RESOURCES OVERLAP AND THE DISTRIBUTION OF GRAZER ASSEMBLAGES AT TELPERION AND EZEMVELO NATURE RESERVES

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A Research Report submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in partial fulfilment of the requirements for the degree of Master of Science.

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DECLARATION

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

27th of September, 2017

ABSTRACT

The distribution of grazing herbivores is influenced by several factors, including spatial and temporal availability of resources. The Telperion and Ezemvelo Nature Reserves (TENR), located on the border between Gauteng and Mpumalanga Provinces, experienced a declining hartebeest (*Alcelaphus buselaphus caama)* distribution over the last years. Simultaneously, an increase in the density of plains zebra (*Equus quagga*) occurred in the reserves. In this study, I investigated the changes in the distribution of four herbivore species, namely red hartebeest, plains zebra, blue wildebeest and black wildebeest in TENR, and the possible influence that biotic and abiotic factors had on the distribution of hartebeest between 2010 and 2016. Data of aerial surveys conducted in the wet season of each year were used to assess the variation in herbivores distribution along the period. Furthermore, the influence of variables known to affect herbivore distribution (e.g. distance to water, slope gradient, spatial distribution of other herbivore species and vegetation greenness) was tested on hartebeest distribution in TENR. The results indicate that blue wildebeest (*Connochaetes taurinus*) had the highest distribution variation, while plains zebra presented the most spread distribution among the four species, and black wildebeest (*Connochaetes gnou*) concentrated their distribution almost entirely at the Ezemvelo nature reserve. Hartebeest avoided areas with the highest concentration of plains zebra, but did not show the same avoidance for areas with prevalence of wildebeest species. Further, high quality forage resources influenced the hartebeest distribution in TENR. Thus, competition for forage resources with bulk feeders may have affected the population and distribution of hartebeest between 2010-2016.

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MOTIVATION TO THE STUDY

Populations of specialist herbivore species may be susceptible to decrease in numbers and distribution when exposed to interspecific competition with species that can handle a more generalized food intake, especially in a limited resource environment. Resource availability influences grazer species distribution (Murray and Brown, 1993), and in areas with resource use overlap the increase in the distribution of one species can directly influence the decrease in distribution of another species. Hence, the understanding of ecological factors involved in species distribution is crucial to better manage and conserve wildlife assemblages (Bailey *et al.*, 1996).

Resources involve biotic and abiotic factors that can be directly exploited by an organism (Morrison, 2001). Abiotic factors include, among others, rainfall (Coe *et al*., 1976), water availability (Western, 1975) and slope (Bailey *et al*., 1996). Biotic factors involve, for instance, the abundance of forage resources, which is directly affected by abiotic factors (Benshahar and Coe, 1992). In addition, interactions between the animals themselves are important factors mediating the species distribution (Murray and Illius 1996, 2000; Arsenault and Owen-Smith, 2002).

In African grazers, resource partitioning could explain how these animals can coexist in the same areas even though they have similar ecological requirements (Voeten and Prins, 1999) and, therefore, it may be one reason for the coexistence of the high diversity of species (Prins and Olff, 1998). Alternatively, if the availability of food resources is exploited and diminished by one species such that it cannot be exploited by other species, a competition may emerge (Murray and Illius, 1996; Prins and Olff, 1998; Arsenault and Owen-Smith, 2002). Competition can significantly affect the distribution and abundance of species as well as influence the community structure (Anderson *et al*., 2002; Richie *et al*., 2009).

Forage selection of grazers not only embraces ecological attributes of the food resources (Senft *et al*., 1987), but also involves feeding behaviour and physiological digestive differences (Bell, 1971; Cromsigt and Olff, 2006). For instance, while non-ruminant grazers such as the plains zebra (*Equus quagga*) (bulk feeders) can exploit a wide variety of food quality to supply their feeding requirements, ruminant grazers require high quality resources (Bailey *et al.*, 1996; MacNaughton and Georgialis, 1998; Murray and Illius, 2000). For example, the red hartebeest (*Alcelaphus buselaphus caama*) is described to select for high quality food resources (Jarman, 1974), and thus, the availability of such resources may influence their distribution. Furthermore, the hartebeest is considered to be dominated by other species in interspecific interactions (Estes, 1991), and therefore its' distribution may be affected by spatial and resource overlap with bulk feeders.

The Telperion and Ezemvelo Nature Reserves (TENR) had a decrease in red hartebeest distribution over the last years, especially in the Telperion section, but the specific reasons for this change are still unclear. For the reserves to maintain their herbivores assemblages, it is important to assess the distribution of the species, as well as factors and interactions guiding it, especially for species with decreasing distribution and population size. Thus, the aim of this study was to compare the distribution of different herbivores assemblages (plains zebra, black and blue wildebeest) as well as environmental variables (forage resources, distance to water and slope gradient) in order to determine whether these variables affected the distribution of red hartebeest between 2010-2016.

INTRODUCTION

Factors Guiding Herbivores Distribution

The Telperion and Ezemvelo Nature Reserves have a broad distribution of bulk feeders (e.g plains zebra) which may narrow the distribution of specialist herbivores, such as the hartebeest. The distribution of herbivores is determined, among other aspects, by spatial and temporal availability of resources (Seagle and McNaughton, 1992). Morrison (2001) defined resource as any biotic or abiotic factor that is directly used by an organism and has relevance for the fitness of the animal. Thus, both biotic and abiotic factors may contribute to herbivores distribution (Redfern *et al*., 2003), but not all factors had their influence individually quantified (Groom and Harris, 2009). Further, as the habitat for herbivores in Africa is becoming more restricted into fenced protected areas (Newmark, 1996; Cromsigt and Olff, 2006), the influence that the distribution of one species has on another species' distribution may be aggravated (Morrison, 2001).

Biotic factors

The hartebeest, as specialist feeders (Estes, 1991) are expected to forage in areas with high quality resources within TENR. Forage quality and quantity influence herbivores distribution (Bailey and Provenza, 2008). Large herbivores seem to prefer areas with high-quality forage availability, spending more time on these compared to areas with low quality food resources (Senft *et al*., 1987; Senft, 1989; Bergman *et al*., 2001). Moreover, studies of wild herbivores (e.g. hartebeest, wildebeest and plains zebra) show that these grazers select for greener grass at local scale, indicating a preference for high quality resources (Sinclair, 1985; Groom and Harris, 2009; Boyers, 2011). For instance, the study of Boyers (2011) using NDVI (Normalised Difference Vegetation Index, which is a measure of green biomass) found plains zebra selecting feeding stations based on greenness during the late dry season, indicating their selectiveness for high quality forage.

In the present study, I wanted to investigate if the change in the hartebeest distribution has been affected by spatial overlap and possibly interspecific interactions with other grazers, specifically the plains zebra, blue wildebeest and black wildebeest. Over the last decades, many ecology studies have been carried out to try to understand how areas with a low diversity of food resources (e.g. grasses) could support a high diversity of herbivores in African savannas (Bell, 1971; Cromsigt and Olff, 2006; Kleynshans *et al*., 2010). Suggestions proposed by some authors argue that these animals can coexist due to their difference in size and digestive strategy (Illius and Gordon, 1992; Cromsigt *et al*., 2009), which would allow them to forage on resources of different quality and availability (Illius and Gordon, 1993; Kleynshans *et al*., 2010). For instance, hartebeest and wildebeest are ruminants and thus, have a slow and highly efficient digestion (Munn *et al*., 2008), which enables these animals to supply their feeding requirements with a trade-off between food quantity and quality: a large quantity of forage is not necessary, provided it is of a high quality (Bell, 1971; McNaughton and Georgiadis, 1986). On the other hand, non-ruminant grazers such as the plains zebra have to compensate their less efficient digestive system by feeding on large quantity of food (Estes, 1991). One explanation of how different species can coexist even though they overlap in ecological requirements may be resource partitioning (MacArthur, 1972; Voeten and Prins, 1999). Resource partitioning is defined as the differential use of similar resources, such as food or space (Schoener, 1974; Voeten and Prins, 1999), and it may occur through distinct resource selectivity, such as grass species composition, grass height (Macandza, 2009), grass greenness (Sinclair, 1985) and different parts of plants. For example, studies showed plains zebra and wildebeest coexisting with extensive overlap on their diet (MacNaughton and Giogiadis, 1986), but the proportion of distinct parts of plants in their *ingesta* indicated feeding distinction between the species (Gwynne and Bell, 1968; MacNaughton and Giogiadis, 1986). Hence, for coexistence of species that overlap in resource selection, there must be a proportion of these resources that one species can exploit and the other cannot, or alternatively, resources need to be abundant enough to allow all species to meet their nutritional requirements (Gordon and Illius, 1989).

Competition for resources may be influencing the distribution of hartebeest in TENR. These herbivores are considered to be susceptible to interspecific interactions (e.g. competition) with other herbivores (Sinclair, 1985), even smaller ones such as the blesbok (Estes, 1991). In areas with coexistence of herbivore species, if the availability of shared food resources is reduced by one species such that it cannot be exploited efficiently by other species, a competition situation may arise (Murray and Illius 1996; Prins and Olff, 1998; Arsenault and Owen-Smith, 2002). For competition to occur, besides the shared resource being in an insufficient supply, it is necessary that the exploitation by one (or more) herbivore species lead to a reduced performance (e.g. narrow distribution) of the other competing species (Odadi *et al*., 2011). Murray and Illius (2000) studying interspecific competition (i.e. competition between different species) for food between wildebeest and topi (*Damaliscus lunatus*), suggested that one species can prejudice the other by eating the available forage, and also by modifying the forage in a way that it makes it less profitable to the other species to exploit it. Thus, they argued that the modification in the forage brought by grazers themselves can be an important factor limiting grazing ungulates species diversity (Murray and Illius, 2000).

Abiotic factors

The distribution of hartebeest in TENR may possibly be affected by water sources and slope gradient. The relationship between herbivore distribution patterns and environmental characteristics may vary from one location to another, but abiotic factors such as distance to water (Redfern *et al.*, 2003; Ogutu *et al.*, 2014), slope gradient (Bailey *et al.*,1996) and fire regimes (Rowe-Rowe, 1982; Vermeire *et al*., 2004) are noticed to be determinants of grazing distribution patterns. The study of Redfern *et al.* (2003) assessed the relative influence that surface water has on herbivores distribution, and revealed that distance to water sources was correlated with the distribution of several herbivore species. However, the strength of this correlation may vary among species, and trade-off between water availability constraints and nutritional requirements are expected to differ according to species' water dependence, size and gut morphology (Redfern *et al*., 2003). For example, the hartebeest is described to have the lowest water consumption within the Alcelaphini subfamily (Jarman, 1974; Estes, 1991). Yet, Western (1975) described these herbivores as strong water dependent, and they were not found in areas further than 1-2 km away from the closest water source (Western, 1975; Ogutu *et al*., 2014). The studies of Redfern *et al*. (2003) and Groom and Harris (2009) did not found strong relationships between the density of zebra and wildebeest populations and distance to water. Further, high density population of these species have been observed foraging in areas up to 4-5 km away from water sources (Western, 1975; Redfern, 2003; Ogutu *et al.*, 2014). These findings might be related with the fact that both species have been documented facing a water constraint in order to forage in areas of high grass biomass (Groom and Harris, 2009).

The effect that slope gradient has on the hartebeest distribution in TENR has still not been explored, although a previous a study showed that it affected the distribution of other large herbivores (Helm, 2007). Slope represented one important abiotic factor affecting the wildebeest distribution, as these herbivores were most likely to occur in areas with gentle to moderate slope (i.e. never steeper than 20º), and therefore, seemed to avoid great slopes variation in TENR (Helm, 2007). Bailey *et al.* (1996) reported that slope gradient act as crucial determinant of grazing distribution, and herbivores seem to not only notice changes in elevation, but also avoid more elevated places while foraging. Ganskopp and Vavra (1987) also found that herbivores limited their foraging in steep areas, and stated that variation in topography should be considered when assessing herbivores distribution.

Study Species

Red hartebeest

The red hartebeest is a large ruminant antelope with an elongated forehead and oddly shaped horns (Estes, 1991). It is a typical plains antelope, although it is highly tolerant to tall grass and woodlands, and presents the lowest metabolic rate within the Alcelaphini subfamily (Estes, 1991), which also includes wildebeest, blesbok (*Damaliscus dorcas phillipsi*), topi and tsessebe (*Damaliscus lunatus lunatus*). They are also the least migratory members of the subfamily (Estes, 1991), and as high quality food resources are dispersed in low quality food and non-food material, they need to forage selectively. To maximise their selective food intake, these animals have a narrow muzzle that allows them to forage successfully in tall green grass even in a quality-constrained environment (Janis and Ehrhardt, 1988; Gordon and Illius, 1988).

Plains zebra

The Plains zebra or Burchell´s zebra is one of Africa's most adapted and successful grazers. They are found mostly in open savannas with the presence of some trees or in open woodlands (Schoenecker *et al*., 2016), occurring through eastern and southeastern parts of the African continent (Estes, 1991).

Their diet consists of grasses (Schoenecker *et al*., 2016) and they are equipped with strong incisors and sensitive mobile lips that enable them to feed on both tough-tall and short grasses (Estes, 1991). These characteristics allows them to select for areas with high grass biomass, regardless of forage quality (Groom and Harris, 2009), portraying them as bulk (or generalist) feeders. However, Boyers (2011) reported these grazers selecting for greener forage resources during the late dry season, suggesting that, although these herbivores are described as generalist feeders, they seem to feed on low quality food when better quality resources are not available (McNaughton and Georgiadis, 1986). Hence, an overlap in forage resources between the plains zebra and hartebeest may arise in areas where they coexist, and in TENR specifically, the decrease in hartebeest distribution may be related with the increase in plains zebras' distribution.

Wildebeest

The wildebeest is a large, high-shouldered ruminant antelope with broad muzzle and cowlike horns (Estes, 1991). There are two species of wildebeest: the blue or common wildebeest and the black or white-tailed wildebeest, and both co-occur in South Africa (Codron and Brink, 2007).

The black wildebeest is generally smaller than the blue wildebeest, and morphological separation between the two species is based mostly on the horn shape and tail colour (Helm, 2007). While the blue wildebeest distribution extends from East Africa into northeast Mozambique, Zambia, Namibia, Botswana, Zimbabwe and northern and northeastern parts of South Africa, the black wildebeest are endemic to South Africa (Codron and Brink, 2007). Further, their distribution seems to be related with their habitat tolerance: blue wildebeest occupying a variety of savanna habitats (e.g. woodlands, grasslands and semi desert areas) and black wildebeest are mostly restricted to open grasslands habitats (Codron and Brink, 2007).

These differences in habitat selection do not appear to be related with the species feeding behaviour, as both ruminants are referred to as short grass specialists (Cromsigt and Olff, 2006), and as such they also rely on high quality food resources to supply their feeding requirements. Furthermore, they have morphological adaptations such as incisor arcade structure (Gordon and Illius, 1988) that also indicate similar feeding selectivity (Codron and Brink, 2007). As the wildebeest are described as short grass specialist (Cromsigt and Olff, 2006) and the hartebeest as tall grass specialist (Estes, 1991), areas with spatial overlap may not necessarily indicate forage resources overlap between these herbivore species.

OBJECTIVES AND HYPOTHESIS

The objectives of this study were:

1) To analyse the variation in the distribution of red hartebeest, plains zebra, black and blue wildebeest along the study years;

2) To investigate whether the distribution of plains zebra, black wildebeest and blue wildebeest, and environmental factors influenced the distribution of hartebeest between 2010-2016.

Considering the stated objectives, the study hypotheses were, respectively:

1) The hartebeest spatial distribution has changed more than the other species distribution over the years;

2) Forage quality (indicated by NDVI) and spatial overlap with plains zebra were the main factors guiding the hartebeest distribution along the analysed period.

METHODS

Study Area

Telperion and Ezemvelo Nature Reserves (TENR) are located at the boundaries of Gauteng and Mpumalanga Provinces, between the cities of Bronkhorstspruit and Witbank (Figure 1). The area, with extent of approximately 8500 ha, is a private reserve owned by the Oppenheimer family and has operated as a unit since 2002 (Helm, 2007). The perennial Wilge River runs through the TENR from south to north, dividing the area in two sections: East Section, composed by Telperion Nature Reserve, and West Section, which includes

Ezemvelo Nature Reserve and Bohlokwa, which is another section of Telperion Nature Reserve (Figure 1).

Acocks (1988) classified the vegetation of the reserves as a variation of Bankenveld (i.e. a transitional zone between grassland and savanna). The landscape is dominated by open grassy plains with some scattered trees in the West Section, whilst the East Section is dominated by undulating hilly terrain, with a rocky and broken topography close to the Wilge River (Helm, 2007). The reserves presented fire regimes and wildfire in some areas (especially in Ezemvelo Nature Reserve), but as it did not occur regularly and was not possible to access the burned areas register, its' influence on herbivores distribution could not be assessed on this study.

The reserves are situated in a summer rainfall region, with the wet period from October to March and dry period from May to August (Helm, 2007). The mean annual rainfall in Bronkhorstspruit and Witbank are, respectively, 625 mm and 674 mm (Swanepoel, 2006). The TENR has 2 perennial water sources: the Wilge River and the Imvubu Dam, located in the West Section (Appendix I), while other water sources and streams depend on the rainfall.

The area hosts more than 20 species of herbivores, including large ones such as plains zebra, kudu (*Tragelaphus strepsiceros*), black and blue wildebeest, red hartebeest and giraffe (*Giraffa Camelopardalis*), small carnivores such as the black-backed jackal (*Canis mesomelas*), African civet (*Civettictis civetta*) and caracal (*Caracal caracal*), reptiles and a high diversity of birds with more than 250 species estimated (Helm, 2007). There are not large predators in TERN and the small predators that exist do not prey on large herbivores.

Hence, predation will not be considered as a variable affecting the distribution of large herbivores in the reserves.

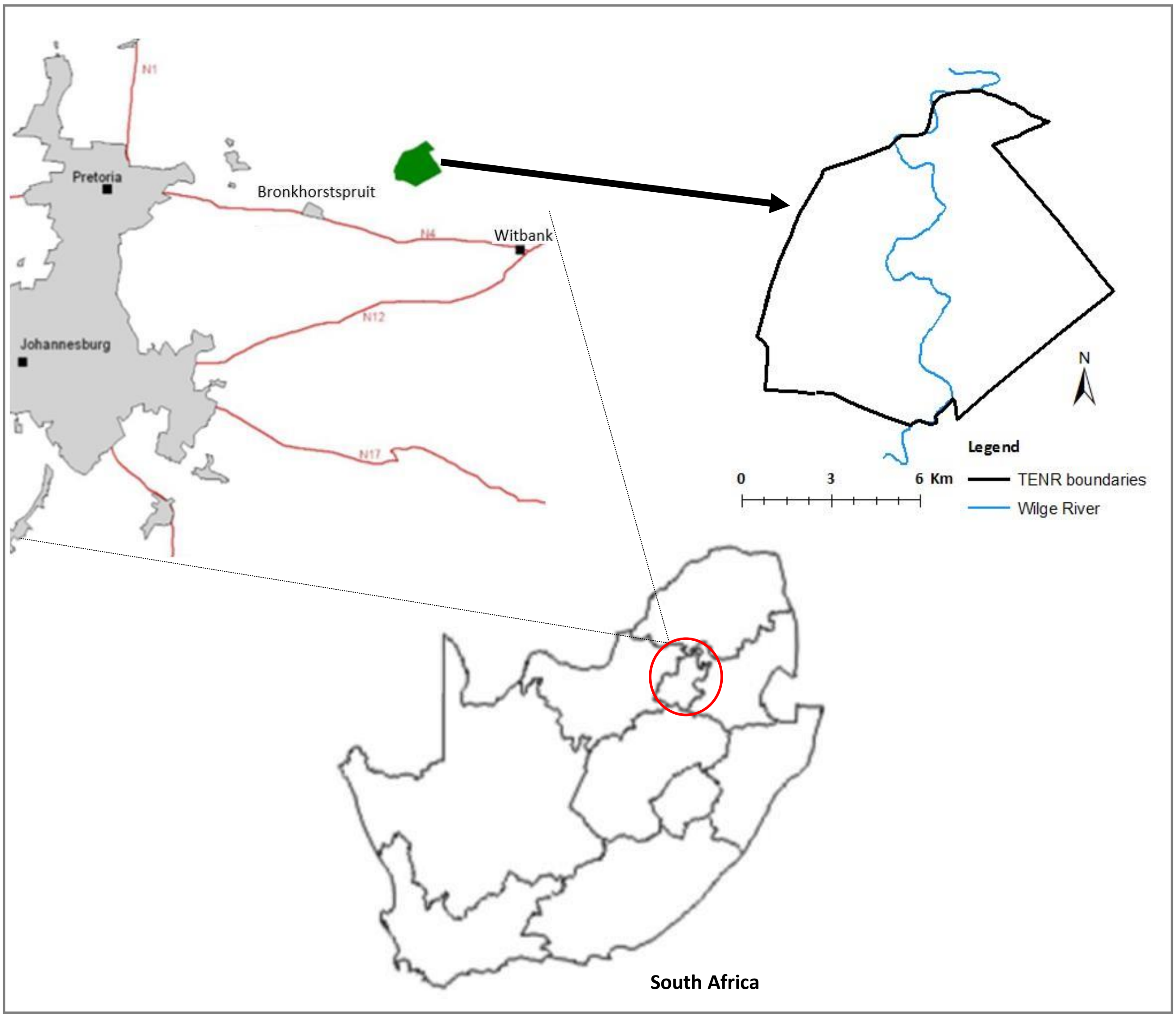

Figure 1: Location of Ezemvelo and Telperion Nature Reserves, between the cities of Bronkhorstspruit and Witbank (modified from Swanepoel, 2006).

Data Collection

Aerial surveys

To investigate the species distribution, data of aerial surveys conducted during February, March or April of each year from 2010 to 2016 were provided by the TENR managers. The surveys were made in a helicopter, using transects that ran from the east border to the Wilge River, and then from the Wilge River to the west border of the reserves (Appendix II). During the surveys, the helicopter was at 50 m above ground, and two spotters (one on each side of the helicopter) recorded all large herbivores sighted within 400 m on each side, as well as the number of individuals when herds were observed (Appendix III).

For every record, the GPS location of the helicopter was recorded. Thus, for each of sighting location, I added a buffer of 400 meters around the location. This bias was based on the survey team information of the maximum distance that they could accurately identify and count the herbivores from the helicopter, and was included to take into account the error associated with the animals’ position in the field.

Factors affecting the species distribution

Possible variables that may have affected the distribution of hartebeest included water sources, slope variation and vegetation greenness. Besides the mentioned factors, the monthly and yearly rainfall records for the study area were obtained from South Africa Weather Service (http://www.weathersa.co.za) to investigate any relationship with the species distribution (Appendix IV). However, these records were not included as a variable directly affecting the hartebeest distribution in the analysis, but as a complementary factor.

Slope gradient

I used geographic coordinates from the whole extension of TENR to generate a slope raster file, which allowed me to access the slope gradient value at any point within TENR. This gradient was reclassified into 4 categories according to the steepness adopted by Helm (2007): flat (0º), gentle (>0º - 10º), moderate (>10º - 20º) and steep (>20º).

Distance to water sources

To include the species' distance to water as a variable, I obtained information about the TENR water sources from the reserves managers. According to the information, the only perennial water sources are the Wilge River and the Imvubu Dam (in the West Section, Appendix I). From a water sources shapefile including the mentioned water points, I generated a raster file that allowed me to obtain the distance to the closest water source from any point within the study area.

NDVI

To include the Normalized Difference Vegetation Index (NDVI), I obtained data from MODIS13Q1 NDVI, freely available from the U.S. Geological Survey website (earthexplorer.usgs.gov). MODIS provides images at 250 m x 250 m spatial and 16 days temporal resolution, meaning that for each 16 days period the highest NDVI is chosen to represent the index for the specific area (modis.gsfc.nasa.gov). This imagery selection tries to diminish the effect that clouds and weather may have on the index. High values of NDVI are associated with a continuous green vegetation such as woodlands or developed grass fields, while low values are associated with vegetation gaps, areas with brown vegetation or without vegetation (e.g. bare soil and water points) (van Bommel *et al*., 2006; Boyers, 2011). Further, I downloaded the images for the specific months (February, March and April) and years (2010-2016) of the study, which are already georeferenced and directly compatible with ArcMap 10.3, where I could superimpose on the study area map.

Data Analysis

Species distribution

The geographic distribution of each species for each year, was generated according to the geographic coordinates obtained from aerial surveys taking into account the spatial bias. From the GPS locations of each species, I generated utilization distribution (UD) estimates. The UD represents a probability function of animals' distribution (Silverman, 1986; Marzluff *et al*., 2004), which includes a density approach that allows to quantify the relationship between the species' density and the resources availability in the area of interest (Marzluff *et al*., 2004). In the specific case of this study, as only actual geographic location of herbivores was used to obtain the species distribution, the UD could be assessed as areas with prevalence of each species, instead of probability of finding them. Further, the UDs were compared in terms of variation in spatial distribution across the years and among species. I used the fixed-kernel methods (Silverman, 1986; Worton, 1989) with reference (standard) bandwidth to create isopleths of 50% of species distribution, using the HRT 2.0 extension (Rogers *et al*., 2015). The 50% isopleths represent the area where the species concentrate their distribution (Chirima, 2009). Fixed kernel method is expected to better define the edges of the distribution ranges rather than the fine-scale discontinuities in occupancy patterns (Gitzen, Millspaugh & Kernohan 2006; Chirima, 2009). Further, kernel density estimation have been used frequently for home ranges estimators (Worton 1987, 1989). The advantage of using the fixed-kernel is that it enables the creation of a smoothed function of the animals' locations, which avoid telemetry errors that the data may contain (Withey *et al*. 2001; Millspaugh *et al*., 2006). For instance, Chirima (2009) used kernel methods techniques to minimize bias of geographic positions inaccuracies from the aerial survey in generating distribution ranges.

All the procedures and analyses involving geographic features were done in ArcMap 10.3 (GIS).

Factors affecting hartebeest distribution

Based on the UD graphs, I could analyse the relationship between the hartebeest distribution and the different factors that may have affected it. As the UD indicates the areas with prevalence of each species, it allowed me to assess the relationship between the occurrence of hartebeest with the distribution of other herbivores, and with the environmental factors. At each sighting point I had specific values for the presence (and abundance) of hartebeest, slope gradient, distance to water, NDVI, and the values for the specific concentration of plains zebra, black wildebeest and blue wildebeest populations. Thereafter, I applied a multiple regression model, using the concentration of hartebeest individuals as the dependent variable. Further, I added the other mentioned variables as independent variables, which had specific values at each hartebeest sighting, and I analysed with a multiple regression method. From the multiple regression statistical results, I was to identify which variables presented relationship with the hartebeest distribution, as well as the magnitude of this relationship according to their individual correlation coefficients. One multiple regression analysis was performed per year of study (2010-2016), and analysed in order to find patterns and differences among the correlations over the years. The multiple regression analysis was performed using Statistica v.7 (http://www.statsoft.com).

RESULTS

Species Spatial Distribution

The UD estimates revealed that the hartebeest concentrated their distribution in the West Section of TENR. Although the sighting locations shows presence of hartebeest in the East section (Appendix III), the prevalence of the species clearly occurred in the west of the Wilge River on most years (Figure 2). For instance, based on the UD that emphasizes the concentration of individuals, besides the years of 2012, 2013 and 2016, the species was almost absent east of the Wilge River (Figure 2). Further, areas with high prevalence of hartebeest were also areas with lower concentrations of plains zebras (Figure 2 and Appendix III).

Plains zebra occurred in both sections of TENR, but their peaks in the UD estimates and therefore their highest concentrations, were always in the East Section (Figure 2 and Appendix III). For instance, in 2010 the prevalence of plains zebra distribution was observed close to the Wilge River, but still in the east side of the river (Figure 2 and Appendix III).

The black wildebeest distribution showed that the species concentrated its' distribution almost entirely in the West Section, and was the only species with no expressive UD estimation on the East Section (Figure 2 and Appendix III). The areas with higher concentration of the species varied every year within the West Section, but were never across the Wilge River.

The blue wildebeest presented a high distribution in both sections of TENR (Figure 2 and Appendix III). Although the species concentrated its distribution mostly in the West Section, it also had significant occurrence in the East Section (e.g. UD graphs for 2010, 2014, 2015 and 2016). An exception occurred in 2011, when the species presented low distribution in the East Section compared with other years, but was not absent (Figure 2 and Appendix III).

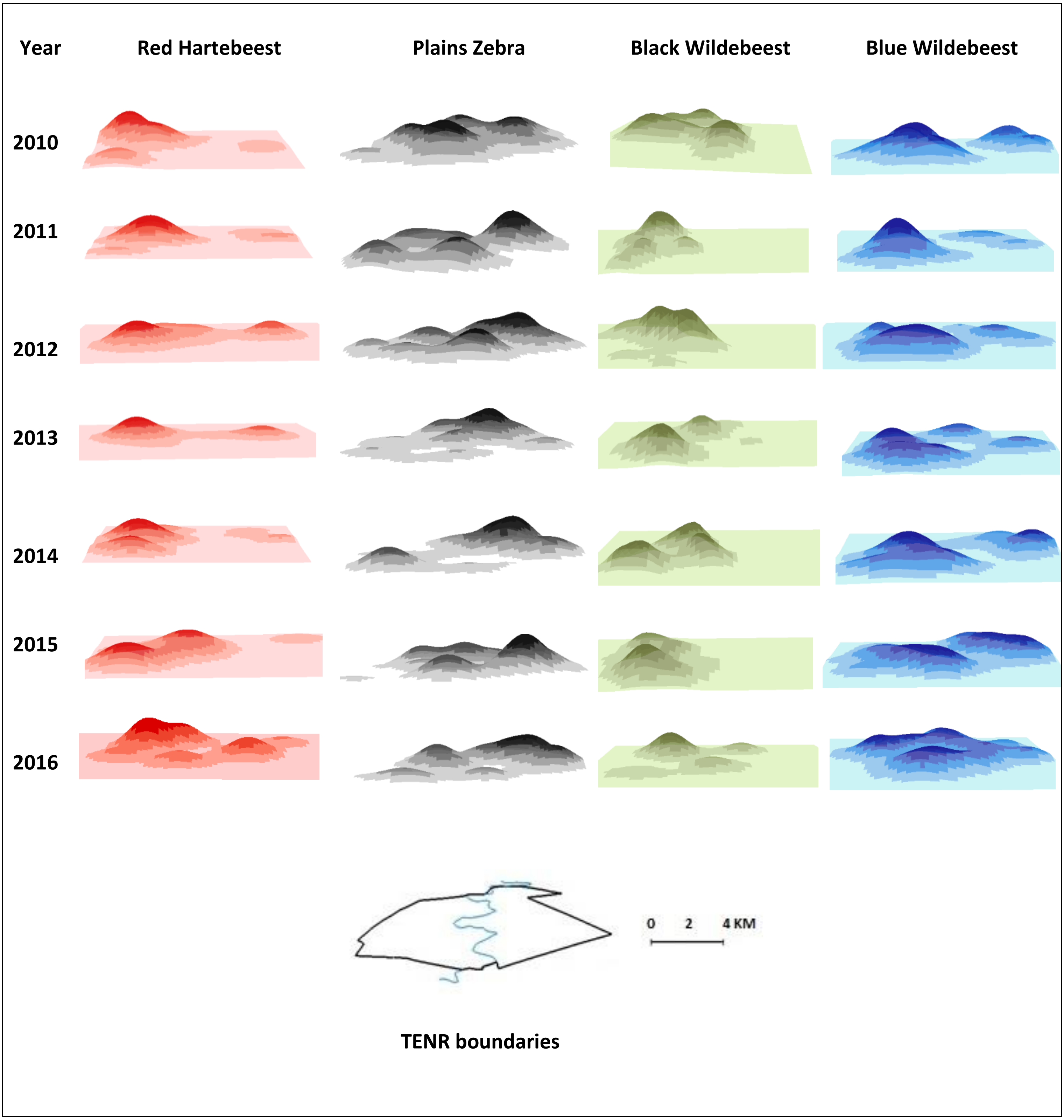

Figure 2: Utilization Distribution (UD) graphs based on the location sightings of the herbivores in Telperion and Ezemvelo Nature Reserves (TENR), for the different study years. The height of the curves indicates the concentration of individuals of the species. The contours at the bottom represents the area of TENR in which the distribution was based on.

Factors Affecting Hartebeest Distribution

The results from the multiple regression models assessing the variables that might have influenced the distribution of hartebeest for the period 2010-2016 were analysed separately for each year (Table 1 and Appendix V). The influence that each factor had on hartebeest distribution varied across the years, assuming either positive, negative or not significant relationship (Figure 3 and Table 1). It is important to notice that for the variable distance to water, the positive relationship means that the hartebeest concentrated their distribution in areas further from water sources, while the negative relationship indicates that the species showed prevalence in areas closer to the water sources.

From the six variables, four of them (distribution of plains zebra, distribution of black wildebeest, distribution of blue wildebeest and distance to water sources) were correlated with the distribution of hartebeest in six of the seven years included in the study (Figure 3). Along the years, the hartebeest distribution was negatively related with the distribution of plains zebras on most years. This negative relationship occurred in five over the six years that the two species' distribution were correlated. The only exception occurred in 2015, when the distribution of hartebeest and plains zebra were positively correlated, but yet the areas with the highest concentration of each species did not overlap, with the prevalence of hartebeest and plains zebra located in the West and East Section, respectively (Table 1, Figure 2 and Appendix III). Thus, the hartebeest seemed to have their population concentrated in areas where the concentration of plains zebra was not the highest, reinforcing what was observed on the spatial distribution.

The same pattern of avoidance was not observed between hartebeest distribution and the distribution of the two wildebeest species. The hartebeest distribution was positively related in four over six years with the distribution of black wildebeest, and negatively related only in 2012 and 2016 (Table 1). Furthermore, the distribution of hartebeest was positively related with the distribution of blue wildebeest in five over six years that the species were correlated (Figure 3 and Table 1).

Distance to water sources was the factor that showed the most variation across the years, presenting three positive (2010, 2012 and 2013) and three negative (2011,2014 and 2016) correlations with hartebeest distribution (Figure 3 and Table 1).

The availability of high quality forage resources was the only factor that presented only positive correlation with the distribution of hartebeest (Figure 3). These grazers seemed to concentrate their distribution in areas with high NDVI values in 2012, 2013, 2015 and 2016 (Table 1). The factor that showed the lowest numbers of relationships with the distribution of hartebeest was the slope gradient (Figure 3). The species concentrated their distribution on flatter areas in 2010, but on a steeper area in 2014 (Table 1).

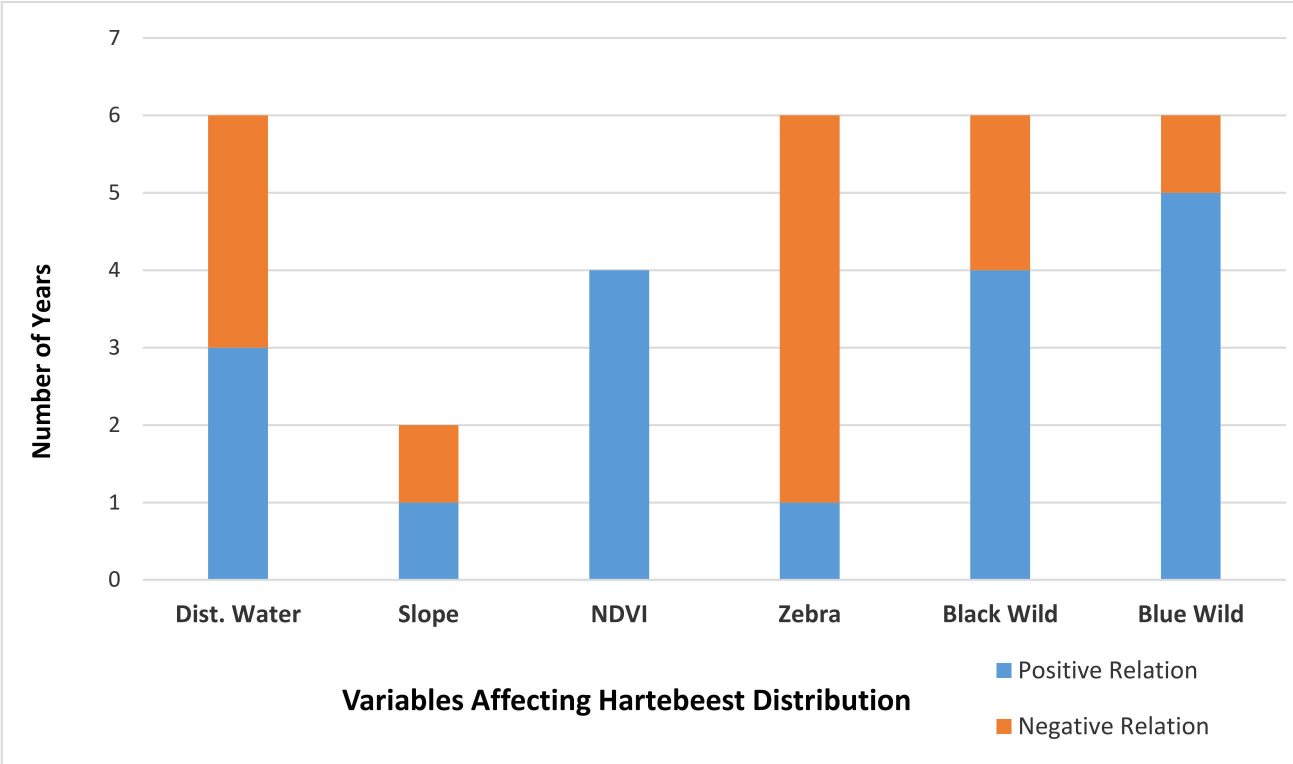

Figure 3. Number of years that each factor tested for statistically significance on affecting the hartebeest distribution, having either a positive (blue) or negative (orange) influence during the seven-year period (2010-2016).

Table 1: The relationship that the distribution of hartebeest had with each independent variable each year, including the related p-value. The regression coefficients (β) indicate if the relationship was either positive, negative or not statistically significant (0).

	Distance to Water Sources	**Slope Gradient**	**NDVI**	**Concentration of Plains Zebra Distribution**	**Concentration of Black Wildebeest Distribution**	**Concentration of Blue Wildebeest Distribution**
2010	β = 1,026 p-value < 0,0001	β = -0,1784 p-value = 0,0013	0 p-value = 0,6487	β = - 0,1202 p-value = 0,0396	β = 0,4716 p-value < 0,0001	β = 1,1321 p-value < 0,0001
2011	β = -0,2222 p-value = 0,0082	0 p-value = 0,5794	0 p-value = 0,1483	0 p-value = 0,2048	β = 0,2526 p-value = 0,0095	β = 0,2918 p-value 0,0043
2012	β = 0,1996 p-value = 0,0061	0 p-value = 0,2049	β = 0,1444 p-value = 0,0016	β = - 0,2583 p-value = 0,0032	β = - 0,3949 p-value < 0,0001	β = 0,1977 p-value < 0,0001
2013	β = 0,1402 p-value = 0,0052	0 p-value = 0,9983	β = 0,1335 p-value = 0,0008	β = - 0,3235 p-value = 0,0001	0 p-value = 0,1598	β = 0,8421 p-value < 0,0001
2014	β = -0,1407 p-value = 0,0177	β = 0,2217 p-value = 0,0001	0 p-value = 0,3325	β = - 0,1483 p-value = 0,0405	β = 0,3542 p-value < 0,0001	0 p-value = 0,7742
2015	0 p-value = 0,9181	0 p-value = 0,7495	β = 0,3311 p-value < 0,0001	β = 0,5798 p-value < 0,0001	β = 0,6821 p-value < 0,0001	β = - 0,419 p-value < 0,0001
2016	β = -0,3970 p-value < 0,0005	0 p-value = 0,152679	β = 0,1908 p-value < 0,0005	β = - 0,2670 p-value < 0,0005	β = - 0,1098 p-value = 0,0455	β = 0,7612 p-value < 0,0005

DISCUSSION

The distribution of hartebeest was concentrated on the West Section of TENR in the period of 2010-2016, with a lower concentration of individuals in the east side of the Wilge River compared to the west side. Hence, it was not the distribution that changed the most over the years, as I expected from hypothesis 1. Among all the variables analysed, two of them influenced the distribution of hartebeest the most: the presence of plains zebra and the availability of high quality food resources, corroborating what was expected from the second hypothesis. While the hartebeest were observed avoiding areas with high prevalence of plains zebra, the same avoidance pattern was not noticed between hartebeest and the other two wildebeest species. Among the environmental factors, distance to water sources and slope gradient did not have a strong influence on the hartebeest distribution.

Variation Occurred in the Distribution of Grazer Species Along the Years

From the four species, three of them concentrated their distribution in the West Section (hartebeest, black wildebeest and blue wildebeest). The distribution of hartebeest and black wildebeest were concentrated in the West Section over the years, while the distribution of blue wildebeest was the one that varied the most among the four species, presenting higher concentration of individuals on both sections, depending on the year analysed. The distribution of plains zebra was the most spread of all four species, and had the peak of concentration in the East Section in all the years. The differences in the distribution of the four herbivore species may be explained by distinct factors, such as differences in foraging behaviour, availability of forage resources, and interactions between the species (e.g.

competition for resources and resource partitioning). For instance, both wildebeest species are described to be adapted to feed on short swards (Duncan *et al*., 1975; Murray and Illius, 2000), and the difference in distribution between the two species in TENR seemed to support earlier studies, showing that black wildebeest were mostly restricted to open grasslands (the same vegetation that prevails in the West Section), while blue wildebeest were observed occupying a variety of savanna habitats (Codron and Brink, 2007). As the East and the West section have differences in the topography and vegetation (Swanepoel, 2006), and both were occupied by the blue wildebeest, the wide species' distribution pattern (Codron and Brink, 2007) may also be an explanation for the change in areas with the species prevalence along the analysed years. Moreover, both wildebeest species concentrated their distribution in areas further from the east border of the Wilge River, supporting the idea that wildebeest seem to avoid rocky grassland habitats (Helm, 2007). Conversely, plains zebra showed no avoidance for the rocky areas and irregular topography existent in the East Section. These herbivores are known as roughage grazers and are found in grassland areas with high green standing crop (McNaughton, 1985; Schoenecker *et al*., 2016) which may have allowed them to occur on both sections of TENR, and thus, to have the most spread distribution among the four species (Figure 2 and Appendix II). The hartebeest is described as tall grass specialist (Estes, 1991) and thus, the open grasslands of the West Section may have provided favourable conditions for the species to concentrate its' distribution, instead of the rocky and undulating hills present in the East Section. In addition, if the presence of plains zebra affected the hartebeest distribution, as expected from the hypothesis 2, the most spread distribution presented by the plains zebra may have influenced the hartebeest distribution. These factors possibly contributed to the prevalence of hartebeest distribution in the West Section over the period of 2010-2016.

Factors that Might Have Affected the Hartebeest Distribution in TENR

The spatial distribution of hartebeest appeared to be influenced by the distribution of other herbivores. For instance, areas with high concentration of hartebeest did not overlap with areas of highest prevalence of plains zebra over the years (Figure 2). Although these two species were not excluded from spatial overlap with each other, hartebeest concentrated their distribution on the West Section of TENR and may have avoided areas where plains zebra had the highest concentration, which is reinforced by their negative relationship in most of the years. In addition, the positive relationships observed between the hartebeest distribution and the wildebeest distribution also reinforced the idea that hartebeest mostly avoided areas with prevalence of plains zebra, but not of all the herbivore species. This difference may be related with the species foraging behaviour and interspecific interactions, such as resource partitioning and competition for forage resources. As the hartebeest are described to feed on tall (Estes, 1991) and high quality grass (McNaughton and Georgiadis, 1986) they can possibly support spatial and resources overlap with wildebeest species, which are described as short grass specialists (Cromsigt and Olff, 2006). Hence, resource partitioning between the hartebeest and the wildebeest species may be one explanation for the high concentration of individuals in overlapped or surrounding areas within the East Section (Figure 2), instead of spatial avoidance between these herbivores. By contrast, the same kind of overlap may not be viable between the hartebeest and the plains zebra. Plains zebra are described to feed on tall grass and to be selective for high quality forage (Boyers, 2011; Bradley, 2012), and thus with resources overlap, a competition for resources may arise between the two species. It is important to notice that these interactions between herbivores species vary according to the seasons, with the increase of productivity and spatial availability of resources influencing competition and even facilitation between the species (Odadi *et al*., 2011). For instance, the study of Ego *et al.* (2003) described hartebeest and wildebeest with forage overlap during the wet season, but the abundance of these resources allowed the species to coexist without competition. Hence, as I analysed data from the wet season only, it is possible that details from the herbivores interactions could not be captured. Nevertheless, the fact that hartebeest and plains zebra never presented their highest distribution concentrations on the same area, and that the hartebeest populations appear to be susceptible to decrease in interspecific competition situations (Estes, 1991), here I suggest that hartebeest avoided areas with the prevalence of plains zebra, where a possible competition for forage resources may arise.

Among the environmental variables included, the NDVI was the only one that was only positively related with the hartebeest distribution. This relationship suggests that hartebeest selected to forage in areas with high NDVI values. As the study analysed data from the wet season and primary production is described to be directly related to precipitation in African savannas (Coe *et al*., 1976; East, 1984), this relationship may indicate not only that hartebeest selected for high quality forage resources, but also for a higher biomass availability of forage resources. Moreover, it is possible that the availability of these forage resources was widely dispersed in TENR during the analysed periods, and thus, the relationship between hartebeest distribution and NDVI could not be noticed in some years (i.e. the variable was not statistically significant). However, the two years that had the lowest rainfall (2013 and 2015, Appendix IV) and thus possibly less plant productivity (Coe *et al*., 1976), were also years that hartebeest presented positive relationship with vegetation greenness. These findings corroborate what was documented by McNaughton and Georgiadis (1986), showing that hartebeest selected for higher quality forage during the wet season, and more, that they seemed to increase the selectivity during seasons with low rainfall.

The distance to water sources did not seem to highly affect the hartebeest distribution. This suggestion was based on two main observations: (1) the high variability between positive and negative correlations involving hartebeest distribution and distance to water across the years, and (2) in the two driest years, 2013 and 2015, hartebeest showed a positive correlation (i.e. the highest concentration of hartebeest was further from water sources), and no correlation, respectively. Although the hartebeest was described as concentrating their distribution in areas close to water sources (Western, 1975; Ogutu *et al.*, 2014), this weak relationship observed in TENR can be related with the probable existence of additional water points during the wet season. Even though TENR has only two perennial water sources, in the rainy period, the herbivores may have access to water in several other localities that could not be assessed in this study, and hence, their necessity to concentrate their distribution in areas close to these analysed water sources may decrease (e.g. positive relationship in 2010, 2012 and 2013). However, as the hartebeest concentrated their distribution in the West Section of TENR, they were also close to both perennial water sources (Appendix I), what may explain the negative relationship observed in 2011, 2014 and 2016 (Table 1), and support the studies by Western (1975) and Ogutu *et al.* (2014). An analysis in the dry season, with probably less or none additional water points, may enhance the findings of how distance to water sources influences the hartebeest distribution in TENR.

The last abiotic factor, slope gradient, had the lowest influence among all the variables affecting the hartebeest distribution. This weak correlation may be related with the fact that hartebeest concentrated their distribution in the West Section of TENR, where the topography consists mostly of flat grasslands with gentle hills (Helm, 2007), and the variation in slope gradient is so subtle that it did not vary enough to represent an influence in the species distribution. Hence, I suggest that the slope did not influence the hartebeest distribution as it affected the wildebeest distribution in the same area (Helm, 2007).

The effect that abiotic factors, such as distance to water and slope gradient had on hartebeest distribution, did not support the ideas of Bailey *et al*. (1996) that these are the principal variables affecting herbivores distribution. Yet, Senft (1989) argues that abiotic constraints should be combined with biotic factors such as forage quantity and quality, in order to better investigate how they affect herbivores distribution. In the present study, it is possible that the wet season made the availability of high quality forage more homogenous in TENR, and thus, the hartebeest did not have to forage in steeper or further areas to obtain high forage resources. However, during the dry season, when high quality resources may be diluted in the lower quality forage, these herbivores may have to forage in different and even steeper areas to achieve their feeding requirements. This comparison may better demonstrate the effect that slope have on hartebeest distribution in TENR.

LIMITATIONS OF THE STUDY

The assessment of changes in grazers distribution was based on aerial surveys conducted once a year during the wet season, from 2010 to 2016. Aerial surveys are susceptible to generate bias on estimations of total numbers of individuals in herbivore populations (Redfern *et al*., 2002), and thus, it is possible that the distribution estimates obtained in this study do not represent the total population of each species, and thus, not their whole detailed distribution. In addition, some of the sighting data had no geographic references and therefore, were discarded. Although these mentioned issues can diminish the sample size of individuals, the distribution of species was based on the total sightings (Appendix VI), which guaranteed the analysis of this study. Furthermore, several studies have described seasonal variation in the feeding selectivity and distribution of herbivores (McNaughton, 1985; Macandza, 2009; Kleynhans *et al*., 2010). Thus, as argued in the discussion above, many variables may affect the hartebeest distribution differently according to the season, and comparison between wet season and dry season can improve the assessment of the factors dictating the hartebeest distribution within TENR.

It is possible that other variables not included in this study may also influence the hartebeest distribution. For instance, geology and soil composition (Bell, 1982; East *et al*., 1984) are factors that influence herbivores distribution, but were out of the scope of this study. Furthermore, the inclusion of other herbivores species existent in the area, as well as a deeper investigation on the forage selection by the herbivores may improve the analysis on how interspecific interactions affect their distribution within TENR.

CONCLUSION

In the present study, I suggest that the plains zebra had the most spread distribution, and the blue wildebeest the distribution that varied the most during the wet seasons between 2010 and 2016. In the context of investigating the reasons for the declining population and distribution of hartebeest in TENR, this study suggests that even in the wet season the hartebeest concentrated their distribution in areas with high forage quality, while avoiding areas with high prevalence of plains zebra. As these bulk feeders were found widely spread on both sections of the reserves and affected the hartebeest distribution, it is possible that the population of hartebeest may become more restricted and their numbers diminish if the population of plains zebra keep increasing. In order to TENR improve the understanding of their herbivore community, and their management decisions, especially for the conservation of the hartebeest, my suggestions are:

1) Investigate with further research, which factors may influence the hartebeest distribution during the dry season (including factors mentioned in the limitations above). Moreover, compare it with findings of this study (wet season), and try to clarify the reasons for concentration of these herbivores in the West Section and their almost absence in the East Section;

2) Analyse the herbivores populations periodically and check for decrease in numbers and distribution. If the population and distribution of hartebeest continue to decrease, a conservation alternative must be discussed in order to maintain the species with abundant numbers and wide distribution within the reserves, especially if the population of plains zebra continue to increase.

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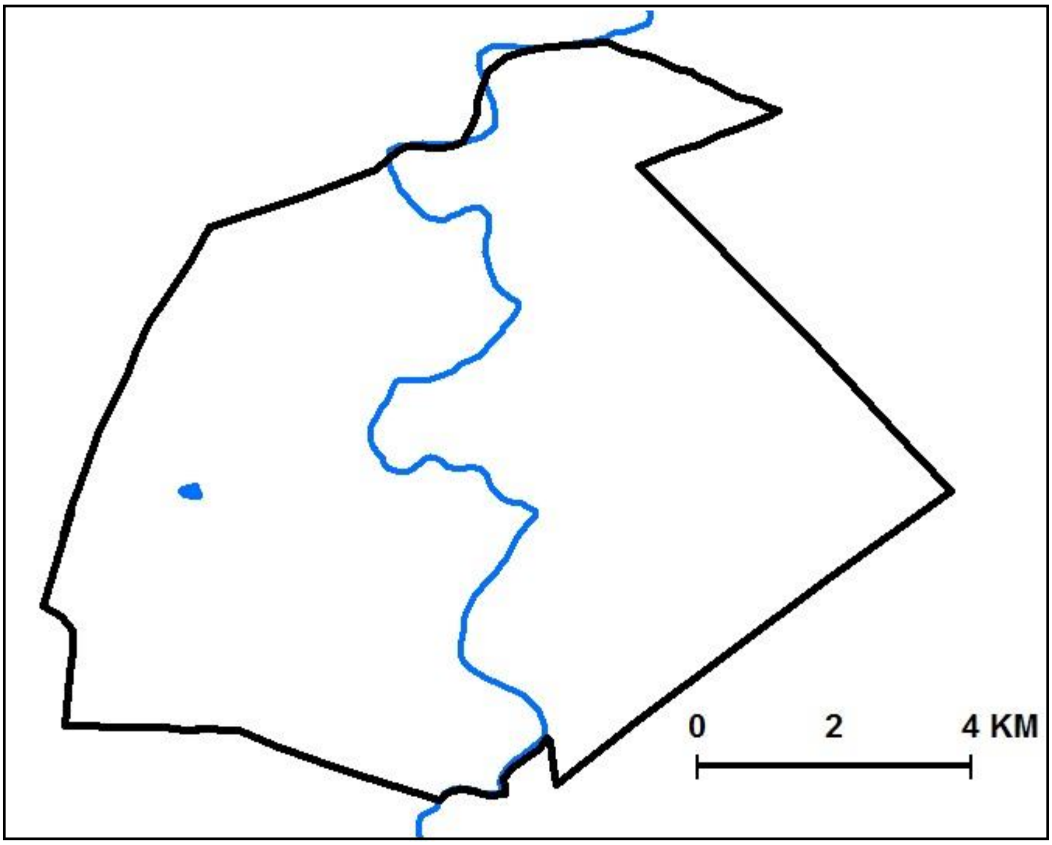
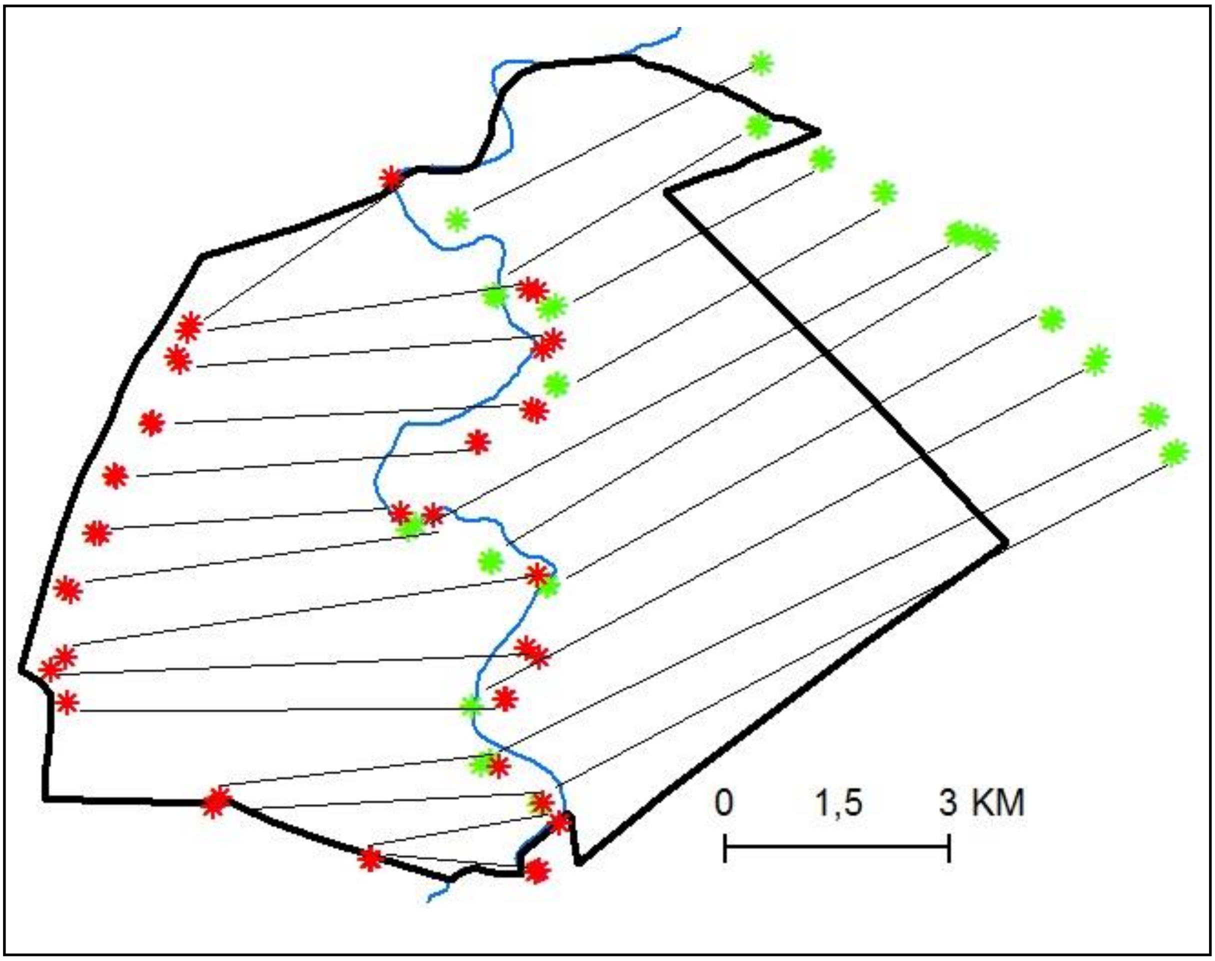
APPENDICES

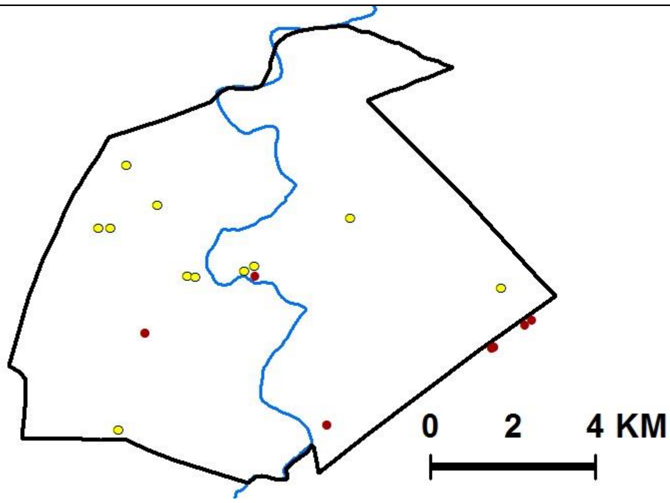
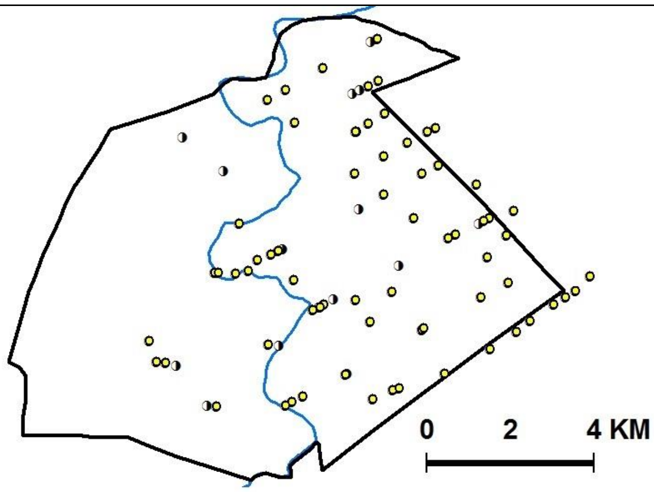
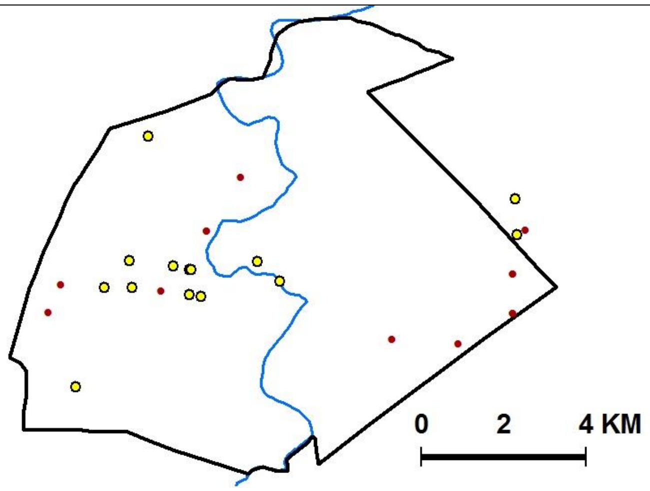
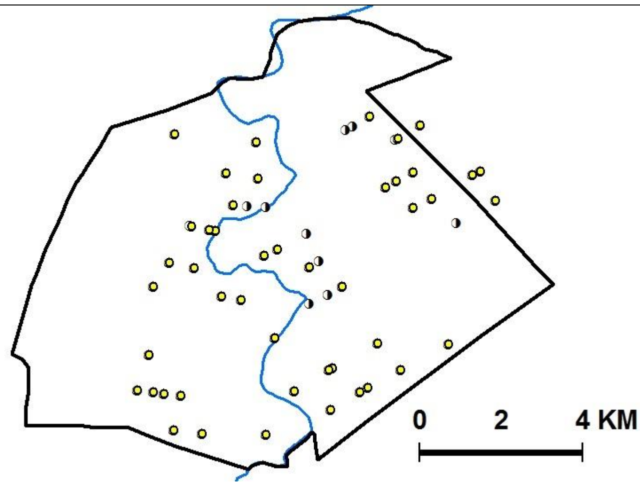
Appendix I: Map representing the area of TENR including the two perennial water sources: the Wilge River dividing the East and the West sections, and the Imvubu Dam, located on the West Section.

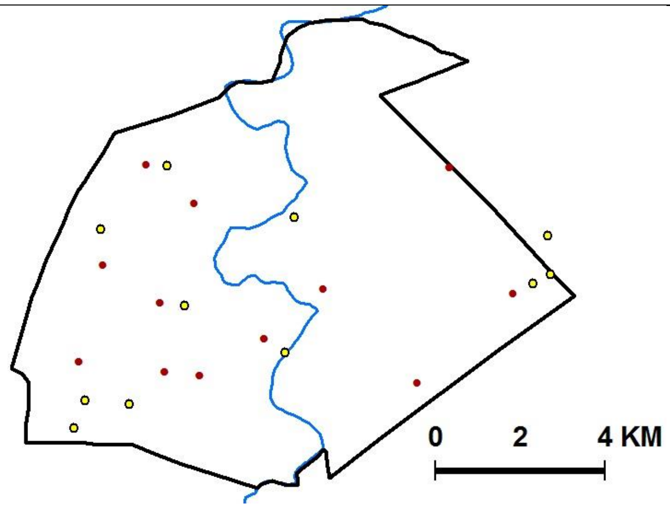
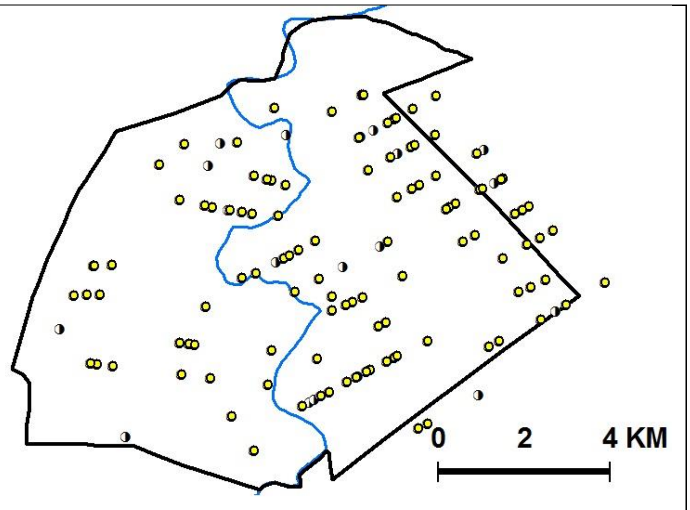
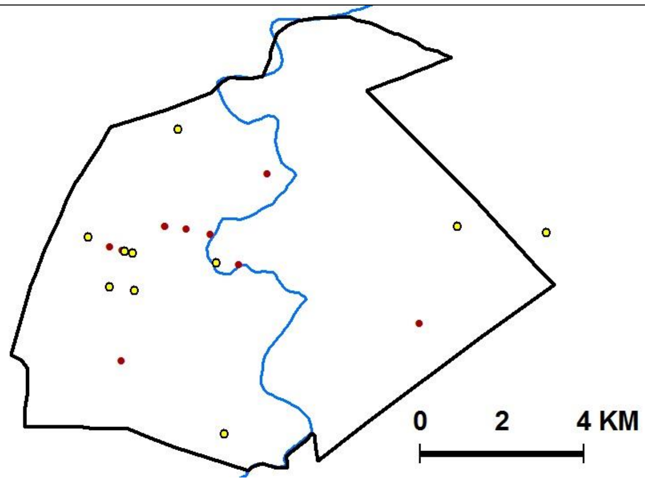
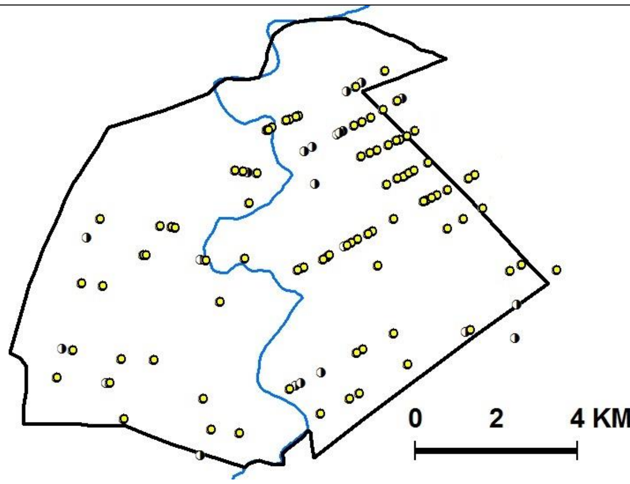
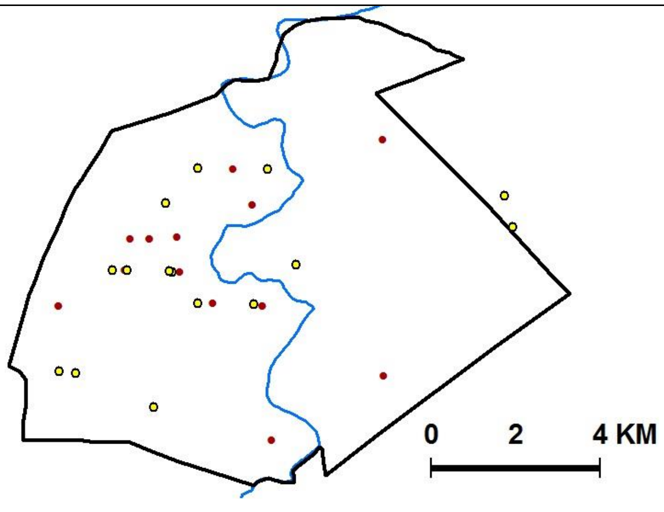
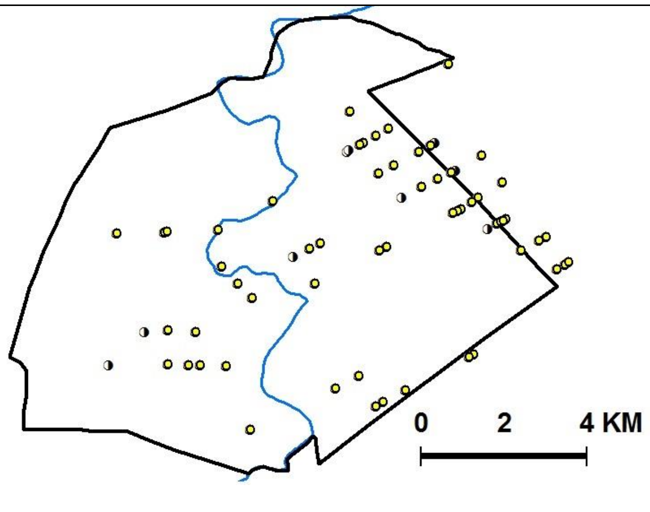


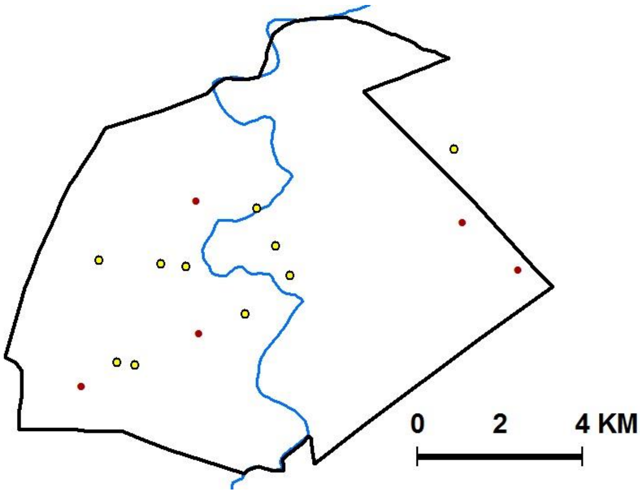
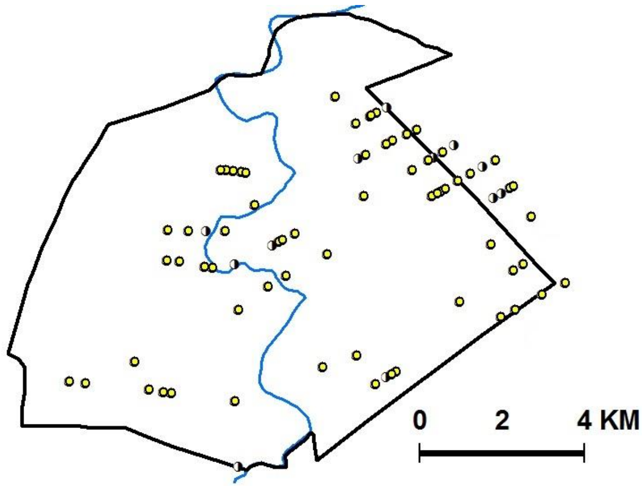
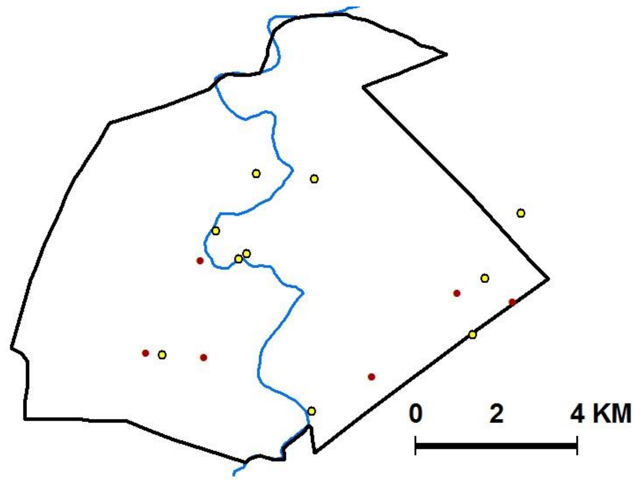
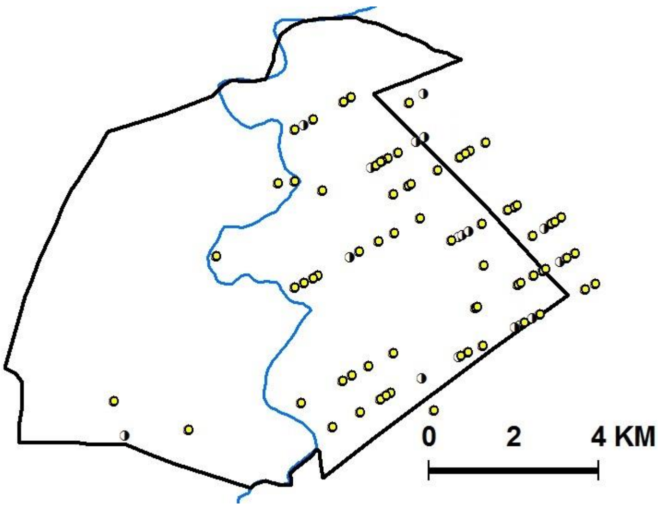
Appendix II: Map showing the transects made during the aerial surveys. The green asterisks on the further east represent the coordinates where the aerial surveys for the East Section started, and the green asterisks close to the Wilge River where these transects ended. The red asterisks close to the Wilge River represent where the aerial surveys for the West Section started, and the red asterisks close to the West border where these transects ended. The black lines between the start and end asterisks represent the approximate path made on the aerial survey.

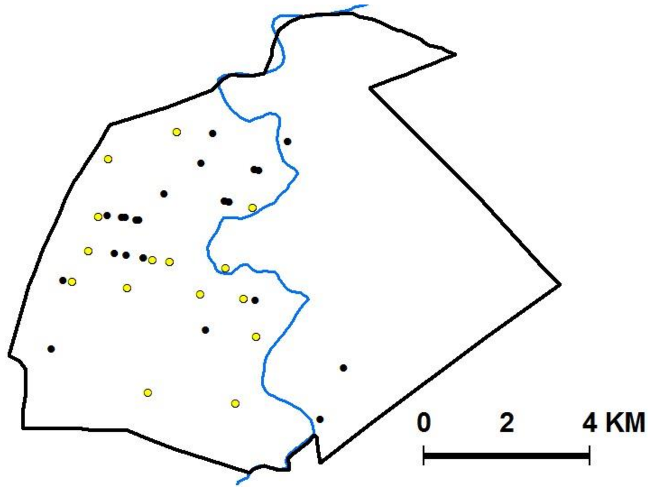
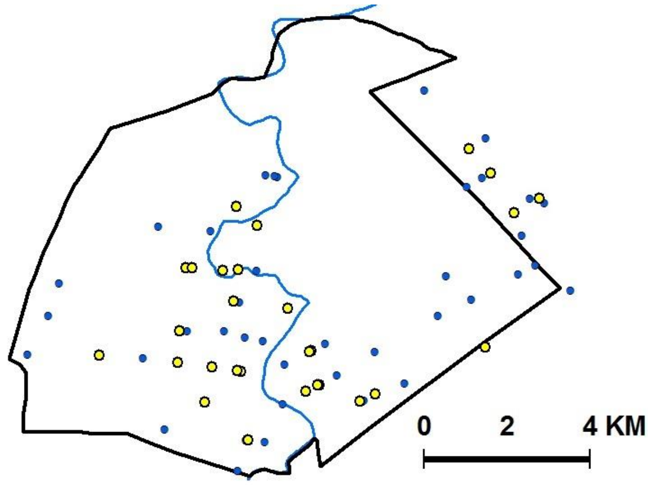
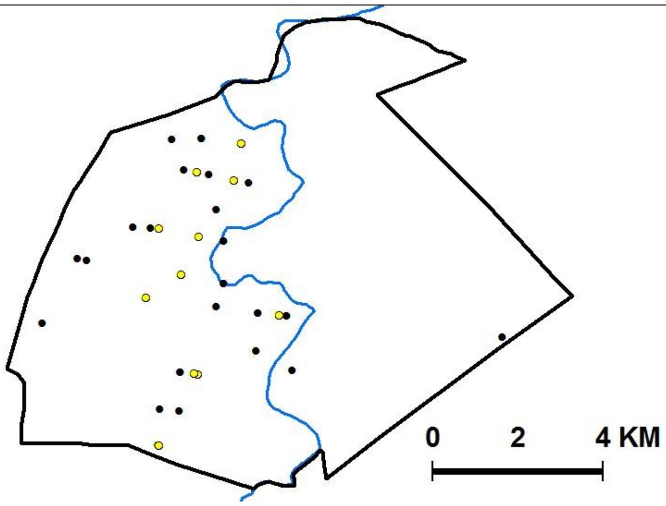
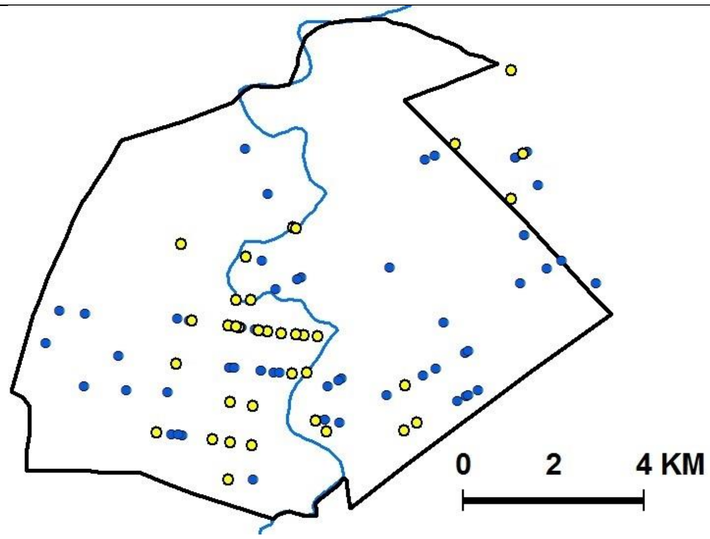
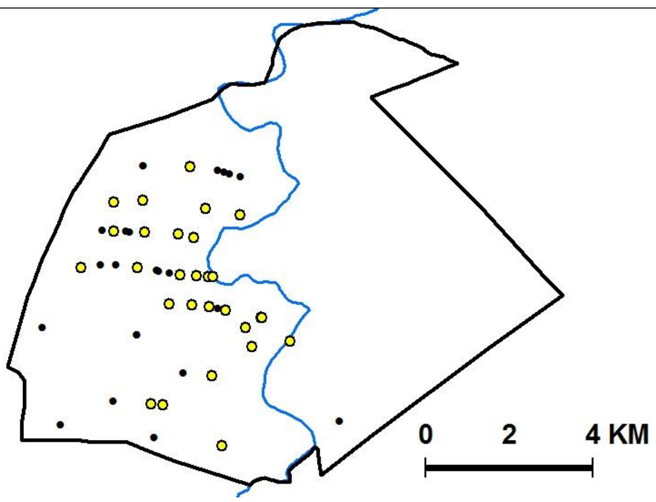
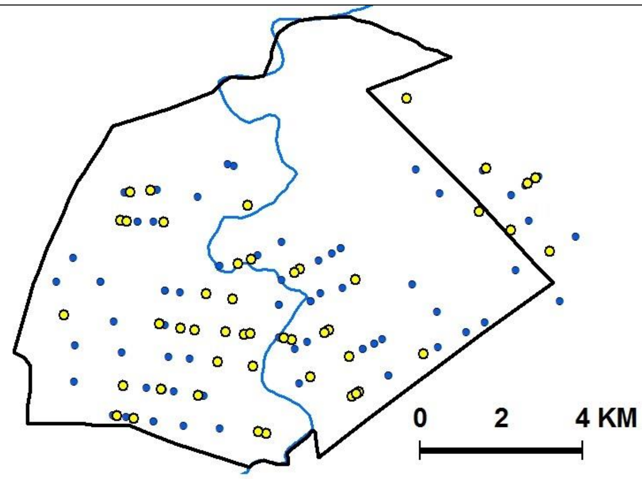


Appendix III: Table including the maps from the aerial surveys showing the distribution of the different herbivore species on each year in TENR. On each map, the yellow points indicate the locations of herds, whereas the other colours indicate individual sightings. The GIS layers obtained for this study do not include recently added sections of TENR, and therefore, the locations observed outside the boundaries were also herbivores sighted within the actual area of the reserves.

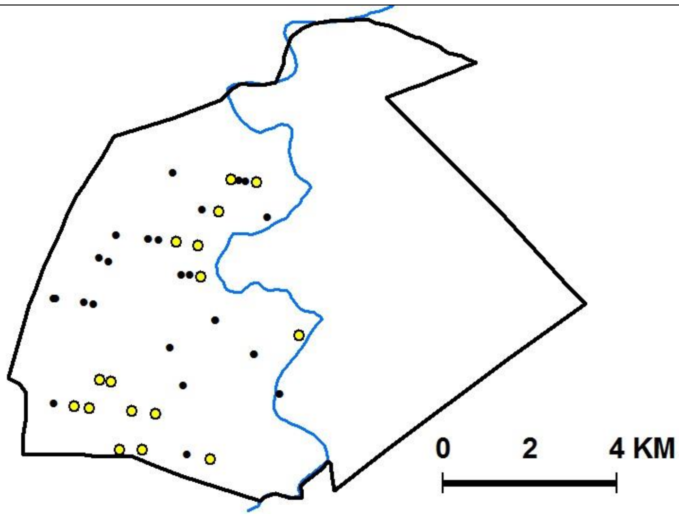
YEAR	Hartebeest	Plains Zebra
2010		
2011		

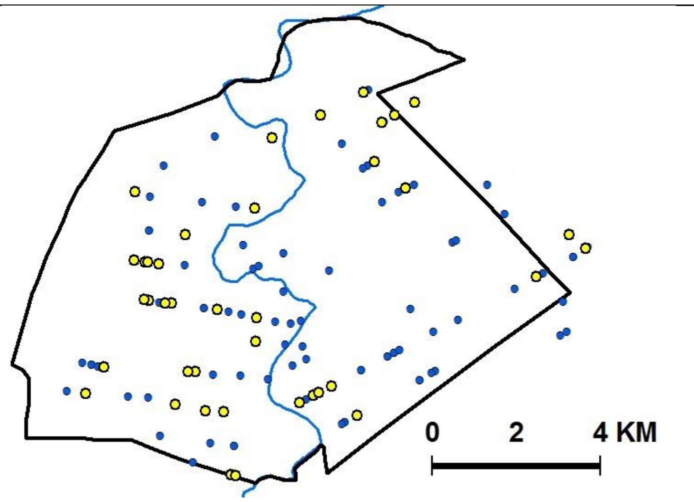
2012		
2013		
2014		

2015		
2016		

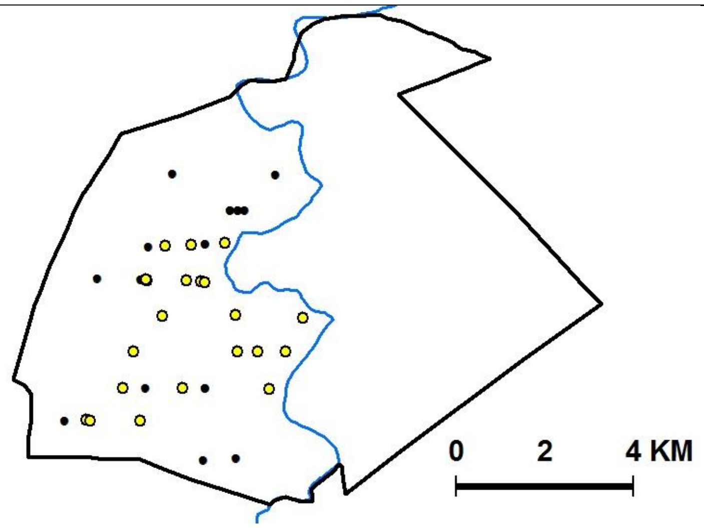
YEAR	Black Wildebeest	Blue Wildebeest
2010		
2011		
2012		

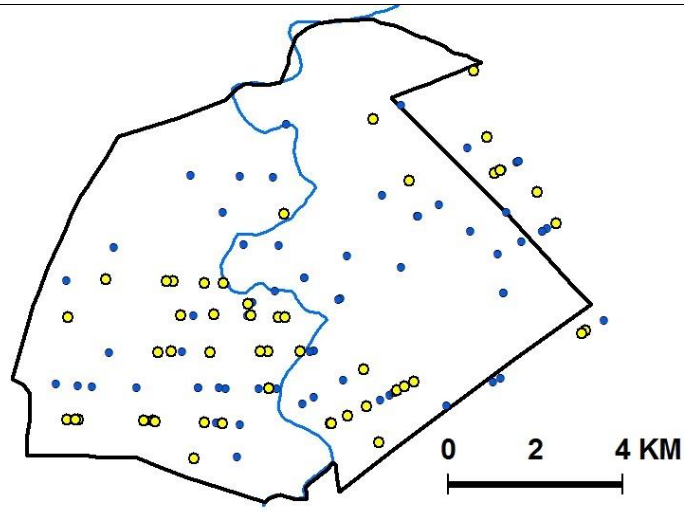
2013



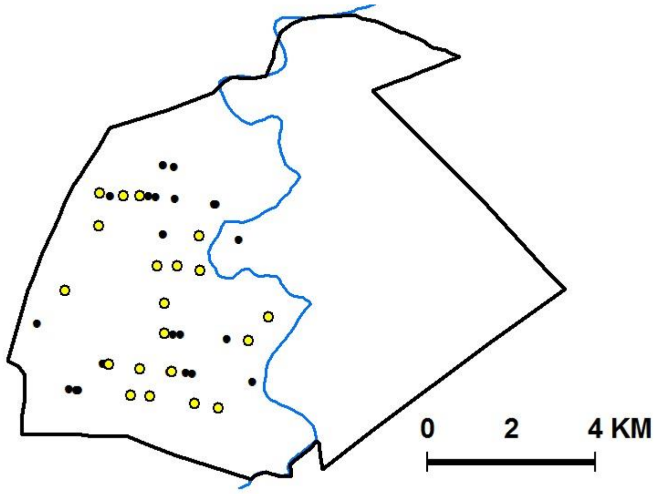


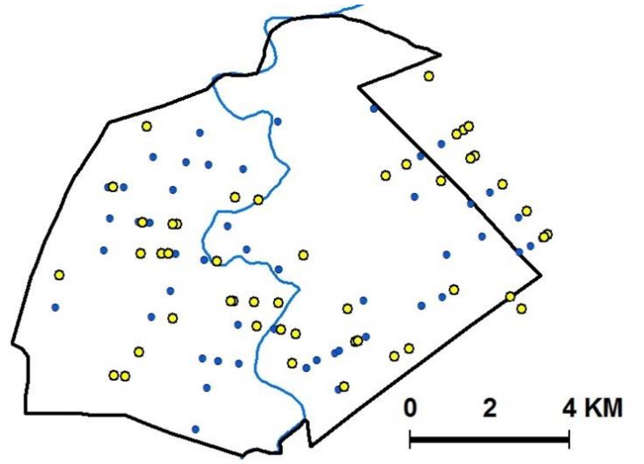
2014

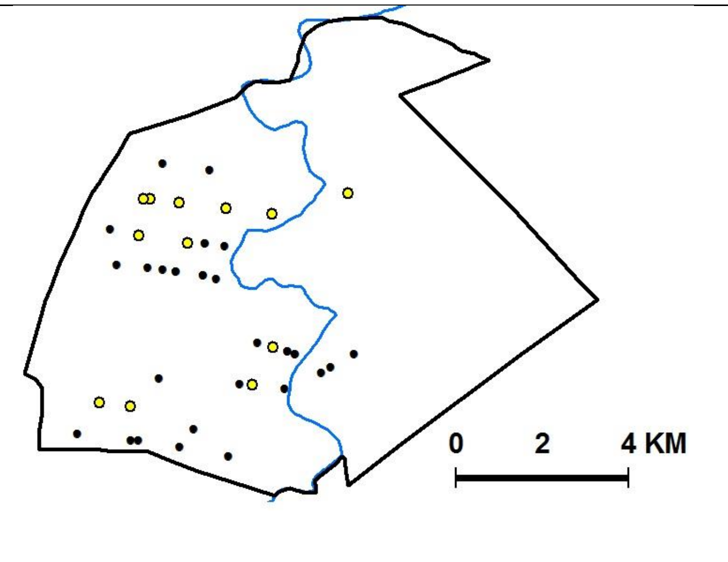
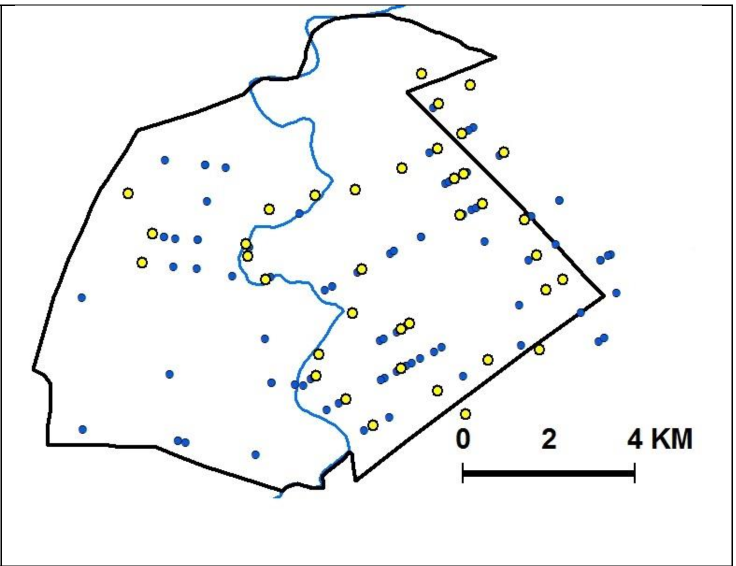




2015





2016		

Appendix IV*:* Table representing the monthly rainfall records for Bronkhorstspruit during the study period (2010-2016). The light-blue highlight indicates the months when the aerial surveys occurred on each year. The grey highlight indicates the total rainfall occurred in the wet season until the aerial survey (i.e. from October of the previous year until the month of data collection).

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC		Total/year	Wet Season Rainfall
2009	185	110,7	133,3	5,5	21,6	25,8	1,4	9,6	12,4	133,8	141,6	157,2		937,9	
2010	121,8	77,8	49,6	176,6	57,2	0,2	0,2	0	6	44	42,6	167,6		743,6	681,8
2011	167	52,6	77,2	37	3,2	4,4	0	19	6,6	87,4	24	132,6		611	473,8
2012	100	93,4	71,2	9,6	0	8,4	0	11,4	152,8	158,2	84,8	91,2		781	508,6
2013	93,2	29,2	39	79,8	6,8	0	3	2	21,6	118	160,6	114,6		667,8	427,4
2014	75,4	111,2	247,4	22,2	0,6	0	0	0,2	1,2	31,2	154	150,2		793,6	468,6
2015	40,8	23,8	44,2	15,2	0,4	0,6	1,8	0	27,4	41,2	57	135,2		387,6	376,2
2016	85,4	40,8	176	30,6	56,6	11,2	0.0	0,4	8,6	73,2	199,6	0,8		683,2	535,6

Appendix V: Table showing the results obtained from the multiple regression involving the distribution of hartebeest (dependent variable) and several independent variables, separated by years.

	F-value	**R^2**	**$R^2_{adjusted}$**
2010	$F_{3,210} = 28{,}66$	$R^2 = 0{,}4502$	$R^2_{adj} = 0{,}4345$
2011	$F_{6,212} = 8{,}40$	$R^2 = 0{,}1922$	$R^2_{adj}= 0{,}1693$
2012	$F_{6,422} = 31{,}185$	$R^2 = 0{,}3071$	$R^2_{adj} = 0{,}2973$
2013	$F_{6,406} = 53{,}475$	$R^2 = 0{,}4414$	$R^2_{adj} = 0{,}4331$
2014	$F_{6,271} = 10{,}564$	$R^2 = 0{,}1895$	$R^2_{adj}= 0{,}1716$
2015	$F_{6,229} = 22{,}29$	$R^2 = 0{,}3687$	$R^2_{adj}= 0{,}3521$
2016	$F_{6,260} = 108{,}21$	$R^2 = 0{,}7140$	$R^2_{adj} = 0{,}7074$

Appendix VI: Table representing the number of total sightings for each species, on each study year**.**

	2010	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**
Hartebeest	148	207	148	97	283	120	156
Plains Zebra	707	462	925	902	843	955	771
Black Wildebeest	217	208	379	223	345	199	184
Blue Wildebeest	567	511	645	584	694	634	574