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Does predation or competition shape the home range and resources selection by sable antelope (*Hippotragus niger*) in the Gorongosa National Park, Mozambique?

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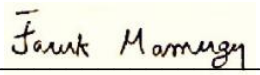
Supervisor: Prof. Jason Marshal

Co-Supervisors: Prof. Francesca Parrini & Prof. Valério Macandza

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

DECLARATION

I declare that this dissertation is my own, unaided, original work. It is being submitted for the Master of Science degree at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or any other examination at any other university.



(Signature if candidate)

16 Day of August 2016

ABSTRACT

Resource selection by herbivores is driven by processes operating across a multitude of spatial scales and is influenced by a variety of biotic and abiotic environmental conditions and resources across the landscape. Spatial scales levels are crucial in habitat selection studies because they affect the interpretation of results and what may appear important at one level may not be relevant at another. Decisions made by animals at these levels can influence animal movements and hence the spatial distribution of populations. 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. Within home ranges, habitat use is mostly influenced by variation of food resources and water availability together with competition and predation risk. The study aimed to determine sable home range extent and habitat use and to test how predation, competition and other environmental factors influenced the selection of areas within these home ranges, in the thriving sable population of the Gorongosa National Park (GNP), Mozambique. Two adult females, one per herd, were fitted with GPS collar providing 5 hours interval GPS coordinates over a year, which were used to determine the annual and seasonal home ranges extents. Home ranges were then overlaid with vegetation map to analyse habitat use. Contrary to expectation, sable home ranges in this study were larger than those found in previous studies. The herds did not limit their habitat use to woodlands, using also open grasslands, drainage lines and bottomlands that retained green grasses during the dry season. Both herds expanded their ranges during the dry season, searching for those areas that still retained green grasses and searching for remaining water sources. For the resources selection within home ranges, I used the same GPS collar coordinates to fit seasonal logistic regression models with biotic factors (predation risk and competition) and with environmental variables (distance from water, distance from roads, elevation, slope, NDVI, vegetation types and landscape). Results show that sable were less prevalent in areas with high predation risk, but herds differed in prevalence with competitors, one herd favouring areas with high reedbuck concentrations and the other favouring low concentrations. Effects of environmental variables were different between seasons and between herds, being distance from water, distance from roads, greenness and elevation the most influential environmental. Both herds, however, avoided low elevation areas during the wet season, probably in order to avoid areas flooded during this period. As conclusion, predation risk

and competition influenced selection within home ranges by sable in the GNP, despite low densities of potential competitors and lions. Nevertheless, this influence seems to not be enough yet to limit the success of the population. The herds also showed evidences of being affected by dry season, as demonstrated by the home ranges expansions during this period. With increase of herbivores population other that sable, and consequently increase competition and decrease of availability of resources, this could lead to reduction of growths percentages of the sable population in the park in the future.

In memory of mother

Isabel Maria Pires Semedo Mamugy

1960 – 2014

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CHAPTER 1

GENERAL INTRODUCTION

THE NEED OF THE STUDY

Decreasing abundance and lack of recovery of large herbivore species has been a cause for concern across a number of conservation areas in Africa (Gasaway *et al*., 1996; Ottichilo *et al*., 2000; Owen-Smith & Mills, 2006). In order to make effective decisions on how to counteract effects of population decline, establishing and understanding causal influences on population dynamics is essential (Owen-Smith & Mills, 2006). Effective conservation and management of endangered wildlife species is dependent on knowledge of the species range of occurrence and understanding the factors influencing their distribution as well as those causing endangerment. Knowledge of species distribution and important habitat resources, coupled with spatial representation of this information, can be used to implement population decline mitigation measures, establish protection sanctuaries or ecological reserves, initiate reintroductions in known ranges, and in planning further research (Johnson *et al*., 2004; Rushton *et al*., 2004).

Among the species exhibiting long-term declines in abundance are sable antelope (*Hippotragus niger*). In the southern African sub-region sable antelope formerly had a wide distribution, but have progressively been eliminated from different parts of their range, being restricted now to conservation areas covering a small portion of their former range (Skinner & Chimimba, 2005). Even in conservation areas, numbers continue to decrease. In the Kruger National Park, South Africa, numbers decreased from 2240 in 1986 (Harrington *et al*., 1999; Grant & van der Walt, 2000) to about 300 animals in 2006 (Whyte, 2006) and in Malilangwe Wildlife Reserve, Zimbabwe, number have decreased from 197 in 1994 to only 62 by 2005 (Goodman, 2009). Reasons suggested to explain the decline include increase predation by lions, coupled with shifts in prey selection (Harrington *et al.,* 1999; Owen-Smith & Mills, 2006), rainfall variation and increased temperature, limiting the availability of forage resources (Harrington *et al.*, 1999; Ogutu & Owen-Smith, 2003; Owen-Smith and Mills, 2006), competition with other grazers (Harrington *et al.*, 1999; Owen-Smith *et al*., 2011) and habitat

loss (Grant & van der Walt, 2000), but it is still unclear what is the main reasons of this decline. However, the sable population of the Gorongosa National Park (GNP), Mozambique, shows fast population growth in the last 14 year. Numbers have increased from less than 100 in 2000 to more than 750 in 2014 (Stalmans *et al.*, 2014), surpassing the maximum historic population size attained before the civil war, estimated at 700 individuals (Tinley, 1977).

The Gorongosa National Park is an area where all the large grazing herbivores were nearly extirpated as a result of the civil conflict two decades ago (Anderson *et al*., 2006). Historic studies of wildlife in GNP prior to the mass reduction of herbivores showed that park resources were capable of sustaining highly diverse and abundant herbivore species (Tinley, 1977). Prior to the civil war that started in 1976, the GNP was home to 42 species of mammals including 200 lions (*Panthera leo*), 2,200 elephants (*Loxodonta africana*), 14,000 buffalo (*Syncerus caffer*), 5,500 wildebeest (*Connochaetes taurinus*), 3,000 zebra (*Equus burchellii*), 3,500 waterbucks (*Kobus ellipsiprymnus*), 3,000 hippos (*Hippopotamus amphibius*), about 500 eland (*Taurotragus oryx*), 700 sable (*Hippotragus niger*) and 800 Lichtenstein's hartebeest (*Alcelaphus lichtensteinii*) (Tinley, 1977). By the end of Mozambique's civil war in 1992, some populations of herbivores had been reduced by 90-95% and others had been wiped out completely (Anderson *et al*., 2006). Since 2004, wildlife populations are recovering rapidly in the park and some species have already recovered the maximum historic populations sizes attained before war (Stalmans *et al*., 2014), mainly due to law enforcement and protection of the park from illegal hunting, combined with reintroductions of large grazer species. However, numbers of potential competitors with sable (zebras, wildebeest, buffalo and impala) are still low, despite the very fast increasing rate in the numbers of waterbuck and reedbuck (Stalmans *et al*., 2014). The lion population is also still small, estimated at 50 to 70 individuals.

The knowledge of species home range, habitat use and factors determining resources selection in an environment where the population is thriving can be important for comparison with the results found in places where the specie is not thriving, and thus, help understand the mechanisms that explain the decline of the species. In addition, the GNP has very few studies on wildlife populations, and only recently studies are starting to be undertaken. So, do competition and/or predation still playing an important role on habitat selection by sable within home ranges,

despite low numbers? Are low numbers of predators and competitors the reason why the population has recovered the park? Hence my study is a baseline for the area relating aspects of habitat use and resources selection of sable. The aim of my study is to determine sable home range extent and habitat use and test the influence of predation, competition and other environmental factors in the selection of areas within these home ranges. The specific objectives of the project were to: 1) analyse sable home ranges extent and compare with previous studies; 2) establish patterns of sable habitat use; 3) investigate effects of predation risk and potential competition in sable selection of areas within home ranges and 4) establish environmental factors influencing selection of areas within sable home ranges.

LITERATURE REVIEW

Spatial scales and resource selection hierarchies

Distribution of large herbivores across the landscape is influenced by aspects of animal behaviour, but many other factors have been demonstrated also influencing resource selection by ungulates including food availability (Senft *et al*., 1987; Bailey *et al.*, 1996), water availability (Redfern *et al*., 2003), interspecific competition (Sinclair, 1985; Chirima, 2009), predation risk (Sinclair, 1985; Valeix *et al.*, 2009a), among others. Moreover, resource selection by animals can occur at different hierarchical levels (Senft *et al*., 1987), ultimately determining where an animal lives. Johnson (1980) described resource selection as a hierarchical process in which resource selection could occur, from a geographic range (1st order of selection), home range or landscape selection (2nd order), to usage of various components within home ranges (3rd order of selection) (e.g. feeding sites), to procurement of items (e.g. food) from those available at a site (4th order of selection). Hierarchical levels are crucial in habitat selection studies because the affect the interpretation of results (Johnson, 1980) and what may appear important at one level may not be relevant at another (Johnson, 1980; Boyce, 2006). 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). Decisions made by animals at these levels influence animal movements and hence the spatial distribution of populations (Turchin, 1991). 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. Furthermore, Senft *et al*. (1987) and Bailey *et al*. (1996) argued that, in order to select, herbivores must perceive differences among or within these levels so that they can discriminate and select among alternatives.

Home range extent

Understanding why home range size varies between and within species remains a fundamental issue in ecological research (McLoughlin & Ferguson, 2000; Borger *et al*., 2008). Home range is defined as the area normally traversed by an animal over a period and within which it meets its needs for food, shelter, security and reproduction (Burt, 1943). Between species, home range size varies depending on the body size and the metabolic requirements of the animal (Harestad & Bunnell, 1979; Lindstedt *et al*., 1986; Owen-Smith, 1988), herbivore aggregation patterns (Owen-Smith, 1988) and food production in the habitat (Harestad & Bunnell, 1979; Lindstedt *et al*., 1986). Among populations of same species, habitat productivity is the main factor determining differences in home range size (McLoughlin & Ferguson, 2000). Other factors such as such as sex (Mikesic & Drickamer, 1992), food availability, patchiness in the environment and predation (McLoughlin & Ferguson, 2000) have been demonstrated influencing home range size and patterns of its utilization by individuals within a population.

Home range size should increases with increasing body mass because larger animals require higher food quantity than smaller animals (Owen-Smith, 1988) and tend to be generalist feeders (Bell 1970). Difference in nutritional requirements and social structure deriving from different body size are generally considered as sufficient explanation of interspecific variation in home range extent (Du Toit & Owen Smith, 1989; van Beest *et al*., 2011). For example, in African savannah ecosystems, relatively smaller and solitary antelopes constantly occupy smaller home ranges throughout the year than larger and gregarious species (Jarman, 1974; Du Toit & Owen Smith, 1989). The larger home ranges in herding herbivores can be viewed as a cost of sharing a home range with companions.

Forage quality and availability (food productivity) and distribution of surface water can also determine the size of home ranges. If resources are concentrated in relative small areas, and

available at acceptable quality levels throughout the year, the home range will be smaller in extend (Owen-Smith *et al*., 2010). Seasonal change in the quality and quantity of resources may 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 (*Ceratotherium simum*) and African buffalo (*Syncerus caffer*) respectively, all had larger home ranges in dry season (when food was scarce) than in the wet season (when food was more abundant). Differentiated seasonal home ranges, and eventually migratory movements between spatially distinguished ranges, are observed when resources are cyclically found at certain, predictable locations, as in the case of migratory species such as wildebeest (*Connochaetes taurinus*) and Thomson's gazelle (*Gazzella thomsonnii*) of Serengeti ecosystem (Fryxell *et al*., 2004; Boone *et al*., 2006).

Many methods for estimating home ranges have been developed (e.g., minimum convex polygons; kernels density estimator and local convex hull) (Kernohan *et al*., 2001; Getz & Wilmers, 2004). The minimum convex polygon (MCP) is the oldest and was the most common method and connects the outer points to define the overall area of use (Kernohan *et al.,* 2001). This method can produce exaggerated estimates if a few points are well beyond the usual centres of activity. Because it was the most used method in the past, 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). A UD assesses the probability of an animal or group of animals occurring at any point (van Winkle, 1975; Worton, 1989; Kernohan *et al.,* 2001). Kernel methods estimate different intensities of space use by creating isopleths containing a certain probability of animal occurrence based on the distribution of density of animal observations. Density of animal observations is suggestive of the frequency of use of an area (Worton, 1989; Seaman & Powell, 1996). The local convex hull (LoCoH) is a relatively new method proposed by Getz & Wilmers (2004) that produces bounded home ranges and has been shown to have superior convergence properties compared to kernel methods used in constructing home ranges and UDs (Getz *et al*., 2007). The method tends to not include areas where a species was not recorded and are more adept comparing to previous methods at locating geographical features such as reserve boundaries, rivers, lakes, inhospitable terrain, and so on (Getz *et al.*, 2007). Essentially, the LoCoH show outside boundaries of location records and construct isopleths that join areas which

exhibit same probability of use by an individual animal or herd, constructing local hulls from a user-specified number of nearest points to each location in a data set (Getz & Wilmers, 2004).

For sable, a wide range of annual home range sizes have been documented in different areas, using minimum convex polygons (Wilson & Hirst, 1977; Grobler, 1981; Parrini, 2006; Magome *et al.*, 2008). Sizes varied between 2.4 km^2 (Rhodes Matopos National Park, Zimbabwe; Grobler, 1981) to 196 km^2 (KNP; Henley, 2005). Seasonally, sable have been reported expanding their home ranges in the dry season comparing (Henley, 2005; Parrini, 2006; Rahimi & Owen-Smith, 2007; Owen-Smith & Cain, 2007) in order to take advantage of green grass growth, following burns or drainage sump grasslands that retained greenness, and in searching of remaining water sources.

Habitat use within home ranges

Within home ranges, habitat use by large herbivores is partly influenced by the spatial and temporal variation in the quantity and quality of forage and by water availability (Owen-Smith, 1988). However, apart from differences in food preference among grazers and differences in the availability of preferred food among habitats, differences in predation risk among habitats as well as differences in anti-predator behaviour (Jarman, 1974; Sinclair & Arcese, 1995) and social system (Duncan, 1983) might contribute in explaining differential habitat use among ungulate species. Therefore, a suitable home range must contain a mixture of habitats that provide opportunities for all activities essential for reproduction and survival (Mysterud & Ims, 1998). 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).

In African savannas, vegetation varies in woody cover from open areas with very few trees to dense, almost closed woodlands. This variation affects the distribution of food resources for herbivores, as areas with high tree density may have less grass because the trees occupy a larger percentage of the habitat (Riginos & Grace, 2008). However, high tree density can have 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 also result in alterations of grass species composition and forage abundance (Angassa & Baars, 2000). Studies also suggested that prey species select habitats partly on the basis of structural features that modulate risk and that prey respond to coursing and stalking predators in different ways (Creel *et al*., 2005; Valeix *et al*., 2009a). 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).

Sable antelope seem to prefer a mosaic arrangement of open woodlands and grasslands (Wilson & Hirst, 1977; Magome, 1991; Estes, 1991; Skinner & Chimimba, 2005). Wilson and Hirst (1977) reported sable using habitat with woody canopy cover ranging from 15% in the Percy Fyfe Nature Reserve (South Africa) to 25% in the Matetsi area (Zimbabwe). The species have been reported ranging in vleis and grasslands with no canopy cover (Parrini 2006; Hensman *et al*., 2013). During the dry season, sable increase use of vleis, grasslands, drainage lines and valley bottoms (Grober, 1981; Magome, 1991; Parrini, 2006), where grass greenness is retained.

Competition

Food is a fundamental requirement for all living organisms. It is not surprising that herbivores choose habitats in areas with abundant food resources that can meet their body maintenance requirements (Senft *et al.*, 1987). Competition is when the resource use by one species reduces the availability or quality of resources to be used by another species (Tilman, 1982). Within the herbivore grazing guild, the mechanism of competition is mainly exploitative through the depletion of grass resources during limiting seasons (Owen Smith, 2002). Harrison *et al.* (1995) suggested that a superior competitor may relegate inferior competitors to establish residency in areas where the former species is less abundant. Competition and the effect of

herbivores on the quality and quantity of resources are recognized to be related to body size. Smaller herbivores are expected to be superior competitors to larger herbivores on high quality but sparse resources (Owen Smith, 2002; Murray & Baird, 2008), as they may have the ability to maintain grasslands at very short grass heights, making them less beneficial to large bulk grazers (Illius & Gordon, 1987), but should be out-competed by larger herbivores when food is abundant but of poor quality (Owen Smith, 2002). Larger herbivores can utilize lower quality resources and have a greater diet breadth than smaller species (du Toit & Owen Smith, 1989). Du Toit & Owen-Smith (1989) found that, by feeding in habitats less suitable for smaller species, larger species were more evenly spread throughout the environment, whereas, smaller selective feeders, decreased their diet breadth and used less available habitats. Sinclair (1985) in the Serengeti-Mara ecosystem found that, abundances and movements of ungulates were determined by concentration of potential competitors. Evidences of competition with sable antelope had been recorded by Macandza *et al*. (2012) in Kruger National Park (KNP), where grazers such as African buffalo and plains zebra restricted distribution and densities of sable by contributing to depletion of common resources.

Sinclair (1985) also noted how ungulates in the Serengeti-Mara system were not only influenced by direct competition for resources but also by the concentration of principal prey for predators. Apparent competition, whereby some prey species support the build-up of predator numbers resulting in an increased predation pressure on other prey species (Holt, 1977), might also influence resource use and spatial separation between the prey species sharing the predator. In KNP, Owen-Smith & Mills (2008) documented that a shift from principal to alternative prey species by lions was the prime cause of decline of some ungulate populations, including sable. The abundance of zebra and wildebeest influenced lion abundance, thereby limiting sable distribution by apparent competition (Owen-Smith *et al*., 2011; Chirima *et al*., 2012).

Predation

Predators may influence prey populations not only through direct lethal effects, but also indirectly through indirect behavioural changes. Indirect effects of predation are expected to have an impact on the fitness of prey individuals, and hence on prey demography (Valeix *et al*.,

2009a). Behavioural responses to predation include: (i) avoidance by herbivores of areas characterized by high risk of predation (Sinclair & Arcese, 1995; Valeix *et al*., 2009a), leading herbivores, in some cases, to use marginal sites/patches where food quantity and quality is low; (ii) selection of specific habitat structure, because habitat structure affects visibility and hence capacity to detect a predator, ease of escape from a predator, and camouflage and ambush opportunities for predators (Creel *et al*., 2005; Kie, 1999); (iii) temporal and spatial changes in activity patterns, avoiding high risk periods coinciding with predator hunting (Valeix *et al*., 2009b); (iv) increased vigilance and reduced foraging time in high predation risk areas (Childress & lung, 2003; Creel *et al*., 2014); (v) altering group size, with species aggregating into larger groups when predators are present (Childress & Lung, 2003; Valeix *et al*., 2009b; Creel *et al*., 2014).

Chirima (2009) suggested that sable herds in KNP were more prevalent in areas where predation risks appeared lower than elsewhere. Thaker *et al*. (2011) found that all ungulates species in Karongwe Game Reserve, South Africa, avoided high predation risk areas and most selected safer habitats, thus reducing their probability of being killed. Sinclair (1977) reported that wildebeest herds avoided places surrounded by thick vegetation, which might conceal predators when approaching a river. Ungulates can reduce risk of predation by aggregating in open areas with increased visibility, and group sizes generally increase when predators are present (Kie, 1999). Creel *et al*. (2014) found that zebra (*Equus burchellii*) and impala (*Aepyceros melampus*) both aggregated into larger groups when predators were present in order to increase vigilance. It is not easy for a predator to approach a bigger group of ungulates without being detected (Sinclair, 1977). Studies on carnivores in KNP (Mills & Funston, 2003) confirmed that lions were less successful in open areas and with larger groups of herbivores.

Interactions between predation, resources, and habitat use may arise, with resource deficiencies causing animals to move into more risky areas, and predation risk causing them to crowd into depleted areas (Lingle, 2002). Herbivores with similar food, environmental and resource requirements may end up selecting different habitats because they differ in their susceptibilities to predation (Lingle, 2002).

Study species

The sable antelope found in southern Africa, *Hippotragus niger niger* (Harris, 1938) is one of four subspecies of *H. niger*. The others *H. n. variani*, *H. n. kirkii* and *H. n. roosevelti* are found in Angola, Zambia and East Africa respectively (Estes, 1991; Skinner & Chimimba, 2005). 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 and has the largest distribution range. They occur in Zimbabwe, Botswana, South Africa, Zambia, Mozambique and Malawi (Skinner & Chimimba, 2005).

Sable antelope are gregarious, medium-sized grazers with an average body mass of 227 kg (Estes, 1997), and typically occurring in herds of 20-25 individuals composed mostly by females, calves, sub-adults (Wilson & Hirst, 1977; Skinner & Chimimba, 2005), although herds up to 75 are not uncommon (Estes, 1991; Estes 1997), one having been spotted in GNP with approximately 80 individuals (Stalmans *et al*., 2014). Sable herds display a strong social order and within each breeding herd there is a dominant female who leads the herd to feed or to water (Wilson & Hirst, 1977; Skinner & Chimimba, 2005). Males are territorial and defend their territories from other males. Territorial males will also repel young bulls from the breeding herd when they reach about 24 months of age (Skinner & Chimimba, 2005; Bothma & van Rooyen, 2005). These young bulls then move off to form small bachelor herds until they are old enough to establish their own territory (Grobler, 1974).

Sable antelope can be described as an ecotonal species, undertaking seasonal movements between woodlands and grasslands and are highly selective in food resources (Estes, 1991). Sable generally prefer medium – tall grass swards, selecting leafy, palatable grasses with the most important species in their diets being *Panicum maximum*, *Heteropogon contortus* and *Themeda triandra* (Parrini, 2006; Magome *et al*., 2008; Macandza, 2009). Many studies suggest that sable antelope have distinct wet season and dry season home ranges, although they may

overlap (Estes, 1974; Wilson & Hirst, 1977; Henley, 2005; Owen-Smith & Cain, 2007; Macandza, 2009). The species has also been described as being highly water dependent, relying on water every day and never moving further than 3 km from a permanent water source (Grobler, 1981; Skinner & Chimimba, 2005). However, recent studies (Rahimi & Owen-Smith, 2007; Cain *et al*., 2012) have reported sable travelling more than 8 km to water sources at 2-4 day intervals in the Kruger National Park during the dry season, showing more water independent behaviour the species.

STUDY AREA

The Gorongosa National Park (GNP), located in central Mozambique, at the southern tip of the African Rift Valley (Fig. 1), is approximately 3970 km^2 and was created in 1960 (previously having been a hunting reserve). The park together comprises four regions, which are from West to East: the Gorongosa Mountain, Midlands (Báruè Platform), Rift Valley and Cheringoma Plateau (Tinley, 1977; Stalmans & Beilfuss, 2008). Within these regions, 15 landscapes and different vegetation types, ranging from lowland floodplain grassland to montane rainforest interspersed with savanna and woodland, have been identified (Stalmans & Beilfuss, 2008).

I conducted this study in the southwest of the park, in an area of approximately 1011 km^2 close to Chitengo camp (main camp of the park) (Fig. 1). In the area selected for the study, 3 landscapes types are present, namely Rift Valley Alluvial Fan Landscape, Rift Valley Riverine & Floodplain Landscape and Rift Valley Lake Urema Landscape, being all part of the Rift Valley region. In the Rift Valley Alluvial Fan the vegetation consists of a complex mix of open to closed woodlands and dry forest/thickets reflecting the structural soil characteristics and moisture regime of the alluvial fans. The Rift Valley Riverine & Floodplain Landscape consists of a mix of mostly open plant communities ranging from pure grasslands to sparse palm veld and open *Acacia xanthophloea* and *Faidherbia albida* woodlands and it is normally subject to prolonged floods. The Rift Valley Lake Urema Landscape consists of Lake Urema, characterized by open water, but along the margins floating mats of the alien water hyacinth *Eichornia crassipes* are common (Stalmans & Beilfuss, 2008). I further divided the vegetation of the study area into 18 classes based on visual interpretation of Landsat imageries from June and August

2015 and from plant communities discriminated by Stalmans & Beilfuss (2008). Reference data (ground truth) for the classification were based on field observations and data from vegetation surveys of the park provided by the park managers. Vegetation classes varied from shrublands, different types of grasslands and woodlands to dense forest (Fig 2, Table 1)

Following Köppen's Climate Classification (Köppen, 1948), Gorongosa is designated as a Wet-Dry Tropical Savanna Climate with a moist, warm season from November to April and a cool, dry period from May to October (Böhme *et al*., 2006). Rainfall is strongly seasonal, with the wet season months (November – April) experiencing the majority of the rainfall (approximately 90% of the rainfall). On average, the ecosystems receive about 800 – 1000 mm of rain annually (Tinley, 1977), with large variation between the four regions of the park. The Rift valley floor experiences the lowest amount of rainfall, ranging from 600-1000 mm/yr (Owen, 2004). The weather station in Chitengo, situated in the Rift Valley, has registered a mean annual precipitation (Oct 1 – Sept 30) for the years 1956-1969 and 1998-2009 of about 850±269 mm (mean ±standard deviation), giving a coefficient of variation of 0.32 (ARAC, 2005; Weather data from Chitengo, 2005-2009). Gorongosa Mountain receives very high annual precipitation (1800-2200 mm per annum) due to orographic rainfalls (Beilfuss *et al*., 2007) and between these two precipitation extremes are the Bárué Midlands and the Cheringoma Plateau with 800–1200 mm and 1000–1400 mm, respectively (Owen, 2004). During the year of data collection, from August 2015 to July 2016, Rift Valley received only 674 mm (Weather data from Chitengo, 2011-2016).

Gorongosa had in the past one of the greatest densities of wildlife in Africa, but as result of sixteen year civil conflict (1976-1992), all the large grazing herbivores were nearly extirpated (Anderson *et al*., 2006), leaving most animal populations decimated by 90-95 per cent (Table 2). By 1994 Mozambique's government stepped in with preliminary restoration efforts but progress was slow until 2004. Since 2004, with the support of the Gregory Carr Foundation in restoring and conserving the park, wildlife populations are recovering rapidly and some species have already recovered the maximum historic populations sizes attained before war (Table 2) (Stalmans *et al*., 2014), mainly due to protecting the park from illegal hunting, combined with reintroductions of large grazer species.

STUDY DESIGN

Two adult sable females were captured on 23 June and 11 July 2015 respectively, using well-established capture techniques by an experienced veterinarian and fitted with GPS Sirtrack collars (ID 112047 and 112048) around the neck (Wits animal ethics number 2013/47/2A). The first herd (ID 112047) had around 21-25 individuals, was found ranging most of the time far North from Chitengo camp and was first seen in ecotones of mopane woodland with grasslands (from now on referred as mopane herd). The second herd (ID 112048) was always close to Chitengo camp, and had around 45 individuals (from now on referred as Chitengo herd). For the capture, *Thiafentenal* with *Azaperone* was delivered by intra-muscular dart, fired from a Dan-inject rifle. Captured animals were blind-folded to reduce stress and temperature and respiration were monitored during animal collar placement to ensure no adverse physiological reactions to the immobilization agents. After collaring process is completed, an antagonist (*Naltrexone*) was administered by hand syringe, and the capture crew retreated to a safe distance. The animals were then monitored until it was clear that the chemical immobilization had been reversed.

Collars were fitted on adult females to ensure that the movements of the individuals bearing the collar represented the movements of the herds because adult females remain within the breeding herds (Estes, 1991; Skinner and Chimimba, 2005). These collars contained a GPS and radiotelemetry tracking device. Collars information was recorded over one year period, from August 2015 to July 2016. The collars were programmed to record GPS coordinates every 5 hours to obtain GPS positions at different times each day. The coordinates were downloaded every week using the sirtrack GPS software v1.6.3 (http://www.sirtrack.co.nz). Using Minimum Convex Polygons (MCP) and adaptive Local Convex Hulls (*a*-LoCoH) at the 95% and 50% isopleths levels, I calculated sable seasonal and annual home ranges, compared them with home ranges extents from other areas studies on sable and looked use of different vegetation types by sable in the park.

In order to analyse influence of predation, competitors and environmental factors in resources selection by sable within home ranges, I collect information about other herbivores and signs of predation in the field, during the months of August until middle November of 2015.

During this time I conducted walking transects and used the transect information to create models for potential competitors (waterbuck and reedbuck) and for predation risk proxy (prey availability biomass and signs of predation). Distance from water, distance from roads, elevation, slope, NDVI, vegetation types and landscapes were used as environmental variables. I then fitted logistic regression models, considering sable collar locations as used resources and random points created within their MCP as available resources and predation risk/competitors and environmental factors as independent variables.

DISSERTATION STRUCTURE

The dissertation is made up of one introduction chapter, two data chapters and one conclusion chapter. The two data chapters are written up in article format, each with a separate introduction, methods, results and discussion section. Study area, study species and collaring operations are described in chapter 1 and not repeated again in the two data chapters to avoid unnecessary repetitions.

In the general introduction I justified the need of the study, presented the aim and objectives and reviewed the relevant literature on factors influencing home ranges and selection by herbivores. The main two chapters were written addressing aspects of the third order of resource selection as defined by Johnson (1980). First, I examined sable home range extent and habitat use (Chapter 2). I calculated sable seasonal and annual home ranges, compared them with extents found in previous studies made in other areas, and discussed probable factors contributing to differences in the home range extents. I also examined sable use of different vegetation types and analyzed variations between different seasons. Next (Chapter 3), I examined influence of predation risk, competitors and environmental factors in resources selection within sable home ranges. The aim was to determine which factors restricted sable within their home ranges. Positions of the herds were obtained from collars and predation risk and competitors probability maps were made using data collected from transects in the field. Logistic regression models were fitted to estimate the probability of presence/absence of sable herds within their home ranges as a function of predation/competitors and environmental factors. At the end (Chapter 4) I synthesised the findings from the two data chapters. I highlighted areas that still need further

research in sable in the park and consideration was also given to what this study has achieved in terms of sable management and conservation.

TABLES

Table 1: Characteristics of the vegetation types found in southwest of Gorongosa National Park

Vegetation Type	**Defining Characteristics (adapted from Stalmans & Beilfuss (2008).**
Dry Forest/Thicket	Very dense formation typified by woody species such as *Cleistochlamys kirkii, Diospyros senesis, Craibia zimmermannii, Alchornea laxiflora, Milletia stuhulmannii, Markhamia acuminata, Capparis sp.* and *Thilachium africanum*. The grass layer is sparse occurring when present *Brachiaria deflexa, Digitaria sp.* and *Oplismenus sp.*
Gallery Forest	Woody formation found on humid soils close to permanent drainage lines.
Miombo Woodlands	Open to close woodland dominated by species such as *Brachistegia boehmii, Julbernardia globiflora, Acacia nigrescens, Diplorhynchus condylocarpon, Sterculia quinqueloba, Strychnos potatorum* and *Pterocarpus rotundifolius*. Grass layer varies from short to tall, dominated by *Panicum maximum, Digitaria eriantha, Themeda triandra* and *Sporobolus sp.*
Inselberg Miombo	Closed miombo woodland with a more open canopy on rock outcrops. This formation occurring on small inselbergs that occur in the park.
Mixed Forest (Riverine)	Open to closed woody formation occurring close to Pungue river and Pungue drainage lines. Species such as *Hyphaene petersiana, Borassus aethiopium, Piliostigma thonningii, Philenoptera violacea, Combretum adenogonium, Acacia sieberana* dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata, Panicum maximum, Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Acacia xanthophloea Woodland	Open to close woodland dominated by *Acacia xanthophloea*. This formation is seasonally inundated. Grass layer is usually tall dominated by *Panicum maximum, Setaria incrassata* and *Cynodon dactylon*
Acacia-Combretum Woodland	This is the most extensive community. Characterised by open to close woodlands dominated by *Combretum adenogonium, C. imberbe, Acacia nigrescens, A. robusta* and also occurring frequently *Sclerocarya birrea,*

	Dalbergia melanoxylon, Philenoptera violacea e *Ziziphus mucronata*. Grassland layer varies from short to tall dominated by *Panicum maximum, Digitaria eriantha, Heteropogon contortus, Urochloa mossambicensis* and *Themeda triandra*. Often with termite mounds.
Colospermum mopane Woodland	Short closed woodland dominated by Mopane (*Colophospermum mopane*). Grass cover is sparse dominated by *Enteropogon macrostachyus* with *Digitaria eriantha* and *Chloris sp.* on the edges.
Faidherbia albida Woodland	Open to close woodland dominated by *Faidherbia albida*, found close to Urema Lake and subjected to temporary inundations. Grass layer ranges from short to tall, dominated by *Cynodon dactylon, Digitaria swazilandensis* and *Echinochloa pyramidalis*.
Dichrostachys cinerea Shrubland	Closed shrubland dominated by *Dichrostachys cinerea*, found mostly at edge of mopane and other woodlands. Grass cover is sparse, occurring when present *Panicum maximum* and *Brachiaria deflexa*
Dalbergia melanoxylon Shrubland	Closed shrubland dominated by *Dalbergia melanoxylon*, found mostly at edge of other taller woodlands. Grass layer is usually short and open, dominated by *Panicum maximum, Heteropogon contortus, Aristida sp.* and *sporobolus sp.*
Palm Veld	Open to closed woody formation subjected to temporary inundation. Species such as *Hyphaene petersiana, Borassus aethiopium* and *Phoenix reclinata* dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata, Panicum maximum, Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Short Grassland	Short closed grassland formation dominated by *Cynodon dactylon* and *Digitaria swazilandensis*. This formation is being invaded by alien specie *Mimosa pigra,* and during wet seasons is subjected to floods
Saline Grasslands	Short open grassland formation dominated by *Sporobolus iocladus*. This formation usually occurs associated with Acacia.
Pan Grasslands	Short closed grassland formation that occurs along pans dominated by *Paspalidium obtusifolium, Echinochloa sp., Oryza longistaminata* and *Hemarthiria altissima*.

Shrub Grassland	Medium to tall grassland with patches of *Dichrostachys cinerea* shrubs. Grass species such as *Panicum maximum, Setaria incrassata*, *Vetiveria nigritana* and *Brachiaria deflexa*
Medium-Tall Grassland	Medium to tall grassland dominated by *Panicum maximum, Panicum coloratum, Setaria incrassata, Vetiveria nigritana* and *Brachiaria deflexa*
Tall Grassland	Tall grassland, normally adjacent to permanent water and seasonally inundated. Dominated *Echinochloa pyramidalis* and *Vetiveria nigritana*.
Shifting Cultivation	Seasonal cultivation by the communities. Found mainly south of Pungue river.
Water	Open water, typified by Urema lake, Pungue river and other permanent water streams.

Table 2: Estimated wildlife populations size in Gorongoza National Park over time. The 1972 estimates represent the number of animals before the civil war. By 1994, the number of animals were at an all-time low but started to increase by 2000, as animals were reintroduced to the park. Source: Stalmans et al. (2014)

Species	1972 estimate (Tinley, 1977)	2000 estimate	Loss 1972 – 2000	2014 Numbers	Current recovery as % of historical levels
Buffalo	14000	<100	>99%	>650	<5%
Elephant	2500	<200	>92%	>500	>20%
Hippp	3500	<100	>97%	>430	>15%
Waterbuck	3500	<300	>91%	>34000	>100%
Reedbuck	–	<200	–	>12000	–
Zebra	3500	<20	>99%	<40	<2%
Blue wildebeest	6500	<20	>99%	>350	<7%
Sable antelope	700	<100	>86%	>750	>100%
Hartebeest	800	<100	>88%	>600	>75%
Lion	200	–	–	>50	>25%

Note 1: Historical surveys were made using Fixed wing aeroplanes with recent surveys were made using helicopters. Therefore some historical numbers were likely much greater as the fixed wing counts would tend to underestimate the true numbers. Even sable antelope numbers may have been underestimated as they often occur in closed woodlands.

Note 2: Little reliable historical information is available on some species, especially browsers.

FIGURES

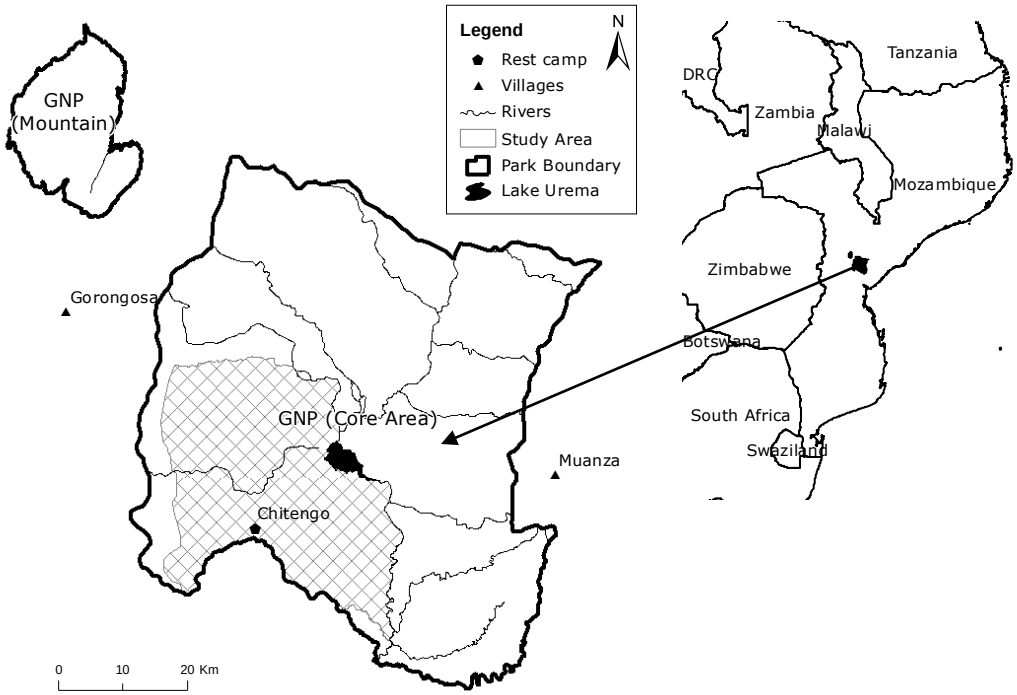


Figure 1: Gorongosa National Park, Mozambique and location of study area in Gorongosa National Park.

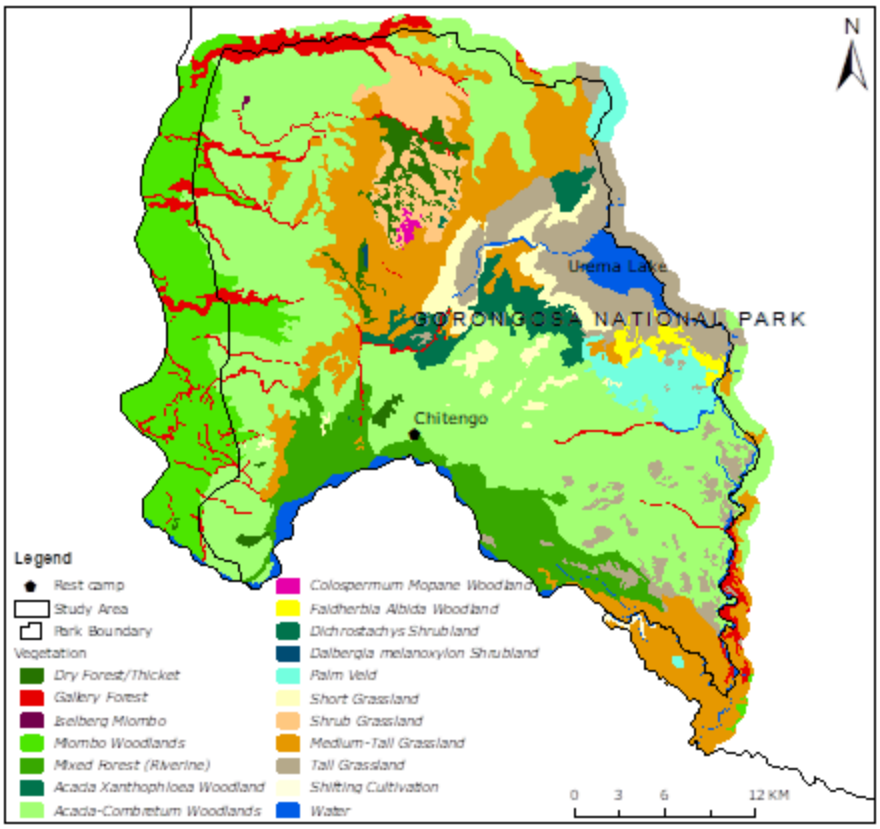


Figure 2: Vegetation Map of the study area in Gorongosa National Park.

REFERENCES

Anderson, J. L., Beilfuss, R. D., Pereira, C. L., & Zolho, R. (2006). *Proposed strategy to reintroduce and supplement wildlife populations in Gorongosa National Park, Mozambique*. Technical report submitted to Gorongosa National Park, Mozambique.

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.

ARAC (2005). *Spreadsheets with precipitation and evaporation data of Chitengo*. Administração Regional de Águas Centro. Beira, Mozambique.

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

Beilfuss, R., Steinbruch, F. & Owen, R. (2007). *Long-term plan for hydrological research: adaptive management of water resources at Gorongosa National Park.* Internal report, Gorongosa National Park. 26pp.

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

Böhme, B., Steinbruch, F., Gloaguen, R., Heilmeier, H. & Merkel, B. (2006). Geomorphology, hydrology and ecology of Lake Urema, central Mozambique, with focus on lake extent changes. *Physics and Chemistry of the Earth* **31**: 745-752.

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.

Bothma, J. d. P. & van Rooyen, N. (2005). *Intensive wildlife production in southern Africa*. Van Schaik Publishers. Pretoria, South Africa.

Boyce, M. S. (2006). Scale for resource selection functions. *Diversity and Distributions* **12**: 269-276.

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

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 Wiwatersrand, Johannesburg, South Africa.

Chirima, G. J., Owen-Smith, N., Erasmus, B. F. N. & Parrini, F. (2012). Distributional niche of relatively rare sable antelope in a South African savanna: habitat versus biotic relationships. *Ecography* **35**: 68-79.

Childress, M. J. & Lung, M. A. (2003): Predation risk, gender and the group size effect: Does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour* **66**: 389-398.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**: 3387-3397

Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size,vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology* **25 (4)**: 773-784.

Du Toit, J. T. & Owen-Smith, N. (1989). Body size, population metabolism and habitat specialization among large African herbivores. *American Naturalist* **133**: 736-740

Duncan P. (1983). Determinants of the use of habitat by horses in a Mediterranean wetland. *Journal of Animal Ecology* **52**: 93-109

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

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

Fryxell, J. M., Wilmshurst, J. F. & Sinclair, A. R. (2004). Predictive models of movements by Serengeti grazers. *Ecology* **85(9)**: 2429-2435

Gasaway, W. C., Gasaway, T. K. & Berry, H. H. (1996) Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food regulation hypothesis. *Canadian Journal of Zoology* **74(8)**: 1556-1572.

Getz, W. M & Wilmers, C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* **27**: 498-505.

Getz, W. M., Fortmann-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.

Goodman, P.S. (2009). *Large mammal population estimates for Malilangwe Estate: September/October 2008*. Internal Management Report. Malilangwe Trust, Zimbabwe.

Grant, C. C. & van der Walt, J. J. (2000). Toward 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. (1974). *Aspects of the biology, population ecology and behaviour of sable (Hippotragus niger niger) (Harris 1838) in the Rhodes Matopos National Park, Rhodesia*. M.Sc thesis, University of Pretoria, Pretoria, South Africa

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.

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

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. *Biological Conservation* **90:** 69-78.

Harrison, S., Thomas, C. D. & Lewinsohn, T. M. (1995). Testing metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). *The American Naturalist* **145**: 546-562.

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.

Hensman, M. C., Owen-Smith, N., Parrini, F. & Bonyongo, C. M. (2013). Home range occupation and habitat use of sable antelope in the Okavango Delta region of northern Botswana. *African Journal of Ecology* **52**: 237-245

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

Illius, A. W. & Gordon, I. J. (1987). The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**: 989-999

Jarman, P. J. (1974). The social organization of antelope in relation to their ecology. *Behaviour* **48**: 215-266

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

Johnson, C. J., Seip, D. R. & Boyce, M. S. (2004). A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales, *Journal of Applied Ecology* **41:** 238-251.

Kernohan, B. J.; Gitzen, R. A & Millspaugh, J. J. (2001). Analysis of Animal Space Use and Movements. In: *Radio Tracking and Animal Populations* (Eds: Millspaugh, J. J. & Marzluff, J. M.), Academic Press California, pp. 125-166

Kie, G.J. (1999). Optimal foraging and risk of predation: Effects on Behavior and social structure in Ungulates. *Journal of Mammalogy* **80**: 1114-1129.

Köppen, W. (1948). *Climatologia: con un estudio de los climas de la tierra*. Fondo de Cultura Econômica, México. 479p.

Lindstedt, S. L., Miller, B. J. & Buskirk, S. W. (1986). Home range, time, and body size in mammals. *Ecology* **67:** 413-418.

Lingle, S. (2002). Coyote predation and Habitat segregation of white-tailed deer and mule deer. *Ecology* **83**: 2073-2048.

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. & Cain, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* **121:** 891-898

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., & 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.

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

Mikesic D. G. & Drickamer L. C. (1992). Factors affecting home-range size in house mice (Mus musculus domesticus) living in outdoor enclosures. *American Midland Naturalist* **127**: 31-40.

Mills, M.G.L. & Funston, P.J. (2003). Large carnivores and savanna heterogeneity, In: *The Kruger experience- ecology and management of Heterogeneity*. (Eds: du Toit, J.T., Rogers, K.H., & Biggs, H.C). Island Press. Washington DC. pp 371-388:

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

Murray, M. G. & Baird, D. R. (2008). Resource-ratio theory applied to large herbivores. *Ecology* **89**: 1445-1456

Ogutu, J. & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters.* **6**: 412-419.

Ottichilo, W. K., de Leeuw J. & Skidmore A. K. (2000) Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *African Journal of Ecology* **38**: 202–216

Owen, R. (2004). *The Millennium Ecosystem Assessment (MA): GM SAFMA Hydrogeology condition and trend report*. Mineral Resources Centre, University of Zimbabwe.

Owen-Smith, N. (1988). *Megaherbivores – The influence of a very large body size onecology*. Cambridge University Press. Cambridge

Owen-Smith, N. (2002). *Adaptive Herbivore Ecology – from resources to populations in variable environments*. Cambridge University Press. Cambridge

Owen-Smith, N. & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* **76:** 73-92.

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. & Mills, M. G. L. (2008). Predator–prey size relationships in African large-mammal food web. *Journal of Animal Ecology* **77**: 173-183.

Owen-Smith, N., Fryxell, J. M. & Merrill, E. H. (2010). Foraging theory upscaled: the behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society B: Biological Sciences* **36(1550)**: 2267-2278.

Owen-Smith, N., Chirima, G. J., Macandza, V. & Le Roux, E. (2011). Shrinking sable antelope numbers in Kruger National Park: what is suppressing population recovery? *Animal Conservation* **15**: 195-204.

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.

Rahimi, 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**: 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.

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.

Rushton, S. P., Ormerod, S. J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology* **41 (2)**: 193-200.

Seaman, D. E. & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**: 2075-2085.

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

Sinclair, A. R. E. (1977). *The African Buffalo*. University Press, Chicago.

Sinclair, A. R. E. (1985) Does interspecific competition or predation shape the African ungulate community. *Journal of Animal Ecology* **54(3)**: 899-918.

Sinclair, A. R. E. & Arcese, P. (1995). Population consequences to predation – sensitive foraging: the Serengeti wildebeest. *Ecology* **76**: 882-891

Skinner, J. D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*, 3rd ed. Cambridge University Press, Cape Town.

Stalmans, M. & Beilfuss, R. (2008). *Landscapes of the Gorongosa National Park*. Unpublished report to the Gorongosa Restoration Project. 103p.

Stalmans, M., Peel, M. & Massad, T. (2014). *Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion*. Unpublished report to the Gorongosa Restoration Project.

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.

Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B., Niemann, S. M. & Slotow, B. (2011). Minimizing predation risk in a landscape of multiple predators: Effects on the spatial distribution of African ungulates. *Ecology* **92**: 398-407.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.

Tinley. K.L. (1977). *Framework of the Gorongosa Ecosystem*. PhD thesis. University of Pretoria.

Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**: 1253-1266

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

Valeix, M., Loveridge, A. J., Chamaille´-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D. W. (2009a). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**: 23-30.

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. (2009b). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology* **63**:1483-1494.

Van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M. & 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 Winkle, W. (1975). Comparison of several probabilistic home-range models. *Journal of Wildlife Management* **39**: 118-123

Weather data from Chitengo 2005-2009. University of Edinburgh and Envirotrade. Available at http://www.geos.ed.ac.uk/homes/cryan.

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**: 1-111.

Worton, J.B. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164-168.

CHAPTER 2

HOME RANGE EXTENT AND HABITAT USE BY SABLE ANTELOPE IN GORONGOSA NATIONAL PARK

ABSTRACT

Understand how species establish home ranges and habitat use is fundamental to conservations and management decisions. In Gorongosa National Park (GNP), Mozambique, wildlife populations are recovering rapidly since 2004, including sable antelope (*Hippotragus niger*), however studies on their ranging behaviour remain lacking. I analysed home range extents and where home ranges were established by two herds of sable antelope in the southwest of the park. GPS collars were fitted in two adult females within different herds (Mopane and Chitengo herds respectively), recording coordinates every 5 hours over a year. The annual and seasonal extents of the home ranges were determined using Minimum Convex Polygons (MCP) and adaptive Local Convex Hulls (*a*-LoCoH) at the 95% and 50% isopleths levels. I overlaid the home ranges with a vegetation map that I created for the study area and determined percentages of vegetation types used by the herds. The home ranges of the two herds in the GNP were larger than those reported in previous studies on sable. Between herds, mopane herd had much larger MCP home range that the Chitengo herd. It seems that water had a larger influence in the size of sable home ranges in the park. The mopane herd established home ranges further from permanent water sources, needing to make regular movements to water sources during the dry season, while Chitengo herd was always close to water sources throughout the year. Both herds expanded their home ranges during the late dry season, but had a different habitat use over the year. The mopane herd used grassland areas during the dry season and moved to woodlands in the wet season, while the Chitengo herd used woodlands during most of the year and increased use of riverine mixed forest in the dry season.

INTRODUCTION

Understanding how animals use different habitat types to meet their requirements for resources (food, water and breeding habitat) and how those animals establish and use their home ranges is important for conservation and management of wildlife species (Morrison *et al*., 1998; Kernohan *et al*., 2001). For species in decline, such as sable antelope (*Hippotragus niger*), understanding their movement patterns and home range is particularly crucial. Sable antelope had in the past a wide distribution in the Southern African sub-region (Skinner & Chimimba, 2005), but have progressively declined in different parts of their range (Harrington *et al.,* 1999; Grant & van der Walt, 2000; Goodman, 2009). However, in Gorongosa National Park (GNP), the sable population is thriving. GNP in Mozambique, is an area that had a very high density of herbivores in the past, but all the large grazing herbivores were nearly extirpated as a result of civil conflict two decades ago (Anderson *et al*., 2006). Since 2004, wildlife populations are recovering rapidly in the park (Stalmans *et al*., 2014). As the sable population in the park is thriving, contrary to many other areas where the specie exists, it is important to understand how sable herds are establishing home ranges and using the habitat during different seasons, especially as species other than sable are also recovering, and that might have effects on sable population.

Home range, by definition, represents a specific area normally covered by an animal in meeting its requirements for food, shelter, security and reproduction (Burt, 1943; Jewell, 1966). Home range size, movement patterns and habitat use are driven by the abundance, availability and distribution of resources, as well as the structure of the landscapes in which they are distributed (Jenkins, 1981; Brandt & Cresswell, 2008). Resources can vary from place to place within home ranges limits, so that use may be concentrated within certain core areas or centers of activity, while other sections are visited occasionally. Resource availability and other conditions also vary seasonally. Seasonal variation is particularly influential for large mammalian herbivores, which depend on vegetation both as a food resource and for defining habitat features such as visibility affecting security against predation (Owen-Smith & Cain, 2007).

Between populations of the same species, habitat productivity determines differences in home range sizes, whereas food availability, patchiness in the environment and predation are the factors influencing home range size and patterns of its utilization by individuals within a population (McLoughlin & Ferguson, 2000). Grazers home range sizes should increase with decrease in food density towards the end of the dry season (Harestad & Bunnell, 1979; Scoones, 1995; Ryan *et al*., 2006; Owen-Smith & Cain, 2007) or if sections of the landscape retain key resources for the population, such as drainage lines retaining green forage (Scoones, 1995; Knoop & Owen-Smith, 2006), foraging animals might concentrate use of space on these smaller areas during the dry season than during periods when food is widely distributed. When water sources starts to dry up, grazers start to move over long distances in searching of remaining water sources and patches of food (Cain *et al*., 2012). Unusually large home range extents for a species may indicate poor habitat resources and conditions requiring the animal to occupy larger home ranges to meet their survival requirements (Reid *et al.*, 2007). Habitat productivity also influences animal densities, as differences in local population densities can be expected to match differences in local habitat characteristics (Maier *et al*., 2005). Thereby, if an animal population is thriving, it would be expected to have smaller range sizes compared to an animal population that is not thriving.

Within home range, habitat and resource use is a complex process involving trade-offs between forage intake and risks such as predation. Thus, a suitable home range must contain a mixture of habitats that can provide required resources for survival, growth and reproduction (Mysterud & Ims, 1998). For large herbivores the structure and species composition of the vegetation form the foundation of an animal's habitats and consequently affects the distribution and habitat use patterns of herbivores (Senft *et al*., 1987; Owen-Smith, 2002). In order to thrive, herbivores depend on the availability of particular vegetation components to offer food resources throughout the year (Owen-Smith, 2002; Henley, 2005). Animals may also select specific structure of the vegetation in order to reduce predation risk, because habitat structure affects visibility and hence capacity to detect a predator, ease of escape from a predator, and camouflage and ambush opportunities for predators (Creel *et al*., 2005). In previous studies, sable have been described as woodlands with about 25% woody vegetation cover (Estes & Estes,1974; Wilson & Hirst, 1977; Magome, 1991; Parrini, 2006), and also using grassland areas during the dry season

(Estes & Estes, 1974; Sekulic, 1981; Parrini, 2006). 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 (Henley, 2005). Therefore, the need for refuge from adverse weather is another determinant of habitat use by the species (Duncan, 1983; Owen-Smith, 1988).

Sable home ranges have been reported varying between 2.4 km^2 (Rhodes Matopos National Park, Zimbabwe; Grobler, 1981) and 196 km^2 (Kruger National Park; Henley, 2005). Sable are not a migratory species but have been reported to make seasonal movements of up to 50 kilometres (Estes, 1997), especially during the dry season. In this study, I will report findings from two collars placed in two females, one per herd, which supplied data on locations over a complete year. Given that no information exists in GNP relating to sable habitat use, my objective was to assess where sable are establishing home ranges and what are the variations of home range sizes during different season. For that I created three prediction: (1) Sable herds will occupy relatively smaller home ranges compared to sable in areas where they are not thriving, such as Kruger National Park; (2) sable will occupy larger home ranges during the dry season than during the wet season and (3) sable will establish home ranges in wooded vegetation types, using open grasslands only during the late dry season.

METHODS

Study site

The study was conducted in the southwest of Gorongosa National Park (GNP), Mozambique, in an area close to the park main camp (Chitengo), covering approximately 1011 km^2 (Fig. 1). In the study area, 3 landscapes types are present (Rift Valley Alluvial Fan Landscape, Rift Valley Riverine & Floodplain Landscape and Rift Valley Lake Urema Landscape; Stalmans & Beilfuss, 2008) and 18 vegetation types, varying from open to closed woodlands and dry forest/thickets to pure grasslands (Fig. 2, Table 1). The area has distinct wet (November– April) and dry (May–October) seasons, with approximately 90% of the rainfall in the wet season months. Mean rainfall of 850 mm (SD: ±269 mm) has been registered by a weather station in Chitengo, calculated as average for the years 1956-1969 and 1998-2009 (ARAC, 2005; Weather data from

Chitengo, 2005-2009). During the study period (August 2015 to July 2016), the area received 674 mm of rainfall.

Sable capture and collaring

Two female sable from two different breeding herds were fitted with GPS Sirtrack collars (ID 112047 and 112048) in June and July 2015 respectively (Wits animal ethics number 2013/47/2A). All handling procedures were conducted by an experienced veterinarian using well-established capture techniques. I will refer to the two groups as "mopane herd" and "Chitengo herd" respectively from now on. Mopane herd had around 21-25 individuals, and used to be found far North from Chitengo camp and on ecotones of mopane woodland or acacia-combretum woodland with grasslands. Chitengo herd had around 45 individual and was found ranging always close to Chitengo camp. Collars contained a GPS and radiotelemetry tracking device to locate the animal, and recorded GPS coordinates at 5 hours interval, with were downloaded weekly, using the sirtrack GPS software v1.6.3 (http://www.sirtrack.co.nz).

Home range extent and habitat use

I carried out the study during a period of one year, from August 2015 to July 2016. I used rainfall data recorded at a weather station situated in Chitengo to define different seasons. I divided the study period into 4 seasons, late dry season (August – 15 November 2015, the day when it started to rain in the park), early wet season (16 November 2015 – 31 January 2016), late wet season (1 February – 30 April 2016), and early dry season (1 May 2016 – 31 July 2016) (Fig. 3).

I calculated home ranges using two methods, Minimum Convex Polygons (MCP – Hayne, 1949; Harris *et al*., 1990) using 100% convention for annual home ranges, in order to compare the results of the present study with previous studies that used MCP 100% (Sekulic, 1981; Magome, 1991; Jooste, 2000; Owen-smith & Cain, 2007), and adaptive-Local Convex Hull (*adaptive*-LoCoH - Getz & Wilmers, 2004; Getz *et al*., 2007) using 50% isopleths as representing the core range areas and 95% representing total home range areas, for both annual and seasonal home ranges.

The Minimum Convex Polygon simply joins the outer herd locations, creating a range extent that can include gaps and occasional excursions beyond the limits of the range normally traversed by the animal, producing large overestimates of range size (Kernohan *et al*., 2001). The MCP simply join the outer herd locations, creating a range extent that can include gaps and occasional excursions beyond the limits of the range normally traversed by the animal, producing large overestimates of range size (Kernohan *et al*., 2001).

Local Convex Hulls is an alternative kernel method proposed by Getz & Wilmers (2004) for estimating utilization distributions based on local nearest neighbour convex hulls. LoCoH was used in previous sable antelope studies (Chirima, 2009; Hensman, 2011) and according to Getz and Wilmers (2004) and Getz *et al*. (2007) is better than the kernel method for constructing home ranges. 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). The adaptive or *a*-LoCoH is particularly good at identifying shifts, disruptions, gaps and sharp boundaries within a home range (Getz & Wilmers, 2004; Getz *et al*., 2007). The main constraint to the accuracy of *a*-LoCoH is that selecting the appropriate *k* (minimum number of points used to construct a polygon) and *a* (distance from the root point) values is somewhat subjective and requires experience with the method (Getz & Wilmers, 2004; Getz *et al*., 2007) or knowledge of where gaps and sharp boundaries occur in the range beforehand. Values that are too small for both parameters, could result in underestimates of the used area, leading to gaps in the distribution where they should not exist, whilst values that are too large often cause the inclusion of real gaps, including areas that are not actually used by the animal (Getz *et al*., 2007).

For the MCP's, I transferred all the sable collar locations to ArcGIS 10.2 and projected to Universe Transverse Mercator (UTM) zone 36S WGS 1984 spheroid. Then, using the Hawth's Analysis Tools extension MCP's were created for both herds. The LoCoH home ranges were made in R 3.3.1 using the t-LoCoH package (Lyons *et al*., 2013, Lyons, 2014). Since timestamps associated with locations, which can be accounted for in t-LoCoH, were not necessary for the

scope of the present study, I simply built utilization distribution (UDs) by setting the time parameter as zero (s=0) (Lyons *et al*., 2013; Lyons, 2014).

In order to assess the vegetation types used by herds, I overlaid the home ranges with the vegetation map of the study area. I divided the vegetation of the study area into 18 classes based on visual interpretation of Landsat imageries from June and August 2015 and from plant communities discriminated by Stalmans & Beilfuss (2008). Reference data (ground truth) for the classification were based on field observations and data from vegetation surveys of the park provided by the park managers. Vegetation classes varied from shrublands, different types of grasslands and woodlands to dense forest (Fig. 2, Table 1). I then calculated the areas of each vegetation type within 50% and 95% isopleths for the annual and seasonal home ranges and the proportion of the home range covered by each vegetation type.

RESULTS

I analysed location data for 2 sable herds. There were in total 2131 locations across both herds, with the mopane herd having 1187 and the Chitengo herd 994 locations.

Home ranges

Sable annual home ranges (MCP) at GNP (181.5 km^2 for mopane herd and 98.7 km^2 for Chitengo herd) were larger than in other areas where sable exists (annual home ranges ranging from 10 to 65 km^2), except between the Chitengo herd and one herd from Kruger National Park that had 118 km^2 of annual home range (Table 2). However, annual LoCoH range areas showed similar values from those found in previous studies (Table 3). Between the two herds, the mopane herd occupied about double of annual MCP home range of the Chitengo herd (Fig. 4, Table 2). The two herds showed small overlap in their annual MCP home range (9% overlap for the mopane herd and 16.6% overlap for the Chitengo herd, Fig. 4). Mopane herd also had larger LoCoH home ranges than Chitengo herd, but with smaller differences compared to differences found in MCPs (Fig. 4, Table 3). Seasonal home ranges showed the same pattern as annual home ranges, with the mopane herd having larger home ranges (differences from 234 ha to 710 ha) and

core areas (differences from 41 ha to 208 ha) than the Chitengo herd, except during the late dry season, when the core area of the Chitengo herd was 91 ha larger than the mopane herd (Fig. 5, Table 4).

Seasonal variations in home ranges showed that both herds expanded their ranges during the late dry season. The mopane herd reduced its home range as the wet season progressed. During the late wet season sable used the smallest home range, which was almost half of the late dry season home range. Core areas were larger in the early wet season and smaller in the late wet season (Fig. 5, Table 4). Smallest home range for Chitengo herd was in the early dry season, same pattern for the core areas. This herd doubled its home range in the late dry season comparing to the other seasons (Fig. 5, Table 4).

The mopane herd in the late dry season used two distinct ranges. Initially was staying in ecotones of mopane woodlands and grasslands, close to Lake Urema and moved to woodlands west of the lake as the late dry season progressed (Fig. 5a). The herd used the same woodlands during the wet seasons, but with smaller range used in the late wet season (Fig. 5b and Fig. 5c). The herd continued to use the same areas in the beginning of early dry season, and stated to move back to ecotones of woodlands and grasslands in the middle of the season, staying there until the end of the season (Fig. 5d). The Chitengo herd, in other hand, showed one large distinct range, in the woodlands east to Chitengo camp, used in the beginning of the season and other small ranges, most of them close to the Pungue River, used as the dry season progressed (Fig. 5a). In the early wet season the herd used the same woodlands east to Chitengo camp in the beginning of the season and mover to woodlands north-west to the camp by middle of the season (Fig. 5b), same area used in the late wet season, but with a southward expansion (Fig. 5c). In the early dry season the herd used areas closer to Pungue River west to Chitengo camp, showing a small overlap with the late wet season range (Fig 5d).

Habitat use

The two herds used different vegetation types. The mopane herd used mostly grassland areas (61% of annual home range), but also woodlands throughout the year (Fig. 6). During late dry

season the herd establish home range and core areas predominantly in medium-tall and shrubby grasslands, moving to established home range and core areas in the *Acacia-Combretum* woodland during the entire wet season. In the early dry season the herd moved back to areas frequently used in the late dry season, establishing home range and core areas predominantly in medium-tall and shrubby grasslands, where water and green grass remain (Fig. 6). Differences in use of grasslands and woodlands were more evident in core areas along different seasons.

The Chitengo herd established home ranges mainly in *Acacia-Combretum* woodlands (67% of annual home range) and riverine mixed forest (29% of annual home range) during most of the year (Fig. 7). During the wet season, the home range was covered by predominantly *Acacia-Combretum* woodlands (97% and 86% for early wet season and late wet season respectively). With the progress of the dry season, the herd increased the use of riverine forests, where water and green grass remain (Fig. 7). Intensively used areas (core areas) however, were made up during all season, by open to dense *Acacia-Combretum* woodlands (Fig. 7). This herd only moved to grasslands at the end of the late dry season, with grasslands contributing only with 4% of the dry season home range (Fig. 7).

DISCUSSION

Sable antelope home ranges in GNP are larger than in other area were sable exists, mainly due large expansions during the late dry season. Home range expansion during the dry season is consistent with a number of previous studies (Wilson & Hirst, 1977; Henley, 2005; Parrini, 2006; Owen-Smith & Cain, 2007; Macandza, 2009). I was expecting both herds to range most of the year in wooded areas. The Chitengo herd confirmed this pattern. The mopane herd however, stayed most of the year in grassland areas. The use of grasslands during large periods of the year, despite not very common in sable, was also report in the past by Estes (1991) and Tinley (1977) in a previous study in GNP.

Home range comparisons with other studies

I expected sable annual MCP's to be smaller than in previous studies in other areas were sable exists but in a declining trend. Sable home ranges in GNP, although the species is thriving in the park, were much larger comparing to MCP's home ranges from previous studies (Table 2). However, annual LoCoH (95%) isopleths areas showed similar values from those found in Okavango Delta by Hensman (2011) (Table 3). Some of the areas where previous studies were conducted such as Pilanesberg National Park, Sandveld National Reserve and Kgaswane Mountain Reserve in South Africa (Magome, 1991; Jooste, 2000; Parrini, 2006) and Shimba Hills Game Reserve in Kenya (Sekulic; 1981), are fenced and much smaller comparing to the Gorongosa area, limiting thus the movements of animals and influencing home range extents. In addition to size of the reserves, an important limitation in Gorongosa is the accessibility to water. Both herds expanded considerably their home ranges during the dry season, having in both cases doubled the area when comparing with late wet season areas, when water was scarce (Table 4). During the late dry season, most of the pans and rivers dried out in the park, and available water remained only in the Urema Lake and Pungue River. Therefore animals needed to walk long distances to find water (collar data and personal observation), contributing thus to their large home ranges. Kruger National Park annual MCP's (Owen-Smith & Cain, 2007) however, have much smaller differences in size when comparing to the MCP's in this study.

The Chitengo herd used nearly half the size of the mopane herd MCP annual home range. This difference can be related with movements to water sources. The Chitengo herd stays all the year within 3 km from water, as it used most of the time woodlands with many small pans and close to Púnguè River. The area used by mopane herd however, has few seasonal water points and permanent water sources were far. Therefore, during the dry season, the mopane herd needed to walk long distances beyond their core area to the Urema Lake in order to find water. Water has been reported influencing sable home range sizes (Cain *et al*., 2012). Previous studies documented that sable depend on regular access to drinking water (Estes, 1997, Skinner & Smithers, 1990; Skinner & Chimimba, 2005). Some literature suggests that sable remain less than 4 km from water (Wilson & Hirst, 1977; Grobler, 1981; Magome, 1991), while some other

studies had reported movements of over 7 km to water at 3-4 day intervals (Rahimi & Owen-smith, 2007; Owen-Smith & Cain, 2007).

Size of the herd was suggested also influencing home range size of sable in Kruger National Park, South Africa, due to greater local resource depletion when the grass resources became non-renewing. As consequence, is expected that larger herds have also larger home ranges (Owen-Smith & Cain, 2007). However, according to Gilchrist & Otali (2002) the importance of group size on home range size variation is not clear as it has hardly been investigated. In GNP, herd size did not seem to have much influence on home range size, as the Chitengo herd had around 45 individual, about the double of mopane herd (around 21-25 individual only), but had smaller home ranges comparing with the mopane herd. Macdonald (1983) stated that there is no direct correlation between home range size and group size, suggesting that dispersion of available food resources influences home range size, whereas food resources abundance independently influences group size. So, if the resources are widely dispersed, territories are correspondingly larger. In contrast, abundance of resources in each territory correlates with group size. Kruuk & Macdonald (1985) predicted that home range behaviour in group living species should conform to one of two strategies. They should either expand their range to encompass sufficient additional resources to support more group members or increase group size only up to the size that can be sustained on the resources within the range.

Seasonal variations in home ranges

As expected, home range extent of both herds increased in the late dry season, nearly doubling the size when compared with the home range used in other seasons, with exception of the early wet season for the mopane herd, which approached the size of the late dry season home range, probably as a result of prolonged effects of the dry season. Previous studies on sable (Wilson & Hirst, 1977; Henley, 2005; Parrini 2006; Owen-Smith & Cain, 2007; Macandza, 2009) also documented larger home range sizes during the dry season than during the wet season, in search for water and remaining high quality food. For the mopane herd water had much larger influence in late dry season home range expantion, as mentioned above. However, food availability also influenced expansion of home ranges in the late dry season, as during this

time, it was common to see the herd moving to recent burned areas to feed on regrowthing green grasses (personal observation). The Chitengo herd in other hand, seemed to be influenced by both, scarcity of water and decline in the availability of food at different stages. After the small pans dried out, the herd moved to areas close to Pungue River, and at the end of the late dry season, it moved to drainage lines that retained green grasses. It was also common to see this herd move to recently burned areas during the late dry season. When resources decrease in quantity and quality herds can be forced to use areas out of their usual range. Wilson & Hirst (1977) noted that burning can attract sable away from their usual localities. Sable were also found occasionally aggregating on recent burnt pastures that provide best grazing compared with non-burned areas in other studies (Grobler, 1973; Sekulic, 1981; Parrini & Owen-Smith 2009) and utilizing valley bottomlands such as floodplains during the late dry season to exploit the characteristic retention of green grass associated with such areas (Jarman, 1972; Estes & Estes, 1974; Parrini, 2006; Magome *et al*., 2008).

Habitat use

The use of vegetation types differed between the two sable herds. I was expecting both herds to use more frequently wooded vegetation types, moving to grasslands only on the late dry season. The mopane herd occupied both wooded and open areas (grasslands), at different times in the year. The herd established core home ranges in grasslands during the dry season and in *acacia-combretum* woodlands during the wet season. The Chitengo herd however, occupied almost exclusively wooded areas, establishing home ranges and core areas in *acacia-combretum* woodlands mostly of the year, with exception of early wet season were the herd used more riverine mixed forest. Similar pattern showed in this study for both herds was also found in previous studies. Tinley (1977), in a previous study on the park, reported the largest number of sable on the floodplain grasslands and open savannas during the dry season and largest numbers on miombo woodlands during the wet season, a similar pattern to that found for the mopane herd in this study. Dabengwa (2009) in Kruger National Park reported that sable avoided home range areas with more woody cover during the dry season and Estes (1991) also found that sable herds range the open grasslands in the dry season in search of green plants. My study also found similar behaviour. Beyond movement between grasslands and miombo woodlands, Tinley (1977)

documented that sable in the park prefer ecotones of savanna with dambos and floodplains grasses. This was also found in this study, were mopane herd was found, during the field work, foraging on ecotones of floodplains grasslands and adjacent woodlands and the Chitengo herd foraging on woodland areas with dambos and pans. Sable have been described as favouring ecotones in other previous studies (Jarman, 1972; Sekulic, 1981; Henley, 2005) where the interface between different vegetation types provides diverse opportunity for foraging, shelter and predator avoidance.

Acacia-cumbretum woodlands were the most used vegetation type by the Chitengo herd and the second most used by the mopane herd. This may have been attractive to sable because *acacia-Coumbretum* woodlands are characterized by palatable medium-tall grasses, such as *Panicum maximum, Heteropogon contortus* and *Themeda triandra*. *P. maximum, H. contortus* and *T. triandra* were documented in other studies as species favoured by sable antelope (Parrini, 2006; Magome *et al*., 2008; le Roux, 2010; Macandza *et al*., 2012). These woodlands were also associated with termite mounds, where highly nutritious and palatable grasses grow (van Oudtshoorn, 1999). Sekulic (1981) also found sable frequently grazing at the edges of termite mounds in Shimba Hills Game Reserve, Kenya. Termites can redistribute soil nutrients and have profound influences on savanna vegetation (Dangerfield *et al.*, 1998; Sileshi *et al.*, 2010), acting as keystone structures that provide nutrient-rich patches (Davies *et al*., 2014). John & Stein (2004) and Ragnhild *et al.* (2005) revealed that some plants grow well on termite mounds because the soil of the mounds is rich in nutrients. However, according to Arshad (1982) the soil nutrient enrichment effects of termite mounds are far reaching and have been shown to affect areas within a radius of up to 25 m of the actual mound. Therefore, sable may nutritionally benefit merely by foraging in areas with a high density of termite mounds. Mopane herd used mostly the medium-tall grasslands and shrubby grasslands, especially in the dry season, probably also attracted by palatable grasses such as *Setaria incrassata* and *P. maximum* and high grass biomass in these areas.

Summary

Sable antelope herds in Gorongosa National Park, despite sable is doing well in the park, have larger home ranges than in areas where species is declining, mainly due to scarcity of water during late dry season. Both herds expanded their home ranges during the late dry season, when water and green grasses started to become scarce in the park. One herd (the mopane herd) used open areas (grasslands) more frequently during the dry season and wooded areas in the wet season, while the other herd (the Chitengo herd) stayed in wooded areas throughout the year, only making movement to grasslands in the end of the late dry season. Results presented in this study suggests that sable can adapt to limitation of the dry season by using grasslands as key resource areas or moving over a wide range in order to find and exploit key resources. Looking at the home range sizes and the size of the herds, seems that the mopane herd established home ranges in poor resources areas comparing to Chitengo herd, water playing an important role as a limiting factor.

TABLES

Table 1: Characteristics of the vegetation types found in southwest of Gorongosa National Park

Vegetation Type	**Defining Characteristics (adapted from Stalmans & Beilfuss (2008).**
Dry Forest/Thicket	Very dense formation typified by woody species such as *Cleistochlamys kirkii, Diospyros senesis, Craibia zimmermannii, Alchornea laxiflora, Milletia stuhulmannii, Markhamia acuminata, Capparis sp.* and *Thilachium africanum*. The grass layer is sparse occurring when present *Brachiaria deflexa, Digitaria sp.* And *Oplismenus sp.*
Gallery Forest	Woody formation found on humid soils close to permanent drainage lines.
Miombo Woodlands	Open to close woodland dominated by species such as *Brachistegia boehmii, Julbernardia globiflora, Acacia nigrescens, Diplorhynchus condylocarpon, Sterculia quinqueloba, Strychnos potatorum* and *Pterocarpus rotundifolius*. Grass layer varies from short to tall, dominated by *Panicum maximum, Digitaria eriantha, Themeda triandra* and *Sporobolus sp.*
Inselberg Miombo	Closed miombo woodland with a more open canopy on rock outcrops. This formation occurring on small inselbergs that occur in the park.
Mixed Forest (Riverine)	Open to closed woody formation occurring close to Pungue river and Pungue drainage lines. Species such as *Hyphaene petersiana, Borassus aethiopium, Piliostigma thonningii, Philenoptera violacea, Combretum adenogonium, Acacia sieberana* dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata, Panicum maximum, Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Acacia xanthophloea Woodland	Open to close woodland dominated by *Acacia xanthophloea*. This formation is seasonally inundated. Grass layer is usually tall dominated by *Panicum maximum, Setaria incrassata* and *Cynodon dactylon*
Acacia-Combretum Woodland	This is the most extensive community. Characterised by open to close woodlands dominated by *Combretum adenogonium, C. imberbe, Acacia nigrescens, A. robusta* and also occurring frequently *Sclerocarya birrea,*

	Dalbergia melanoxylon, Philenoptera violacea e *Ziziphus mucronata*. Grassland layer varies from short to tall dominated by *Panicum maximum, Digitaria eriantha, Heteropogon contortus, Urochloa mossambicensis* and *Themeda triandra*. Often with termite mounds.
Colospermum mopane Woodland	Short closed woodland dominated by Mopane (*Colophospermum mopane*). Grass cover is sparse dominated by *Enteropogon macrostachyus* with *Digitaria eriantha* and *Chloris sp.* on the edges.
Faidherbia albida Woodland	Open to close woodland dominated by *Faidherbia albida*, found close to Urema Lake and subjected to temporary inundations. Grass layer ranges from short to tall, dominated by *Cynodon dactylon, Digitaria swazilandensis* and *Echinochloa pyramidalis*.
Dichrostachys cinerea Shrubland	Closed shrubland dominated by *Dichrostachys cinerea*, found mostly at edge of mopane and other woodlands. Grass cover is sparse, occurring when present *Panicum maximum* and *Brachiaria deflexa*
Dalbergia melanoxylon Shrubland	Closed shrubland dominated by *Dalbergia melanoxylon*, found mostly at edge of other taller woodlands. Grass layer is usually short and open, dominated by *Panicum maximum, Heteropogon contortus, Aristida sp.* and *sporobolus sp.*
Palm Veld	Open to closed woody formation subjected to temporary inundation. Species such as *Hyphaene petersiana, Borassus aethiopium* and *Phoenix* reclinata dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata, Panicum maximum, Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Short Grassland	Short closed grassland formation dominated by *Cynodon dactylon* and *Digitaria swazilandensis*. This formation is being invaded by alien specie *Mimosa pigra,* and during wet seasons is subjected to floods
Saline Grasslands	Short open grassland formation dominated by *Sporobolus iocladus*. This formation usually occurs associated with Acacia.
Pan Grasslands	Short closed grassland formation that occurs along pans dominated by *Paspalidium obtusifolium, Echinochloa sp., Oryza longistaminata* and *Hemarthiria altissima*.

Shrub Grassland	Medium to tall grassland with patches of *Dichrostachys cinerea* shrubs. Grass species such as *Panicum maximum, Setaria incrassata*, *Vetiveria nigritana* and *Brachiaria deflexa*
Medium-Tall Grassland	Medium to tall grassland dominated by *Panicum maximum, Panicum coloratum, Setaria incrassata, Vetiveria nigritana* and *Brachiaria deflexa*
Tall Grassland	Tall grassland, normally adjacent to permanent water and seasonally inundated. Dominated *Echinochloa pyramidalis* and *Vetiveria nigritana*.
Shifting Cultivation	Seasonal cultivation by the communities. Found mainly south of Pungue river.
Water	Open water, typified by Urema lake, Pungue river and other permanent water streams.

Table 2: Annual home range size (MPC 100% and LoCoH 95%) for sable in the Gorongosa National Park compared to previous studies

Study Area	**Study**	**MCP HR Size (Km^2)**	**Study Area Size (Km^2)**
Gorongosa NP, MZ	Present – mopane herd	181.5	3,970
Gorongosa NP, MZ	Present – Chitengo herd	98.7	3,970
Kruger NP, SA	Owen-smith & Cain 2007	118	19,485
Kruger NP, SA	Owen-smith & Cain 2007	65	19,485
Kgaswane MR, SA	Parrini 2006	19.1	42.57
Kgaswane MR, SA	Parrini 2006	15.6	42.57
Pilanesberg NP, SA	Magome 1991	44	500
Sandveld NR, SA	Jooste 2000	24.7	370
Shimba Hills GR, Kenya	Sekulic 1981	10-24	250

Table 3: Annual home range size (LoCoH 95%) for sable in the Gorongosa National Park compared to previous studies.

Study Area	**Study**	**LoCoH (95%) HR Size (Km^2)**
Gorongosa NP, MZ	Present – Chitengo herd	26.8
Gorongosa NP, MZ	Present – Mopene herd	23.5
Okavango Delta, BTZ	Hensman 2011	20.7
Okavango Delta, BTZ	Hensman 2011	21.5
Okavango Delta, BTZ	Hensman 2011	31.0

Table 4: Sable antelope seasonal home ranges in the Gorongosa National Park, calculated using LoCoH 95% and LoCoh 50%. All values are in hectares.

Seasons	LoCoH 95%		LoCoH 50% (core area)	
	Mopane herd	**Chitengo herd**	**Mopane herd**	**Chitengo herd**
Late dry	1556.9	1223.2	280.2	371.4
Early wet	1338.8	628.7	342.1	134
Late wet	766.9	533.4	181	139.9
Early dry	989.5	467.4	240	107.8

FIGURES

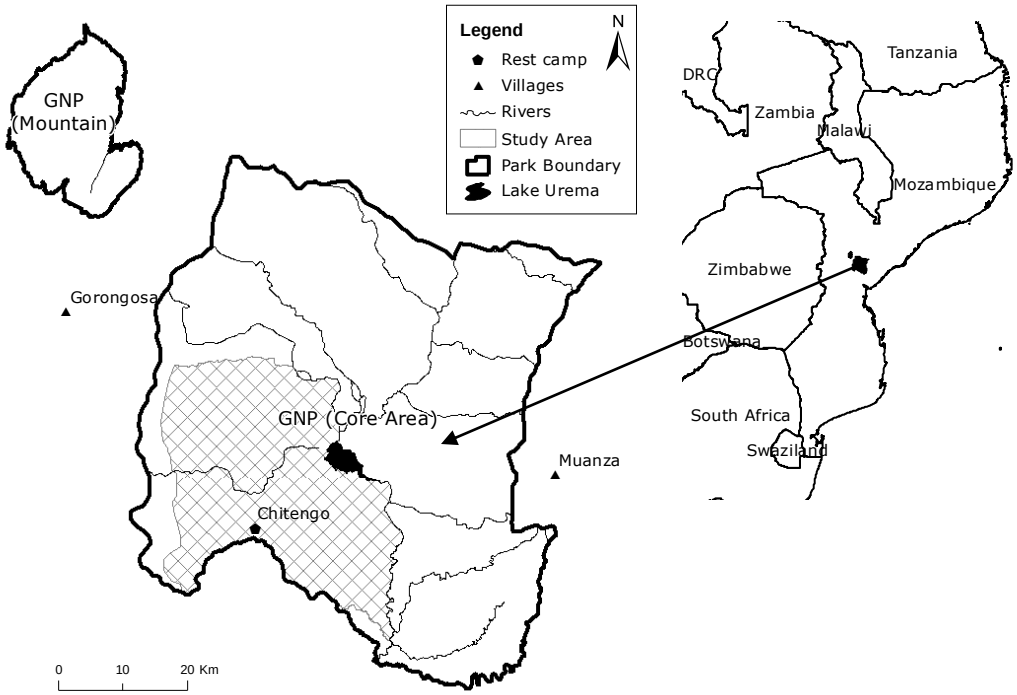


Figure 1: Gorongosa National Park, Mozambique and location of study area in Gorongosa National Park.

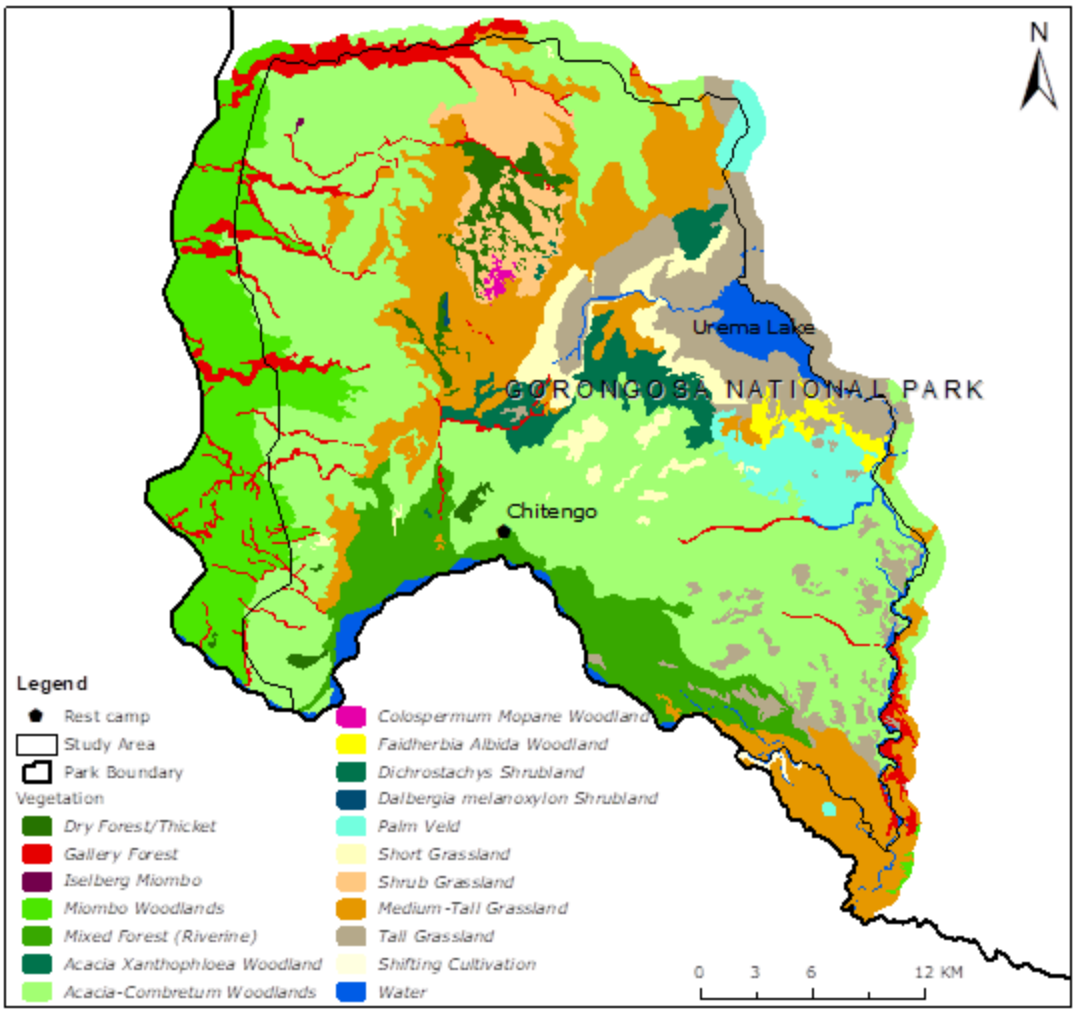


Figure 2: Gorongosa National Park, Mozambique and location of study area in Gorongosa National Park.

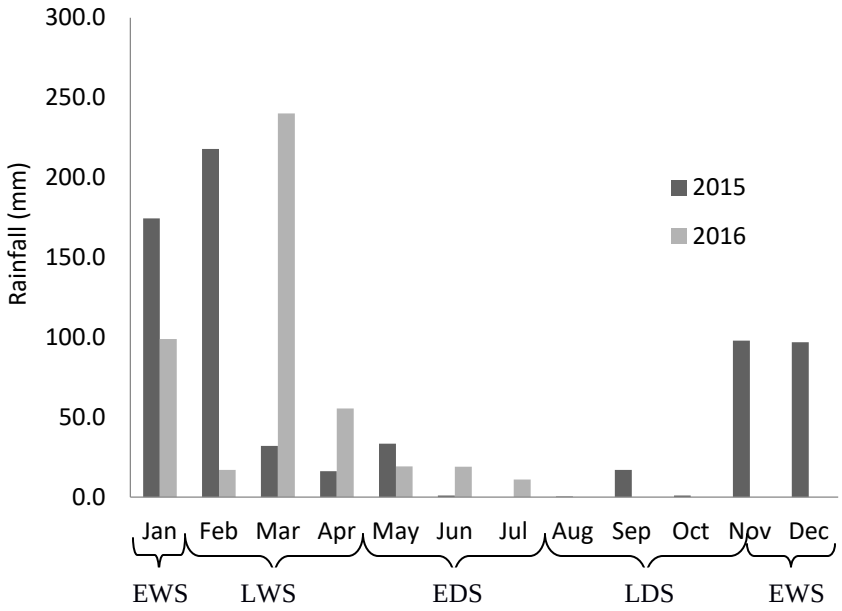


Figure 3: Rainfall in study area from January 2015 to July 2016 (source: weather station in Chitengo, GNP)

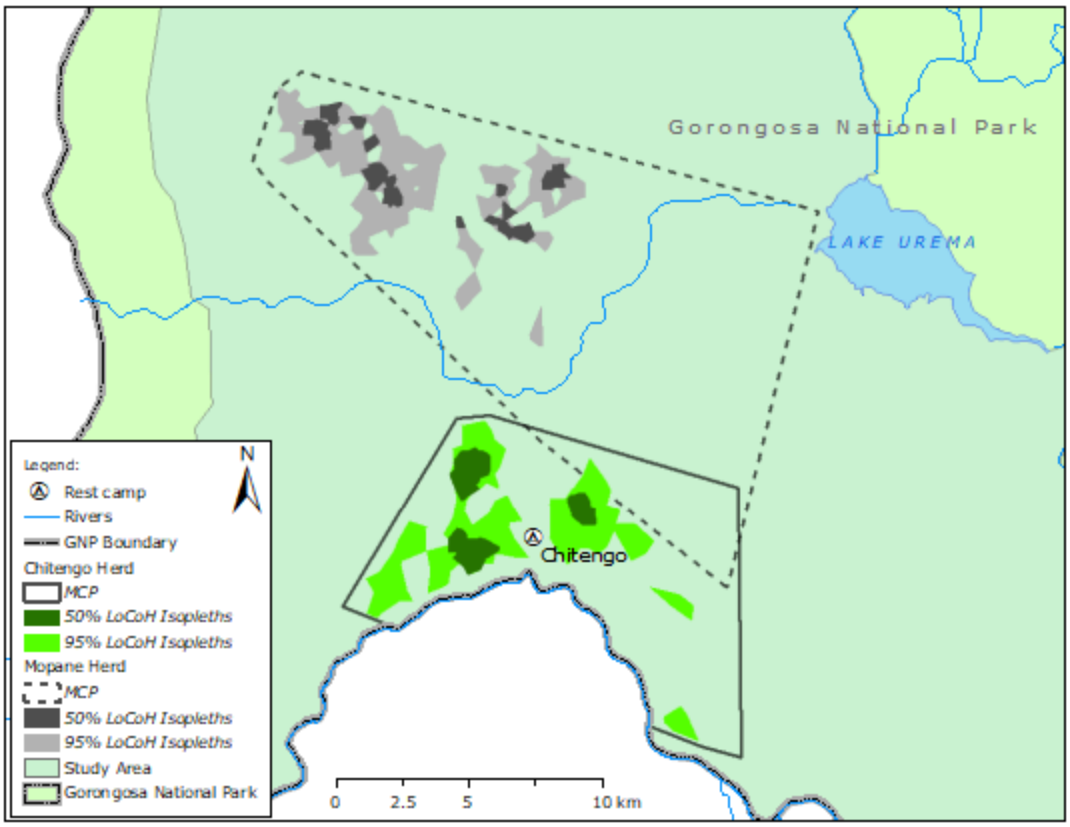


Figure 4: Annual Minimum Convex Polygons (MCPs) and annual LoCoH (95% and 50% isopleths) of two collared herds in Gorongosa National Park from August 2015 to July 2016

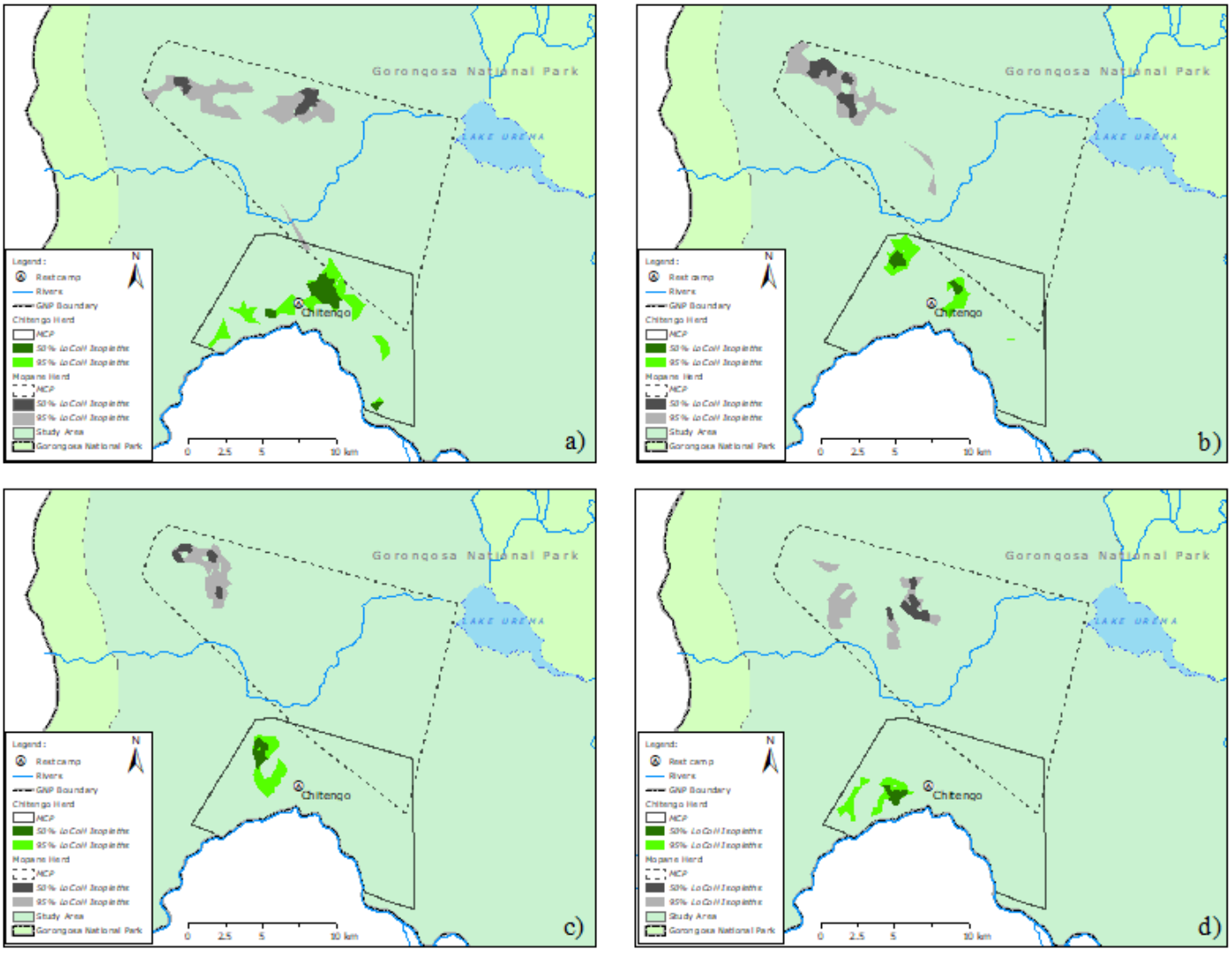


Figure 5: Seasonal home ranges (a-LoCoH 95% and 50% isopleths) of the two collared herds in Gorongosa National Park. a) Late dry season; b) Early wet season; c) Late wet season and d) Early dry season

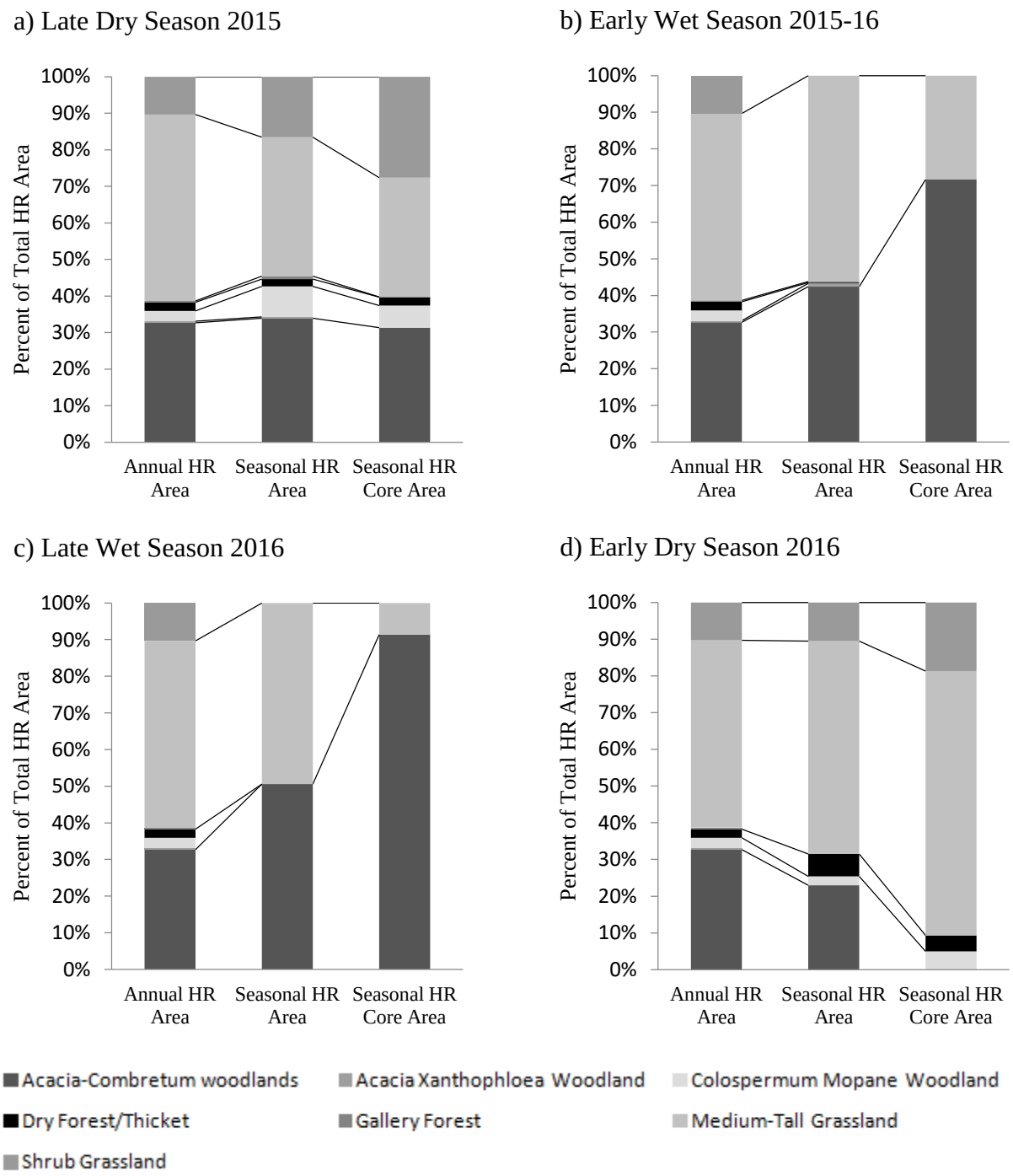


Figure 6: Proportion of vegetation types on the a-LoCoH annual, seasonal, core seasonal and variations between different seasons for the mopane herd

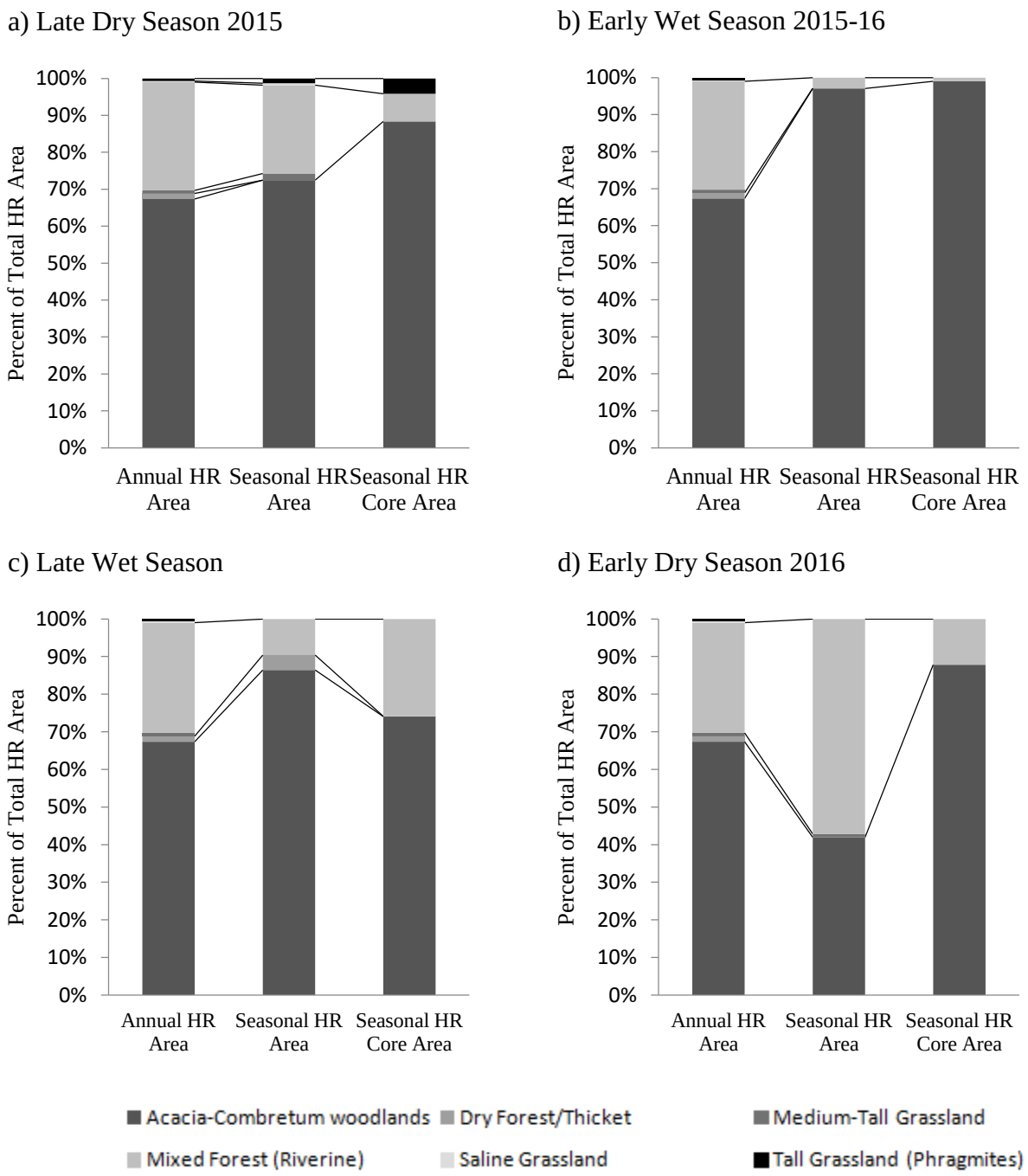


Figure 7: Proportion of vegetation types on the a-LoCoH annual, seasonal, core seasonal and variations between different seasons for the Chitengo herd

REFERENCES

Anderson, J. L., Beilfuss, R. D., Pereira, C. L., & Zolho, R. (2006). *Proposed strategy to reintroduce and supplement wildlife populations in Gorongosa National Park, Mozambique*. Technical report submitted to Gorongosa National Park, Mozambique.

ARAC (2005). *Spreadsheets with precipitation and evaporation data of Chitengo*. Administração Regional de Águas Centro. Beira, Mozambique.

Arshad, M. A. (1982). Influence of the termite Macrotermes michaelseni (Sjöst) on soil fertility and vegetation in a semi-arid savannah ecosystem. *Agro-Ecosystems* **8**: 47-58.

Brandt, M. J. & Cresswell, W. (2008). Breeding behaviour, home range and habitat selection in Rock Firefinches Lagonosticta sanguinodorsalis in the wet and dry season in central Nigeria. *Ibis* **150(3)**: 495-507.

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

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 Wiwatersrand, Johannesburg, South Africa.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**: 3387-3397

D'Ammando, G. (2016). *Patterns of home range use and resource selection by eland (Tragelaphus oryx) in the Kgaswane Mountain Reserve*. M.Sc Thesis. University of the Wiwatersrand, Johannesburg, South Africa.

Dabengwa, A. N. (2009). *Assessing the role of woody cover in resource selection by sable antelope (hippotragus niger) in northern Kruger National Park*. M.Sc Thesis. University of the Wiwatersrand, Johannesburg, South Africa.

Dangerfield, J. M., McCarthy, T. S. & Ellery, W. N. (1998). The mound-building termite Macrotermes michaelseni as an ecosystem engineer. *Journal of Tropical Ecology* **14**: 507-520.

Davies, A. B., Robertson, M. P., Levick, S. R., Asner, G. P., van Rensburg, B. J. & Parr. C. L. (2004). Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. *Journal of Vegetation Science* **25**: 1405-1416

Duncan P. (1983). Determinants of the use of habitat by horses in a Mediterranean wetland. *Journal of Animal Ecology* **52**: 93-109

Estes, R. D. & Estes, R. K. (1974). The biology and conservation of the giant sable, *Hippotragus niger variani* Thomas, 1916. *Proceedings of 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.

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

Getz, W. M & Wilmers, C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography* **27**: 498-505.

Getz, W. M., Fortmann-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.

Gilchrist, J. S. & Otali, E. (2002). The effects of refuse-feeding on home-range use, group size, and intergroup encounters in the banded mongoose. *Canadian Journal of Zoology* **80**: 1795-1802.

Goddard, J. (1967). Home range, behaviour, and recruitment rates of two black rhinoceros populations. *African Jornal of Ecology* **5**: 133-150.

Goodman, P. S. (2009). Large mammal population estimates for Malilangwe Estate: September/October 2008. *Internal Management Report*. Malilangwe Trust, Zimbabwe.

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. (1973). *Aspects of the biology, population ecology and behaviour of sable (Hippotragus niger niger) (Harris 1838) in the Rhodes Matopos National Park, Rhodesia*. M.Sc thesis, University of Pretoria, Pretoria, South Africa

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.

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

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. *Biological Conservation* **90:** 69-78.

Harris S., Cresswell, W. J., Forde, P. G., Trewhelle, W. J., Wollard, T. & Wray, S. (1990). Home range analyis using radio-tracking data. A review of problems and tecniques particularly as applied to the study of mammals. *Mammal Review* **20**: 97-123

Hayne, D. W. (1949). Calculation of size of home range. *Journal of Mammalogy* **30**: 1-18

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.

Hensman, M. C. (2011). *Home range and resource use of sable antelope in the okavango delta.* M.Sc. thesis, University of the Witwatersrand, Johannesburg.

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

Jenkins, S. H. (1981). Common Patterns in Home Range-Body Size Relationships of Birds and Mammals. *The American Naturalist* **118(1)**: 126-128.

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

John, P. L. & Stein, R. M. (2004). Termitaria as browsing hotspots for African megaherbivores in miombo woodland. *Journal of Tropical Ecology* **20**: 337-343.

Jooste, M. H. (2000). *Die ekologie van die swartwitpens in die Sandveld Natuurreservaat, Vrystaat Provinsie*. M.Sc thesis, University of Pretoria, Pretoria, South Africa.

Kernohan, B. J., Gitzen, R. A & Millspaugh, J. J. (2001). Analysis of Animal Space Use and Movements. In: *Radio Tracking and Animal Populations* (Eds: Millspaugh, J. J. & Marzluff, J. M.), Academic Press California, pp. 125-166

Knoop, M-C. & Owen-Smith, N. (2006). Foraging ecology of roan antelope: key resources during critical periods. *African Journal of Ecology* **44**: 1-9

Kruuk, H. & Macdonald, D. W. (1985). Group territories of carnivores: empires and enclaves. In: *Behavioural ecology* (Eds: Sibly, R. M. & Smith, R. H.), Blackwell, pp. 521-536.

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.

Lyons, A. J., Turner, W. C. & Getz, W. M. (2013). Home range plus: a space-time characterization of movements over real landscapes. *Movement Ecology* **1(1)**: 1-14.

Lyons, A. J. (2014). *T-LoCoH for R: Tutorial and Uses Guide*. University of California, 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.

Macandza, V. A., Owen-Smith, N. & Cain, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* **121:** 891-898

Macdonald, D. W. (1983). The ecology of carnivore social behaviour. *Nature* **301**: 379-384.

Maier, J. A. K., Ver-Hoef, J. M., McGuire, A. D., Bowyer, R. T., Saperstein, L., Maier, H.A. (2005). Distribution and density of moose in relation to landscape characteristics: effects of scale. *Canadian Journal of Forest Research*. **35**: 2233–2243.

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., & 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.

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

Morrison, M. L.; Marcot, B. G. & Mannan, R. W. (1998). *Wildlife-habitat relationships. Concepts and applications*. Second ed: The University of Wisconsin Press.

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

Murray, M. G. (1982). Home range, dispersal and the clan system of impala. *African Journal of Ecology*, **20(4)**: 253-269

Owen-Smith, N. (1979). Assessing the foraging efficiency of a browsing ungulate, the kudu. *South African Journal of Wildlife Research* **9**:102-110.

Owen-Smith, N. (1988). *Megaherbivores – The influence of a very large body size onecology*. Cambridge University Press. Cambridge

Owen-Smith, N. (2002). *Adaptive Herbivore Ecology – from resources to populations in variable environments*. Cambridge University Press. Cambridge

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.

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. (2009) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology*. **48(2):** 526-534.

Ragnhild, M., Anne, K. N. & Stein, R. M. (2005). Termitaria are focal feeding sites for large ungulates in Lake Mburo National Park, Uganda. *Journal of Zoological Society* **267**: 97-102.

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

Reid, C., Slotow, R., Howison, O. & Balfour, D. (2007). Habitat changes reduce the carrying capacity of HluhluweUmfolozi Park, South Africa, for Critically Endangered black rhinoceros Diceros bicornis. *Oryx* **41**: 247-254

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.

Sekulic R. (1981). Conservation of the sable Hippotragus niger roosvelti 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. & Swift, D. M. (1987). Large Herbivore Foraging and Ecological Hierarchies. *Bioscience* **37**: 789-799

Sileshi, G. W., Arshad, M. A., Konaté, S. & Nkunika, P. O. Y. (2010). Termite-induced heterogeneity in African savanna vegetation: mechanisms and patterns. *Journal of Vegetation Science* **21**: 923-937.

Skinner, J. D. & Smithers, R. H. N. (1990). The *mammals of the Southern African subregion*. University of Pretoria, Pretoria, South Africa.

Skinner, J. D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion,* 3rd ed. Cambridge University Press, Cape Town.

Stalmans, M. & Beilfuss, R. (2008). *Landscapes of the Gorongosa National Park*. Unpublished report to the Gorongosa Restoration Project. 103p.

Stalmans, M., Peel, M. & Massad, T. (2014). *Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion*. Unpublished report to the Gorongosa Restoration Project.

Tinley. K.L. (1977). *Framework of the Gorongosa Ecosystem*. PhD thesis. University of Pretoria.

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

Weather data from Chitengo 2005-2009. University of Edinburgh and Envirotrade. Available at http://www.geos.ed.ac.uk/homes/cryan.

Wilson, D. E. & Hirst, S. M. (1977). Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife Monographs* **54**: 1-111.

CHAPTER 3

RESOURCES SELECTION WITHIN HOME RANGES BY SABLE ANTELOPE IN GORONGOSA NATIONAL PARK

ABSTRACT

The aim was to determine the role of predation and competition in resource selection by sable within home ranges and which other factors are contributing to the selection of those areas in Gorongosa National Park (GNP). Sable antelope (*Hippotragus niger*) numbers in the GNP have substantially increased since 2000, and understand witch factors are influencing resource selection by the specie is crucial to help with their recovery in the park. I used coordinates from two GPS collars that were fitted in two sable females from different herds in the park (referred as mopane and chitengo herd respectively) to obtain locations of sable and conducted walking transects in the field to collect information on competitors and predators. I used the most abundant grazers reedbuck and waterbuck to assess competition and, as predation proxy, prey availability biomass and signs of predation. Distance from water, distance from roads, elevation, slope, NDVI, vegetation types and landscapes were considered as environmental variables that could affect selection by sable within home ranges. I fitted season logistic regression models using biotic predictors (competitions and predation) and environmental variables. For biotic variables I fitted only for the late dry season, period where transects were conducted. Sable were more prevalent in areas with low predation risk within their home ranges. Influence of competition differed between herds, with mopane herd avoiding areas with high concentrations of reedbuck while Chitengo herd favoured those areas. Distance from water, distance from roads, greenness and elevation appeared as the most influential environmental variables in selection of areas within home ranges by sable, but influence varied between herds and seasonally. However, both herds proffered high elevation areas during the wet season, probably as a response of the floods frequents in the park during this time. Results presented here show that, despite low densities, competition and predation risk influences selection of areas within home ranges by sable.

INTRODUCTION

Decreasing numbers of large mammalian herbivores have been a cause for concern across a number of conservation areas in Africa (Owen-Smith & Mills, 2006; Goodman, 2009; Ogutu *et al*., 2011). Sable antelope (*Hippotragus niger*) is one of the species that had a wide distribution in the Southern African sub-region (Skinner & Chimimba, 2005), but is exhibiting long-term declines in abundance in different parts of their range. In the Kruger National Park (KNP), South Africa, sable have decreased from 2240 in 1986 (Harrington *et al.,* 1999; Grant & van der Walt, 2000) to about 300 animals in 2006 (Whyte, 2006) and in Malilangwe Wildlife Reserve, Zimbabwe, number have decreased from 197 in 1994 to only 62 by 2005 (Goodman, 2009). Many reasons have been suggested to explain the decline and lack of recovery of sable antelope, including: increased predation (Harrington *et al.,* 1999; Owen-Smith & Mills, 2006), decreased dry season rainfall and increased temperature, reducing the availability of green foliage through the critical dry period (Harrington *et al.,* 1999; Ogutu & Owen-Smith, 2003; Owen-Smith & Mills, 2006), competition with other grazers (Harrington *et al.*, 1999; Owen-Smith *et al*., 2011) and habitat loss (Grant & van der Walt, 2000). However, in contrast to populations in many other parts of Southern Africa, the sable population of the Gorongosa National Park (GNP) appears to be thriving. Numbers have increased from less than 100 in 2000 to more than 750 in 2014, but species other than sable are also recovering (Stalmans *et al.,* 2014). GNP has a small number of lions and the number of potential competitors with sable antelope is still low, despite the very fast increasing rate in the numbers of waterbuck (*Kobus ellipsiprymnus*) and common reedbuck (*Redunca arundinum*).

Both abiotic and biotic factors have been demonstrated to influence distribution of ungulates (Senft *et al*., 1987; Bailey *et al*., 1996). Quantifying the relationships between ungulates distributions and their abiotic or biotic environments is central to understanding species ecology (Johnson *et al*., 2004; Rushton *et al*., 2004). Senft *et al*. (1987) suggested that resource selection by animals operates at a number of different spatial scales, ultimately determining where an animal lives. At different scales a variety of factors play a role in determining whether an animal chooses a specific area or not. Johnson (1980) described resource selection as a hierarchical process in which resource selection could occur, from a geographic range (1st order of selection), home range or landscape selection (2nd order), to usage of various components within home ranges (3rd order of selection) (e.g. feeding sites), to procurement of items (e.g. food) from those available at a site (4th order of selection). At the within-home-range scale, habitat selection is usually linked to the animals daily foraging, resting rhythms and also security against predation, in contrast to selection of home ranges at broader scales, which is often linked to dispersal processes or seasonal migrations (Morris, 1987).

In theory, herbivores should select areas with optimal food quantity and quality within their home ranges (Owen-Smith & Novellie, 1982; Belovsky, 1984; Manly *et al.*, 2002). However, in practice, herbivores are influenced by numerous other factors including distance from water, topography, vegetation types, quantity and quality of food resources, human disturbances, and interspecific interaction which modifies their selection criteria (Senft *et al.*, 1987; Bailey *et al*., 1996; Godvik *et al*., 2009; Morin, 2011). Habitat conditions, available resources, and risks of predation vary from place to place, so that use may be concentrated within certain core areas or centres of activity, while other sections are infrequently visited (Owen-Smith & Cain, 2007). Topography present soil sequences that are associated with different plant communities from uplands to bottomlands (Belsky, 1995), having effects on water availability for plants and determining, thus, the proportion of green leaf that remains in the sward through the dry season (Owen-Smith, 2002). Bell (1971) in the Serengeti found that herbivores selected habitats on high ground in the wet season where nutritious short grass dominated. However, with the progression of the dry season the herbivores selected habitats towards the bottom of the catena where tall and medium grasses of poor quality prevailed. Herbivores, in order to survive, depend 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 search for areas retaining plant species of better quality and quantity and, in most cases, progressively include species of lower nutritive value in order to survive, until the next period of food abundance (Owen-Smith, 2002; Henley, 2005). Animals often select different habitats in each season depending upon the seasonal distribution and availability of resources (Burt, 1943; Western, 1975; Boyce *et al.*, 2016).

Predators have direct effects on prey populations through lethal consumption and non-lethal effects. Lima (1998) suggested that indirect effects of predators on prey, such as the alteration of prey behaviour, have larger ecological impacts than actual predation. Herbivores tend to avoid areas characterized by high risk of predation (Sinclair & Arcese, 1995; Valeix *et al*., 2009a), leading them, in some cases, to use marginal sites/patches were food quantity and quality is low and to select specific vegetation structure. Vegetation structure affects visibility and hence capacity to detect a predator, ease of escape from a predator, and camouflage and ambush opportunities for predators (Creel *et al*., 2005).

Interspecific competition may arise where one species reduces shared food resources below the level that can be exploited efficiently by another species (Murray & Illius, 1996). Among large herbivores, competition results from resources exploitation through the depletion of food resources during seasons of food limitations

(Owen-Smith, 2002). Harrison *et al.* (1995) suggested that a superior competitor may relegate inferior competitors to establish residency in areas where the former species is less abundant. Apart from exploitative competition, apparent competition might also influence resource use and spatial separation between prey species sharing the predator (Holt, 1977). Beyond interspecific competition, intraspecific competition can also lead to changes in foraging behaviour and space use by herbivores (Sinclair, 1985; Clutton-Brock *et al*., 1987; Smith & Cain, 2008), result in species searching larger areas to satisfy their nutritional requirements (Redfern *et al*., 2003).

Hensman (2011) suggested that predation and interspecific competition played an important role on sable movements and home ranges in Botswana. However, Hensman (2011) did not have strong evidence to disentangle if floodplains were largely avoided because of direct competition with other grazers or because of increased predation risk as a consequence of the increase in prey species attracting predators to the floodplains, suggesting that further studies should be undertaken. Data from the last aerial wildlife count of the GNP (Stalmans *et al*., 2014) show that sable seem to avoid the Riverine & Floodplain landscape, a landscape subjected to prolonged flooding, where theoretically the probability of founding green, high value grass species should be higher in the late dry season when food resources are limited, and are instead found in the woodlands. According to Tinley (1977), the largest numbers of sable were found on ecotones of woodlands with floodplain grasslands in the dry season. Therefore, the aim of this study was to assess what is the relationship between of predation and competition on sable habitat use and which other factors are contributing to sable select specific areas within home range in GNP in order to survive. For that I created three prediction: (1) sable will select areas within their home ranges avoiding those with high predation risk, (2) sable should concentrate on the sections infrequently used by main competitors (waterbuck and reedbuck), to reduce competition for resources, and (3) other factors such as distance from water, vegetation type and greenness (NDVI) should have influence on sable habitat use, especially during the critical dry season.

METHODS

Study site

I conducted this study in the southwest of Gorongosa National Park (GNP), Mozambique, in an area covering 1011 km^2 close to Chitengo camp (main camp of the park) (Fig. 1). The Park is approximately 3970

km^2 and is located in central Mozambique at the southern tip of the African Rift Valley. The area is situated in a region with distinct wet (November-April) and dry (May to October) seasons, and receives relatively high mean annual rainfall of 850 mm (SD: ±269 mm), calculated as average from 1956-1969 and 1998-2009 (ARAC, 2005; Weather data from Chitengo, 2005-2009). During the study period (August 2015 to July 2016) rainfall in the area was 21% above long term-mean (674 mm).

Based in a combination of plant communities, Stalmans & Beilfuss (2008) described tree landscape types covering the study area: (1) the Rift Valley Alluvial Fan consisting in a mix of open to closed woodlands and dry forest/thickets reflecting the structural soil characteristics and moisture regime of the alluvial fans, (2) The Rift Valley Riverine & Floodplain Landscape consisting in a mix of mostly open plant communities and normally subject to prolonged flooding and (3) The Rift Valley Lake Urema Landscape characterized by open water that forms the Lake Urema. Using Landsat imageries, field observation and vegetation surveys of the park I then divided the area into 18 different types (Fig 2, Table 1).

Numbers of lions are still low in the park. Potential competitors densities are also low,, with the exception of waterbuck and reedbuck. Lions (*Panthera leo*) are estimated to be around 50 to 70. On the last aerial count (Stalmans *et al*., 2014) were counted 33 zebras (*Equus burchellii*), 361 wildebeest (*Connochaetes taurinus*), 670 buffalo (*Syncerus caffer*), 2,735 impala (*Aepyceros melampus*), 11,912 Common reedbuck (*Redunca arundinum*) and 34,507 waterbuck (*Kobus ellipsiprymnus*).

Sable capture and collaring

Two adult sable females from two different herds were captured on 23 June and 11 July 2015 respectively (ID 112047 and 112048, from now on referred as Mopane herd and Chitengo herd respectively), using well-established capture techniques by an experienced veterinarian and fitted with GPS Sirtrack collars around the neck (Wits animal ethics number 2013/47/2A). Collars were fitted on adult females to ensure that the movements of the individuals bearing the collar represented the movements of the herds because adult females remain within the breeding herds (Estes, 1991; Skinner & Chimimba, 2005). The collars were programmed to record GPS coordinates every 5 hours to obtain GPS positions at different times each day. Coordinates were downloaded every week using the sirtrack GPS software v1.6.3 (http://www.sirtrack.co.nz).

Field data collection

With the aid the study area map and road network of the park stored in ArcGIS 10.2 (Environmental Systems Research Institute Inc, USA), I distributed 12 walking transects, arranged at regular intervals (4 km apart between lines and 2 km between transects in the same line) covering all area used by the sable herds and all landscapes in the study area (Fig. 4), following the methodology used by Treydte *et al*. (2005). Transects were conducted in order to obtain locations of potential competitors and predators. Each transect was oriented when possible east-west, 3 km long and was located on the ground using a handheld GPS device. Transects were walked once between August 2015 and November 2015, during the periods of greatest animal activities (6:30– 10:00 am and 3:00–6:30 pm; Davis, 1982) and all live individuals of herbivores were counted. For each animal sighting, the GPS observer location, the specie, distance from the animal to the transect using a range finder, and the angle of the animal to the transect using a compass was recorded. Perpendicular distance of the animal was estimated and all data loaded in the Program DISTANCE. Signs of predation (kills carcasses, spoors and dung of lions) along transects, were also recorded.

Data analysis

GIS layers processing

Seven environmental variables (elevation, slope, distance from roads, distance from water, NDVI, vegetation and landscape) that could potentially influence large herbivores movements and resource selection (Senft *et al*., 1987; Bailey *et al*., 1996; Godvik *et al*., 2009) were selected, to assess distribution of competitors and predation risk and habitat selection by sable within home ranges.

I obtained elevation data from the ASTER Global Digital Elevation Model (GDEM) (NASA LP DAAC, 2009) with 30 m spatial resolution and derived the slope using the Slope tool in ArcGIS 10.2 (Environmental Systems Research Institute Inc, USA). For distance from roads and distance from water, roads network of the park and water surfaces were obtained from the park managers and distance rasters with 30 m spatial resolution were derived using the Euclidean distance tool in ArcGIS 10.2 (Environmental Systems Research Institute Inc, USA). Two distances from water maps were created, one for the late dry season, excluding the pans that dried up during this time, and other one for the other seasons. Monitoring of seasonal pans was made during the field

work and using Google earth images. MODIS NDVI imageries, having a temporal resolution of 16 days and a spatial resolution of 250 m were download from the GLOVIS website (http://glovis.usgs.gov/) and used as a measure of vegetation greenness. I calculated NDVI seasonal means and reformulated them in four equal categories, associated with low to high greenness in order to avoid convergence failures. Convergence failures occur when the algorithms for fitting a model do not converge on maximum likelihood estimates for that model (Allison, 2004). I also reformulated the spatial resolution to 30 m to be in conformity with other variables. Convergence failures occur when the algorithms for fitting a model do not converge on maximum likelihood estimates for that model (Allison, 2004). This imagery provides a measure of spatial variability in the quantity and greenness quality of vegetation (Huete *et al*., 2002; Pettorelli *et al*., 2005; van Bommel *et al*., 2006) and has demonstrated close correspondence with aboveground vegetation biomass for savannas (Huete *et al*., 2002). The range of MODIS NDVI values varies from 0–10.000, with larger values representing greener vegetation and smaller values representing no vegetation (Pettorelli *et al*., 2011). I created a vegetation map of the study area from a visual interpretation of Landsat imageries from June and August 2015 in ArcGIS 10.2 (Environmental Systems Research Institute Inc, USA). Eighteen vegetation classes were defined, adapted from plant communities discriminated by Stalmans & Beilfuss (2008). I used field observations and data from vegetation surveys of the park provided by the park managers as a reference data (ground truth) for the classification (Fig 2, Table 1). Landscaps of the park were obtained as shapefile form the park managers and descriptions of the different landscapes can be obtained in Stalmans & Beilfuss (2008).

Field data processing

To assess distribution of competitors and predation risk, logistic regressions were used to build resource selection functions (RSFs), under the used-availability design (Boyce *et al.*, 2002; Manly *et al.*, 2002). For competitors, I created individual models for species that can compete with sable and were observed when walking transects and, as proxy of predation risk I considered 3 approaches, which will be described further below. To create the RSFs, I defined the observations recorded in transects as used resources. To define available resources, I created buffers around transects based on maximum detection distance, estimated by Program DISTANCE (Thomas *et al*., 1998), and then created random points at a ratio of 1:1 to the number of used locations. The explanatory variables were all the GIS layers described above. The values of different GIS layers at each used and random location were then extracted. A set of different combination of GIS layers,

including the global model was constructed using the resource selection probability function (Manly *et al*., 2002):

$$w * (x) = \frac{\exp\left(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ \ldots \ + \ \beta_p x_p\right.}{1 + \exp\left(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ \ldots \ + \ \beta_{\mathrm{p}} x_{\mathrm{p}}\right.}$$

Where β_0 to β_p are coefficients of each independent variable (abiotic factors) and x_0 to x_p are the abiotic factors that the probability of success is related to.

For competitors, I considered data from waterbuck (*Kobus ellipsiprymnus*) and common reedbuck (*Redunca arundinum*) only, because the number of potential competitors with sable is still low, with very few observation points in transects. In total I recorded 53 and 39 locations of waterbuck and reedbuck respectively.

For predation risk, I used 3 proxy methods to create the models. The first method was using signs of predation recorded during field work (kills and direct observation) as used resources. The second method was using prey available biomass of all species recorded along transects (bushbuck, hartebeest, impala, kudu, nyala, oribi, reedbuck, warthog, waterbuck and wildebeest), following the methods used by Chirima (2009) in the Kruger National Park. Each species was weighted based on relative selection shown by lions for these species (Owen-Smith & Mills, 2008) (i.e. a species will be weighted relative to how much it contributed to lion diet elsewhere). The relative degree of selection for different prey species by lion was derived by comparing the proportion in the prey killed with the proportion in the herbivore assemblage, as proposed by Manly *et al*. (2002). Because there is no information published on prey selection by lion in Gorongosa, information from KNP (see Owen-Smith & Mills, 2008 and Chirima, 2009 for details) was used (Table 2). The third method for risk of predation was the use of presence/absence data of all prey species recorded in transects, considering all record in transect as "presence" and creating equal number of random points and considering them as "absence".

Model selection was based on Akaike weights (w) of the models. I calculated Akaike weights (w) based on the Akaike's Information Criterion (AIC) values of the models and selected the model with the best fit, i.e. the models with $w \geq 0.90$ (Burnham & Anderson, 2002). When none of the models had $w \geq 0.90$, i.e. model selection was uncertain, I used the multi-model inference approach by computing the average model parameters weighted by the Akaike weights of each model (Burnham *et al*., 2011). Selected models were then converted into maps.

Resource selection by sable

Resource selection functions (RSF) were estimated using use-availability logistic regressions (Boyce *et al.*, 2002; Manly *et al.*, 2002) following the same equation used for the predators and competition maps. For this, first I created Minimum Convex Polygons (MCP – Hayne, 1949; Harris *et al*., 1990) using 100% convention for annual home ranges in ArcGIS using the Hawth's Analysis Tools extension MCPs. I defined sable collar locations as used resources and random points created within their MCP as available resources (Manly *et al*., 2002). For the mopane herd I used 388 locations for the late dry season, 214 for the early wet, 246 for the late wet and 339 for the early dry. For the Chitengo herd I used 277 locations for late dry season, 181 for the early wet, 229 for the late wet and 257 for the early dry. I sampled random points at a ratio of 1:1 to the number of used locations to ensure that the random points representing the available resources were accessible to the animals at that particular spatial scale (Recio *et al*., 2014). I included in the models all biotic variables (waterbuck probability use, reedbuck probability use, predation risk by signs, predation risk by prey available biomass and predation risk by location of all herbivores) and GIS layers (elevation, slope, distance to roads, distance to water, NDVI, vegetation and landscape). I tested all variables for correlation first. Predation risk model using presence/absence of all prey species recorded in transects was removed from analysis because of high correlation with reedbuck and waterbuck models. I created RSF for each herd for different seasons and created models for biotic variables separated from models for GIS layers. The main reason was because, for biotic variables I only created models for the late dry season, as transects only covered this season of the year. Model selection was based on Akaike weights (*w*) of the models, the same approach used for predators and competition maps.

RESULTS

Predation risk and competitors

Information for competitors and predation risk were recorded along 12 walking transects, providing 338 ground locations. Among the biotic factors, predation risk and probability use of the area by reedbuck appeared to be the more important factors for both herds within their home ranges (Table 3). For mopane herd, models that combined predation risk using prey biomass, predation risk using signs of predation and reedbuck

probability use of the area received more statistical support for explaining selection within home ranges (Table 4). For the Chitengo herd, models that combined predation risk using prey biomass and reedbuck probability use of the area received more statistical support for explaining selection within home ranges (Table 5).

The mopane herd avoided high prey biomass areas and high concentrations of reedbuck but seemed to favour areas with high evidence (signs) of predation. Herd prevalence decreased by a factor of 0.003 (-0.004, -0.002) in high prey biomass areas and by 3.44 (-4.57, -2.3) in areas of high probability use of the area by reedbuck, increasing of 0.86 (0.23, 1.5) in areas of high signs of predation, but the effect of signs of predations was less influential than the other two factors. The Chitengo herd also avoided high prey biomass areas, but seemed to favour areas of high concentrations of reedbuck, contrary to the pattern showed by the mopane herd. Herd prevalence decreased by a factor of 0.002 (-0.003, -0.001) in high prey biomass areas and with an increase of 2.97 (1.78, 4.15) in high probability use of the area by reedbuck areas (Table 3).

Environmental variables

The mopane herd was most influenced by distance from water, distance from roads and DEM (Table 6). However, none of the models generated for the different seasons was strongly superior to others in explaining where sable mopane herd occurred (Table 7). During the late dry season, the mopane herd were more prevalent in the alluvial fan landscape rather than the riverine and floodplain landscape, with prevalence increasing by 1.98 (1.42, 2.54) in alluvial fan landscape areas. The herd also demonstrated evidence of selection for areas far from roads and from water (Table 6). In wet seasons, the mopane herd was positively associated with elevation and distance from water. Probability use of areas by the herd was higher in high elevation areas and far from water. Probability use also increased with the proximity to roads in the early wet season (Table 6). During the early dry season, prevalence was higher far from roads and close from water sources, contrary to patterns demonstrated during wet season (Table 6). Although effects of vegetation types on where the herd occurred appeared weak for all season, it improved the fit of the models in both late and early dry seasons, appearing in all best models supported (Table 7).

The Chitengo herd demonstrated evidence of selection among greenness categories and DEM. Distance from roads and slope also influenced selection in some seasons (Table 8). The herd late dry season selection within home ranges was associated with greenness category 3 more than category 4 and lowest categories of

greenness. The herd also used more frequently areas close to roads (table 8). During the wet seasons, the herd was more prevalent in high elevation areas and seemed to avoid the highest categories of greenness. Early wet season probability use of areas increased also in acacia-cumbretum woodlands while in late wet season herd did not demonstrated evidences of preferring a specific vegetation type. Probability use of areas during this season was also influenced by distance from water and slope, decreasing with the increase of distance from water sources and in areas with high slope. Herd continued to favour high elevation areas and low slopes during early dry season, also increasing prevalence with proximity to roads. Effects of vegetation on where herd occurred, despite appearing weak during dry season, improved the fit of the models in both late and early dry season, appearing in all models best supported (Table 9).

DISCUSSION

Findings presented in this study demonstrate that effects of predation risk and competition influenced recourses selection within both sable herds home ranges. Sable herds were less prevalent areas with high predation risk, but competition differed between herds. Mopane herd were less prevalent areas with high reedbuck probability use while the Chitengo herd seemed to favour those areas. Avoidance of high predation and competition risk areas by sable is consistent with results reported for a number of studies (Sinclair & Arcese 1995; Chirima, 2009; Valeix *et al*., 2009a; Macandza *et al*., 2012). In terms of environmental variables, factors influencing selection within home ranges were different between the two herds. Distance to water, distance to roads and elevation were the best supported environmental factors explaining use of areas by the mopane herd while the Chitengo herd demonstrated evidences of selection among greenness categories and elevation.

Predation risk and competitors

I predicted that competition effects and predation risk would be negatively associated with sable selection within home ranges. My results suggest that both herds favoured low predation risk areas within their home ranges, despite the low number of predators in the park. Predation risk using prey biomass appeared more influential on both herds, followed by predation risk using signs of predation. However, predation risk using signs of predation had a positive influence on mopane herd selection, contrary to what I was expecting. This can be explained in part because the search of signs of predation was made along transect, but also when

searching for the herds during the field work. This could influence the results found here, as within the herds home ranges the effort on searching for signs of predation was higher than elsewhere in the study area. Effect of predation risk using signs of predation on the Chitengo herd was also positive, but it was not significant. In fact, in the field, more lion kill sites were found around the mopane herd ranges, than around the Chitengo herd. Previous studies documented that risk of predation by lions influences the behaviour of African herbivores (Sinclair & Arcese, 1995; Creel *et al*., 2005; Valeix *et al*., 2009a; Valeix *et al*., 2009b; Creel *et al*., 2014). Lima (1998) suggested that indirect effects of predators on prey, such as the alteration of prey behaviour, have larger ecological impacts than actual predation. Chirima (2009) found that the highest sable herd densities in Kruger National Park, South Africa were located where prey abundance and lion sightings were both relatively low. Sable prevalence dropped from about 0.50 (50%) in areas of lowest predation risk to 0.25 in highest predation risk areas. Sinclair & Arcese (1995) and Valeix *et al*. (2009a) also reported that herbivores, including sable, avoid areas characterised by high risk of predation, leading herbivores, in some cases, to use marginal sites/patches were food quantity and quality is low.

Previous studies suggest that competition could influence selection within home range level (Grobler, 1981, Sinclair 1985; Macandza *et al*., 2012). I predicted that competition effects would have negative association with sable prevalence within home ranges. Due to their abundance, only reedbuck and waterbuck were considered for this study as potential competitors with sable. Reedbuck appeared to have more influence on sable herds prevalence within home ranges compared with the effects of waterbuck. However, Marshall *et al*. (2016), in Kgaswane Mountain Reserve, documented waterbuck having an effect on sable, contrary to founding on this study, showing that sable numbers decreased with the increase on waterbuck numbers. From the results, reedbuck seems to have different effects in both herds prevalence. The mopane herd appeared be less prevalent in high concentration of reedbuck while the Chitengo herd seems to favour such areas. Numbers of other herbivores documented in previous studies as potential competitors with sable, such as buffalo and zebra, which utilize a similar height grass range to sable (Macandza *et al*., 2012) or wildebeest through apparent competition (Chirima *et al*., 2012; Owen-Smith *et al*., 2011) are still low in the park (about 700 buffalos, 40 zebras and 360 wildebeest on last count in the park; Stalmans *et al*., 2014). The low number of potential competitors can be one of the reasons why sable are thriving in the park. Hofer *et al*. (2004), using survey records of sable antelope in the Selous-Niassa corridor suggested that the population of the species is reportedly increasing likely because abundances of impala, wildebeest, zebra, and buffalo are very low in this area.

Chirima (2009) suggested that competition influences from zebra, buffalo, impala, and wildebeest could be exerting negative effects on sable prevalence, thus relegating the latter to areas of low abundances of these species. In his study, effects from impala and wildebeest appearing to be more influential on where sable herds established home ranges than effects of zebra and buffalo, probably because of predation risk associated with areas with high concentration of impala and wildebeest. Wildebeest constitute the most preferred species for lions in KNP (Owen-Smith & Mills, 2008). However, effects of competition and predation on sable in this study need to be analyzed with caution, because they may be associated with environmental variables, as the models were originated from these environmental variables. For example, reedbuck model (Table 10), shows landscape as the most influential variable, followed by distance from roads. Reedbuck seems to prefer rift valley riverine & floodplain landscape and areas close to roads. As showed above, the mopane herd seemed to avoid reedbuck while Chitengo herd seemed to prefer areas close to reedbuck. Looking to the environmental factors we can find that mopane herd, during the late dry season seemed to prefer areas far from roads and preferred rift valley alluvial fan landscape over rift valley riverine & floodplain landscape, just the opposite of reedbuck. Chitengo herd meanwhile, preferred areas close to roads and avoided rift valley alluvial fan landscape (this was not significant), same as reedbuck, making it difficult to conclude whether it is in fact the effect of reedbuck or the effect of the environmental variables.

Environmental variables

Water was the best supported environmental factor in explaining use of areas within home ranges by the mopane herd followed by distance from roads, and NDVI. Elevation was the most influential for the Chitengo herd. I was expecting herds to prefer areas close to water during dry seasons. Mopane herd however, preferred areas far from water instead of being close to water sources during the late dry season. It seems that the herd was forced to range far from water points. During this time of the year, all water sources close to the herd home range were dry, remaining only a small pan that in October also dried out, and the Urema Lake. Both sources of water however, were far from the suitable habitats for sable (personal observations). During the field work months it was possible to note that the areas surrounding the remaining water points were composed by short grasslands or medium and tall grasslands transformed practically in bare soils by fire, becoming unsuitable for sable. In the wet seasons, the herd also seemed to prefer areas far from water. According to Tinley (1977), during wet seasons, the Lake Urema increases its extension from 10 km^2 (dry season minimum)

up to 200 km^2 (wet season maximum) and large grasslands areas are regularly inundated. So, it seems that the herd was probably avoiding these inundated areas. The Chitengo herd was always less than 3 km from water, and from models, distance from water only influenced selection during the late wet season, where the herd favoured areas close to water. Because the Chitengo herd uses almost exclusively woodlands during all seasons (chapter 2) which have higher elevations, inundations have less effect in their selection during wet seasons. It has been reported in a number of studies that sable are a highly water dependent species (Estes & Estes 1974, Western 1975, Wilson & Hirst 1977, Grobler, 1981, Skinner & Chimimba, 2005, Smit *et al*. 2007). However, similar to the mopane herd in this study, Rahimi & Owen-Smith (2007) have documented more water independent behaviour in sable in the Kruger National Park. They suggest sable may be more water independent, drinking only every 3-4 days and travelling up to 7 km from water sources. Capon (2011), in Malilangwe Wildlife Reserve (MWR), south-eastern Zimbabwe, also recorded that sable consistently foraged further than average from water sources, particularly during the dry season.

Human presence through road network may influence the spatial distribution of medium-sized herbivores such as sable, reducing sense of security and cover on hunting areas (Setsaas *et al.*, 2007; Ciuti *et al.*, 2012; Muposhi *et al.*, 2016) or attracting them to avoid predation if human presence creates refugee from predators (Hebblewhite & Merrill, 2009). The mopane herd preferred areas far from roads in the dry season and Chitengo herd areas close to roads. The differences showed by the models may be related to the park road network. Mopane herd established home range in areas with very low road network and the Chitengo herd in areas with high road network, influencing thus the results found here. Chitengo herd was observed during field work in many times feeding close to roads.

Elevation in the study area does not change much, ranging from about 20 to 30 m in the floodplain landscape to about 50 to less than 100 m on wooded landscapes according to the study area DEM. However, even with this small variation in elevation, both herds seemed to favour high elevation areas in the wet season. Chitengo herd continued to favour high elevation areas also during early dry season. This may be associated with the flooding regime in the park, as during the wet season and beginning of dry season many areas get flooded, so animals tend to move to high elevation areas to avoid the floods. Previous studies demonstrated influence of elevation on sable only in the dry season, with herds selecting bottomlands areas, in searching for green grasses retained in these areas during this time (Grober, 1981; Magome, 1991; Parrini, 2006). From field observation and collar data, same behaviour was possible to note for the mopane herd in the end of the dry season, as the herd moved to bottomland areas such as drainage line. It is important to point that none of the

study areas of these previous studies were subjected to temporary long floods such as these in Gorongosa. Evidences from NDVI also suggested selection of high greenness categories for mopane herd during late dry season, probably as consequence of herd moving to areas that still retained green grasses. Chirima (2009), in Kruger National Park also found that sable was positively associated with dry season NDVI, but contrary to founding in this study, were Chitengo herd avoided high NDVI areas during wet season, he found also positive association with wet season NDVI. Mordecai (2016) also found, in Kgaswane Mountain Reserve, South Africa, one sable herd associated to higher NDVI values comparing with what was available. I was expecting also preference of high NDVI values during wet season, as the herd used more dense habitats during those periods (Chapter 2), reflecting contributions of tree canopy cover to NDVI values. The only probably justification of low NDVI values preferences by the mopane herd may be related to influence of water in the NDVI values. Because water has a much lower NDVI value than other surfaces, inundated areas may also result in low NDVI values.

Slope, landscape and vegetation type were the less influential factors within sable home ranges. Slope only influenced Chitengo herd during late wet and early dry season, where the herd favoured low slope areas. Glover (1969) also observed that sable avoid slopes, attributing this preference to lower density of grass on steeper inclines, many of which show signs of extensive soil erosion. Landscape only influenced selection for mopane herd during the late wet season, where the herd preferred the Rift Valley Alluvial Fan landscape that consists of a complex mix of open to closed woodlands and dry forest/thickets reflecting the structural soil characteristics and moisture regime of the alluvial fans. The tendency of sable selecting landscapes with a high proportion of the woodland component of vegetation is in agreement with patterns observed elsewhere (Estes & Estes, 1974, Wilson & Hirst, 1977, Grobler, 1981; Chirima, 2009).

Research on sable has described selection by the specie at different levels, from which plants species or parts of plants to select (Parrini, 2006; Magome *et al*., 2008; Macandza, 2009; le Roux, 2010), to what drives selection of where to establish home ranges (Chirima, 2009), in order to find which factors are responsible for the declining abundance of sable antelope. My findings here demonstrate that predation and competition and effects of environmental factors influence selection by sable within their home ranges. Predation and competition can lead sable to use areas less favourable areas within home ranges. Thus, monitoring of population dynamics of main competitors and lions in the park, and how these can affect sable, could contribute to sable continue to thrive. This study also revealed several unexpected responses of sable to

seasonal changes in the habitat. Sable selected areas within their home range based on distances from roads, distances from water, elevation and greenness. These data suggest that sable may indirectly be sensitive to changes in water distribution and food availability through the seasons. Distances from roads may be associated with the park network, as one herd established home ranges in areas with low roads density and the other herd in areas with high road densities.

TABLES

Table 1: Characteristics of the vegetation types found in southwest of Gorongosa National Park

Vegetation Type	**Defining Characteristics (adapted from Stalmans & Beilfuss (2008).**
Dry Forest/Thicket	Very dense formation typified by woody species such as *Cleistochlamys kirkii, Diospyros senesis, Craibia zimmermannii, Alchornea laxiflora, Milletia stuhulmannii, Markhamia acuminata, Capparis sp.* and *Thilachium africanum*. The grass layer is sparse occurring when present *Brachiaria deflexa, Digitaria sp.* And *Oplismenus sp.*
Gallery Forest	Woody formation found on humid soils close to permanent drainage lines.
Miombo Woodlands	Open to close woodland dominated by species such as *Brachistegia boehmii, Julbernardia globiflora, Acacia nigrescens, Diplorhynchus condylocarpon, Sterculia quinqueloba, Strychnos potatorum* and *Pterocarpus rotundifolius*. Grass layer varies from short to tall, dominated by *Panicum maximum, Digitaria eriantha, Themeda triandra* and *Sporobolus sp.*
Inselberg Miombo	Closed miombo woodland with a more open canopy on rock outcrops. This formation occurring on small inselbergs that occur in the park.
Mixed Forest (Riverine)	Open to closed woody formation occurring close to Pungue river and Pungue drainage lines. Species such as *Hyphaene petersiana, Borassus aethiopium, Piliostigma thonningii, Philenoptera violacea, Combretum adenogonium, Acacia sieberana* dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata, Panicum maximum, Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Acacia xanthophloea Woodland	Open to close woodland dominated by *Acacia xanthophloea*. This formation is seasonally inundated. Grass layer is usually tall dominated by *Panicum maximum, Setaria incrassata* and *Cynodon dactylon*
Acacia-Combretum Woodland	This is the most extensive community. Characterised by open to close woodlands dominated by *Combretum adenogonium, C. imberbe, Acacia nigrescens, A. robusta* and also occurring frequently *Sclerocarya birrea,*

	Dalbergia melanoxylon, Philenoptera violacea e *Ziziphus mucronata*. Grassland layer varies from short to tall dominated by *Panicum maximum, Digitaria eriantha, Heteropogon contortus, Urochloa mossambicensis* and *Themeda triandra*. Often with termite mounds.
Colospermum mopane Woodland	Short closed woodland dominated by Mopane (*Colophospermum mopane*). Grass cover is sparse dominated by *Enteropogon macrostachyus* with *Digitaria eriantha* and *Chloris sp.* on the edges.
Faidherbia albida Woodland	Open to close woodland dominated by *Faidherbia albida*, found close to Urema Lake and subjected to temporary inundations. Grass layer ranges from short to tall, dominated by *Cynodon dactylon*, *Digitaria swazilandensis* and *Echinochloa pyramidalis*.
Dichrostachys cinerea Shrubland	Closed shrubland dominated by *Dichrostachys cinerea*, found mostly at edge of mopane and other woodlands. Grass cover is sparse, occurring when present *Panicum maximum* and *Brachiaria deflexa*
Dalbergia melanoxylon Shrubland	Closed shrubland dominated by *Dalbergia melanoxylon*, found mostly at edge of other taller woodlands. Grass layer is usually short and open, dominated by *Panicum maximum, Heteropogon contortus, Aristida sp.* and *sporobolus sp.*
Palm Veld	Open to closed woody formation subjected to temporary inundation. Species such as *Hyphaene petersiana*, *Borassus aethiopium* and *Phoenix reclinata* dominates. Grass layer varies from short to tall, dominated by *Setaria incrassata*, *Panicum maximum*, *Vetiveria nigritana, Hyparrhenia sp.* and *Oplismenus sp.*
Short Grassland	Short closed grassland formation dominated by *Cynodon dactylon* and *Digitaria swazilandensis*. This formation is being invaded by alien specie *Mimosa pigra,* and during wet seasons is subjected to floods
Saline Grasslands	Short open grassland formation dominated by *Sporobolus iocladus*. This formation usually occurs associated with Acacia.
Pan Grasslands	Short closed grassland formation that occurs along pans dominated by *Paspalidium obtusifolium, Echinochloa sp., Oryza longistaminata* and *Hemarthiria altissima*.
Shrub Grassland	Medium to tall grassland with patches of *Dichrostachys cinerea* shrubs.

	Grass species such as *Panicum maximum, Setaria incrassata, Vetiveria nigritana* and *Brachiaria deflexa*
Medium-Tall Grassland	Medium to tall grassland dominated by *Panicum maximum, Panicum coloratum, Setaria incrassata, Vetiveria nigritana* and *Brachiaria deflexa*
Tall Grassland	Tall grassland, normally adjacent to permanent water and seasonally inundated. Dominated *Echinochloa pyramidalis* and *Vetiveria nigritana*.
Shifting Cultivation	Seasonal cultivation by the communities. Found mainly south of Pungue river.
Water	Open water, typified by Urema lake, Pungue river and other permanent water streams.

Table 2: Prey species for lion, body mass and weighting factor (kill likelihood) used to calculate the predation index (Adapted from Owen-Smith & Mills, 2008)

Species	**Body mass**	**Weighting factor**
Wildebeest	208	1
Warthog	83	0.8
Waterbuck	210	0.8
Kudu	214	0.7
Zebra	270	0.6
Buffalo	600	0.5
Eland	463	0.5
Sable antelope	230	0.5
Hartebeest	135	0.5
Nyala	86	0.2
Bushbuck	73	0.2
Reedbuck	58	0.2
Impala	52	0.2

Table 3: Resource selection function model average, describing predation and competitors influence within sable late dry season home ranges in Gorongosa National Park, 2015

Variables	Estimate	95% CI	
		Lower	Upper
Mopane herd			
(Intercept)	0.746	0.476	1.015
Biomass	-0.003	-0.004	-0.002
Signs	0.864	0.234	1.495
Reedbuck	-3.435	-4.573	-2.297
Waterbuck	1.278	-0.034	3.792
Chitengo Herd			
(Intercept)	-0.723	-1.104	-0.341
Biomass	-0.002	-0.003	-0.001
Reedbuck	2.967	1.78	4.153
Waterbuck	-0.487	-1.175	-0.023
Signs	0.0312	-1.888	2.175

Table 43: Summary of the sixteen models utilised to explain resource selection by sable mopane herd as function of predation and competitors within late dry season home ranges in Gorongosa National Park, 2015. Models are ranked according to their AICc value and best models are indicated in boldface

Models	**logLik**	**K**	**AICc**	**ΔAICc**	w_i**AICc**
Biomass + signs + reedbuck + waterbuck	**-381**	**5**	**772.1**	**0.00**	**0.642**
Biomass + signs + reedbuck	**-382.8**	**4**	**773.6**	**1.51**	**0.302**
Biomass + reedbuck	-386	3	778.0	5.91	0.033
Biomass + reedbuck + waterbuck	-385.4	4	778.8	6.64	0.023
Signs + reedbuck	-401.7	3	809.4	37.25	0.000
Signs + reedbuck + waterbuck	-400.9	4	809.9	37.80	0.000
Reedbuck + waterbuck	-403	3	812.0	39.82	0.000
Reedbuck	-404.4	2	812.8	40.64	0.000
Biomass + waterbuck	-406.3	3	818.6	46.45	0.000
Biomass + signs + waterbuck	-406.3	4	820.6	48.47	0.000
Biomass	-410.7	2	825.3	53.21	0.000
Biomass + signs	-410.6	3	827.3	55.18	0.000
Waterbuck	-425.8	2	855.7	83.57	0.000
Signs + waterbuck	-425.5	3	857.0	84.85	0.000
Signs	-466.1	2	936.1	164.01	0.000
Intercept	-468.6	1	939.1	167.01	0.000

Notes: Biomass – predation risk model using prey biomass; Signs - predation risk model using signs of predation; Reedbuck – reedbuck probability use model; Waterbuck - waterbuck probability use model; LogLik – Natural logarithm of the maximum likelihood; *K*- number of parameters; AICc – Akaike's Information Criterion; ΔAICc – calculated as AICi-minAIC; w_iAICc – rounded Akaike weights

Table 5: Summary of the sixteen models utilised to explain resource selection by Chitengo herd as function of predation and competitors within late dry season home ranges in Gorongosa National Park, 2015. Models are ranked according to their AICc value and best models are indicated in boldface

Models	**logLik**	**K**	**AICc**	**ΔAICc**	w_i**AICc**
Biomass + reedbuck + waterbuck	**-368.5**	**4**	**745.1**	**0.00**	**0.552**
Biomass + signs + reedbuck + waterbuck	**-368.5**	**5**	**747.1**	**2.02**	**0.201**
Biomass + reedbuck	**-370.7**	**3**	**747.4**	**2.33**	**0.172**
Biomass + signs + reedbuck	-370.6	4	749.3	4.16	0.069
Reedbuck + waterbuck	-374.7	3	755.5	10.36	0.003
Signs + reedbuck + waterbuck	-374.7	4	757.4	12.30	0.001
Reedbuck	-378.1	2	760.1	15.03	0.000
Signs + reedbuck	-377.8	3	761.6	16.53	0.000
Waterbuck	-381	2	766.1	21.01	0.000
Biomass + waterbuck	-381	3	768.0	22.92	0.000
Signs + waterbuck	-381	3	768.0	22.94	0.000
Biomass + signs + waterbuck	-380.9	4	770.0	24.85	0.000
Intercept	-384	1	770.0	24.92	0.000
Signs	-383.8	2	771.6	26.47	0.000
Biomass	-384	2	772.0	26.93	0.000
Biomass + signs	-383.8	3	773.6	28.48	0.000

Notes: Biomass – predation risk model using prey biomass; Signs - predation risk model using signs of predation; Reedbuck – reedbuck probability use model; Waterbuck - waterbuck probability use model; LogLik – Natural logarithm of the maximum likelihood; *K*- number of parameters; AICc – Akaike's Information Criterion; ΔAICc – calculated as AICi-minAIC; w_iAICc – rounded Akaike weights

Table 6: Resource selection function model average, describing environmental variables influence within sable mopane herd home ranges Gorongosa National Park, 2015-16

Variables	Estimate	95% Confidence Interval	
		Lower	Upper
Late dry season			
(Intercept)	-18.53	-1212	1175
Acacia-combretum wood.	14.78	-1179	1208
Mopane Woodland	16.73	-1177	1211
Dalbergia Shrubland	-0.42	-7860	7859
Dry Forest/Thicket	14.49	-1179	1208
Gallery Forest	13.87	-1180	1208
Medium-Tall Grassland	16.25	-1178	1210
Saline Grassland	14.09	-1180	1208
Short Grassland	14.70	-1179	1209
Tall Grassland	15.94	-1178	1210
Shrubs Grassland	16.95	-1177	1211
Alluvial Fan landscacpe	1.977	1.417	2.538
Slope	0.018	-0.011	0.081
Distance from roads	< 0.001	< 0.001	< 0.001
Distance from water	< 0.001	< 0.001	< 0.001
NDVI3	-0.218	-1.042	0.161
DEM	0.002	-0.022	0.037
Early wet season			
(Intercept)	-4.983	-6.32	-3.646
NDVI3	-0.699	-1.444	-0.131
Acacia-Combretum wood.	-0.7685	-1.896	3.587
Dry Forest/Thicket	-18.24	-3052	3016
Gallery Forest	-15.40	-5465	5434
Medium-Tall Grassland	0.211	-0.812	1.233
Saline Grassland	-0.207	-2.634	2.222
Short Grassland	-1.888	-4.217	0.441
Tall Grassland	-15.09	-2129	2099
Shrubs Grassland	0.171	-2.925	3.265
DEM	0.135	0.1	0.171
Distance from roads	> -0.001	> -0.001	> -0.001
Distance from water	< 0.001	< 0.001	< 0.001
Alluvial Fan landscape	-0.129	-1.095	0.357
Slope	0.004	-0.049	0.080
Late wet season			
(Intercept)	-25.59	-3963	3912
NDVI3	-0.513	-1.357	0.142
Acacia-Combretum wood.	17.77	-3920	3955

Mopane Woodland	0.901	-21496	214944
Dalbergia Shrubland	-0.922	-21496	21494
Dry Forest/Thicket	15.12	-3923	3953
Gallery Forest	-0.548	-9239	9238
Medium-Tall Grassland	18.28	-3919	3.956
Pan Grassland	1.683	-21493	21497
Saline Grassland	1.054	-7567	7571
Short Grassland	1.493	-5332	5335
Tall Grassland	2.503	-5875	5880
Shrubs Grassland	-2.775	-6691	6685
DEM	0.144	0.107	0.172
Distance from water	0.001	< 0.001	0.002
Distance from roads	> -0.001	> -0.001	<0.001
Alluvial Fan landscape	-0.052	-0.519	0.804
Slope	0.002	-0.059	0.778
Early dry season			
(Intercept)	-17.5	-1670	1635
NDVI3	-0.569	-1.318	-0.12
Acacia-Combretum wood.	17.72	-1635	1670
Mopane Woodland	20.31	-1632	1673
Dalbergia Shrubland	18.96	-1634	1671
Dry Forest/Thicket	-0.921	-5047	5045
Gallery Forest	19.24	-1633	1672
Medium-Tall Grassland	-0.72	-9182	9180
Saline Grassland	-0.118	-4711	4711
Short Grassland	15.96	-1637	1668
Tall Grassland	-1.412	-3362	3359
Shrubs Grassland	20.59	-1632	1673
Alluvial Fan landscape	-0.320	-0.927	0.150
Distance from roads	< 0.001	< 0.001	< 0.001
Distance from water	> -0.001	-0.001	> -0.001
Slope	0.003	-0.032	0.054
DEM	-0.001	-0.033	0.02

Notes: DEM – Digital Elevation Model, NDVI – Normalized Difference Vegetation Index

Table 7: Summary of the twenty best models (over a hundred) per season utilised to explain resource selection by sable mopane herd as function of predation and competitors within late dry season home ranges in Gorongosa National Park, 2015-16. Models are ranked according to their AICc value and supported models are indicated in boldface

Models	**logLik**	**K**	**AICc**	**ΔAICc**	w_i**AICc**
Late dry Season					
Slope + dist_roads + dist_water + landsc + veget	**-325.8**	**15**	**682.4**	**0.00**	**0.183**
Slope + dist_roads + dist_water + NDVI + landsc + veget	**-324.8**	**16**	**682.4**	**0.03**	**0.180**
Dist_roads + dist_water + landsc + veget	**-327**	**14**	**682.7**	**0.27**	**0.160**
Dist_roads + dist_water + NDVI + landsc + veget	**-326**	**15**	**682.7**	**0.33**	**0.155**
DEM + dist_roads + dist_water + landsc + veget	**-326.7**	**15**	**684.2**	**1.75**	**0.076**
DEM + dist_roads + dist_water + NDVI + landsc + veget	**-325.7**	**16**	**684.2**	**1.77**	**0.075**
DEM + slope + dist_roads + dist_water + landsc + veget	**-325.8**	**16**	**684.5**	**2.07**	**0.065**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-324.8**	**17**	**684.5**	**2.09**	**0.064**
DEM + dist_water + landsc + veget	-329.7	14	688.0	5.59	0.011
DEM + dist_water + NDVI + landsc + veget	-329.1	15	689.0	6.61	0.007
DEM + slope + dist_water + landsc + veget	-329.2	15	689.2	6.81	0.006
Slope + dist_water + landsc + veget	-330.7	14	690.0	7.59	0.004
DEM + slope + dist_water + NDVI + landsc + veget	-328.7	16	690.3	7.91	0.004
Dist_water + landsc + veget	-332.1	13	690.8	8.41	0.003
Slope + dist_water + NDVI + landsc + veget	-330.4	15	691.5	9.13	0.002
Dist_water + NDVI + landsc + veget	-331.9	14	692.4	9.96	0.001
DEM + dist_roads + NDVI + landsc + veget	-330.9	15	692.6	10.22	0.001
DEM + slope + dist_roads + NDVI + landsc + veget	-330.2	16	693.2	10.84	0.001
DEM + dist_roads + landsc + veget	-332.5	14	693.6	11.17	0.001
DEM + slope + dist_roads + landsc + veget	-331.8	15	694.2	11.85	0.000
Early wet season					
DEM + dist_roads + dist_water + NDVI + veget	-190.2	13	407.2	0.00	0.353
DEM + dist_roads + dist_water + NDVI + landsc + veget	-189.7	14	408.5	1.32	0.183
DEM + slope + dist_roads + dist_water + NDVI + veget	-190	14	409.1	1.86	0.139
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	-189.7	15	410.5	3.33	0.067
DEM + dist_roads + dist_water + landsc + veget	-191.9	13	410.7	3.48	0.062
DEM + dist_water + NDVI + veget	-193.2	12	411.2	4.02	0.047
DEM + dist_roads + dist_water + veget	-193.4	12	411.6	4.40	0.039
DEM + slope + dist_water + NDVI + veget	-192.9	13	412.6	5.38	0.024
DEM + slope + dist_roads + dist_water + landsc + veget	-191.9	14	412.8	5.58	0.022
DEM + dist_water + NDVI + landsc + veget	-193.6	13	413.2	6.00	0.018
DEM + slope + dist_roads + dist_water + veget	-193.3	13	413.5	6.33	0.015
DEM + slope + dist_water + NDVI + landsc + veget	-192.8	14	414.6	7.45	0.009
DEM + dist_roads + dist_water + NDVI	-202.4	5	415.0	7.82	0.007
DEM + dist_roads + dist_water + NDVI + landsc	-202.2	6	416.6	9.36	0.003
DEM + dist_water + veget	-197.1	11	416.9	9.69	0.003
DEM + slope + dist_roads + dist_water + NDVI	-202.4	6	417.0	9.80	0.003
DEM + dist_water + landsc + veget	-196.3	12	417.4	10.24	0.002
DEM + dist_roads + NDVI + veget	-196.5	12	417.7	10.55	0.002

DEM + slope + dist_water + veget	-196.8	12	418.3	11.14	0.001
DEM + slope + dist_roads + dist_water + NDVI + landsc	-202.2	7	418.6	11.40	0.001
Late wet season					
DEM + dist_water + NDVI + veget	**-145.5**	**15**	**322.0**	**0.00**	**0.205**
DEM dist_water + veget	**-146.8**	**14**	**322.6**	**0.52**	**0.158**
DEM + dist_roads + dist_water + NDVI + veget	**-145.3**	**16**	**323.7**	**1.69**	**0.088**
DEM + dist_roads + dist_water + veget	**-146.4**	**15**	**323.9**	**1.82**	**0.083**
DEM + dist_water + NDVI + landsc + veget	**-145.4**	**16**	**323.9**	**1.83**	**0.082**
DEM + slope + dist_water + NDVI + veget	**-145.5**	**16**	**324.1**	**2.07**	**0.073**
DEM + slope + dist_water + veget	**-146.8**	**15**	**324.5**	**2.49**	**0.059**
DEM + dist_water + landsc + veget	**-146.8**	**15**	**324.7**	**2.64**	**0.055**
DEM + dist_roads + dist_water + NDVI + landsc + veget	**-145.1**	**17**	**325.6**	**3.54**	**0.035**
DEM + slope + dist_roads + dist_water + NDVI + veget	**-145.3**	**17**	**325.8**	**3.80**	**0.031**
DEM + slope + dist_roads + dist_water + veget	**-146.4**	**16**	**325.9**	**3.87**	**0.030**
DEM + slope + dist_water + NDVI + landsc + veget	**-145.3**	**17**	**325.9**	**3.90**	**0.029**
DEM + dist_roads + dist_water + landsc + veget	**-146.4**	**16**	**326.0**	**3.94**	**0.029**
DEM + slope + dist_water + landsc + veget	**-146.8**	**16**	**326.7**	**4.62**	**0.020**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-145.1**	**18**	**327.7**	**5.65**	**0.012**
DEM + slope + dist_roads + dist_water + landsc + veget	**-146.4**	**17**	**328.0**	**6.00**	**0.010**
DEM + dist_roads + dist_water + NDVI	-171.5	5	353.1	31.09	0.000
DEM + dist_water + NDVI	-173.2	4	354.4	32.34	0.000
DEM + dist_roads + dist_water	-173.4	4	354.8	32.74	0.000
DEM + dist_roads + dist_water + NDVI + landsc	-171.4	6	354.9	32.84	0.000
Early dry season					
Dist_roads + dist_water + NDVI + veget	**-316.3**	**14**	**661.2**	**0.00**	**0.224**
Dist_roads + dist_water + NDVI + landsc + veget	**-315.3**	**15**	**661.3**	**0.13**	**0.210**
DEM + dist_roads + dist_water + NDVI + veget	**-316.2**	**15**	**663.0**	**1.86**	**0.088**
Slope + dist_roads + dist_water + NDVI + veget	**-316.2**	**15**	**663.1**	**1.91**	**0.086**
Slope + dist_roads + dist_water + NDVI + landsc + veget	**-315.2**	**16**	**663.3**	**2.08**	**0.079**
DEM + dist_roads + dist_water + NDVI + landsc + veget	**-315.3**	**16**	**663.4**	**2.19**	**0.075**
Dist_roads + dist_water + landsc + veget	**-317.7**	**14**	**664.1**	**2.88**	**0.053**
DEM + slope + dist_roads + dist_water + NDVI + veget	**-315.8**	**16**	**664.4**	**3.25**	**0.044**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-315.1**	**17**	**665.1**	**3.95**	**0.031**
Dist_roads + dist_water + veget	**-319.4**	**13**	**665.3**	**4.08**	**0.029**
Slope + dist_roads + dist_water + landsc + veget	**-317.6**	**15**	**666.0**	**4.83**	**0.020**
DEM + dist_roads + dist_water + landsc + veget	**-317.7**	**15**	**666.1**	**4.92**	**0.019**
DEM + dist_roads + dist_water + veget	**-319.2**	**14**	**667.0**	**5.78**	**0.012**
Slope + dist_roads + dist_water + veget	**-319.3**	**14**	**667.2**	**5.97**	**0.011**
DEM + slope + dist_roads + dist_water + landsc + veget	**-317.5**	**16**	**667.8**	**6.63**	**0.008**
DEM + slope + dist_roads + dist_water + veget	**-318.7**	**15**	**668.2**	**6.98**	**0.007**
DEM + dist_water + NDVI + landsc + veget	-322.8	15	676.3	15.12	0.000
DEM + dist_water + landsc + veget	-324.5	14	677.6	16.40	0.000
DEM + slope + dist_water + NDVI + landsc + veget	-322.7	16	678.3	17.13	0.000
Dist_water + NDVI + landsc + veget	-324.9	14	678.3	17.16	0.000

Notes: LogLik – Natural logarithm of the maximum likelihood; *K*- number of parameters; AICc – Akaike's Information Criterion; ΔAICc – calculated as AICi-minAIC; w_iAICc – rounded Akaike weights; DEM – Digital Elevation Model; NDVI – Normalized Difference Vegetation Index; dist_roads – Distance from roads; dist_water – Distance from water; landsc – Landscapes of study area; veget – vegetation types of study area

Table 8: Resource selection function model average, describing environmental variables influence within sable Chitengo herd home ranges, Gorongosa National Park, 2015-16

Variables	Estimate	95% CI	
		Lower	Upper
Late dry season			
(Intercept)	-17.15	-1655	1621
NDVI3	2.063	0.874	3.252
NDVI4	0.466	-2.070	3.001
Acacia-Combretum wood.	16.19	-1622	1655
Medium-Tall Grassland	16.43	-1622	1655
Mixed Riverine Forest	14.96	-1623	1653
Open Water	-0.367	-2159	2158
Saline Grassland	31.18	-2570	2633
Tall Grassland	17.05	-1621	1655
Alluvial Fan landscape	-0.322	-1.247	0.119
Distance from roads	> -0.001	-0.001	> -0.001
Distance from water	> -0.001	> -0.001	<0.001
DEM	0.012	-0.016	0.071
Slope	-0.003	-0.789	0.534
Early wet season			
(Intercept)	-20.65	-1597	1556
NDVI3	-1.826	-2.574	-1.078
NDVI4	-2.242	-7941	7936
Acacia-Combretum wood.	2.011	-0.274	4.297
Gallery Forest	-16.70	-7797	7764
Medium-Tall Grassland	0.754	-5712	5713
Mixed Riverine Forest	-0.146	-2.548	2.256
Open Water	0.941	-4189	4190
Alluvial Fan landscape	16.06	-1560	1593
DEM	0.130	0.064	0.196
Distance from water	> -0.001	> -0.001	<0.001
Distance from roads	> -0.001	> -0.001	<0.001
Slope	0.008	-0.036	0.085
Late wet season			
(Intercept)	-20.44	-7796	7755
NDVI3	-1.422	-2.154	-0.691
NDVI4	-18.24	-3411	3375
Acacia-Combretum wood.	18.99	-7756	7794
Dry Forest/Thicket	16.66	-7758	7792
Gallery Forest	-0.619	-9450	9449
Medium-Tall Grassland	1.360	-10994	10997
Mixed Riverine Forest	17.24	-7758	7792

Open Water	-1.149	-8021	8018
DEM	0.134	0.070	0.197
Slope	-0.079	-0.154	-0.019
Distance from roads	<0.001	>-0.001	0.001
Distance from water	-0.002	-0.002	-0.001
Early dry season			
(Intercept)	-8.179	-11.652	-4.705
Acacia-Combretum wood.	0.292	-2.214	2.797
Dry Forest/Thicket	-17.98	-2739	2703
Medium-Tall Grassland	3.152	-0.336	6.640
Mixed Riverine Forest	-0.155	-2.664	2.354
Open Water	-16.07	-1537	1505
Tall Grassland	-15.57	-3058	3027
DEM	0.264	0.197	0.330
Slope	-0.192	-0.261	-0.122
Distance from roads	-0.002	-0.003	-0.001
Distance from water	>-0.001	-0.000	0.000
Alluvial Fan landscape	-0.016	-0.719	0.592
NDVI3	0.018	-0.738	1.243
NDVI4	0.052	-1.097	2.526

Notes: DEM - Digital Elevation Model, NDVI – Normalized Difference Vegetation Index

Table 9: Summary of the twenty best models (over a hundred) per season utilised to explain resource selection by sable Chitengo herd as function of predation and competitors within late dry season home ranges in Gorongosa National Park, 2015-16. Models are rank according to their AICc value and best models are indicated in boldface

Models	logLik	K	AICc	ΔAICc	w_iAICc
Late dry Season					
Dist_roads + dist_water + NDVI + landsc + veget	**-339.2**	**12**	**703.0**	**0.00**	**0.166**
Dist_roads + dist_water + NDVI + veget	**-340.5**	**11**	**703.5**	**0.52**	**0.128**
DEM + dist_roads + dist_water + NDVI + landsc + veget	**-338.6**	**13**	**703.9**	**0.89**	**0.106**
DEM + dist_roads + dist_water + NDVI + veget	**-339.7**	**12**	**704.0**	**1.00**	**0.100**
Dist_roads + NDVI + landsc + veget	**-341**	**11**	**704.4**	**1.44**	**0.081**
DEM + dist_roads + NDVI + landsc + veget	**-340.2**	**12**	**705.0**	**1.98**	**0.062**
Slope + dist_roads + dist_water + NDVI + landsc + veget	**-339.2**	**13**	**705.1**	**2.10**	**0.058**
DEM + slope + dist_roads + dist_water + NDVI + veget	**-339.4**	**13**	**705.4**	**2.42**	**0.050**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-338.3**	**14**	**705.5**	**2.49**	**0.048**
Slope + dist_roads + dist_water + NDVI + veget	**-340.5**	**12**	**705.6**	**2.61**	**0.045**
DEM + dist_roads + + NDVI + veget	**-341.8**	**11**	**706.1**	**3.13**	**0.035**
Dist_roads + NDVI + veget	**-342.9**	**10**	**706.2**	**3.24**	**0.033**
Slope + dist_roads + NDVI + landsc + veget	**-340.9**	**12**	**706.5**	**3.49**	**0.029**
DEM + slope + dist_roads + NDVI + landsc + veget	**-340**	**13**	**706.7**	**3.77**	**0.025**
DEM + slope + dist_roads + NDVI + veget	**-341.6**	**12**	**707.8**	**4.77**	**0.015**
Dist_water + NDVI + veget	**-342.9**	**11**	**708.2**	**5.27**	**0.012**
DEM + slope + dist_roads + veget	-344.5	11	711.4	8.47	0.002
DEM + slope + dist_water + landsc + veget	-343.6	12	711.7	8.73	0.002
DEM + slope + dist_roads + dist_water + NDVI + landsc	-344.6	11	711.7	8.75	0.002
Dist_water + NDVI + landsc	-345.8	10	712.0	8.99	0.002
Early wet season					
DEM + dist_water + NDVI + landsc + veget	**-183.6**	**11**	**390.0**	**0.00**	**0.215**
DEM + dist_roads + dist_water + NDVI + landsc + veget	**-182.7**	**12**	**390.3**	**0.30**	**0.185**
DEM + dist_roads + NDVI + landsc + veget	**-184**	**11**	**390.7**	**0.70**	**0.152**
DEM + slope + dist_water + NDVI + landsc + veget	**-183.4**	**12**	**391.7**	**1.71**	**0.092**
DEM + slope + dist_roads + NDVI + landsc + veget	**-183.5**	**12**	**391.8**	**1.86**	**0.085**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-182.4**	**13**	**391.8**	**1.87**	**0.085**
DEM + NDVI + landsc + veget	**-186**	**10**	**392.5**	**2.59**	**0.059**
DEM + slope + NDVI + landsc + veget	**-185.5**	**11**	**393.8**	**3.86**	**0.031**
DEM + dist_water + NDVI + veget	**-187**	**10**	**394.5**	**4.56**	**0.022**
DEM + dist_roads + dist_water + NDVI + veget	**-186.1**	**11**	**395.0**	**5.05**	**0.017**
DEM + dist_roads + NDVI + veget	**-187.3**	**10**	**395.2**	**5.22**	**0.016**
DEM + slope + dist_water + NDVI + veget	**-186.6**	**11**	**396.0**	**6.01**	**0.011**
DEM + slope + dist_roads + NDVI + veget	**-186.6**	**11**	**396.0**	**6.07**	**0.010**
DEM + slope + dist_roads + dist_water + NDVI + veget	**-185.7**	**12**	**396.3**	**6.34**	**0.009**
DEM + NDVI + veget	**-189.1**	**9**	**396.7**	**6.72**	**0.007**
DEM + slope + NDVI + veget	**-188.5**	**10**	**397.6**	**7.69**	**0.005**
Slope + dist_roads + dist_water + NDVI + landsc + veget	-189	12	402.9	12.93	0.000
Slope + dist_water + NDVI + landsc + veget	-190.2	11	403.2	13.27	0.000

Slope + dist_roads + NDVI + landsc + veget	-190.3	11	403.3	13.36	0.000
Slope + NDVI + landsc + veget	-193	10	406.5	16.57	0.000
Late wet season					
DEM + slope + dist_roads + dist_water + NDVI + veget	**-214.4**	**13**	**455.6**	**0.00**	**0.567**
DEM + slope + dist_water + NDVI + veget	**-216.2**	**12**	**457.2**	**1.52**	**0.266**
DEM + dist_roads + dist_water + NDVI + veget	-217.5	12	459.8	4.16	0.071
DEM + dist_water + NDVI + veget	-219	11	460.6	4.93	0.048
DEM + slope + dist_roads + dist_water + veget	-219	11	460.6	4.93	0.048
DEM + dist_roads + dist_water + veget	-224.1	11	470.7	15.10	0.000
Dist_roads + dist_water + NDVI + veget	-226.1	10	472.6	16.97	0.000
Dist_water + NDVI + veget	-225.8	11	474.2	18.54	0.000
Slope + dist_roads + dist_water + NDVI + veget	-227	10	474.5	18.84	0.000
DEM + dist_water + NDVI + veget	-225.7	12	476.2	20.56	0.000
DEM + slope + dist_water + veget	-228.7	10	478.0	22.32	0.000
DEM + dist_water + veget	-230.1	9	478.5	22.90	0.000
Dist_roads + dist_water + veget	-232.6	9	483.6	27.94	0.000
Slope + dist_roads + dist_water + veget	-232.5	10	485.5	29.89	0.000
Dist_water + veget	-236.1	8	488.6	32.95	0.000
Slope + dist_water + veget	-235.9	9	490.3	34.62	0.000
DEM + slope + NDVI + veget	-244.4	11	511.4	55.73	0.000
DEM + slope + dist_roads + NDVI + veget	-243.5	12	511.8	56.14	0.000
DEM + dist_roads + NDVI + veget	-247.4	11	517.4	61.74	0.000
DEM + NDVI + veget	-248.9	10	518.2	62.60	0.000
Early dry season					
DEM + slope + dist_roads + veget	**-267.9**	**10**	**556.2**	**0.00**	**0.397**
DEM + slope + dist_roads + dist_water + veget	**-267.4**	**11**	**557.3**	**1.09**	**0.230**
DEM + slope + dist_roads + landsc + veget	**-267.8**	**11**	**558.2**	**2.02**	**0.144**
DEM + slope + dist_roads + dist_water + landsc + veget	**-267.4**	**12**	**559.3**	**3.18**	**0.081**
DEM + slope + dist_roads + NDVI + veget	**-267.6**	**12**	**559.7**	**3.56**	**0.067**
DEM + slope + dist_roads + dist_water + NDVI + veget	**-267**	**13**	**560.7**	**4.50**	**0.042**
DEM + slope + dist_roads + NDVI + landsc + veget	**-267.5**	**13**	**561.8**	**5.62**	**0.024**
DEM + slope + dist_roads + dist_water + NDVI + landsc + veget	**-267**	**14**	**562.8**	**6.61**	**0.015**
DEM + slope + dist_roads	-284.4	4	576.9	20.75	0.000
DEM + slope + dist_roads + landsc	-284.4	5	578.9	22.76	0.000
DEM + slope + dist_roads + dist_water	-284.4	5	578.9	22.77	0.000
DEM + slope + dist_roads + NDVI	-284.3	6	580.8	24.66	0.000
DEM + slope + dist_roads + dist_water + landsc	-284.4	6	581.0	24.79	0.000
DEM + slope + dist_water + veget	-281	10	582.4	26.27	0.000
DEM + slope + dist_water + NDVI + veget	-279.1	12	582.8	26.59	0.000
DEM + slope + dist_roads + NDVI + landsc	-284.3	7	582.8	26.66	0.000
DEM + slope + dist_roads + dist_water + NDVI	-284.3	7	582.8	26.68	0.000
DEM + slope + dist_water + landsc + veget	-281	11	584.4	28.26	0.000
DEM + slope + dist_water + NDVI + landsc + veget	-279.1	13	584.8	28.66	0.000
DEM + slope + dist_roads + dist_water + NDVI + landsc	-284.3	8	584.9	28.71	0.000

Notes: LogLik – Natural logarithm of the maximum likelihood; *K*- number of parameters; AICc – Akaike's Information Criterion; ΔAICc – calculated as AICi-minAIC; w_iAICc – rounded Akaike weights; DEM – Digital Elevation Model; NDVI – Normalized Difference Vegetation Index; dist_roads – Distance from roads; dist_water – Distance from water; landsc – Landscapes of study area; veget – vegetation types of study area

Table 10: Probability use averaging models for potential competitors and predation risk in southwest of Gorongosa National Park, 2015

Variables	Estimate	95% CI	
		Lower	Upper
Reedbuck			
(Intercept)	0.248	-1.822	2.318
Distance from roads	-0.002	-0.003	> -0.001
Riverine & floodplain landscape	2.186	0.588	3.783
Distance from water	> -0.001	>-0.001	< 0.001
Slope	-0.036	-0.387	0.137
DEM	-0.001	-0.117	0.105
Waterbuck			
(Intercept)	-8.179	-8.214	9.384
DEM	-0.101	-0.29	-0.012
Slope	0.254	0.015	0.544
Distance from roads	-0.002	-0.003	> -0.001
Riverine & floodplain landscape	3.927	-1.798	9.652
Distance from water	> -0.001	-0.001	<0.001
Acacia-Combretum wood.	1.904	-2.175	9.436
Mopane Woodland	3.430	-1.272	14.35
Medium-Tall Grassland	0.192	-2.048	2.779
Mixed Forest (Riverine)	10.47	-3314	3353
Saline Grassland	1.805	-2.669	9.553
Short Grassland	1.543	-0.092	5.978
Tall Grassland	0.486	-1.661	3.514
Shrub Grassland	3.631	0.345	13.50
Predation risk by signs			
(Intercept)	1.505	-0.663	3.674
Slope	-0.343	-0.567	-0.119
Acacia-Combretum wood	-3.133	-5.328	-0.937
Mopane Woodland	-1.891	-5.06	1.279
Dry Forest/Thicket	-0.114	-3.085	2.857
Gallery Forest	16	-3487	3519
Medium-tall grassland	0.4	-1.53	2.33
Mixed Forest	-15.08	-4464	4435

Palm Veld	-16.48	-7850	7818
Saline Grassland	-2.539	-5.043	-0.036
Short Grassland	-3.082	-5.779	-0.384
Tall Grassland	-3.577	-5.971	-1.184
Shrub Grassland	-0.968	-3.392	1.455
Distance from roads	< 0.001	>-0.001	< 0.001
Riverine & floodplain landscape	0.245	-0.758	2.765
Distance from water	>-0.001	-0.001	< 0.001
DEM	-0.002	-0.146	0.097
Predation risk by prey available biomass			
(Intercept)	1012	654.6	1368
Distance from water	-0.242	-0.369	-0.115
Alluvial Fan landscape	-891.5	-1333	-449.9
Distance from water:Riverine & floodplain landscape.	0.239	0.066	0.411
Slope	-0.584	-28.9	22.32
Distance from roads	-0.003	-0.22	0.191
DEM	-0.08	-16.48	15.55
Predation risk by prey species presence/absence			
(Intercept)	1.102	-0.059	2.262
DEM	-0.044	-0.083	-1.187
Slope	0.094	0.029	1.594
Distance from water	>-0.001	>-0.001	9.471
Distance from roads	>-0.001	-0.001	-3.24
Riverine & floodplain landscape	1.173	0.725	1.62

Notes: DEM – Digital Elevation Model, NDVI – Normalized Difference Vegetation Index

FIGURES

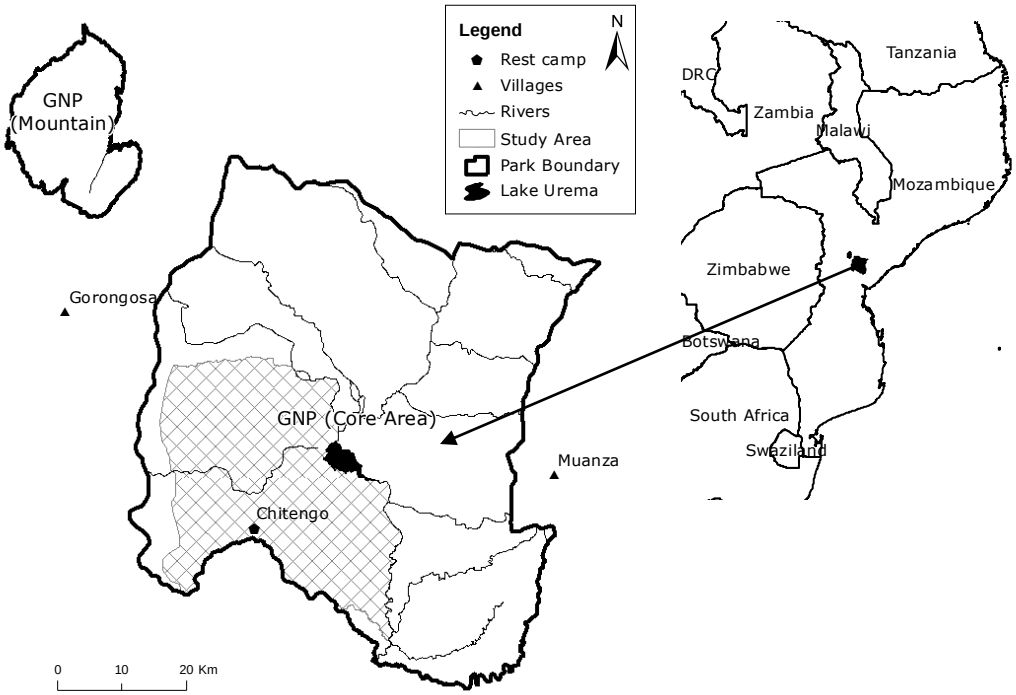


Figure 1: Gorongosa National Park, Mozambique and location of study area in Gorongosa National Park.

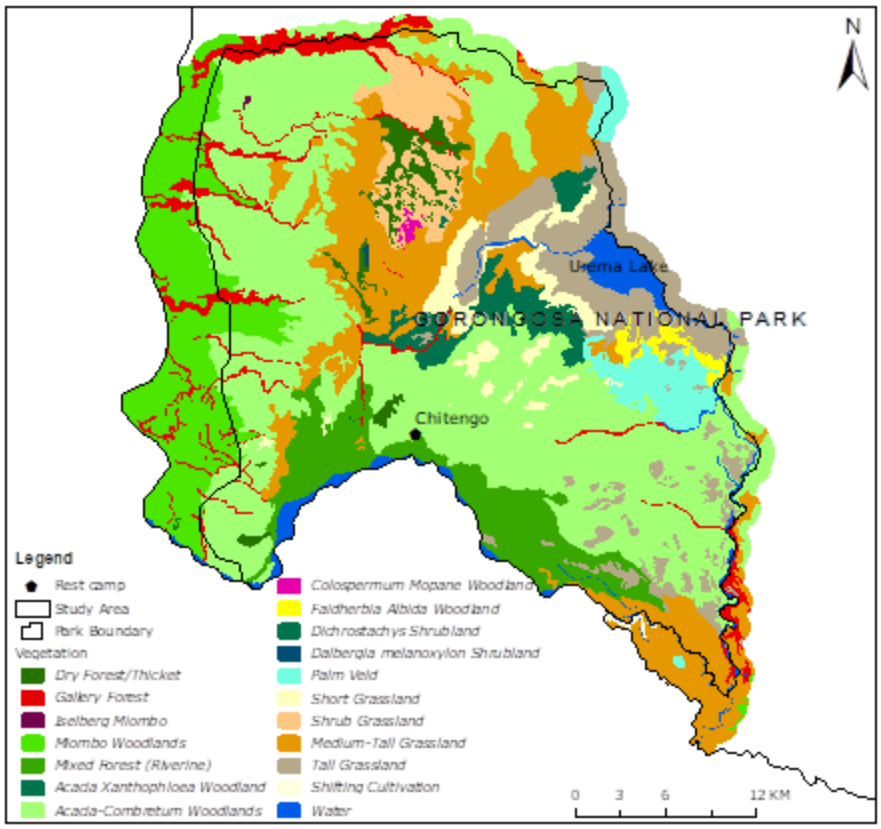


Figure 2: Vegetation Map of study area, southwest of Gorongosa National Park

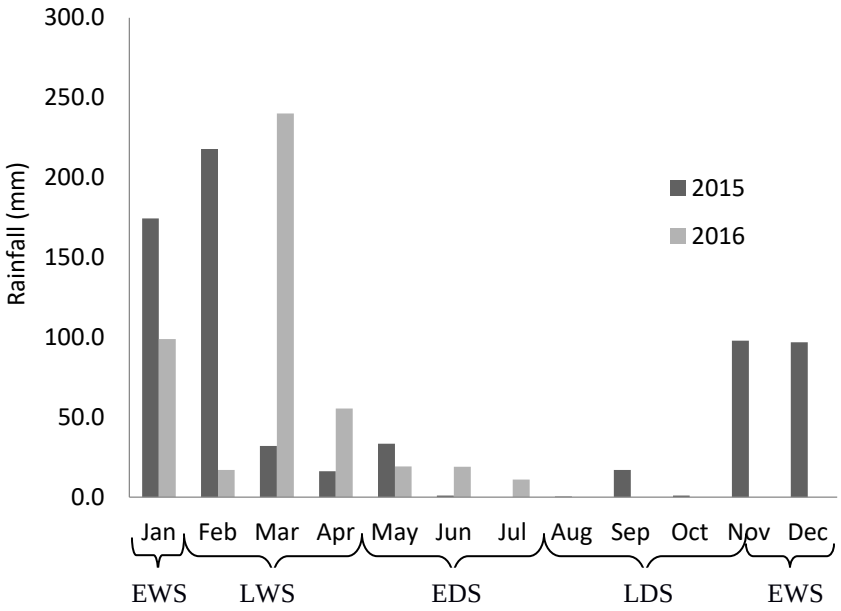


Figure 3: Rainfall in study area from January 2015 to July 2016 (source: weather station in Chitengo, GNP)

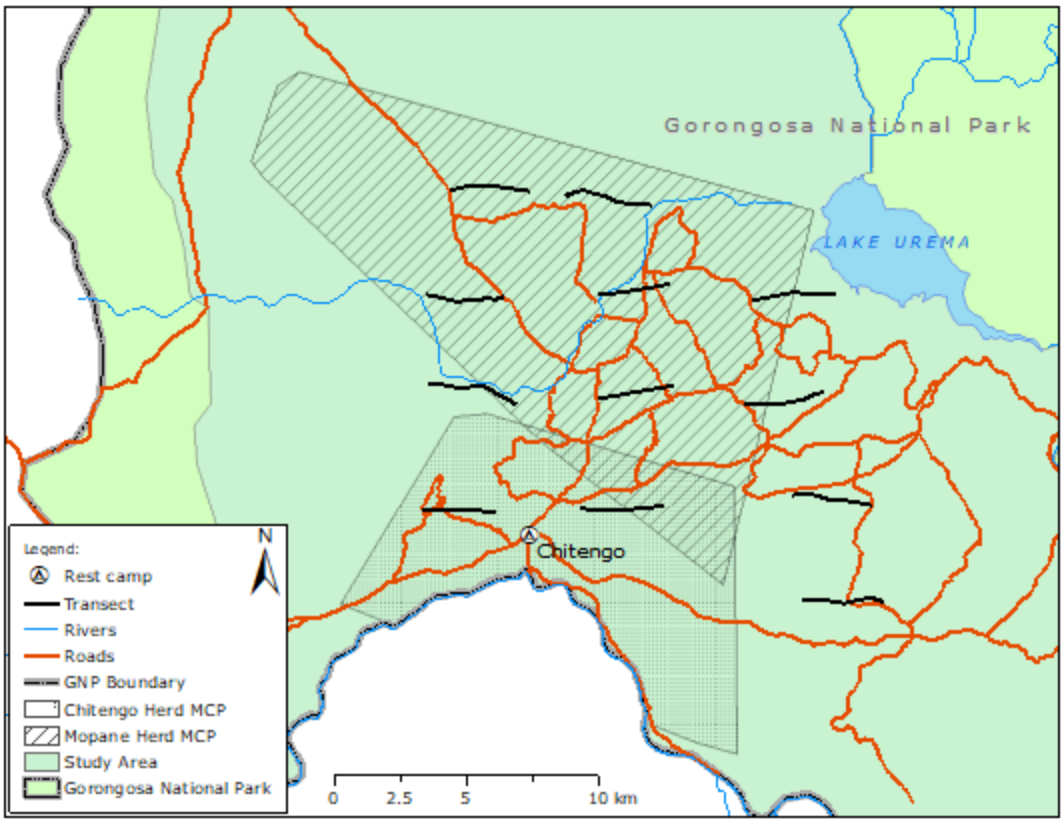


Figure 4: Transects used to obtain locations of potential competitors and predators during field work

REFERENCES

Allison, P. D. (2004). Convergence problems in logistic regression. In: *Numerical issues in statistical computing for the social scientist*. (Eds: Altman, M., Gill, J. & McDonald, M. P.). Wiley, Hoboken, New Jersey, pp. 238-252.

ARAC (2005). *Spreadsheets with precipitation and evaporation data of Chitengo*. Administração Regional de Águas Centro. Beira, Mozambique.

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

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

Belovsky, G. E. (1984). Herbivore Optimal Foraging: A Comparative Test of Three Models. *The American Naturalist*, 124(1): 97-115

Belsky, A. J. (1995). *Landscape and landscape ecology in African savannas. Mosaic Landscapes and Ecological Processes.* (eds). Hansson, L.F., Fahrig, L., and Merriam, G. London, Chapman and Hall.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling* **157**: 281-300.

Boyce, M. S., Johnson, C. J., Merrill, E. H., Nielsen, S. E., Solberg, E. J. & van Moorter, B. (2016). Can habitat selection predict abundance? *Journal of Animal Ecology* **85**: 11-20

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York, USA: Springer-Verlag.

Burnham, K. P., Anderson, D.R. & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* **65(1)**: 23-35.

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

Capon, S. D. (2011). *The ecology and potential factors limiting the success of sable antelope in southeastern Zimbabwe: Implications for conservation*. M.Sc Thesis. University of Stellenbosch, South Africa.

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

Chirima, G. J., Owen-Smith, N., Erasmus, B. F. N. & Parrini, F. (2012). Distributional niche of relatively rare sable antelope in a South African savanna: habitat versus biotic relationships. *Ecography* **35**: 68-79.

Clutton-Brock, T. H., Iason, G. R. & Guinness, F. E. (1987). Sexual segregation and density-related changes in habitat use in male and female red deer (Cervus elaphus). *Journal of Zoology* **211**: 275-289.

Creel, S., Winnie, J., Maxwell, B., Hamlin, K. & Creel, M. (2005) Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**: 3387-3397

Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size,vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology* **25(4)**: 773-784.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M. & Pitt, J. A. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS One* **7(11)**: e50611.

Davis, D. E. (1982). *CRC Handbook of Census Methods for Terrestrial Vertebrates*. Library of congress cataloguing in publication data, Boca Raton, Florida, USA.

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

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

Glover, P. E. (1969) *Report on an ecological survey of the proposed Shimba Hills National Reserve*. East African Wild Life Society, Kenya.

Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009). Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology* **90(3)**: 699-710.

Goodman, P.S. (2009). *Large mammal population estimates for Malilangwe Estate: September/October 2008*. Internal Management Report. Malilangwe Trust, Zimbabwe.

Grant, C. C. & Van der Walt, J. J. (2000). Toward 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(1)**: 50-58.

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. *Biological Conservation* **90:** 69-78.

Harris S., Cresswell, W. J., Forde, P. G., Trewhelle, W. J., Wollard, T. & Wray, S. (1990). Home range analyis using radio-tracking data. A review of problems and tecniques particularly as applied to the study of mammals. *Mammal Review* **20**: 97-123

Harrison, S., Thomas, C. D. & Lewinsohn, T. M. (1995). Testing metapopulation model of coexistence in the insect community on ragwort (Senecio jacobaea). *The American Naturalist* **145**: 546-562.

Hayne, D. W. (1949). Calculation of size of home range. *Journal of Mammalogy* 30: 1-18

Hebblewhite, M. & Merrill, E. H. (2009). Trade-offs between wolf predation risk and forage at multiple spatial scales in a partially migratory ungulate. *Ecology* **90:** 3445-3454.

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.

Hensman, M. C. (2011). *Home range and resource use of sable antelope in the okavango delta.* M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Hofer, H., Hildebrandt, T. B., Göritz, F., East, M. L., Mpanduji, D. G., Hahn, R., Siege, L & Baldus, R. D. (2004). *Distribution and movements of elephants and other wildlife in the Selous-Niassa wildlife corridor, Tanzania*. Published Report, Eschborn, p. 1-83

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

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.

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

Johnson, C. J., Seip, D. R. & Boyce, M. S. (2004). A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* **41:** 238-251.

Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* **48**: 25-34.

LP DAAC, NASA, USGS. (2009). *ASTER Global Digital Elevation Model (GDEM).* Available at http://gdex.cr.usgs.gov/gdex/

Macandza, V. A., Owen-Smith, N. & Cain, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* **121:** 891-898

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.

Marshal, J. P., Rankin, C., Nel, H. P., & Parrini, P. (2016). Drivers of population dynamics in sable antelope: forage, habitat or competition? *European Journal of Wildlife Research* **62**: 549-556

Manly, B. F., McDonald, L., Thomas, D., McDonald, T. L. & Erickson, W. P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. New York, US: Kluwer Academic Publishers.

Mordecai, K. (2016). *The value of using landsat 8 indices to describe large herbivore distribution.* M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Morin, P. J. (2011). *Community Ecology*. Blackwell Publishing, Chichester, UK.

Morris, D. W. (1987). Ecological scale and habitat use. *Ecology* **68**: 362-369

Muposhi, V. K., Gandiwa, E., Chemura, A., Bartels, P., Makuza, S. M. & Madiri, T. H. (2016). Habitat Heterogeneity Variably Influences Habitat Selection by Wild Herbivores in a Semi-Arid Tropical Savanna Ecosystem. *PLoS ONE* **11(9)**: e0163084

Murray, M. G. & Illius, A. W. (1996). Multispecies grazing in the Serengeti. – In: *The ecology and management of grazing* (eds: Hodgson, J. & Illius, A. W.). CAB Int., Wallingford, pp. 247-272.

Ogutu, J.O., Owen-Smith, N., Piepho, H. P., Said, M. Y. (2011). Continuing wildlife population declines and range contraction in the Mara region of Kenya during 1977-2009. *Journal of Zoology* **285**: 99-109

Ogutu, J. & Owen-Smith, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters* **6**: 412-419.

Owen-Smith, N. & Novellie, P. (1982) What should a clever ungulate eat? *The American Naturalist*. **119(2)**: 151-178.

Owen-Smith, N. (2002). *Adaptive Herbivore Ecology – from resources to populations in variable environments*. Cambridge University Press. Cambridge

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. & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* **76:** 73-92.

Owen-Smith, N. & Mills, M. G. L. (2008). Predator–prey size relationships in African large-mammal food web. *Journal of Animal Ecology* **77**: 173-183.

Owen-Smith, N., Chirima, G. J., Macandza, V. & Le Roux, E. (2011). Shrinking sable antelope numbers in Kruger National Park: what is suppressing population recovery? *Animal Conservation* **15**: 195-204.

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.

Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C.J. & Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* **20**: 503-510

Pettorelli, N., Ryan, S. J., Mueller, T., Bunnefeld, N., Jedrzejewsk, B., Lima, M. & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Climate Research* **46**: 15-27.

Rahimi, S. & Owen-Smith, N. (2007). Movement patterns of sable antelope in the Kruger National Park from GPS/GSM collars: a preliminary assesment. *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**: 2092-2107.

Recio, M. R., Mathieu, R., Virgós, E. & Seddon, P. J. (2014). Quantifying fine-scale resource selection by introduced feral cats to complement management decision-making in ecologically sensitive areas. *Biological Invasions* **16(9)**: 1915-1927.

Rushton, S. P., Ormerod, S. J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology* **41(2)**: 193-200.

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

Setsaas, T. H., Holmern, T., Mwakalebe, G., Stokke, S. & Røskaft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas?±A case study from the Serengeti Ecosystem, Tanzania. *Biological Conservation* **136(4)**:563-570.

Sinclair, A. R. E. (1985) Does interspecific competition or predation shape the African ungulate community, *Journal of Animal Ecology* **54(3)**: 899-918.

Sinclair, A. R. E. & Arcese, P. (1995). Population consequences to predation – sensitive foraging: the Serengeti wildebeest. *Ecology* **76**: 882-891

Skinner, J. D. & Chimimba, C.T. (2005). *The Mammals of the Southern African Subregion*, 3rd ed. Cambridge University Press, Cape Town.

Smit, I. P. J., Grant, C. C. & Devereux, B. J. (2007). Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation* **136**: 85-99.

Smith, S. M. & Cain, J. W. (2008). Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density. *African Jornal of Ecology* **47**: 109-118

Stalmans, M. & Beilfuss, R. (2008). *Landscapes of the Gorongosa National Park*. Unpublished report to the Gorongosa Restoration Project. 103p.

Stalmans, M., Peel, M. & Massad, T. (2014). *Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion*. Unpublished report to the Gorongosa Restoration Project.

Thomas, L., Laake, J. L., Derry, J. F., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Strindberg, S., Hedley, S. L., Burt, M. L., Marques, F. F. C., Pollard, J. H. & Fewster, R. M. (1998). *Distance 3.5 Release 6*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. Available: http://www.ruwpa.st-and.ac.uk/distance/

Tinley. K.L. (1977). *Framework of the Gorongosa Ecosystem*. PhD thesis. University of Pretoria.

Treydte, A. C., Edwards, P. J. & Suter, W. (2005). Shifts in native ungulate communities on a former cattle ranch in Tanzania. *African Jornal of Ecology* **43**: 302-311

Valeix, M., Loveridge, A. J., Chamaille´-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D. W. (2009a). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**: 23-30.

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. (2009b). Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behavioral Ecology and Sociobiology* **63**:1483-1494.

Van Bommel, F. P. J., Heitkonig, 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. *Journal of Tropical Ecology* **22**: 101-110

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.

Weather data from Chitengo 2005-2009. University of Edinburgh and Envirotrade. Available at http://www.geos.ed.ac.uk/homes/cryan.

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**: 1-111.

CHAPTER 4

CONCLUSION

SYNTHESIS AND KEY FINDINGS

The broad aim of this study was to determine sable home range extent and habitat use and which factors influence resource selection by sable antelope within home ranges in the thriving population in Gorongosa National Park (GNP), with more emphasis on influences of competition by other herbivores and predation by lions. One of the hypotheses for the decline of sable population in other conservation areas suggests that they may suffer from competition with other grazers (Harrington *et al.*, 1999; Owen-Smith *et al*., 2011) and increased predation (Harrington *et al.,* 1999; Owen-Smith & Mills, 2006). GNP lost most of their wildlife population because of the Mozambique civil war (1976-1992). Since the beginning of the restoration program of the park in 1995, most wildlife populations are recovering rapidly in the park, including sable. However, populations of potential competitors with sable (zebra, wildebeest, and buffalo) reported in previous studies and of lions are struggling to recover (Stalmans *et al*., 2014). Is competition and/or predation still playing an important role on habitat selection by sable within home ranges, despite low numbers? Are low numbers of predators and competitors the reason why the population has recovered in the park? The study incorporated two key elements: (i) a study of space-use and habitat selection by sable; and (ii) an investigation of the influence of predation risk, potential competition, and environmental factors on sable selection within home ranges.

Contrary to expectation, the Minimum Convex Polygon (MCP) home ranges for the GNP sable herds were larger than those found in previous studies (Sekulic, 1981; Magome, 1991; Jooste, 2000; Parrini, 2006; Owen-smith & Cain, 2007), but sable showed similar annual Local Convex Hulls (LoCoH) (95%) isopleths areas than those found in Okavango Delta by Hensman (2011). Differences in the MCP can be attributed first, to the small size of the reserves where most of the previous studies were made, and second, to large range expansions during the late dry season. Expansion of home ranges during the dry season is consistent with a number of previous studies (Wilson & Hirst, 1977; Henley, 2005; Parrini, 2006; Owen-Smith & Cain, 2007; Macandza, 2009). One herd changed the area used and walked long distances to and from water in the late dry season, while the other herd changed the area used frequently in searching for remaining water sources and food

resources. During the late dry season surface water becomes restricted to a few perennial sources, while the food resources remaining at this time of the year were also of inadequate quantity and quality.

Most previous studies showed that sable antelope prefer woodland areas to open grasslands (Pienaar 1974, Wilson & Hirst, 1977; Magome, 1991). The only exception was in Kenya where sable preferred open grasslands. This, however, was likely due to the absence of open woodlands (Estes & Estes 1974). However, more recently, Parrini (2006) reported sable using woodlands, but also open grasslands in Kgaswane Mountain Reserve, South Africa. Similar to what Parrini (2006) found, my results indicate different vegetation uses between herds. One herd used mostly grasslands, but also woodlands, establishing core areas in grasslands during the dry season and in woodlands during the wet season, while the herd other used only woodlands and riverine forests. The use of riverine forests increased during the dry season, because of proximity with water and presence of drainage lines that provided green grasses.

I expected sable to select areas with low predation risk, low competition with other herbivores and factors such as distance from water, vegetation and greenness having large influence in habitat area selection within home ranges. The findings of my study suggest that predation and competitors do influence selection within home range by sable, despite low densities of predators and competitors. Both herds avoided areas with high prey biomass, but contrary to expectations, one herd favoured areas with high evidence (signs) of predation. This can be associated probably to how signs of predation (kill carcass, lion sights, lion dung and spoors) were collected in the field, as search of signs of predation was made both along transects and when searching for the herds during the field work. Therefore within the herds home ranges, search for signs of predation efforts were higher than elsewhere in the study area. For competitors, only reedbuck appeared to influence within home range resource selection by the herds, with one herd avoiding and one herd favouring high reedbuck concentrations. Predation risk and competition have also been demonstrated affecting sable resource selection in a number of previous studies (Chirima, 2009; Valeix *et al*., 2009; Macandza *et al*., 2012). Although predation risk and competitors influenced prevalence by sable within home ranges, low density of lions and main competitors can be one of the reasons why the sable populations are doing well in the park.

Herds were influenced differently by environmental variables. Mopane herd had larger influence by distance from water, distance from roads and elevation. The herd favoured areas far from roads during the dry season and, contrary to what I expected, far from water during late dry season, but close to water during early

dry season. From the field observations it seems that the herd was forced to range far from the remaining water sources during the late dry season, as all remaining water sources were far from the suitable habitats for sable. During the wet season selection was influenced by elevation and distance from water, with the herd prevalence increasing in high elevation areas and areas far from water, probably avoiding the floods frequents in the park during this time. Chitengo herd was largely influenced by greenness categories and elevation, followed by distance to roads and slope. During late dry season this herd favoured high NDVI areas and areas close to roads, increasing prevalence during wet season in high elevation areas, probably avoiding low elevation areas because of the inundations, and preferring also low NDVI areas contrary to expected. The herd were also more prevalent in high elevation areas during the early dry season. Besides low densities of competitors and predators, other factors contributing to success of the sable population in the park is the ability that the herds have to adapt to the limitation of the dry season by increasing home range sizes to include key resources areas such as grasslands and drainage lines that provide grass species preferred by sable such as *Setaria incrassata* and *Panicum maximum*, and the ability to establish home ranges further from permanent water sources, drinking only every 3-4 days. The park also have large areas covered by open to close *Acacia-Cumbretum* woodlands, which are associated with grasslands layers dominated by *Panicum maximum*, *Heteropogon contortus* and *Themeda triandra* favoured by sable (Parrini, 2006; Magome *et al*., 2008; Macandza, 2009). However, the size of the home ranges together with the herds sizes, suggests that water can be a limiting factor in the success of the sable population in the park, as the herd that established home range further from permanent water sources had a smaller herd (around 21-25) comparing with the herd that was always close to water (around 45 individual in the herd), but much larger home range.

Recommendations for future research

Few studies have been made in Gorongosa National Park related to wildlife and how they are interacting with each other and with the environmental, now that the herbivores populations are increasing in the park. For sable this is the fists study, and still exist much to explore. This work would have benefitted greatly through the inclusion of further two levels of selection i.e. at a finer scale, investigating selection at the food level and at a broader scale, investigating resource selection at home range or landscape level. Finer scale selection would provide detailed information on plants and plants parts selected by sable, and also the role of competitors in the selection of these plants and plants parts. At the broader scale of selection, research could address the major biotic and abiotic drivers of resource selection by sable at landscape level. Results could be

used to compare with results found in areas where the specie is not thriving and provide insights to help understand the decline of the population in these areas.

Future research could also look at faecal nitrogen and phosphorus levels of sable throughout the dry season. Faecal nitrogen is positively correlated to dietary protein. Measuring nutritional gains through faecal analyses can provide an alternative to direct field observations or rumen content analysis and is a useful research tool (Holecheck *et al.*, 1982; Parrini & Owen-Smith, 2010) to predict dietary quality of free-ranging grazers (Verheyden *et al.*, 2011). 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).

Competitions between herds have been also noted in previous studies, with home ranges of different herds rarely overlapping each other (Parrini, 2006; Hensman, 2011). This study didn't take into account this aspect because I only had two herds. Future studies would benefit if this aspect is included, helping to see better patterns for some of the questions highlighted in this study.

Water availability affected the herds home ranges and movements, especially during the dry season. One study could look at movements made by the herds in searching for water and food resources, to see if there is a change in the behaviour of the herds in different seasons, such as diel displacement movements, extent of activity during the night.

Management implications

The findings in this study provide some insights into what could be done to improve conditions for sable antelope in GNP. The knowledge that predation risk and competition have effects on where sable herds occur within home ranges can help improve management of potential competitors or prey for lions. Understanding that a ‘hands off’ approach to wildlife management is adopted in the park, the management recommendations I suggest following this study mostly represent further research and monitoring needs. Therefore, for continued growth of the sable population in the park, I recommend monitoring the abundance of high densities species

such as reedbuck and waterbuck, which could influence sable through direct competition or apparent competition. I also recommend monitoring of calves and adult mortality due predation by lions, perhaps with the help of information provided by the ongoing "GNP lion project".

Both herds in this study were affected by water availability through the year, either walking long distances to water sources, or avoiding low elevation areas during the wet season, probably avoiding inundations that affect these areas of the park annually. Floods are also a key feature to the functionality of floodplains that provide food resources during the dry season to sable and other herbivores in the park. Therefore, monitoring of water regime throughout the year should be done in order to ensure that floodplain grasslands remain functional and provide high quality resources towards the end of the dry season. The physiological effects of scarcity of water in the individuals that established home ranges further from permanent water sources should also be investigated to determine if wide ranging movements outside their core home ranges in search of water could lead to high stress levels.

REFERENCES

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

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

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. *Biological Conservation* **90:** 69-78.

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.

Hensman, M. C. (2011). *Home range and resource use of sable antelope in the okavango delta.* M.Sc. thesis, University of the Witwatersrand, Johannesburg.

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.

Jooste, M. H. (2000). *Die ekologie van die swartwitpens in die Sandveld Natuurreservaat, Vrystaat Provinsie*. M.Sc thesis, University of Pretoria, Pretoria, South Africa.

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. & Cain, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos* **121:** 89-98

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., & 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.

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

Owen-Smith, N. (2002). *Adaptive Herbivore Ecology – from resources to populations in variable environments*. Cambridge University Press. Cambridge

Owen-Smith, N. & Mills, M. G. L. (2006). Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* **76:** 73-92.

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., Chirima, G. J., Macandza, V. & Le Roux, E. (2011). Shrinking sable antelope numbers in Kruger National Park: what is suppressing population recovery? *Animal Conservation* **15**: 195-204.

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. (2009) The importance of post-fire regrowth for sable antelope in a Southern African savanna. *African Journal of Ecology*. **48(2):** 526-534.

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

Sekulic R. (1981). Conservation of the sable Hippotragus niger roosvelti in the Shimba Hills, Kenya. *African Journal of Ecology* **19**: 153-165

Stalmans, M., Peel, M. & Massad, T. (2014). *Aerial wildlife count of the Parque Nacional da Gorongosa, Mozambique, October 2014. Approach, results and discussion*. Unpublished report to the Gorongosa Restoration Project.

Wilson, D. E. & Hirst, S. M. (1977). Ecology and factors limiting roan and sable antelope populations in South Africa. *Wildlife Monographs* **54**: 1-111.

Valeix, M., Loveridge, A. J., Chamaille´-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. & Macdonald, D. W. (2009a). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology* **90**: 23-30.

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.