caluzi). US Peace Corps, Washington D.C.

BUTCHARD, D., (2000) *Wildlife of the Okovango – common animals and plants*. Struik Publishers. Cape Town.

BONYONGO, M.C. (2009) *Okavango river basin technical diagnostic analysis: environmental flow module.* Okavango river basin transboundary diagnostic analysis technical report, Botswana.

BONYONGO, M.C. & MUBYANA, T. (2004) Soil nutrient status in vegetation communities of the Okavango Delta floodplains. *S. Afr. J. Sci.,* 100 (7-8), 337-340

CAIN III, J.W., OWEN-SMITH, N., & MACANDZA, V.A. (in press) The costs of drinking: comparative water dependency of sable antelope and zebra. *J. Zool.*

CHOUBERT, G. & FAURE-MURET, A. (1990) International geological map of Africa. Commision for the geological map of the world, (UNESCO, Paris).

CODRON, D., CODRON, J., LEE-THORP, J.A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R., & FOURIE, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.,* 273, 21-29.

ELLERY, K. & ELLERY, W. (1997) *Plants of the Okavango Delta: a field guide*. Tsaro Publishers, Durban.

ESTES, R.D. (1991) *The Behavior Guide to African Mammals: including hoofed mammals, carnivores, primates.* The University of California Press, California.

ESTES, R.D. & ESTES, R.K. (1974) The biology and conservation of the giant sable antelope, *Hippotragus niger variani* (Thomas 1961). *P. Acad. Nat. Sci. Phila.,* 126, 73-104.

FASSNACHT, K.S., COHEN, W.B., & SPIES, T.A. (2006) Key issues in making and using satellite-based maps in ecology: A primer. *Forest Ecol. Manag.,* 222, 167–181.

GRANT, C.C. & VAN DER WALT. (2000) Towards an adaptive management approach for the conservation of rare antelope in the Kruger National Park – outcome of a workshop held in May 2000. *Koedoe,* 43, 103-111.

GROBLER, J.H. (1981) Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. *S. Afr. J. Zool.,* 16 (1), 50-58.

GUMBRICHT, T., McCARTHY, J., & McCARTHY, T.S. (2004) Channels, wetlands and islands in the Okavango Delta, Botswana, and their relation to hydrological and sedimentological processes. *Earth Surf. Proc. Land.,* 29, 15–29

HARRINGTON, R., OWEN-SMITH, N., VILJOEN, P.C., BIGGS, H.C., MASON, D.R. & FUNSTON, P. (1999) Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Conserv.,* 90**,** 69 – 78.

HEITKONIG, I.M.A. (1993) *Feeding strategy of roan antelope in a low nutrient savanna.* PhD thesis. University of Witwatersrand.

HENLEY, S. (2005) *Habitat dependency and nutritional ecology of sable antelope in two regions of the Kruger National Park.* Report to South African National Parks. Centre for African Ecology. University of the Witwatersrand, Johannesburg.

ILLIUS, A.W. & O'CONNOR, T.G. (1999) On the relevance of non-equilibrium concepts to arid and semi-arid grazing systems. *Ecol. Appl.,* 9 (3), 798-813.

ILLIUS, A.W. & O'CONNOR, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos,* 89 (2), 283-294.

JARMAN, P.J., (1972) Seasonal distribution of large mammal populations in the unflooded middle Zambezi valley. *J. Appl. Ecol.,* 9 (1), 283-299.

JOHNSON, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology,* 61 (1), 65-71.

KNOOP, M. & OWEN-SMITH, N. (2006) Foraging ecology of roan antelope: key resources during critical periods. *Afr. J. Ecol.,* 44, 228-236.

LE ROUX, E. (2010) *Habitat and forage dependency of sable antelope (Hippotragus niger) in the Pretoriuskop region of the Kruger National Park.* MSc Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A. (2009) *Resource partitioning between low-density and high-density grazers: sable antelope, zebra and buffalo.* PhD Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A., OWEN-SMITH, N., & CROSS, P.C. (2004) Forage selection by buffalo in the late dry season in two landscapes. *S. Afr. J. Wildl. Res.,* 34 (2), 113-121.

MAGOME, D.T. (1991). *Habitat selection and the feeding ecology of the sable antelope (Hippotragus niger niger) (Harris 1838), in Pilanesberg National Park, Bophuthatswana.* MSc Thesis, University of the Witwatersrand, Johannesburg.

MAGOME, H., CAIN, J.W., OWEN-SMITH, N., & HENLEY, S.R. (2008) Forage selection of sable antelope in Pilansberg Game Reserve, South Africa. *S. Afr. J. Wildl. Res.,* 38 (1), 35–41.

McCARTHY, T. S. (1992) Physical and biological processes controlling the Okavango Delta – a review of recent research. *Botswana notes and records.,* 24, 57-86.

McCARTHY, T. S., BLOEM, A. & LARKIN, P. A. (1998) Observations on the hydrology and geohydrology of the Okavango Delta. *S. Afr. J. Geol.,* 101 (2), 101–117.

McCARTHY, T.S. (2006) Groundwater in the wetlands of the Okavango Delta, Botswana, and its contribution to the structure and function of the ecosystem. *J. Hydrol.,* 320, 264–282.

OGUTU, J.O. & OWEN-SMITH, N. (2005) Oscillations in large mammal populations: are they related to predation or rainfall? *Afr. J. Ecol.,* 43, 332–339.

O'REAGAIN, P.J. & SCHWARTZ, J. (1995) Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and temporal variability. In: *Recent developments in the nutrition of herbivores. Proceedings of the IVth International Symposium on the Nutrition of Herbivores* (Eds. M. Journet, E. Grenet, M-H. Farce, M. Theriez & C. Demarquilly). 407 – 423. INRA Editions, Paris.

OWEN-SMITH, N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of Tropical Savannas* (Eds. B.J. Huntley & B. H. Walker) Springer-Verlag, Berlin, 359-404.

OWEN-SMITH, N. (1988) *Megaherbivores – The influence of a very large body size on ecology*. Cambridge University Press. Cambridge, UK.

OWEN-SMITH, N. (2002) *Adaptive Herbivore Ecology (Student Edition).* Wits University Press, Johannesburg.

OWEN-SMITH, N. & COOPER, S.M. (1987) Assessing the food preferences of ungulates by acceptability indices. *J. Wildlife Manage.*, 51, 372-378.

OWEN-SMITH, N. & NOVELLIE, P. (1982) What should a clever ungulate eat?
Am. Nat., 119, 151-178.

PARRINI. F. (2006) *Nutritional and social ecology of the sable antelope in the Magaliesberg Nature Reserve.* PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

PARRINI, F. & OWEN-SMITH, N. (2010) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *Afr. J. Ecol.*, 48 (2), 526-534.

ROBBINS C.T. (1996) *Wildlife feeding and nutrition*. Academic Press, San Diego, California, USA.

SCOONES, I. (1995) Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *J. Arid. Environ.,* 29, 221-237.

SCHAEPMAN-STRUB, G., SCHAEPMAN, M. E., PAINTER, T. H., DANGEL, S. & MARTONCHIK, J. V. (2006) Reflectance quantities in optical remote sensing – definitions and case studies. *Remote Sens. Environ.,* 103, 27-42.

SENFT, R.L., COUGHENOUR, M.B., BAILEY, D.W., RITTENHOUSE, L.R., SALA, O.E. & SWIFT, D.M. (1987) Large herbivore foraging and ecological hierarchies. *BioScience.* 37, 789 – 799.

SHAEFER, J.A. & MESSIER, F. (1995) Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography.* 18, 333-344.
SHAW, J.A. (2011) *Adaptive resource use in a re-introduced black rhinoceros population.* PhD Thesis. University of the Witwatersrand, Johannesburg.

SINCLAIR, A.R.E. (1977) *The African Buffalo. A study of Resource Limitations on Populations.* University of Chicago Press, Chicago.

SKINNER, R.H.N. & CHIMIMBA, C.T. (2005) *The mammals of the Southern African Subregion*. 3rd edn. Cambridge University Press, Cambridge, UK.

VAN BOMMEL, F.P.J., HEITONIG, I.M.A., EPEMA, G.F., RINGROSE, S., BONYONGO, C., & VEENENDAAL, E.M. (2006) Remotely sensed habitat indicators for predicting distribution of impala (*Aepyceros melampus*) in the Okavango Delta, Botswana. *J. Trop. Ecol.,* 22, 101–110.

VAN OUDTSHOORN, F. (1999) *Guide to grasses of southern Africa (2nd Edition)*. Briza Publications, Pretoria.

WALKER, B.H. (1976) An approach to monitoring the changes in composition of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.,* 6, 1-32.

WHITE, I.J. (2006) *Rare antelope in the Kruger National Park: Trends, current status, and options for future management.* Scientific Report, South African National Parks.

WILSON, D.E. & HIRST, S.M. (1977) Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife Monographs.* 54, 3-111.

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Please note that the following chapter is NOT solely my own work because my supervisor and co-supervisors (see front page for details) contributed to the draft that has recently been submitted to the African Journal of Ecology for publication as a short note. This section is co-authored by my supervisors and includes revision following reviewers comments.

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CHAPTER 4 – DRY SEASON BROWSING BY SABLE ANTELOPE IN NORTHERN BOTSWANA

Introduction

The late dry season is a crucial period for grazing ungulates because the nutritional value of the remaining brown grass is lowest then and levels of crude protein and digestible organic matter may fall below the maintenance requirements of herbivores (Owen-Smith, 1982). During this adverse period, mixed feeders like impala (*Aepyceros melampus*) increase the proportion of browse in the form of the leaves of the woody plants they consume (Owen-Smith & Cooper, 1985). Crude protein levels are generally higher and seasonally more constant in foliage of woody plants than in grasses (Owen-Smith, 1982), but the foliage is commonly defended by tannins or spines that restrict consumption by grazers not adapted to cope with them (Cooper & Owen-Smith, 1985; Cooper & Owen-Smith, 1986; Cooper, Owen-Smith & Bryant, 1988).

Sable antelope (*Hippotragus niger*) are predominantly grazers and are distributed throughout southern African savannas (Estes, 1991; Skinner & Chimimba, 2005) where the dry season is prolonged and ambient temperatures are high before the rains begin. Grass quality is especially poor on infertile, sandy soils (Bell, 1984). Sable typically depend on green grass persisting in drainage sump grasslands or in recently burned areas during the dry

season (Estes & Estes, 1974; Parrini & Owen-Smith, 2009). However, contrary to previous reports, we observed a substantial amount of browsing by sable in our study area during the dry season. Here, we quantify the contribution made by browse to the diet of sable in our study area.

Methods

The study area was located on the northern edge of the Okavango Delta in Botswana. An adult female sable in each of three herds was fitted with a GPS collar to facilitate observations. When the herd being observed from a vehicle was foraging, we selected the closest female and watched her feeding from 10-50 m away. Beginning on any tenth minute of the hour, we recorded whether this animal was browsing, grazing or performing other activities on every tenth second over a minute ($n = 879$ one-minute observations). Records were pooled for each morning and afternoon observation session ($n = 113$). Following initial observations of browsing in late 2009, records representing early wet season conditions were collected from December 2009 through January 2010 ($n=46$), mid dry season conditions through August- September 2010 ($n=36$), and late dry season conditions through October-November 2010 ($n=31$).

The beginning of a foraging path was identified as the location of the closest observed female to the vehicle on any 15th minute of the hour if the majority of the herd was foraging. Foraging paths identified by fresh tracks of the selected sable were typically 25 m in length. We recorded which woody species were available within 5 m of the foraging path with foliage below 2 m above ground. Fresh bite marks were counted on each woody plant. Grouping morning and afternoon foraging paths separately yielded 91 foraging sites assumed to be independent. The availability of each woody species was estimated from the number of

foraging sites where it was present divided by the total of foraging sites. The acceptability of each species was estimated as the number of foraging sites where it was browsed once or more divided by the number of foraging sites where it was present (Owen Smith & Cooper 1987). Only woody species present in more than 10 foraging sites in at least one season were considered. The proportion contributed by each species was assessed as the number of bites taken from it divided by the total number of bites across all woody plants. Acceptability and relative browse contributions were not estimated for the wet season because too little browsing occurred then.

Results

Browsing by sable was observed in over half of foraging periods in the dry season of 2010 (Fig. 1) and amounted to about a quarter of feeding time towards the end (Fig. 2). Feeding on sausage tree (*Kigelia africana*) flowers took place frequently during the mid dry season. Of the seven woody species encountered in ten or more foraging sites in any seasons, Kalahari apple-leaf (*Philenoptera nelsii*) made the greatest dietary contribution, although knobbly combretum (*Combretum mossambicense*) was equally highly acceptable (Table 1). Other commonly available woody species were eaten rarely or not at all. Very little browsing took place during the early wet season.

Discussion

Wilson & Hirst (1977) did not observe any browsing by sable antelope in northern South Africa, and reported that browse fragments were infrequent in the rumen contents of sable from other regions of South Africa. Stable carbon isotopes in faeces indicated that C3 (non-grass) plants made no contribution to the year-round diet of sable antelope in Kruger National

Park (Codron *et al.*, 2007). In Zimbabwe, browsing by sable amounted to only 0.1% of feeding records, made up of newly flushed leaves of camphor bush (*Tarchonanthus camphoratus*) and common wild currant (*Rhus pyroides*) eaten during the hot dry season (Grobler, 1981). Studies summarised by Gagnon and Chew (2000) suggested a mean dicot content of around 10% in the diet of sable in southern Africa. However, a sable antelope shot in the Matetsi region of Zimbabwe had mainly dicotyledonous plant parts in its rumen (Wilson & Hirst 1977). Our observations indicated that woody plant parts including flowers contributed about a quarter of the diet of sable antelope in northern Botswana during the late dry season. Our impression was that the browse component consumed by sable, including flowers of Kalahari apple-leaf trees, was even greater during the dry season of 2009. Browsing took place at a time of the year when the green leaf content of grasses was generally low and their nutrient content likely to be especially low on the prevalent sandy soils. Sable did not exploit nearby floodplains presenting greener grass, apparently avoiding concentrations of other grazers there (Hensman, unpublished observations). A feature of the extended hot dry season typical of our study region is that many trees and shrubs produce new leaves before the rains commence, offering forage much higher in protein content than available in grasses at this time of the year (Cooper *et al*., 1988; Owen-Smith, 1994).

Congeneric roan antelope (*Hippotragus equinus*) have been recorded consuming more browse than any other grazer during the dry season (Hashim, 1987; Owen-Smith, 1997). Both roan and sable depend on quite tall, fibrous grasses (Wilson & Hirst 1977; Knoop & Owen-Smith, 2006; Macandza *et al*., 2012). Heitkonig (1993) found that roan antelope have an unusually high digestive passage rate for a grazer, which could facilitate processing lignified fibre in browse as well as in these grasses. We surmise that sable antelope share a similar dietary adaptation, although studies of their digestive adaptation are lacking.

Acknowledgements

References

BELL, R.H.V. (1984) Soil–plant–herbivore interactions. In: *Conservation and Wildlife Management in Africa* (Eds. R.H.V. Bell and E. McShane-Caluzi). US Peace Corps, Washington D.C.

CODRON, D., CODRON, J., LEE-THORP, J.A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R., & FOURIE, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *J. Zool.* 273, 21-29.

COOPER, S.M. & OWEN-SMITH, N. (1985) Condensed tannins deter feeding by browsing ruminants in a South African Savanna. *Oecologia.* 67 (1), 142-146.

COOPER, S.M. & OWEN-SMITH, N. (1986) Effects of plant spinescence on large mammalian herbivores. *Oecologia.* 68, 446-455.

COOPER, S.M., OWEN-SMITH, N. & BRYANT, J.P (1988) Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry in woody plants in a South African savanna. *Oecologia.* 75, 336-342.

ESTES, R.D. (1991) *The Behavior Guide to African Mammals: including hoofed mammals, carnivores, primates.* The University of California Press, California.

ESTES, R.D. & ESTES, R.K. (1974) The biology and conservation of the giant sable antelope, *Hippotragus niger variani* Thomas 1961. *P. Acad. Nat. Sci. Phila.* 126, 73-104.

GAGNON, M. & CHEW, A.E. (2000) Dietary preferences in extant African Bovidae. *J. Mammal.* 81, 490-511.

GROBLER, J.H. (1981) Feeding behaviour of sable *Hippotragus niger niger* (Harris, 1838) in the Rhodes Matopos National Park, Zimbabwe. *S. Afr. J. Zool.* 16 (1), 50-58.

HASHIM, I.M. (1987) Relationship between biomass of forage used and masses of faecal pellets of wild animals in meadows of the Dinder National Park. *Afr. J. Ecol.* 25, 217-223.

HEITKONIG, I.M.A. (1993) *Feeding strategy of roan antelope in a low nutrient savanna.* PhD thesis. University of Witwatersrand, Johannesburg.

KNOOP, M. & OWEN-SMITH, N. (2006) Foraging ecology of roan antelope: key resources during critical periods. *Afr. J. Ecol.* 44, 228-236.

LE ROUX, E. (2010) *Habitat and forage dependency of sable antelope (Hippotragus niger) in the Pretoriuskop region of the Kruger National Park.* MSc Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A., OWEN-SMITH, N. & CAIN, J.W (2012) Habitat and resource partitioning between abundant and relatively rare grazing ungulates. *J. Zool.* (Only early view available at present).

MAKHABU, S.W. (2005) Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *J. Trop. Ecol.* 21, 641-649.

OWEN-SMITH, N. (1982) Factors influencing the consumption of plant products by large herbivores. In: *Ecology of Tropical Savannas* (Eds. B.J. Huntley & B. H. Walker) Springer-Verlag, Berlin, 359-404.

OWEN-SMITH, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology.* 75, 1050-1062.

OWEN-SMITH, N. (1997) Distinctive features of the nutritional ecology of browsing versus grazing ruminants. *Z. Saugetierkd.* 62, 176-191.

OWEN-SMITH, N. & COOPER, S.M (1985) Comparative consumption of vegetation components by kudus, impalas and goats in relation to their commercial potential as browsers in savanna regions. *S. Afr. J. of Sci.* 81, 72-76.

OWEN-SMITH, N. & COOPER, S.M. (1987) Assessing the food preferences of ungulates by acceptability indices. *J. Wildlife Manage.* 51, 372-378.

PARRINI, F. & OWEN-SMITH, N. (2009) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *Afr. J. Ecol*. 48 (2), 526-534.

SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The mammals of the Southern African Sub-region (3rd Edition).* Cambridge University Press, Cape Town.

WILSON, D.E. & HIRST, S.M. (1977) Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife Monog.* 54, 3-111.

Tables

Table 1: Seasonal availability, acceptability and proportion of browse consumed by sable from woody species. Wet season (WS) = December 2009 through January 2010; mid dry season (MDS) = August through September 2010 and; late dry season (LDS) = October through November 2010.

Browse species	Availability			Acceptability		Proportion of browse consumed	
	WS	MDS	LDS	MDS	LDS	MDS	LDS
Philenoptera nelsii	0.22	0.60	0.53	0.44	0.65	0.78	0.89
Combretum mossambicense	0.30	0.23	0.18	0.25	0.71	0.18	0.11
Croton megalobotrys	0.39	0.09	0.08	0.20	0.00	0.02	0.00
Terminalia sericea	0.61	0.26	0.42	0.07	0.06	0.01	0.00
Colophospermum mopane	0.22	0.38	0.26	0.05	0.00	0.01	0.00
Diospyros lycioides	0.70	0.32	0.16	0.00	0.00	0.00	0.00
Gymnosporia senegalensis	0.00	0.21	0.08	0.00	0.00	0.00	0.00

Figure legends

Figure 1: The proportion of foraging periods in which grazing, browsing or feeding on fallen flowers by sable was recorded during the wet season (WS, December-January), mid dry season (MDS, August-September) and the late dry season (LDS, October-November). Vertical bars represent 95% binomial confidence intervals.

Figure 2: Proportion of foraging time spent grazing, browsing or consuming fallen flowers by sable antelope in the wet season (WS, December - January), mid dry season (MDS, August – September) and late dry season (LDS, October –November) months.
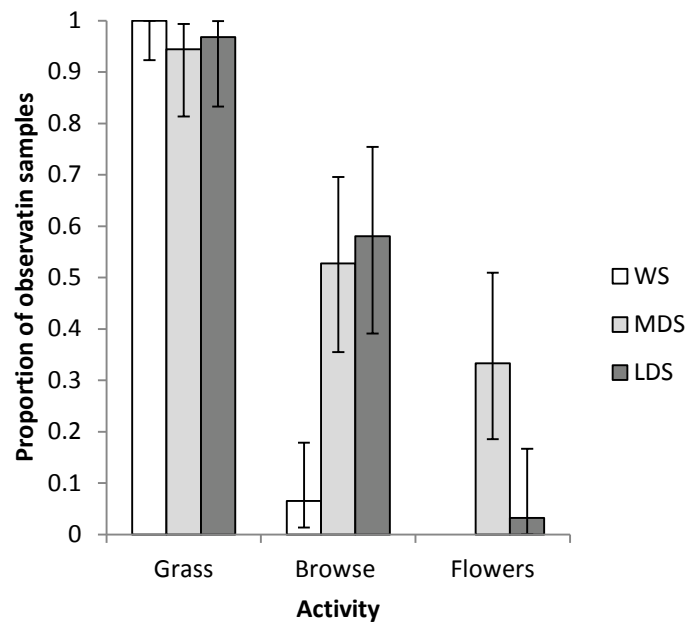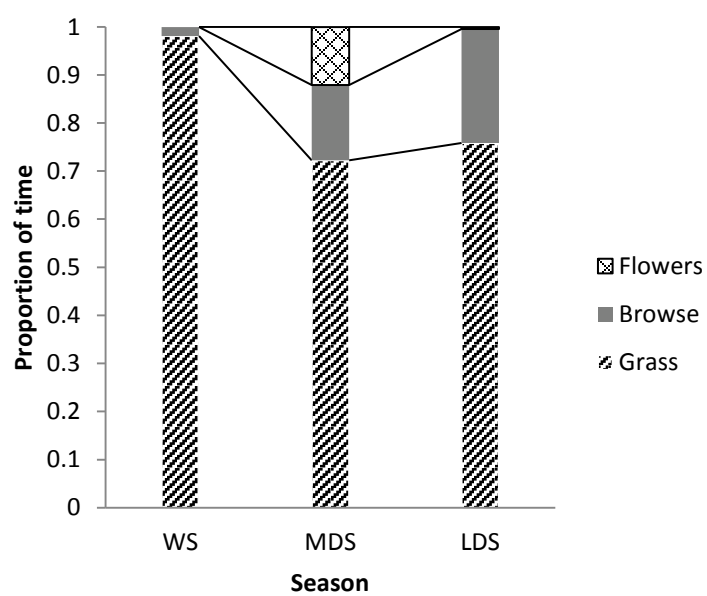
Figures

Figure1

Figure 2

CHAPTER 5 – SYNTHESIS

Key findings and study complications

This study was a contribution to a broader research programme of the Centre for African Ecology (CAE). Specifically, the study was aimed at establishing the home range and habitat use of sable antelope in the Kwedi concession where they were believed to be thriving because of their general abundance in northern Botswana. The study was structured within a hierarchical framework encompassing three orders of habitat selection (2nd, 3rd and 4th) as defined by Johnson (1980).

During the study years (2009 and 2010), the Okavango region experienced exceptionally high floods (http://www.eyesonafrica.net/updates/flood-update.htm) so this study reflects the movements and behaviour of sable under high flood conditions rather than the conditions previously prevailing in the study area. Unfortunately, the study was also compromised by the failure of all three GPS collars at different stages of the study. Two of the collars failed and were replaced at a similar time. The third collar failed 2 months after the first 2 had failed. It was the only collar that provided reliable data for the entire wet season, but did not record locations during the late dry seasons when the other two collars were functioning. All three collars only functioned simultaneously for three of the 16 months in the study period. This affected attainment of the study aims, particularly those related to the 2nd and 3rd orders of habitat selection, because there was very little scope for comparison between herds and very few GPS locations were provided during the late dry season which was identified as the critical period because resources then are most limited.

The greatest limitation on the distribution of sable within the landscape was imposed by the lack of surface drinking water in the north of the study area where large expanses of Kalahari apple-leaf and Mopane woodlands occurred. Areas more than 7 km from Permanent water and Floodplain grasslands where green grass and water were scarce, were simply not occupied by sable herds. Most of the landscape within 7 km of Permanent water and Floodplain grasslands represented suitable areas for three sable herds that occupied by three adjacent home ranges there. During the dry season, Kalahari apple-leaf and Mopane woodlands were also generally avoided despite being close to available drinking water. All three herds also avoided large expanses of open vegetation (i.e.: Floodplain grasslands and Open savannah) but utilised Floodplain grasslands interspersed with clumps of mixed woodlands that may have offered shelter from direct sunlight and may have provided some cover against predation. Sable herds seemed to prefer a mosaic arrangement of open woodlands and grasslands and areas ranging from vleis with no canopy cover (Parrini, 2006) as well as areas with reasonably high canopy cover as observed in other studies (Wilson & Hirst, 1977; Grober, 1981; Magome, 1991; Estes, 1991; Skinner & Chimimba, 2005).

Contrary to expectations, sable herds foraged far less on the floodplains than expected between August and November despite the floodwater having receded then and despite the floodplains being much greener than the surrounding vegetation then too. An abundance of

other grazers such as zebra, tsessebe, wildebeest and buffalo were casually recorded on the floodplains and the number of predator sightings on the floodplains was especially high. These observations, combined with sightings book records, also indicated that more sable were found killed on the Floodplain grasslands than other vegetation types. Since effects of competition or predation were not part of the initial objectives, the gathered evidence (from sightings book records) is too weak to disentangle if floodplains were largely avoided during the dry season because of direct competition with other grazers or because of increased predation risk because of the increase in prey species attracting predators to the floodplains. During the rainy season about three months after the floodwater had receded the herds began utilizing the floodplains extensively.

The home ranges extents of the Kwedi sable herds were reasonably small in comparison to those of herds from other areas where sable populations are doing poorly. Nutritional indicators suggested that sable herds in the Kwedi sustained crude protein levels above the recommended maintenance requirements throughout the study period. The combination of small home ranges and moderately high faecal crude protein levels indicate that the sable in the Kwedi were able to satisfy their nutritional requirements within a relatively small area. The sable herds on the Kwedi did not show distinctly larger home ranges during the late dry than the wet season either, suggesting that even during the late dry season when resources are most limiting, sable did not have to range wider in search of resources. The home ranges of adjacent herds did not overlap indicating that trespassing on neighbours ranges to acquire resources that were unavailable within their own home ranges was not necessary.

The study has also reported the contribution of several grass and sedges species previously not documented in the diet of sable as well as the contribution of browse to the diet of sable which has rarely been documented. In the upland vegetation that was used during the dry season, the sable herds were dependant on tall, stemmy, fibrous grass species often considered to be poor forage value species for grazing by cattle. A high tolerance of stemmy species has been documented for sable antelope by Parrini (2006), Macandza (2009) and Le Roux (2010) and for the closely related roan antelope (Heitkonig, 1993). Sedges and other low value grasses that retained greenness made up a considerable portion of the dry season diet. Sable herds were more likely to feed from grass that was green during the dry season and generally ignored completely brown grass unless they were palatable species. Faecal samples indicated that even during the dry season, sable were able to maintain higher faecal N and P levels than required for maintenance. Even during the harshest time of year sable were not nutritionally vulnerable even though they seemed to have adopted a risk free foraging strategy by avoiding the floodplains where competitors and predators concentrated. During December and January when all grass encountered was green, sable selected high value grass species that were generally located on the floodplains and which were reflected by elevated faecal N and P levels during that period. Although limited browsing by sable has been documented in previous studies, sable herds in the study area spent more time browsing than documented for sable elsewhere. Unfortunately, I was unable to record enough samples

of the browsing that took place during the 2009 late dry season, even though the sable herds spent a considerable amount of time browsing then as noted from casual observations. Sable appear to be able to cope with the browse component of their diet by selecting young leaves (expected to be high in protein and low in tannin concentration; Cooper *et al*., 1988; Owen-Smith, 1994) and flowers.

One of the main concerns about the population performance of sable in the Kwedi concession is that the few herds occurring there remained small. Based on information from the sightings books, nine sable were killed by predators within a four month period in 2007. During the study period, three adult sable were killed by lion, including one that was collared. Through my personal observations which have not been reported in previous chapters, only 4 out of 15 sable calves born during the study period survived. Predation by lion on adult sable and the poor survival rate of the calves seem to be primarily responsible for the small herd sizes of the remaining sable herds in the Kwedi concession.

Recommendations for future research

Henley (2005) presented a conceptual model in which he suggested that sable population declines (such as that experienced in Kruger National Park) are initiated first by environmental stress leading to sable foraging in areas with high predation risk exacerbating the decline to below a certain threshold. Once the threshold is surpassed, even if environmental conditions improve, the small sable population would struggle to recover due to relative predation pressure being excessive, coupled with an Allee effect. Although supporting data are weak, there is evidence of high predation pressure on sable in the Kwedi concession. Sightings book records and personal observations indicate that10 sable were killed by lion in the study area between August 2007 and December 2010. The risk of predation may influence the use of various habitat components and may play a role in preventing sable from being more abundant in the Kwedi concession. It may therefore be worthwhile for future studies to determine the distribution of large predators in the study area so that it can be assessed as a habitat parameter, influencing predation risk for sable. In the Kwedi, at least 15 sable calves were born of which only four survived. The cause of calf death is unknown because carcasses were not found. There were also no reports of unhealthy or sick calves from the guides who regularly did game drives in the study area, nor did I observe any unhealthy and sick calves while driving to and from foraging sites. Habitat selection at finer temporal scales may be able to provide some insight explaining the high mortality of sable calves.

During the late dry season after floodwater had receded, sable spent surprisingly little time foraging on the floodplain grasslands where green, high value grass species were found. During the same period the number of predator and competitor sightings on the floodplains were considerably higher making it difficult to disentangle whether competition or predation were the main factors behind the reduced use of the floodplain grasslands by sable. A detailed differential habitat selection and foraging study between sable and other species of grazing

herbivores may be useful for determining how different species of grazing herbivores partition the grass resource available on the floodplain grasslands. Such a study may be fundamentally important in helping to determine how the species co-exist. It may also help disentangle if the floodplains are largely avoided by sable due to competition or predation.

Future research could also potentially look to expand on observations reported in Chapter 4 by incorporating the chemical features of the woody plant species that were browsed to help explain their consumption by sable. A study directed towards determining the anatomical features of sable that enable them to cope with the tannins (i.e. enlarged salivary glands), high fibre content of the woody browse component and the fibrous grass species that they repeatedly consume would also be extremely beneficial.

Management implications

A 'hands off' approach to wildlife management is adopted in the Kwedi concession. Under extreme circumstances where intervention of a more applied nature may be contemplated, provision of environments where predation pressure is reduced (i.e. enclosures) may be necessary to facilitate population growth. However, Henley (2005) emphasised that such a system has been previously been criticized for breeding naïve prey which are normally killed by predators soon after release unless they are released in large numbers (100's as opposed to 10's). Water provision, in the north of the study area beyond 7km from permanent water where sable do not currently occupy home ranges may also be cautiously contemplated. In Kruger National Park, heightened predation following excessive water provision and a consequential influx of prey species when artificial water points were opened proved problematic for sable and other rare antelope species.

The management recommendations I suggest following this study mostly represent further research and monitoring needs due to the hands off approach. Before this study, information on the population performance of sable antelope in the Kwedi concession was largely scattered and unassimilated and there is very little information on long-term population trends of sable in the Kwedi concession. Monitoring of the size, composition, mergers and disappearance of different herds within the study area should be continued so that long-term trends in sable abundance within the study area can be established. Determining long term trends in sable abundance will be futile unless population performance can be related to potentially influential factors which should also be continuously monitored in the study area. For example, sable prevalence has been negatively associated with the occurrence of predators and competitors (Chirima, 2009). The abundance and movements of predators (not just high-profile species like wild-dog and lion but also hyena and jackal that seem to be preying on sable calves during the lying out period) and competitors (such as buffalo and zebra that share similar food selection) should also be monitored. Understanding how these aforementioned factors interact and work together could be vital to building a knowledge base ensuring that animal populations, particularly rare antelope species in the Kwedi concession do not follow similar paths of decline to those in so many other southern African reserves. Although sightings of high profile species (i.e. lion,

leopard, sable, etc.) are recorded in the sightings books, the information is largely unreliable because the locations are not precise enough (descriptions are based on road names rather than co-ordinates) and often information is not transferred from the sightings book into the 'Capture Sightings' programme. Similarly, the records on the level of floodwater were inconsistent and poorly recorded. The data that had been collected was too unreliable to make use of in this study.

During the critical dry season the population size that can be supported is dependent on animals being able to find sufficiently high quality vegetation components or key resource areas to meet nutritional requirements (Illius & O'Connor, 2000) or at least retard starvation. Faecal N and P levels were lower when floodplains were used less (i.e. during the dry season) and higher when floodplains were used more (i.e. wet season). Floodplain grasslands, though used comparatively less than the upland grasslands, may have been important in maintaining faecal N levels above the maintenance requirements. From this study sable appear dependent on availability and extent of the seasonal floodplains which may be influenced by flooding events and changes in water flow into the Okavango. Increased water flow could be detrimental to floodplain grazers because seasonally flooded areas may become permanently inundated thereby reducing the floodplain grassland area and under prolonged high floods, seasonal floodplains could be converted to semi-permanently flooded swamps where high quality grasses are likely to give way to lower quality forage (Bonyongo 2009 cited Bonyongo & Ugutu, unpublished manuscript). However, water levels higher than normal is likely to also result in the creation of new areas of permanent swamp, seasonal swamp and outer elevated floodplain improving forage productivity in otherwise dry areas (Bonyongo, 2009). The worst case scenario would be reduced flow of water resulting in the progressive desiccation and destruction of floodplain grasslands which would be detrimental to grazers' dependant on them during the dry season (Bonyongo, 2009). Much like the timing of burns during the seasonal cycle is an important determinant of the forage quality and quantity produced to sustain herbivores through the dry season (Parrini & Owen-Smith, 2009), the timing of the departure of the floodwaters is also a key determinant of the quantity and quantity of the forage resources on the floodplains and the period over which sable must survive on low quality forage. In this way, the timing of the floods are just as important, if not more important, than the extent of the floods and is likely to have an impact on population performance of sable. If the floodplains remained inundated until the end of the late dry season (April to end of November) and high value forage grasses were not accessible before the end of the dry season, sable would have to depend entirely upon upland vegetation types to meet their nutritional requirements thought the critical bottleneck period. If the floodwaters receded earlier, the forage resource on the floodplains may be diminished through desiccation or consumption by other floodplain grazers before the critical dry season period. In both scenarios, sable would be nutritionally worse off because they would have to depend entirely on forage in the upland vegetation to maintain nutritional levels above the maintenance requirements. Under such circumstances, they may become weaker and more susceptible to disease and predation.

Flow changes into the Okavango can be effected either naturally or through anthropogenic influences. Naturally induced changes in water flow occur as a result of dislodged vegetation causing channel blockages or the opening or unblocking of channels by hippo and other large animals (i.e. Nqoga channel, Wilson, 1973; McCarthy, 1992). Human induced changes to the hydrological flows of the Okavango include processes such as the abstraction of water from upstream and large scale developments such as damming (Bonyongo, 2009). One needs only consider the effect that the construction of three major dams in the Zambezi delta had on altering the floodplain systems above and below the walls that resulted in the loss of important habitats for both livestock and wildlife (Jarman, 1972; Funston, 2006 cited by Bonyongo, 2009). There is no question that climate is changing and could also affect seasonal patterns of rainfall, flooding and temperature in the Okavango region (Mbaiwa & Mmopelwa, 2009) with a consequential influence on the timing of the floods and the distribution and extent of certain forage resources on which sable depend prior to calving and during the dry season. If climate change reduces the distribution of the floodplain grasslands that support sable through the dry season then they could easily become threatened. Water flow, particularly the abstraction of water from upstream, needs to be managed to ensure that floodplain grasslands remain functional and provide high quality resources towards the end of the dry season.

References

BONYONGO, M.C. (2009) Okavango river basin technical diagnostic analysis: Environmental flow module specialist report. Botswana.

CHIRIMA, J.G. (2009) *Habitat suitability assessments for sable antelope.* PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

COOPER, S.M., OWEN-SMITH, N. & BRYANT, J.P (1988) Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry in woody plants in a South African savanna. *Oecologia*. 75, 336-342.

HEITKONIG, I.M.A. (1993) *Feeding strategy of roan antelope in a low nutrient savanna.* PhD Thesis. University of Witwatersrand, Johannesburg, South Africa.

ILLIUS, A.W. & O'CONNOR, T.G. (2000) Resource heterogeneity and ungulate population dynamics. *Oikos*. 89, 283-294.

JARMAN, P.J. (1972) Seasonal distribution of large mammal populations in the unflooded middle Zambezi valley. *Journal of Applied Ecology*. 9 (1), 283-299.

LE ROUX, E. (2010) *Habitat and forage dependency of sable antelope (Hippotragus niger) in the Pretoriuskop region of the Kruger National Park.* MSc Thesis. University of the Witwatersrand, Johannesburg.

MACANDZA, V.A. (2009) *Resource partitioning between low-density and high-density grazers: sable antelope, zebra and buffalo.* PhD Thesis. University of the Witwatersrand, Johannesburg.

MBAIWA, J.E. & MMOPELWA, G. (2009) Okavango river basin technical diagnostic analysis: Climate change and tourism development. Botswana.

McCARTHY, T. S. (1992) Physical and biological processes controlling the Okavango Delta – a review of recent research. *Botswana Notes and Records*. 24, 57-86.

OWEN-SMITH, N. (1994) Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*. 75, 1050-1062.

PARRINI. F. (2006) *Nutritional and social ecology of the sable antelope in the Magaliesberg Nature Reserve*. PhD Thesis. University of the Witwatersrand, Johannesburg, South Africa.

PARRINI, F. & OWEN-SMITH, N. (2010) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology*. 48 (2), 526-534

WILSON, B. H. (1973) Some natural and man-made changes of channels of the Okavango Delta. *Botswana Notes and Records.* 5, 132-153.