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D'Ammando, Giacomo

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Patterns of home range use and resource selection by eland (*Tragelaphus oryx*) in the Kgaswane Mountain Reserve

MSc Candidate: Giacomo D'Ammando
E-mail: giacomo_dammando@hotmail.it

Supervisor: Prof Francesca Parrini

Centre for African Ecology
School of Animal, Plant & Environmental Sciences
University of the Witwatersrand, Johannesburg

DECLARATION

I declare that this thesis represents the original product of my own work, and does not involve plagiarism or collusion. It is being submitted for the Degree of Master of Science to the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other university.



Giacomo D'Ammando (973014)

Date: 09th March 2016

ABSTRACT

Resource selection by animals is a hierarchical process, reflecting the spatio-temporal heterogeneity in biotic and abiotic environmental conditions and resources. In savannah ecosystems, the availability and nutritional quality of forage resources across the seasonal cycle constitute two of the main drivers of feeding choices, seasonal movements, and, ultimately, population dynamics of large herbivores. As a consequence of the increasing insularisation of protected areas in southern Africa, the understanding of the ecological requirements of confined populations of nomadic ungulates constitutes a crucial issue for their management.

The study aimed at determining the effects of forage quality and availability across the seasonal cycle on the home range occupation and resource selection by eland in an insular-like protected area, the Kgaswane Mountain Reserve (KMR) in South Africa. I focused on three spatio-temporal scales of selection: seasonal home range selection over the available landscape; habitat selection within the seasonal home range; and selection for plant species included in the diet.

The main objectives at the scales of landscape and habitat selection were: 1) to determine the extent and location of the seasonal home ranges utilised by collared adult female eland in the KMR, in order to identify the seasonally favoured resource units within the available landscape; and 2) to determine the influence of environmental drivers, including the seasonal variation in forage quality and abundance, on resource selection by eland at the two different scales. Four adult female eland were fitted with GPS collars, over the course of two years. The extent and location of annual and seasonal home ranges were estimated using *a*-LoCoH. The influence of environmental factors, including vegetation-type, burnt areas, and NDVI, on landscape- and habitat-scale selection of used locations at peak feeding times over available scattered points was tested using mixed-effects logistic regression models. Despite the small size of the KMR, eland occupied spatially distinct dry and wet season ranges. The dry season ranges were smaller than their wet season counterparts, and During the dry season, seasonal ranges were small, and were located in moderate to very green (as indicated by NDVI values) woodland areas in respect to the available landscape. Eland selected for dry grassland, wet grassland, and open shrubland (associated with low NDVI levels) during the wet season, when they coalesced into a nursery herd and occupied a relatively large home range. The

selective use of burnt areas over the available landscape units was mostly restricted to the wet season, after a green herbaceous flush had been prompted by rainfall events. Within the seasonal home ranges, eland preferentially foraged on burnt woodland and open shrubland, where re-growth of woody plants was also available. The study animals also selected for locations characterized by low vegetation greenness and biomass as a consequence of the concentration of foraging activities in open areas where low-lying browse was accessible.

At the smallest scale considered for this study, the two main objectives were: 1) to determine the changes in the use of vegetation types and burnt areas during foraging activities between two different seasons; 2) to determine forage selection at the plant species scale, as influenced by the phenophase of grasses and browse. In March-April 2015 (wet-early dry transition season) and July-August 2015 (mid-dry season), feeding sites of eland were located through both VHF-tracking and scanning from vantage points. Characteristics of used feeding sites were only descriptively addressed, and included vegetation type, burning, canopy cover, and soil catenal position. The greenness and basal cover of plant species were also recorded. Availability, acceptance, and dietary contribution for each species were calculated for the two seasons, while the influence of phenological traits on plant species selection was investigated through mixed-effects logistic regression models. Woody plants were consumed in larger proportions than grasses and herbaceous forbs during the entire study period. Woody forbs and shrublets such as *Lippia javanica* and *Athrixia elata* were particularly favoured. Eland targeted species offering high proportions of green leaves. During the wet-early dry transition, the deciduous *Vangueria parvifolia* was particularly selected for, while the consumption of evergreen species, including *Searsia lancea*, increased during the dry season. Most of the observed grazing took place on flushing burns during the wet-early dry transition. The decline in grass consumption was paralleled by a considerably lowered use of the burns and of the dry grassland during the dry season, as also reflected by collars data.

The results indicated that eland in the KMR adjusted their landscape and habitat selection in response to spatio-temporal variations in the availability and quality of food resources. During the wet season, flushing burns provided accessible green forage to nursery herds. Conversely, evergreen woody plants probably represented a crucial resource for eland during the limiting dry season, when herbaceous plants were mostly dormant and foliage on deciduous species

was unavailable. Therefore, environmental heterogeneity at different spatial scales likely constitutes a key factor for the persistence of eland populations in small, fenced reserves.

To my family, to Irene, and to all the people and the wild nature of Africa

"We became human in a very specific setting – within rich communities of African animals and plants. To destroy these communities is to detach ourselves, irrevocably, from our biological, even intellectual past".

Jonathan Kingdon

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deserves a special mention in this thesis for her true friendship (despite the worries I caused her by “disappearing” into the dark continent). Thanks to Patience and Innocentia Lushaba (and to the newly-arrived Lesedi), who are my “family from another continent”.

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Thank you Irene; you have always been in my mind, and in my heart, as the most beautiful part of my life.

This thesis is dedicated to Africa,to its magnificent wildlife and landscapes, and to all the people living on this continent (but especially to Bongimusa and Siphesihle). It will always be my home away from home.

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ACRONYMS AND ABBREVIATIONS

AIC	Akaike's Information Criterion
AICc	Akaike's Information Criterion corrected for small sample size
AWT	Africa Wildlife Tracking
CAE	Centre for African Ecology
Dicots	Dicotyledonous plants
GR	Game Reserve
IUCN	International Union for the Conservation of Nature
KMR	Kgaswane Mountain Reserve
Monocots	Monocotyledonous plants
MODIS	Moderate Resolution Imaging Spectroradiometer
NDVI	Normalized Difference Vegetation Index
NIR	Near-infrared radiation
NP	National Park
NR	Nature Reserve
Pers. comm.	Personal communication
Pers. obs.	Personal observation
Red	Red spectral radiation

Note 1: The complete word form for acronyms and abbreviations is used at first mention in each chapter. References follow the rules for the *African Journal of Ecology*: papers or reports written by three authors are referred to using the three complete names at first mention in each chapter, and later referred to with only the first author plus "*et al.*"

Note 2: The generic name *"Acacia*" was utilized to designate species now assigned by many authors to the *Vachellia* and *Senegalia*. The choice was made in order to allow for a clear comparison with information present in previous studies.

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CHAPTER 1: GENERAL INTRODUCTION

MOTIVATION FOR THE STUDY

African savannahs are home to the highest species diversity of mammalian herbivores on the planet (Du Toit, 1995; Shorrocks, 2007). However, most populations of large mammals are nowadays confined to protected wildlife areas (especially in southern Africa), and these populations often need intensive management interventions in order to survive (Du Toit, 1995). Small populations of large herbivores in isolated areas may be excluded from access to seasonal key resources (Scoones, 1995; Kröger & Rogers, 2005), and are extremely susceptible to local extirpation risk due to environmental, demographic, and genetic stochasticity (Gilpin & Soule, 1986), and due to potential exacerbation of intra- and interspecific competition (Jarman, 1971; Leuthold, 1978; Landman, Schoeman & Kerley, 2013). Catastrophic climatic events, such as prolonged droughts in southern Africa, have negatively affected particularly those herbivores living in areas with little scope for seasonal movements in search of high-quality forage (Walker *et al.*, 1987; Holdo *et al.*, 2011). Investigating the scales of resource use and selection within protected areas is therefore fundamental in order to understand the long-term viability of herbivore populations, and to prevent the risk of local population extirpation.

Over the last two decades, conservation areas in East and southern Africa have experienced a severe decline in antelope species which are relatively rare within herbivore communities (Harrington *et al.*, 1999; Dunham, Robertson & Grant, 2004; Ogutu *et al.*, 2011). The habitat preferences, foraging behaviour, and population ecology of the species commonly ascribed to the conceptual category of the "rare antelopes", including sable antelope (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), and tsessebe (*Damaliscus lunatus*), and the possible causes for this observed decline, have therefore been investigated into detail (Heitkönig & Owen-Smith, 1998; Dunham, Robertson & Swanepoel, 2003; Parrini, 2006; Macandza, Owen-Smith & Cain, 2012; Hensman *et al.*, 2014 a & b). However, one of these rare species, the common eland (*Tragelaphus oryx*) has received very little attention (Watson & Owen-Smith, 2000; D'Ammando *et al.*, 2015). Although eland are considered as "Least Concern-Conservation dependent" by the IUCN (Thouless, 2014), and their numbers appear to be stable across the continent (East, 1999), the range of this ungulate has been greatly

reduced during the last thirty years (East, 1999). A local decline in free-ranging populations has been observed in the Kruger National Park (South Africa; Ogutu & Owen-Smith, 2003; Whyte, 2006), in the Ngorongoro Conservation Area (Tanzania; Estes, Atwood & Estes, 2006), in the Masai Mara National Reserve-communal ranchland complex (Kenya; Ogutu *et al.*, 2011), and in the central-southern Kalahari ecosystem (Botswana; Spinage & Matlhare, 1992). As the eland is one of the largest nomadic ruminants in sub-Saharan Africa (Hillman, 1988), the long-term persistence of populations in national parks and game reserves is under significant threat from landscape fragmentation, and especially from the erection of artificial barriers, such as fences or agricultural fields, preventing large-scale movements. For example, the increasing environmental isolation, caused by expanding agricultural development, of the Ngorongoro Crater (Estes *et al.*, 2006), and of the Biharamulo Game Reserve (Tanzania; Stoner *et al.*, 2006; Okello *et al.*, 2015), probably resulted in the observed declines in eland numbers. Today, a substantial proportion (50%) of the estimated 136 000 eland present in Africa live in formally protected areas (Thouless, 2014). Moreover, populations reintroduced to private ranchland and fenced game farms and reserves in South Africa and neighbouring countries account for 30% of the total population, and, despite the limitations imposed to nomadism in these areas, show an overall increasing trend in numbers (Thouless, 2014). Since free-ranging populations of this antelope are likely to decline over the next century as a result of further range contraction and severe human encroachment into national parks and reserves, the only effective conservation measure to be taken *in situ* may thus be the sound management of eland in fenced reserves (IUCN 2014; East, 1999). However, little is known about the adaptations of this nomadic ungulate to cope with the limited landscape and habitat heterogeneity offered by insular-like wildlife areas. Research oriented towards the understanding of forage- and habitat-related limiting factors is therefore urgently needed.

The Kgaswane Mountain Reserve (KMR; South Africa) hosts a small but relatively stable eland population (Nel, *pers. comm.*). As the largest and most numerous mixed-feeders in the reserve, eland are responsible for extensive over-browsing of *Acacia caffra* woodland and subsequent reduction of forage biomass at accessible canopy levels for small browsers (Nel, 2000). Restrictions to seasonal movements imposed by the reserve's fences may exacerbate the impact of this large ungulate on woody plants, leading to potentially detrimental vegetation changes for other valuable species (from both economic and conservation perspectives), such as sable antelope. This study was therefore oriented to provide the

management authorities of the reserve with detailed information about habitat and forage requirements of eland, in light of its potential impact on vegetation and on other herbivores species in the KMR.

The study is also part of the "rare antelopes research programme" of the Centre for African Ecology (CAE), which aims at investigating the causes of the drastic population decline in low-density ungulates across southern Africa (Henley, 2005; Parrini, 2006; Parrini & Owen-Smith, 2010; Hensman *et al.,* 2014 a & b). It represents the first CAE study focusing on the spatial ecology of eland, thus constituting a baseline for future eland-oriented research, and a new insight into the ecology of this species in insular-like protected areas.

AIM OF THE STUDY

This study was aimed at determining the effects of forage quality and availability across the seasonal cycle on the home range occupation and resource selection by eland in an insular-like protected area, the Kgaswane Mountain Reserve in South Africa.

LITERATURE REVIEW

Study species

Common eland (*Tragelaphus oryx* Pallas, 1796)

The common eland is the second largest "antelope" (intended as wild Bovidae with the exception of buffalo) species in Africa, after the closely related Lord Derby's (or Giant) eland, which inhabits the Sahel belt in Central and Western Africa (Pappas, 2002; Thouless, 2014). Three subspecies of common eland have been recognized (Kingdon, 1997): Cape eland (*T.o.oryx*), found south of the Zambezi river; Livingstone eland (*T.o.livingstonii*), typical of the miombo belt of south-central Africa; and East African eland (*T.o.pattersonianus*), distributed over the Somali-Maasai Arid Zone. The Cape eland (the subspecies of this study) range encompasses Mozambique, Botswana, Zimbabwe, Namibia, South Africa, Lesotho and Swaziland (Thouless, 2014). In South Africa, the species formerly occurred throughout the country, but it was extensively eliminated outside and inside protected areas, as a tse-tse control measure and as it was supposed to compete with domestic livestock (Thouless, 2014). Today, the largest populations inhabit the Kgalagadi Transfrontier Park, Kruger NP and Ukhalamba-Drakensberg Park (Thouless, 2014). Reintroduced eland

populations have however been established on many small reserves and private game farms (Thouless, 2014).

Eland present an extreme sexual dimorphism, with adult males reaching a body mass of 500-600 kg, almost doubling the mass of an adult female (340-445 kg; Kingdon, 1982; Pappas, 2002; Thouless, 2014). Males presumably continue to grow until old age, thus reaching, in exceptional cases, a body mass of almost 1000 kg (Kingdon, 1982, 1997; Thouless, 2014). Both sexes have spiralled horns (usually only one spiral is observed; Kingdon, 1997), but horns of males are on average shorter (43-67 cm), thicker and with more pronounced spirals than those of females (51-69.6 cm; Estes, 1991). Although the coat of Livingstone's and East African eland have up to twelve stripes, adult Cape eland usually lose the stripes and therefore have an almost uniform tawny fur (Kingdon, 1997). The fur of male eland changes to grey as the animal ages, and a frontal, black hair tuft is often observed in adult bulls; Kingdon (1982) and Bro-Jørgensen & Dabelsteen (2008) suggested that the development and regression of the frontal tuft is under hormonal control. Although a dewlap is present in both sexes, it is much smaller in females than in males (Estes, 1991). As for other members of the Tragelaphins tribe, the muzzle is narrow and pointed, and jaw muscles are small if compared to similar-sized herbivores (Kingdon, 1982).

Eland are highly gregarious mammals, forming herds numbering many hundreds (up to 500), especially during the wet season (Jarman, 1974; Kingdon, 1982; Hillman, 1987, 1988). "Wet season gatherings" of eland, which are unusual among antelopes, have been observed in eastern Africa by many researchers, although very little is known about the environmental and social factors driving these associative patterns (Kingdon, 1982; Hillman, 1988). Females aggregate in herds, and small calves are usually found in "nursery herds" led by a group of females (probably unrelated to the calves; Underwood, 1981; Hillman, 1987). Herd composition is extremely variable through time, and single females have been observed to stay in a herd for periods ranging from several hours to several months (Underwood, 1975; Hillman, 1979; Hillman, 1987). Males form small herds or live solitarily, adjoining female herds only temporarily (Hillman, 1988). Territorial behaviour is absent (Hillman, 1987; Underwood 1981), but a rigid pecking hierarchy is established both within female herds and within bull associations (Jarman, 1974; Underwood, 1981; Hillman, 1988). The presence of horns in both sexes, and the slow development of secondary sexual attributes in bulls (such as

grey colouration, frontal tuft, or dewlap), probably allow them to remain in female herds for longer than in other Tragelaphins (Kingdon, 1982, 1997; Estes, 1991). Although a breeding and a calving season have not been clearly identified, and probably varies from one population to another (Kingdon, 1982; Pappas, 2002), calving in southern Africa usually peaks during the late months of the dry season and the early wet season (Underwood, 1975; Scotcher, 1983; Buys & Dott, 1991; Thouless, 2014). The calf is dependent on its mother only for the first two weeks of life, during which it is hidden in thick bush (Kingdon, 1982; Estes, 1991). Eland are reportedly crepuscular and foraging activities are concentrated during the early morning and evening (Lewis, 1978; Hillman, 1979). Additional information on home range use, habitat and forage preferences of eland is discussed in the following paragraphs.

The scales of resource selection

Ecological heterogeneity in resource quality and distribution, at multiple spatial and temporal scales, influences the complex behavioural patterns of large herbivores, determining diverse processes such as movements, social organization, habitat use and dietary selection (Jarman, 1974; Wiens, 1989; Bailey *et al.,* 1996). Nowadays, one of the most important topics in ecology is the study of the relationships between ecological heterogeneity and the resource selection scale (Wiens, 1989), as a possible way to understand how the environmental variability, through the behavioural responses that it generates, affects population-level dynamics (Owen-Smith, 2014).

Resource selection is considered to take place over the four ordering levels identified by Johnson (1980):

1) Geographic distribution;
2) Home range selection (within a landscape);
3) Habitat selection within the home range;
4) Forage selection.

The present study investigated the 2nd, 3rd, and 4th orders of resource selection of four GPS-collared adult female eland in the Kgaswane Mountain Reserve (KMR).

Home ranges

The "home range" of an individual animal is the area traversed by this animal over a pre-determined temporal extent (day, month, season or year), and within which the requirements for forage, cover, and social interactions (including reproduction) can be satisfied (Burt, 1943). Home range extent, shape, location, and patterns of utilisation are not strictly species-specific: they can vary between different populations and even between different individuals in a population, and the drivers of this extreme variability constitute one of the core issues in movement ecology (McLoughlin & Ferguson, 2000; Borger, Dalziel & Fryxell, 2008; Wittemyer *et al.,* 2007; Van Beest *et al.,* 2011; Naidoo *et al.,* 2012). Differences in nutritional requirements and social structure deriving from different body size are generally considered as sufficient explanations of interspecific variation in home range extent (Jarman, 1974; Owen-Smith, 1988; Carbone *et al.,* 2005). For example, in African savannah ecosystems, small antelopes (e.g. steenbok *Raphicerus campestris*) tend to occupy smaller home ranges than larger species (Jarman, 1974; Owen-Smith, 1988). A large body size is associated with high absolute food requirements, thus resulting in the necessity to move over wide areas in search of forage (Owen-Smith, 1988). Similarly, in species with pronounced sexual dimorphism in body size, home range extent differs greatly between males and females (again, scaling positively with body mass), as it has been observed for elephant (*Loxodonta africana*) in South African reserves (Shannon *et al.* 2010). The larger home range size reported for highly gregarious herbivores in respect to solitary species, is probably a consequence of the rapid depletion of water and forage resources caused by large numbers of individuals sharing the same space for prolonged periods (Hillman, 1988; Owen-Smith, 1988). Intraspecific variations in home range extent are generally attributed to the interactions between intrinsic life-history traits of individual animals, and extrinsic environmental conditions (Borger *et al.,* 2008; Van Beest *et al.,* 2011). As an intrinsic, individually-variable factor, the reproductive state can influence the movements and space use of an ungulate (Owen-Smith, 1988). Female moose (*Alces alces*), for example, moved over restricted areas shortly after parturition, as a consequence of the reduced mobility of newborn calves (Van Beest *et al.,* 2011). Social interactions between single individuals or social groups also affect the characteristics of home ranges (Owen-Smith, 1988). Territoriality, intended as the active defence of resources in area (often coincident with the home range itself; Owen-Smith, 1977),

poses a constraint to the spatial extent, shape, and location of a home range (Owen-Smith, 1988).

Among the environmental factors affecting the ranging behaviour of mammalian herbivores, the distribution of surface water and the availability of forage generally play a predominant role (Owen-Smith, 1988; Mueller & Fagan, 2008; Owen-Smith, Fryxell & Merrill, 2010; Van Beest *et al.,* 2011; Naidoo *et al.,* 2012; Owen-Smith, 2014). When food resources are concentrated in relatively small areas, and available at relatively high quality throughout the year, a home range will be small in extent, presenting constant patterns of use within its boundaries (Mueller & Fagan, 2008; Owen-Smith *et al.,* 2010). Differentiated seasonal home ranges, and eventually directional migratory movements between spatially distinguished ranges, will be observed when green forage and water are cyclically found at predictable locations (Owen-Smith, 1988). This is the case of migratory wildebeest (*Connochaetes taurinus*) and Thomson's gazelle (*Gazella thomsonii*) of the Serengeti ecosystem (Fryxell, Wilmshurst & Sinclair, 2004; Boone, Thirgood & Hopcraft, 2006; Holdo, Holt & Fryxell, 2009). Nomadism, as the occupation of extremely large, distinct home ranges during the same season over different years, has been observed in highly mobile species living in areas where the forage and warter resources are subjected to dramatic stochasticity in availability and quality over time (Bailey *et al.,* 1996; Mueller *et al.,* 2008; Owen-Smith *et al.,* 2010). The growth cycle of plant species and the distribution of surface water in African savannahs and other semi-arid ecosystems is largely governed by regional rainfall patterns (Owen-Smith, 2008). The mean home range extent of herbivores generally increases in arid regions, where forage and water are often scattered over large areas and extensive movements are therefore necessary in order to satisfy nutritional and water requirements (e.g. African buffalo *Syncerus caffer*; Sinclair, 1977; Ryan, Knechtel & Getz, 2006; Mongolian gazelle *Procapra gutturosa*; Mueller *et al.,* 2008). Home range size for browsers (herbivores feeding on dicotyledonous plants) is also affected by the spatial dispersion of favoured woody species (Leuthold & Leuthold, 1978; Owen-Smith, 1988). Giraffe (*Giraffa camelopardalis*), for example, were observed to occupy larger home ranges in open savannah, where trees and shrubs are patchily distributed within a grass-dominated matrix, than in thickets and miombo woodland (Berry, 1978; McQualter *et al.,* 2015).

Only one peer-reviewed study (Hillman, 1988) reported on home range extent and seasonal movements of eland, focusing on the Nairobi National Park-Athi Kapiti Plains ecosystem of Kenya. Home range sizes estimated for herds of females and calves ("nursery herds") were among the largest ever recorded for an African ungulate (mean extent 222 km^2; maximum extent 422 km^2; Hillman, 1988). Unpublished results from the arid Kgalagadi Transfrontier Park (Botswana) and reported in Thouless (2014) also indicated extremely large annual home ranges covering up to 20 000 km^2. In Kenya, movements between distinct wet and dry season ranges were observed, although the high inter-annual variability in the location of seasonal ranges within the available landscape implied a nomadic lifestyle rather than regular migrations (Hillman, 1988). As for other browsing mammals, range size was much smaller during the dry season than during the wet season (about 12% of the wet season home range; Hillman, 1988). According to Hillman (1988), adult males were mostly sedentary, occupying small home ranges throughout the year and showing little seasonal variation in home range extent. Keep, Barnes & Root (1972) similarly found that artificially marked eland males in the Drakensberg mountain range (South Africa) moved for relatively short distances from the original marking point (unfortunately, the home range size was not estimated). Eland in the fenced Pilanesberg National Park (South Africa), occupied relatively small home ranges (~60 km^2), but still maintained seasonal dispersal over a large area during the wet season (Kelso, 1986). High levels of spatial home range overlap between different herds suggest a lack of territorial behaviour for this species (Hillman, 1988), as confirmed by descriptive behavioural observations (Kingdon, 1982; Estes, 1991; Thouless, 2014).

Landscape and habitat selection

Landscape and habitat

The distribution of large herbivores at the landscape scale is influenced by a wide range of biotic and abiotic factors (Senft *et al.*, 1987; Du Toit & Owen-Smith, 1989; Mduma & Sinclair, 1994; Bailey *et al.*, 1996; Redfern *et al.*, 2003; Fynn, Chase & Roder, 2014). A landscape is defined as a heterogeneous mosaic of land units, characterized by different topography, vegetation structure and composition, and local conditions of anthropogenic use (Urban, O'Niel & Shugart, 1987; Owen-Smith, 2014). Abiotic elements of the landscape, including topographic and edaphic attributes and presence and accessibility of surface water, are usually considered as the main constraints to herbivore distribution at this scale (Bailey *et*

al., 1996; Redfern *et al.,* 2003; Winnie, Cross & Getz, 2008). Habitat selection takes place within the borders of a home range, established over the available landscape (Johnson, 1980). The concept of habitat has a species-specific (or population-specific) connotation and can be defined as the area where a species or a population can survive and persist (by reproducing) due to a suitable combination of resources and conditions (Morrison, Marcott & Mannan, 2006; Wiens,1989). Resources defining a habitat often present a patchy spatial distribution (Arditi & Dacorogna, 1988; Wiens, 1989), and also vary in quality and availability over time (Scoones, 1995; Owen-Smith, 2002), thus resulting in uneven usage of home ranges by individual animals (Owen-Smith, 1988). At both scales, selection by mammalian herbivores is largely driven by: forage quality, availability, and accessibility (Mysterud, Pèrez-Barberìa & Gordon, 2001; Van Beest *et al.,* 2010; Fynn *et al.,* 2014); presence of potential competitors (Macandza *et al.,* 2012; Hensman *et al.,* 2014b); real or perceived predation risk (Mech, 1977; Fischhoff *et al.,* 2007); micro-climatic characteristics associated with elevation and shade availability (Sheehy & Vavra, 1996; Owen-Smith, 1998; Bjørneraas *et al.* 2012); availability and accessibility of surface water (Bergström & Skarpe, 1999; Traill, 2004; Cain *et al.,* 2012).

Vegetation characteristics and forage quality at different spatial scales

The vegetation structure and the floristic composition of a particular landscape unit or habitat patch can influence the patterns of resource selection by large mammalian herbivores at different spatio-temporal scales (Holdridge, 1947; Pienaar, 1974; Wiens, 1969). The presence and relative availability of frequently consumed plant species in vegetation communities has often been considered as a reliable proxy index for habitat quality by several studies (Gordon, 1989b; Watson & Owen-Smith, 2000; Morrison *et al.,* 2006). However, in savannah ecosystems, the growth cycle of individual plants is controlled by seasonal and inter-annual changes in regional rainfall and temperature patterns (interacting with landscape-scale topo-edaphic conditions), and thus the nutritional value of food material for herbivores is subjected to extensive inter-seasonal and inter-annual fluctuations (Bell, 1971; Owen-Smith, 2002, 2008; Illius & O'Connor, 2000; Skarpe *et al.,* 2000; Redfern *et al.,* 2003; Fynn *et al.,* 2014, 2015). Nutritional value is determined by the proportion of cell content (in which nutrients, and especially protein and minerals, are concentrated) versus the proportion of cell wall (which contains semi-digestible or undigestible fibre, such as cellulose and lignin), and it is commonly expressed as the protein:fibre ratio of a plant (Demment & Van Soest, 1985;

Bergström, 1992; Owen-Smith, 2005). Protein levels in grasses decrease from peak concentrations in young, green leaves during the early wet season, to very low levels (~60% lower than those recorded during the growing season) during the late dry season (or "dormant season"), when grass tufts are mostly brown and digestible material is at minimum levels (Owen-Smith, 1982, 2008; Bergström, 1992). During maturation, grasses, though retaining green leaves, increase in height and stemminnes, with the subsequent dilution of nutrients in a matrix of undigestible structural carbohydrates (Fynn *et al.,* 2015). For what concerns browse, the production of green leaves often presents a lagged response to rainfall, and it is not always coincident with the early phase of the wet season (Owen-Smith, 2005). In some woody species and forbs (herbaceous dicotyledonous plants), a flush of new leaves is observed immediately before the onset of the first rains (Shorrocks, 2007; Owen-Smith, 2002). Senescent, brown leaves of woody plants generally contain 30-40% lower protein levels than those recorded in young, green leaves (Owen-Smith, 2005). Furthermore, many woody species in southern Africa are deciduous, thus limiting the availability of green browse during the dry season (Bergström, 1992). The greenness of an entire vegetation community is therefore positively related to the proportion of green leaves versus brown leaves and stems on individual plants and, ultimately, to the yield of metabolizable protein and energy available for mammalian herbivores (Owen-Smith & Cooper, 1987a; Pettorelli *et al.,* 2005; Parrini, Macindoe & Erasmus, 2013).

The use of indices derived from satellite imagery has become an incredibly valuable tool for estimating spatial and temporal patterns of vegetation greenness and production (Pettorelli *et al.*, 2005, 2011). NDVI (Normalized Difference Vegetation Index), calculated from satellite images provided by the MODIS (MODerate Resolution Spectroradiometer; Pettorelli *et al.,* 2005), is positively correlated to the chlorophyll level of plants (and therefore to greenness), and to the Leaf Area Index, which determines the degree of vegetation thickness (Pettorelli *et al.*, 2005). NDVI has been successfully applied to the study of large herbivores distribution and habitat selection (Pettorelli *et al.*, 2011). At various spatio-temporal scales, herbivores from boreal and austral ecosystems, including elephant in southern Africa (Young, Ferreira & van Aarde, 2009), mule deer (*Odocoileus hemionus*) in the Sonoran Desert (USA; Marshal *et al.*, 2006), and migratory wildebeest of the Serengeti ecosystem (Boone *et al.,* 2006), have been observed to associate positively with high values of NDVI at different spatial scales. However, high values of NDVI may not correspond to the most nutrient-rich forage, as

mature grasses (and, possibly, browse) usually offer high food biomass (in respect to areas devoid of vegetation), but also hold high fibre levels in respect to young, growing swards or foliage (McNaughton, 1985; Bergström, 1992). Mongolian gazelle of the Asian steppe, for example, selected for grassland patches of intermediate greenness, presumably corresponding to young, growing grass swards (Mueller *et al.,* 2008). The spatial scale at which NDVI is measured is also important for resource selection studies. Ryan *et al.* (2006) concluded that buffalo did not select for high NDVI values at a spatial resolution of 1 km^2, mainly due to the fact that at this scale the presence and abundance of green grasses under woodland or shrubland canopy was impossible to detect. Similarly, the density of large savannah browsers, including eland and giraffe, did not scale positively with NDVI across protected areas in Africa, possibly because these species were mostly selective for greenness at the level of individual plants, indiscernible from the surrounding matrix using satellite imagery (Pettorelli *et al.,* 2009). It is therefore important to always couple measures of forage quality from satellite-derived indices with ground estimates of vegetation composition, structure, and phenology, in order to determine the actual drivers of resource selection at small spatial scales (Ryan *et al.,* 2006; Marshal *et al.,* 2011).

The dry season in savannah ecosystems imposes conditions of limited forage availability to large herbivores, due to the fact that green leaves on both herbaceous and woody plants enter a dormant phase and experience a dramatic decrease in protein content (Sinclair, 1975; Owen-Smith, 2002). During periods of severe resource limitation (such as during the late phases of the dry season), the presence of "key resource areas" in a landscape, offering enough forage biomass as a buffer against death from starvation, is thus crucial to the long-term persistence of herbivore populations (Scoones, 1995; Illius & O'Connor, 2000; Owen-Smith, 2002, 2004; Yoganand & Owen-Smith, 2014). Key resource areas for grazers (grass-eaters) are often associated with bottomlands, where the water table is high and allows for grass growth during dry months (Scoones, 1995; Ngugi & Conant, 2008). Dry season movements along the soil catena towards bottomlands were observed in many non-migratory ungulates of the Serengeti (Bell, 1971), and in sable and roan antelope in southern Africa (Parrini, 2006; Heitkönig & Owen-Smith, 1998). Wetlands, including *vlei* grassland and floodplains, although associated with a high biomass of green grasses throughout the year, generally offer forage of extremely low quality to grazers (Fynn *et al.,* 2015). However, wild or human-induced fires can promote new growth, providing herbivores with a relatively high-quality "bridging resource" to

alleviate nutritional stress during the severe conditions of forage limitation between the end of the dry season and the onset of the rains (Fynn *et al.*, 2015). Zebra (*Equus quagga*) in northern Botswana, for example, made use of grasses on burnt *vleis* during the dry season (Fynn *et al.*, 2014), while the Nile river floodplains in South Sudan, regularly burnt by pastoralists, constituted an important dry season pasture for migratory populations of white-eared kob (*Kobus kob leucotis*) and tiang (*Damaliscus korrigum tiang*; Fryxell & Sinclair, 1988). For browsers (herbivores feeding on dicotyledons), key resources are usually determined by the availability of woody vegetation patches retaining foliage during the dry season (Owen-Smith, 2002). Green leaves on trees and shrubs are available year-round in riparian vegetation along drainage lines (Pellew, 1983; Du Toit, 1986; O'Kane *et al.*, 2013), or in stands of evergreen woody species (Kerr, Wilson & Roth, 1970; Owen-Smith & Cooper, 1987a). During exceptionally dry periods, evergreen plants of low nutritional value also constitute an important resource for browsers (Owen-Smith, 2002). Greater kudu (*Tragelaphus strepsiceros*) in the Kruger NP were observed to extensively use open plains during the wet season, when plains-dwelling forbs and creeper were green, but abandoned this vegetation type during the dry season, moving to the hill-base ecotone where green foliage of woody species was still available (Owen-Smith, 2002). Similarly, kudu are absent from open *Acacia tortilis* savannahs, typical of the Serengeti ecosystem and of the central region of the Kruger NP, mainly due to the scarcity, in this vegetation type, of evergreen plant species providing these large browsers with an adequate protein yield during the critical late dry season (Du Toit, 1990; Owen-Smith, 2002). For a mixed feeder, a key resource during critical months may be constituted by low-quality grass swards still available in the late dry season (Owen-Smith, 2002). However, eland feeding on dry grass starved in Kenya during a drought (Hillman, 1979), indicating that a moribund sward did not meet the basic nutrient and energy requirements of these large antelopes.

Mammalian herbivores actively modify the heterogeneity of forage resources at the landscape scale. Megaherbivores, such as white rhinoceros (*Ceratotherium simum*), and species present at high local densities such as wildebeest in the Serengeti ecosystem, often maintain, through intensive feeding activity, areas of short, green grasses, known as "grazing lawns" (McNaughton, 1976, 1984; Cromsigt & Olff, 2008; Waldram, Bond & Scott, 2008). Similarly, "browsing lawns" can be established on patches of woody vegetation coppicing after heavy consumption by elephant or other large browsers and mixed-feeders (Fornara &

Du Toit, 2007; Cromsigt & Kuijper, 2011). In savannah ecosystems, localized combinations of heavy and continued grazing pressure and elevated concentrations of soil minerals often lead to the formation of "nutrient hotspots" for herbivores (Grant & Scholes, 2006). Soil minerals, including Phosphorus, Calcium, and Sodium, are usually deficient in tropical plant-based forage, but constitute key elements for a nutritionally balanced diet, especially during crucial phases of the life cycle (for example, Calcium is essential for milk production; Kreulen, 1975; Seagle & McNaughton, 1992). High concentrations of minerals in the soil are promoted by deposits of volcanic material, fungal cultivations associated with termite mounds, and accumulation of cattle dung in areas previously occupied by corrals (McNaughton, 1988; Augustine, 2004; Grant & Scholes, 2006). Hotspots constitute sites of aggregation for herbivores of different species and also provide them, in a positive feedback generated by high grazing pressure, with green food resources in areas often far from water sources and interspersed within a matrix of low quality forage and nutrient poor soils (Redfern *et al.*, 2003; Winnie *et al.*, 2008; Anderson *et al.*, 2010).

Vegetation structure is also an important biotic spatial element for herbivores, not only because it determines the accessibility of food to the different species, but also as a source of shade (Owen-Smith, 1998; Bjørneraas *et al.* 2012), and as potential cover from predators (Bro-Jørgensen, 2008; Bjørneraas *et al.* 2012). Thermal stress constitutes an important constraint to the time that herbivores can devote to foraging activities, and shade-seeking behaviour during the hottest hours of the day has been observed in various African ungulates, including kudu (Owen-Smith, 1998; Owen-Smith, 2002) and eland (Taylor, 1969; Hillman, 1979). The anti-predator strategies of small Bovids, including Tragelaphins such as bushbuck (*Tragelaphus scriptus*), are based on freezing and camouflage in thick vegetation cover, while large species tend to rely on fleeing or collective defence in open areas (Bro-Jørgensen, 2008). By contrast, medium- and large-sized browsers in Hwange National Park (Zimbabwe) were found to select for feeding sites with higher visibility than available control sites, probably because of enhanced probabilities of predators detection (Valeix *et al.*, 2011). Predation risk is also significantly high in areas close to water, such as rivers and waterholes, where thick woody cover provides ambush predators with effective concealment (Hopcraft, Sinclair & Packer, 2005).

The common eland is widely distributed across East and southern Africa, with presence recorded in virtually all land types (except for dense rainforest and true desert; Kingdon, 1997; Pappas, 2002). Owen-Smith (2002) suggested that eland, according to their dietary requirements, should select for broad-leaf savanna woodland and forb-rich grassland providing green foliage throughout the year. Seasonal landscape and habitat use by eland is therefore supposedly driven by changes in forage quality and abundance conditions, and in fact a number of studies suggested that eland in savanna areas move from woodland to open grassland during the early wet season to forage on new growing grasses (Lamprey, 1963; Hillman, 1988; Buys, 1990; Fabricius & Mentis, 1990; Watson & Owen-Smith, 2000). Similarly, eland of the Drakensberg mountain range move from afromontane forest and sub-alpine scrubland into grassland at the onset of the rains (Skinstad, 1972; Scotcher, 1983).

Burnt areas

In savannah ecosystems, natural or human-ignited fires promote the establishment of high quality herbaceous forage, by removing senescent, dry vegetal matter and stimulating the re-growth of new leaves on grass tufts (Vesey-Fitzgerald, 1971; Moe & Wegge, 1997). Mammalian grazers of different body sizes have been observed to select for previously burnt foraging areas when available within the landscape (Gureja & Owen-Smith, 2002; Magome *et al.*, 2008; Parrini & Owen-Smith, 2010), because of the high quality of the resprouting grass sward (McNaughton, 1985). However, grasses on burnt areas (burns from now onwards) are typically short and, although often providing a reliable source of protein during the dry season, they offer low fodder biomass to large herbivores (McNaughton, 1985; Wilsey, 1996). Medium-sized grazers on short grass like tsessebe and blue wildebeest, would therefore have to commute for unburnt vegetation patches in order to meet their high absolute food requirements (Wilsey, 1996). Medium- and tall-grass grazers, including roan and sable antelope, would instead make use of the burns only after the sward had reached a suitable height in grass leaves and stems to be efficiently cropped (around 6 cm for sable antelope; Grobler, 1981; Gureja & Owen-Smith, 2002; Tomor & Owen-Smith, 2002). Impala (*Aepyceros melampus*) and nyala (*Tragelaphus angasii*), which are referred to as mixed-feeding ungulates (consuming both grasses and browse according to local availability and quality), were seemingly attracted to burns in the Hluhluwe-iMfolozi Park during the dry season, when growing, young grasses often constitute the highest quality source of protein

(O'Kane *et al.,* 2011a). Feeding on burns has rarely been observed among African browsers, although kudu in Nylsvley Nature Reserve (South Africa) sometimes fed on post-fire grass flushes during the early wet season (Owen-Smith, 2002). In the area of lake Eyasi in northern Tanzania, browsers moved into burns later than grazers, as resprouting forbs and foliage on woody plants presented a lagged response to burning in respect to grasses (Moe, Wegge & Kapela, 1990). Burning can also remove tall grass cover, which is used for concealment by small herbivores, while at the same time providing large open areas with enhanced opportunities of detecting predators (FitzGibbon, 1990).

Available information on the use of burns by eland is scarce, although observations on the Drakensberg Mountains (South Africa; Rowe-Rowe, 1983) and in the Pilanesberg National Park (South Africa; Kelso, 1986) suggested that grazing on flushing grasses was restricted to the wet season, when the protein content of grasses was higher than that of woody fodder species (Buys, 1990). Immediate response to fires was recorded for the sister-species of the common eland, the Lord Derby's eland (*Tragelaphus derbianus*) of the Guineo-Sudanian savannahs, which were attracted by ashes and burnt woody material (Planton & Michaux, 2014).

Water availability

The availability and accessibility of surface water is a major constraint to herbivores distribution and movements in African savannahs (Bergström & Skarpe, 1999; Owen-Smith, 2002; Traill, 2004; Valeix *et al.,* 2009). Water availability changes over the seasonal cycle, with seasonal rivers and waterholes holding water almost exclusively during the wet season (Sinclair, 1975; Shorrocks, 2007). In many South African protected areas, water is artificially provided through boreholes and therefore does not constitute a limiting factor to large herbivores. Although the frequency of visits to water points is primarily affected by the capacity of animals to reduce water losses through faeces and urine (Cain *et al.,* 2012), it is also influenced by the perceived risk of predation while drinking (Hopcraft *et al.,* 2005), and and by the distance of suitable foraging areas from the water source (Redfern *et al.,* 2003). Sable antelope, for example, usually foraged far from water and reduced their visitation rate to waterholes and rivers during the dry season, probably in order to avoid the risks associated with the congregation of large numbers of zebra and buffalo, and of their predators, in these areas (Cain *et al.,* 2012). The availability of water seems to be less constraining for browsers

than for grazers, because of the generally higher moisture contents of browse material compared to grasses (Owen-Smith, 2002; Cain *et al.,* 2012). Large ruminant browsers (including giraffe and greater kudu) of Hwange NP and Kruger NP, for example, seemed to be less affected in their distribution patterns by water availability than similar-sized grazers (Redfern *et al.,* 2003; Valeix *et al.,* 2009). Only anecdotal information is available on eland water dependency. All sources confirm that these ungulates are water-independent and can survive for indetermined periods of time without drinking, probably obtainining the necessary moisture from the diet (Estes, 1991; Thouless, 2014). Accordingly, eland in the Amboseli basin (Kenya) were observed to occupy areas at a greater distance to water than any other ungulate (Western, 1975), while populations in the Kgalagadi TP actively avoided waterholes in fossil riverbeds during the dry season (Thouless, 2014). By contrast, eland are reported to drink regularly in areas where water is readily available and accessible (Estes, 1991; Kingdon, 1997; Pappas, 2002).

Forage selection

Foraging strategies

Browsing (feeding on dicotyledonous plants; dicots from now onwards), and grazing (feeding on monocotyledonous plants; monocots from now onwards) represent the two main foraging strategies adopted by herbivores (McNaughton & Georgiadis, 1986; Janis, 2008; Prins & Fritz, 2008). Jarman (1974) and Hofmann (1989) distinguished also herbivorous species, often referred to as “mixed feeders” or “intermediate feeders”, which regularly switch from grazing to browsing during different periods of the year in response to changes in nutritional value of both dicots and monocots. Grasses and dicots constitute two extremely different forage types (Owen-Smith, 2002), and for this reason the morphophysiology of the digestive system presents evident differences between grazers and browsers (Jarman, 1974; Hofmann, 1989). Although grasses in tropical and sub-tropical savannahs usually offer higher protein contents than dicots during the early growing season, when their nutritional value decreases rapidly, while woody plants and forbs maintain high levels of metabolizable nutrient and energy for longer into the dry season (Field, 1975; Buys, 1990). Grazers are therefore adapted to digest lower quality food than browsers (Hofmann, 1989). Body mass is also negatively associated with the degree of forage selectivity observed in mammalian herbivores (Bell, 1971; Jarman, 1974; Demment & Van Soest, 1985; Du Toit & Owen-Smith, 1989). Large

body size was traditionally considered by various authors as an adapatation to process large quantities of low-quality food, according to the Jarman-Bell principle (Bell, 1971; Jarman, 1974; Demment & Van Soest, 1985). However, a recent study by Steuer *et al.* (2013) largely disproved the assumption of superior digestive capacities for large herbivores. Therefore, differences in the quality of consumed forage associated with body mass are likely correlated with the different energy requirements of large and small species. Small herbivores present low absolute metabolic requirements, but feed on high-quality food items (i.e. green leaves, fruit) in order to satisfy higher energy requirements per unit of body mass than larger species (Jarman, 1974; Owen-Smith, 1988; Fynn *et al.,* 2016). Conversely, the high absolute metabolic requirements of large-bodied species largely determine the consumption of abundant forage of general lower quality (Steuer *et al.,* 2014; Fynn *et al.,* 2016). In addition, mouth anatomy constitutes a major physical constraint for forage selection (Fynn *et al.,* 2016). A narrow mouth allows species such as reedbuck (*Redunca arundinum*; Jungius, 1971) and sable antelope (Grobler, 1981), to select for green leaves in tall grass swards. By contrast, broad-mouthed ungulates, such as white rhinoceros, preferentially feed on uniform short swards, where grasses of acceptable quality can be efficiently cropped in large quantities (Arsenault & Owen-Smith, 2008). Although large-bodied species possess relatively broader mouths than smaller ones, the interspecific variation in the width of the dental arcades for similar-sized grazers is indicative of different feeding adaptations and can be extremely variable between species of similar body size (Fynn *et al.,* 2016). For example, the narrow-mouthed hartebeest (*Alcelaphus buselaphus*) can selectively feed on tall, low quality grass swards, while wildebeest, characterized by wide, square-shaped mouths, tend to prefer short grass lawns (Murray, 1993). Browsers are characterized by relatively narrower mouths than grazers (Owen-Smith, 1988); however, the ability of biting off single green leaves from woody plants decreases with increasing body size (O'Kane *et al.,* 2011a). Recent field observations reported selective feeding by very large browsers/mixed feeders, including moose (Van Beest *et al.* 2010), elephant (Owen-Smith & Chafota, 2012), and eland (Watson & Owen-Smith, 2000; D'Ammando *et al.,* 2015). It is therefore likely that other factors, including fine-scale physiological characteristics of the digestive systems and the heterogeneity of forage at different spatial scales, also affect the foraging strategies adopted by large mammalian herbivores.

Scales of foraging

The "palatability" (i.e. the likelihood of being consumed as food) of a plant species to a herbivore is determined by physical and chemical characteristics encompassing various scales, from the cellular structure to the stage of the life cycle (Owen-Smith & Cooper, 1987a; Owen-Smith, 2002). Structural defences include thorns and spines for dicots (Cooper & Owen-Smith, 1986) and silica bodies for monocots (McNaughton *et al.,* 1985), which increase the time required to handle food items and, ultimately, reduce the food intake rate (Cooper & Owen-Smith, 1986). Greenness, intended as the proportion of green leaves versus brown leaves on an plant (Walker, 1976), is generally considered as a good proxy indicator for plant phenophase and forage quality, as it is positively correlated with the protein and nutrient contents (Parrini, 2006; Pettorelli *et al.*, 2005). However, green leaves of woody plant species may contain variable concentrations of secondary compounds, which can act as deterrents of herbivory (Bryant, Reichardt & Clausen, 1992; Owen-Smith, 2002). Alkaloids, for example, are toxic to most mammalian herbivores, while high concentrations of condensed tannins slow down the digestive rates of ruminants (Cooper, Owen-Smith & Bryant, 1988; Bryant *et al.*, 1992). Thus, greenness of plant species and individual plants should be considered among the drivers of browse selection, provided that the potential effects of secondary metabolites is also taken into consideration. Forage quality also varies between single parts (leaves, stems, etc.) of an individual plant (Bryant *et al.*, 1992; Watson & Owen-Smith, 2000), and, as reported in previous paragraphs, is also influenced by the stage of the seasonal cycle and by local environmental conditions (Bailey *et al.,* 1996; Owen-Smith, 2002). Given the heterogeneity in nutritional quality of plant species across different spatio-temporal scales, forage selection can be viewed as a hierarchical decision-making process, nested within habitat selection (Novellie, 1978; Senft *et al.,* 1987; Bailey *et al.,* 1996; Owen-Smith *et al.,* 2010). By modifying the "scales of grazing" proposed by Bailey *et al.* (1996), and adapting them to the forage requirements of a browsing-mixed feeding ungulate, we can distinguish, along with plant species selection, the following scales of foraging:

a. Plant part (grass tuft): at the bite scale, herbivores tend to maximize the intake rate by selecting for single plant parts. The nutrient concentration, as well as the presence of secondary compounds and physical structures as herbivore-deterrents (thorns, spines), constitute the main driver of feeding selection at this scale (Owen-Smith & Cooper,

1987a; Bryant *et al.,* 1992; Bailey *et al.,* 1996; van der Merwe & Marshal, 2012). The morphology of the muzzle and of various mouth structures (including the width and inclination of the lower incisors arc in Bovids), also pose a constraint to selectivity, by determining the bite size and the thus the relative size of the selected plant part (e.g. shoot diameter or grass height; Hofmann, 1989; Bailey *et al.,* 1996; Arsenault, 2002; Arsenault & Owen-Smith, 2002).

b. Feeding station: a feeding station is the area immediately available for exploitation to a foraging herbivore, without any movement of the forelegs (Novellie, 1978). The quality and quantity of forage and the plant species composition influence the proportion of time spent at the station (and, subsequently, the food intake rate) versus the time needed for relocating to another station, thus constituting the main selection drivers (Novellie, 1978; Owen-Smith & Novellie, 1982; Underwood, 1983). Grazers of the Kyle National Park (Zimbabwe), for example, increased the time spent per feeding station during the dry season, probably as a consequence of the greater amount of time required to select green leaves among a matrix of senescent plant material (Underwood, 1983).

c. Feeding patch

   A feeding patch is a cluster of feeding stations (Bailey *et al.,* 1996). Patches can be identified as distinct spatial units when an individual animal reprises its feeding sequence after a relocating movement (Bailey *et al.,* 1996). Although little information is available about selectivity at this scale, male and female elephant, for example, show differential preferences towards patches presenting differences in plant species composition and small-scale topography (Stokke, 1999).

d. Feeding site

   A feeding site is a cluster of feeding patches, which is exploited during a foraging bout (a foraging session which is interrupted by other activities, such as relocation between patches; Bailey *et al.,* 1996). Selection for feeding sites falls within microhabitat selection, and it is influenced by distance to water, topography, and vegetation structure and composition (Bailey *et al.,* 1996; Boyers, 2011; Macandza *et al.,* 2012).

The eland: browser or mixed feeder?

Eland have been described as browsers, mixed feeders, and also as preferential grazers in different regions of the African continent (Lamprey, 1963; Kerr, Wilson & Roth, 1970; Hofmann, 1973; Nge'the & Box, 1976; Hofmann, 1989; Buys, 1990; Gagnon & Chew, 2000; Watson & Owen-Smith, 2000; Cerling, Harris & Passey, 2003; Codron *et al.,* 2005, 2007; Wallington *et al.,* 2007). Due to the very large body size and relatively broad muzzle of these ungulates, Jarman (1974) classified them as "roughage eaters", presenting adaptations to forage on a wide diversity of plant species and to digest plants and plant parts of very low nutritional value. However, despite their large body size, eland possess a browser-like digestive system, and are therefore unable to cope with poor quality forage, such as senescent grasses (Hofmann, 1973, 1989; Owen-Smith, 2002). Accordingly, several field studies reported that eland selected for green plant species and plant parts (Kerr *et al.,* 1970), and generally for either protein-rich or fibre-deficient forage (Field, 1975; Watson & Owen-Smith, 2000). At Galana Ranch (Kenya) and in the lowveld of Zimbabwe, eland fed on young grasses after the onset of the first rains, and, as grasses matured, they concentrated on deciduous browse plants, switching to browse on evergreen shrubs after the foliage of deciduous species had become unavailable (Kerr *et al.,* 1970; Field, 1975). The proportions of monocots in the diet of the eland vary according to the nutritional quality of grasses in different seasons and different eco-regions (Cerling *et al.,* 2003; Thouless, 2014). Although Gagnon & Chew (2000), in a review of the diet of extant African Bovids, reported that the average annual diet of the eland was constituted by up to 50% by grasses, high levels of grass consumption were recorded almost exclusively for the early months of the wet season, when short, green grasses are available (Hillman, 1979; Watson & Owen-Smith, 2000). East African populations of eland consume more grasses than their southern counterparts, probably because of an extended growing season resulting from bimodal rainfall patterns at equatorial latitudes (Owen-Smith & Ogutu, 2013). Cerling *et al.* (2003) found, by analysing the isotopic ratios between monocots (C^4 plants) and dicots (C^3 plants) in faecal and tooth enamel samples, that eland from Athi-Kapiti Plains and Laikipia plateau (Kenya) included on average 20% grasses in the annual diet. In southern Africa, the Cape eland has been usually considered as a browser consuming appreciable proportions of grasses only during the early growing season (Sponheimer *et al.,* 2003; Codron *et al.,* 2006, 2007; Wallington *et al.,* 2007). For example, grasses contributed by only 5.7 % to the eland annual diet in Mountain

Zebra NP, while constituting the favoured food type (up to 45% of the diet) during the early months of the wet season. The very low proportions of C^4 plants in the diet recorded in the Suikersbosrand Nature Reserve (South Africa) were ascribed by Wallington *et al.* (2007) to browsing on *Aloe marlothii* (though information on dietary composition was not available for the early wet season). Nevertheless, grazing on remaining green tufts during the late wet or dry seasons has been reported for various southern African populations in grassland-dominated areas (Buys, 1990; D'Ammando *et al.*, 2015). It is thus possible, as suggested by Wallington *et al.* (2007), that eland may be able to adapt their dietary preferences to local conditions of forage quality and availability. This extreme versatility in feeding habits may explain the wide geographic distribution and the catholic habitat preferences of this large ungulate (Kingdon, 1997).

STUDY AREA

The Kgaswane Mountain Reserve (KMR, 35° 43'S 27° 11'E; altitude: 1300-1660 m a.s.l) is situated in the North-West Province of South Africa (**Fig. 1**). The reserve was proclaimed in 1967 as the Rustenburg Nature Reserve, assuming its current name in 2002. The area protects part of the Magaliesberg mountain range, and borders, to the south-east and east, the suburban areas of Rustenburg. The reserve covers an area of about 4257 ha (Nel, 2000). Annual rainfall average is 682 mm (CV 27%, calculated over 44 years); 88% of the annual rainfall occurs between October and March. Mean daily temperature ranges from 9.7°C in July to 21.3°C in January (additional information on rainfall and temperature during the study period can be found in Appendix I).

The geomorphology of KMR allows for the distinction between a plateau region, and fluvial valleys (Nel, 2000; Parrini, 2006). In the northern area of the reserve, the plateau is flat and constituted by quartzite; it extends into a *vlei* (or *dambo*) occupying the central basin of KMR (Wilson & Hirst, 1977; Carruthers, 2014; Parrini, 2006). A *vlei* is defined as a seasonally-waterlogged and treeless depression in the upper catchment of a river system (Fynn *et al.*, 2015). In the KMR, a main *vlei* is found along the main drainage line in the central basin, but smaller seasonally flooded areas are also present in the valleys (Nel, 2000). The valleys lay on a preponderantly diabasic substrate, and quartzite hill ranges abruptly divide them from the plateau (Carruthers, 2014). The Waterkloofspruit originates from the upper plateau within the reserve, and, flows through a gorge and down to the south-eastern valley, exiting the reserve

to become a tributary of the Hex river (Nel, 2000). Small streams also originate from the plateau and join the main watercourse in the central basin (Nel, 2000).

The soils are mostly constituted by quartzitic sandstone, and therefore they are nutrient deficient (Carruthers, 2014). Deep and well-differentiated soils are present on the northern plateau and in the *vlei*, where they are constituted by alluvial deposits of black clays (Nel, 2000). The valleys present young alluvial soils, while shallow and poorly differentiated soils characterize the hills range (Nel, 2000).

Nel (2000) classified the reserve into four main vegetation types differentiated by species composition, nature of the underlying mother rock, soil depth, clay content, and moisture content (**Fig. 2**):

1) Dry grassland: this vegetation type is found mostly in the northern plateau and in the central basin, where the following grass species are common: *Brachiaria serrata, Eragrostis racemosa, Loudetia simplex, Schizachyrium sanguineum, Themeda triandra*, and *Trachypogon spicatus*. In the central basin, grassland is often associated with scattered individuals of *Protea caffra, Acacia caffra* and *Faurea saligna*. Grassland communities are also patchily found on hill slopes.
2) Wet grassland: found almost exclusively in the *vlei* on the central basin, although small patches are also present on the plateau and in the valleys. It is mostly constituted by *Phragmites australis* reedbeds located close to the main rivercourse;
3) Open shrubland: found mostly on slopes along the hills range. Common species in this community include: *Englerophytum magalismontanum, Zanthoxylum capense, Ancylobotrys capensis* and *Vangueria parvifolia*; associated grass species include *Diheteropogon amplectens, T. triandra* and *Melinis nerviglumis*;
4) Woodland: associated with the main valleys. Vegetation communities are dominated by *A. caffra* and *P. caffra.* Other common trees are *Celtis africana, Combretum molle, Combretum zeyheri, Grewia occidentalis, Searsia leptodictya,* and *Ziziphus mucronata*, with common species in the grass layer constituted by *T. triandra, Setaria sphacelata, Heteropogon contortus, Panicum maximum* and *Setaria lindenbergiana.*

The main protected area borders with privately-owned lands, namely the Hunter's Rest Farm, which has been effectively incorporated into the reserve, and the Rainbow Farms, which have

been alternatively included or excluded from sharing an unfenced boundary with KMR (Thsenkeng, *pers. comm.*). However, as Rainbow Farms seemed to be easily accessible to eland even in the presence of a low boundary fence, I considered them as part of the study area.

Regular controlled burning has been used as a management tool since 1975, in order to remove moribund or death plant material and stimulate grass growth (Nel, 2000). The burning usually takes place during the late wet season or early dry season, in order to alleviate nutritional stress to economically valuable grazing herbivores during the course the critical season (Nel, 2000; Parrini & Owen-Smith, 2010). The sable antelope population of the KMR, for example, extensively graze on burns after green regrowth is available (Parrini & Owen-Smith, 2010), and recent observations suggest that eland may also take advantage of green grass on burns during the mid-dry season (D'Ammando *et al.*, 2015).

The large mammal populations present in the KMR are mostly a result of systematic reintroductions after the proclamation of the reserve (Nel, 2000). Aerial counts of medium- to large-sized animals were started in 1985; the most recent game count show high numbers of herbivores on the terrain of the reserve, including zebra (90) and antelopes such as eland (94), sable antelope (41), greater kudu (27), common reedbuck *Redunca arundinum* (11), mountain reedbuck *Redunca fulvorufula* (22), blesbok *Damaliscus pygargus* (26), impala (73), red hartebeest *Alcelaphus buselaphus* (90), roan antelope (3), springbok (5), waterbuck (71), klipspringer *Oreotragus oreotragus* (6), and oribi *Ourebia ourebi* (2) (Nel *et al.*, 2011; Thsenkeng, *pers. comm.*). Very small numbers of predators, including caracal (*Felis caracal*), aardwolf (*Protele cristatus*), black-backed jackal (*Canis mesomelas*) and leopard (*Panthera pardus*) also occur in the reserve. Leopard are however very uncommon and sightings are probably restricted to vagrant animals originating from the main Magaliesberg population (Power, *pers. comm.*).

The study population

The population of eland in KMR, despite oscillations in number over the years, has never shown any alarming sign of decline since the initiation of aerial surveys of large mammals by the North-West Parks and Tourism Board in 1999 (Thsenkeng, *pers. comm.*; **Fig. 3**). Although decreasing abundance seemed to be correlated with low annual rainfall, differences

in total counts between consecutive years could also account for the reported oscillations. This could be especially true when considering that adjoining areas to KMR, such as the Rainbow Farms, have been discontinuously surveyed. Moreover, varying numbers of adult eland were occasionally removed from KMR prior to 2013, thus further affecting the population structure and dynamics of this species in the area. P. Theskeng, the ecologist of the reserve, has suggested that the period of the year in which the aerial surveys are conducted may also play a crucial role in determining the effective number of eland visible to the observers. In fact, individuals of this species (as confirmed by my own observations reported in Appendix II and by other studies across East and southern Africa) tend to aggregate in large nursery herds in open vegetation communities during the wet season, whilst living in very small social groups and utilising woodland and thickets during the dry months. Thereof, the results of aerial counts conducted at the apex of the dry season would produce an underestimate of the number of eland, which would be a consequence of the lowered visibility of small groups under the canopy of the wooded valleys and gorges of KMR. Conversely, an aerial survey in late October 2015, reported a very high number of eland, most of them in a large nursery herd. I could therefore assume eland in KMR to represent a relatively thriving population, as numbers over 16 years preceding the present study, despite the removal of individuals and the varying rainfall patterns, never decreased abruptly, without any visible threat of local extirpation.

THESIS STRUCTURE

The broad aim of this study was to investigate resource selection at different spatio-temporal scales by a low-density, nomadic antelope, the common eland, within the context of an insular-like protected area. The characteristics of the KMR, and especially its absence of predators, sub-temperate climate (excluding prolonged situation of potential thermal stress), and year-round availability of surface water, contributed to define an ideal study site in which to quantify resource selection at various scales under the influence of forage quality and availability.

The thesis is made up of two data chapters (chapter 2 and 3), a general introduction chapter (chapter 1) and a conclusion chapter (chapter 4). The sub-division into two research chapters reflected the different approaches to data acquisition, with GPS-collars and remote sensing providing the base for the second chapter (3^{rd} and 2^{nd} order resource selection), and field-

collected data constituting the core of the work on forage selection in the third chapter (1st order selection). Initially, the project should have spanned only one year of collars data, restricting to information collected at hourly intervals by GPS units between 25th September 2014 and 30th September 2015. However, the year 2015 was characterized by very low rainfall, well below the average calculated over forty years from data provided by KMR's meteorological station. I thus decided to include data collected over the preceding year in chapter 2, in order to get a comparison of pre-drought conditions with movement patterns and resource selection during year of average rainfall.

The objectives of Chapter 2 were:

1) To determine the extent and location of the seasonal home ranges utilised by collared adult female eland in the KMR, in relationship to the available resources at the landscape scale (3rd order selection).
2) To determine the influence of environmental drivers, including abundance and quality of forage and its variation in space and time, vegetation structure, and availability of burns, on habitat selection by eland across the seasonal cycle (2nd order selection).

These objectives were achieved by the use of GPS locations from collared individuals and by the use of data available from satellite imagery (greenness) and from ongoing ecological monitoring work in the KMR (maps of vegetation and burnt areas). Annual home ranges proved to hold very little significance to the ecology of eland in KMR, where they evidently occupied discrete areas during the wet and dry season. Therefore, the study of eland spatial ecology was entirely based on used locations within seasonal home ranges, rather than within annual ranges, compared to available locations generated across the entire reserve (landscape selection), and within the same seasonal home ranges (habitat selection). This procedure, despite comparing the same set of used points with available locations at two spatial scales, was considered to be the most accurate representation of space use by eland over the seasonal cycle.

In Chapter 3, I presented a study on forage selection and its interaction with phenology of grasses and browse at the plant species scale, with additional information on the seasonal characteristics associated with feeding sites. The original study was designed to conduct an individual-based assessment of plant species selection, to be included in a full-scale

investigation of hierarchical forage and habitat selection of each individual animal, within the seasonal and annual home range. However, collar failures during the course of 2015 prevented this procedure to be fully implemented during the two data collection sessions in the field, requiring the addition of observations on other non-collared individuals and social units. For this reason, I also included observations on characteristics of feeding sites, as a term of comparison with collar-based estimates of habitat selection presented in Chapter 2. The objectives of Chapter 3 were:

1) To determine the changes in the use of vegetation types and burnt areas during foraging activities between two different seasons.
2) To determine forage selection at the plant species scale, as influenced by phenological characteristics of grasses and browse.

During an early phase of the eland project in July 2013 (part of my work as a visiting student at the Centre for African Ecology and of my previous degree), I observed that eland were extensively grazing on grass species retaining green leaves into the driest period of the year (D'Ammando *et al.*, 2015). This was considered as rather extraordinary for eland during the dry season, especially as it happened during a year characterised by above-the-average rainfall, thus not forcing eland to feed on dry grasses as recorded in situations of nutritional stress (Hillman, 1979). The focus on forage selection at different times of the year thus provided an opportunity to compare the relative dietary contribution of grasses and browse to the seasonal diet; this aspect was considered as a "sub-objective" of objective 2. The main limitation to the field work was constituted by the human-shy and ever-alert nature of the species in general and of the population inhabiting KMR (which is not exposed to high photo-tourism volumes) in particular, which impeded detailed observations at close quarters of the study animals during foraging activities. However, the field protocol adopted allowed for general direct observations of feeding sites use and herd size and structure, and at the same time ensured the least bias possible for the indirect evaluation of plant species selection.

While conducting field work, I noticed that the size and composition of the herds with which collared individuals associated, were seemingly in constant flux, and that, similarly to what reported by early researchers (Underwood, 1975; Hillman, 1987), the social structure of eland appeared to be correlated with the use of different vegetation types at different times of the

year. For this reason, I included in Appendix II a small account regarding the size and age-sex structure of eland social groups I encountered in the study area.

Each chapter of this thesis presents a paper-like structure, and is organized into an introduction, materials and methods, results, discussion, and conclusions, while also accompanied by references of the literature cited in the chapter itself. Tables and figures are not embedded in the text but presented at the end of each chapter. In order to avoid unnecessary repetition, the study area is described only once in the first, introductory chapter. Information presented in the literature review is often re-discusses within the introduction or discussion of each research chapter, and therefore I apologise to the reader for potential repetitions, which were however necessary to the flowing of the text. The final chapter is written in the form of a summary of the entire research project, also presenting management suggestions based on the data collected and on the results achieved. Additionally, broad implications of my findings for the management and conservation of eland populations on insular-like reserves are also discussed, as well as an examination of the findings within the evolutionary history and ecological role played by eland in African savannah ecosystems.

FIGURES

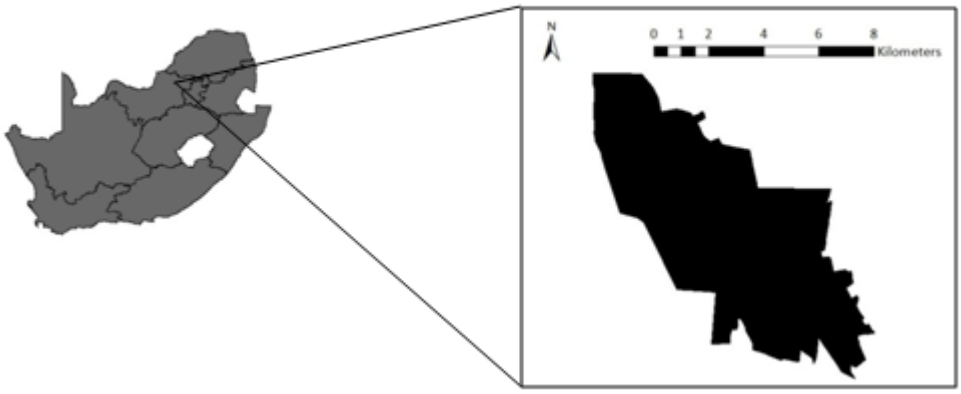


Fig. 1 : Location of Kgaswane Mountain Reserve in the North-West Province, South Africa.

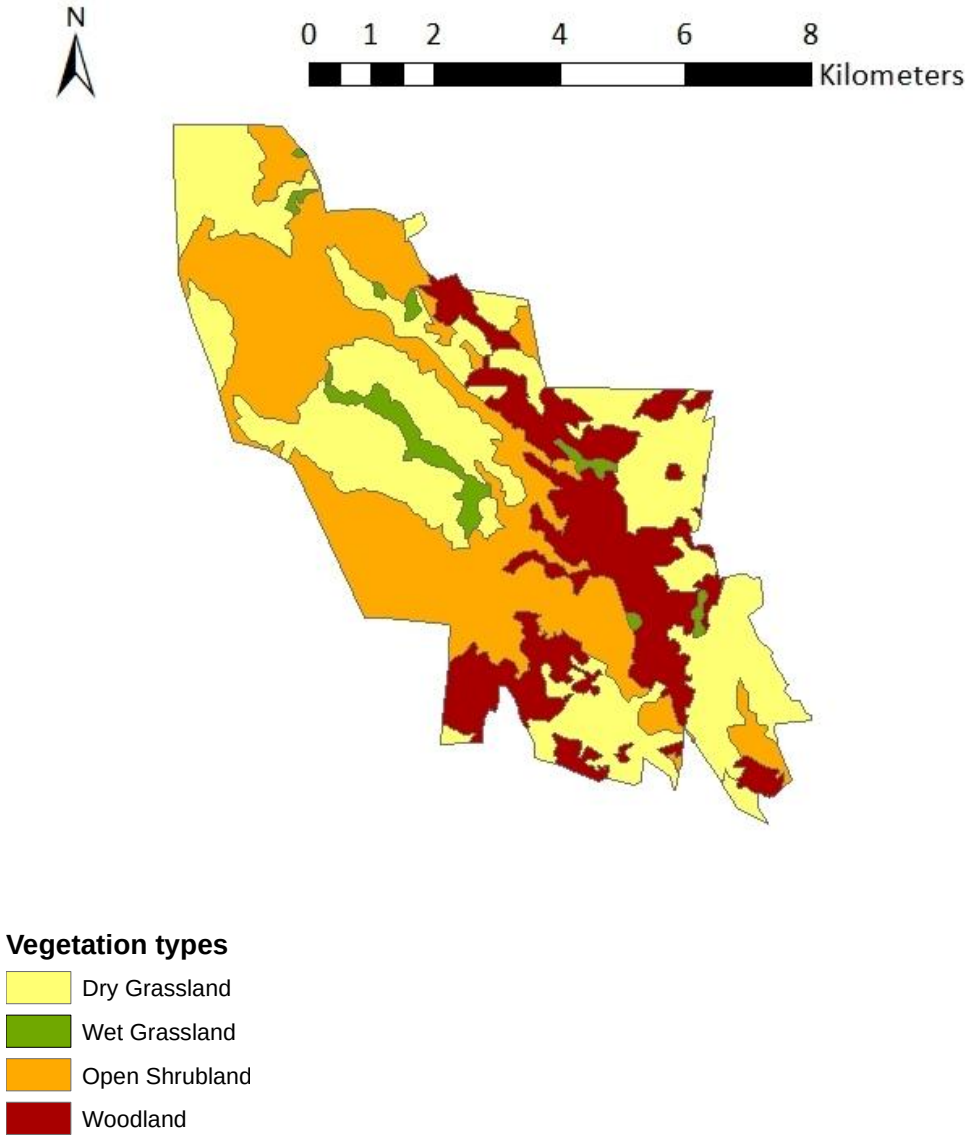


Fig. 2: Map of the four main vegetation types characterizing the Kgaswane Mountain Reserve. The contours of each vegetation type were drawn according to aerial images, and later validated through field relevès.

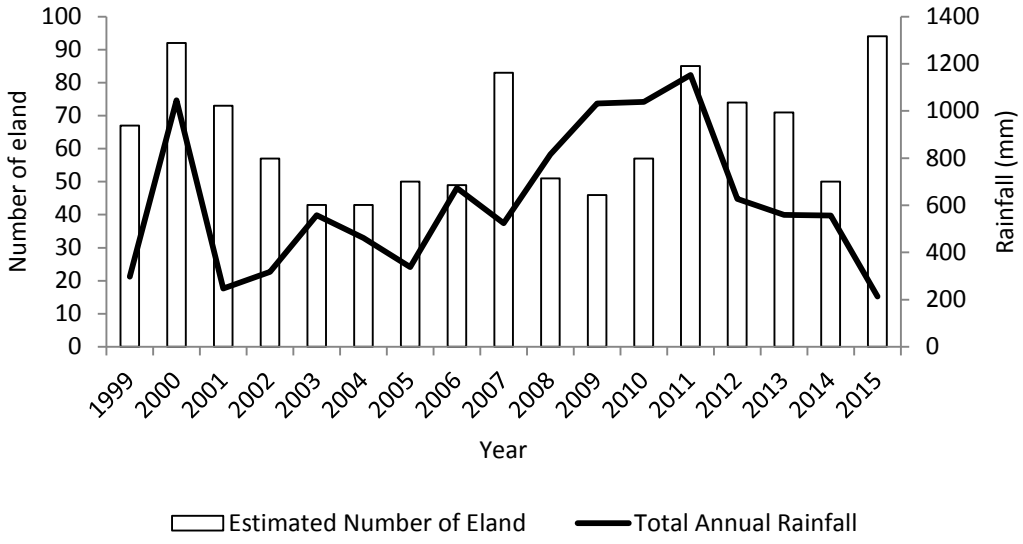


Fig. 3: Estimated number of eland in the Kgaswane Mountain Reserve. Estimates were derived from total aerial counts conducted from a helicopter and on an annual basis by the staff of the North-West Parks and Tourism Board. Total annual rainfall, recorded at the Kgaswane Meteorological Station, was also included in the graph, as a possible determinant of population dynamics of eland.

REFERENCES

ANDERSON, T. M., HOPCRAFT, J. G. C., EBY, S., RITCHIE, M., GRACE, J. B., & OLFF, H. (2010). Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. *Ecology*, **91**(5), 1519-1529.

ARDITI, R., & DACOROGNA, B. (1988). Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist*, **136**(6), 837-846.

ARSENAULT, R. (2008). *Competition vs facilitation: Species interactions within the short grass grazing guild*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

ARSENAULT, R., & OWEN-SMITH, N. (2008). Facilitation versus competition in grazing herbivore assemblages. *Oikos*, **97**(3), 313-318.

AUGUSTINE, D. J. (2004). Influence of cattle management on habitat selection by impala on central Kenyan rangeland. *Journal of Wildlife Management*, **68**(4), 916-923.

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

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

BERGSTRÖM, R. (1992). Browse characteristics and impact of browsing on trees and shrubs in African savannas. *Journal of Vegetation Science*, **3**(3), 315-324.

BERGSTRÖM, R., & SKARPE, C. (1999). The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *African Journal of Ecology*, **37**(1), 12-26.

BERRY, P. S. M. (1978). Range movements of giraffe in the Luangwa Valley, Zambia. *African Journal of Ecology*, **16**(2), 77-83.

BJØRNERAAS, K., HERFINDAL, I., SOLBERG, E. J., SÆTHER, B. E., VAN MOORTER, B., & ROLANDSEN, C. M. (2012). Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. *Oecologia*, **168**(1), 231-243.

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

BÖRGER, 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**(6), 637-650.

BOYERS, M. (2011). *Do zebra (Equus quagga) select for greener grass within the foraging area?*PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

BRO-JØRGENSEN, J. (2008). Dense habitats selecting for small body size: a comparative study on bovids. *Oikos*, **117**(5), 729-737.

BRO-JØRGENSEN, J., & DABELSTEEN, T. (2008). Knee-clicks and visual traits indicate fighting ability in eland antelopes: multiple messages and back-up signals. *BMC biology*, **6**(1), 1.

BRYANT, J. P., REICHARDT, P. B., & CLAUSEN, T. P. (1992). Chemically mediated interactions between woody plants and browsing mammals. *Journal of Range Management*, **45**, 18-24.

BURT, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**(3), 346-352.

BUYS, D. (1990) Food selection by eland in the western Transvaal. *South African Journal of Wildlife Research*, **20**, 16-20.

BUYS, D. & DOTT. H. M. (1991). Population fluctuations and breeding of eland Taurotragus oryx in a western Transvaal nature reserve. *Koedoe-African Protected Area Conservation and Science*, **34**(1), 31-36.

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**(1), 58-67.

CAMERON, E. Z., & DU TOIT, J. T. (2007). Winning by a neck: tall giraffes avoid competing with shorter browsers. *The American Naturalist*, **169**(1), 130-135.

CARBONE, C., COWLISHAW, G., ISAAC, N. J., & ROWCLIFFE, J. M. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, **165**(2), 290-297.

CARRUTHERS, V. (2014). *The Magaliesberg*. Protea Book House Pretoria, Pretoria, South Africa.

CERLING, T. E., HARRIS, J. M., & PASSEY, B. H. (2003) Diets of East African Bovidae based on stable isotope analysis. *Journal of Mammalogy* **84**(2), 456-470.

CODRON, D., CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., & DE RUITER, D. (2005) Animal diets in the Waterberg based on stable isotopic composition of faeces. *South African Journal of Wildlife Research,* **35**(1), 43-52.

CODRON, D., CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R., & FOURIE, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology,* **273**(2), 21-29

COOPER, S. M., & OWEN-SMITH, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia*, **68**(3), 446-455.

COOPER, S. M., OWEN-SMITH, N., & BRYANT, J. P. (1988). Foliage acceptability to browsing ruminants in relation to seasonal changes in the leaf chemistry of woody plants in a South African savanna. *Oecologia*, **75**(3), 336-342.

CROMSIGT, J. P., & KUIJPER, D. P. (2011). Revisiting the browsing lawn concept: Evolutionary Interactions or pruning herbivores?. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**(3), 207-215.

CROMSIGT, J. P., & OLFF, H. (2008). Dynamics of grazing lawn formation: an experimental test of the role of scale-dependent processes. *Oikos*, **117**(10), 1444-1452.

D'AMMANDO, G., PARRINI, F., ATTORRE, F., & BOITANI, L. (2015). Observations on dry season grazing by eland in a Magaliesberg Nature Reserve, South Africa.*African Journal of Ecology,* **53**(1), 112-115.

DEMMENT, M. W., & VAN SOEST, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, **125**(5), 641-672.

DU TOIT, J. T. (1986). *Patterns of resource use within the browsing ruminant guild in the central Kruger National Park*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

DU TOIT, J. T. (1990). Feeding-height stratification among African browsing ruminants. *African Journal of Ecology*, **28**(1), 55-61.

DU TOIT, J. T. (1995). Determinants of the composition and distribution of wildlife communities in southern Africa. *Ambio*, **24**(1), 2-6.

DU TOIT, J. T., & OWEN-SMITH, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist*, **133**(5), 736-740.

DUNHAM, K. M., ROBERTSON, E. F., & SWANEPOEL, C. M. (2003). Population decline of tsessebe antelope (*Damaliscus lunatus lunatus*) on a mixed cattle and wildlife ranch in Zimbabwe. *Biological conservation*, **113**(1), 111-124.

DUNHAM, K. M., ROBERTSON, E. F., & GRANT, C. C. (2004). Rainfall and the decline of a rare antelope, the tsessebe (Damaliscus lunatus lunatus), in Kruger National Park, South Africa. *Biological conservation*, **117**(1), 83-94.

EAST, R. (Editor). (1999). *African antelope database 1998* (Vol. 21). IUCN.

ESTES, R. D. (1991). *The behaviour guide to African mammals.* University of California Press, Berkeley, USA, and London, UK.

ESTES, R. D., ATWOOD, J. L., & ESTES, A. B. (2006). Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. *Biological Conservation*, **131**(1), 106-120.

FABRICIUS, C., & MENTIS, M. T. (1990) Seasonal habitat selection by eland in arid savanna in southern Africa. *South African Journal of Zoology* **25**(4), 238-244.

FIELD, C. R. (1975) Climate and the food habits of ungulates on Galana Ranch. *African Journal of Ecology*, **13**, 203-220.

FISCHHOFF, I. R., SUNDARESAN, S. R., CORDINGLEY, J., & RUBENSTEIN, D. I. (2007). Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology*, **18**(4), 725-729.

FITZGIBBON, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour*, **39**(6), 1116-1126.

FORNARA, D. A., & DU TOIT, J. T. (2007). Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African savanna. *Ecology*, **88**(1), 200-209.

FRYXELL, J. M., & SINCLAIR, A. R. E. (1988). Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology*, **26**(1), 17-31.

FRYXELL, J. M., WILMSHURST, J. F., & SINCLAIR, A. R. (2004). Predictive models of movement by Serengeti grazers. *Ecology*, **85**(9), 2429-2435.

FYNN, R. W., CHASE, M., & RODER, A. (2014). Functional habitat heterogeneity and large herbivore seasonal habitat selection in northern Botswana. *South African Journal of Wildlife Research*, **44**(1), 1-15.

FYNN, R. W. S., MURRAY-HUDSON, M., DHLIWAYO, M., & SCHOLTE, P. (2015). African wetlands and their seasonal use by wild and domestic herbivores.*Wetlands Ecology and Management*, **23**(4), 559-581.

FYNN, R. W., AUGUSTINE, D. J., PEEL, M. J., & GARINE-WICHATITSKY, M. (2016). REVIEW: Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence. *Journal of Applied Ecology*, **53**(2), 388-397.

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

GILPIN, M. E., & SOULE, M. E. 1986. Minimum viable populations: processes of species extinction. *Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts*, 19-34.

GORDON, I. J. (1989). Vegetation community selection by ungulates on the Isle of Rhum. II. Vegetation community selection. *Journal of Applied Ecology*, **26**(1), 53-64.

GRANT, C. C., & SCHOLES, M. C. (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, **130**(3), 426-437.

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

GUREJA, N., & OWEN-SMITH, N. (2002). Comparative use of burnt grassland by rare antelope species in a lowveld game ranch, South Africa. *South African Journal of Wildlife Research*, **32**(1), p-31.

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**(1), 69-78.

HEITKÖNIG, I., & OWEN-SMITH, N. (1998). Seasonal selection of soil types and grass swards by roan antelope in a South African savanna. *African Journal of Ecology*, **36**(1), 57-70.

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, Skukuza, South Africa.

HENSMAN, M. C., OWEN-SMITH, N., PARRINI, F., & BONYONGO, C. M. (2014a). Resource use and the nutritional status of sable antelope in the Okavango Delta region of northern Botswana. *African Journal of Ecology*, **52**(3), 265-273.

HENSMAN, M. C., OWEN-SMITH, N., PARRINI, F., & BONYONGO, C. M. (2014b). Home range occupation and habitat use of sable antelope in the Okavango Delta region of northern Botswana. *African journal of ecology*, **52**(2), 237-245.

HILLMAN, J. C. (1979). *The biology of the Eland (Taurotragus oryx) in the wild*. PhD Thesis, University of Nairobi, Nairobi, Kenya.

HILLMAN, J. C. (1987). Group size and association patterns of the common eland (Tragelaphus oryx). *Journal of Zoology*, **213**(4), 641-663.

HILLMAN, J. (1988). Home range and movement of the common eland (*Taurotragus oryx* Pallas 1766) in Kenya. *African Journal of Ecology*, **26**(2), 135-148.

HOFMANN, R. R. (1973) *The ruminant stomach. Stomach structure and feeding habits of East African game ruminants.* East African Monographs in Biology, 2. East African Literature Bureau, Nairobi.

HOFMANN, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, **78**(4), 443-457.

HOLDO, R. M., HOLT, R. D., & FRYXELL, J. M. (2009). Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**(4), 431-445.

HOLDO, R. M., FRYXELL, J. M., SINCLAIR, A. R., DOBSON, A., & HOLT, R. D. (2011). Predicted impact of barriers to migration on the Serengeti wildebeest population. *PloS one*, **6** (1), e16370.

HOLDRIDGE, L. R. (1947). Determination of world plant formations from simple climatic data. *Science*, **105**, 367-368.

HOPCRAFT, J. G. C., SINCLAIR, A. R. E., & PACKER, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, **74** (3), 559-566.

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

JANIS, C. (2008). An evolutionary history of browsing and grazing ungulates. In GORDON, I. J., & PRINS, H. H. (Eds.). (2008). *The ecology of browsing and grazing* (pp. 21-45), Springer, Heidelberg, Germany.

JARMAN, P. J. (1971). Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia*, **8**(2), 157-178.

JARMAN, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(3/4), 215-267.

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

JUNGIUS, H. (1971). Studies on the food and feeding behaviour of the reedbuck *Redunca arundinum* Boddaert, 1785 in the Kruger National Park. *Koedoe*, **14**(1), 65-98.

KEEP, M.E., BARNES, P.R. & ROOT, A.E.A. *(*1972*)* The marking of adult male eland to study seasonal movements. *The Lammergeyer*, **17**, 10–17.

KELSO, D. L. (1986). *Resource Partitioning Between Browsing Ungulates: Kudu (Tragelaphus strepsiceros) and Eland (Taurotragus oryx) in Pilansberg National Park, Bophuthatswana*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

KERR, M. A., WILSON, V. J., & ROTH, H. H. (1970) Studies on the agricultural utilization of semi-domesticated eland (*Taurotragus oryx*) in Rhodesia. 2. Feeding habits and food preferences. *Rhodhesian Journal of Agricultural Research*, **8**, 71-77.

KINGDON, J. (1982). *East African Mammals: an atlas of evolution in Africa. Volume III, Part C (Bovids).* Academic Press, London, UK.

KINGDON, J. (1997). *The Kingdon field guide to African mammals.* A & C Black Publishers, London, UK.

KREULEN, D. (1975). Wildebeest habitat selection on the Serengeti plains, Tanzania, in relation to calcium and lactation: a preliminary report. *African Journal of Ecology*, **13**(3-4), 297-304.

KRÖGER, R., & ROGERS, K. H. (2005). Roan (*Hippotragus equinus*) population decline in Kruger National Park, South Africa: influence of a wetland boundary. *European journal of wildlife research*, **51**(1), 25-30.

LAMPREY, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika1. *African Journal of Ecology*, **1**(1), 63-92.

LANDMAN, M., SCHOEMAN, D. S., & KERLEY, G. I. (2013). Shift in black rhinoceros diet in the presence of elephant: evidence for competition?. *PloS one*, **8**(7), e69771.

LEUTHOLD, W. (1978). Ecological separation among browsing ungulates in Tsavo East National Park, Kenya. *Oecologia*, **35**(2), 241-252.

LEUTHOLD, B. M., & LEUTHOLD, W. (1978). Ecology of the giraffe in Tsavo East National Park, Kenya. *African Journal of Ecology*, **16**(1), 1-20.

LEWIS, J. G. (1978). Game domestication for animal production in Kenya: shade behaviour and factors affecting the herding of eland, oryx, buffalo and zebu cattle. *The Journal of Agricultural Science*, **90**(03), 587-595.

MACANDZA, V. A., OWEN-SMITH, N., & CAIN III, J. W. (2012). Dynamic spatial partitioning and coexistence among tall grass grazers in an African savanna. *Oikos*, **121**(6), 891-898.

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

MARSHAL, J. P., BLEICH, V. C., KRAUSMAN, P. R., REED, M. L., & ANDREW, N. G. (2006). Factors affecting habitat use and distribution of desert mule deer in an arid environment. *Wildlife Society Bulletin*, **34**(3), 609-619.

MARSHAL, J. P., RAJAH, A., PARRINI, F., HENLEY, M., HENLEY, S. R., & ERASMUS, B. F. (2011). Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. *European Journal of Wildlife Research*, **57**(3), 537-548.

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.

MCNAUGHTON, S. J. (1976). Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science*, **191**(4222), 92-94.

MCNAUGHTON, S. J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *American Naturalist*, **124**(6), 863-886.

MCNAUGHTON, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological monographs*, **55**(3), 259-294.

MCNAUGHTON, S. J., TARRANTS, J. L., MCNAUGHTON, M. M., & DAVIS, R. D. (1985). Silica as a defense against herbivory and a growth promotor in African grasses. *Ecology*, **66**(2), 528-535.

MCNAUGHTON, S. J., & GEORGIADIS, N. J. (1986). Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics*, **17,** 39-65.

MCQUALTER, K. N., CHASE, M. J., FENNESSY, J. T., MCLEOD, S. R., & LEGGETT, K. E. (2015). Home ranges, seasonal ranges and daily movements of giraffe (*Giraffa camelopardalis giraffa*) in northern Botswana. *African Journal of Ecology*, **54**(1), 99-102

MDUMA, S. A., & SINCLAIR, A. R. E. (1994). The function of habitat selection by oribi in Serengeti, Tanzania. *African Journal of Ecology*, **32**(1), 16-29.

MECH, L. D. (1977). Wolf-pack buffer zones as prey reservoirs. *Science*, **198**(4314), 320-321.

MOE, S. R., WEGGE, P., & KAPELA, E. B. (1990). The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. *African journal of Ecology*, **28**(1), 35-43.

MOE, S. R., & WEGGE, P. (1997). The effects of cutting and burning on grass quality and axis deer (*Axis axis*) use of grassland in lowland Nepal. *Journal of Tropical Ecology*, **13**(02), 279-292.

MORRISON, M. L., MARCOT, B., & MANNAN, W. (2006). *Wildlife-habitat relationships: concepts and applications*. Island Press, Washington, D.C., USA.

MUELLER, T., & FAGAN, W. F. (2008). Search and navigation in dynamic environments–from individual behaviors to population distributions. *Oikos*, **117**(5), 654-664.

MUELLER, T., OLSON, K. A., FULLER, T. K., SCHALLER, G. B., MURRAY, M. G., & LEIMGRUBER, P. (2008). In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *Journal of Applied Ecology*, **45**(2), 649-658.

MURRAY, M. G. (1993). Comparative nutrition of wildebeest, hartebeest and topi in the Serengeti. *African Journal of Ecology*, **31**(2), 172-177.

MYSTERUD, A., PÉREZ-BARBERÍA, F. J., & GORDON, I. J. (2001). The effect of season, sex and feeding style on home range area versus body mass scaling in temperate ruminants. *Oecologia*, **127**(1), 30-39.

NAIDOO, R., DU PREEZ, P., STUART-HILL, G., WEAVER, L. C., JAGO, M., & WEGMANN, M. (2012). Factors affecting intraspecific variation in home range size of a large African herbivore. *Landscape ecology*, **27**(10), 1523-1534.

NEL, H. P. (2000). *Ecological management objectives and monitoring procedures for Rustenburg Nature Reserve, North West Province* . MSc Thesis, University of Pretoria, Pretoria, South Africa.

NEL, P., KNOOP, C., SEITHLAMO, W., TSHENKENG, P. (2011). *Animal population estimates for protected areas in the North-West Province.* Scientific Report, North West Parks and Tourism Board, Mafikeng, South Africa.

NGE'THE, J.C., & BOX, T. W. (1976) Botanical composition of eland and goat diets on an Acacia-grassland community in Kenya. *Journal of Range Management,* **29**, 290-293.

NGUGI, M. K., & CONANT, R. T. (2008). Ecological and social characterization of key resource areas in Kenyan rangelands. *Journal of Arid Environments*, **72**(5), 820-835.

NOVELLIE, P. A. (1978). Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. *South African Journal of Wildlife Research*, **8**(4), 137-144.

OGUTU, J. O., & OWEN-SMITH, N. (2003). ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. *Ecology Letters*, **6**(5), 412-419.

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**(2), 99-109.

O'KANE, C. A., DUFFY, K. J., PAGE, B. R., & MACDONALD, D. W. (2011a). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, **27**(3), 249-258.

O'KANE, C. A., DUFFY, K. J., PAGE, B. R., & MACDONALD, D. W. (2013). Effects of resource limitation on habitat usage by the browser guild in Hluhluwe-iMfolozi Park, South Africa. *Journal of Tropical Ecology*, **29**(1), 39-47.

OKELLO, M. M., KIRINGE, J. W., WARINWA, F., MURUTHI, P., KENANA, L., MASSAWE, E., KANGA, E., MURUTHI, P., BAKARI, S., SITATI, N. W., NDAMBUKI, S., GICHOI, N., KIMUTAI, D., MWITA, M., MUTETI, D., & MALITI, H. (2015). Status and population trend of the common eland in the Kenya Tanzania borderland: 2010 and 2013 survey analysis. *International Journal of Biodiversity and Conservation*, **7**(4), 254-266.

OWEN-SMITH, N. (1982). Factors influencing the consumption of plant products by large herbivores. (pp. 359-404). In HUNTLEY, B.J., *et al.* (Editors) *Ecology of tropical savannas.* Springer Berlin, Heidelberg.

OWEN-SMITH, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, UK.

OWEN-SMITH, N. (1998). How high ambient temperature affects the daily activity and foraging time of a subtropical ungulate, the greater kudu (*Tragelaphus strepsiceros*). *Journal of Zoology*, **246**(2), 183-192.

OWEN-SMITH, N. (2002). *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge University Press, UK.

OWEN-SMITH, N. (2004). Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, **19**(7), 761-771.

OWEN-SMITH, N. (2005), Incorporating fundamental laws of biology and physics into population ecology: the metaphysiological approach. *Oikos*, **111**(3), 611–615.

OWEN-SMITH, N. (2008). Effects of temporal variability in resources on foraging behaviour. In PRINS, H. H. T., & VAN LANGEVELDE, F. (Eds). (2008). *Resource ecology: spatial and temporal dynamics of foraging* (pp 159-181). Springer, Netherlands.

OWEN-SMITH, N. (2014), Spatial ecology of large herbivore populations. *Ecography*, **37**, 416–430.

OWEN-SMITH, N., & CHAFOTA, J. (2012). Selective feeding by a megaherbivore, the African elephant (Loxodonta africana). *Journal of Mammalogy*, **93**(3), 698-705.

OWEN-SMITH, N., & COOPER, S. M. (1987a). Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, **68**(2), 319-331.

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*, **365**(1550), 2267-2278.

OWEN-SMITH, N., & NOVELLIE, P. (1982). What should a clever ungulate eat?. *American Naturalist*, **119**(2), 151-178.

OWEN-SMITH, N., & OGUTU, J. O. (2013). Controls over reproductive phenology among ungulates: allometry and tropical-temperate contrasts. *Ecography*, **36**(3), 256-263.

PAPPAS, L. A. (2002). Taurotragus oryx. *Mammalian species*, **689**, 1-5.

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

PARRINI, F., MACINDOE, M., & ERASMUS, B. F. (2013). A comparison between field-measured NDVI and visual estimates of grass greenness in buffalo-foraging areas. *African journal of ecology*, **51** (4), 641-643.

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

PELLEW, R. A. (1983). The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse. *African Journal of Ecology*, **21**(4), 241-267.

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**(9), 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.

PIENAAR, U. D. V. (1974). Habitat-preference in South African antelope species and its significance in natural and artificial distribution patterns. *Koedoe*, **17**(1), 185-195.

PRINS, H. H., & FRITZ, H. (2008). Species diversity of browsing and grazing ungulates: consequences for the structure and abundance of secondary production. In GORDON, I. J., & PRINS, H. H. (Eds.). (2008). *The ecology of browsing and grazing* (pp. 21-45), Springer, Heidelberg, Germany.

PLANTON, H. P., & MICHAUX, I. G. (2014). *Tragelaphus derbianus* Giant Eland (Lord Derby's Eland). In KINGDON, J., HAPPOLD, D., BUTYNSKI, T., HOFFMANN, M., HAPPOLD, M., & KALINA, J. *Mammals of Africa*, *Volume VI* (186-193), A & C Black, UK.

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

ROWE-ROWE, D. T. (1983). Habitat preferences of five Drakensberg antelopes. *South African Journal of Wildlife Research*, **13**, 1-8.

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**(3), 764-776.

SCOONES, I. (1995). Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments*, **29**(2), 221-237.

SCOTCHER, J. S. B. (1983). *Interrelations of vegetation and eland (Taurotragus oryx Pallas) in Giant's Castle Game Reserve, Natal*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

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**(11), 789-795.

SHANNON, G., PAGE, B. R., DUFFY, K. J., & SLOTOW, R. (2010). The ranging behaviour of a large sexually dimorphic herbivore in response to seasonal and annual environmental variation. *Austral Ecology*, **35**(7), 731-742.

SHEEHY, D. P., & VAVRA, M. (1996). Ungulate foraging areas on seasonal rangeland in northeastern Oregon. *Journal of Range Management*, **49**(1), 16-23.

SHORROCKS, B. (2007). *The biology of African savannahs*. Oxford University Press, Oxford, Uk.

SINCLAIR, A. R. E. (1975). The resource limitation of trophic levels in tropical grassland ecosystems. *The Journal of Animal Ecology*, **44**(2), 497-520.

SINCLAIR, A. R. E. (1977). *The African buffalo: a study of resource limitation of populations*. University of Chicago Press, Chicago, USA.

SKARPE, C., BERGSTRÖM, R., BRÅTEN, A. L., & DANELL, K. (2000). Browsing in a heterogeneons savanna. *Ecography*, **23**(5), 632-640.

SKINSTAD, J.R. *(*1972*) Factors Influencing the Distribution and Seasonal Movements of the Cape Eland* (Taurotragus oryx) *in the Giant's Castle Game Reserve. Natal Parks Board, South Africa.* Natal Parks Board, mimeo report, South Africa.

SPINAGE, C. A., & MATLHARE, J. M. (1992). Is the Kalahari cornucopia fact or fiction? A predictive model. *Journal of applied Ecology*, 605-610.

SPONHEIMER, M., LEE-THORP, J. A., DERUITER, D. J., SMITH, J. M., VAN DER MERWE, N. J., REED, K., GRANT, C.C., ALYFFE, L.K., ROBINSON, T.F. HEIDELBERGER, C., & MARCUS, W. (2003) Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy,* **84**, 471-479.

STOKKE, S. (1999). Sex differences in feeding-patch choice in a megaherbivore: elephants in Chobe National Park, Botswana. *Canadian Journal of Zoology*, **77**(11), 1723-1732.

STEUER, P., SÜDEKUM, K. H., MÜLLER, D. W., KAANDORP, J., CLAUSS, M., & HUMMEL, J. (2013). Fibre digestibility in large herbivores as related to digestion type and body mass—An in vitro approach. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **164**(2), 319-326.

STEUER, P., SÜDEKUM, K. H., TÜTKEN, T., MÜLLER, D. W., KAANDORP, J., BUCHER, M., CLAUSS, M., & HUMMEL, J. (2014). Does body mass convey a digestive advantage for large herbivores?. *Functional Ecology*, **28**(5), 1127-1134.

STONER, C., CARO, T., MDUMA, S., MLINGWA, C., SABUNI, G., BORNER, M., & SCHELTEN, C. (2007). Changes in large herbivore populations across large areas of Tanzania. *African Journal of Ecology*, **45**(2), 202-215.

TAYLOR, C. R. (1969). Metabolism, respiratory changes, and water balance of an antelope, the eland. *American Journal of Physiology--Legacy Content*, **217**(1), 317-320.

THOULESS, C. (2014). *Tragelaphus oryx* Common Eland. In Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. *Mammals of Africa, Volume VI* (186-193), A & C Black, UK.

TOMOR, B. M., & OWEN-SMITH, N. (2002). Comparative use of grass regrowth following burns by four ungulate species in the Nylsvley Nature Reserve, South Africa. *African Journal of Ecology*, **40**(2), 201-204.

TRAILL, L. W. (2004). Seasonal utilization of habitat by large grazing herbivores in semi-arid Zimbabwe. *South African Journal of Wildlife Research*, **34**(1), 10-13.

UNDERWOOD, R. (1975). Social behaviour of the eland (*Taurotragus oryx*) on Loskop Dam Nature Reserve.MSc Thesis, University of Pretoria, Pretoria, South Africa.

UNDERWOOD, R. (1981). Companion preference in an eland herd. *African Journal of Ecology*, **19**(4), 341-354.

UNDERWOOD, R. (1983). The feeding behaviour of grazing African ungulates. *Behaviour*, **84**(3), 195-242.

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

VALEIX, M., LOVERIDGE, A. J., CHAMAILLÉ-JAMMES, S., DAVIDSON, Z., MURINDAGOMO, F., FRITZ, H., & MACDONALD, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90** (1), 23-30.

VALEIX, M., FRITZ, H., SABATIER, R., MURINDAGOMO, F., CUMMING, D., & DUNCAN, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, **144**(2), 902-912.

VAN BEEST, F. M., MYSTERUD, A., LOE, L. E., & MILNER, J. M. (2010). Forage quantity, quality and depletion as scale-dependent mechanisms driving habitat selection of a large browsing herbivore. *Journal of Animal Ecology*, **79**(4), 910-922.

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**(4), 771-785.

VAN DER MERWE, J., & MARSHAL, J. P. (2012). Hierarchical resource selection by impala in a savanna environment. *Austral Ecology*, **37**(3), 401-412.

VESEY-FITZGERALD, D. (1971). Fire and animal impact on vegetation in Tanzania National Parks. In *Proceedings Annual Tall Timbers Fire Ecology Conference*, **11**, 297-317.

WALDRAM, M. S., BOND, W. J., & STOCK, W. D. (2008). Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems*, **11**(1), 101-112.

WALKER, B. H. (1976). An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research*, **6**(1), 1-32.

WALKER, B. H., EMSLIE, R. H., OWEN-SMITH, R. N., & SCHOLES, R. J. (1987). To cull or not to cull: lessons from a southern African drought. *Journal of Applied Ecology*, **24**(2), 381-401.

WALLINGTON, B. P., MCKECHNIE, A. E., OWEN-SMITH, N., & WOODBORNE, S. (2007) Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *South African Journal of Wildlife Research,* **37**(2), 127-131.

WATSON, L. H., & OWEN-SMITH, N. (2000). Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*., **38**(2), 130-137.

WESTERN, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, **13**(3-4), 265-286

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

WIENS, J. A. (1969). *An approach to the study of ecological relationships among grassland birds*. American Ornithologists' Union, USA.

WIENS, J. A. (1989). Spatial scaling in ecology. *Functional ecology*, **3**(4), 385-397.

WILSEY, B. J. (1996). Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, **34**(1), 32-38.

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

WINNIE JR, J. A., CROSS, P., & GETZ, W. (2008). Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). *Ecology*, **89**(5), 1457-1468.

WITTEMYER, G., GETZ, W. M., VOLLRATH, F., & DOUGLAS-HAMILTON, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, **61**(12), 1919-1931.

YOGANAND, K., & OWEN-SMITH, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, **37**(10), 969-982.

YOUNG, K. D., FERREIRA, S. M., AARDE, V., & RUDOLPH, J. (2009). The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. *Austral Ecology*, **34**(3), 329-342.

CHAPTER 2: HOME RANGE OCCUPATION AND RESOURCE SELECTION AT THE LANDSCAPE AND HABITAT SCALE BY ELAND IN THE KGASWANE MOUNTAIN RESERVE

INTRODUCTION

Resource selection by large mammalian herbivores is a scale-dependent, hierarchical process (Johnson, 1980; Wiens, 1989), which reflects the ecological heterogeneity of a wide range of biotic and abiotic environmental conditions and resources, ranging from availability of water and forage to shelter from thermal stress and predation (Watson & Owen-Smith, 2000; Ryan, Knechtel & Getz, 2006; Winnie, Cross & Getz, 2009). Selection is operated by individuals and social units over four broad spatio-temporal scales: geographic distribution (1st order of selection); home range or landscape selection (2nd order of selection), habitat selection within the home range (3rd order of selection), and forage or dietary selection (4th order of selection; Johnson, 1980; Bailey *et al.*, 1996; Owen-Smith, 2014). In this chapter, I report on home range and habitat selection (2nd and 3rd order selection) of GPS-collared adult female common eland (*Tragelaphus oryx*) in the Kgaswane Mountain Reserve (KMR) of the North-West Province, South Africa.

Fitness and population dynamics of large herbivores are inherently influenced by spatial and temporal variation in resource availability and quality at the landscape scale (Du Toit & Owen-Smith, 1989; Owen-Smith, Fryxell & Merrill, 2010; Owen-Smith, 2014). According to the optimal foraging theory, home range selection (2nd order of selection) implies selection for particular areas within a landscape that would maximize energy and nutrient intake, while minimizing losses and predation risk (Pyke, 1984; Owen-Smith *et al.*, 2010). A home range generally describes the area traversed over a specified period of time by an individual animal while performing its "routine" activities (Burt, 1943; Jewell, 1966), and offering a combination of both environmental conditions and resources favouring the resilience and long-term viability of a population (Bolger *et al.*, 2008). The extent of a home range is not a species-specific property and presents a considerable level of inter- and intra-population variation, due to a range of intrinsic and extrinsic factors also affecting the location, topology, and occupation patterns of the range (Owen-Smith, 1988; Van Beest *et al.*, 2011; Owen-Smith *et al.*, 2010). Notable biological constraints to space use and home range extent are

constituted by territoriality (Owen-Smith, 1977), social ranking (Wittemyer *et al.,* 2007), and changes in reproductive state (Van Beest *et al.,* 2011). Extrinsic factors affecting the establishment of a home range and patterns of landscape selection by herbivores include the nutritional quality of forage, the availability and accessibility of favoured plant species and palatable surface water, the real or perceived predation risk (in the form of actual predator presence, escape terrain, or as topographic and vegetation-related characteristics determining predators detectability), and the presence and distribution patterns of potential competitors (Owen-Smith, 1988; Valeix *et al.,* 2009; Cain, Owen-Smith & Macandza, 2012; Hensman *et al.,* 2014b). Patches of different vegetation communities are rather fixed and spatially discrete units with usually little appreciable variation in their landscape-scale distribution over the lifetime of an individual animal (Owen-Smith *et al.,* 2010). However, vegetation (considered from both compositional and structural perspectives) in tropical savannah systems could undergo extreme changes in terms of the nutritional value of forage and of the availability of digestible plant parts, as a primary consequence of unimodal or bimodal rainfall patterns over the seasonal cycle (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013). Thus, most tropical ungulates undergo seasonal shifts in range use, mainly through migration between seasonal discrete home ranges across an unsuitable landscape matrix (Boone *et al.,* 2006; Holdo, Holt, & Fryxell, 2009), opportunistic nomadic movements driven by unpredictable rainfall and vegetation growth patterns (Hillman, 1988; Cushman, Chase, & Griffin, 2005), or commutation between adjacent wet and dry season ranges (Ryan *et al.,* 2006; Naidoo *et al.,* 2012; Owen-Smith, 2014).

Patterns of home range selection and utilisation differ substantially between browsing and grazing ungulates (Owen-Smith, 2014). The landscape-scale distribution of grazers is notably influenced by the availability of surface water and by the phenophase of the grass sward (Western, 1975; Redfern *et al.,* 2003). During the wet season, grazers selectively exploit the abundance of green grass on pastures situated in close proximity to surface water (Owen-Smith & Cain, 2007; Cain *et al.,* 2012). When water sources dry up and the grass sward within walking distance of them (defined by the movement capability of the study species) is ultimately depleted by grazing pressure, grazers start to move over long distances between water and remaining patches of green grasses, thus exploring a far larger area than during the rainy season (Murray, 1982; Shrader, Owen-Smith & Ogutu, 2006; Cain *et al.,* 2012; Owen-Smith, 2014). By contrast, water-independent browsers, and, to a lesser extent, mixed feeders,

are mainly constrained in their landscape-scale distribution and movements by the fine-grained dispersion of browse resources, such as clumps of shrubs or trees holding green leaves (Pellew, 1984; Kelso, 1986; Owen-Smith, 1988, 2002). As green foliage on woody browse remains available for longer into the dry season than herbaceous plants (Pellew, 1983), browsers thus minimize their energy expenditures by restricting their movements around landscape units offering green dicotyledonous plants (Hillman, 1988; Owen-Smith, 1988). Conversely, movements over large areas in search of flushing forbs and young, protein-rich grasses, are commonly observed during the wet season (Kelso, 1986; Bro-Jørgensen, 1997; Owen-Smith, 1988).

For tropical herbivores, which do not accumulate fat stores, areas of the landscape offering forage in sufficient quantity to prevent death from starvation make a crucial contribution to population viability during periods of severe resource limitation and nutritional stress (Scoones, 1995; Owen-Smith, 2002). Grazers rely on key resource areas on bottomlands retaining moisture and a high biomass of green grasses to survive through the late dry season (Scoones, 1995). By contrast, landscape units presenting stands of evergreen woody vegetation provide browsers with a dry season buffer against starvation (Owen-Smith, 2002, 2014).

Selection at the home range scale, despite providing a clear advantage to individuals and social units by allowing for extensive knowledge and spatial memory of resource dispersion in a familiar area (Owen-Smith, 1988), constitutes a major constraint to the decision-making process of habitat and forage selection at the intermediate and fine scales (Johnson, 1980; Senft *et al.,* 1987). "Habitat" is a species-specific concept and designates the set of conditions and resources necessary for the occupancy and persistence of a population of a given species within the broader home range context (Hall, Krausmann & Morrison, 1997; Morrison, 2001). Furthermore, habitat selection by large herbivores is itself a scale-dependent hierarchical process which parallels the heterogeneity of vegetation structure and composition, including differences in species availability and in their chemical properties (Novellie, 1978; Bailey *et al.,* 1996). Within the annual or seasonal home range, mammalian herbivores are mainly influenced in their selection for patches of habitat by the availability of plants at the optimal growth stage, according to the "forage maturation hypothesis" (Fryxell, Greever & Sinclair, 1988; Hebblewhite, Merrill & McDermid, 2008), or by the real or perceived risk of predation

("predation sensitive hypothesis"; Stephens & Krebs, 1986; Sinclair & Arcese, 1995). According to the predation sensitive hypothesis, herbivores would therefore avoid patches offering highly digestible foods, but impeding the detection of approaching predators or the access to escape terrains (Hamel & Cotè, 2007; Valeix *et al.,* 2011). Furthermore, habitat quality for large herbivores in savannah ecosystems is substantially altered by fires (McNaughton, 1985). Post-burning green flushes of short, nutritious grasses established through the removal of old, dry leaves and stems constitute attractive patches for selective grazers and mixed feeders (McNaughton, 1985; Mduma & Sinclair, 1994; O'Kane *et al.,* 2011a), while at the same time offering enhanced visibility for predators detection (Fitzgibbon, 1990). The biomass of the re-growing swards is however low, and forces herbivores of large body size to limit their use of burns during bouts of feeding and to revert to unburnt patches where plant biomass is sufficient to meet their high absolute metabolic requirements (Wilsey, 1996; Sensenig, Demment & Laca, 2010).

Eland are large, non-territorial mixed feeding-browsing ruminants inhabiting a wide range of vegetation communities, from miombo woodland to afro-alpine moorlands (Hillman, 1979; Watson & Owen-Smith, 2000). They have been variously described as migratory (Ansell, 1960), nomadic (Hillman, 1988; Thouless, 2014), or sedentary ungulates (Kelso, 1986). From the few studies offering an estimate of seasonal and annual home range size, eland reportedly move over very large areas (up to 15 000 Km^2 in the semi-desert of southern Kalahari) and mostly use open grassland during the wet season, while concentrating around smaller areas of woodland and scrub during the dry season, as typical for most browsing antelopes (Hillman, 1988; Buys, 1990; Owen-Smith, 2014; Thouless, 2014). Changes in home range size and habitat use are usually reflected by variation in herd composition, as large "nursery" herds are formed during the rains and then break into smaller sub-units at the onset of the dry season (Underwood, 1975; Scotcher, 1983). Eland have undergone a substantial decline across protected areas of southern and East Africa over the last two decades, especially within the Greater Kruger Ecosystem, where the local decrease in abundance has been associated with the decline of other low-density antelope species (Ogutu & Owen-Smith, 2005; Whyte, 2006). According to Thouless (2014), potential causes of dwindling eland numbers can be identified in the ongoing fragmentation of savannah landscapes, resulting in a substantial restriction to their migratory or nomadic movements. As eland already occur at low densities (East, 1999), the further contraction of their range and isolation of small populations would likely result in

an increased vulnerability to environmental changes, such as exceptional drought spells or tick-born diseases (Thouless, 2014). By contrast, localised high densities of eland established in small reserves presenting optimal environmental conditions, frequently exert a deep impact on vegetation communities due to extensive browsing on favoured woody species and "horning" of trees and shrubs (Wilson, 1969; Nyengera & Sebata, 2010). However, the ecology of eland populations in insular-like reserves of southern Africa is poorly known, and the potential for resilience of these confined populations to environmental change remains doubtful. The KMR in the North-West Province of South Africa, harbours a reintroduced population of eland in a small, insular-like environment (Nel, 2000), and offers a unique opportunity to disentangle the effects of forage quality and availability on resource selection at different scales, thanks to the unrestricted accessibility to surface water and to the virtual absence of large predators. The little scope for seasonal or nomadic movements between the KMR and the rest of the Magaliesberg range constitutes a matter of concern for management authorities, mainly because of the potential for interspecific exploitative competition over limited food resources with associated herbivores, such as the regionally rare and economically valuable sable antelope (*Hippotragus niger*; Nel, *pers. comm.*). Furthermore, a severe impact on *Acacia* woodlands was reported by Nel (2000) for the KMR, and the effectiveness of the fire management programme in relieving dry season nutritional stress has not been assessed in relation to the eland population. This study aimed at determining home range occupation and resource selection at the 3rd and 2nd orders (Johnson, 1980), and at providing baseline information about the ecological requirements of eland in an insular-like reserve. The two main objectives of the study were:

1) To determine the extent and location of the seasonal home ranges utilised by collared adult female eland in the KMR, in relationship to the available resources at the landscape scale (3rd order selection).
2) To investigate the influence of environmental drivers, including abundance and quality of forage across the seasonal cycle (assessed through satellite imagery), vegetation structure, and availability of burns, on selection of foraging areas by eland at the habitat scale (2nd order selection).

Given the insular-like nature of the study area, and the fact that the study population never showed any sign of serious decline in the KMR, I expected eland not to be under resource-

stressful conditions and to show patterns of space use across the seasonal cycle similar to those reported for populations in "open", unfenced ecosystems with low restrictions in forage availability at the landscape and habitat scales. Relatively to Objective 1, I expected that:

a) Eland would have not used the reserve uniformly, and selected for landscape units providing high-quality resources at any time of the year.
b) Eland, as non-territorial ungulates, would have occupied overlapping home ranges, regularly trespassing into each other's range and not segregating in the use of resources during dry periods.
c) During the dry season, when grasses tend to dry out rapidly while woody plants still maintain green foliage, eland would have selected for greenness at the landscape ("broad") scale by establishing seasonal home ranges in woodland areas. By contrast, during the wet, "green" season, eland would have selected against greenness (as measured by NDVI), as they would have mostly grazed on grasses and browsed on herbaceous forbs in grassland areas, with sparse woody cover and thus attaining lower greenness (NDVI) levels than woodland or shrubland.
d) At the landscape scale, eland would have selected for burnt over unburnt patches during the wet season, when high biomasses of growing grasses and forbs would have been made available, establishing seasonal home ranges in areas of the reserve landscape where flushing green grasses allow for regular exploitation of nutritionally rich grazing pastures. Burns would have also been selected over the landscape during the dry season, when recent ignition may have prompted the growth of green grasses and forbs.

For selection at the habitat scale (Objective 2), I expected that if adequate resources were available to eland over the study period within the KMR:

a) Eland would have selected for greener areas than the surrounding woodland matrix within the dry season range, as they would have chosen patches of green browse (especially those presenting evergreen woody plants). Similarly, eland would have selected for greener grassland patches during the wet season, which would correspond to high-quality grass swards or clumps of shrubs and trees, offering young, growing leaves and shoots.

b) There would have been no evident selection for burnt patches, as large-sized eland, despite taking advantage of the high-quality, growing herbaceous layer, would still have had to commute to unburnt areas where plant material is available at high biomass levels as a trade-off necessary to sustain their high absolute metabolic requirements.

c) Eland would have selected for grassland during the wet season, when young growing grasses and forbs are available. By contrast, eland would have selected for woodland and shrubland areas over grassland during the dry season, when they would have mostly browsed and concentrated their movements around clusters of woody plants. Wet grassland would have been negatively selected year-round, as it would have offered only tall, fibrous grasses, and extremely low availability of browse.

MATERIALS AND METHODS

Data acquisition

GPS collars data

Four adult female eland were fitted with GPS collars. One female (SAT1399) was captured and collared on 5th July 2013 and later re-captured on 25th September 2014 and fitted with a newly functioning collar. In both cases, the eland was in mixed-sex herds with no dependant calves (respectively, accompanied by five individuals during the 2013 operation and by three individuals in 2014). Three additional females were captured on 25th September 2014, two of which (SAT1396 and SAT1397) in the same, 16-individual group spotted in the central *vlei* of KMR. The last animal (SAT1398) was in a seemingly independent herd in the plateau area of the reserve. Captures and collaring were performed by a qualified veterinarian hired by the North-West Parks and Tourism Board, in full respect of ethic guidelines required for wildlife capture and handling by the University of the Witwatersrand (Wits ethic clearance certificate: 2013/14/04).

Collars were manufactured by Africa Wildlife Tracking (www.awt.co.za; AWT from now onwards). Each collar contained an Iridium GPS (Global Positioning System) unit and a VHF (Very High Frequency) transmission unit. The GPS units recorded animal location at five-hour intervals between July 2013 and September 2014 for SAT1399. Between September 2014 and September 2015, all deployed collars were set to provide GPS locations at hourly

intervals. Individual SAT1396 was discovered to be seriously affected by tick infestation in early March 2015, which caused severe necrosis of the front left leg, and eventually death. The collar on individual SAT1397 started to work discontinuously from 14th March 2015, and stopped all transmissions shortly after. Individual SAT1399 died on the first week of June 2015; due to advanced tooth wear, large body size, and very dark colouration of forequarters, it was reasonable to indicate old age as the primary cause of the death. The last collar (SAT1398), worked continuously until the second week of October 2015, when GPS transmission was interrupted.

Determination of seasons

The study encompassed a temporal range of two years and two months, from 15th July 2013 to 30th September 2015. Over this period, I identified two wet seasons (from 1st December to 31st March) and three dry seasons (from 1st June to 30th September, although June 2013 was not included in the study), based on monthly rainfall patterns as provided by the KMR meteorological station, and on average maximum and minimum monthly temperatures obtained from the South African National Weather Service, from the nearby Rustenburg weather station. The highest wet season rainfall was recorded in February 2014 (189.6 mm) for the first wet season (2013-2014), and in January 2015 (77 mm). By contrast, lowest rainfall levels were recorded for the June-September period in all three dry seasons, when no rainfall was recorded (apart from anomalous but small rainfall events totalling 3.5 mm in August 2013). Mean maximum temperature was highest in November 2013 and February 2015 (31.8 °C and 33°C, respectively), while lowest minimum temperatures were always reported in July (July 2013: 5.9 °C; July 2014; 3.8 °C; July 2015: 3.9 °C).

I defined April-May and October-November as “transition periods”, which presented very high mean maximum temperature (always over 30 °C), and were characterised by varying rainfall (for example, October 2013 experienced high rainfall of 64.6 mm, while very little rain fell in October 2014). April and May were also associated with little to no rainfall and high maximum temperatures (~25 °C). Graphs depicting seasonal variation in rainfall can be consulted in Appendix I. The traditional sub-division into “early dry season” and “late dry seasons” for African savannah ecosystems was not respected in the present study, as KMR presents a sub-temperate climate typical of the South African Highveld, with only two clearly defined stages of the seasonal cycle (Nel, 2000).

Seasons over the study period were referred to as: first dry season, 2013 (D1); first October-November transition period. 2013 (TO1); first wet season, 2013-2014 (W1); first April-May transition period, 2014 (TA1); second dry season, 2014 (D2); second October-November transition period, 2014 (TO2); second wet season, 2014-2015 (W2); second April-May transition period, 2015 (TA2); third dry season, 2015 (D3).

Vegetation map, burnt areas, and satellite imagery

Quality and availability of forage in terms of vegetation greenness and biomass within the study area were determined using the Normalized Difference Vegetation Index (NDVI) at 250 x 250 m spatial resolution and 16-days temporal resolution, derived from MODIS satellite images. Thirty-eight images were downloaded from Earth Explorer (https://earthexplorer.usgs.gov) and later re-projected into Universal Transverse of Mercator (UTM) zone 35 South in ArcMap 10.1. Images were already corrected for the presence of water vapour, clouds, and aerosols, and did not need any further processing (de Jong *et al.,* 2012). The satellite-based NDVI has been widely and successfully used in the study of herbivores spatial ecology and distribution, and has also been applied to predict the density of African ungulates across different ecosystems (Pettorelli *et al.,* 2009). NDVI is calculated according to the formula:

$$(\mathrm{NIR} - \mathrm{Red})/(\mathrm{NIR} + \mathrm{Red})$$

Where NIR stands for the near infrared radiation and Red for the red spectral radiation reflected by the Earth's surface (Rouse *et al.,* 1974). The value of NDVI ranges between 0 and 1, but is presented by MODIS imagery into a scale of 0 to 10 000. Green leaves, through their photosynthetic pigments, absorb solar radiation in the blue and red bands of the visible spectrum, and are reflective of green radiation both in the visible and infra-red spectral regions (Pettorelli *et al.,* 2011). For this reason, high NDVI values (close to 10 000), correspondent to high reflectance of the green spectral band due to extensive vegetation on the ground, indicates presence of green foliage, while values close to zero coincides with areas with no vegetation cover, or to cloudy zones. NDVI is positively associated with net primary production and leaf biomass (usually estimated using the Leaf Area Index, LAI), thus constituting a useful index of the phenophase of terrestrial plant communities (Wang *et al.,* 2005; Pettorelli *et al.,* 2011). Pixels of uniform canopy cover would hold higher NDVI values

than open grassland, even in case of a homogeneously green grass sward, because of the higher foliage biomass growing on trees and shrubs in respect to herbaceous plants (Pettorelli *et al.*, 2011). Satellite-based measures of greenness and forage abundance need therefore to be interpreted in relation to the vegetation structure of the study area.

A map and detailed description of the vegetation communities present in the reserve was compiled by Nel (2000). The map was realised using aerial images followed by ground-truthing relevès (Nel, 2000). However, vegetation communities are often of scarce relevance in evaluating habitat characteristics for large mammals primarily because they are based on the definition of the diagnostic, not the most abundant, plant species in area (Morrison, 2001). For this reason, I adopted the four main management and structural units identified by Nel (2000) as the "vegetation types" of KMR. These included: valley woodland (referred to as woodland in this study); open shrubland; dry grassland; and wet grassland. This classification was similarly used for a study on habitat selection by the population of sable antelope inhabiting the reserve (Parrini, 2006; Parrini & Owen-Smith, 2010), and was chosen as an accurate representation of the structural and compositional vegetation diversity within the small study area. The boundaries around the four main vegetation types were re-designed using aerial images in 2014 by KMR technicians, addressing for potential variation in woody plant cover.

A detailed dataset of burnt areas was made available by the ecological monitoring staff of the KMR. Spatial extent, date of start, and cause of ignition were all recorded for each fire, and later entered as shapefiles into ArcMap 10.1.

Surface water in KMR is available year-round, due to the presence of a perennial stream and of several small pans in the valleys retaining water for long into the dry months (Nel, 2000; Carruthers, 2014). Field surveys during the dry seasons (D1, D2, and D3) evidenced how water was also largely available in the form of shaded rock pools along deep drainage lines which were apparently used by various ungulates (*pers.obs.*), thus not constituting an apparent limiting factors to large mammals in KMR.

All shapefiles of vegetation types and burns were converted into raster files using the Polygon to Raster function in ArcMap 10.1, and re-sampled at a resolution of 250 m x 250 m in order to meet the same spatial arrangement of MODIS images.

Statistical analysis

Seasonal home range extent and composition of individual animals

All GPS locations were used for determining annual and seasonal home range extent. Various authors suggest to consider only one location per day in order to avoid spatial autocorrelation of data (Ryan *et al.*, 2006), but the use of a large sub-set of locations per day, such as those collected at hourly intervals, generally improves the accuracy of the home range estimates (de Solla *et al.*, 1999). Furthermore, according to the theoretical framework, a "home range" should include all those areas utilised in routine activities, and not only during foraging and/or resting, thus precluding any specific selection for locations at "peak foraging times". However, caution should be taken when comparing home range size between the 2013-2014 and 2014-2015 periods, as sampling intervals were different between the two years. All GPS locations were loaded into R 3.2.2 and, using the t-LoCoH package (Lyons, Turner, & Getz, 2013), transformed from geographic coordinates into UTM coordinates within the zone 35 South. Outlying points, were visually identified via scatterplots and later removed from the dataset. Annual home ranges were calculated only for those collars whose battery lifetime corresponded to at least 12 months of continuous and regular functioning, thus including SAT1399 (15th July 2013- 31st July 2014), and SAT1398 for the period ranging from 1st October 2014 to 30th September 2015 (**Tab. 1**). A "total" home range was also calculated for locations of SAT1399 in October 2014-May 2015, as the dry season was excluded due to collar failure (**Tab. 1**). Seasonal home ranges were calculated over the two different years of the study.

I used the t-LoCoH package, based on the LoCoH (Local Convex Hull) family of algorithms, in R 3.2.2, in order to develop seasonal and annual home range estimates. The LoCoH method is based on the algorithmic construction of convex polygons from user-selected nearest-neighbouring points associated with each GPS location of an individual animal (Getz & Wilmers, 2004). The polygons, also termed as "hulls", are later used to determine isopleths, or borders defining areas with the same probability of being utilised by the study animal (Getz & Wilmers, 2004; Lyons *et al.*, 2013). The number of nearest-neighbours necessary to build local convex hulls is determined by the user as the value assigned to the *k*, *a*, *r*, or *t* parameters of the algorithm (Getz *et al.*, 2007). The *a*-LoCoH (adaptive LoCoH) methodology was selected, according to which local polygons are constructed around a set of

nearest neighbours whose cumulative distance from the root point is defined as equal or smaller than the value of *a* (Getz & Wilmers, 2004; Getz *et al.,* 2007). 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 distributions (UDs) by setting the *s* parameter to zero (*s*=0; Lyons *et al.,* 2013; Lyons, 2014). The main constraint to the accuracy of *a*-LoCoH for home range estimates was posed by the subjectivity in the selection of the *k* and *a* parameters (Getz & Wilmers, 2004). Small values of both parameters could result in underestimates of the used area, while too large values often cause the inclusion of real gaps into the total calculated range (Getz *et al.,* 2007; Lyons *et al.,* 2013). Field surveys contributed by providing a general, though time-limited, knowledge of where gaps in distribution would have had most likely occurred, in zones rarely visited by eland. During the data analysis process, I adopted the Minimum Spurious Holes Covering method, and plotted a range of values for *k* against the isopleths area and edge:area ratio, in order to identify the values at which a plateau distribution was observed (Ryan *et al.,* 2006; Lyons, 2014). Consequently, a fixed *k* (k=3, the minimum value for polygon construction) was entered in the function, and contrasting values of *a* were then plotted against isopleths area and edge:area ratio in order to identify the interval at which a plateau distribution was reached (Getz & Wilmers, 2004). According to this procedure, a plateau distribution is characteristic of a home range where all spurious gaps have been covered, while the plotted curves should start to grow again when real holes in the utilization distribution are added to the isopleths-building process (Getz & Wilmers, 2004; Ryan *et al.,* 2006). After a plateau value for *a* had been fixed, different values of *k* were similarly against isopleths area and edge:area ratio until a plateau was identified. The home range was then determined using both values (*a* and *k*). In the case of multiple levelling off points while plotting the area curves against *a* values, a conservative approach was taken in order to select the correct parameter.

The *a*-LoCoH method, in particular, was selected above the Minimum Convex Polygon (MCP), Kernel analysis, and *k* or *r* LoCoH, since it is generally regarded as the best estimator for gaps within UDs and hard boundaries around total home ranges. Conversely, the MCP is drawn around the entire set of animal locations, and it is thus extremely sensitive to outlying points, including occasional extra-range excursions, which often produce large overestimates of range size (Nilsen, Pedersen & Linnell, 2008). LoCoH merges together the local hulls while calculating UDs in increasing order of size; the smallest hulls are commonly considered

as the “areas of core use” or “activity centres”, with a high density of used locations and thus presenting the highest probability of use (Ryan *et al.,* 2006). The 95% isopleths were utilised to represent the total home range area, while the 100% isopleths, as they correspond to MCPs, were excluded from the analysis in order not to include extra-limital excursions and large gaps in distribution between routinely traversed areas (Nilsen *et al.,* 2008). The only available studies on eland spatial ecology and home range extent and use were based on calculations of MCPs, but they did not provide any useful comparison to the present study as they all differed for what pertained the collection of individuals location (assessed through photo identification along transects or VHF triangulation), and were also conducted in areas of overtly larger extent than KMR (Kelso, 1986; Hillman, 1988). The MCPs approach was thus deemed unnecessary and regarded as a less effective tool for comparative purposes than mere descriptive comparisons. Given the small and fenced nature of the study area, the calculation of “core ranges” was excluded from the analysis and considered as of little significance for the overall study; however, the different isopleths generated in *a*-LoCoH were qualitatively presented as part of home range maps.

The area of the 95% isopleths, and the surface extent of the four different vegetation types within the reserve, were extracted in the Geospatial Modelling Environment for ArcMap 10.1. I then estimated the availability of vegetation types as the proportional area of each vegetation type within the study area (area of vegetation type/total area of KMR). A first estimate of landscape-scale selection (second order selection) for vegetation types was obtained from the proportional area of each vegetation type within the wet or dry season home range over the total area covered by the vegetation type. I used the “home range composition”, or the of vegetation types within a seasonal home range, as a proxy for habitat use. Indexes of selection were assessed separately for each individual animal, assuming independence of space use. Although there was evidence that all collared eland joined in one nursery herd during the wet season of 2014-2015, individuals within this large association were observed to abandon it frequently on their own or accompanied by an ever-changing (in age and sex structure) groups of adults and subadults, thus suggesting a loose social structure were decision-making is restricted to the individual level (Appendix II; Underwood, 1975; and Hillman, 1987).

Landscape and habitat selection

Resource selection by eland were investigated at two scales: selection of seasonal home ranges within the landscape (landscape scale), and habitat selection within the seasonal home ranges (habitat scale). I considered the entire surface of KMR (together with the adjoining Rainbow Farms) as the total available landscape for all the collared eland. Equal accessibility to the study area for each animal was assumed, mainly because of the lack of internal barriers to movements (apart from a low perimeter fence between the KMR and Rainbow Farms to the south-east, a border which was however easily and frequently trespassed by adult eland thanks to their jumping ability). Only the GPS locations of SAT1398 and SAT1399 were included in this analysis, as they represented the most complete set of data over the study period. Extra-limital movements were excluded from the analysis, which included only points falling within the seasonal 95% UDs of both individuals. Selection at both scales was assessed only for the wet and dry seasons, to compare space use between these two contrasting periods over the years. Transition periods were not included since they presented a much lower number of locations in respect to wet and dry seasons (thus possibly leading to multiple convergence errors), and were also associated with variable environmental conditions which would have required an accurate inter-annual estimate in the field to give a reliable *a posteriori* interpretation of space use patterns. GPS locations of collared animals were labelled as "used", and compared to a set of scattered available random points, generated in ArcMap 10.1, with a 1:1 available to used ratio. Given the small size of the study area, this ratio was chosen as the best representation of the available landscape and habitat. Larger ratios than 1:1 were considered but immediately rejected after graphical assessment in ArcMap, where it was evident that a large number of available locations would have fallen within the same pixels. Since I was interested in investigating selection for areas where eland had been foraging during the study period, and in order to minimize the effects of spatial autocorrelation on the independence of residuals and overall overfitting of resource selection models (Burnham & Anderson, 2001), I chose to only include the locations collected at peak feeding times (07:00 am and 18:00 pm, determined during field work) in the dataset. Eland usually moved daily over long distances, and were rarely found foraging in the same area during morning and afternoon field observations. For scattered random points, spatial independency of locations was assumed. For each set of points falling within a 16-days period, I generated an equal number of scattered random points in ArcMap 10.1, at both

landscape and habitat scales. Available points were then labelled with an ID (SAT1398 or SAT1399), thus estimating use and availability of landscape and habitat at the individual scale, following a Type III Design (Manly *et al.,* 1993).

Resource selection by eland was tested using mixed effects binary logistic regression models. Two sets of models, one for landscape-scale selection and another for habitat-scale selection, were built in R 3.2.2, using the glmer function in the lme4 package. I set the binary response variable as used (1) or available location (0). Explanatory variables were all categorical and included: a) vegetation type (four categories: woodland; open shrubland; dry grassland; wet grassland); b) burnt area (as a dichotomous variable with two classes coded as: 1-burnt and 0-unburnt); c) NDVI (divided into five levels, each with the same number of observations); d) season (consisting of two categories: wet and dry). Month, season ID (D1,D2,D3,W1,W2), and individual ID of collared animals were also included in the models as random factors. Season ID was considered as exerting a random effect on resource selection because the lagged effects of low rainfall on the wet season on browse or grass greenness and availability during the following year could not be ascertained through remote sensing or in the field. A warning advice for false convergence errors was encountered in R 3.2.2 when running the logistic regression models with NDVI as a continuous explanatory variable. False convergence arises from disproportional distribution of continuous explanatory variables, causing a failure to converge on maximum likelihood estimates (Allison, 2004; Marshal *et al.,* 2011). One way to overcome this error is to transform continuous variables into categories (van der Merwe & Marshal, 2012). Thus I divided the continuous NDVI data into five arbitrary levels of greenness, each of them with the same number of observations, following recommendations by Marshal *et al.* (2011). I considered all points to be in a burnt area in the dry season only if the fire had occurred during that same dry season or during the previous April-May transition period. Burns resulting from ignition during the previous year were in fact likely to have already exhausted the fire-stimulated growth potential after the rains of the intervening wet season (confirmed during field surveys). For wet season locations, I considered only those areas which had been burnt during the previous dry season and October-November transition period (because rainfall would have triggered further regrowth; confirmed during field surveys). There was no record of fires during the wet season (December-March).

Using multi-model inference, I developed a series of models for landscape and habitat selection, each presenting a different combination of fixed-effects explanatory variables. Interactions between the four variables were also tested, when considered as biologically meaningful. Model selection was based on two statistical estimates of model fit, the Akaike's Information Criterion corrected for small sample size (AICc), with the models presenting the lowest AICc considered as the best ones to explain variation in the data (Burnham & Anderson, 2001). The Δ AICc was calculated between all the candidate models and the best model. When the Δ AICc showed a small difference (≤ 2) between two models, I selected the most parsimonious (presenting the lowest number of explanatory variables) as the best one (Burnham & Anderson, 2001). Additionally, I compared the candidate models by calculating Akaike's weigths (w_iAICc), representing the probability that the selected model was also effectively the best at explaining the data (Burnham & Anderson, 2001; Anderson, 2008). Evidence ratios, as likelihood estimate of relative weights of evidence, were also calculated to provide a comparison between models presenting similar or equivalent statistical estimates of fit (Anderson, 2008). Influence of vegetation types, burnt areas, and greenness categories across the seasonal cycle on landscape and habitat selection was identified by deriving log-odds ratio (with 95% confidence intervals) from the coefficients of the best model for each scale. The natural logarithm of the odds ratio constitutes indeed a measure of selection probability (Zuur *et al.,* 2009; Marshal *et al.,* 2011). However, log-odds ratios do not correspond to absolute probability values but are expressed relatively to a reference category (Zuur *et al.,* 2009). In this case, I used the most available vegetation type in the reserve (dry grassland), the most available type of burning regime (unburnt area), the wet season (the non-limiting period), and the lowest NDVI class (following Marshal *et al.,* 2011), as the reference levels for the explanatory variables. Within this framework, positive log-odds ratios indicate a higher likelihood of being selected for a specific class variable in respect to the reference, while negative ratios (lower than the reference category) represent a lowered likelihood of selection for a variable class (Peng, Lee & Ingersoll, 2002; Zuur *et al.,* 2009). If the lower and upper limits of 95% confidence intervals overlapped with the reference, likelihood of selection was interpreted as equal to the reference (Zuur *et al.,* 2009). NDVI levels were obtained by conveniently and arbitrarily lumping together different values of this index, and therefore did not represent the real vegetational greenness and biomass recorded in each pixel. In order to provide the reader with a graphical and close-to-reality interpretation of the

interaction between NDVI and season, I compared the mean values (± Standard Error, S.E.) of NDVI at GPS locations and scattered random points.

RESULTS

Most collars showed consistent patterns of home range and habitat use during the period of simultaneous collar functioning. The vast majority of GPS locations were recorded from within the borders of the formally protected area, but adjacent private land within Rainbow Farms proved to be widely utilised at certain times of the year, and especially by SAT1398 during the dry season of 2015. SAT1398, which was most often found alone or accompanied by adult males during field surveys, presented slightly different patterns of home range and landscape use compared to the other adult females. In fact, SAT1398 made frequent use of the gorges and uplands mosaic in the northern sector of the KMR, and was generally associated with areas where the other collared individuals rarely ventured.

Home range extent and composition

Annual home ranges occupied an overall smaller area than the reserve itself (**Tab. 2**; **Fig. 1-3**). Individual SAT1399 occupied a slightly larger annual range between 15th July 2013 and 31st August 2014 (21.2 km^2) than SAT1398 during the period ranging from 1st October 2014 to 30th September 2015 (20.87 km^2; **Tab. 2**). Nevertheless, comparisons should be taken with caution as sampling frequency of GPS locations increased from five hours in 2013-2014 (when only SAT1399 was fitted with a GPS collar) to one hour in 2014-2015, thus resulting in a smaller set of locations utilised in estimating home range for SAT1399 prior to October 2014 (**Tab. 2**). Furthermore, annual ranges for SAT1399 referred to different years with different pluviometric and temperature patterns, and thus should be considered within their intra-annual environmental context. The total home range of SAT1399 during 1st October 2014-31st May 2015, although excluding the entire dry season of 2015, covered an area of 17.4 km^2 (**Tab. 2**).

Within the study area, dry grassland represented the most available vegetation-type (39% of KMR), followed by open shrubland (37.5%), woodland (20.7%), and wet grassland (2.8%). The annual home range of SAT1399 (1st July 2013 - 31st August 2014), was constituted, in decreasing order of areal proportion, by dry grassland (48%), open shrubland (26%), woodland (27%), and wet grassland (4%; **Fig. 1**). Proportions of each vegetation-type

included within the annual home range were slightly different for SAT1398 (1st October 2014 – 31st May 2015), with a pronounced contribution of open shrubland to the total area (43%), and a reduced fraction of both dry grassland (33%) and woodland (20%; **Fig. 2**). On an annual scale, wet grassland was the only vegetation-type used more than its proportional availability within the study area by both SAT1399 in 2013-2014 and SAT1398 in 2014-2015 (**Fig. 1-2**). Conversely, dry grassland was selected over its landscape-scale availability by SAT1399 in 2013-2014, but substantially rejected by SAT1398; a similar but opposite pattern was observed for open shrubland. Woodland was only apparently selected for over the available landscape by SAT1399 in 2013-2014. Despite representing only a partial estimate of utilization distribution, the total home range for SAT1399 between October 2014 and May 2015 showed similar compositional characteristics to those estimated for the same individual during the previous year, with a preponderance of dry grassland over the total range area (43% of the home range size; **Fig. 3**).

Annual home ranges effectively constituted a composite range of partially discrete wet and dry season home ranges (**Tab. 3; Fig. 4-8**). The smallest 95% home range was estimated for SAT1399 in the dry season of 2014, whilst the largest one (16.37 km^2) was utilised by the same individual during the previous wet season (**Tab. 3**). Adult female eland occupied small dry season home ranges (4.09-5.83 km^2; **Tab. 3**), and SAT1399 in particular concentrated in the south-eastern valley woodland in 2013 and 2014 (**Fig. 4a & e**). SAT1398, during the dry months of 2015, reduced its activities to the close proximity of a deep, well-wooded gorge in the northern area of the reserve, but shifted to Rainbow Farms on the southern slopes of the mountainous range in July 2015 (**Fig. 6d**). During the October-November transition periods, home ranges tended to increase, shifting towards the central basin and northern plateau of the KMR (**Tab. 3**; **Fig. 4-8**). Evident overlap between the 95% UDs of all collared animals in October and November 2014 probably corresponded to congregation in one large nursery herd prior to the start of the rains (**Fig. 5a, 6a, 7a & 8a**). Although this social unit was most probably not cohesive, all collared individuals were seen together in March 2015. The wet season home ranges were the largest seasonal ranges in all years of the study (**Tab. 3**). Individuals SAT1397 and SAT1396 occupied relatively small and topologically identical wet season 95% ranges (**Fig. 7b & 8b**); in the case of SAT1396, small range size was probably correlated with reduced mobility due to tick infestation, which ultimately caused its death. Although showing similar patterns of home range occupancy to the other animals during the

wet season, SAT1398 vacated the nursery herd at the beginning of March 2015 (earlier than the other collared females), and subsequently moved to the northern uplands of the reserve, which were utilised until the first week of July 2015 (**Fig. 6b**). Small seasonal home ranges (4.62-5.05 km^2) were occupied during the April-May transition period, as a result of contracting range size with the progression of the dry season (**Tab. 2**; **Fig. 4-8**). At this time of the year in 2015, SAT1399 returned to its habitual (at least for what concerns the two years of the study) home range in the south-eastern valley, while SAT1398 remained in the northern uplands which it had occupied during the last phases of the wet season (**Fig. 5-6**).

Woodland made a major contribution the dry season range of SAT1399 in both years (contributing by 49% and 59% of seasonal home range proportional area, respectively, in 2013 and 2014), and was selected over its availability in the landscape (**Fig. 9a & e**). By contrast, woodland was negatively selected at the landscape scale by SAT1398 during the course of the dry season in 2015, but contributed to a somewhat large proportion of the seasonal range (**10a & d**). Woodland constituted an important component of the seasonal home ranges of these two individuals during the October-November and April-May transition periods in all years (**Fig. 9-12**), but during April and May 2015, woodland was apparently not selected for and its contribution to home range size was reduced to 19% for SAT1399 and 13% for SAT1398 (**Fig. 10c and 11c**). By contrast, for SAT1397 and SAT1396, woodland formed only a minor proportion of the home range during the October-November transition period in 2014 (**Fig. 12a & b**). Woodland was negatively selected for and made up a small fraction of the wet season range (<10% of the total area) of all individuals and across the two years of the study for SAT1399 (**Fig. 9-13**). Open shrubland was generally less used than its availability within the study area by SAT1399 (**Fig. 9c and 11b**), SAT1397 (**Fig. 12a**), and SAT1396 (**Fig. 12b**), but during the wet seasons it constituted a high proportion of the seasonal range (**Fig.9-12**). It was particularly under-utilised by SAT1399 during the dry season of 2013 and 2014, when it made up less than 10% of the seasonal home range (**Fig. 9a & e**). By contrast, SAT1398 selected for open shrubland during the wet season of 2014-2015 and also made extensive use of this vegetation-type during April-May 2015 and during the dry season of 2015 (**Fig. 10c & d**), probably as a result of its range shift towards the northern (April-May) and southern slopes (dry season) of the reserve. Dry grassland made up large proportions (between 30% and 50%) of the home ranges of all individuals during the wet season and also during the October-November and April-May transition periods, but it was

generally utilised according to its landscape-scale availability (**Fig. 9-12**). The proportion of dry grassland within the seasonal range was however high, though not indicative of selection, in the dry season of 2013 (**Fig. 9a**). Wet grassland formed small proportions of all home ranges across the seasonal cycle, but generally increased in its areal contribution to 6%-7% of the seasonal ranges during the October-November transition and during the wet season (**Fig. 9-12**). Conversely, the proportion of wet grassland within seasonal home ranges of all individuals was always higher than its availability in the landscape.

Landscape selection

Fifty models were tested for landscape-scale selection (**Tab. 4**). The best model (Model 31), which had the lowest AICc estimate, included vegetation-type, burnt area, and NDVI, all of them in their interaction with season, as categorical predictors (w_i AICc=0.80; **Tab. 4**). Thus, selection of vegetation-types varied according to season, with woodland less selected (log-odds= -1.189 ± 0.195), and wet grassland more selected (log-odds= 0.755 ± 0.292), than dry grassland (the reference category) during the wet season (**Fig. 13**). Eland decreased their selectivity towards dry grassland during the dry season compared to the wet season, while showing consistent patterns of selection for open shrubland in both seasons (**Fig. 13**). According to the best model, areas burnt during the previous dry season or October-November transition were positively selected against unburnt landscape patches during wet season months (log-odds=0 .994 ± 0.267; **Fig. 14**). Conversely, selection for burns decreased significantly (relatively to the reference) during the course of the dry season (**Fig. 14**). However, log-odds evidenced a significant selectivity for areas associated with intermediate levels of NDVI (category two and three) during the wet season, if compared with category five (**Fig. 15**). Locations with very low (category one) and high (category four) greenness were not differentially selected in respect to the reference (**Fig. 15**). The lowest two categories of NDVI had lower influences on landscape selection during the dry season than during the wet season, and were negatively selected in respect to the reference during the driest months of the year (**Fig. 15**). During the dry season of 2013, SAT1399 used areas at peak foraging times within the seasonal range which did not apparently differ in mean NDVI values from what was available at the landscape scale (**Fig. 16a**); conversely, both SAT1399 during the dry season of 2014 and SAT1398 during the dry season of 2015 utilised locations of higher NDVI than the available random points (**Fig. 16a & c**). Locations within the seasonal home

ranges of both individuals were, by contrast, always associated with areas characterized by lower NDVI values than available (**Fig. 17**).

Despite the absolute lowest AICc estimate of fit associated with the best model, evidence for a model including season, burnt area, and NDVI, all interacting with the vegetation-types, was also encountered ($E_{1,2}$= 6.78). However, the significant differences in AIC with the best model (ΔAICc > 2), and the relatively low weight (w_iAICc= 0.15), suggested a low statistical confidence for this model. Furthermore, results pertaining the landscape-scale selection of resources by eland closely paralleled those derived from home range analysis, thus prompting me to retain the above-described model as the best at explaining the present data.

Habitat selection

Habitat selection was mainly influenced by vegetation-type (varying according to season), burnt areas interacting with vegetation-types, and by level of NDVI depending on the vegetation-type (**Tab. 5**). The selected model, presenting all of the above-mentioned categorical variables with their respective interactions, hold the lowest AIC estimate and a 99% likelihood of representing the best model at explaining data variation (w_i AICc= 0.99; **Tab. 5**). During the wet seasons, there was a much lower probability of selection towards woodland in respect to dry grassland (log-odds= -1.477 ± 0.247; **Fig. 18**). Locations on open shrubland were also less selected than those situated on dry grassland in the wet season (log-odds= -0.666 ± 0.26), while selection for wet grassland did not differ significantly from the reference (log-odds= 0.311 ± 0.333; **Fig. 18**). Conversely habitat selection during the dry season appeared to be less directed towards dry grassland than during the wettest months of the year (**Fig. 18**). The influence of burnt areas on habitat selection varied according to the vegetation type in which the burnt or unburnt patches were available (**Fig. 19**). Burns in open shrubland (log-odds= 0.967 ± 0.231) and woodland (log-odds= 0.676 ± 0.25) were favoured against unburnt patches of dry grassland, while at the same time burnt dry grassland (log-odds= -0.284 ± 0.158) was slightly less favoured than its unburnt counterpart (**Fig. 19**). Burnt wet grassland had a weak influence on habitat selection, compared to the reference category (log-odds= -1.106 ± 0.907; **Fig. 19**). Conversely, unburnt areas on wet grassland were used in similar proportions to those located on dry grassland (log-odds=0.0287±0.333; **Fig. 19**).

Within the seasonal home ranges, NDVI varied its effect on habitat selection according to the vegetation-type. Woodland at the lowest level of NDVI was less influential on habitat selection than dry grassland in NDVI category five (log-odds= -1.308 ± 0.271). Wet grassland at low NDVI levels was also negatively selected if compared to the reference (Category one, log-odds: -2.566 ± 1.138; Category two, log-odds: -3.383 ± 1.451; Category three, log-odds: -2.626 ± 1.139), possibly indicating avoidance for wide open areas devoid of woody canopy cover. As graphical comparison of odds-ratios would have revealed very little information about habitat selection in relation to NDVI, I calculated the mean NDVI for used locations at peak feeding times and available scattered random points for each vegetation-type, within the seasonal home ranges of collared animals. During the dry seasons of 2013 and 2014, SAT1399 tended to be associated with areas of woodland and dry grassland characterised by mean NDVI values not apparently different from those recorded for available points (**Fig. 20a & b**). Conversely, GPS locations in open shrubland or wet grassland tended to be characterised by higher NDVI than the available points in the respective vegetation-types (**Fig, 20a & b**). By contrast, SAT1398 in the dry season of 2015 was associated with higher than available NDVI only on wet grassland, but not on the other vegetation-types (**Fig. 19c**). Locations from both collared individuals on open shrubland were characterised by lower NDVI than respective available points during the two wet seasons (**Fig. 21**). Used locations of SAT1398 always presented low mean NDVI compared to availability in the wet season of 2014-2015 across all vegetation-types (**Fig. 21c**). During the wet seasons, both SAT1399 and SAT1398 on wetland were associated with higher mean NDVI than those calculated for random points (in both years for SAT1399; **Fig. 21**).

DISCUSSION

Annual home range extent

Confirming my expectations, eland did not make a uniform use of the entire area of the KMR, establishing smaller annual and seasonal home ranges than the total extent of the study area. Unsurprisingly, annual home ranges in the insular-like KMR were much smaller than those estimated for migratory-nomadic populations of eland in the Kgalagadi Transfrontier Park in Botswana (1691 km^2-19 761 km^2; Thouless, 2014) and in the Nairobi National Park and surrounding Athi-Kapiti Plains in central Kenya (174.9-422 km^2; Hillman, 1988). Constrains to long-distance movements, as reported by early authors (Ansell, 1960; Lamprey, 1963),

were patently posed by the presence of perimeter fences. The small size of the KMR, coupled with the extremely limited availability of data on the spatial ecology of eland and with the diversity of quantitative approaches adopted in order to estimate home range extent (MCPs in all previous studies against the *a*-LoCoH chosen for the present one), prevented any meaningful comparison with existing literature on ranging patterns of eland. Underwood (1975) concluded that the areal extent of the Loskop Dam Nature Reserve (120 km^2; South Africa) was too small to accommodate the nutritional and social requirements of eland, which repeatedly broke free from the reserve. In comparison, none of the collared individuals ever left the KMR, apart when using the adjacent Rainbow Farms (which were formerly part of KMR; Thsenkeng, *pers. comm.*), suggesting that the study population, despite the undeniable anthropogenic limits imposed to nomadism and dispersal, was able to satisfy its socio-ecological requirements within the small and insular-like study area.

Seasonal home ranges and landscape-scale selection

As expected, season had a marked influence on home range extent. All collared individuals occupied a smaller and spatially distinct home range during the dry season than during the wet season. The observed patterns of seasonal space use thus closely reflected, albeit on a restricted spatial scale, the seasonal home range patterns reported for both central Kenya and southern Kalahari (Hillman, 1988; Verlinden, 1998; Thouless, 2014). Shifts in the size and location of seasonal home ranges corresponded, in East and southern Africa, to a shift in landscape use between open areas with low woody cover during the wet season, and closed canopy areas, such as woodland or thickets, during the dry season (Underwood, 1975; Rowe-Rowe, 1983; Hillman, 1988; Watson & Owen-Smith, 2000). Similarly, and partially confirming predictions, eland in KMR selected for woodland at the home range scale during the dry season, while dry grassland, wet grassland, and open shrubland were positively selected for during the wet season. The seasonal range shift occurred as a gradual expansion of the dry season range in October and November, which culminated in a movement into open and lightly wooded vegetation-types during the wet season.

Seasonal variation in home range size and location has been observed across a wide variety of large herbivores (Murray, 1982; Owen-Smith, 1988; Ryan *et al.*, 2006; Van Beest *et al.*, 2011; Naidoo *et al.*, 2012). Among the members of the guild of savannah browsers and mixed-feeders, to which the eland is commonly assigned, the water-dependent elephant (*Loxodonta*

africana) and impala (*Aepyceros melampus*), regardless of their conspicuous evolutionary and eco-physiological differences, occupy small dry season ranges, centred around remaining water sources (Murray, 1982; Owen-Smith, 1988). Eland, however, are notoriously considered as water-independent (Thouless, 2014), and were never seen drinking in KMR during the course of the present study. Browsers, such as greater kudu and black rhinoceros (*Diceros bicornis*), restrict their movements to patches offering high-quality browse, in the form of evergreen shrubs and small trees, during the dry season (Owen-Smith, 1979, 1994; Frame, 1980). At the onset of the tropical rains, high-quality forage in the form of flushing, protein-rich herbaceous dicotyledons becomes widely available across the landscape, and draws mammalian browsers out of their habitual dry season refuges (Evans, 1979; Owen-Smith, 1988, 2002). These patterns of seasonal resource availability could potentially explain the shift in home range location for eland in KMR, which most likely lost their bond with evergreen woody plants as soon as scattered patches of high-quality herbaceous plants became available and drew the animals outside of their formal dry season range. The shifts in landscape use by eland from areas characterized by extensive grass cover to wooded vegetation patches are also generally associated with a marked dietary change, from a grazing-dominated diet during the wet season to almost exclusive browsing on trees and shrubs as the protein content in grasses fell below acceptable levels (Field, 1975; Scotcher, 1983; Buys, 1990). Dietary changes throughout the seasonal cycle have also been recorded for the population in KMR, thus suggesting that differences in home range location may reflect differential use of the array of plant species available to the individual animals. A time-lag response to rainfall was also noted in the present study (and also in central Kenya by Hillman, 1988), with adult female eland completely commuting for a seasonal home range centred on the open areas of the central basin in KMR only in December, when a sufficient regrowth of grass had already been triggered by the first, sporadic rainfall events during the previous month. Eland in KMR probably moved into dry grassland when flushing grasses were available at an optimal height to be efficiently cropped (forage maturation hypothesis; Fryxell *et al.*, 1988). Grass species associated with woodland in KMR, such as *Panicum maximum* and *Sporobolus africanus*, are mostly tall and stemmy and probably not attractive to eland, in comparison to the shorter sward typical of the basin and of the plateau (Nel, 2000). Positive landscape-scale selection for open shrubland during the wet season, although unexpected, coincided with the sprout of new leaves on some frequently consumed deciduous

woody species associated with this vegetation-type, such as *Vangueria parvifolia* and *Ancylobotrys capensis* (see Chapter 3). During the dry season, eland reverted back to woodland as soon as grasses entered the dormant stage and leaves of palatable woody plants in open shrubland started to turn brown (*pers.obs.*), probably because of the low moisture-retention properties of soils underlying this vegetation community (Nel, 2000). Within this broad pattern of interaction between nutritional requirements, species composition of vegetation-types, and seasonal movements, selection of home ranges within the landscape was also influenced by greenness and primary production of landscape units. Although lower values of NDVI than available associated with GPS locations at feeding sites during the wet season seemed counter-intuitive, they simply paralleled the shift in home range location to areas of the reserve characterized by lower woody cover than those mostly utilised during the dry months. In fact, Pettorelli *et al.* (2005) noticed that NDVI values were positively correlated with the percentage of woody cover in a pixel, mainly due to the increased leaf area index and plant biomass in respect to open areas. Thus, eland selected for green grassland or open shrubland during the wet season, which presented intrinsically lower NDVI levels than wooded areas.

Another possible explanation of the smaller dry season home ranges compared to the wet season home ranges, could be linked to the fact that between October and March all collared individuals most likely remained, at least temporarily, associated together and as part of a single, large nursery herd, varying in size between 33 and 55 individuals (Appendix II). During the dry seasons in 2013 and 2015, collared eland were always observed in small herds containing only adult individuals of both sexes. Thus, herd size was substantially larger during the wet season than during the dry season. Several authors suggested that home range size might scale positively with herd size for herbivores, mainly because large numbers of individuals might accelerate the depletion of food resources in a foraging area (Sinclair, 1977; Ryan *et al.*, 2006; Owen-Smith & Cain, 2007). Additionally, the conspicuous presence of calves and yearlings in the large nursery herd where all the collared individuals were found in the wet season possibly forced the entire social unit to feed in vegetation-types were forage was either: a) high in protein contents and low in fibre concentrations, in order to sustain the fast growth rate and metabolic requirements of weaned, growing calves (Underwood, 1975); and b) accessible at low levels above the ground, where it could be reached by both calves and yearlings.

The long-term population resilience of migratory and nomadic ungulates is often determined by their ability to switch between different ranges at crucial stages of the seasonal cycle (Bolger *et al.*, 2008; Morrison & Bolger, 2012). Eland in Kenya and in southern Botswana showed their adaptability to unpredictable inter-annual variation in rainfall patterns by shifting their seasonal ranges during prolonged droughts, in order to track remaining patches of green herbage and foliage (Hillman, 1988; Verlinden, 1998). In the southern Kalahari, eland were able to persist in large numbers despite the erection of veterinary cordon fences which halted the migratory movements of other large ruminants, by selecting for new unrestricted dry season pastures (Verlinden, 1998; Thouless, 2014). Collared individuals in KMR were observed in different woodland areas during the dry seasons of the study period, with SAT1399 most often restricted to the south-eastern valley and slopes abutting the main drainage line (during all three dry seasons of the study). At the same time, SAT1397, despite the interruption of all GPS transmission in April 2015, was frequently observed during the following dry season, mostly around a patch of woodland extending into the central basin. The individual SAT1398, during the dry season of 2015, returned to the same area characterized by deep, well- vegetated gorges, where it had been captured in the previous year (September 2015). These patterns suggested that heavily wooded landscape units within the KMR could represent "dry season refuges" of suitable forage for the adult female eland. However, SAT1398 exhibited a shift in what was most probably its dry season range of choice in the north-eastern gorges and hills of the reserve, moving southwards to the Rainbow Farms in July 2015, when low rainfall during the preceding wet season (**Fig. 2**) depressed the availability of green forage (*pers. obs.*). The border between KMR and Rainbow Farms remained fenced for most of the study period (apart from 2013), but eland did not seem to be restricted in their movements by this barrier, and regularly crossed (presumably jumped over) it. Rainbow Farms thus constitute a possible reservoir of green and palatable browse (maintained by the low exposure to sunlight of the southern slopes of the Magaliesberg range; Carruthers, 2014) during exceptionally dry periods.

Habitat use and selection

Eland in different eco-regions of the African continent have been documented to select for open, grass-dominated vegetation-types during the wet season (Rowe-Rowe, 1983; Kelso, 1986; Hillman, 1979; Buys, 1990; Fabricius & Mentis, 1990; Watson & Owen-Smith, 2000).

Consistently with these observations, and similarly to what reported for landscape-scale selection, eland in KMR included a generally larger proportional area of dry grassland within their wet season ranges than within their dry season ranges, and also selected this vegetation-type over woodland during the dry season, confirming my expectations. During the dry season of 2013, dry grassland constituted an unusually large proportion of the home range of SAT1399. The utilisation of this vegetation-type was probably facilitated by the availability of green grass tufts for long into the dry season (probably as a leftover of early dry season fires), which also prompted extra-seasonal grazing by eland (D'Ammando *et al.*, 2015). During the dry season of 2015, the home range of SAT1398 was still composed of a conspicuous proportion of open shrubland. Because of the low rainfall characterizing the preceding wet season, eland expanded their diet to include also coriaceous and lowly palatable (according to van Wyk & van Wyk, 2002) evergreens, such as *Englerophytum magalismontanum*, which were largely available on open shrubland and probably constituted an attractive source of green leaves during drought conditions (see Chapter 3). Wet grassland formed a small but detectable fraction of the seasonal home ranges throughout the year, in contrast to what was expected. Use of floodplains by eland has been rarely documented (Sheppe & Osborne, 1971), but the pattern observed in KMR could be explained by the abundance of weeds and other dicots on the central "*vlei"* during the wet season.

The influence of NDVI, in its interaction with the vegetation-type, on habitat selection remains unclear, although apparently significant from a modelling perspective. I could anyway exclude that eland were selecting greener areas than available within the seasonal ranges, as initially hypothesized. Eland seemingly fed in areas of lower than available greenness within the woodland, which suggested the avoidance of densely wooded patches. This is in accordance with the large body size of the study species, evolved as an adaptation to mobility in open savannah (Hillman, 1979), and probably constituting an impediment to movement in dense vegetation (Bro-Jørgensen, 2008). Furthermore, eland were mostly seen while feeding in grassy glades interspersed within valley woodland, where browse was available at accessible levels above the ground, in stark contrast with the almost complete lack of undergrowth in the presence of developed canopy cover (Nel, 2000). Selection for very green locations on wet grassland reflected the preference for mat-forming weeds and dwarf shrubs commonly found in this community. The main driver of habitat selection was

thus constituted by the structural and compositional heterogeneity of vegetation over the landscape of the reserve and according to the stage of the seasonal cycle.

Use of burnt areas

The use of burnt areas by eland has been qualitatively observed, but never quantified into detail, in several of the ecosystems where this species has been studied (Underwood, 1975; Rowe-Rowe, 1982, 1983; Kelso, 1986; Moe *et al.,* 1990). Confirming initial predictions, foraging on burnt areas in the KMR was mostly limited to the wet season, when burns were actively selected for at the landscape scale and offered young herbaceous vegetation in a matrix of tall, fibrous grasses. However, burns were generally avoided during the dry season, being relatively devoid of green forage (although burning in the dry season of 2013 triggered the growth of a detectable proportion of green grass tufts; *pers. obs.*). Use of flushing burns as elective feeding grounds was also mostly recorded during wet months in the Drakensberg (Rowe-Rowe, 1982, 1983), in Loskop Dam NR (Underwood, 1975), and in the Pilanebserg NP (Kelso, 1986). The need to forage on burns during the rains might have been caused by the presence of calves in nurseries, which necessitated the access to food items within their height range. Although some grazing events were witnessed in July 2013 on areas likely to had been subjected to fire prior to the rains (D'Ammando, *unpubl. data*), eland avoided burns during the dry season. Rowe-Rowe (1982) hypothesized that broad-muzzled eland could not successfully harvest the scattered and extremely short flush which established immediately after fires. Accordingly, eland in the Ol-Pejeta Conservancy (Kenya) fed on burnt patches which offered higher grass biomass and lower proportions of green leaves than extremely short swards established immediately after fires (Sensenig *et al.,* 2010). Confirming these observations, eland presented a time-lagged response to burning in the KMR, and patches of vegetation where fire had occurred during the previous dry season were only intensively used after rainfall had promoted the growth of a substantially uniform layer of green grasses, several months after the fire ignition date. Within the home ranges, eland selected for burnt patches in woodland and shrubland, where the presence of accessible and palatable food both in the herbaceous layer and in the newly-established foliage on woody plants probably constituted a magnet for mixed feeders. Burns on wet grassland were actively avoided, probably because fires removed the fernbeds of *Pteridium aquilinum* (usually associated with

areas undisturbed by fires; Nel, 2000) which facilitates the growth of dense stands of tall forbs and thus likely constituted attractive habitat patches for eland.

Apparently, the avoidance of burns during the dry season eliminated any management concern over the potential for interspecific competition between the eland and the sable antelope populations in KMR. Sable antelope usually concentrated on burnt wet grassland during the late dry season, when foraging on young grasses allows for an increase in the protein intake (Parrini & Owen-Smith, 2010). Eland, by contrast, clearly avoided burns on wet grassland and made a selective use of burnt areas over the available landscape only during the wet season. However, wet grassland was only marginally affected by fires during the present study period (*pers. obs.*), and thus whether extensive flushes of grass would attract eland to this vegetation type or not remains unknown. Grobler (1981) found that the grass sward on burns, when exposed to heavy grazing pressure by short-grass grazers, was prevented from reaching an optimal height at which it could be efficiently cropped by sable antelope. For this reason, the eventual grazing on burnt wetland by eland in years of regular dry season burning should be monitored in order to disentangle potential detrimental effects on the short-term growth rate of the sward, and, ultimately, on the population performance of the vulnerable and economically valuable sable antelope.

The severe decline of large herbivores, including eland, in the Nairobi NP (Kenya), and in the Ngorongoro Crater (Tanzania) has been put in correlation with the degradation of pastures following the abandonment of rotational burning practices by local pastoralists (Estes, Atwood, & Estes, 2006; Ogutu *et al.,* 2013). The present study, together with previous evidence from descriptive studies, highlights the importance of flushing burns for eland during the wet season. Shift in sward composition towards tall grass species might not favour mixed feeders and browsers, which sought after protein-rich (and fibre-deficient), short grasses (Field, 1975; Owen-Smith & Cooper, 1987a; Watson & Owen-Smith, 2000; O'Kane *et al.,* 2011a). For this reason, fire policies in insular-like game reserves of southern Africa should take into account the nutritional requirements of eland across the seasonal cycle, not only during the limiting season, and include burning as a management tool in order to simulate, on a much smaller spatial scale, the natural heterogeneity characterising large savannah ecosystems.

Summary

Eland occupied distinct seasonal home ranges, and dispersed over a large area under favourable conditions during the wet season, when green forage was widely distributed across the landscape of the reserve, and green grasses on burns constituted an attractive forage resource for adult females. Conversely, they established dry season ranges in woodland to take advantage of the local availability of green foliage during the limiting period. Thus, according to the forage maturation hypothesis, eland established seasonal ranges on landscape units providing them with plant species at stages of maturation offering green and easily processed forage during the course of the year. These results suggests that, despite limitations imposed by the insular-like nature of the study area, eland can still diversify the seasonal use of landscape and habitat according to forage availability and quality. Chemical characteristics of plant species, as well as local conditions of browse accessibility and vegetation structure, might affect habitat selection within the home ranges, and therefore need further investigation. The importance of burns as foraging areas during the wet season has been highlighted by resource selection models, and the use of fire as a managing tool for fenced-in populations of eland needs also to be explored into detail.

TABLES

Tab. 1: Chart illustrating the sub-division of the study period into seasons (based on rainfall and temperature), and the functioning period for each GPS collar. C=collaring operations. Dark rows=individuals not yet collared. The seasons are the following: D1=Dry season 2013; TO1=October-November transition 2013; W1=Wet season 2013-2014; TA1=April-May transition 2014; D2=Dry season 2014; TO2=October-November transition 2014; W2=Wet season 2014-2015; TA2=April-May transition 2015; D3=Dry season 2015.

	July '13	August '13	September '13	October '13	November '13	December '13	January '14	February '14	March '14	April '14	May '14	June '14	July '14	August '14	September '14	October '14	November '14	December '14	January '15	February '15	March '15	April '15	May '15	June '15	July '15	August '15	September '15
Season	D1			TO1		W1				TA1		D2				TO2		W2				TA2		D3			
SAT1399	Working														C	Working									Failed		
SAT1398															C	Working											
SAT1397															C	Working									Failed		
SAT1396															C	Working									Failed		

Tab. 2: Annual home range extent (95% isopleths) for the two collared eland in Kgaswane Mountain Reserve whose collars lifespan allowed for estimates in a-LoCoH at the temporal scale of one year.

Individual ID	Sampling period	Herd size at capture	Days of sampling	Number of GPS locations	Annual 95% home range extent (km^2)
SAT1399	15/07/2013-31/08/2014	6	412	2060	21.2
	01/10/2014-31/05/2015	4	242	5808	17.38
SAT1398	01/10/2014-30/09/2015	8	364	8736	20.87

Tab. 3: Estimates of seasonal home range extent (95% isopleths) as obtained in a-LoCoH, for each individual eland in the Kgaswane Mountain Reserve. The number of operational days per season, the duration of each season, and the number of GPS locations collected are also indicated.

Individual ID	Season	Period of collected GPS locations	Days of sampling	Number of GPS locations	Seasonal 95% home range size (km^2)
SAT1399	Dry 2013 (D1)	15/07-30/09	77	385	5.83
	Oct-Nov 2013 (TO1)	01/10-30/11	60	300	12.07
	Wet 2013-2014 (W1)	01/12-31/03	120	600	16.37
	Apr-May 2014 (TA1)	01/04-31/05	60	300	5.48
	Dry 2014 (D2)	01/06-25/09	116	580	4.09
	Oct-Nov 2014 (TO2)	01/10-30/11	60	1440	7.3
	Wet 2014-2015 (W2)	01/12-31/03	120	2880	11.37
	Apr-May 2015 (TA2)	01/04-31/05	60	1440	5.05
SAT1398	Oct-Nov 2014 (TO2)	01/10-30/11	60	1440	13.53
	Wet 2014-2015 (W2)	01/12-31/03	120	2880	14.3
	Apr-May 2015 (TA2)	01/04-31/05	60	1440	4.62
	Dry 2015 (D3)	01/06-30/09	121	2904	5.16
SAT1397	Oct-Nov 2014 (TO2)	01/10-30/11	60	1440	10.5
	Wet 2014-2015 (W2)	01/12-31/03	120	2880	10.49
SAT1396	Oct-Nov 2014 (TO2)	01/10-30/11	60	1440	11.38
	Wet 2014-2015 (W2)	01/12-31/03	120	2880	9.95

Tab. 4: Table presenting twenty of the fifty candidate models for explaining landscape-scale selection. Models are ordered in decreasing order of fit, according to their statistical estimates, and especially to the Akaike's Information Criterion (AICc). The model evidenced in the first row was considered as the best model, due to lowest AICc, and highest Akaike's weights (w_iAICc). The table continues on the following page.

Models	**Fixed effects**	**K**	**AICc**	**ΔAICc**	***w*$_i$AICc**	**logLik**	**Deviance**	**Df.dev**
Model 31	**NDVI*Season+Vegetation-type*Season+Burns*Season**	**17**	**3588.9**	**0**	**0.80**	**-1773.4**	**3546.9**	**2772**
Model 44	Vegetation-type*Burns+Vegetation - type*Season+Vegetation-type*NDVI	21	3592.2	3.3	0.15	-1765.1	3530.2	2762
Model 46	Vegetation-type*NDVI+Vegetation - type*Season+Burns	17	3594.7	5.8	0.04	-1769.3	3538.7	2765
Model 35	Vegetation-type*Season+Burns*Season+ NDVI*Vegetation-type	19	3596.3	7.4	0.02	-1769.2	3538.2	2764
Model 42	Vegetation-type*Season+Burns*Vegetation- type+NDVI	17	3605.9	17	0.0001	-1783.9	3567.9	2774
Model 23	Habitat-type*Season+NDVI+Burns	13	3607.9	19	0	-1788.0	3575.9	2777
Model 38	NDVI*Season+Vegetation - type*Season+Burns*Season+ NDVI*Vegetation -type	26	3615.4	26.5	0	-1774.7	3549.4	2760
Model41	Vegetation-type*Season+Burns*Vegetation-type	12	3632.5	43.3	0	-1801.2	3605.8	2778
Model33	Vegetation-type*Season+Burns*Season	10	3635.7	46.8	0	-1804.9	3609.7	2780
Model25	Vegetation-type*Season+Burns	8	3636.1	47.2	0	-1806.0	3612.1	2781
Model28	NDVI*Vegetation-type+Burns	11	3652.3	63.4	0	-1802.2	3604.3	2769
Model27	NDVI*Vegetation - type+Burns+Season	13	3654.3	65.4	0	-1802.1	3604.3	2768
Model36	Burns*Season+NDVI*Vegetation -type	13	3656.2	67.3	0	-1802.1	3604.2	2767
Model40	NDVI*Season+Vegetation - type*Season+Burns*Season+ Burns*Vegetation-type	23	3681.3	92.4	0	-1819.7	3639.3	2772

Model39	NDVI*Season+NDVI*Vegetation -type	16	3684.7	95.8	0	-1814.3	3628.7	2765
Model49	Burns*NDVI+Vegetation -type	11	3686.6	97.7	0	-1827.3	3654.6	2777
Model47	Burns*NDVI	7	3687.9	99	0	-1831.0	3661.9	2780
Model48	Burns*NDVI+Vegetation -type+Season	13	3688.1	99.2	0	-1827.0	3654.1	2776
Model50	Burns*NDVI+Season	9	3688.7	99.8	0	-1830.3	3660.7	2779
Model 1	NDVI+Habitat-type+Burns+Season	13	3714.2	125.3	0	-1844.1	3688.2	2780
NULL	-		3870		0	-	-	-

Tab. 5: Summary of the twenty models (over the fifty tested) utilised to explain habitat-scale selection by eland in the KMR. Models are ordered in decreasing order of fit, according to their the Akaike's Information Criterion (AICc). The model in bold cases was selected as the best one, because of its lowest AICc and highest Akaike's weights (w_iAICc). The table continues on the following page.

Models	**Fixed effects**	**K**	**AICc**	**ΔAICc**	w_i**AICc**	**logLik**	**Deviance**	**Df.dev**
Model 44	**Vegetation-type*Burns+Vegetation -type*Season+Vegetation-type*NDVI**	21	3590.2	0	0.99	-1764.1	3528.2	2657
Model 42	Vegetaion-type*Season+Burns*Vegetation -type+NDVI	11	3604.1	13.9	0.001	-1783.0	3566.1	2669
Model 46	Vegetation-type*NDVI+Vegetation-type*Season+Burns	17	3618.4	28.2	0	-1781.2	3562.4	2660
Model 35	Vegetation-type*Season+Burns*Season+NDVI*Vegetation-type	19	3619.4	29.2	0	-1780.7	3561.4	2662
Model 31	NDVI*Season+Vegetation-type*Season+Burns*Season	16	3627.7	37.5	0	-1792.9	3585.7	2667
Model 41	Vegetation-type*Season+Burns*Vegetation -type	12	3630.5	40.3	0	-1800.2	3600.5	2673
Model 43	Vegetation-type*Season+Burns*Season+NDVI	15	3630.6	40.4	0	-1798.3	3596.6	2671
Model 23	Vegetation-type*Season+NDVI+Burns	13	3631.4	41.2	0	-1799.7	3599.4	2672
Model 32	NDVI*Season+Vegetation-type*Season	13	3638.9	48.7	0	-1800.4	3600.9	2669
Model 24	Vegetation-type*Season+NDVI	11	3643.8	53.6	0	-1806.9	3613.8	2673
Model 38	NDVI*Season+Vegetation-type*Season+Burns*Season+NDVI*Vegetation-type	26	3656.6	66.4	0	-1795.3	3590.6	2655
Model 33	Vegetation-type*Season+Burns*Season	10	3657.8	67.6	0	-1815.9	3631.8	2675
Model 25	Vegetation-type*Season+Burns	8	3661.8	71.6	0	-1818.9	3637.8	2676
Model 40	NDVI*Season+Vegetation-type*Season+Burns*Season+Burns*Vegetation-type	24	3667.6	77.4	0	-1812.8	3625.6	2667
Model 28	NDVI*Vegetation-type+Burns	11	3673.4	83.2	0	-1812.7	3625.4	2664

Model 27	NDVI*Vegetation-type+Burns+Season	13	3675.4	85.2	0	-1812.7	3625.4	2663
Model 36	Burns*Season+NDVI*Vegetation-type	13	3676.9	86.7	0	-1812.5	3624.9	2677
Model 26	Vegetation-type*Season	6	3679.4	89.2	0	-1828.7	3657.4	2677
Model49	Burns*NDVI+Vegetation-type	11	3680.3	90.1	0	-1824.2	3648.3	2672
Model48	Burns*NDVI+Vegetation-type+Season	13	3682.0	91.8	0	-1824.0	3648.0	2671
NULL	-	-	3728.4	138.2	0	-	-	-

FIGURES

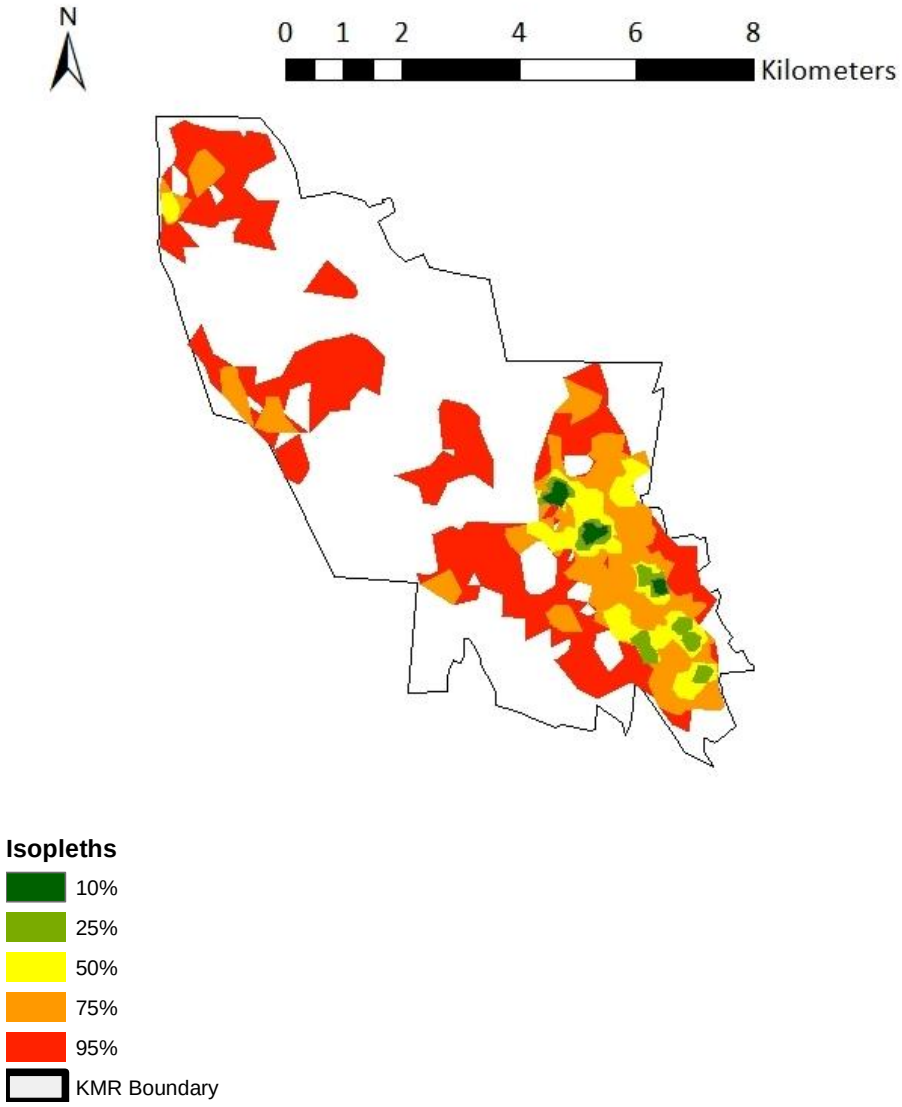


Fig. 1: Annual utilization distributions, as represented by different isopleths, for SAT1399 between 15th July 2013 and 31st August 2014. The 95% isopleth contour should be interpreted as the total annual home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at five -hour intervals.

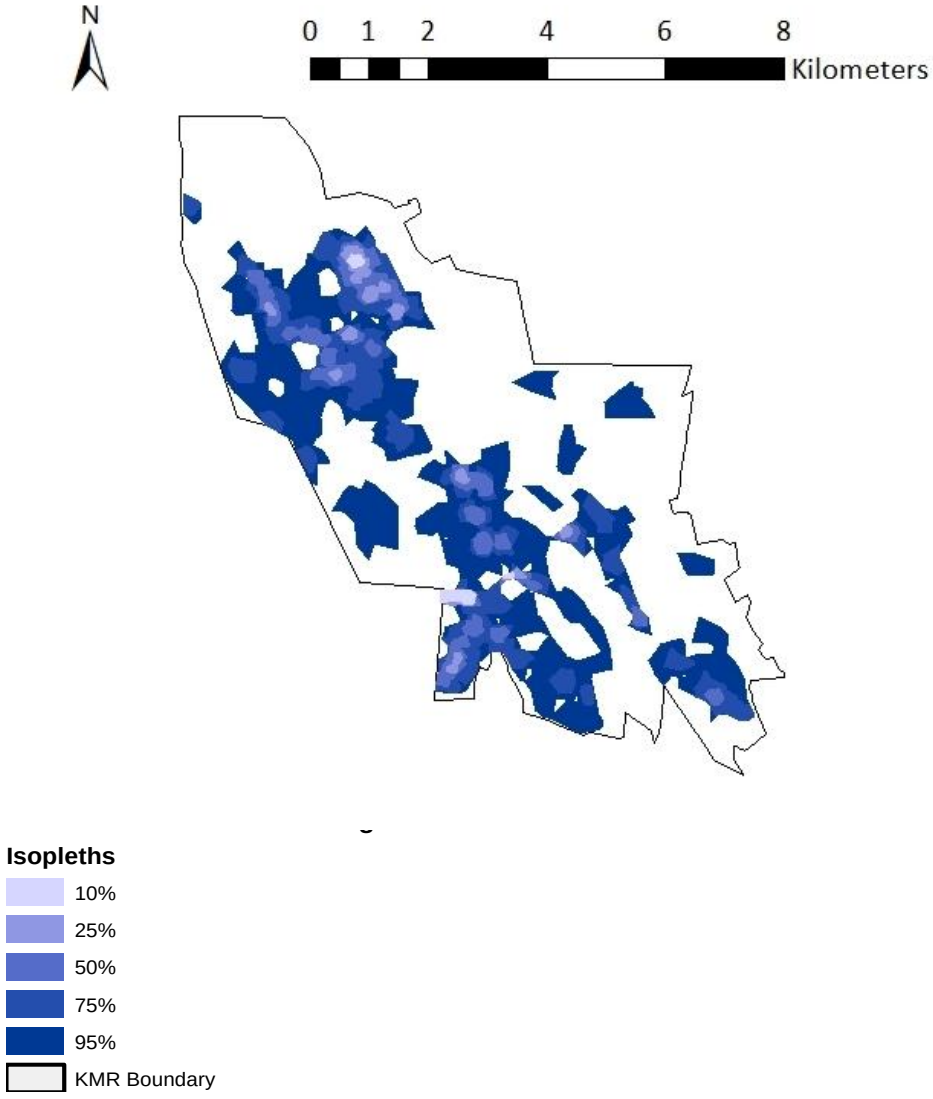


Fig. 2: Annual utilization distributions, as represented by different isopleths, for SAT1398 between 1st October 2014 and 30th September 2015. The 95% isopleth contour should be interpreted as the total annual home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals.

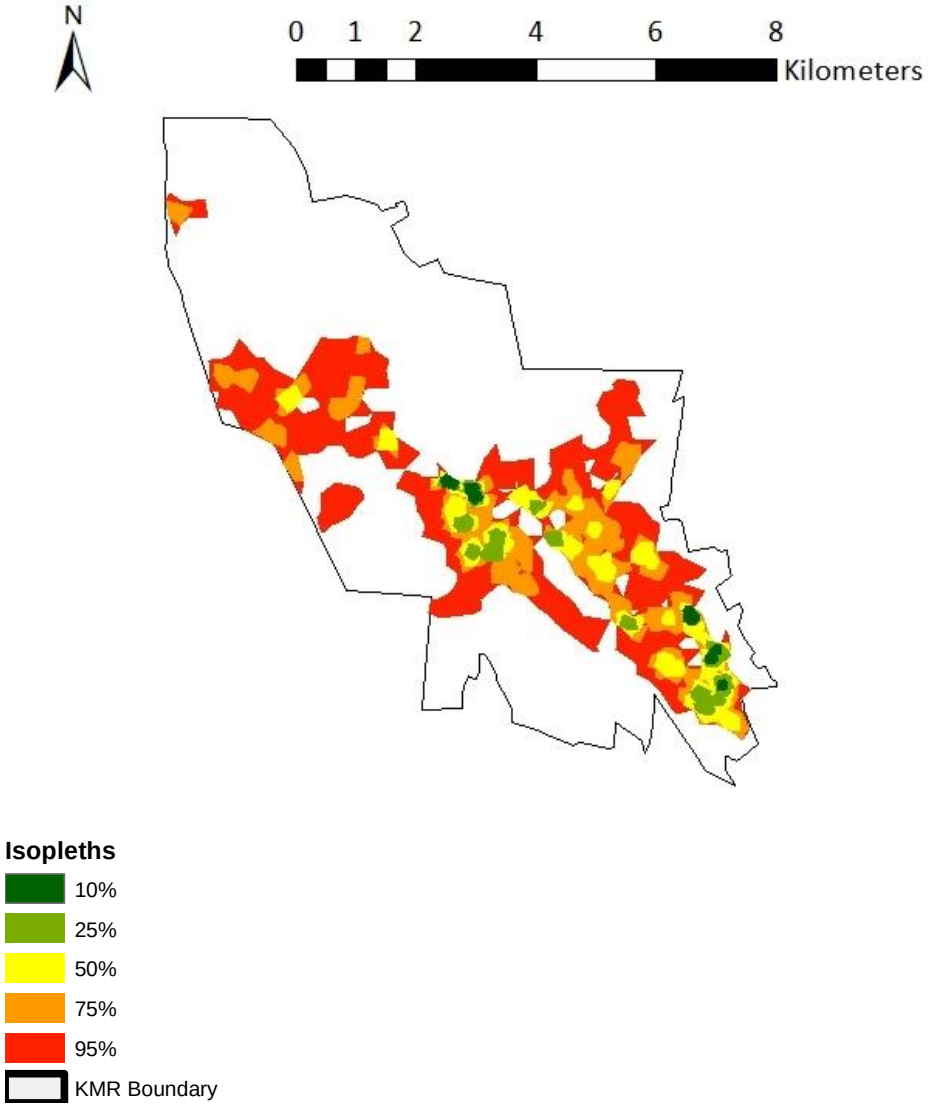
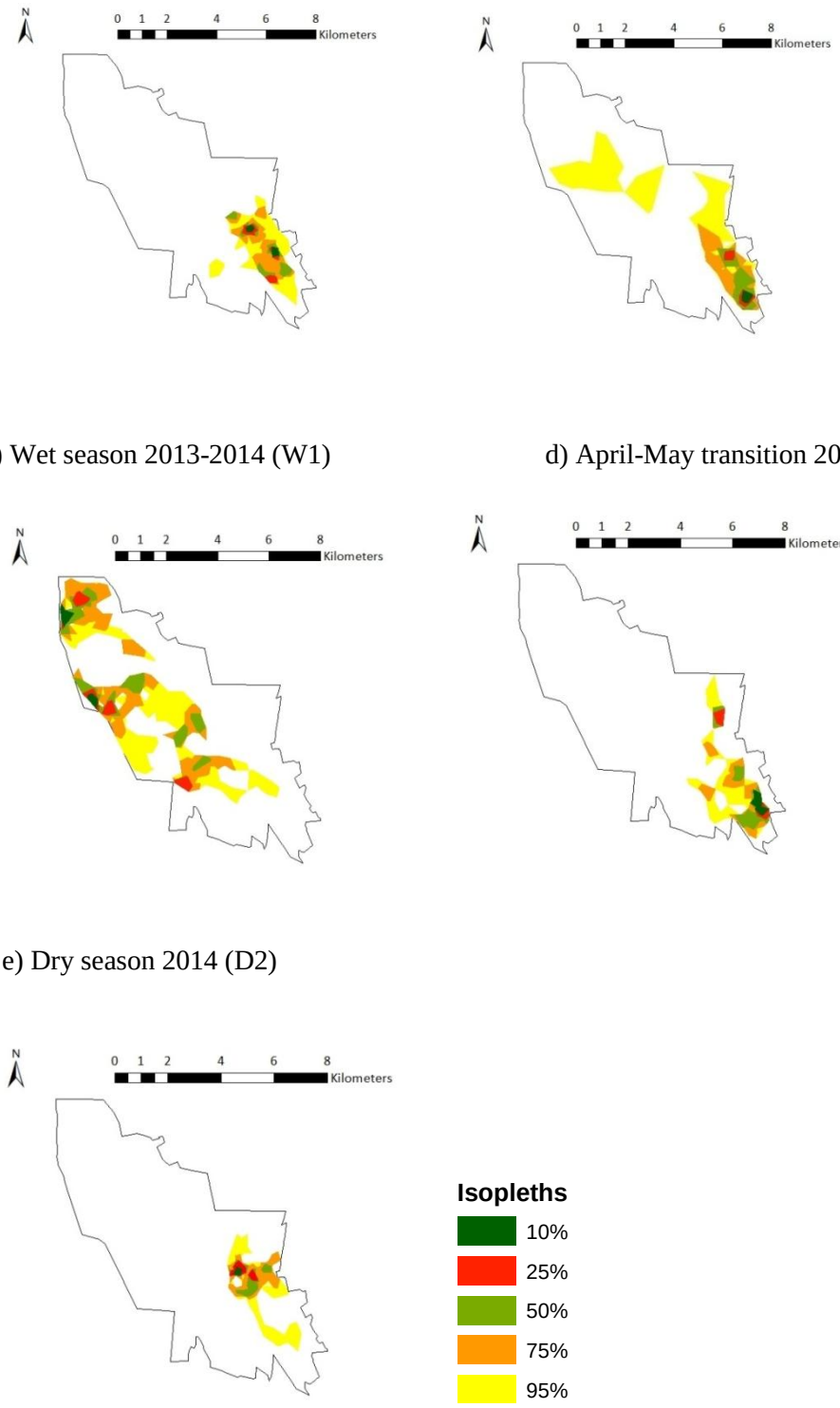


Fig. 3: Total utilization distributions, as represented by different isopleths, for SAT1399 between 1st October 2014 and 31st May 2015. The 95% isopleth contour should be interpreted as the total annual home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals.

a) Dry season 2013 (D1)

b) October-November transition 2013 (TO1)



c) Wet season 2013-2014 (W1)

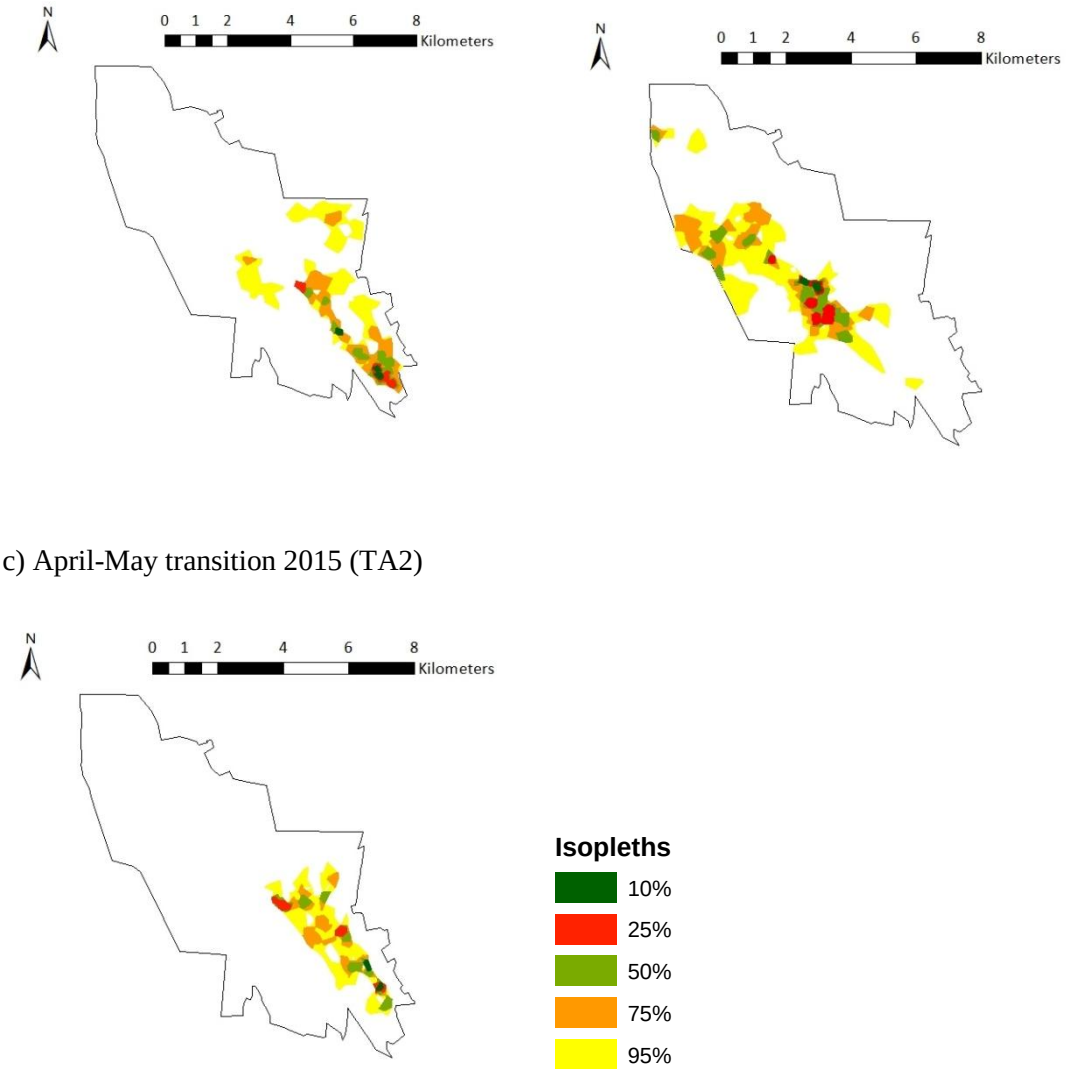
d) April-May transition 2014 (TA1)

e) Dry season 2014 (D2)

Fig. 4: Seasonal utilization distributions, as represented by different isopleths, for SAT1399 between 15th July 2013 and 31st August 2014. The 95% isopleth contour should be interpreted as the seasonal home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at five-hour intervals. The images refers to the following seasons: a) Dry season 2013 (D1); b) October-November transition 2013 (TO1); c) Wet season 2013-2014 (W1); d) April-May transition 2014 (TA1); e) Dry season 2014 (D2).

a) October-November transition 2014 (TO2)

b) Wet season 2014-2015 (W2)



c) April-May transition 2015 (TA2)

Fig. 5: Seasonal utilization distributions, as represented by different isopleths, for SAT1399 between 1st October 2014 and 31st May 2015. The 95% isopleth contour should be interpreted as the seasonal home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals. The images refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2); c) April-May transition 2015 (TA2).

a) October-November transition 2014 (TO2)

b) Wet season 2014-2015 (W2)

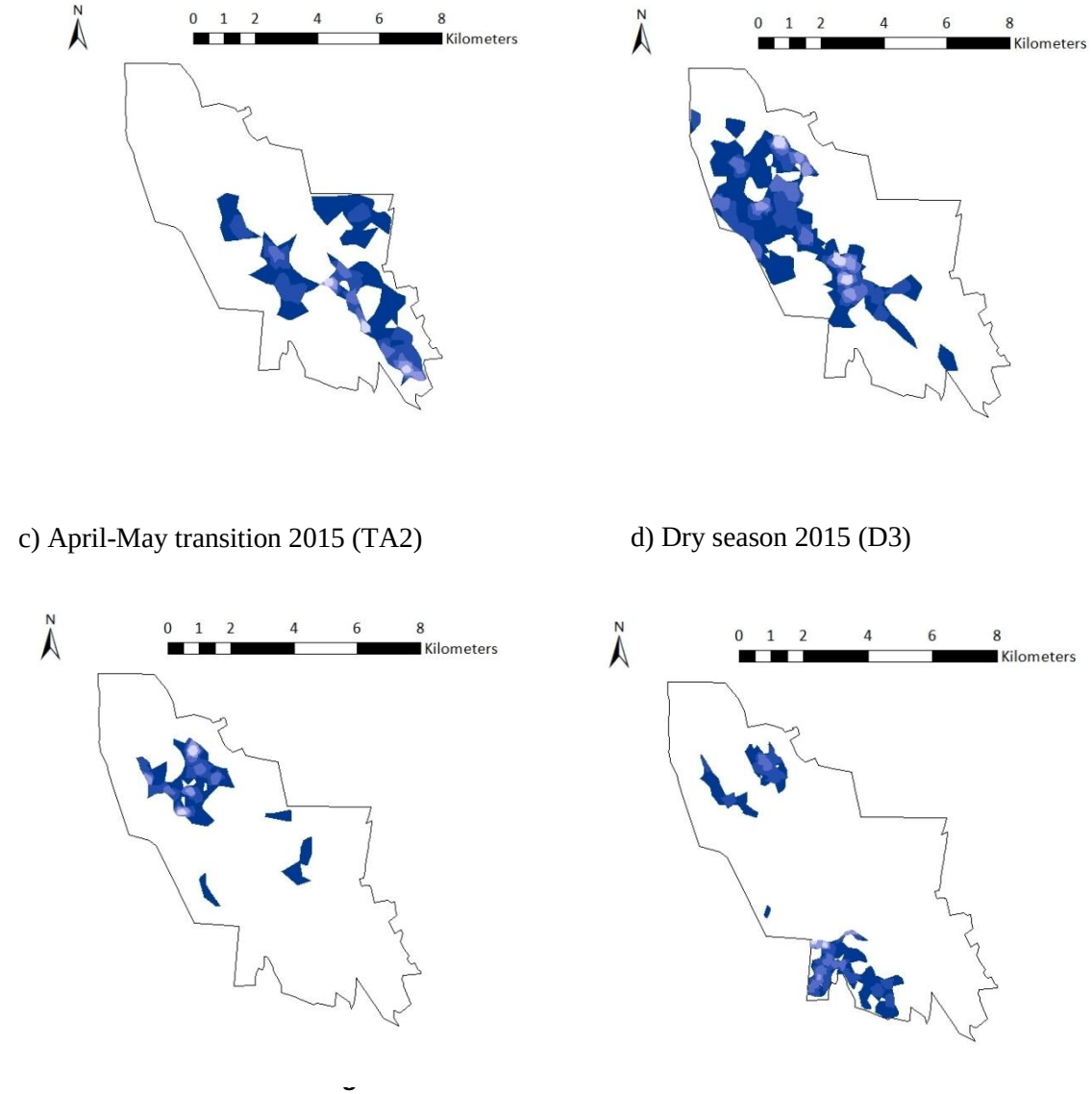


Fig. 6: Seasonal utilization distributions, as represented by different isopleths, for SAT1398 between 1st October 2014 and 30th September 2015. The 95% isopleth contour should be interpreted as the seasonal home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals. Images refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2); c) April-May transition 2015 (TA2); d) Dry season 2015 (D3).

a) October-November Transition 2014 (TO2)

b) Wet season 2014-2015 (W2)

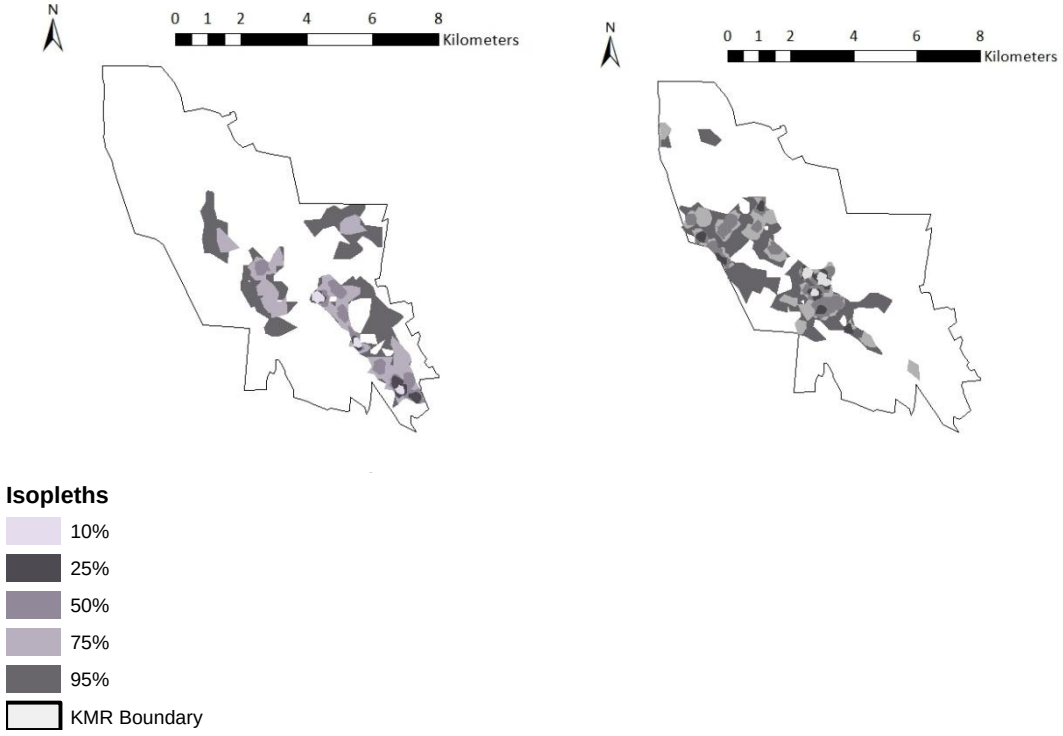


Fig. 7: Seasonal utilization distributions, as represented by different isopleths, for SAT1397 between 1st October 2014 and 28th February 2015. The 95% isopleth contour should be interpreted as the seasonal home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals. The images refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2).

a) October-November transition 2014 (TO2)

b) Wet season 2014-2015 (W2)

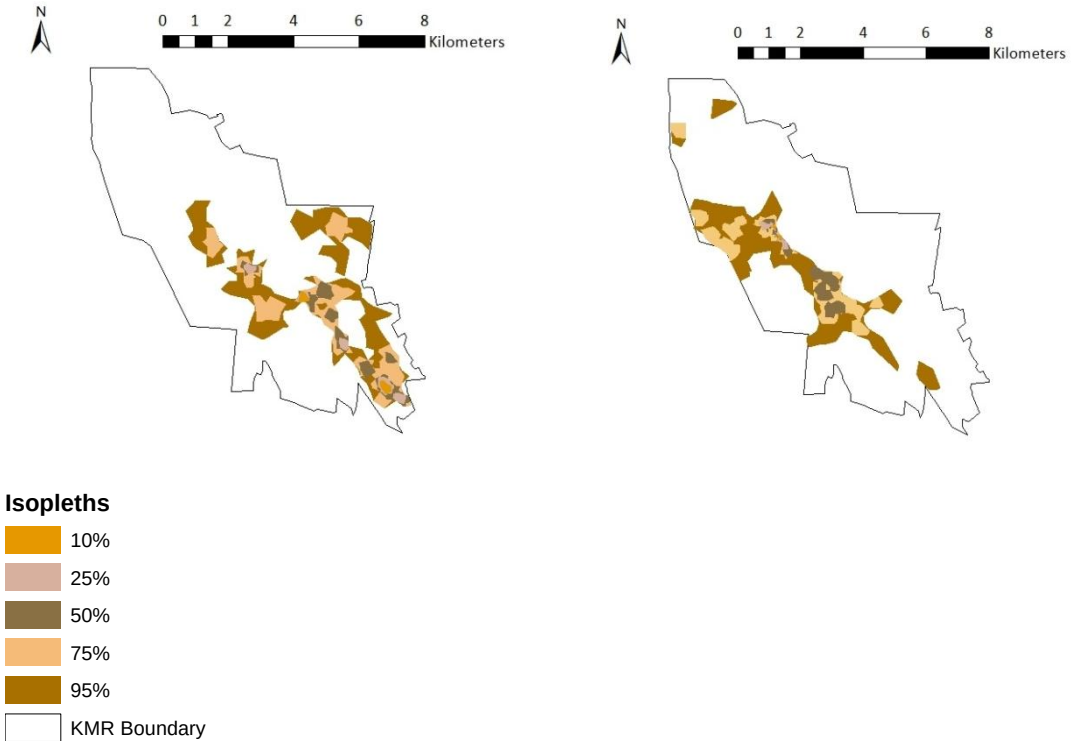


Fig. 8: Seasonal utilization distributions, as represented by different isopleths, for SAT1396 between 1st October 2014 and 28th February 2015. The 95% isopleth contour should be interpreted as the seasonal home range. The estimate was calculated in a-LoCoH, on the basis of GPS locations collected at hourly intervals. The images refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2).

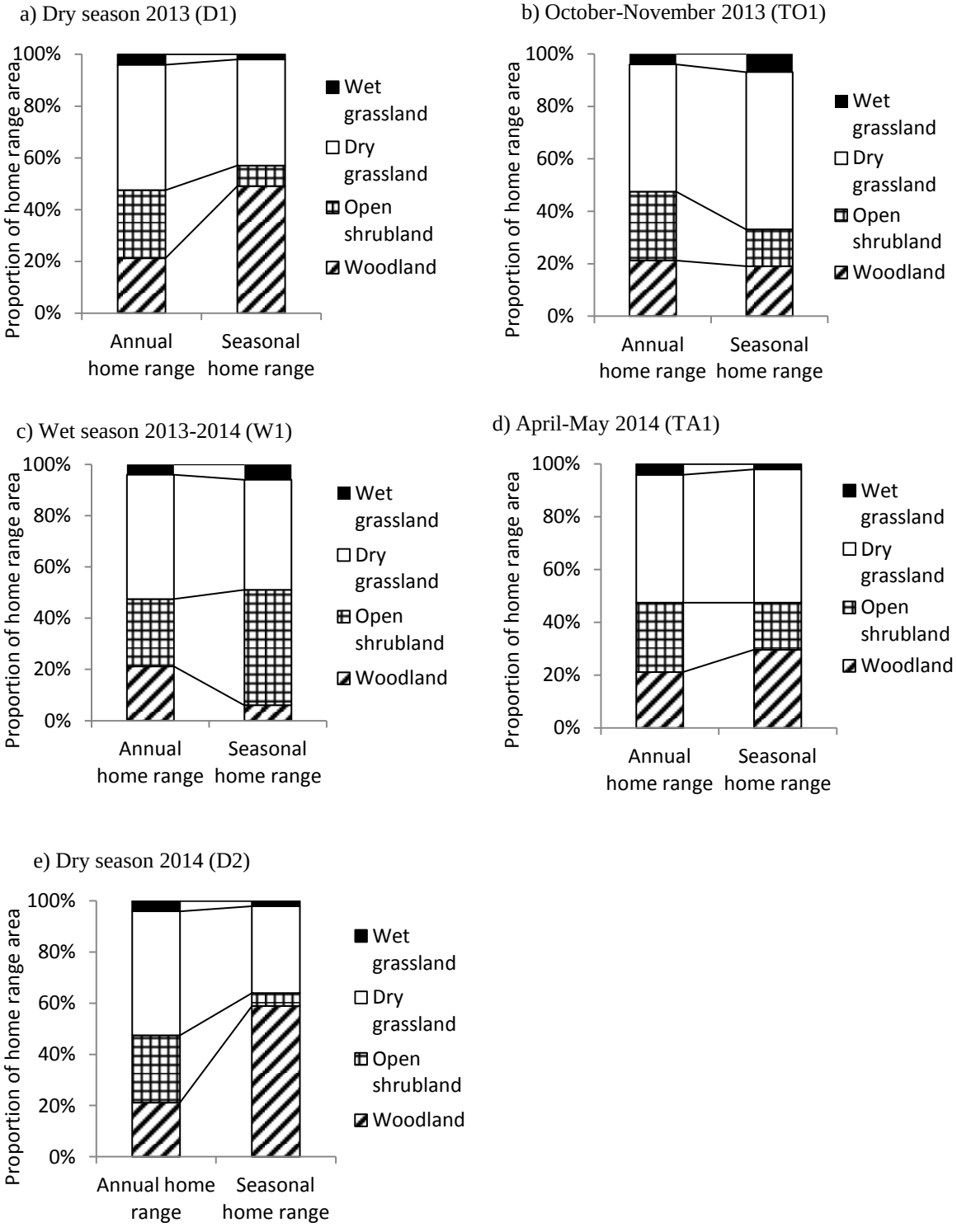


Fig. 9: Composition of seasonal home ranges by vegetation-types, compared with the composition of the annual home range for eland SAT1399 in the Kgaswane Mountain Reserve, during the period between the dry season of 2013 and the dry season of 2014 (GPS locations collected at five-hour intervals). The graphs refer to the following seasons: a) Dry season 2013 (D1); b) October-November transition 2013 (TO1); c) Wet season 2013-2014 (W1); d) April-May transition 2014 (TA1); e) Dry season 2014 (D2).

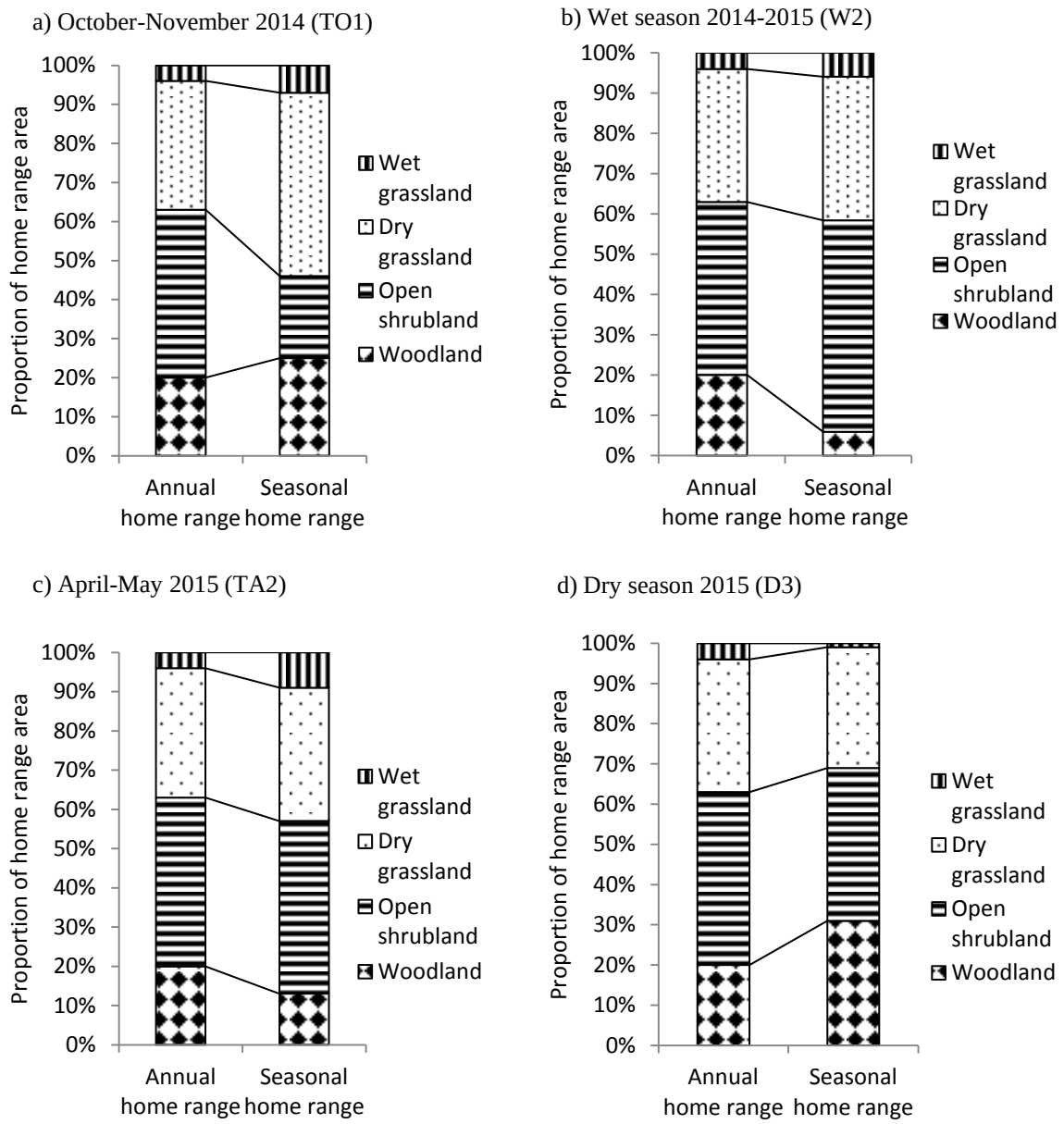


Fig. 10: Composition of seasonal home ranges by vegetation-types, for eland SAT1398 in Kgaswane Mountain Reserve. The seasonal contribution of each vegetation-type to the home range is compared with the contribution to the annual home range, area, for the period comprised between 1st October 2014 and 30th September 2015. The graphs refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2); c) April-May transition 2015 (TA2); d) Dry season 2015 (D3).

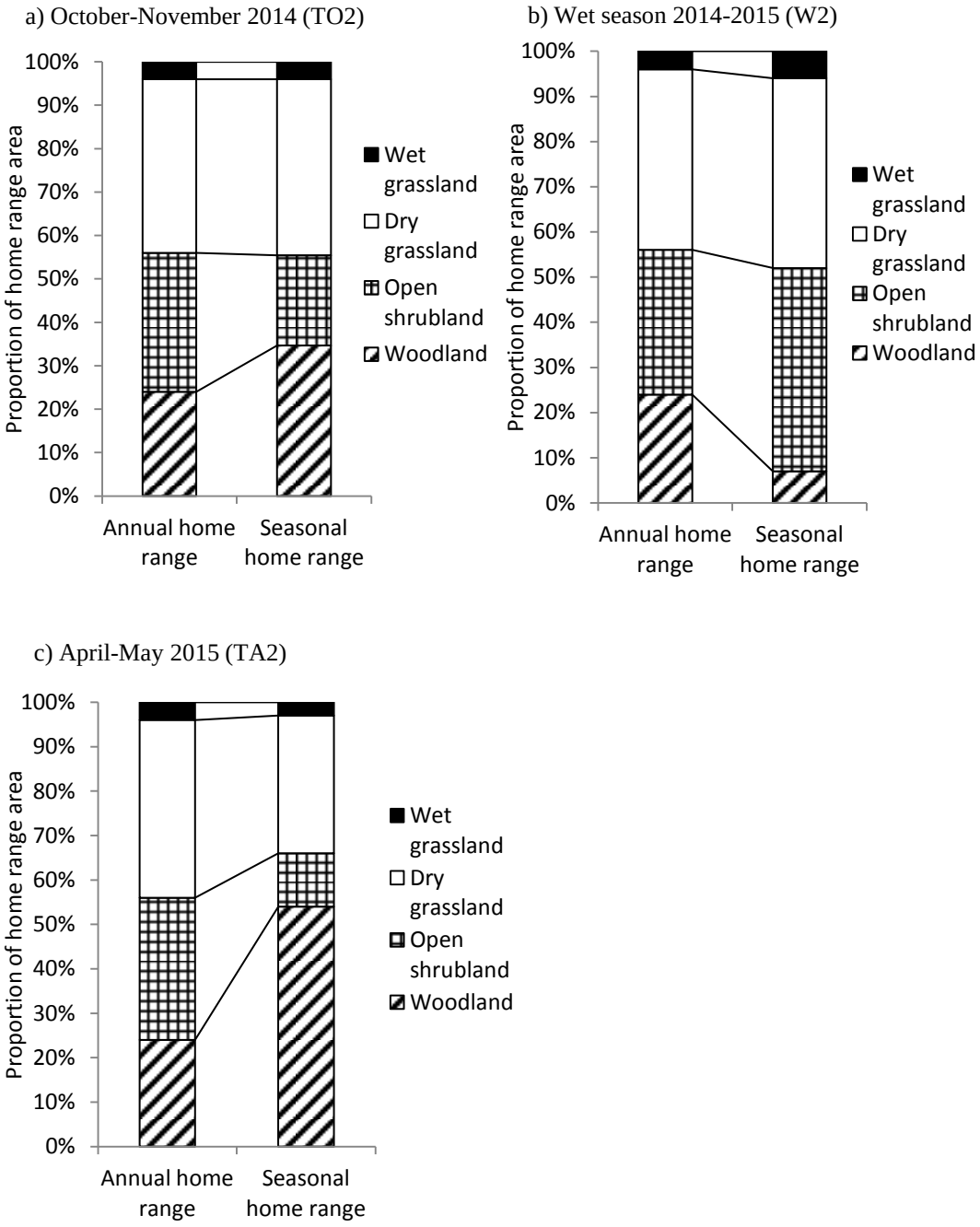
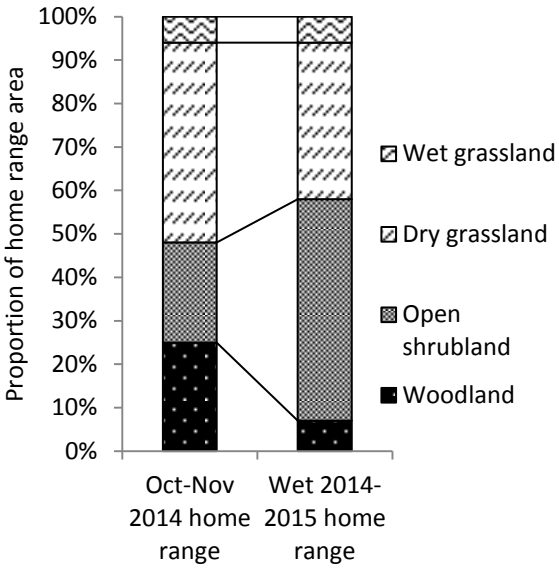


Fig. 11: Composition of seasonal home ranges by vegetation-types for eland SAT1399 in the Kgaswane Mountain Reserve, during the period comprised between 1st October 2014 and 31st May 2015. Composition is compared with that of the total home range for October 2014-May 2015 (GPS locations collected at hourly intervals). The graphs refer to the following seasons: a) October-November transition 2014 (TO2); b) Wet season 2014-2015 (W2); c) April-May transition 2015 (TA2).

a) Seasonal home ranges of SAT1397



b) Seasonal home ranges of SAT1396

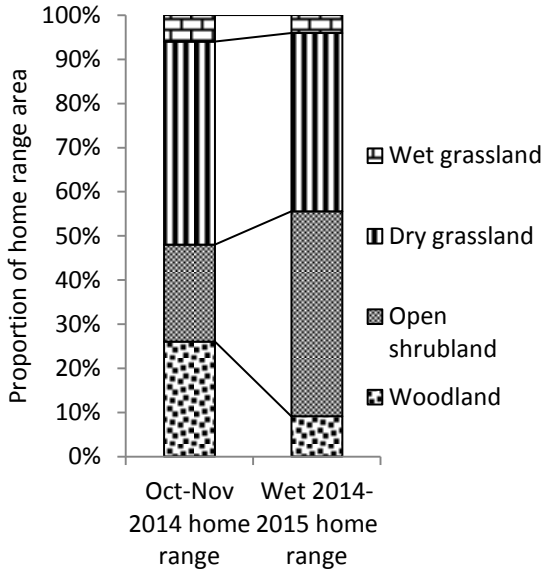


Fig. 12: Composition of seasonal home ranges for eland SAT1397 and SAT1396 in the Kgaswane Mountain Reserve, by vegetation-types. Home ranges during the October-November 2014 transition period are compared with home ranges during the wet season of 2014-2015, in the impossibility to estimate an annual home range (due to collar failure). The graphs refer to: a) Individual SAT1397; b) Individual SAT1396

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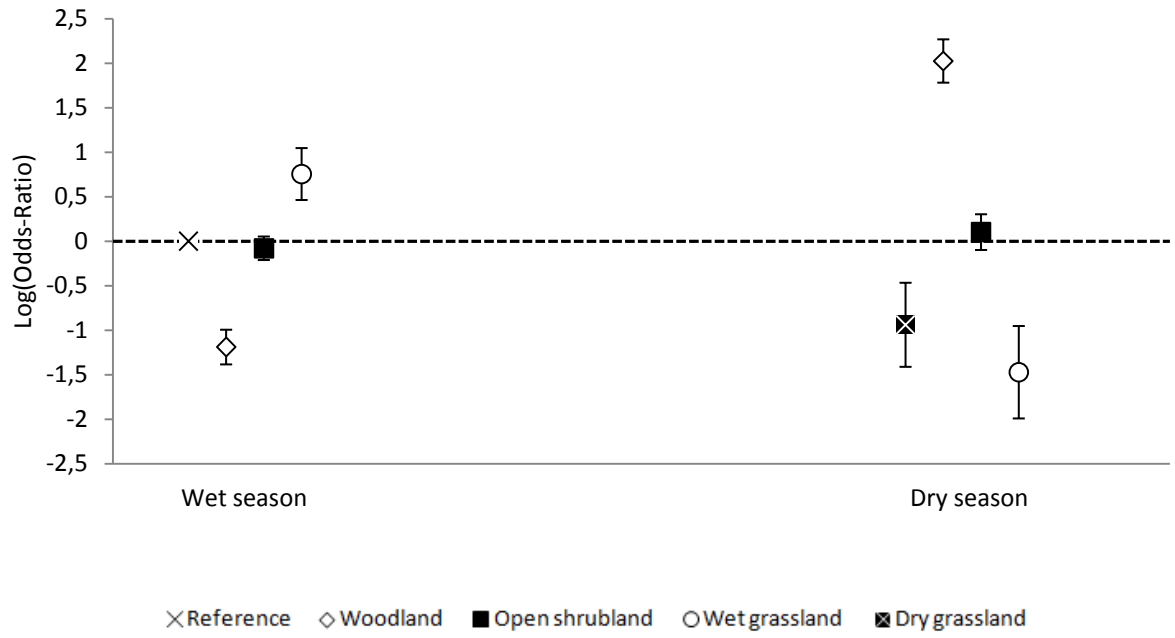


Fig. 13: Selection estimates for different vegetation-types at the landscape scale, based on the natural logarithms of odds-ratios derived from logistic regression models, for the interaction between vegetation-type and season. Estimates refer to both eland SAT1399 and SAT1398 in the Kgaswane Mountain Reserve, over the wet and dry seasons of the two years of the study. The reference category is dry grassland during the wet season. Log(Odds-ratios) are presented with their respective 95% Confidence Intervals; intervals overlapping the reference are not selected over the reference itself, while higher or lower values are associated, respectively, to positive and negative selection in respect to the reference.

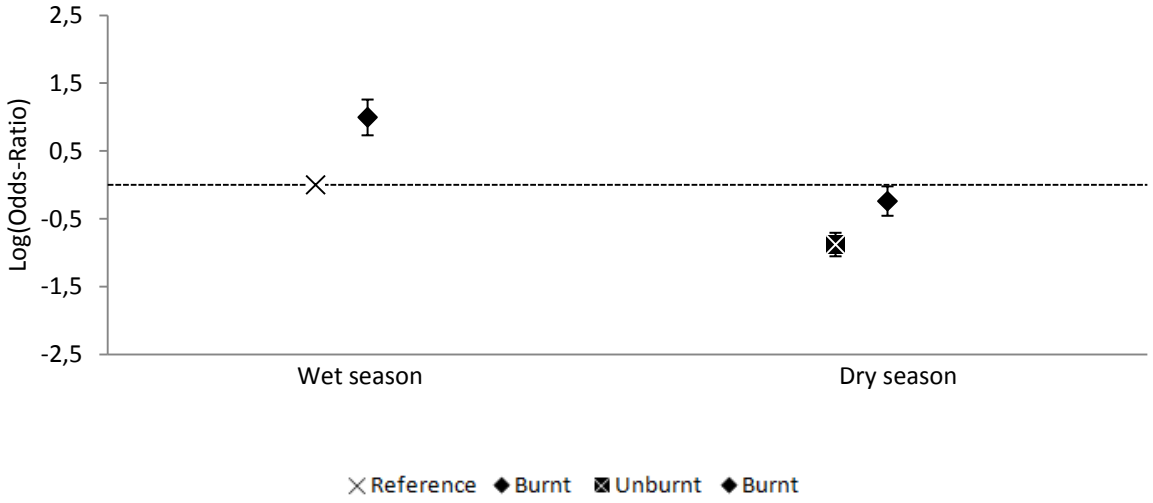


Fig. 14: Selection estimates for burnt and unburnt areas interacting with seasons at the landscape scale, based on the natural logarithms of odds-ratios derived from logistic regression models. Estimates refer to both eland SAT1399 and SAT1398 in the Kgaswane Mountain Reserve, over the wet and dry seasons of the two years of the study. The reference category is unburnt area during the wet season. Log(Odds-ratios) are presented with their respective 95% Confidence Intervals; intervals overlapping the reference are not selected over the reference itself, while higher or lower values are associated, respectively, to positive and negative selection in respect to the reference.

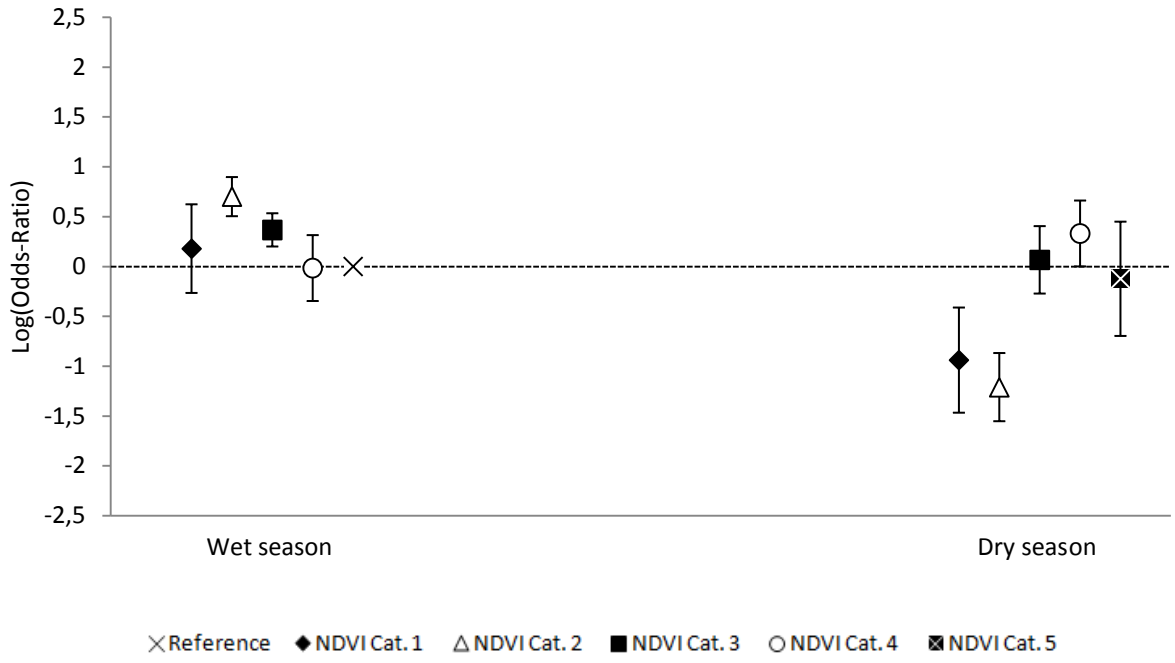


Fig. 15: Selection estimates for the five levels of NDVI according to season at the landscape scale, based on the natural logarithms of odds-ratios derived from logistic regression models. Estimates refer to both eland SAT1399 and SAT1398 in the Kgaswane Mountain Reserve, over the wet and dry seasons of the two years of the study. The reference category is NDVI level 5 on dry grassland. Log(Odds-ratios) are presented with their respective 95% Confidence Intervals; intervals overlapping the reference are not selected over the reference itself, while higher or lower values are associated, respectively, to positive and negative selection in respect to the reference.

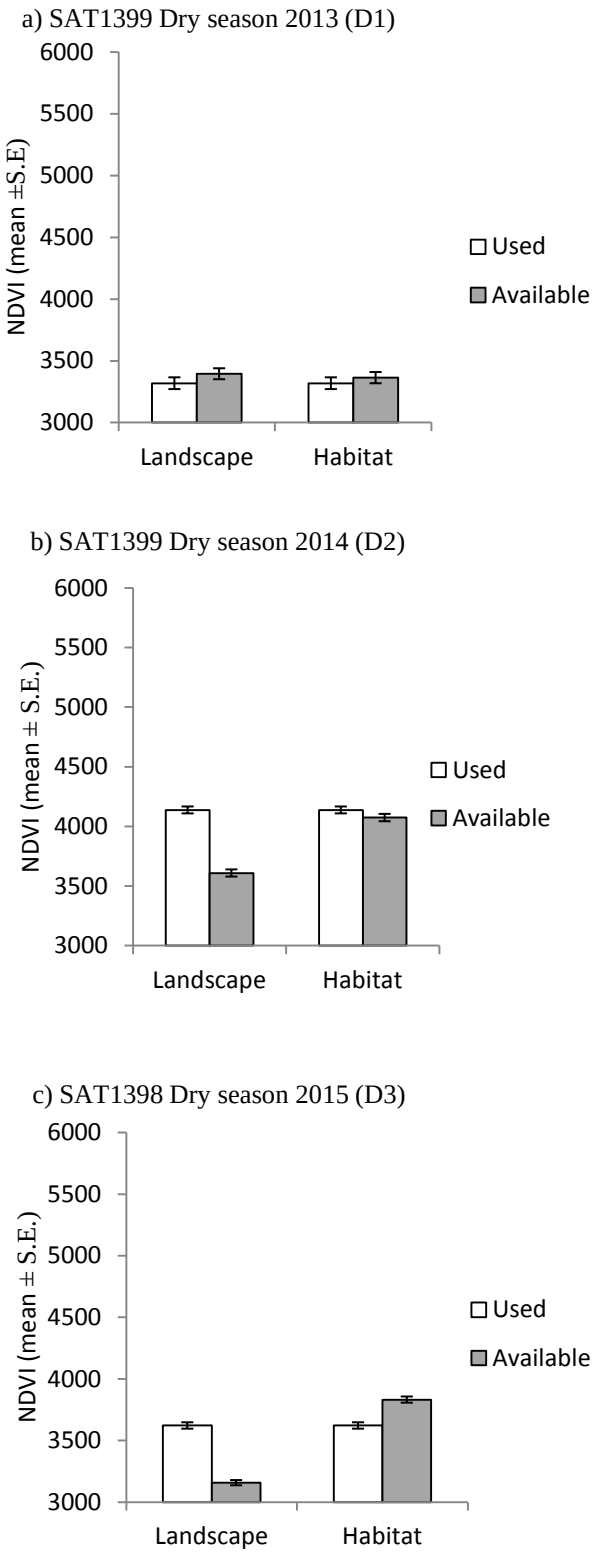
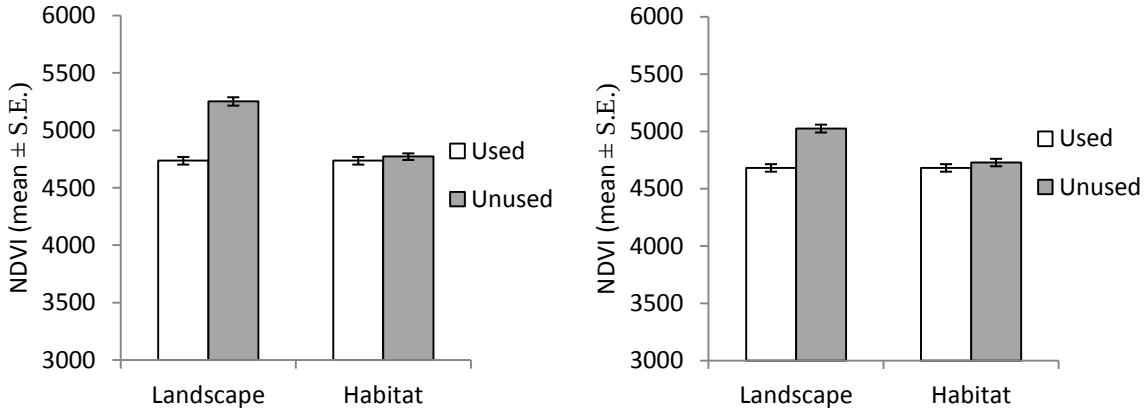


Fig. 16: Comparison of mean NDVI values (± Standard Errors) associated with used GPS locations and available scattered random points during all the dry seasons of the study period (D1, D2, and D3), at both landscape (seasonal home ranges vs total study area) and habitat (within seasonal home ranges) scales. Overlap between error bars indicates no significant difference between used and available locations. Data presented are derived from SAT1399 (a,b) and SAT1398 (c).

a) SAT1399 Wet season 2013-2014 (W1)

b) SAT1399 Wet season 2014-2015 (W2)



c) SAT1398 Wet season 2014-2015 (W2)

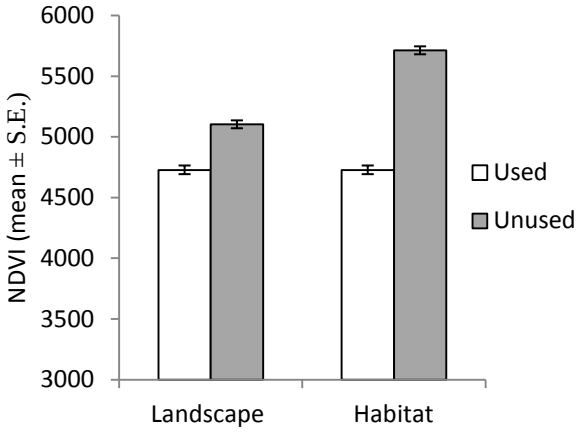


Fig. 17: Comparison of mean NDVI values (± Standard Errors) associated with used GPS locations and available scattered random points during all the wet seasons of the study period (D1, D2, and D3), at both landscape (seasonal home ranges vs total study area) and habitat (within seasonal home ranges) scales. Overlap between error bars indicates no significant difference between used and available locations. Data presented are derived from SAT1399 (a,b) and SAT1398 (c).

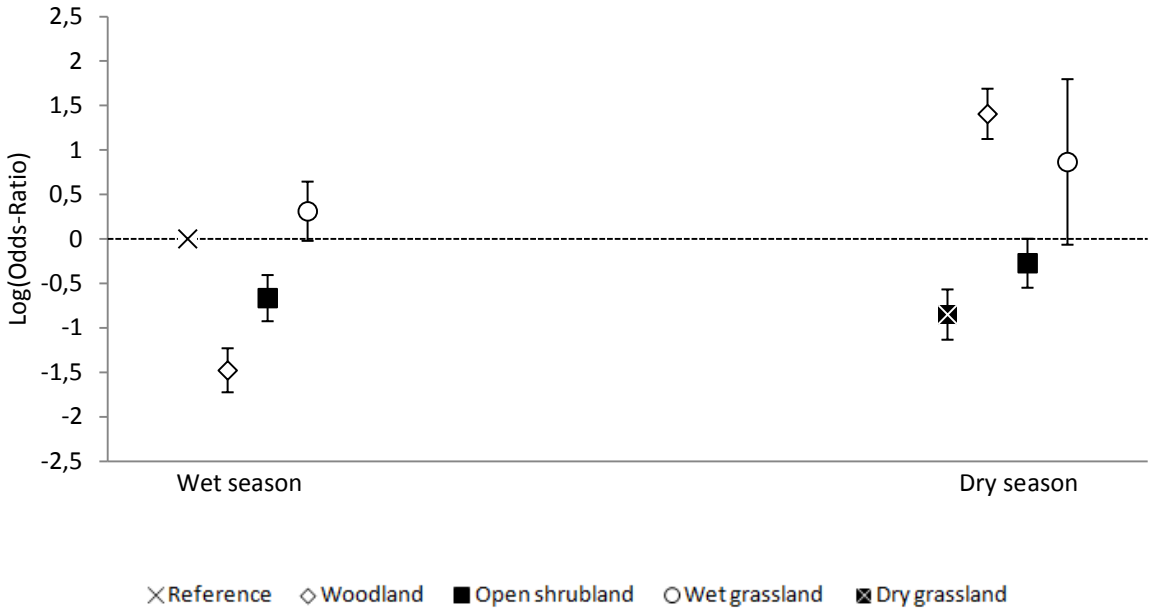


Fig. 18: Selection estimates for different vegetation-types at the habitat scale, based on the natural logarithms of odds-ratios derived from logistic regression models, for the interaction between vegetation-type and season. Estimates refer to both eland SAT1399 and SAT1398 in the Kgaswane Mountain Reserve, over the wet and dry Seasons of the two years of the study. The reference category is dry grassland during the wet season. Log(Odds-ratios) are presented with their respective 95% Confidence Intervals; intervals overlapping the reference are not selected over the reference itself, while higher or lower values are associated, respectively, to positive and negative selection in respect to the reference.

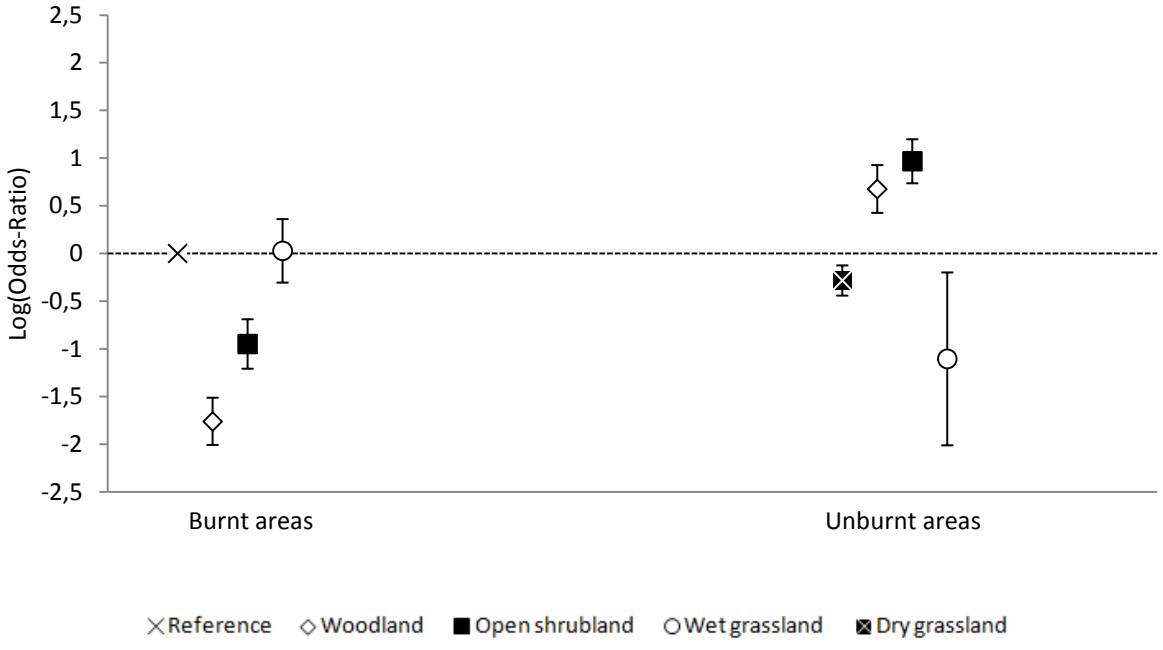


Fig. 19: Selection estimates for burnt and unburnt areas in their interaction with vegetation-types at the habitat scale, based on the natural logarithms of odds-ratios derived from logistic regression models. Estimates refer to both eland SAT1399 and SAT1398 in the Kgaswane Mountain Reserve. The reference category is unburnt dry grassland.

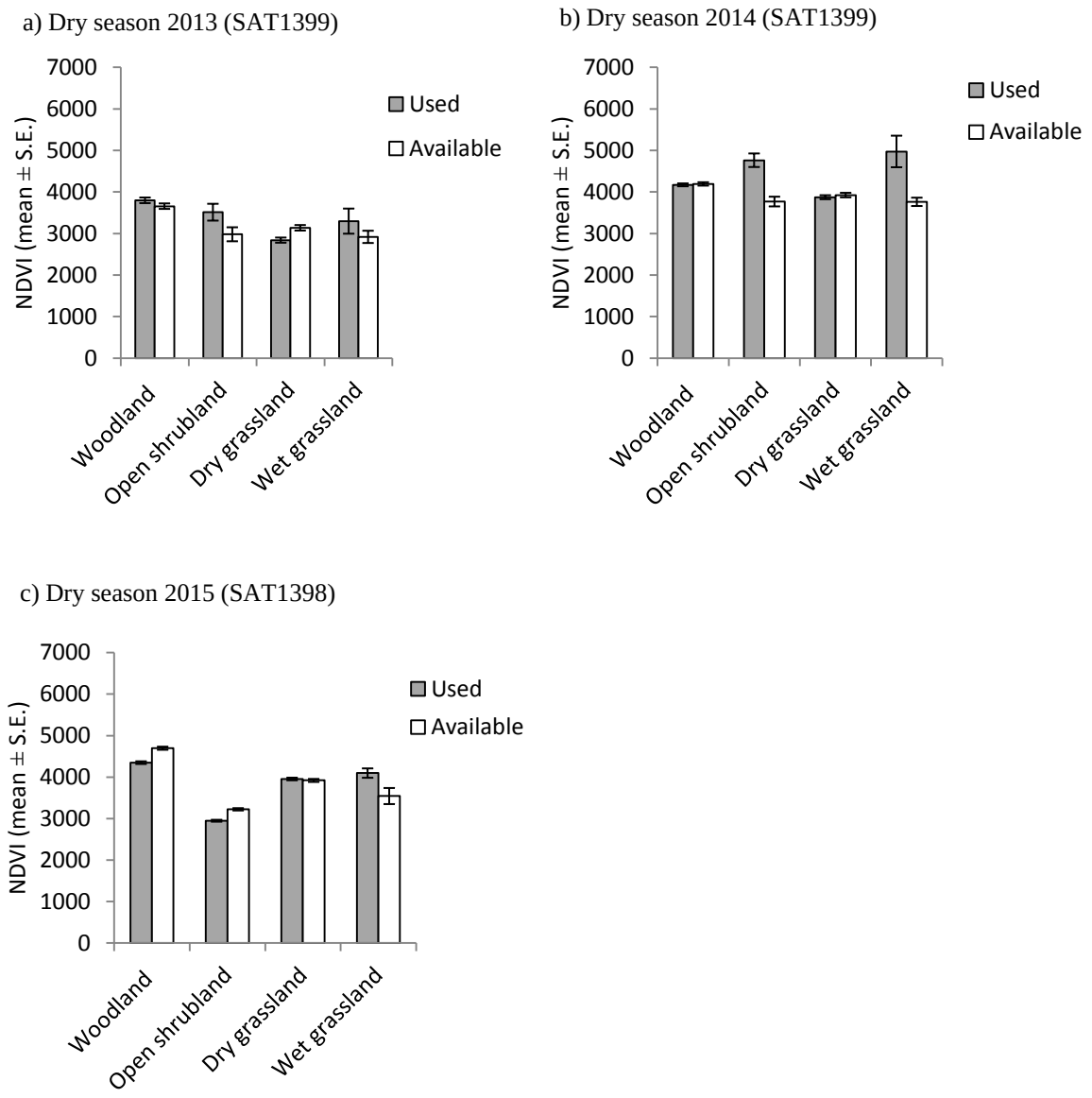


Fig. 20: Comparison of mean NDVI values (± Standard Errors) for each vegetation-type associated with used GPS locations and available scattered random points during all the dry seasons of the study period (D1, D2, and D3), at both landscape (seasonal home ranges vs total study area) and habitat (within seasonal home ranges) scales. Overlap between error bars indicates no significant difference between used and available locations. Data presented are derived from eland SAT1399 and SAT1398.

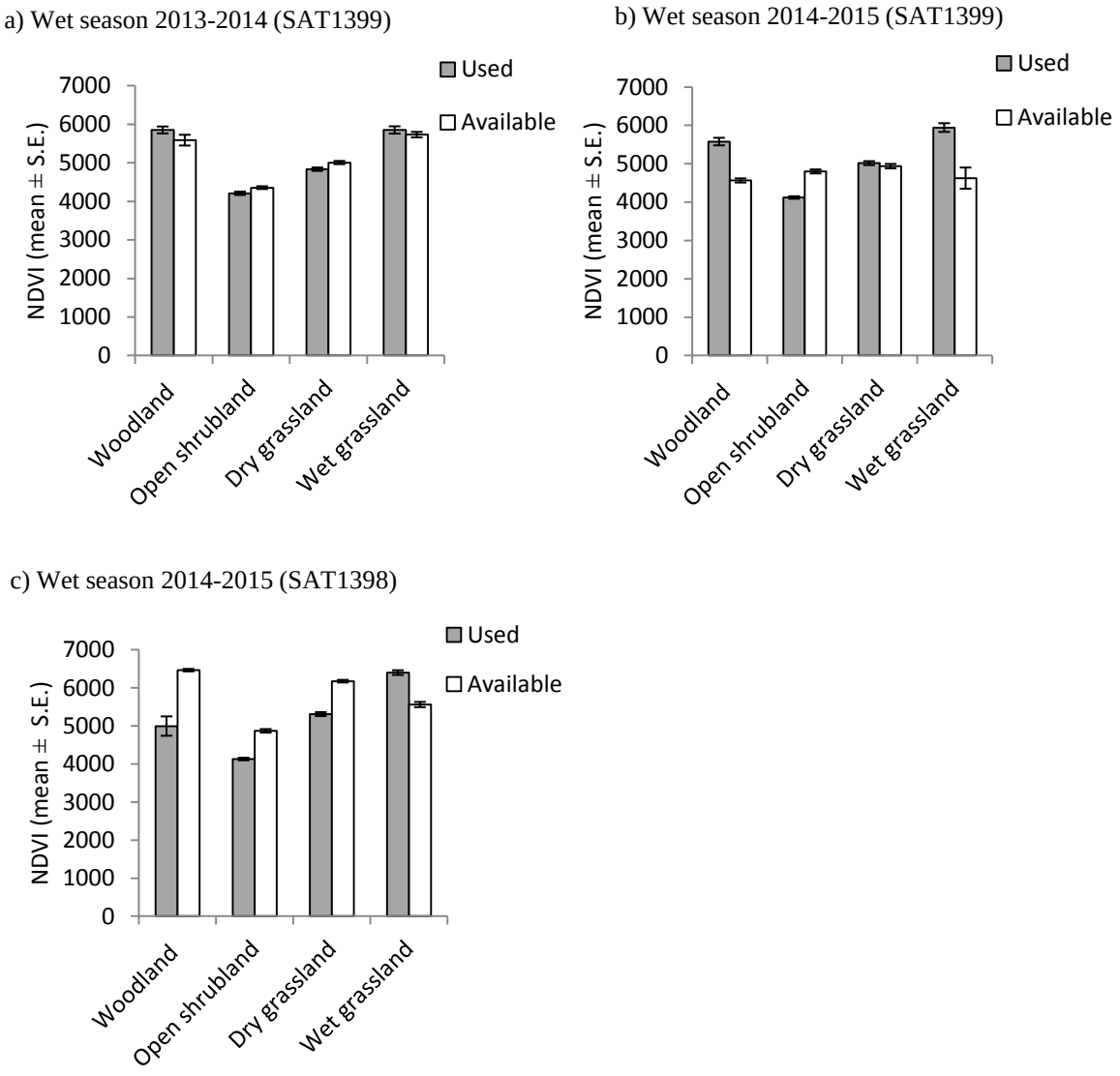


Fig. 21: Comparison of mean NDVI values (± Standard Errors) for each vegetation-type associated with used GPS locations and available scattered random points during all the wet seasons of the study period (W1 and W2), at both landscape (seasonal home ranges vs total study area) and habitat (within seasonal home ranges) scales. Overlap between error bars indicates no significant difference between used and available locations. Data presented are derived from eland SAT1399 and SAT1398.

REFERENCES

ALLISON, P. (2004). Convergence problems in logistic regression. In ALTMAN, M., GILL, J., & MCDONALD, M. P. *Numerical issues in statistical computing for the social scientist*, 238-252, John Wiley & Sons, Hoboken, USA.

ANDERSON, D. R. (2008). *Model based inference in the life sciences: a primer on evidence*. Springer Science & Business Media, New York, USA.

ANSELL, W. F. H. (1960). *Mammals of northern Rhodesia*. Rhodesian Department of Game and Fisheries, Lusaka, Zambia.

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

BOLGER, D. T., NEWMARK, W. D., MORRISON, T. A., & DOAK, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, **11**(1), 63-77.

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

BRO-JØRGENSEN, J. (1997). *The ecology and behaviour of the Giant Eland (Tragelaphus derbianus, Gray 1847) in the wild*. Masters Thesis, University of Copenhagen, Copenhagen, Denmark.

BRO-JØRGENSEN, J. (2008). Dense habitats selecting for small body size: a comparative study on bovids. *Oikos*, **117**(5), 729-737.

BURT, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of mammalogy*, **24**(3), 346-352.

BURNHAM, K. P., & ANDERSON, D. R. (2001). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife research*, **28**(2), 111-119.

BUYS, D. (1990) Food selection by eland in the western Transvaal. *South African Journal of Wildlife Research.* **20**, 16-20.

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**(1), 58-67.

CARRUTHERS, V. (2014). *The Magaliesberg*. Protea Book House Pretoria, Pretoria, South Africa.

CUSHMAN, S. A., CHASE, M., & GRIFFIN, C. (2005). Elephants in space and time.*Oikos*, **109**(2), 331-341.

D'AMMANDO, G., PARRINI, F., ATTORRE, F., & BOITANI, L. (2015). Observations on dry season grazing by eland in a Magaliesberg Nature Reserve, South Africa.*African Journal of Ecology*, **53**(1), 112-115.

DE SOLLA, D. E., SHANE, R., BONDURIANSKY, R., & BROOKS, R. J. (1999). Eliminating autocorrelation reduces biological relevance of home range estimates. *Journal of Animal Ecology*, **68**(2), 221-234.

DU TOIT, J. T., & OWEN-SMITH, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. *American Naturalist*, **133**(5), 736-740.

ESTES, R. D., ATWOOD, J. L., & ESTES, A. B. (2006). Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. *Biological Conservation*, **131**(1), 106-120.

EVANS, P. G. H. (1979). Habitat preferences of ungulates in closed savanna of central Africa. *Mammal Review*, **9**(1), 19-32.

FABRICIUS, C., & MENTIS, M. T. (1990) Seasonal habitat selection by eland in arid savanna in southern Africa. *South African Journal of Zoology* **25**(4), 238-244.

FIELD, C. R. (1975) Climate and the food habits of ungulates on Galana Ranch. *African Journal of Ecology*, **13**, 203-220.

FITZGIBBON, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour*, **39**(6), 1116-1126.

FRAME, G. W. (1980). Black rhinoceros (*Diceros bicornis* L.) sub-population on the Serengeti Plains, Tanzania. *African Journal of Ecology*, **18**(2-3), 155-166.

FRYXELL, J. M., GREEVER, J., & SINCLAIR, A. R. E. (1988). Why are migratory ungulates so abundant?. *American Naturalist*, **131**(6), 781-798.

GETZ, W. M., & WILMERS, C. C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*, **27**(4), 489-505.

GETZ, W. M., FORTMANN-ROE, S., CROSS, P. C., LYONS, A. J., RYAN, S. J., & WILMERS, C. C. (2007). LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS one*, **2**(2), e207.

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

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

HAMEL, S., & CÔTÉ, S. D. (2007). Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety?.*Canadian Journal of Zoology*, **85**(9), 933-943.

HEBBLEWHITE, M., MERRILL, E., & MCDERMID, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population.*Ecological monographs*, **78**(2), 141-166.

HENSMAN, M. C., OWEN-SMITH, N., PARRINI, F., & BONYONGO, C. M. (2014b). Home range occupation and habitat use of sable antelope in the Okavango Delta region of northern Botswana. *African journal of ecology*, **52**(2), 237-245.

HILLMAN, J. C. (1979). *The biology of the Eland (Taurotragus oryx) in the wild*. PhD Thesis, University of Nairobi, Nairobi, Kenya.

HILLMAN, J. C. (1987). Group size and association patterns of the common eland (*Tragelaphus oryx*). *Journal of Zoology*, **213**(4), 641-663.

HILLMAN, J. (1988). Home range and movement of the common eland (*Taurotragus oryx* Pallas 1766) in Kenya. *African Journal of Ecology*, **26**(2), 135-148.

HOLDO, R. M., HOLT, R. D., & FRYXELL, J. M. (2009). Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, **173**(4), 431-445.

JARMAN, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(3/4), 215-267.

JEWELL, P. A. (1966). The concept of home-range in mammals. *Symposium of the Zoological Society of London*, **18**, 85-109.

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

KELSO, D. L. (1986). *Resource Partitioning Between Browsing Ungulates: Kudu (Tragelaphus strepsiceros) and Eland (Taurotragus oryx) in Pilansberg National Park, Bophuthatswana*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa

LAMPREY, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika1. *African Journal of Ecology*, **1**(1), 63-92.

LYONS, A. J., TURNER, W. C., & GETZ, W. M. (2013). Home range plus: a space-time characterization of movement over real landscapes. *Movement Ecology*, **1**(1), 1-14.

LYONS, A.J. (2014). T-LoCoH for R: Tutorial and Users Guide. University of California, USA.

MANLY, B. F., MACDONALD, L. L., THOMAS, D. L., MCDONALD, T. L., & ERICKSON, W. P. (1993). *Resource selection by animals*. Chapman & Hall, London, UK.

MARSHAL, J. P., RAJAH, A., PARRINI, F., HENLEY, M., HENLEY, S. R., & ERASMUS, B. F. (2011). Scale-dependent selection of greenness by African elephants in the Kruger-private reserve transboundary region, South Africa. *European Journal of Wildlife Research*, **57**(3), 537-548.

MCNAUGHTON, S. J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological monographs*, **55**(3), 259-294.

MCNAUGHTON, S. J. (1986). Grazing lawns: on domesticated and wild grazers. *The American Naturalist*, **128**(6), 937-939.

MDUMA, S. A., & SINCLAIR, A. R. E. (1994). The function of habitat selection by oribi in Serengeti, Tanzania. *African Journal of Ecology*, **32**(1), 16-

MOE, S. R., WEGGE, P., & KAPELA, E. B. (1990). The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. *African journal of Ecology*, **28**(1), 35-43.

MORRISON, M. L. (2001). A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *The Journal of wildlife management*, **65**(4), 613-623.

MORRISON, T. A., & BOLGER, D. T. (2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*, **81**(3), 543-552.

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

NAIDOO, R., DU PREEZ, P., STUART-HILL, G., JAGO, M., & WEGMANN, M. (2012). Home on the range: factors explaining partial migration of African buffalo in a tropical environment. *PLoS One*, **7**(5), e36527.

NEL, H. P. (2000). *Ecological management objectives and monitoring procedures for Rustenburg Nature Reserve, North West Province* . MSc Thesis, University of Pretoria, Pretoria, South Africa.

NILSEN, E. B., PEDERSEN, S., & LINNELL, J. D. (2008). Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions?.*Ecological Research*, **23**(3), 635-639.

NOVELLIE, P. A. (1978). Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. *South African Journal of Wildlife Research*, **8**(4), 137-144.

NYENGERA, R., & SEBATA, A. (2010). Effect of eland density and foraging on *Combretum apiculatum* physiognomy in a semi-arid savannah. *African Journal of Ecology*, **48**(1), 45-50.

OGUTU, J. O., & OWEN-SMITH, N. (2005). Oscillations in large mammal populations: are they related to predation or rainfall?. *African Journal of Ecology*, **43**(4), 332-339.

OGUTU, J. O., OWEN-SMITH, N., PIEPHO, H. P., SAID, M. Y., KIFUGO, S., REID, R. S., & ANDANJE, S. (2013). Changing wildlife populations in Nairobi National Park and adjoining Athi-Kaputiei Plains: collapse of the migratory wildebeest. *Open Conservation Biology Journal*, **7**, 11-26.

O'KANE, C. A., DUFFY, K. J., PAGE, B. R., & MACDONALD, D. W. (2011a). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, **27**(3), 249-258.

OWEN-SMITH, N. (1977). On territoriality in ungulates and an evolutionary model. *Quarterly Review of Biology*, **52**(1),1-38.

OWEN-SMITH, N. (1979). Assessing the foraging efficiency of a large herbivore, the kudu. *South African Journal of Wildlife Research*, **9**(3/4), 102-110.

OWEN-SMITH, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, UK.

OWEN-SMITH, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. Cambridge University Press, UK.

OWEN-SMITH, N. (2002). *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge University Press, UK.

OWEN-SMITH, N. (2014), Spatial ecology of large herbivore populations. Ecography, **37** (5), 416–430.

OWEN-SMITH, N., & CAIN, J. W. (2007). Indicators of adaptive responses in home range utilization and movement patterns by a large mammalian herbivore. *Israel Journal of Ecology & Evolution*, **53**(3/4), 423-438.

OWEN-SMITH, N., & COOPER, S. M. (1987a). Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, **68**(2), 319-331.

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*, **365**(1550), 2267-2278.

OWEN-SMITH, N., & OGUTU, J. O. (2013). Controls over reproductive phenology among ungulates: allometry and tropical-temperate contrasts. *Ecography*,**36**(3), 256-263.

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

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

PELLEW, R. A. (1983). The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse. *African Journal of Ecology*, **21**(4), 241-267.

PELLEW, R. A. (1984). Food consumption and energy budgets of the giraffe. *Journal of Applied Ecology*, **21**(1), 141-159.

PENG, C. Y. J., LEE, K. L., & INGERSOLL, G. M. (2002). An introduction to logistic regression analysis and reporting. *The Journal of Educational Research*, **96**(1), 3-14.

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**(9), 503-510.

PETTORELLI, N., BRO-JØRGENSEN, J., DURANT, S. M., BLACKBURN, T., & CARBONE, C. (2009). Energy availability and density estimates in African ungulates. *The American Naturalist*, **173**(5), 698-704.

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.

PYKE, G. H. (1984). Optimal foraging theory: a critical review. *Annual review of ecology and systematics*, **15**, 523-575.

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

ROUSE JR, J., HAAS, R. H., SCHELL, J. A., & DEERING, D. W. (1974). Monitoring vegetation systems in the Great Plains with ERTS. *NASA special publication*, **351**, 309.

ROWE-ROWE, D. T. (1982). Influence of fire on antelope distribution and abundance in the Natal Drakensberg. *South African Journal of Wildlife Research*, **12**(4), 124-129.

ROWE-ROWE, D. T. (1983). Habitat preferences of five Drakensberg antelopes. *South African Journal of Wildlife Research*, **13**(1), 1-8.

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**(3), 764-776.

SCOONES, I. (1995). Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments*, **29**(2), 221-237.

SCOTCHER, J. S. B. (1983). *Interrelations of vegetation and eland (Taurotragus oryx Pallas) in Giant's Castle Game Reserve, Natal*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

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**(11), 789-795.

SENSENIG, R. L., DEMMENT, M. W., & LACA, E. A. (2010). Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology*, **91**(10), 2898-2907.

SHEPPE, W., & OSBORNE, T. (1971). Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs*, **41**(3), 179-205.

SHRADER, A. M., OWEN-SMITH, N., & OGUTU, J. O. (2006). How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Functional ecology*, **20**(2), 376-384.

SINCLAIR, A. R. E. (1977). *The African buffalo: a study of resource limitation of populations*. University of Chicago Press, Chicago, USA.

SINCLAIR, A. R. E., & ARCESE, P. (1995). *Serengeti II: dynamics, management, and conservation of an ecosystem* (Vol. 2). University of Chicago Press.

STEPHENS, D. W., & KREBS, J. R. (1986). *Foraging theory*. Princeton University Press.

THOULESS, C. (2014). *Tragelaphus oryx* Common Eland. In Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. *Mammals of Africa, Volume VI* (186-193), A & C Black, UK.

UNDERWOOD, R. (1975). Social behaviour of the eland (*Taurotragus oryx*) on Loskop Dam Nature Reserve. MSc Thesis, University of Pretoria, Pretoria, South Africa.

VALEIX, M., FRITZ, H., SABATIER, R., MURINDAGOMO, F., CUMMING, D., & DUNCAN, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, **144**(2), 902-912.

VALEIX, M., LOVERIDGE, A. J., CHAMAILLÉ-JAMMES, S., DAVIDSON, Z., MURINDAGOMO, F., FRITZ, H., & MACDONALD, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**(1), 23-30.

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**(4), 771-785.

VAN DER MERWE, J., & MARSHAL, J. P. (2012). Hierarchical resource selection by impala in a savanna environment. *Austral Ecology*, **37**(3), 401-412.

VAN WYK, B. V., & VAN WYK, B. E. (2002). *Photographic guide to trees of Southern Africa*. Briza Publications, Pretoria, South Africa.

VERLINDEN, A. (1998). Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, **36**(2), 117-128.

WANG, Q., ADIKU, S., TENHUNEN, J., & GRANIER, A. (2005). On the relationship of NDVI with leaf area index in a deciduous forest site. *Remote sensing of environment*, **94**(2), 244-255.

WATSON, L. H., & OWEN-SMITH, N. (2000). Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, **38**(2), 130-137.

WESTERN, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, **13**(3/4), 265-286.

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

WIENS, J. A. (1989). Spatial scaling in ecology. *Functional ecology*, **3**(4), 385-397.

WILSEY, B. J. (1996). Variation in use of green flushes following burns among African ungulate species: the importance of body size. *African Journal of Ecology*, **34**(1), 32-38.

WILSON, V. J. (1969). Eland, *Taurotragus oryx*, in eastern Zambia. *Arnoldia (Rhodesia)*, **4**(12), 1-9.

WINNIE JR, J. A., CROSS, P., & GETZ, W. (2008). Habitat quality and heterogeneity influence distribution and behavior in African buffalo (Syncerus caffer). *Ecology*, **89**(5), 1457-1468.

WITTEMYER, G., GETZ, W. M., VOLLRATH, F., & DOUGLAS-HAMILTON, I. (2007). Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behavior. *Behavioral Ecology and Sociobiology*, **61**(12), 1919-1931.

YOGANAND, K., & OWEN-SMITH, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, **37**(10), 969-982.

ZUUR, A. F., IENO, E. N., WALKER, N. J., SAVELIEV, A. A., & SMITH, G. M. (2009). Mixed effects modelling for nested data. In *Mixed effects models and extensions in ecology with R* 101-142). Springer New York, New York, USA.

CHAPTER 3: SEASONAL USE OF FEEDING SITES AND PLANT SPECIES SELECTION BY ELAND IN THE KGASWANE MOUNTAIN RESERVE

INTRODUCTION

The structural and compositional variety of monocotyledonous (monocots) and dicotyledonous (dicots) plant species found in African savannahs offer a diversity of food, ranging from single plant parts to vegetation communities, to large mammalian herbivores, which is at the basis of the diversity and coexistence of an extremely diversified herbivore guild in tropical savannahs (Shorrocks, 2007; Kartzinel *et al.,* 2015). Within this variety of Bovid species, single taxa are usually classified, according to the morpho-physiological characteristics of their digestive system, into three feeding types, namely browsers, grazers, and intermediate or mixed feeders (herbivores which can subsist both on grasses and dycots; Hofmann, 1989). Browsers are limited in their utilisation of grasses by the high proportions of structural fibre typical of grass leaves and stems, but young, green grass tufts do present higher protein:fibre ratio than browse during the early phase of the growing season, with new sprout of green leaves usually prompted by rainfall or fires (Field, 1975; Owen-Smith, 1997). By contrast, dicots maintain high (albeit lowered in respect to the wetter months) protein levels during the dry season (Owen-Smith, 1997), and are therefore targeted as a preferred food source by mixed feeders during the dry, limiting period (Owen-Smith, 1997), despite containing tannins, alkaloids, and other toxic or indigestible secondary metabolites (Bryant *et al.* 1991). African herbivores are therefore distributed along a browser-grazer continuum, which ensures dietary niche separation in relation to feeding preferences and physical characteristics (McNaughton & Georgiadis, 1986; Owen-Smith, 2008). Additionally, the Jarman-Bell principle states that herbivores of large body-size will feed on coarser forage than smaller species (Bell, 1970, 1971; Jarman, 1974). However, small browsers like dik dik (*Madoqua guentherii*) do include small proportions of grass and other low-quality foods in their diet (Kartzinel *et al.,* 2015), while large species, such as elephant (*Loxodonta africana*), can show patterns of selectivity for the plant parts consumed (Owen-Smith & Chafota, 2012).

Forage selection is a hierarchical process, which implies a range of feeding choices at spatial and temporal scales, over different levels of resource availability, dispersion, and distribution (Senft *et al.,* 1987; Bailey *et al.,* 1996). Thereof, resource selection according to varying body

size and nutritional-energetic requirements has been largely resolved with differential selectivity at the plant parts scale (Jarman, 1974; Owen-Smith & Chafota, 2012). However, differences in microhabitat use at the level of feeding site can result in fine-scale spatial and temporal partitioning between similar-sized species, and are therefore important drivers of resource use and selection (Cromsigt & Olff, 2006; Owen-Smith, Martin & Yoganand, 2015), thus underlining the importance of the often overlooked selectivity at a coarser scale than the single species or plant part.

The distribution of herbivores species is mainly constrained by the availability of landscapes presenting high forage productivity and biomass (Fernàndez & Vrba, 2005). At the habitat scale, herbivores of small body size are usually described as specialists, while large-bodied species inhabit a wide variety of habitat-types (Du Toit & Owen-Smith, 1989). Browsing ruminants are of general smaller size than grazers, and usually inhabit densely wooded areas where woody browse is abundant (Du Toit & Owen-Smith, 1989; Hofmann, 1989). By contrast, some species of small body size (i.e. steenbok *Raphicerus campestris* and Grant's gazelle *Nanger granti*) are adapted to subsist on the spatially and temporally unpredictable herbaceous and low-lying browse of open savannah and grassland (Kingdon, 1982; Du Toit, 1986).

Phylogenetic constraints, in addition to morphology, physiology, and size of the digestive system, should also be considered when evaluating the habitat and dietary preferences of an ungulate (Brashares, Garland & Arcese, 2000). Members of the tribe Tragelaphini are usually classified as "browsers", but most species will include various proportions of grasses in their diet (Hillman, 1986; Gagnon & Chew, 2000; Apio & Wronski, 2005). Among them, the common eland (*Tragelaphus oryx*) has been described, by various authors, either as a selective or unselective herbivore, at different scales of foraging (Lamprey, 1963; Watson & Owen-Smith, 2000). Albeit expected to be roughage eaters and habitat generalists, due to their imposing body size (Jarman, 1974) and to their wide geographic distribution (Kingdon, 1982), eland have been observed to be rather selective at the plant species scale, usually targeting the greenest available food items at different times of the seasonal cycle (Kerr, Wilson & Roth, 1970; Field, 1975; Buys, 1990; D'Ammando *et al.*, 2015). The proportions of grasses versus browse components of the diet in particular have been questioned by different studies. Although eland possess a browser-like gut and a small rumen:body size ratio

(Hofmann, 1973, 1989), grasses (which are usually of lower protein content than dicots), were found as the primary food source during the growing season and on flushing burnt grassland both in East (Lamprey, 1963; Hillman, 1979) and southern Africa (Scotcher, 1983; Buys, 1990). In the study area selected for the present study, a small provincial reserve in the North-West Province of South Africa, grasses were also accepted during the dry season, provided that they offered a sufficient yield of green leaves (D'Ammando *et al.,* 2015).

Eland are nomadic-migratory herbivores, which tend to move over vast areas in order to track the flush of high quality grasses or browse in sufficient biomass to sustain their high absolute metabolic requirements (Hillman, 1988; Thouless, 2014). However, expanding human population of southern Africa, coupled with the increased fragmentation of natural landscapes due to the development of fences, roads, and other anthropogenic infrastructures, has now largely prevented the occurrence of large scale movements, thus effectively confining large herbivores within the borders of protected areas (Fynn & Bonyongo, 2011; Beale *et al.,* 2013). About 30% of the total wild eland population is now restricted to small, fenced reserves in southern Africa (Thouless, 2014), but their use of available resource within these insular-like areas, and its effects on the long term survival of these populations, remain unknown. The study presented in this chapter was aimed at identifying drivers of forage selection by eland the Kgaswane Mountain Reserve (KMR) of the North-West Province (South Africa), in order to determine the resource requirements of this species and to provide information for the management of this fenced-in population. The importance of controlled burning was also accounted for, as it was revealed to offer key resources for other herbivores in the same study area over limiting periods (Parrini & Owen-Smith, 2010). I focused on determining the relative importance of grasses and browse in the seasonal diet, particularly during the limiting mid-dry season, and during the transition between the wet and the early dry season (when the grazing/browsing switch is expected to occur) in order to understand the influence of grass and browse quality on selectivity and to determine foraging requirements of eland.

The main study objectives were:

1) To determine the differential use of vegetation types and burns for foraging purposes during two different seasons (namely the wet-early dry transition in March-April 2015; and the dry season in July-August 2015).
2) To determine the phenological characteristics of forage influencing selectivity at the plant species scale, causing the seasonal dietary switch from grazing to browsing;.

A posteriori, I also compared our results with those obtained during the mid-dry season of 2013 (D'Ammando *et al.,* 2015), as a mean to understand the effect of the 2015 drought on small-scale changes in plant phenology and forage selection during the dry months of the year.

For what concerns the use of feeding sites, I expected that:

a) Eland would mostly feed in woodland and open shrubland over the entire study period (which took place during relatively dry months), but would proportionally make more use of open vegetation types (dry and wet grassland) with low canopy cover during the wet-early dry transition, when green grass and herbage is still available, as compared to the dry season, when they would stick to remaining patches of green browse.
b) I expected burns to be utilised for foraging by eland in both seasons, as sprouting green grasses would be available as a high-quality food resource after dry season fires, amidst the "brown" vegetation matrix.

At the plant species scale, I expected that:

a) Eland would select for the greenest available woody browse during both seasons, but evergreen species and those retaining green foliage during the dry season would be more accepted during the dry season than during the wet-early dry transition.
b) In both seasons, green grasses would be moderately to highly accepted by eland, with highest acceptance on burnt areas, as grasses would be greener on burns than in other areas. Eland would also highly accept herbaceous forbs throughout the year, forming a large part of the diet during the wet-early dry transition, at their peak greenness period.

MATERIALS AND METHODS

Study design

In KMR, observations of eland at close quarters were not possible due to the shy and secretive nature of the study population, prompting me to design a study on forage selection based on feeding site surveys (Litvaitis, 2000). However, I conducted long-distance observations (generally from a vantage point located at 30-200 m from the focal animals), in order to individuate the exact position of a feeding site, and to determine the herd size and age/sex structure (determined according to Hillman, 1979; for details on ageing and sexing of eland, see Appendix II) and the presence of other herbivores which could cause substantial biases in the evaluation of feeding sites usage. Social groups containing various age and sex classes plus calves and yearlings were classified as "nursery herds", while I lumped all other groups constituted by adult and subadult of both sexes as "mixed herds", following recommendations by Underwood (1975) and Hillman (1979). Care was taken in order to minimize the human disturbance to the daily activities of the animals. Foraging eland (both herds and single individuals) and respective feeding sites were observed in the field following two alternative and complementary procedures:

a) **Radio-tracking of collared individuals**: four adult females, in different herds at the time of capture, were fitted with GPS Iridium satellite collars, with VHF transmitting beacons, in September 2014. Collars were manufactured by Africa Wildlife Tracking (www.awt.co.za; AWT), and captures were performed by a qualified veterinarian hired by the North West Parks and Tourism Board, following the standard procedure for large ungulates. The GPS transmitting units in the collars recorded the hourly location of the animals, while the VHF beacons allowed for radio-tracking on the ground. Each individual was tracked at least once a week (until collars failure) using a H-type directional antenna and a receiver. One collar failed in March 2015, while two other individuals experienced fatalities, respectively due to tick infestation (March, 2015), and unknown causes (possibly old age or malnutrition; June, 2015).

b) **Scanning from vantage points**: I searched for foraging herds and individuals of eland from natural vantage points, with the aid of a pair of NIKON Monarch 8x42 binoculars. This second procedure, although less reliable than radio-tracking, was alternated daily with

observations on collared individuals during the transition period in order to get a population-level inference for plant species and feeding site selection, otherwise restricted to the records for individuals associated with the tagged adult females. This methodology became a necessity when collared animals ventured into areas inaccessible to the observer (including deep river gorges and stream lines or privately owned game farms bordering KMR), and after collar failures. Data on feeding site and plant species selection obtained from the two procedures were believed to be comparable, since the visibility bias related to the observation of non-collared animals was largely resolved by directly observing collared animals during foraging activities. Herds or individuals included in our observations will be referred to, from now onwards, as "focal herds" or "focal individuals".

Eland in KMR were mostly active during early-mid morning (06:30-11:30), and late afternoon (15:30-18:30), in both seasons. Thus, observation sessions were concentrated during these two periods of the day. Field work was conducted in March-April 2015 and July-August 2015. In Chapter 2, I considered April as part of a "transition period" between the wet and the dry season, while March was ascribed to the wet season (Appendix I). However,due to the small sample size, data from March and April were lumped together in the present chapter, thus constituting a period that I referred to as "wet-early dry transition". Data collected during July and August fell within the dry season (as defined in Chapter 2), but only covered a fraction of this period, which was referred to as the "mid-dry season".

Data collection

Characteristics of feeding sites

A feeding site was defined as the 20 m-radius area where a herd or single individual had spent at least five minutes foraging (van der Merwe & Marshal, 2012). A site was centred around the location at which the majority of the individuals in a herd had been seen foraging; its exact location was then confirmed by looking at conspicuous fresh bite signs on grasses or dicots while visiting the area on foot (van der Merwe & Marshal, 2012; Hensman *et al.*, 2014a). Feeding sites for the same focal herd were considered as independent when the entire herd clearly started a period of resting and/or ruminating of no less than three hours between two foraging bouts. Feeding sites for different herds were considered as independent samples; individuals were considered as in different herds when they where ~ 500 m apart and in a

social association presenting a clearly different age-sex structure from the one previously sampled during the same observation session. When individuals of other herbivore species were foraging in the immediate proximity of the focal herd, or when fresh hoof prints and/or fresh dung pellets of species other than eland were recorded at the focal herd location, the site was discarded, in order to avoid potential biases associated with including the bites of other ungulates in the dataset. Each feeding site was assigned to one of the four vegetation types: a) woodland; b) open shrubland; c) dry grassland; and d) wet grassland. Canopy cover of large trees at feeding sites was ranked as: no large trees; 1-25%; >25%. Sites were also classified according to their position in the soil catena: a) bottomland; b) footslope; c) midslope; d) topslope; e) upland. I additionally described feeding sites according to their burnt status: a) "green burns" (areas with clear signs of burning and presenting a green flush of herbaceous vegetation); b) "recent burns" (burnt areas where a green flush is not yet established); c) "unburnt sites".

Characteristics of plant species

Fresh bite signs on plants were identified by their bright colour and lack of dried rims (Macandza, 2009; van der Merwe, 2010). A 1 m x 1 m quadrat was placed on the first evidence of a fresh bite sign, and extended up to 2.5 m in height, encompassing the range of potential browse within reach of an adult eland (Underwood, 1975). Each quadrat represented therefore a feeding station, as the area accessible to a large antelope without moving its front feet (Novellie, 1978). Two standardized and complementary protocols for data collection at feeding sites were used during our study (van der Merwe & Marshal, 2012):

a) A quadrat was placed on the first observed sign of grazing or browsing on a herbaceous species, or just below the first sign of browsing on a woody plant. Eight additional quadrats were then positioned around the first one, two along each main cardinal direction, at a distance of at least 3 m from each other. If fresh bite signs could not be identified, quadrats were allowed to flip along the two main diagonals (O'Shaughnessy, Cain & Owen-Smith, 2014).
b) Nine quadrats were placed at 3 m intervals along a feeding path, starting from the first observed sign of fresh browsing or grazing. If fresh bite signs could not be identified in a quadrat, the quadrat was allowed to flip by 1 m at a time along the path, until a fresh bite sign was present within it (Hensman *et al.*, 2014a).

The two sampling protocols were necessarily adopted in order to reflect, as accurately as possible, the plasticity in foraging behaviour of the eland, which tended to disperse over a large foraging area while grazing or browsing on forbs in open grassland, and to move in a single line along a feeding path when browsing in woodland.

All plants in each feeding station were identified to the species level. Plant species which could not be readily identified on the field were collected and dried, and later identified by comparison with KMR herbarium collections. A vast proportion of forbs could not be univocally assigned to a certain species, and was therefore assigned to two major categories: herbaceous forbs and woody forbs (forbs presenting woody stems). Similarly, sedges were grouped together in a single multi-species category. Plant species within a feeding station were scored as "eaten" (1), if presenting recent bite signs, or as "uneaten" (0). An inventory of plant species available within a feeding station was therefore believed to be a satisfactory index of local availability (Du Toit, 1986). Plants were categorized into the following forage types (Du Toit, 1986; Valeix *et al.*, 2011):

1) Grasses;
2) Herbaceous forbs;
3) Creepers;
4) Woody forbs and shrublets/dwarf shrubs;
5) Seedlings (woody species less than 30 cm. in height);
6) Shrubs (height between 30 cm. and 3 m.);
7) Trees (height > 3 m.).

Classification of woody plants into the woody forbs/shrublets/dwarf shrubs category was based on Gill (2012).

The number of bites on each plant species was recorded. A bite was considered as the area of a grass tuft, or of a cluster of branches or leaves, covered by the closed fist of the observer. The proportion of green versus brown leaves on plants ("greenness" from now onwards) and basal cover of each plant species within a feeding station were assigned to frequency intervals according to Walker's eight point visual scale (Walker, 1976):

1) 0%
2) 1-10%

3) 11-25%
4) 26-50%
5) 51-75%
6) 76-90%
7) 91-99%
8) 100%.

Statistical analyses

Feeding site selection

The proportion of feeding sites within each vegetation type and position in the soil catena was computed for each season as the number of sites recorded in a vegetation type/soil catena divided by the total number of sites recorded in that category. Seasonal differences in feeding site use were tested using a one-way χ^2 test of independence, with 95% confidence intervals and significance threshold at $p<0.05$ (Rao & Scott, 1981; Thomas & Taylor, 1990).

Seasonal dietary contribution

The seasonal dietary contribution of each plant species was calculated as the number of bites recorded for each plant species in each season divided by the total number of bites recorded across all the plant species in each season ("bite frequency" from now onwards; Hensman *et al.*, 2014a; O'Shaughnessy *et al.*, 2014). Only plant species recorded in ≥ 10 feeding sites in at least one season were considered for calculations. Dietary contribution was assessed independently for grass and browse species (comprising forbs and woody plants), thus producing estimates for the "seasonal grass diet" and the "seasonal browse diet". Since the removal of plant edible biomass through biting is somewhat different between grass tufts and dicots (Watson & Owen-Smith, 2000), the comparison of the number of bites recorded on grasses and browse will be considered as a mere index of dietary composition, without a real quantitative value in assessing the contribution of grazing versus browsing. Differences in dietary contribution of plant species between the two seasons were tested using a one-way χ^2 test of independence with a significance threshold of $p<0.05$ and binomial confidence intervals. The contribution of each forage type to the total "browse diet" was additionally computed by dividing the number of bites recorded for each type in each season by the total number of bites recorded on for that feeding-type in that same season. Although not

representing an accurate estimate of seasonal contribution of dicot versus monocot species as for the reasons explained above, an index of total dietary contribution for the browse and grass species combined was also calculated for each season and for the annual diet. The contribution by feeding type was also calculated for green burns versus unburnt sites, in order to identify potential dietary changes related to the burning regime.

Site-based availability and acceptance

Site-based availability and frequency of acceptance for each plant species were calculated *sensu* Owen-Smith & Cooper (1987b). Only plant species present in ≥ 10 feeding sites in at least one season were considered for computations of these indexes. Total seasonal availability was calculated as the number of feeding stations in which a plant species is present, divided by the total number of feeding stations. Additionally, I calculated vegetation-type-specific availability as the number of feeding stations in a given vegetation type in which a species is present, divided by the total number of stations in that vegetation type (Hensman *et al.,* 2014a). Vegetation-type-specific availability was calculated by lumping together data from the two seasons (because of the otherwise too small sample size to allow for calculations if division by seasons was maintained), for plant species present in ≥ 10 feeding sites in at least one vegetation-type. Although vegetation-specific availability did not constitute a real estimate of plant species availability over the total spatial extent of a vegetation-type, it still represented a meaningful index to compare plant species availability within the patches selected as feeding sites by eland.

Site-based frequency of acceptance was calculated as the number of feeding stations in which a plant species had been recorded as eaten, divided by the total number of plots in which it had been recorded as present (Owen-Smith & Cooper, 1987b). Owen-Smith & Cooper (1987b) defined site-based acceptance as the proportion of 10 m radius areas in which a kudu had been observed foraging on a certain plant species divided by the total number of areas in which that species had been observed as present. As I was interested in determining the criteria of selectivity at the plant species scale, I considered the feeding stations as our units for frequency calculations, and independent from each other. Acceptance therefore varies between 0 and 1, with species close to 0 regarded as generally discarded, and species approaching a value of 1 (and thus readily eaten at most of the feeding stations) representing the favoured food resources. Frequencies of availability and acceptance were compared across

species using a one-way χ^2 test of independence (significant p-value= 0.05). I computed mean seasonal greenness of all plant species, using the midpoint of each frequency interval for calculations. All statistical analyses were performed in R 3.2.2.

Plant species selection models

In order to establish which phenological characteristics influenced plant species selection, binary logistic regression models with mixed effects were tested using multi-model inference (Burnham & Anderson, 2001; Anderson, 2008). As grasses were seldom consumed during the dry season, I ran models only for dicot species. The binary response variable was constituted by eaten (1) or uneaten (0) plant species within feeding stations, considered as the presence/absence values required by logistic regression assumptions (Peng, Lee & Ingersoll, 2002). The fixed effects explanatory variables were all categorical and included: a) plant species; b) greenness; c) basal cover; d) season (wet-early dry or mid-dry). Biologically meaningful interactions between these variables were also tested. In order to avoid false convergence errors due to small number of records for each greenness category (Allison, 2004), I lumped the eight greenness intervals of the Walker's scale into three classes: 1) < 25% 2) 25%-75%; 3) > 75%. Similarly, I re-classified the basal cover of each species as either less or more than 10% (two classes) of a feeding station. Several plant species ascribed to the same genus were lumped together in the same category, if forage quality and general biological features were similar enough (according to van Wyk & van Wyk, 2002) to justify this procedure. However, I ensured that those species forming the bulk of the seasonal diets were included as single entities. Woody plants which occurred in ≤10 feeding sites in both seasons were grouped together as "other trees/shurbs" or "other woody forbs/shrublets" (according to their foraging type) and subsequently included in the logistic regression analysis. Feeding station nested within feeding site was included as a random effect in order to account for the effective presence of a given plant species at a certain feeding station and site (van der Merwe & Marshal, 2012). A set of candidate models was therefore produced in the lme4 package in R 3.2.2. Models were selected on the basis of their Akaike's Information Criterion (AIC), corrected for small sample size (AICc; Burnham & Anderson, 2001). Models with the lowest AICc values were considered as the best models which explained the majority of our data (Burnham & Anderson, 2001). The Δ AICc was calculated between all the candidate models and the best model; in the case of a model differing in Δ AIC by less than

two points from the best model, the most parsimonious model (the one with the lowest number of explanatory variables) was retained as the best one (Burnham & Anderson, 2001). I further compared the candidate models by calculating Akaike's weights (w_iAICc), representing the probability that the selected best model is also effectively the best at explaining the variation in the data (Burnham & Anderson, 2001). In order to compare models with equivalent validation (those with the lowest AICc and the highest w_iAICc values, and differing by $\Delta AICc \leq 2$), I also computed the evidence ratio ($E_{1,2}$) between them. Evidence ratios gave us an estimate of the likelihood of the models, by comparing their relative weights of evidence (Anderson, 2008). In order to identify the criteria of plant species selection, I calculated log-odds ratios, with 95% confidence intervals, and odds ratios of the coefficients obtained for each explanatory variable (and eventual interactions) for the best models. Log-odds ratios could not be computed as exact probabilities for categorical variables, and therefore were derived from coefficients relatively to a reference category (van der Merwe & Marshal, 2012; Zuur *et al.*, 2009). Log-odds ratios higher than 0 represented variables which were positively selected, and ratios lower than 0 were interpreted as negatively selected, in comparison to the reference category (Peng *et al.*, 2002; Zuur *et al.*, 2009). When 95% confidence intervals overlapped with the baseline category, selection was considered as similar or equal to the reference (Zuur *et al.*, 2009).

RESULTS

Characteristics of feeding sites

A total of 150 feeding sites were sampled over the entire study period (wet-early dry season: n=80; mid-dry season: n=70). A higher proportion of feeding sites was recorded in the woodland vegetation type during the mid-dry season (52% of the total sites) than during the wet-early dry transition period (37%; **Fig. 1**). By contrast, the use of dry grassland was visibly reduced during the mid-dry season (from 24% to 11% of the total feeding sites), while the proportion of sites assigned to open shrubland and wet grassland remained similar over the study period (**Fig. 1**). There was no significant difference in the proportion of feeding sites located in bottomlands or along drainage lines between the wet-early dry transition and the mid-dry season (34% and 31% of the feeding sites; respectively; χ^2=0.016; df=1; p=0.898). Eland also made similar use of footslope (although the frequency of sites in this catenary position increased from 24% to 38% in the mid-dry season; χ^2=3.192; df=1; p=0.07), and

midslope (21% and 26% of the total sites; χ^2=0.2038; df=1; p=0.65) during both seasons, but reduced significantly their foraging activities on topslope and crest areas during the mid-dry season (21% to 4% of the feeding sites; χ^2=7.888; df=1; p= 0.005). The majority of feeding sites over the entire study period was located in areas with medium cover by large canopy trees (37% of the sites in the wet-early dry season, and 45% of the sites in the mid-dry season); the seasonal increase in the proportion of feeding sites with medium canopy cover was statistically significant (χ^2=4.100; df=1; p=0.04). A decline (though not significant) in the frequency of sites located in areas with no trees as the dry season progressed (from 31% to 16% of the sites; χ^2=3.675; df=1; p= 0.06), was also observed. By contrast, the proportion of sites under extensive canopy cover (canopy cover >25%), remained low in both seasons (12% and 9%, respectively, for the transition and mid-dry seasons; χ^2=0.02; df=1; p = 0.88). During the wet-early dry transition, 30% of the feeding sites were located on green burns. Conversely, green growth on burns was apparently not established during the dry season, and eland were never seen feeding on ashes or fire-scorched plant material on recent burns.

Vegetation type-specific availability of plant species

I recorded 120 different species of dicots (excluding unidentified herbaceous and woody forbs and a large proportion of creepers) and 56 species of grasses (excluding sedges and some unidentifiable specimens on burns which were occasionally encountered) at feeding sites. Among dicots, only 21 species of browse occurred in ten or more feeding sites, along with four "generic groups" of species with very similar characteristics of forage value (*Acacia* sp or "straight thorn acacias", excluding *Acacia caffra,* six species; *Combretum* sp, three species; and *Solanum* sp; four species). Clusters of availability among the four habitat types were easily defined. *Acacia caffra*, *Lippia javanica*, *Searsia pyroides*, *Solanum* sp, and *Tagetes minuta* were highly available in woodland (availability ≥ 0.3), but presented medium (between 0.1 and 0.3) to low (≤ 0.1) availability in other habitat types (**Tab. 1**). By contrast, some shrubs and small trees, including *Ancylobotrys capensis*, and *Vangueria parvifolia*, were frequently encountered at sites in open shrubland (>0.5), and rarely recorded in other habitat types. The only highly available (>0.25) woody species on wet grassland was *Diospyros lyciodes*, along with a wetland-dwelling invasive forb (*Verbena bonariensis*; availability=0.66) and with various species of ferns (>0.3). Herbaceous and woody forbs had very high availability (≥ 0.5) in all habitat types, probably because they represented

heterogeneous groups of species with different habitat requirements. A commonly encountered woody species, *Helichrysum kraussii* was never found in ten or more feeding sites per habitat type, but was frequently encountered (8-9 sites) in woodland, shrubland and dry grassland, and therefore perceived as widespread across the study area (except for wet grassland). Among grasses, eleven species plus the *Eragrostis* species and sedges were encountered in more than ten feeding sites and subsequently considered for analysis. Some of the species presenting similar nutritional value (as estimated in literature) were lumped into three "generic groups" (*Aristida* sp, six species; *Cymbopogon* sp, three species; and *Setaria* species other than *Setaria sphacelata*, three species). The only species presenting high availability (>0.4) in all habitat types were those ascribed to the *Eragrostis* genus, while *Themeda triandra* was frequently encountered in all habitat types apart from wet grassland (**Tab. 2**). *Loudetia simplex* and *T. leucothrix* was highly available (>0.4) in open shrubland and dry grassland, while *Cymbopogon* species were typical of wet grassland and *Setaria sphacelata* was commonly encountered (availability > 0.4) only in wooded areas. *Cynodon dactylon* had low levels of availability in all habitat types, and was mainly associated with human-modified grasslands close to settlements (*pers. obs.*). .

Dietary contribution

The diet of the eland was dominated by woody dicots over the study period, although the proportions of utilised grass and forbs varied between the seasons. Bites on grasses constituted 20% of the total bites during the wet-early dry season, but only 1% of the mid-dry season total (**Fig. 2**). The contribution of shrublets, dwarf shrubs, and woody forbs remained relatively unaltered between the two seasons (37% versus 33%), while the proportion of shrubs, seedlings and trees increased by 26% from the wet-early dry transition period to the mid-dry season (34% to 60% of the total bites). Herbaceous forbs contributed to the wet-early dry and mid-dry diets by 8% and 6%, respectively, thus forming a small but appreciable proportion of the annual diet (**Fig. 2**). Ferns and creepers were usually not eaten by eland and contributed marginally to the seasonal diet (less than 0.5% in both seasons for both feeding types). During the wet-early dry season, grasses constituted the dominant food item on green burns (47% of the bites recorded on green burns), if compared to their relatively low contribution (7%) on unburnt feeding sites (species-specific calculations were not possible due to the relatively small sample size of feeding sites on burns; **Fig. 3**). Herbaceous forbs

were inversely more eaten on unburnt areas than on green burns (**Fig. 3**). Average greenness of grasses on green burns was higher than on unburnt areas (76% versus 38%), suggesting that patches burnt prior to the rainy season retained green foliage for long into the late wet season.

Eland fed on 54 species of dicots and 28 species of grasses during the wet-early dry transition (in addition to an unknwon number of unidentified herbaceous and woody forbs). Four woody species (*A. capensis*, *A. elata*, *L. javanica*, and *V. parvifolia*) accounted for 44% of the bites on dicots (**Tab. 3**). The dominant grass in the transition period diet was *T. leucothrix* (53% of the bites), with other species only making a minor contribution to the total number of bites (**Tab. 4**).

A higher number of dicot species (64) was consumed during the mid-dry season than during the wet-early dry transition. By contrast, grass species included in the seasonal diet declined from sixteen to six species, as grasses were very seldom eaten during the mid-dry season (**Tab. 4**). Of the extremely small number of bites recorded on grasses (n=26), the vast majority (n=20) was observed on grass tufts of *T. leucothrix*. Most of the dicots showed statistically significant changes in dietary contribution. *Ancylobotrys capensis* and *V. parvifolia*, which constituted the bulk of the diet during the transition period, were subjected to a sharp decline in dietary contribution (*A. capensis* from 9% to 2% of the seasonal diet: χ^2=108.59; df=1; p =<0.01; *V. parvifolia* from 11% to 3% of the seasonal diet: χ^2=139.85; df=1; p = <0.01), while *L. javanica* and *A. elata* maintained relatively high bite indexes despite a significantly lowered contribution during the mid-dry season (*A. elata*: 8% to 4%; χ^2=38.92; df=1; p =<0.01; *L. javanica*: 16% to 10%; χ^2=42.13; df=1; p =<0.01; **Table 3**). *Searsia lancea* and *H. kraussii*, two woody plants rarely eaten during the wet-early dry season, significantly increased in their bite proportions from 0.2% and 1% during the wet-early dry transition to, respectively, 11% and 12% of the total dry season bites, effectively replacing the above-mentioned dicots as the dietary bulk species of July and August (*S. lancea*: χ^2=462.21; df=1; p =<0.01; *H. kraussii*: χ^2=305.16; df=1; p =<0.01; **Tab. 3**). A number of trees and shrubs which attained a very low or null bite frequency during the wet-early dry transition were significantly more consumed by eland during the limiting season, and included *Diospyros lyciodes* (0.1% to 3%), *Dombeya rotundifolia* (0.0001% to 2%), *Faurea saligna* (0.5% to 3%), and *Englerophytum magalismontanum* (0 to 4%; **Tab. 3**).

Ziziphus mucronata was the only species recorded in the wet-early dry transitional diet which was never encountered as eaten in July and August. In both periods, the herbaceous forbs in the genus *Vernonia* and *Verbena bonariensis*, persisted as a small contribution to the diet. However, while *Vernonia* species were consumed in significantly smaller amounts as the dry season progressed (from 4% in the wet-early dry transition to 2% in the mid-dry season; χ^2=32.46; df=1; p =<0.01), *V. bonariensis* increased (though not significantly) from 3% to 4% in its contribution of the total browse diet (from 3% to 4%; χ^2=1.12; df=1; p =0.29; **Tab. 3**). The small sample size for eaten grass species during the mid-dry season suggested that grass consumption had to be considered as an occasional phenomenon.

Availability, acceptance, and greenness

Site-based frequencies of acceptance of browse species during the wet-early dry transition could be distinguished into three clusters: high acceptance (which I considered as favoured species; acceptance≥ 0.75); medium acceptance (moderately accepted species; between 0.70 and 0.20); low acceptance (neglected species; ≤0.2; **Tab. 3**). Highly accepted species included almost exclusively woody plants, and one group of forbs (*Vernonia* sp). The woody plants forming the bulk of the wet-early dry transitional diet, such as *A. elata*, *A. capensis*, *L. javanica*, and *V. parvifolia*, were also favoured by eland, and all of them were relatively highly available, with *A. elata* and *L. javanica* frequently encountered at feeding stations if compared to other species (availability >0.1; **Tab. 3**). *H. lucida*, *A.caffra*, and *Lantana rugosa*, though highly accepted, accounted for a small fraction of the diet and were infrequently encountered (<0.05). Highly accepted species were also very green (**Fig. 4**), although the proportion of green leaves was also high for some discarded and neglected species and feeding types. Generally, neglected species made a small contribution to the seasonal diet of the eland if taken singly (<5%), and they had low availability (<0.05); notable exceptions include *Solanum* species, *Tagetes minuta* and *V. bonariensis*, which were widely available at feeding stations in this season (>0.05; **Tab. 3**). *Parinari capensis*, a creeper poisonous to domestic cattle (Tshenkeng, *pers. comm.*) was never eaten despite its moderately high availability (>0.05), and ferns were generally discarded, apart from very green individuals of *Pellaea calomelanos* and young shoots of *Pteridium aquilinum*. Grasses were generally eaten according to their availability, and presented higher availability values when compared to dicots (**Tab. 4**). Frequency of acceptance was exceptionally low for grasses, with

T. leucothrix and *C. dactylon* as the only moderately accepted species (acceptance ≥ 0.3). *Tristachya leucothrix* was also the second most available grasses at feeding sites (after *Eragrostis* species), and were also very green, possibly because associated with green burns (**Fig. 5; Tab. 4**). Grasses (here considered as a single category because of the impossibility of species-specific calculations due to the small sample size) were moderately accepted (>0.3), and very green on green burns during this season (on average, more than 75% of the leaves were green), especially if confronted with the low frequencies of acceptance (<0.1) and with the low average greenness (<40%) recorded on unburnt areas.

During the mid-dry season, I found no evidence of direct proportionality between acceptance and greenness of dicots, and woody species in particular tended to be consumed according to their availability (**Fig. 6; Tab. 3**). Clustering was not as evident as during the wet-early dry transition, and a distinction into acceptability classes was therefore deemed impossible for the period spanning July and August. The majority of woody species and forbs which were frequently eaten during March and April did not show any significant decline in their acceptance by eland, but the availability of most species changed evidently between the two seasons, probably as a consequence of changes in fine-scale habitat use. There was an increase in the frequency of acceptance for *H. kraussii* (from 0.6 to 0.9; χ^2=19.66; df=1; p = <0.01), *S. lancea* (0.3 to 0.9; χ^2=11.81; df=1; p =<0.01), and *V. bonariensis* (0.6 to 0.9; χ^2=11.78; df=1; p =<0.01), which subsequently constituted the favoured species of the season together with the already frequently consumed *A. elata*, *L. rugosa*, and *L. javanica* (**Tab. 3**). *H. kraussii* and *S. lancea* increased significantly in their availability at feeding sites at this time of the year if compared to the wet-early dry season (*H. kraussii* from 0.03 to 0.14: χ^2=47.97; df=1; p =<0.01; and *S. lancea* from 0.01 to 0.07; χ^2=30.66; df=1; p =<0.01), thus indicating a change in microhabitat selection, towards those sites offering numerous individuals of seasonally favoured plants (**Tab. 3**). These two evergreen woody plants, which also constituted the bulk of the dry season diet (**Tab. 3**), maintained high levels of greenness (>80% of green leaves) during both seasons, while *V. bonariensis* experienced a decline in average greenness over the seasonal cycle (from ~85% to ~45% of green leaves; **Fig. 6**). *H. lucida*, which was always eaten during the wet-early dry season, was mostly rejected during this period (acceptance decreasing from 1 to 0.06; χ^2=21.53; df=1; p =<0.01), despite maintaining comparably similar availability and proportions of green leaves. Acceptance of *V. parvifolia* also declined significantly (from 0.98 to 0.67; χ^2=13.89; df=1; p =<0.01), thus

reflecting the significant decrease in dietary contribution, coupled with a decline in average leaf greenness (**Fig. 6**), and availability at feeding stations (from 0.08 to 0.03; χ^2=13.38; df=1; p =<0.01). Dicot species rarely or never browsed during the wet-early dry season were readily accepted during the mid-dry season, and these included the highly palatable *D. rotundifolia* (acceptance increasing from 0.05 to 0.5; χ^2=9.08; df=1; p =0.01) and *D. lycioides* (0.05 to 0.5; χ^2=9.19; df=1; p =0.01), which surprisingly presented relatively low proportions of green leaves (<50%, compared to 66% and 92% during the previous season). *E. magalismontanum*, an evergreen shrub or tree never eaten in the wet-early dry transition, attained moderate acceptance frequencies (0.61), despite remaining at similar availability and greenness levels (**Tab. 3**). *Z. mucronata* was never utilised (and significantly under-represented in respect to the wet-early dry transition) during the mid-dry season and presented low greenness compared to the transition period, albeit still producing moderately high proportions of green leaves (>50%). Herbaceous forbs and woody forbs were less green, less available, and less accepted in the mid-dry season than during the wet-early dry transition, a pattern confirmed by their general small contribution to the seasonal diet (woody forbs also showed a significantly decline in the frequency of acceptance from 0.6 to 0.3; χ^2=17.67 df=1; p =<0.01). Grass species composition of feeding sites differed between the two seasons, but the availability of species which were mostly consumed during the wet-early dry transition, including *C. dactylon* and *T. leucothrix*, did not show any significant changes. Grasses were avoided by eland during the mid-dry season, being almost entirely dry (**Fig. 7**), and most of the species were never eaten. There was a significant decline in the frequency of acceptance for *T. leucothrix* (0.6 to 0.06; χ^2=68.62; df=1; p= <0.01) with unaltered inter-seasonal availability (**Tab. 4**), and for *C. dactylon* (0.4 to 0.03; χ^2=9.81; df=1; p =0.01), which offered the greenest tufts available (**Fig. 7; Tab. 4**).

Dicot species selection models

I tested thirty mixed effects logistic regression models for dicot selection (**Tab. 5**). The best model (AICc=2626.4;) included all the fixed effects and the interaction between plant species and season as explanatory variables; none of the other models attained a value of AICc which could fall within a ΔAICc of ≤ 2. This model had a 99% likelihood of being the best one at explaining dicots selection (w_iAICc=0.99), as also supported by evidence ratios ($E_{1,2}$=162.83). The reference level was set as the "other trees and shrubs" during the wet season and at the

highest level of greenness (>75% of green leaves) and cover (>10% of cover within a feeding station). In comparison to the baseline value, selection for low (log-odds=-1.698 ± 0.279) and medium greenness (log-odds=-0.447 ± 0.266) was weak and did not overlap with the high greenness level, indicating that eland selected for the greenest available plant species. Species with low basal cover proportions (≤10% of the cover of a feeding station) were also less selected than species with high basal cover (log-odds=1.37±0.24). During the wet-early dry transition, selectivity was high (compared to the baseline category of the "other trees and shrubs" group during the wet-early dry transition) for *A. elata* (log-odds=2.007 ± 0.276), *A. capensis* (log-odds=2.223 ± 0.441), *L. javanica* (log-odds= 2.7844 ± 0.389), *Solanum* sp (log-odds=0.427 ± 0.304), *T. minuta* (log-odds=0.818 ± 0.333), *V. parvifolia* (log-odds= 3.953 ± 1.002), and the category of "woody forbs and shrublets" (log-odds=0.890 ± 0.187), which were also some the highest accepted species during the transition period (with the exception of *T. minuta*; **Fig. 8**). The species decreased in their selection estimates, in relation to the reference, during the dry season, in correspondence to their decline in dietary contribution (although *A. elata, A. capensis*, *L. javanica,* and *V. parvifolia*, still maintained relatively high levels of acceptance; **Fig. 8**). This pattern was closely mirrored by the rise in the consume of other shrubs and trees during the dry season, as a consequence of dietary broadening to include a large number of woody species during the driest months of the year. *Helichrysum kraussii* and *V. bonariensis* during the wet-early dry season were also selected for (*H. kraussii*: log-odds= 0.895 ± 0.456; *V. bonariensis*: log-odds= 1.958 ± 0.391), and increased in their influence on forage selection during the dry season, when they were also highly accepted (**Fig. 8; Tab. 5**). The "Acacias" and *Searsia* species were conveniently created by lumping together different species of variable acceptability to eland, and thus represented spurious groups, with limited significance for what pertains the interpretation of the results. Eland in our study population therefore selected, within feeding stations, for different plant species at different times of the year (as confirmed by the acceptance/availability analyses and by the log-odds of mixed effects models), and for high greenness and basal cover of woody plants and forbs.

DISCUSSION

Characteristics of feeding sites

In KMR, eland used all of the four main habitat types for foraging purposes, although displaying seasonal differences in the number of feeding sites per habitat type, correlated with marked changes in dietary composition. As expected, eland concentrated their foraging activities in woodland for most of the study period, where the only staple year-round forage species, *L. javanica* , was widely available. Open shrubland and wet grassland presented foods which were moderately to highly accepted year-round, and were therefore utilised in similar proportions during the two seasons. For example, eland used open shrubland in the wet-early dry season for browsing on new shoots of *A. capensis* and *V. parvifolia*, and for feeding on *E. magalismontanum* and *Zanthoxylum capense* in the mid-dry season. There was also extensive use of dry grassland during the wet-early dry transition, when flushing new grasses were available on burns. Dry grassland was only marginally utilised during the mid-dry season, mostly for accessing stands of *F. saligna* and *D. lycioides*. Eland in Mountain Zebra National Park (Watson & Owen-Smith, 2000), S.A. Lombard Nature Reserve (Buys, 1990), and Loskop Dam Nature Reserve (Underwood, 1975), similarly showed preferential use of grassland communities during the wet summer months of southern Africa. In East Africa, populations inhabiting the Athi-Kapiti Plains of Kenya (Hillman, 1988), the Crater Highlands of Tanzania (Estes, Atwood & Estes, 2006), and the Nyika Plateau of Malawi (Munthali & Banda, 1992), undertook long-range seasonal movements while tracking the sprouting of green herbaceous vegetation following rainfall events. Other woodland-dwelling Tragelaphins, such as bushbuck (*Tragelaphus scriptus*) and greater kudu (*Tragelaphus strepsiceros*), are known to utilise open vegetation during the wet season, albeit somewhat less frequently than eland (Evans, 1979; Du Toit, 1986; Owen-Smith, 2002). Eland in KMR congregated on green burns during the austral summer, a phenomenon also observed in the Drakensberg (Rowe-Rowe, 1983) and in the Pilanesberg National Park (Kelso, 1986). Other browsers, such as greater kudu, only utilise burns during the early phase of the rainy season, when flushing grass species remain short and at peak protein contents (Owen-Smith, 2002). However, the high absolute forage requirements and the large muzzle probably forced eland in KMR to make use of burns late in the wet season, after the flushing grasses had reached a suitable biomass yield. Similarly, eland in central Kenya avoided the extremely short and

scattered grasses growing on burnt grasslands immediately after a fire (Sensenig, Demment & Laca, 2010). In the Hluhluwe-Imfolozi Park, mixed feeding nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*) were attracted to recent burns during the dry season (O'Kane *et al.*, 2011a); this was not observed in KMR for eland as burns did not flush with new growth during the mid-dry season. Eland extensively used the *vleis* (wet grasslands) of KMR in both seasons as feeding sites. The wet grasslands were characterised by the presence of a favoured forb (*V. bonariensis*), and generally by an abundance of nutritious green forbs and grasses throughout the year, due to clayey and moisture-retaining properties of the underlying soil (Nel, 2000). Observations reported in Sheppe & Osborne (1971) suggest that herds on the Kafue Flats of Zambia frequented the floodplains of the Kafue river as dry season foraging grounds, while Jarman (1972) noted that the number of eland on the mid-Zambezi floodplain gradually increased from August to an abundance peak in October, during the final spell of the late dry season. Sheppe & Osborne (1971) reported that eland did not feed in water, but I observed herds venturing into the flooded grassland and taking semi-submerged forbs. Evidence of the importance of wetlands for browsers and mixed feeders is scarce, with only one study reporting that impala in the Okavango Delta move into the receding floodplains, tracking fast-disappearing water (Bonyongo, 2005). It is highly unlikely that eland made use of flooded grasslands aiming at accessing surface water, as this resource was highly available in all habitat types of the reserve during the study period, and eland were never observed drinking (*pers. obs.*). Eland are water-independent and were reported at greater distance than any other large herbivore from water sources in the Amboseli Basin (Kenya; Western, 1975) and in the southern Kalahari (Thouless, *unpublished report*; as seen in Thouless, 2014).

Eland did not show any consistent pattern of seasonal movement down the soil catena, as instead observed for both ruminant grazers (Bell, 1970) and browsers (O'Kane *et al.*, 2011a). Nevertheless, they significantly reduced their use of topslope areas during the mid-dry season, and were most often found on bottomlands and drainage lines in both seasons. In African savannahs, high biomass of green herbaceous forage and of foliage on woody plants persist across the seasonal cycle on the lower slopes (Scoones, 1995; Pellew, 1983; Owen-Smith, 1988, 1997, 2002), which are considered as key resource areas for grazing and browsing mammals. As eland possess physiological adaptations related to their large body size, allowing them to consume woody material and leaves of evergreen, sclerophyllous plant species (Jarman, 1974; Hofmann, 1989), they were not entirely dependent on young leaves

and shoots in bottomlands during the dry season and also utilised shrublands and woodlands on hilly slopes. Lactating females often conducted their newborn calves in the main *vlei* of KMR in August (*pers. obs.*), suggesting that low-lying damp areas, with abundant green browse at low levels, provided key forage resources for individuals in specific age classes and life cycle stages and for social units with reduced mobility.

Eland frequently utilised areas with medium cover by large canopy trees throughout the year, as they were often observed feeding in grassy glades or open areas interspersed within woodlands. Although the availability of shade from large canopy trees is often considered as a fundamental habitat characteristic for plains-dwelling ungulates which are too large to seek cover from direct sun exposition in thickets or scrub (Jarman, 1972), eland in the KMR were never seen resting in the shade of large trees, even during the hottest daylight hours of the austral late summer. Similarly, eland in the sub-tropical Kalahari region of South Africa did not use areas of extensive canopy cover as resting sites (Fabricius & Mentis, 1990), while those inhabiting the harsh plains of Tsavo East National Park, a coastal equatorial ecosystem, were mainly crepuscular feeders and rested in shady spots during daytime (Hillman, 1979).

Plant species selection

Eland in KMR showed selectivity at the plant species scale. Selection of dicots was mainly based on the interaction between species and season; it is also positively influenced by greenness and negatively by basal cover of each species. These patterns of plant species selection suggested that eland in the KMR were selective feeders. Greenness is a good proxy index for the quality of dicots (Van Soest, 1994), with high values associated with young leaves rich in metabolizable protein and soluble carbohydrates and containing low levels of structural fibre and toxic allelochemicals as browsing deterrents (Jarman, 1974; Owen-Smith & Novellie, 1982). Despite claims that eland should be considered as unselective roughage eaters (Jarman, 1974; Scotcher, 1983), this study is actually supportive of field evidence describing eland as selective for certain plant species at certain times of the year (Kerr *et al.*, 1970; Field, 1975; Hillman, 1979).

Eland selected for some of the most available green species during the wet-early dry season, but, contrary to expectations, widened their acceptance to low quality forage in the dormant season, instead of increasing their selectivity towards the highest quality species. Broad-leaf

woody plants were favoured, as predicted by Owen-Smith (2002), especially if we include *A. caffra*, with its large compound leaves among them (as suggested by Fabricius, 1989). Eland focused on low-quality deciduous woody plants, such as *V. parvifolia*, during the wet-early dry season, when they offered new leaves and shoots, and subsequently switched to non-favoured but highly palatable deciduous species, including *D. lycioides* and *D. rotundifolia* (Owen-Smith & Cooper, 1987a; van Wyk & van Wyk, 2002), in the mid-dry season. Evergreen trees and shrubs (mainly *F. saligna, S. lancea*), discarded in the wet-early dry transition possibly due to their high contents of waxes and/or tannins (van Wyk & van Wyk, 2002), were moderately to highly accepted during the mid-dry season as the deciduous ones shredded their wet season foliage. Similarly, eland in the Zimbabwean lowveld selected for the woody plants offering the greatest amount of green leaves in each month, reverting to unpalatable species as soon as these produced new growth (Kerr *et al.*, 1970). Greater kudu also increased their consumption of evergreen *Searsia* species as the dry season progressed in Nylsvley Nature Reserve (Owen-Smith & Cooper, 1987a), thus indicating that species ascribed to this genus might constitute important buffer food during the limiting season for large-bodied Tragelaphins. Evergreens, especially those characterized by succulent leaves such as *E. magalismontanum*, also contain high levels of moisture and therefore also constitute an important source of liquids during the dry season for browsers (i.e. for dik dik, *Madoqua kirkii*; Manser & Brotherton, 1995). Fabricius (1989) deemed *Z. mucronata* and other woody plants with spinescent defences as rather unpalatable to the wide-muzzled eland; by contrast, eland in KMR readily fed on leaves and also thorny shoots of several trees and shrubs, including *Zanthoxylum capense* and various *Solanum* species, provided that they offered a high leaf yield. Leptophyllous species with long, straight thorns, such as *Acacia karroo*, were mostly discarded, both in KMR and in the Pilanseberg NP(Kelso, 1986), although figuring as moderately accepted foods in Mountain Zebra NP (Watson & Owen-Smith, 2000). These differences could be explained by the fact that *Acacia* species with large, pinnate leaves, are not present in the karoid shrublands typical of Mountain Zebra NP (Watson & Owen-Smith, 2000). *Acacia caffra* was the only leguminous species significantly accepted by eland in KMR (a favourite also in the nearby Pilanesberg NP; Kelso, 1986), but made a relatively small contribution to the diet. The suggestion that eland in KMR might integrate their dry season diet with a high proportion of Nitrogen-fixing species in the family Fabaceae as an explanation for the isotopic composition of faecal samples (Mìranda, Dalerum

& Parrini, 2014), is therefore unlikely at the present status of the knowledge. At the plant parts scale, although no quantitative measure was attempted in the impossibility of direct observations, eland usually bit off green and sometimes woody shoots (green shoots were especially sought after on *V. parvifolia*), with associated leaves or twigs. In some instances, browsed trees or shrubs which appeared as completely defoliated and lacking green shoots, at a closer inspection revealed green and moisture-rich meristems probably preceding the growth of new twigs and shoots. Plant parts rich in lignin were also present in appreciable percentages in rumen contents of eland from various populations (Hillman, 1979), despite not attaining the same values encountered in samples of large non-ruminants (Owen-Smith, 1988). Browsers of Hluhluwe-Imfolozi Park consumed higher proportions of shoots on woody plants with increasing body size, with kudu consuming more terminal shoots of trees and shrubs than nyala and impala (O'Kane *et al.*, 2011a). Large body size is generally associated with high absolute metabolic requirements and a relatively broad mouth, which constrain the level of selectivity that can be achieved at the plant parts scale (Jarman, 1974; Steuer *et al.*, 2014; Fynn *et al.*, 2016). Following this simple body-size scaling rule, it can be reasonably assumed that eland would consume more lignified shoots than smaller browsers. High-quality plant parts, such as fruit, were also consumed when available, possibly representing an important source of energy and nutrients. The small fruit of *Searsia* species, in particular, were eaten in abundance during both seasons, as well as flowers of various species.

Shrublets, dwarf shrubs, and woody forbs, despite a marked decline in greenness, still retained green leaves during the mid-dry season, and showed moderate to high acceptance in both seasons. *T. minuta*, an invasive alien species, was by contrast moderately accepted in the transition period but mainly rejected in July and August, as it undertook a substantial decline in the proportion of green leaves. Among the favourite species, *L. javanica* and *A. elata*, two aromatic shrublets constituting a significant proportion of the total diet (more than 10% in both seasons in the case of *L. javanica*), were present in a large proportion of feeding sites and usually very green; it was also a favourite for eland populations in the central highlands of Kenya (Hillman, 1979) and in the Suikerbosrand Nature Reserve (Wallington *et al.*, 2007). *H. kraussii*, despite being a microphyllous dwarf shrub and presenting a low leaf yield, was particularly favoured during the driest months of the year, probably because it was the only prostrate species offering an abundance of green shoots during this season. The dietary

composition of eland in the KMR, with its preponderance of woody plants regarded as unpalatable to most mammalian browsers (*V. parvifolia*, *S. pyroides*; van Wyk & van Wyk, 2002), aromatic shrublets, and woody-stemmed forbs (*Bidens pilosa* among the others) was extremely similar to the estimate reported for Suikerbosrand NR by Wallington *et al.* (2007), probably due to the similar vegetation communities present in the two protected areas (Bredenkamp, 1978; Nel, 2000). Herbaceous forbs constituted a small but constant proportion of the wet-early dry season diet, especially in the form of tall and erect *Vernonia* species. Forbs consumption during the mid-dry season was almost exclusively restricted to one weedy invasive, *V. bonariensis*, growing on wet bottomlands, as other species were mostly dormant. The year-round consumption of herbaceous forbs is less pronounced than for greater kudu, but similar, in the selection for woody-stemmed species, to the forb utilisation made estimated for goats (*Capra hircus*) and impala (Owen-Smith & Cooper, 1987a). Selection for forbs and shrublets, including alien invasives species, containing aromatic oils is confirmed by other studies (Hillman, 1979; Fabricius, 1989; Thouless *unpublished data, as seen in* Thouless, 2014), and even for the sister taxon of the common eland, the Lord Derby's eland (*Tragelaphus derbianus*) of the Sudano-Sahelian and Guinean savannahs (Graziani & D'Alessio, 2004; Hejcmanòva *et al.*, 2010).

I noticed significant differences in plant species acceptance between the dry season of 2013 (D'Ammando *et al.*, 2015), and the dry season of 2015. Although *L. javanica* and *A. caffra* were among the highest accepted species in both dry seasons in 2013 and 2015, eland also favoured *Combretum* species and *Z. mucronata* (which constitute high-quality fodder; van Wyk & van Wyk, 2002) in the dry season of 2013. Presumably, they widened their diet to low-quality foods in the dry season of 2015 due to the low and erratic rainfall experienced in the previous wet months. With this ability of dietary switching according to the local phenophase of available forage, eland place themselves halfway along the continuum between "generalist" and "selective" ruminants (Hofmann, 1973, 1989), and are to be considered as "opportunistic selectors" which take advantage of localised changes in the phenological cycle of browse.

The diet of the eland in KMR was undoubtedly dominated by browse (~90% of the total estimated diet), as reported by other studies in southern Africa (Watson & Owen-Smith, 2000; Wallington *et al.*, 2007; Appendix III). Grasses contributed significantly only to the wet-early

dry season diet (especially when considering the totality of bites recorded on burns), and my expectations of grazing on green grass tufts during the dry months (as reported in D'Ammando *et al.*, 2015) was not supported by the evidence. The actual contribution of grasses to the seasonal and annual diet of eland populations has been debated over the past fifty years, as well as the environmental causes triggering the dietary switch from grazing to browsing during the early dry season (Thouless, 2014). Early studies reported a significant contribution of grasses to the annual diet of eland in East and southern Africa, oscillating between 20% and 45% of the total diet (Field, 1975; Buys, 1990). Recent observational research and stable-isotopes analyses of C^3:C^4 ratios, by contrast, confirmed that most populations undoubtedly subsisted on a browse-dominated annual diet (Watson & Owen-Smith, 2000; Wallington *et al.*, 2007; Sponheimer *et al.*, 2003; Codron *et al.*, 2007). Wet season grazing on green burns was descriptively observed in the Drakensberg (Rowe-Rowe, 1983) and in the Pilanesberg NP (Kelso, 1986). Pure browsers, including greater kudu, also take advantage of short and nutritious grass growth on burnt areas after the first rains, when the browse resource is often scarce and severely depleted (Owen-Smith & Cooper, 1985; Owen-Smith, 2002). Eland showed a marked selectivity towards certain grass species which were abundant at feeding sites and presented a high proportion of green leaves. Only one highly palatable species (*C. dactylon*; Ben-Shahar, 1998) contributed in significant quantities to the diet and was also frequently eaten, while the bulk of the grazing, was formed by the medium to lowly palatable *T. leucothrix*, frequently associated with flushing burns (van Outdshoorn, 2006). Field (1975) described how grass species of low nutritional value were selected by buffalo (*Syncerus caffer*) when offering green leaves on burns, where they attained high protein contents, and *T. leucothrix* was also eaten by sable antelope (*Hippotragus niger*) exclusively on burnt patches in the KMR (Parrini, 2006). Furthermore, *T. leucothrix* is favoured by ruminants in the subfamily Caprinae (van Outdshoorn, 2006), thus probably presenting chemical characteristics which make them more digestible to mixed-feeding ungulates than to pure grazers. Effective dietary segregation from other grazers and mixed feeders (suh as impala), as estimated by Mìranda *et al.* (2014) in KMR through stable isotopes analyses of faecal samples, was thus probably achieved by selecting for dicots (including species unpalatable to impala) and for grasses of low quality for medium-sized grazers. Eland in the Athi-Kapiti Plains of Kenya consumed large quantities of dry grasses during a drought, probably starving to death by feeding on such poor quality food (Hillman,

1979). By contrast, eland in KMR, during the dry spell of 2015, almost completely avoided brown grasses (apart from occasional bites on seed-bearing inflorescences) and became exclusive browsers. The small areal extent of KMR seems therefore not to constitute a limiting factor for the foraging requirements of the wide-ranging and nomadic eland, proving drought-buffering resources thanks to its variety of plant species and vegetation communities (Nel, 2000). Apio & Wronski (2005) stated that preferential browsers will revert to grazing only if protein-rich grasses are abundant, grasslands comprise most of the vegetation types of the available area, and interspecific competition for this resource is low. In KMR, green grasses are available during the wet season, and grassland is the dominant land type (Nel, 2000); density of grazers is also relatively low (Nel *et al.*, 2011), and eland maintained a well-differentiated isotopic dietary niche from other grazers and impala, despite consuming variable amount of grasses (Mìranda *et al.*, 2014), as already stated. Wallington *et al.* (2007) suggested that populations of the East African plateau would have included more grasses in their annual diet due to the dominance of grasslands in this eco-geographical region, as also reported for impala (Wronski, 2002). Here (and in a previously published paper: D'Ammando *et al.*, 2015) I suggest that the actual amount of grazing is mostly influenced by the phenophase of the grass sward, which is in turn affected by vegetations structure, rainfall and, in African savannahs, by the incidence of fires (Sinclair, 1975; Archibald *et al.*, 2005). The browse consumption undertake a substantial decline with increasing rainfall (Hillman, 1979), and grasses at their young stage of growth contain a higher fraction of protein (Buys, 1990), and lower secondary metabolites than woody browse (Bryant *et al.*, 1991), therefore constituting a sought after resource by mixed feeders during the early growing season. The bimodal rainfall pattern (which allows for a continuous flush of new leaves, albeit diluting protein contents in the growing grass biomass), rather than the availability of grassland communities, could therefore explain the higher intake of grasses in East Africa than in southern Africa, while inter-annual variation in rainfall (coupled with the availability of burns) could account for the differences in grass species acceptance observed in KMR between the mid-dry seasons of 2013 and 2015 (D'Ammando *et al.*, 2015). Discrepancies in the estimated grass consumption between different study sites could then be reduced to stochastic variations in environmental conditions not taken into consideration by previous studies.

Summary

Eland in KMR fed on both grasses and browse during the wet-early dry transition season, but mostly restricted their diet to woody plants as the dry season progressed. Grazing was mostly limited to flushing grasses on burns, which were heavily utilised only in the wettest period of the study. The differential availability of favoured browse species between the different vegetation-types, coupled with the phenophase of woody plants and forbs, probably constituted the main drivers of habitat use (although further research is needed in this direction). The wet grassland, although offering tall grass species of little appeal to eland, constituted an important feeding ground thanks to its continuous production of green forb growth. Furthermore, the selection of dycotiledonous plant species was affected by their small-scale phenological changes in greenness, which may have reflected variation in chemical composition according to rainfall patterns. Inconsistencies between the estimated foraging preferences during the dry seasons of 2013 and 2015 seemed to indicate that eland are able to take advantage of local patterns of forage quality and availability, mainly by consuming grasses and foliage of deciduous species when high rainfall prompted green leaf retention into the dry months, and expanding their diet to include lowly palatable evergreens during drought or semi-drought conditions. These results largely confirmed my predictions, with eland to be considered as selective mixed feeders at the plant species scale despite their large body size, making use of the vegetation in order to optimize their requirements for foods rich in protein and low in fibre contents.

From a management perspective, KMR seems to offer (in combination with its burning policy) enough heterogeneity at the vegetation type and plant species scale, thus providing potential buffer resources for eland during dry periods. Interspecific competition with sable antelope remains unlikely due to the browse-dominated diet of the eland, although high densities of eland grazing on burns could potentially be detrimental to the establishment of regenerating tall grasslands favoured by the sable antelope (Grobler, 1981).

TABLES

Tab. 1: Availability of dicotyledons found in 10 or more feeding sites in at least one habitat type over the entire study period. Availability was calculated as a frequency, by dividing the number of feeding sites in which a species was present in a habitat type by the number of feeding sites recorded in that habitat type.

	Habitat types			
Dicot species	**Woodland**	**Open shrubland**	**Dry grassland**	**Wet grassland**
Acacia caffra	0.31	0.07	0.00	0.00
Other Acacias	0.20	0.11	0.00	0.14
Ancylobotrys capensis	0.12	0.54	0.25	0.00
Diospyros lycioides	0.28	0.11	0.11	0.28
Dombeya rotundifolia	0.29	0.07	0.00	0.00
Englerophytum magalismontanum	0.09	0.39	0.07	0.00
Faurea saligna	0.26	0.00	0.11	0.07
Ferns	0.17	0.25	0.04	0.34
Herbaceous forbs	0.58	0.54	0.71	0.72
Halleria lucida	0.22	0.04	0.00	0.03
Lippia javanica	0.63	0.07	0.14	0.28
Parinari capensis	0.14	0.25	0.43	0.00
Sersia pyroides	0.37	0.14	0.00	0.10
Solanum sp	0.34	0.29	0.18	0.14
Tagetes minuta	0.43	0.25	0.07	0.10
Vangueria parvifolia	0.09	0.50	0.11	0.00
Verbena bonariensis	0.05	0.07	0.07	0.66
Woody forbs	0.55	0.36	0.50	0.48
Ziziphus mucronata	0.25	0.07	0.11	0.07

Tab. 2: Availability of grass species found in 10 or more feeding sites in at least one vegetation type over the entire study period. Availability was calculated as a frequency, by dividing the number of feeding sites in which a species was present in a habitat type by the number of feeding sites recorded in that habitat type.

	Vegetation types			
Grass species	**Woodland**	**Open shrubland**	**Dry grassland**	**Wet grassland**
Aristida sp	0.11	0.25	0.39	0.31
Cymbopogon sp	0.15	0.50	0.29	0.41
Cynodon dactylon	0.15	0.18	0.25	0.17
Eragrostis sp	0.52	0.71	0.82	0.59
Hyparrhenia hirta	0.11	0.18	0.07	0.41
Hypertelia dissoluta	0.20	0.07	0.07	0.21
Loudetia simplex	0.20	0.43	0.57	0.03
Panicum maximum	0.20	0.04	0.00	0.03
Schizach. sanguineum	0.18	0.46	0.32	0.07
Setaria sphacelata	0.42	0.11	0.25	0.24
Themeda triandra	0.40	0.54	0.64	0.17
Trachypogon spicatus	0.38	0.36	0.36	0.10
Tristachya leucothrix	0.34	0.46	0.64	0.03

Tab. 3: Frequency of acceptance, availability, and contribution of browse species to the seasonal diet of eland in the Kgaswane Mountain Reserve. The "Sig." column reports those species (or groups) for which there was a significant decrease or increase in availability, acceptance, or dietary contribution between the late wet-early dry and the mid-dry season ("*" indicates a significant p-value, $p \leq 0.05$). The "-" symbol indicates a number of samples too small to allow for exact calculations of the p-value.

	Availability			**Acceptance**			**Seasonal dietary contribution**		
Dicot species	**Wet-early dry season**	**Mid-dry season**	**Sig.**	**Wet-early dry season**	**Mid-dry season**	**Sig.**	**Wet-early dry season**	**Mid-dry season**	**Sig.**
Acacia caffra	0.03	0.05		0.79	0.69		0.02	0.03	*
Other acacias	0.02	0.02		0.23	0.36		0.02	0.01	*
Ancylobotrys capensis	0.08	0.03	*	0.88	0.75		0.09	0.02	*
Asparagus sp	0.03	0.02		0.57	0.40		0.01	0.00	*
Athrixia elata	0.18	0.05	*	0.81	0.84		0.08	0.04	*
Combretum sp	0.01	0.05	*	0.40	0.68		0.01	0.05	*
Diospyros lycioides	0.03	0.06	*	0.05	0.47	*	0.00	0.03	*
Dombeya rotundifolia	0.03	0.06	*	0.05	0.49	*	0.00	0.02	*
Englerophytum magalismontanum	0.02	0.03		0.00	0.61	-	0.00	0.04	*
Euclea crispa	0.001	0.02	*	0.00	0.20	-	0.00	0.00	-
Faurea saligna	0.03	0.04		0.28	0.61		0.00	0.03	*
Ferns	0.08	0.03	*	0.05	0.05		0.00	0.00	
Herbaceous forbs	0.28	0.07	*	0.30	0.16		0.04	0.01	*
Halleria lucida	0.02	0.03		1.00	0.06	*	0.01	0.00	*
Helichrysum kraussii	0.03	0.14	*	0.60	0.96	*	0.01	0.11	*
Indigofera sp	0.05	0.01	*	0.03	0.00		0.00	0.00	
Lantana rugosa	0.04	0.01	*	0.82	0.83		0.02	0.01	*
Lippia javanica	0.12	0.13		0.90	0.83		0.16	0.10	*
Parinari capensis	0.08	0.03	*	0.00	0.00		0.00	0.00	
Searsia lancea	0.01	0.07	*	0.29	0.91	*	0.00	0.12	*
Searsia lepodyctia	0.01	0.03	*	0.43	0.33		0.00	0.01	*
Searsia pyroides	0.05	0.06		0.58	0.68		0.03	0.04	
Solanum sp	0.09	0.06		0.44	0.21	*	0.03	0.01	*
Tagetes minuta	0.06	0.04		0.48	0.07	*	0.01	0.00	*
Vangueria parvifolia	0.08	0.03	*	0.98	0.67	*	0.11	0.03	*
Verbena bonariensis	0.08	0.12	*	0.60	0.87	*	0.03	0.04	
Vernonia sp	0.06	0.07		0.78	0.61		0.04	0.02	*
Woody forbs	0.28	0.06	*	0.63	0.25	*	0.11	0.01	*
Ziziphus mucronata	0.04	0.01	*	0.53	0.00	-	0.02	0.00	*

Tab. 4: Frequency of acceptance, availability, and contribution of grass species to the seasonal diet of eland in the Kgaswane Mountain Reserve. The "Sig." column reports those species (or groups) for which there was a significant decrease or increase in availability, acceptance, or dietary contribution, between the late wet-early dry and the mid-dry season ("*" indicates a significant p-value, $p \leq 0.05$). The "-" symbol indicates a number of samples too small to allow for exact calculations of the p-value.

	Availability			**Acceptance**			**Seasonal dietary contribution**		
Species	**Wet-early dry season**	**Mid-dry season**	**Sig.**	**Wet-early dry season**	**Mid-dry season**	**Sig.**	**Wet-early dry season**	**Mid-dry season**	**Sig.**
Andropogon gayanus	0.05	0.00	*	0.18	0.00	-	0.02	0.00	-
Aristida spp	0.07	0.02	*	0.25	0.00	-	0.05	0.00	-
Cymbopogon sp	0.14	0.05	*	0.09	0.00	-	0.04	0.00	-
Cynodon dactylon	0.05	0.05		0.37	0.03	*	0.05	0.04	
Diheteropogon amplectens	0.03	0.00	*	0.13	0.00	-	0.01	0.00	-
Eragrostis sp	0.37	0.16	*	0.12	0.02	*	0.07	0.08	
Hyparrhenia hirta	0.05	0.11	*	0.03	0.00	-	0.00	0.00	-
Hypertelia dissoluta	0.04	0.03		0.00	0.00		0.00	0.00	
Loudetia simplex	0.10	0.10		0.29	0.02	*	0.04	0.04	-
Melinis repens	0.04	0.01	*	0.07	0.00	-	0.00	0.00	
Panicum maximum	0.03	0.01	*	0.16	0.00	-	0.01	0.00	-
Schizachyrium sanguineum	0.04	0.12	*	0.19	0.00	*	0.01	0.00	-
Sedge	0.06	0.03	*	0.07	0.00	-	0.02	0.00	-
Setaria sp	0.05	0.02	*	0.00	0.00		0.00	0.00	
Setaria sphacelata	0.10	0.06	*	0.18	0.00	-	0.04	0.00	
Sporobolus africanus	0.04	0.08	*	0.19	0.00	-	0.02	0.00	
Themeda triandra	0.13	0.13		0.06	0.00	-	0.01	0.00	-
Trachypogon spicatus	0.05	0.15	*	0.06	0.00	-	0.01	0.00	-
Tristachya leucothrix	0.22	0.18		0.56	0.06	*	0.53	0.77	

Tab. 5: Twenty of the candidate mixed-effects logistic regression models (plus the null model) produced in order to investigate selection for dicot species eaten by eland in the Kgaswane Mountain Reserve, as influenced by their phenological characteristics. The table continues on the following page.

Models	**Fixed effects**	**AICc**	**ΔAICc**	**w_iAICc**	**logLik**	**Deviance**	**Df.dev**
Model 12	**Species*Season+Greenness+Cover**	**2626.4**	**0**	**0.99**	**-1274.2**	**2548.4**	**2616**
Model 28	Species*Greenness+Species*Season+ Cover	2634.1	7.6	0.001	-1248.0	2496.1	2586
Model 29	Species*Greenness+Species*Cover+ Species*Season	2642.6	16.2	0	-1237.3	2474.6	2571
Model 8	Species*Greenness+Cover+Season	2674.2	47.8	0	-1283.1	2566.2	2601
Model 24	Species+Greenness+Cover*Season	2675.4	49	0	-1312.7	2625.4	2630
Model 9	Species*Greenness+Cover	2677.2	50.8	0	-1285.6	2571.2	2602
Model 30	Species*Greenness+Species*Cover+ Season	2677.4	51	0	-1269.7	2539.4	2586
Model 27	Species*Greenness+Species*Cover	2680.1	53.7	0	-1272.1	2544.1	2587
Model 1	Species+Greenness+Cover+Season	2698.9	72.4	0	-1325.5	2650.9	2631
Model 18	Species*Cover+Greenness+Season	2701.1	74.7	0	-1311.5	2623.1	2616
Model 2	Species+Greenness+Cover	2701.7	75.3	0	-1327.9	2655.7	2632
Model 19	Species*Cover+Greenness	2703.3	76.9	0	-1313.7	2627.3	2617
Model 13	Species*Season+Greenness	2762.4	136	0	-1343.2	2686.4	2617
Model 26	Species*Greenness+Species*Season	2769.8	143.4	0	-1316.9	2633.8	2587
Model 14	Species*Season+Cover	2782.4	156	0	-1354.2	2708.4	2618
Model 10	Species*Greenness+Season	2816.3	189.9	0	-1355.1	2710.3	2602
Model 11	Species*Greenness	2818.1	191.7	0	-1357.1	2714.1	2603
Model 25	Species+Cover*Season	2841.0	214.6	0	-1397.5	2795.0	2632

Model 4	Species+Greenness+Season	2844.6	218.2	0	-1399.3	2798.6	2632
Model 5	Species+Greenness	2846.3	219.9	0	-1401.2	2802.3	2633
NULL	-	3654.5	1028.1	-	-	-	-

FIGURES

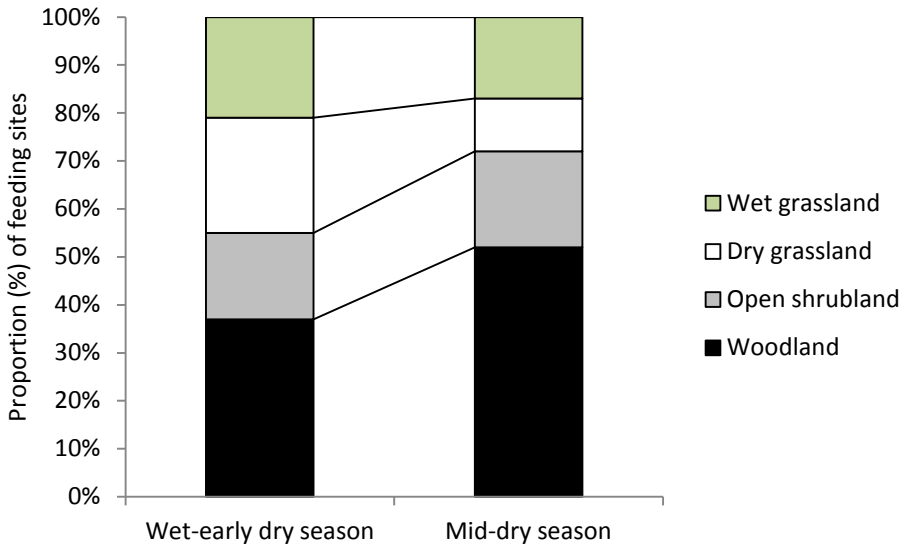
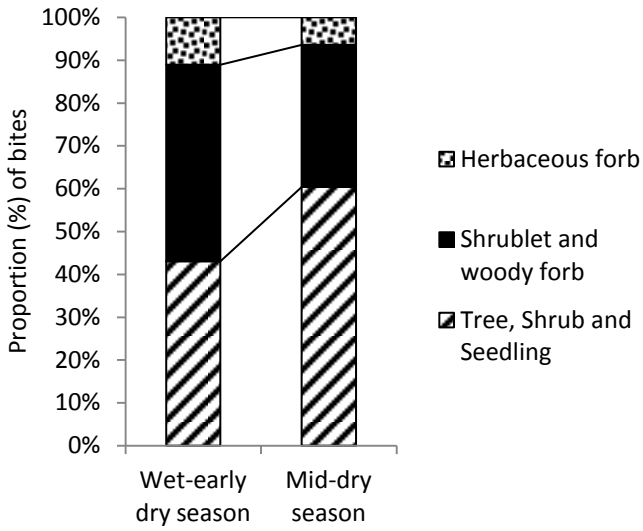


Fig. 1: Proportions of eland feeding sites in each of the four main habitat types of KMR (woodland, open shrubland, dry grassland, and wet grassland). Proportions were calculated as the total number of feeding sites for each habitat type divided by the total number of feeding sites recorded across all habitat types in each season.

a) Browse dietary contribution by growth types



b) Total dietary contribution by growth types

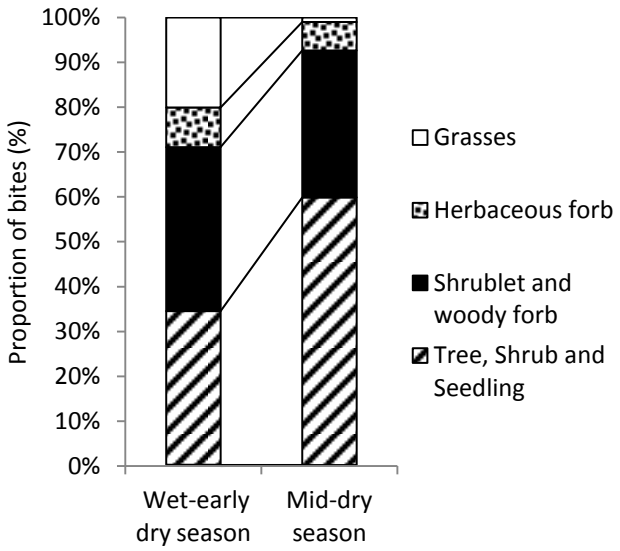


Fig. 2: Dietary contribution of growth forms to the seasonal "browse diet" of the eland (a), and to the "total seasonal diet" (b).

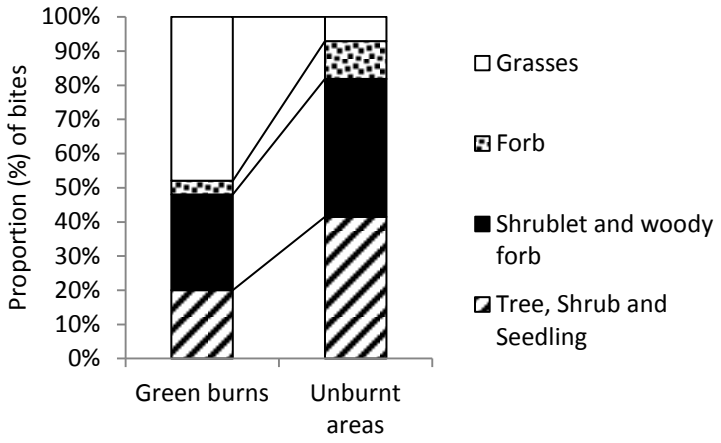


Fig. 3: Proportions of bites recorded on plant species, divided by growth type, on "green" burns, offering a flush of new plant material, and on unburnt areas.

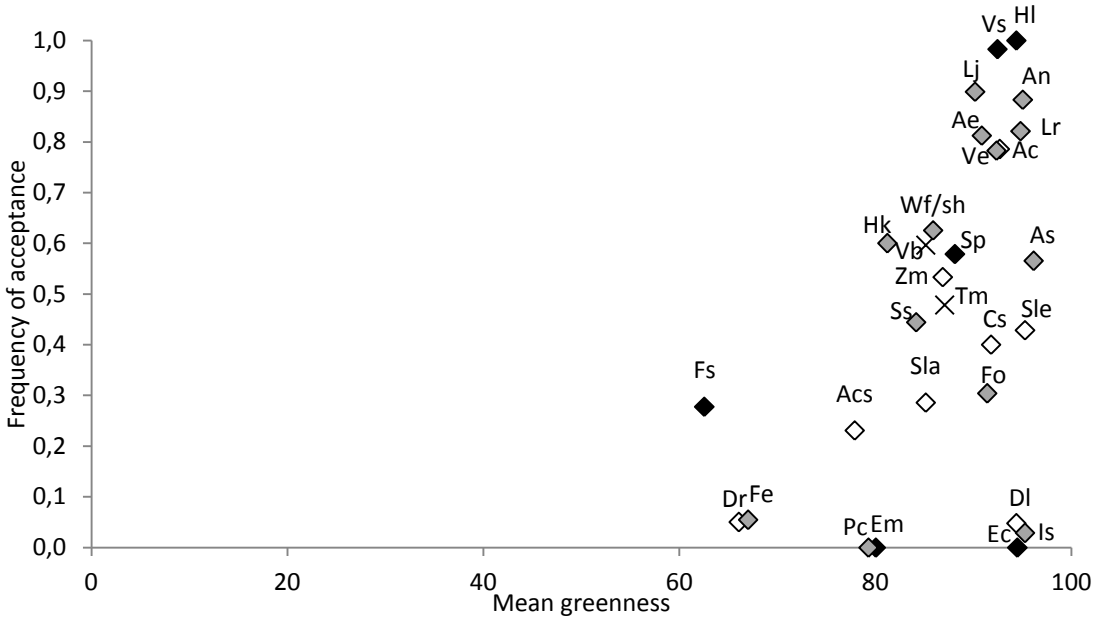


Fig. 4: Frequencies of acceptance and greenness (average) of dicotyledonous plant species recorded at ≥ 10 feeding patches during the late wet-early dry season transition period. The plant species displayed are the following: Ac (*Acacia caffra*); Acs (*Acacia* sp); An (*Ancylobotrys capensis*); As (*Asparagus* sp); Ae (*Athrixia elata*); Cs (*Combretum* sp); Dl (*Diospyros lycioides*); Dr (*Dombeya rotundifolia*); Em (*Englerophytum magalismontanum*); Ec (*Euclea crispa*); Fs (*Faurea saligna*); Fe (Ferns); Fo (Herbaceous forbs); Hl (*Halleria lucida*); Hk (*Helichrysum kraussii*); Is (*Indigofera* sp); Lr (*Lantana rugosa*); Lj (*Lippia javanica*); Pc (*Parinari capensis*); Sla (*Searsia lancea*); Sle (*Searsia lepodyctia*); Sp (*Searsia pyroides*); Ss (*Solanum* spp); Tm (*Tagetes minuta*); Vs (*Vangueria parvifolia*); Vb (*Verbena bonariensis*); Ve (*Vernonia* spp); Wf (Woody forbs); Zm (*Ziziphus mucronata*). Palatability classes have been established according to van Wyk & van Wyk (2007).

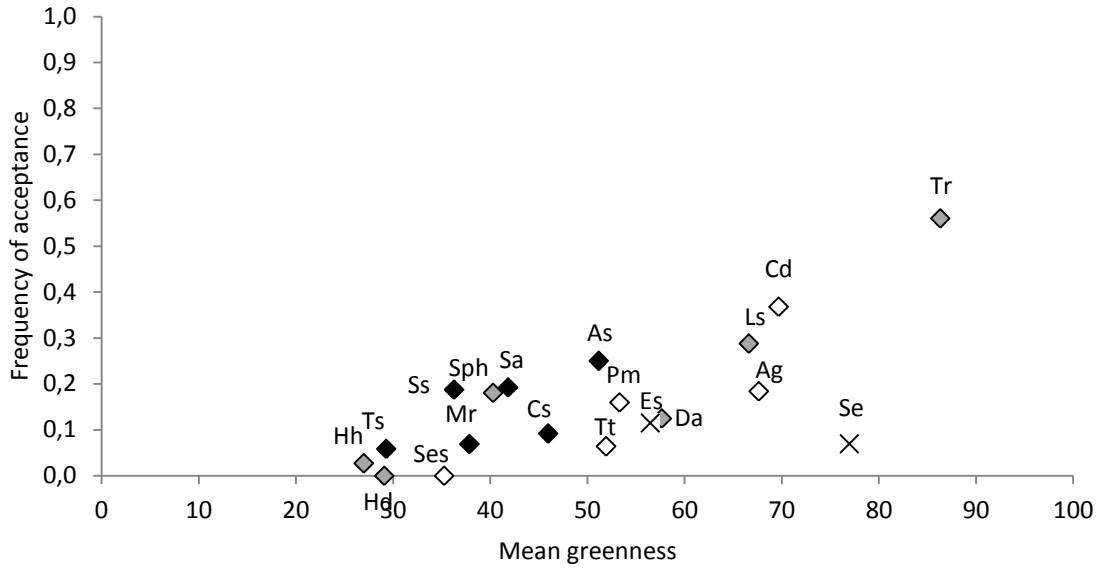


Fig. 5: Frequencies of acceptance and greenness (average) of monocotyledonous plant species recorded at ≥ 10 feeding patches during the late wet season-early dry season transition period. The plant species displayed are the following: Ag (*Andropogon gayanus*); As (*Aristida* sp); Cd (*Cynodon dactylon*); Cs (*Cymbopogon* sp); Da (*Diheteropogon amplectens*); Es (*Eragrostis* spp); Hd (*Hypertelia dissoluta*); Hh (*Hyparrhenia hirta*); Ls (*Loudetia simplex*); Mr (*Melinis repens*); Pm (*Panicum maximum*); Sa (*Sporobolus africanus*); Se (Sedges); Ses (*Setaria* sp); Sph (*Setaria sphacelata*); Ss (*Schizachyrium sanguineum*); Tr (*Tristachya leucothrix*); Ts (*Trachypogon spicatus*); Tt (*Themeda triandra*). Palatability classes have been established according to van Outdshoorn (2006). The *Eragrostis* spp and "Sedges" groups could not be assigned respectively to a single palatability class, due to the heterogeneity in the characteristics of member species.

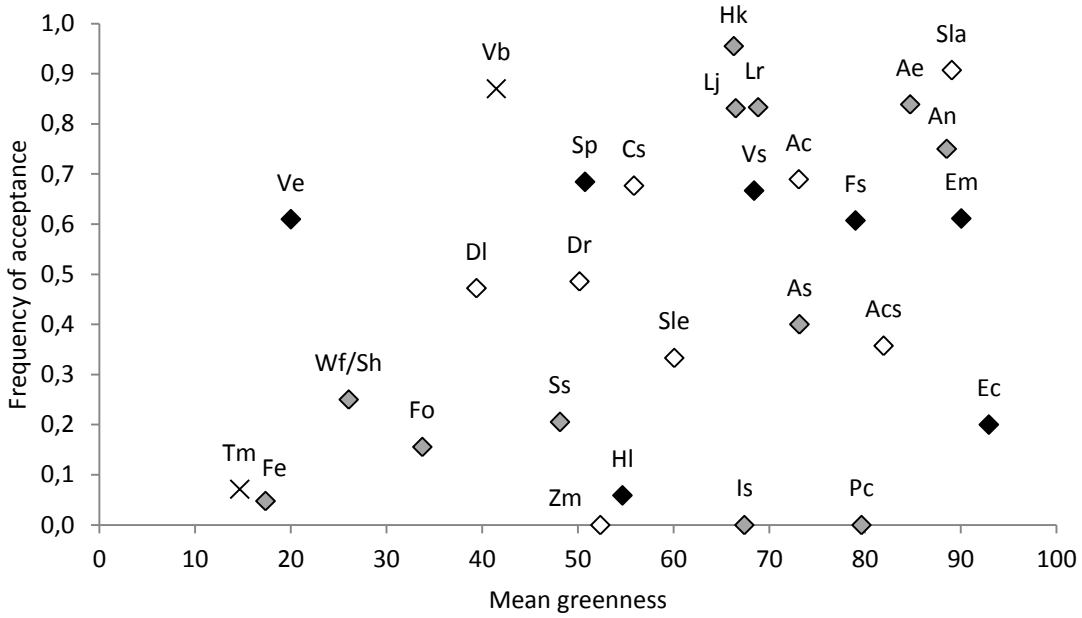


Fig. 6: Frequencies of acceptance and greenness (mean) of dicotyledonous plant species recorded at ≥ 10 feeding patches during the dry season. The plant species displayed are the following: Ac (*Acacia caffra*); Acs (*Acacia* sp); An (*Ancylobotrys capensis*); As (*Asparagus* sp); Ae (*Athrixia elata*); Cs (*Combretum* sp); Dl (*Diospyros lycioides*); Dr (*Dombeya rotundifolia*); Em (*Englerophytum magalismontanum*); Ec (*Euclea crispa*); Fs (*Faurea saligna*); Fe (Ferns); Fo (Herbaceous forbs); Hl (*Halleria lucida*); Hk (*Helichrysum kraussii*); Is (*Indigofera* sp); Lr (*Lantana rugosa*); Lj (*Lippia javanica*); Pc (*Parinari capensis*); Sla (*Searsia lancea*); Sle (*Searsia lepodyctia*); Sp (*Searsia pyroides*); Ss (*Solanum* sp); Tm (*Tagetes minuta*); Vs (*Vangueria parvifolia*); Vb (*Verbena bonariensis*); Ve (*Vernonia* sp); Wf (Woody forbs); Zm (*Ziziphus mucronata*). Palatability classes have been established according to van Wyk & van Wyk (2007).

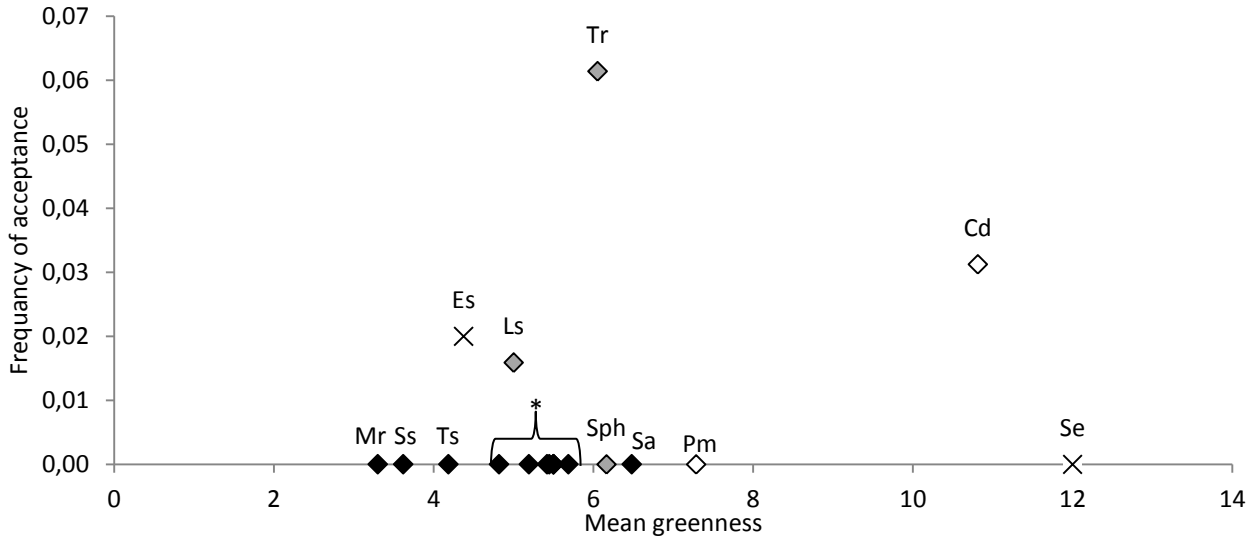


Fig. 7: Frequencies of acceptance and mean greenness of monocotyledonous plant species recorded at ≥ 10 feeding patches during the dry season. The plant species displayed are the following (the species referring to points in the brackets could not be displayed in the graph due to limited space, and are indicated with a *): Ag* (*Andropogon gayanus*); As* (*Aristida* sp); Cd (*Cynodon dactylon*); Cs* (*Cymbopogon* sp); Da* (*Diheteropogon amplectens*); Es (*Eragrostis* sp); Hd* (*Hypertelia dissoluta*); Hh* (*Hyparrhenia hirta*); Ls (*Loudetia simplex*); Mr (*Melinis repens*); Pm (*Panicum maximum*); Sa (*Sporobolus africanus*); Se (Sedges); Ses* (*Setaria* sp); Sph (*Setaria sphacelata*); Ss (*Schizachyrium sanguineum*); Tr (*Tristachya leucothrix*); Ts (*Trachypogon spicatus*); Tt* (*Themeda triandra*). Palatability classes have been established according to van Outdshoorn (2006). The *Eragrostis* spp and "Sedges" groups could not be assigned respectively to a single palatability class, due to the heterogeneity in the characteristics of member species.

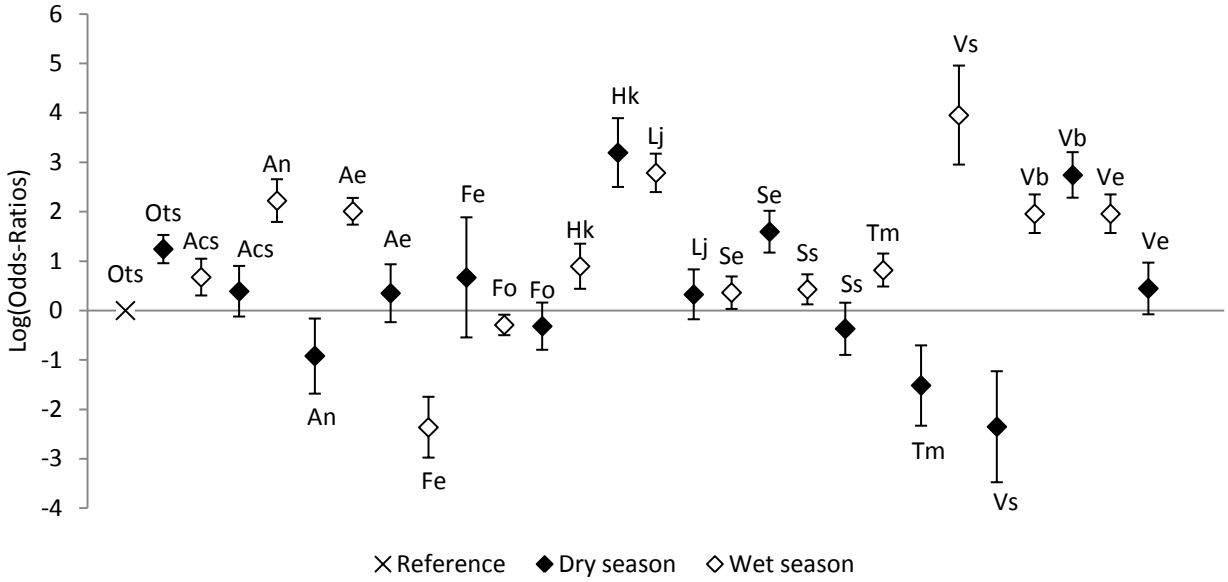


Fig. 8: Log-odds of the interaction between dicot species (or group, when species had been lumped together at the genus or feeding type level), and season (in this case, the late-wet early dry season of the study) derived from the coefficients of the best mixed-effects logistic regression model. The baseline category is represented by the "other trees/shrubs" groups, interacting with the mid-dry season. The plant species and groups displayed in the graph are: Acs (*Acacia* sp); An (*Ancylobotrys capensis*); Ae (*Athrixia elata*); Fe (Ferns); Fo (Herbaceous forbs); Hk (*Helichrysum kraussii*); Lj (*Lippia javanica*); Se (*Searsia* sp); Ss (*Solanum* sp); Tm (*Tagetes minuta*); Vs (*Vangueria parvifolia*); Vb (*Verbena bonariensis*); Ve (*Vernonia* sp); Wf/Sh (Woody forbs and shrublets/dwarf shrubs).

REFERENCES

ALLISON, P. (2004). Convergence problems in logistic regression. In ALTMAN, M., GILL, J., & MCDONALD, M. P. *Numerical issues in statistical computing for the social scientist*, 238-252, John Wiley & Sons, Hoboken, USA.

ANDERSON, D. R. (2008). *Model based inference in the life sciences: a primer on evidence*. Springer Science & Business Media, New York, USA.

APIO, A., & WRONSKI, T. (2005). Foraging behaviour and diet composition of bushbuck (*Tragelaphus scriptus* Pallas, 1766) in Queen Elizabeth National Park, western Uganda. *African Journal of Ecology*, **43**(3), 225-232.

ARCHIBALD, S., BOND, W. J., STOCK, W. D., & FAIRBANKS, D. H. K. (2005). Shaping the landscape: fire-grazer interactions in an African savanna.*Ecological applications*, **15**(1), 96-109.

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

BEALE, C. M., VAN RENSBERG, S., BOND, W. J., COUGHENOUR, M., FYNN, R., GAYLARD, A., GRANT, R., HARRIS, B., JONES, T., MDUMA, S., OWEN-SMITH, N., & SINCLAIR, A.R.E. (2013). Ten lessons for the conservation of African savannah ecosystems. *Biological conservation*, **167**, 224-232.

BELL, R. H. (1970). The use of the herb layer by grazing ungulates in the Serengeti. *Animal populations in relation to their food resources*, **10**, 111-124.

BELL, R. H. V. (1971). A grazing ecosystem in the Serengeti. *Scientific American*, **225**(1), 86-93.

BEN-SHAHAR, R. (1998). Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*, **136**(2), 189-189.

BONYONGO, C. M. (2005). Habitat Utilization by Impala (Aepyceros memmpus) in the Okavango Delta. *Botswana Notes and Records*, **37**, 227-235.

BRASHARES, J. S., GARLAND, T., & ARCESE, P. (2000). Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behavioral Ecology*, **11**(4), 452-463.

BREDENKAMP, G. J. (1978). A synecological account of the Suikerbosrand Nature Reserve. I. The phytosociology of the Witwatersrand geological system. *Bothalia*, **12**(3), 513-529.

BRYANT, J. P., PROVENZA, F. D., PASTOR, J., REICHARDT, P. B., CLAUSEN, T. P., & DU TOIT, J. T. (1991). Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, **22**, 431-446.

BUYS, D. (1990) Food selection by eland in the western Transvaal. *South African Journal of Wildlife Research*, **20**, 16-20.

BURNHAM, K. P., & ANDERSON, D. R. (2001). Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, **28**(2), 111-119.

CODRON, D., CODRON, J., LEE-THORP, J. A., SPONHEIMER, M., DE RUITER, D., SEALY, J., GRANT, R., & FOURIE, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, **273**(2), 21-29

COOPER, S. M., & OWEN-SMITH, N. (1986). Effects of plant spinescence on large mammalian herbivores. *Oecologia*, **68**(3), 446-455.

CROMSIGT, J. P., & OLFF, H. (2006). Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, **87**(6), 1532-1541.

D'AMMANDO, G., PARRINI, F., ATTORRE, F., & Boitani, L. (2015). Observations on dry season grazing by eland in a Magaliesberg Nature Reserve, South Africa.*African Journal of Ecology*, **53**(1), 112-115.

DEMMENT, M. W., & VAN SOEST, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *American Naturalist*, **125**(5), 641-672.

DU TOIT, J. T. (1986). *Patterns of resource use within the browsing ruminant guild in the central Kruger National Park.* PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

DU TOIT, J. T., & OWEN-SMITH, N. (1989). Body size, population metabolism, and habitat specialization among large African herbivores. *The American Naturalist*, **133**(5), 736-740.

ESTES, R. D., ATWOOD, J. L., & ESTES, A. B. (2006). Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. *Biological Conservation*, **131**(1), 106-120.

EVANS, P. G. H. (1979). Habitat preferences of ungulates in closed savanna of central Africa. *Mammal Review*, **9**(1), 19-32.

FABRICIUS, C. (1989). *Habitat suitability assessment for indigenous browsing ungulates in the Northern Cape*, PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

FABRICIUS, C., & MENTIS, M. T. (1990) Seasonal habitat selection by eland in arid savanna in southern Africa. *South African Journal of Zoology*, **25**(4), 238-244.

FERNÁNDEZ, M. H., & VRBA, E. S. (2005). Body size, biomic specialization and range size of African large mammals. *Journal of Biogeography*, **32**(7), 1243-1256.

FIELD, C. R. (1975) Climate and the food habits of ungulates on Galana Ranch. *African Journal of Ecology*, **13**, 203-220.

FYNN, R. W., & BONYONGO, M. C. (2011). Functional conservation areas and the future of Africa's wildlife. *African Journal of Ecology*, **49**(2), 175-188.

GAGNON, M., & CHEW, A. E. (2000). Dietary preferences in extant African Bovidae. *Journal of Mammalogy*, **81**(2), 490-511.

GILL (2012). *Wild flowers of the Magaliesberg*. Gill/Engelbrecht Edition, South Africa.

GRAZIANI, P., & D'ALESSIO, S. G. (2004). *Monitorage radiotelemetrique de l'Eland de Derby- Relatione finale*. ECOFAC-ZVC Project, Istituto di Ecologia Applicata, Roma, Italy.

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.

HEJCMANOVÁ, P., HOMOLKA, M., ANTONÍNOVÁ, M., HEJCMAN, M., & PODHÁJECKÁ, V. (2010). Diet composition of western Derby eland (*Taurotragus derbianus derbianus*) in the dry season in a natural and a managed habitat in Senegal using faecal analyses. *South African Journal of Wildlife Research*, **40**(1), 27-34.

HENSMAN, M. C., OWEN-SMITH, N., PARRINI, F., & BONYONGO, C. M. (2014a). Resource use and the nutritional status of sable antelope in the Okavango Delta region of northern Botswana. *African Journal of Ecology*, **52**(3), 265-273.

HILLMAN, J. C. (1979). *The biology of the Eland (Taurotragus oryx) in the wild*. PhD Thesis, University of Nairobi, Nairobi, Kenya.

HILLMAN, J. C. (1986). Aspects of the biology of the bongo antelope *Tragelaphus euryceros* Ogilby 1837 in South-West Sudan. *Biological Conservation*, **38**(3), 255-272.

HILLMAN, J. C. (1987). Group size and association patterns of the common eland (Tragelaphus oryx). *Journal of Zoology*, **213**(4), 641-663.

HILLMAN, J. (1988). Home range and movement of the common eland (*Taurotragus oryx* Pallas 1766) in Kenya. *African Journal of Ecology*, **26**(2), 135-148.

HOFMANN, R. R. (1973) *The ruminant stomach. Stomach structure and feeding habits of East African game ruminants.* East African Monographs in Biology, 2. East African Literature Bureau, Nairobi.

HOFMANN, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia*, **78**(4), 443-457.

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

JARMAN, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(1), 215-267.

KARTZINEL, T. R., CHEN, P. A., COVERDALE, T. C., ERICKSON, D. L., KRESS, W. J., KUZMINA, M. L., ... & PRINGLE, R. M. (2015). DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences*, **112**(26), 8019-8024.

KELSO, D. L. (1986). *Resource Partitioning Between Browsing Ungulates: Kudu (Tragelaphus strepsiceros) and Eland (Taurotragus oryx) in Pilansberg National Park, Bophuthatswana*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

KERR, M. A., WILSON, V. J., & ROTH, H. H. (1970). Studies on the agricultural utilization of semi-domesticated eland (Taurotragus oryx) in Rhodesia. 2. Feeding habits and food preferences. *Rhodesian Journal of Agricultural Research*, **8**, 71-77.

KINGDON, J. (1982). East African mammals. Vol. III C. University of Chicago Press, Chicago, USA.

LAMPREY, H. F. (1963). Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika1. *African Journal of Ecology*, **1**(1), 63-92.

LITVAITIS, J. A. (2000). Investigating food habits of terrestrial vertebrates. In BOITANI, L., & FULLER, T. K. *Research techniques in animal ecology: controversies and consequences*, 165-190. Columbia University Press, New York, USA.

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

MANSER, M. B., & BROTHERTON, P. N. M. (1995). Environmental constraints on the foraging behaviour of a dwarf antelope (*Madoqua kirkii*). *Oecologia*, **102**(4), 404-412.

MCNAUGHTON, S. J., & GEORGIADIS, N. J. (1986). Ecology of African grazing and browsing mammals. *Annual review of ecology and systematics*, **17**, 39-65.

MIRANDA, M., DALERUM, F., & PARRINI, F. (2014). Interaction patterns within a multi-herbivore assemblage derived from stable isotopes. *Ecological Complexity*, **20**, 51-60.

MUNTHALI, S. M., & BANDA, H. M. (1992). Distribution and abundance of the common ungulates of Nyika National Park, Malawi. *African Journal of Ecology*, **30**(3), 203-212.

NEL, H. P. (2000). *Ecological management objectives and monitoring procedures for Rustenburg Nature Reserve, North West Province* . MSc Thesis, University of Pretoria, Pretoria, South Africa.

NEL, P., KNOOP, C., SEITHLAMO, W., TSHENKENG, P. (2011). *Animal population estimates for protected areas in the North-West Province.* Scientific Report, North West Parks and Tourism Board, Mafikeng, South Africa.

NOVELLIE, P. A. (1978). Comparison of the foraging strategies of blesbok and springbok on the Transvaal highveld. *South African Journal of Wildlife Research*, **8**(4), 137-144.

OUDTSHOORN, F. V. (2002). *Guide to grasses of Southern Africa*. Briza Publications, Pretoria, South Africa.

O'KANE, C. A., DUFFY, K. J., PAGE, B. R., & MACDONALD, D. W. (2011a). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, **27**(3), 249-258.

O'SHAUGHNESSY, R., CAIN, J. W., & OWEN-SMITH, N. (2014). Comparative diet and habitat selection of puku and lechwe in northern Botswana. *Journal of Mammalogy*, **95**(5), 933-942.

OWEN-SMITH, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, UK.

OWEN-SMITH, N. (1997). Distinctive features of the nutritional ecology of browsing versus grazing ruminants. *Proceedings of the 1st International Symposium on Physiologie and Ecology of Wild and Zoo Mammals.* Supplement II, 176-191.

OWEN-SMITH, N. (2002). *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge University Press, UK.

OWEN-SMITH, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, **117**(4), 602-610.

OWEN-SMITH, N., & CHAFOTA, J. (2012). Selective feeding by a megaherbivore, the African elephant (*Loxodonta africana*). *Journal of Mammalogy*, **93**(3), 698-705.

OWEN-SMITH, N., & COOPER, S. M. (1987a). Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, **68** (2), 319-331.

OWEN-SMITH, N., & COOPER, S. M. (1987b). Assessing food preferences of ungulates by acceptability indices. *The Journal of Wildlife Management*, **51**(2), 372-378.

OWEN-SMITH, N., MARTIN, J., & YOGANAND, K. (2015). Spatially nested niche partitioning between syntopic grazers at foraging arena scale within overlapping home ranges. *Ecosphere*, **6**(9), 1-17.

OWEN-SMITH, N., & NOVELLIE, P. (1982). What should a clever ungulate eat?. *American Naturalist*, **119**(2), 151-178.

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

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

PELLEW, R. A. (1983). The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse*. *African Journal of Ecology*, **21**(4), 241-267.

PENG, C. Y. J., LEE, K. L., & INGERSOLL, G. M. (2002). An introduction to logistic regression analysis and reporting. *The Journal of Educational Research*, **96**(1), 3-14.

RAO, J. N., & SCOTT, A. J. (1981). The analysis of categorical data from complex sample surveys: chi-squared tests for goodness of fit and independence in two-way tables. *Journal of the American Statistical Association*, **76**(374), 221-230.

ROWE-ROWE, D. T. (1983). Habitat preferences of five Drakensberg antelopes. *South African Journal of Wildlife Research*, **13**(1), 1-8.

SCOONES, I. (1995). Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. *Journal of Arid Environments*, **29**(2), 221-237.

SCOTCHER, J. S. B. (1983). *Interrelations of vegetation and eland (Taurotragus oryx Pallas) in Giant's Castle Game Reserve, Natal*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

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**(11), 789-795.

SHEPPE, W., & OSBORNE, T. (1971). Patterns of use of a flood plain by Zambian mammals. *Ecological Monographs*, **41**(3), 179-205.

SHORROCKS, B. (2007). *The biology of African savannahs*. Oxford University Press, Oxford, UK.

SENSENIG, R. L., DEMMENT, M. W., & LACA, E. A. (2010). Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology*, **91**(10), 2898-2907.

SINCLAIR, A. R. E. (1975). The resource limitation of trophic levels in tropical grassland ecosystems. *The Journal of Animal Ecology*, **44**(2), 497-520.

SPONHEIMER, M., LEE-THORP, J. A., DERUITER, D. J., SMITH, J. M., VAN DER MERWE, N. J., REED, K., GRANT, C.C., ALYFFE, L.K., ROBINSON, T.F. HEIDELBERGER, C., & MARCUS, W. (2003) Diets of southern African Bovidae: stable isotope evidence. *Journal of Mammalogy,* **84**, 471-479.

THOMAS, D. L., & TAYLOR, E. J. (1990). Study designs and tests for comparing resource use and availability. *The Journal of wildlife management*, **54**(2), 322-330.

THOULESS, C. (2014). *Tragelaphus oryx* Common Eland. In Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. *Mammals of Africa, Volume VI* (186-193), A & C Black, UK.

UNDERWOOD, R. (1975). Social behaviour of the eland (*Taurotragus oryx*) on Loskop Dam Nature Reserve .MSc Thesis, University of Pretoria, Pretoria, South Africa.

VALEIX, M., FRITZ, H., SABATIER, R., MURINDAGOMO, F., CUMMING, D., & DUNCAN, P. (2011). Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, **144** (2), 902-912.

VAN DER MERWE, J. (2010). *Resource selection by impala (Aepyceros melampus) in savanna systems, South Africa: which factors govern forage selection in a mixed feeder?*, PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

VAN DER MERWE, J., & MARSHAL, J. P. (2012). Hierarchical resource selection by impala in a savanna environment. *Austral Ecology*, **37**(3), 401-412.

VAN SOEST, P. J. (1994). *Nutritional ecology of the ruminant*. Cornell University Press, USA.

VAN WYK, B. V., & VAN WYK, B. E. (2002). *Photographic guide to trees of Southern Africa*. Briza Publications, Pretoria, South Africa.

WALKER, B. H. (1976). An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *South African Journal of Wildlife Research*, **6**(1), 1-32.

WALLINGTON, B. P., MCKECHNIE, A. E., OWEN-SMITH, N., & WOODBORNE, S. (2007) Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *SOUTH African Journal of Wildlife Research*, **37**(2), 127-131.

WATSON, L. H., & OWEN-SMITH, N. (2000). Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, **38**(2), 130-137.

WESTERN, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, **13**(3-4), 265-286

WRONSKI, T. (2002). Feeding ecology and foraging behaviour of impala *Aepyceros melampus* in Lake Mburo National Park, Uganda. *African Journal of Ecology*, **40**(3), 205-211.

ZUUR, A. F., IENO, E. N., WALKER, N. J., SAVELIEV, A. A., & SMITH, G. M. (2009). Mixed effects modelling for nested data. In *Mixed effects models and extensions in ecology with R*, 101-142. Springer New York.

CHAPTER 4: CONCLUSIONS

Synthesis and key findings

The study was designed to address the environmental drivers of landscape, habitat, and plant species selection by eland (*Tragelaphus oryx*), and contributed to determine the resource requirements of this species within an insular-like protected area. A major outcome of the project is constituted by the first *a*-LoCoH estimates of home range extent for common eland obtained by GPS-collars in a fenced reserve (only five other home range estimates for eland currently available in the literature). The study also presents the only analysis of resource selection by eland at different spatial scales using a Type III Design (Manly *et al.*, 1993), and the first attempt to include NDVI (at the landscape and habitat scales) and visually-estimated greenness (at the plant species scale) as potential drivers of selectivity for this species. It also provides the only quantitative estimate, for eland, of seasonal selection for burns (exception made for descriptive statistics reported in Rowe-Rowe, 1983).

Building on a previous field survey of feeding sites carried out in the Kgaswane Mountain Reserve in 2013 (which produced a short note on the *African Journal of Ecology;* D'Ammando *et al.,* 2015), the research expanded by incorporating data on spatial ecology obtained from GPS-collars. Inter-seasonal comparisons of resource selection, and of potential drivers of selection, at the three spatial scales, were also made possible by additional field work which was conducted during the course of 2015 (March-April and July-August). Ideally, this study should have included a comparison of the resource-animal interactions between the thriving eland population in the KMR and dwindling populations of eland in other fenced reserves across southern Africa, but it would have been beyond the scope of an MSc project. Conclusions drawn from the present study pertains to the ecology of a population of eland free from predation pressure, and may help to determine if observed declines in other areas can be ascribed to limitations imposed by fences and other barriers to nomadism (Ogutu *et al.*, 2013), rather than to increased vulnerability to predators.

In KMR, I found evidence for occupation of spatially distinct seasonal home ranges by eland, associated with a shift in the use of vegetation types from woodland during the dry season, to grassland (wet and dry) and shrubland during the wet season. Eland are considered as nomadic ungulates in areas where human-made barriers do not (or did not) restrict

movements in response to rainfall and subsequent flushes of forbs and grasses, so that seasonal and inter-annual movements have been frequently reported in East and southern Africa (Hillman, 1988; Verlinden, 1998; Thouless, 2014). However, shift in home range location in small, fenced reserves, had never been observed before, though information presented by Kelso (1986) and Watson (1997) suggest that this pattern of space use may be present in other confined populations. These movements are generally reflected by dispersal from woodland into grassland and other sparsely wooded vegetation communities during the wet season, in both large, unrestricted ecosystems (Western, 1975; Rowe-Rowe, 1983; Hillman, 1988; Verlinden, 1998), and small, fenced reserves (Underwood, 1975; Buys, 1990; Watson & Owen-Smith, 2000). The preferential use of open areas during the wet season seems to be triggered by the availability of green and protein-rich grasses and forbs following rainfall events, causing a switch in dietary preference from browsing on woody plants, typical of the dry season, towards grazing and browsing on the new growth at ground levels (Underwood, 1975; Hillman, 1979; Buys, 1990). Eland in KMR also fed on woody plants during the wet season, and especially on those widely available in sparsely wooded vegetation. For example, the wet season abundance of new leaves on favoured deciduous species typical of sparsely wooded areas, such as *Vangueria parvifolia*, also contributed to attract eland outside of the woodland. As the dry season progressed, it therefore emerged that eland were able to diversify the use that they made of resources even in a fenced reserve. Woodland was already the most utilised vegetation type in March and April, confirming that a gradual shift from open to closed areas was taking place in concomitance with the maturation of grasses and browse in grassland and shrubland. In southern Africa, the wet season dispersal coincides with the coalescence of individuals of different ages and sexes into large nursery herds over the high-quality and abundant flushes of grasses and forbs (Underwood, 1975; Scotcher, 1983; Kelso, 1986; Watson, 1997); the nurseries are also functional to the collective defence of calves (Kruuk, 1972; Hillman, 1979). The use of woodland (or thickets, depending on local availability) during the dry season, similarly to what observed for other mammalian browsers, usually corresponds to a contracted size of the seasonal home range, while dispersal into grassland is paralleled by an increase in the extent of the home range (Owen-Smith, 1979, 1988; Kelso, 1986; Hillman, 1988). In the Pilanesberg National Park, where the area covered by grassland is very limited, eland also occupy large home ranges during the wet season, grazing in the least wooded vegetation communities (Kelso, 1986). In the Mountain

Zebra National Park (South Africa), where eland consume very little amounts of grasses and forbs, grassland is preferentially used during the wet season, mainly because of the availability of favoured shrublets (Watson & Owen-Smith, 2000). Thus, it seems that the use of open areas during the wet season has to be put in correlation with the presence of calves, which require accessible forage (grasses and forbs or dwarf shrubs) at low levels above the ground, and with the accelerated depletion rate of food resources caused by the increase in herd size (Underwood, 1975, Kelso, 1986). Furthermore, non-calving adult females and breeding males would join a nursery herd because of the anti-predator benefits deriving from living with large number of con-specifics (FitzGibbon, 1980), and because of the enhanced possibility of mating, as conceptions in southern Africa seem to coincide with the wet season (Wilson, 1969; Thouless, 2014). Moreover, the herd dynamics remained seemingly unaltered within the KMR, with eland congregating in a nursery herd probably at the start of the wet season (as suggested by largely overlapping home ranges), and remaining together until March-April 2015, when the nursery started to break into smaller sub-units (Appendix II). Evidence from GPS-collars data also suggested that eland were able to maintain their nomadic adaptations by shifting their range into previously unused areas during a particularly dry period in 2015.

I also found evidence of selection for burnt areas during the wet season. Authors including Underwood (1975), Kelso (1986), and Rowe-Rowe (1982, 1983), had also described intensive use of flushing burns. By removing senescent plant material opening up patches of short grasses, favoured by most browsing mammals (Owen-Smith & Cooper, 1987a; Owen-Smith, 1994; O'Kane *et al.*, 2011a), fires can provide weaned calves and yearlings, which cannot successfully harvest leaves and green shoots beyond their reach, with a source of protein-rich and easily-accessed forage. However, burns mostly utilised by eland within the seasonal ranges in KMR were located in open shrubland or woodland, where shrublets were often recorded to grow after fires, including the year-round favoured *Athrixia elata*. For this reason, selection for burns was not only prompted by the availability of green grasses, but also by the presence of new leaves on woody plants at low levels above the ground. In East Africa, the severe decline of large herbivores, including eland, documented in the Nairobi National Park (Kenya), and in the Ngorongoro Crater (Tanzania) has been imputed to the degradation of pastures following the abandonment of rotational burning practices by local pastoralists

(Estes, Atwood & Estes, 2006; Ogutu *et al.*, 2013). Thus, controlled burning should be considered as a valid tool for the management of eland populations.

Eland in KMR can be considered as "mixed feeders preferring browse", reflecting the descriptions of their feeding habits reported by Hofmann & Stewart (1972) and Owen-Smith (1997). Despite feeding on a considerable amount of different plant species, eland were by no means unselective roughage eaters, as suggested by Jarman (1974). Both among grasses and browse, the greenest available species were consumed year-round, and among the very green species, the most abundant ones were selected as staple food. However, the selectivity towards greenness was somewhat impeded by the large muzzle size, which precluded the nibbling of leaves and resulted in general consumption of entire shoots with attached foliage. Similarly, forb-browsing was also mostly restricted to tall, erect species, often presenting lignified central shoots. The trade-off between forage quality and quantity perfectly exemplifies the complex interrelations between a browser-like digestive system and a large body-size coupled with grazer-like habitat preferences and social organization (Hofmann & Stewart, 1972; Hillman, 1979). During the advancing drought of 2015, eland broadened their diet to include a wide variety of woody species, and also waxy and oil-rich leaves from species which had not been eaten during the previous wet-early dry transition period in 2015, nor during the dry season in 2013. The great potential for adaptability to local phenology of plant species was highlighted by the similarity between the acceptance of browse species calculated for the dry seasons of 2013 and the wet-early dry transition of 2015: because of the low rainfall in 2015, eland probably started to feed on species which would have been consumed further on in the dry months, and later in 2015 switched their diet to species of presumable low palatability. This resilience to food shortage, coupled with a tolerance for high level of secondary and toxic chemicals, probably constitute to key to the understanding of the successful persistence of a fenced-in eland population in the diminutive KMR.

Preferences for grass species by eland in KMR showed affinities with the grasses consumed in the Drakensberg. In fact, *Tristachya* species were favoured in both ecosystems, and exclusively during the growing season (Scotcher, 1983). *Lippia javanica*, a shrublet which had already been documented to be highly palatable to eland in both fenced (Kelso, 1986, Wallington *et al.*, 2007) and unfenced ecosystems (Hillman, 1979), constituted the most important fodder species in KMR. Dicot species already documented to feature prominently

in the diet of eland in protected areas of the South African bushveld (such as Loskop Dam Nature Reserve and Pilanesberg NP) were also recorded among the preferred foods in KMR, and included *Acacia caffra, Combretum zeyheri,* and *Searsia lepodyctia* (Underwood, 1975; Kelso, 1986). The estimated dietary preferences in KMR were also similar to those reported for the Suikesbosrand Nature Reserve, with *Searsia pyroides, Tagetes minuta,* and *Vangueria* species among the favoured browse (Wallington *et al.,* 2007). The present study also included the first records of eland feeding on *Englerophytum magalismontanum*, and on an invasive wetland weed, *Verbena bonariensis*. Unexpectedly, *Acacia karoo* was rarely eaten by eland in KMR and also in the nearby Pilanesberg NP (Kelso, 1986), while it gave a major contribution to the annual diet in Mountain Zebra NP (Watson & Owen-Smith. 2000). I suppose that the presence of *A. caffra,* with shorter thorns than *A. karroo* and with comparatively larger leaves, drew most of the browsing pressure away from other *Acacia* species. Generally, the availability of different vegetation communities in KMR, allowed for seasonal dietary switches between highly palatable plant species and buffer dry season forage constituted by evergreen woody plants.

Given these premises, I would like to remark the importance of "functional heterogeneity" (which is the environmental heterogeneity as perceived by ecological entities; Owen-Smith, 2004; Fynn *et al.,* 2016) at different spatial scales for the long-term viability of fenced-in populations of eland. The great variation in geomorphological structures and vegetation composition characterizing the KMR (and likely other small reserves such as Suikersbosrand NR; Wallington *et al.,* 2007), probably constitute a key factor for the persistence of a relatively large population of these nomadic antelopes, in spite of the barriers imposed to long-distance movements. The overall limited food abundance can thus be compensated by the diversified resources available to eland within the landscape, allowing for adaptive responses to phenological and biochemical changes at the different scales of foraging. The decline of eland in the Pilanesberg NP (Tambling & Du Toit, 2005) and Kruger National Park (Ogutu & Owen-Smith, 2006), where a diversified geomorphology is associated with the presence of key ecological gradients over a relatively vast landscape, is likely to be a consequence of changes in predatory pressure by lion (*Panthera leo*) due to human intervention, rather than of limited foraging opportunities arising from restrictions to nomadic movements.

Hillman (1979) described eland as "browsers in a grassland environment". This definition emerged from the combination of the analysis on social behaviour, which was strikingly similar to those of bulk grazers such as buffalo (*Syncerus caffer*; Sinclair, 1977; Winnie, Cross & Getz, 2008), with that of the habitat preferences (grazer-like during the wet season and browser-like during the dry season), and of the composition of the diet, which was invariably dominated by browse scattered over grassland and open savannah. I would add to this definition that southern African populations of eland should be regarded as seasonal visitors to grassland and other open vegetation communities, regularly commuting between a plains-dweller existence in periods of resource abundance, and a "concealed" life in woodland and thickets which hold the key resources for the continuative survival through the limiting periods.

Limitations of the study

During the first phase of the project (July 2013), only one GPS-collar could be deployed, thus limiting inter-annual comparisons to one collared animal (SAT1399). Watson & Owen-Smith (2000) stated that, given the continuously fluxing social system of the eland, patterns of spatial behaviour and forage selection exhibited by an individual would probably constitute a good inferential representation of the same patterns at a population scale. I strongly disagree with this view, on the basis that the apparent independency of adult eland from fixed structures, could lead to inter-individual differences in foraging choices.

The effect of the peculiar dry conditions experienced during the course of 2015 could not be inferred to the entire population of eland in KMR, because of the presence of only one collar (SAT1398) working continuously across the seasonal cycle. Additionally, the range shift exhibited by the only individual fitted with a functioning collar during the dry season of 2015 (SAT1398), into the largely inaccessible Rainbow Farms factually decoupled the study of resource selection at the landscape and habitat scales from the study of plant species selection (conducted on non-collared animals). In some occasions, collared animals ventured into deep gorges which proved to be of very difficult access to people, and thus I was forced to revert to visual scanning of the reserve in order to locate herds containing adult females. Thus, although the results for plant species selection of non-collared animals did not differ substantially from those observed for the tagged ones, caution should be taken when trying to relate estimates obtained from collars and estimates obtained from feeding site surveys.

I simply recorded the characteristics of used feeding sites (canopy cover, catenary position, vegetation-type), but I did not provide any estimate of selection at this scale, because corresponding available sites were not sampled (due to time and logistical constraints). Therefore, other local characteristics which have been overlooked might have shaped selection at the scale of feeding sites.

At the scale of the plant species, the major limitation was posed by the impossibility of observations of focal animals at close quarters. The study had to rely on a very superficial, and potentially inaccurate, estimate of dietary contribution, based on counting the observed fresh bite signs. Other methodologies, such as stable isotopes analysis of faecal samples, could have been adopted for reducing the biases deriving from the count of bite signs.

Management implications

The findings exposed in this study provide basic guidelines for the management of the eland population in KMR and in other insular-like reserves in the South African Highveld and Bushveld. Eland seem to thrive when provided with the opportunity of dispersing from woodland into lightly wooded areas offering different types of resources. The woodland communities offer key food resources in the form of evergreen trees and shrubs, such as *Searsia lancea*. Eventually, woodland would also offer cover during parturition for females, and during the first two-three weeks of calf concealment. At the same time, grassland, or at least vegetation-types with accessible browse at low levels above the ground (forbs and shrublets) coupled with the availability of short, nutritious grasses, provide calves and lactating females with protein-rich fodder plants during the wet season. In areas where tall, fibrous grasses are dominant, a burning policy should be implemented in order to improve the heterogeneity of the sward by creating patches of short, young grasses. Fires should be ignited prior to the rains, in order to provide the nursery herds with a flush of green plant material during the wet season. The presence of a wetland, though possibly not strictly necessary for the subsistence of eland, would constitute a magnet during all seasons by securing a continuous growth of new erect forbs and weeds. Fenced reserves considering the opportunity of introducing eland should therefore present a mosaic of open and closed vegetation-types, in order to accommodate the seasonal changes in the diet and social structure of the eland. The presence of woody species which are favoured throughout most of the geographical range of this antelope, and in particular of aromatic shrublets (*L. javanica, A. elata, Helychrisum* sp)

rarely consumed by other browsers, should also be regarded as a key factor in the successful establishment and persistence of eland populations.

KMR covers an area which is most probably large enough for eland to meet their nutritional and social requirements. Anyway, as there is evidence from this study (to be confirmed in the future) that Rainbow Farms may become a refuge during drought conditions, I would suggest the management authorities to completely remove the fence dividing the protected area from the privately-owned land. The vegetation in Rainbow Farms is thick with a rich understorey of woody plants (*pers. obs.*), and probably unattractive to most grazers. The removal of the fence would thus have a little impact on most species of large mammals present in the reserve, but may contribute to relieve the browsing pressure on woody plants during the dry season and also in conditions of drought.

The potential for interspecific competition between eland and sable antelope (*Hippotragus niger*) in KMR, according to the results of the present study, seems almost non-existent. The two species feed on a completely different array of plant species, and eland include relatively low proportions of grasses in their diet, as opposed to the purely grazing sable antelope (Parrini, 2006). Moreover, the grazing pressure exerted by eland on flushing burns is mostly concentrated during the wet season, while sable antelope make preferential use of the burnt patches of wet grassland during the dry season. I can assume that ecological segregation at the plant species scale seems to prevent competitive interactions in the use of the *vlei*: eland are mainly attracted by stands of wetland-dwelling forbs, while sable antelope usually seek for tall, stemmy grasses, or for flushing burnt areas with reduced forb cover (Parrini, 2006; Parrini & Owen-Smith, 2010). However, the limited extent of burns on wet grassland, which are sought after by sable antelope during the late dry season (Parrini & Owen-Smith, 2010), prevented any further comparison between the feeding ecology of the two species in this particular vegetation type. I would therefore recommend careful observations of both species over the use of the wet grassland during years of extensive burning. Conversely, potential for interspecific competition may actually exist between eland and greater kudu (*Tragelaphus strepsiceros*). Both species rely on browse as the main food source, and select for leaves and young shoots of *S. lancea* during the dry season. Segregation may however still be achieved by the use of different vegetation-types (kudu are seldom seen in grassland or shrubland), but the poor body conditions of kudu encountered during the dry spell of 2015 suggests that this

ungulate is probably under nutritionally-stressing conditions. Options for management should first address the resource requirements of the kudu population, and the causes of their low numbers within the reserve.

The valley woodland constitute a key resource area for eland in KMR, potentially governing the population fluctuations of these large ruminants through the abundance and quality of palatable and evergreen browse during the limiting season (Buys & Dott, 1991). Eland have been documented to exert an intensive browsing impact on woody vegetation, targeting favoured plant species and sensibly altering their physiognomy and recruitment (Nyengera & Sebata, 2010). Moreover, "horn-breaking" of branches from trees and shrubs has been reported as a particularly common behaviour, either for accessing leaves and green shoots or as a dominance display (mostly performed by adult males; Underwood, 1975; Kelso, 1986). Despite the extensive damage allocated to woody plants and the deriving concerns for ungulate management on fenced reserves, the consequences of both browsing and associated horn-breaking behaviour on the availability of browse remain unknown, confining any prediction on consumer-resource interactions to mere speculation. In KMR, horn-breaking was rarely observed, and on these rare occasions targeted plants were mainly constituted by small individuals of *S. lancea* and *A. caffra*. Browsing pressure is most prominent in the woodland during the dry months. Nel (2000) pointed out that eland were severely affecting the growth of *A. caffra* and *Z. mucronata* in the valleys, but I found that the vast majority individuals ascribed to these two species had escaped the height at which it was susceptible to browsing (<2.5 m). Open shrubland should not suffer from high browsing pressure, as this vegetation-type is only targeted during a restricted temporal window, possibly coinciding with green leaves production on *Vangueria parvifolia* (specimens of this tree seemed particularly able to coppice in response to browsing). However, it should be monitored during drought periods, when the long-lasting green leaves of the endemic *E. magalismontanum* are included in the seasonal diet. Dry and wet grassland do not apparently suffer from exposition to grazing by eland, which is selective and restricted to the growing season. The timing and location of burning should be carefully considered. Burning in KMR has been widely utilised to alleviate nutritional stress on sable antelope, resulting in fire ignition mostly confined to moisture-retaining bottomlands allowing for fast and abundant re-growth of grasses (Parrini & Owen-Smith, 2010). In order to maximize the attractive potential for eland, a burnt area should be locate on rocky slopes where fire can trigger new growth on shrublets (mainly *A.*

elata and *Helichrysum kraussii*), and subsequently create a mixed flush of both dicotyledonous and monocotyledonous plants. As woody plants often present a time-lagged response to rainfall (Pellew, 1983; Owen-Smith, 1994), a failure in the establishment of a grass flush due to inadequate rainfall would be compensated by the growth of new foliage on the shrublet layer. Eland were also making use of dry grassland in the dry season of 2013, probably because of flushing burns caused by early fires. Under such circumstances, I suggest that burning should be implemented not only during the mid-dry season (July and August), as to generate flushes lasting to the following wet season, but also immediately after the end of the rains, when new grasses and forbs would delay the home range shift to the woodland and thus alleviate the pressure on woody plants. Although results from this study suggest that eland avoid burns on wet grassland, the sprouting of new, green grasses in this vegetation type may provide lactating females with relatively high-quality forage resources during the critical late dry season (births likely occur between July and November; Appendix II). Further observations, in years of extensive burning of the wet grassland, are needed in order to establish the importance of grasses during the bottleneck in food availbilty between the dry season and the onset of the rains. Additionally, a beneficial fire policy for eland would also extend its scope to the woodland. Eland would indeed take advantage from the removal of the tall, unpalatable stands of *Sporobolus africanus* (van Outdhsoorn, 2006), which would create favourable conditions for the expansion of preferred short grasses, including *Cynodon dactylon*. The generation and consolidation of open glades within the woodland through burning, which can be colonized by forbs and shrublets, associated with the flush of new twigs, leaves, and shoots, on surviving shrubs and trees, may also constitute a benefit to the eland, which avoid the patches of extensive canopy cover where very little browse is available at ground levels. However, these solutions should be taken with enormous caution as they may have potentially irreversible effects on the diversity of woody plants and small animal life which assured the proclamation as UNESCO's World Biosphere Reserve for the Magaliesberg Range (Carruthers, 2014; http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/).

Directions for future research

In KMR, additional information is required on the changes in plant species selection by eland throughout the course of the year. The deployment of GPS-collars on eland should also be

renewed by the managers of the reserve, in order to investigate the relationships between landscape-habitat selection and long-term climatic influences on primary productivity. Moreover, a study on the distribution and abundance of woody plants within the reserve would be of great benefit to the understanding of selection processes at the largest spatial scales. A future research project should ideally be directed on investigating the chemical composition of plants species accepted and rejected by eland, and on its variation at the seasonal and landscape scales. It would especially interesting to determine if feeding choices at the plant species and plant parts scale would be influenced by the content of fibre, as reported by Watson & Owen-Smith (2000), or rather by the levels of crude protein, as instead documented by Field (1975). Accordingly, a study on the physiological changes in the digestive system that enable eland to accommodate the dietary switch from mixed feeding to browsing should also be potentially considered.

There would be the extremely interesting possibility of a study on fusion-fission herd dynamics. The research should focus on the inter-dependence between herd size and seasonal range size, and on the benefits of large associations in nursery herds for calf survival. Eland should however be individually collared or ear-tagged for photographic identification since observations at close quarters are not possible in KMR, resulting in extremely high costs for animal immobilization procedures and for acquiring adequate technologies.

On a much broader scale, research is desperately needed in order to address the major biotic and abiotic drivers of resource selection by eland, under the profound changes in land use and land management which are affecting the populations of nomadic and migratory ungulates across the entire African continent (Serneels & Lambin, 2001; Thirgood *et al.,* 2004; Ogutu *et al.*, 2009). At present, the management of eland populations in most protected areas is almost entirely based on a very limited knowledge of the ecological requirements of this species, and on the assumption that feeding and habitat preferences would be similar between inherently different eco-regions of East and southern Africa. This species is one of a limited number of large mammals lacking a detailed autoecological study in the “charismatic” ecosystems of Africa. Future research should address the long-term viability of eland populations confined to insular-like reserves, and further data is required to draw meaningful comparisons between areas where eland are subjected to predatory pressure. Under these premises, the conservation and successful management of eland populations in the future would receive a substantial

assistance from an improved knowledge of the ecology of this species in its interactions with the biotic and abiotic components of the African savannahs.

REFERENCES

BUYS, D. (1990) Food selection by eland in the western Transvaal. *South African Journal of Wildlife Research.* **20**, 16-20.

BUYS, D. & DOTT. H. M. (1991). Population fluctuations and breeding of eland Taurotragus oryx in a western Transvaal nature reserve. *Koedoe-African Protected Area Conservation and Science,* **34**(1), 31-36.

CARRUTHERS, V. (2014). *The Magaliesberg*. Protea Book House Pretoria, Pretoria, South Africa.

D'AMMANDO, G., PARRINI, F., ATTORRE, F., & Boitani, L. (2015). Observations on dry season grazing by eland in a Magaliesberg Nature Reserve, South Africa. *African Journal of Ecology*, **53**(1), 112-1

ESTES, R. D., ATWOOD, J. L., & ESTES, A. B. (2006). Downward trends in Ngorongoro Crater ungulate populations 1986–2005: conservation concerns and the need for ecological research. *Biological Conservation,* **131**(1), 106-120.

FIELD, C. R. (1975) Climate and the food habits of ungulates on Galana Ranch. *African Journal of Ecology,* **13**, 203-220.

FITZGIBBON, C. D. (1990). Mixed-species grouping in Thomson's and Grant's gazelles: the antipredator benefits. *Animal Behaviour*, **39**(6), 1116-1126.

FYNN, R. W., AUGUSTINE, D. J., PEEL, M. J., & GARINE-WICHATITSKY, M. (2016). Strategic management of livestock to improve biodiversity conservation in African savannahs: a conceptual basis for wildlife–livestock coexistence. *Journal of Applied Ecology*, **53**(2), 388-397.

HILLMAN, J. C. (1979). *The biology of the Eland (Taurotragus oryx) in the wild*. PhD Thesis, University of Nairobi, Nairobi, Kenya.

HILLMAN, J. (1988). Home range and movement of the common eland (*Taurotragus oryx* Pallas 1766) in Kenya. *African Journal of Ecology*, **26**(2), 135-148.

HOFMANN, R. R., & STEWART, D. R. M. (1972). Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants.*Mammalia*, **36**(2), 226-240.

JARMAN, P. (1974). The social organisation of antelope in relation to their ecology. *Behaviour*, **48**(1), 215-267.

KELSO, D. L. (1986). *Resource Partitioning Between Browsing Ungulates: Kudu (Tragelaphus strepsiceros) and Eland (Taurotragus oryx) in Pilansberg National Park, Bophuthatswana*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa

KRUUK, H. (1972). The spotted hyena: a study of predation and social behavior. The University of Chicago Press, Chicago, USA.

MANLY, B. F., MACDONALD, L. L., THOMAS, D. L., MCDONALD, T. L., & ERICKSON, W. P. (1993). *Resource selection by animals*. Chapman & Hall, London, UK.

NEL, H. P. (2000). *Ecological management objectives and monitoring procedures for Rustenburg Nature Reserve, North West Province* . MSc Thesis, University of Pretoria, Pretoria, South Africa.

NYENGERA, R., & SEBATA, A. (2010). Effect of eland density and foraging on *Combretum apiculatum* physiognomy in a semi-arid savannah. *African Journal of Ecology*, **48**(1), 45-50.

OGUTU, J. O., PIEPHO, H. P., DUBLIN, H. T., BHOLA, N., & REID, R. S. (2009). Dynamics of Mara–Serengeti ungulates in relation to land use changes. *Journal of Zoology*, **278**(1), 1-14.

OGUTU, J. O., OWEN-SMITH, N., PIEPHO, H. P., SAID, M. Y., KIFUGO, S., REID, R. S., & ANDANJE, S. (2013). Changing wildlife populations in Nairobi National Park and adjoining Athi-Kaputiei Plains: collapse of the migratory wildebeest. *Open Conservation Biology Journal*, **7**, 11-26.

O'KANE, C. A., DUFFY, K. J., PAGE, B. R., & MACDONALD, D. W. (2011a). Overlap and seasonal shifts in use of woody plant species amongst a guild of savanna browsers. *Journal of Tropical Ecology*, **27**(3), 249-258.

OWEN-SMITH, N. (1979). Assessing the foraging efficiency of a large herbivore, the kudu. *South African Journal of Wildlife Research*, **9**(3/4), 102-110.

OWEN-SMITH, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, UK.

OWEN-SMITH, N. (1994). Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, **75**(4), 1050-1062.

OWEN-SMITH, N. (1997). Distinctive features of the nutritional ecology of browsing versus grazing ruminants. *Proceedings of the 1st International Symposium on Physiologie and Ecology of Wild and Zoo Mammals.* Supplement II, 176-191.

OWEN-SMITH, N. (2002). *Adaptive herbivore ecology: from resources to populations in variable environments*. Cambridge University Press, UK.

OWEN-SMITH, N. (2004). Functional heterogeneity in resources within landscapes and herbivore population dynamics. *Landscape Ecology*, **19**(7), 761-771.

OWEN-SMITH, N., & COOPER, S. M. (1987a). Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*, **68**(2), 319-331.

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

PELLEW, R. A. (1983). The giraffe and its food resource in the Serengeti. I. Composition, biomass and production of available browse*. *African Journal of Ecology*, **21**(4), 241-267.

ROWE-ROWE, D. T. (1982). Influence of fire on antelope distribution and abundance in the Natal Drakensberg. *South African Journal of Wildlife Research*, **12**(4), 124-129.

ROWE-ROWE, D. T. (1983). Habitat preferences of five Drakensberg antelopes. *South African Journal of Wildlife Research*, 13, 1-8.

SERNEELS, S., & LAMBIN, E. F. (2001). Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti–Mara ecosystem. *Journal of Biogeography*, **28**(3), 391-407.

SINCLAIR, A. R. E. (1977). *The African buffalo: a study of resource limitation of populations*. University of Chicago Press, Chicago, USA.

SCOTCHER, J. S. B. (1983). *Interrelations of vegetation and eland (Taurotragus oryx Pallas) in Giant's Castle Game Reserve, Natal*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

TAMBLING, C. J., & DU TOIT, J. T. (2005). Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, **42**(3), 431-441.

THIRGOOD, S., MOSSER, A., THAM, S., HOPCRAFT, G., MWANGOMO, E., MLENGEYA, T., & BORNER, M. (2004). Can parks protect migratory ungulates? The case of the Serengeti wildebeest. *Animal Conservation*, **7**(02), 113-120.

THOULESS, C. (2014). *Tragelaphus oryx* Common Eland. In Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., & Kalina, J. *Mammals of Africa, Volume VI* (186-193), A & C Black, UK.

UNDERWOOD, R. (1975). Social behaviour of the eland (*Taurotragus oryx*) on Loskop Dam Nature Reserve.MSc Thesis, University of Pretoria, Pretoria, South Africa.

VAN OUDTSHOORN, F. V. (2002). *Guide to grasses of Southern Africa*. Briza Publications, Pretoria, South Africa.

VERLINDEN, A. (1998). Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *African Journal of Ecology*, **36**(2), 117-128.

WALLINGTON, B. P., MCKECHNIE, A. E., OWEN-SMITH, N., & WOODBORNE, S. (2007) Stable carbon isotope analysis of eland (*Taurotragus oryx*) diet in the Suikerbosrand Nature Reserve. *South African Journal of Wildlife Research,* **37**(2), 127-131.

WATSON, L. H. (1997). *The feeding ecology of eland in Mountain Zebra National Park*. PhD Thesis, University of the Witwatersrand, Johannesburg, South Africa.

WATSON, L. H., & OWEN-SMITH, N. (2000). Diet composition and habitat selection of eland in semi-arid shrubland. *African Journal of Ecology*, **38**(2), 130-137.

WESTERN, D. (1975). Water availability and its influence on the structure and dynamics of a savannah large mammal community. *African Journal of Ecology*, **13**(3-4), 265-286

WILSON, V. J. (1969). Eland, *Taurotragus oryx*, in eastern Zambia. *Arnoldia (Rhodesia)*, **4**(12), 1-9.

WINNIE JR, J. A., CROSS, P., & GETZ, W. (2008). Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). *Ecology*, **89**(5), 1457-1468.

APPENDIX I: RAINFALL AND TEMPERATURE IN THE KGASWANE MOUNTAIN RESERVE DURING THE STUDY PERIOD

Monthly rainfall parameters were collected by the Kgaswane Meteorological Station in the study area, by staff members of the North-West Parks and Tourism Board. The total monthly rainfall was chosen as the best index of precipitation during the study period, in order to define the different phases of the seasonal cycle. Data on temperature were sourced by the South African National Weather Service and referred to the Rustenburg Weather Station (~5 km from the study site). Mean monthly maximum and minimum temperatures were chosen to define, together with rainfall, the limits of each season (which, however, remained arbitrary).

FIGURES

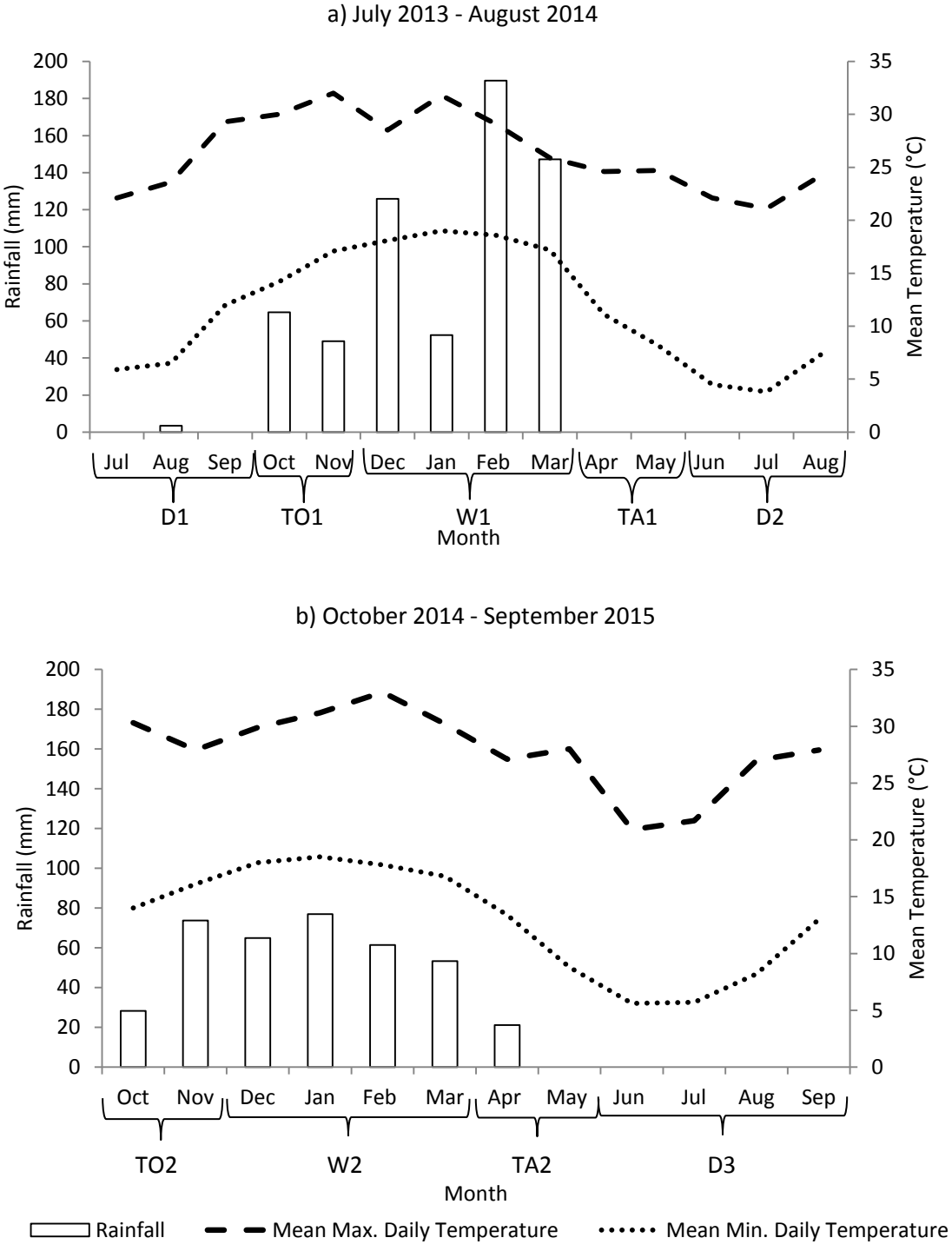


Fig. 1: Summary of rainfall and temperature data utilised to determine the phases of the seasonal cycle in KMR. Rainfall data represent the total monthly rainfall (mm) recorded by park's staff at the pluviometric station of KMR. Temperature is represented by monthly means of daily maximum and minimum temperatures, recorded at the Rustenburg Meteorological Station and sourced by the South African National Weather Service.

APPENDIX II: SIZE AND COMPOSITION OF ELAND GROUPS IN THE KGASWANE MOUNTAIN RESERVE

During field surveys in March-April 2015 and July-August 2015, I collected data on sex and age structure of focal herds in order to determine the potential association between seasonal changes in plant species selection and seasonal changes in social structure. Accurate estimates of age structure were not possible due to the above-mentioned impediments to close range observations, but individuals were qualitatively assigned, according to visible morphological features, to one of the following age/sex classes derived and modified from Hillman (1979):

1) Grey males: adult males with greyish colour of the neck and forequarters, extensive dewlap with absent hair tuft, and evident frontal brush of black hair.
2) Brown males: mature individuals with sexual secondary characters not fully developed, brown coat colour, tuft of black hair on the dewlap, and little development of frontal hair brush.
3) Adult females: fully grown females with long, sharp horns, and presenting a thin spiral at the base of the horns. The dewlap is smaller than in adult males and presents a black hair tuft.
4) Subadults: immature individuals , smaller in body size than adults, with horn tips pointing laterally. All subadults lumped in one category, as it was impossible to determine the sex of subadults through direct observation.
5) Yearlings and large calves: individuals presenting "spike" horns of various length, from half ear length to more than the ear length and pointed anteriorily. Due to the shyness of the study population, yearling and large calves could not be assigned accurately to two different age classes according to accurate estimates horn length and rotation.
6) Newborn calves: small calves lacking horns and generally showing an association bond with an adult female (presumably their mother) for lactation, sometimes hidden in tall grasses or scrub.

Focal herds were categorized as "mixed herds", when composed by adult males, females and subadults, and "nursery herds", when comprising individuals of the above-mentioned age/sex classes associated with yearlings/large calves or newborn calves. This distinction was based

on observations reported by Hillman (1988). In some cases, it was impossible to count all of the individuals in a herd for each age/sex class, and therefore for these incomplete observations the only information retained in our dataset was that pertaining the herd type (mixed or nursery).

Mean herd size was calculated (with associated Standard Error, SE) separately for the two data collection periods, along with mean size of nursery and mixed herds. Additionally, I calculated the mean number of individual per age/sex class per herd for each season, and repeated the calculations separately for the nursery and mixed herds.

The mean number of individuals in nursery herds slightly declined between March and April (from 34.42 ± 3.46 to 27.5 ± 2.63), and was reduced to very low numbers in July (10 ± 1.22) and August (13.67 ± 2.11; **Fig. 1**). The size of mixed herds remained similar throughout the study period, but was somewhat larger in March (8.07 ± 1.24) than during the other months (**Fig. 1**). Grey and brown males completely vacated the nursery in July and August (**Fig. 2**). The number of adult females associated with the nursery was very low in July, but increased again in August (**Fig. 1**). At least four lactating and very small calves were seen during the third week of August while following their respective mothers, indicating that calving started by the first week of the same month (calves are usually hidden for a couple of weeks before being able to follow their mothers during foraging activities). Females with dependent offspring frequently joined the nursery, thus resulting in the increased numbers of adult females observed in the nursery herd. Conversely, all calves observed during March and April in the nursery were already weaned, and there was no evidence that adult females gave birth during the late phases of the wet season. The number of weaned calves and yearlings in the nursery decreased during the dry season, along with the number of subadults, possibly as a consequence of increasing independence of growing individuals from the protection offered by the crèche (**Fig. 2**). The composition of mixed herds did not show any significant variation during the study period, except for the high number of adult females observed in March (**Fig. 3**). In fact, large groups of adult females sometimes departed from the main nursery herd during this month, with no attached calves, and were ascribed to the mixed herds category, thus possible contributing to an over-estimated abundance of this age class (**Fig. 3**).

FIGURES

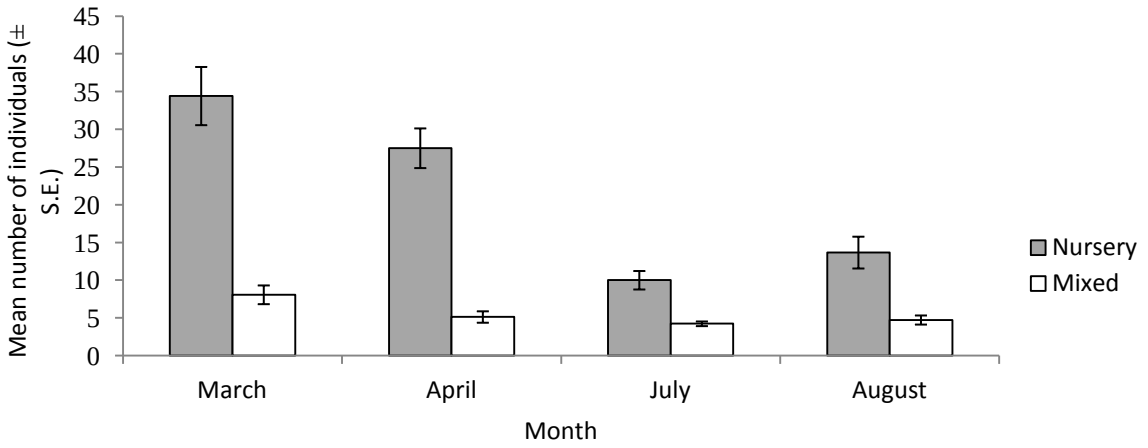


Fig. 1: Mean number of individuals (± SE) recorded for each month of the study period in nursery herds (containing calves and yearlings) or mixed herds (containing only adult and subadult animals).

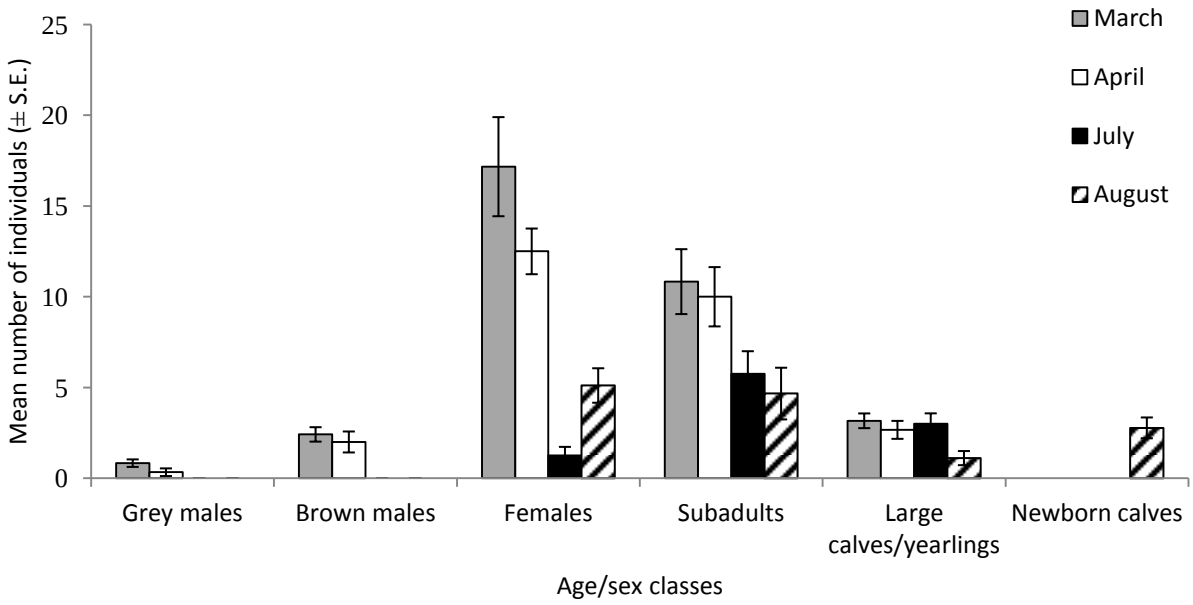


Fig. 2: Mean number of individuals (± SE) recorded in each age/sex class in the mixed-sex herds for each month of the study period. Note that newborn calves (calves still being lactated and left behind hidden in tall grasses/scrub when the herd is moving) were reported only for the month of August.



Fig. 3: Mean number of individuals (± SE) recorded in each age/sex class in the mixed-sex herds for each month of the study period.

APPENDIX III: LIST OF PLANT SPECIES EATEN BY ELAND IN THE KGASWANE MOUNTAIN RESERVE

Family and Species	Eaten (+)
Anacardiaceae	
Ozoroa paniculosa	+
Sclerocarya birrea	
Searsia discolor	
Searsia lancea	+
Searsia lepodyctia	+
Searsia magalismontana	
Searsia pyroides	+
Searsia rigida	
Apocynaceae	
Ancylobotrys capensis	+
Cryptolepis oblongifolia	+
Diplorhynchus condylocarpon	
Gomphocarpus fruticosus	+
Rauvolfia caffra	+
Asparagaceae	
Asparagus flavicaulus	+
Asparagus transvaalensis	+
Asteraceae	
Artemisia afra	+
Athrixia elata	+
Bidens pilosa	+
Brachylaena rotundata	+
Helichrysum kraussii	+
Hilliardiella hirsuta	+
Polydora poskeana	+
Senecio sp	+
Seriphium plumosum	+
Tagetes minuta	+
Vernonia sp	+
Boraginaceae	
Ehretia rigida	+

Cactaceae

Opuntia ficus-indica

Cannabaceae

Celtis africana +
Trema orientalis +

Capparaceae

Maerua caffra +

Chrysobalanaceae

Parinari capensis

Celastraceae

Gymnosporia buxifolia
Gymnosporia polyacanthus
Gymnosporia tenuifolia

Combretaceae

Combretum erythrophyllum +
Combretum molle +
Combretum zeyheri +

Ebenaceae

Diospyros lycioides +
Euclea crispa +

Euphorbiaceae

Acalypha villicaulus +
Clutia pulchella +

Fabaceae

Acacia (Senegalia) caffra +
Acacia dealbata +
Acacia (Vachellia) karroo +
Acacia (Vachellia) nigrescens
Acacia (Vachellia) nilotica
Acacia (Vachellia) robusta

Burkea africana	+
Dicrostachys cinerea	+
Elephanthorriza burkei	
Indigofera sp	+
Mundulea sericea	
Peltophorum africanum	+
Philenoptera violacea	
Rynchosia adenodes	
Rynchosia monophylla	+
Rynchosia nitens	+
Sutherlandia sp	+
Tephrosia sp	
Zornia linearis	+
Icacinaceae	
Apodytes dimidiata	+
Cassinopsis ilicifolia	
Lamiaceae	
Becium obovatum	
Plectranthus sp	+
Loganiaceae	
Strychnos madagascariensis	
Strychnos pungens	+
Malvaceae	
Grewia flava	+
Grewia monticola	+
Grewia occidentalis	+
Hibiscus calyphyllus	+
Moraceae	
Ficus albutilifolia	
Myricaceae	
Morellia serrata	+
Myrtaceae	
Syzigium cordatum	

Ochnaceae	
Ochna pulchra	
Olacaceae	
Ximenia caffra	+
Pentapetaceae	
Dombeya rotundifolia	+
Proteaceae	
Faurea saligna	+
Protea caffra	+
Protea gaguedii	+
Rhamnaceae	
Berchemia zeyheri	+
Helinus integrifolius	+
Ziziphus mucronata	+
Rosaceae	
Cliffortia linearifolia	+
Rubiaceae	
Canthium suberosum	+
Vangueria infausta	+
Vangueria parvifolia	+
Rutaceae	
Zanthoxylum capense	+
Salicaceae	
Salix mucronata	
Sapindaceae	
Pappea capensis	+

Sapotaceae	
Englerophytum magalismontanum	+
Scrophulariaceae	
Alectra sessiliflora	+
Buddleja saligna	+
Selago sp	
Solanaceae	
Solanum delagoense	+
Solanum giganteum	+
Solanum mauritianum	+
Solanum pseudocapsicum	
Stilbaceae	
Halleria lucida	+
Nuxia congesta	
Thymelaeaceae	
Gnidia kraussiana	
Verbenaceae	
Lantana rugosa	+
Lippia javanica	+
Verbena bonariensis	+
Vitaceae	
Rhoicissus tridentata	+

Grass species found at feeding sites of eland, with species consumed by eland indicated as (+).

Family and species	Eaten
Poaceae	
Agrostis lachnantha	
Andropogon gayanus	+
Andropogon schirensis	+
Aristida adscensionis	
Aristida canescens	+
Aristida congesta	+
Aristida diffusa	+
Aristida scabrivalvis	
Aristida vestita	+
Bewsia biflora	
Bothriochloa bladhii	
Bothriochloa insculpta	
Brachiaria nigropedata	+
Brachiaria serrata	
Chloris virgata	
Cymbopogon excavatus	+
Cymbopogon plurinodis	
Cymbopogon validus	+
Cynodon dactylon	+
Digitaria eriantha	+
Diheteropogon amplectens	+
Eilonurus muticus	
Eragrostis sp	+
Eustachys paspaloides	
Heteropogon contortus	
Hyparrhenia hirta	+
Hyparrhenia thamba	
Hypertelia dissoluta	
Imperata cilindrica	
Loudetia simplex	+
Melinis repens	+
Miscanthus junceus	
Panicum maximum	+
Panicum natalense	+
Panicum repens	
Pennisetum sphacelatum	
Perotis patens	
Phragmites australis	+

Pogonarthria squarrosa	
Schizachyrium jeffreysii	+
Schizachyrium sanguineum	+
Setaria incrassata	
Setaria lindbergiana	
Setaria megaphylla	
Setaria sphacelata	+
Sporobolus africanus	+
Sporobolus festivus	
Sporobolus pyramidalis	+
Themeda triandra	+
Trachypogon spicatus	+
Triraphis andropogonoides	
Tristachya biseriata	+
Tristachya leucothrix	+
Tristachya rehmanii	+
Urelytrum agropyroides	

Species of ferns recorded at feeding sites, with those consumed by eland reported as (+).

Family and species	Eaten
Dennstaedtiaceae	
Pteridium aquilinum	+
Pteridaceae	
Pellaea calomelanos	+
Pellaea viridis	