SPATIAL AND TEMPORAL VARIATION IN UNGULATE LANDSCAPE USE IN RELATION TO RESOURCES AND CONSTRAINTS

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

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DECLARATION

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

(Signature of candidate)

22/05/2019

ABSTRACT

Ungulate resource use and distribution are shaped by resources and constraints present in the environment, which are in turn modified by herbivory. Knowing the relationships between ungulates and their environment is particularly critical when managing enclosed areas, which can contain only a limited amount and variety of resources. When resources are limited and used by many species, competition can arise with the result that some species decline in number and may eventually disappear. To investigate how ungulate landscape use varies in relation to resources and constraints in an enclosed area, four ungulate species, one generalist, plains zebra, and three specialists, black and blue wildebeest, and red hartebeest, were observed foraging over one year at Telperion and Ezemvelo nature reserves, a grassland-savanna transition zone in the eastern Highveld of South Africa. Distance between the species, elevation and forage characteristics such as grass greenness, biomass, height and distribution were compared at used and available locations at feeding patch and landscape scale across the East and West sections of the reserves. Red hartebeest and black wildebeest were mainly limited to the West section of the reserves, while blue wildebeest and zebra selected areas on both sections. Large burnt areas were selected by both wildebeest species at landscape scale while being avoided at feeding patch scale, confirming the importance of investigating different spatial scales. Changes in season triggered changes in grass selection in all species. In the dry season, red hartebeest and black wildebeest switched to feeding patches offering more biomass, blue wildebeest accepted taller grass and zebra used less green feeding patches than in other seasons. In addition, results suggest the presence of interspecific competition between black and blue wildebeest at both spatial scales, and an inability for both red hartebeest and black wildebeest to use the eastern half of the study area, probably due to lack of grass of adequate quality. Therefore, this study shows how resources and constraints interact to shaping ungulate distribution and resource use, underlining the

importance of considering different spatial scales, and giving important insight for management.

For

My parents,

Who made it all possible.

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CHAPTER ONE: *General introduction*

This study was conducted as part of a larger project on herbivore feeding strategies at different spatial scales undertaken by the Centre for African Ecology at the University of the Witwatersrand. The aim of this project was to investigate factors affecting landscape use of specialist and generalist grazers across seasons and reserves sections with different forage distribution (heterogeneity), and fire management at Telperion and Ezemvelo nature reserves (TENR), South Africa.

The need for the study

Fenced protected areas are a common occurrence across South Africa. Their establishment has contributed to the conservation of several species of ungulates, but has also created constraints. Indeed, fenced areas are generally smaller than animals' geographical ranges, preventing natural migrations (Ogutu & Owen-Smith, 2003; Western *et al.*, 2009) and increasing the chances of competition, predation and spread of diseases (Soulé *et al.*, 1979; Harrington *et al.*, 1999). In addition, fenced areas prevent immigration of new individuals, thus increasing the chances of inbreeding and, eventually, localised extinction of some species (Soulé *et al.*, 1979). A heterogeneous landscape contributes to sustaining a high biodiversity (Owen-Smith, 2004) and can counteract the negative effects of fences (Cromsigt *et al.*, 2009). Therefore, it is important for the management of enclosed areas to be informed and focused on maintaining an adequate level of both heterogeneity and biodiversity to support the ecosystem functions (Senft *et al.*, 1987; Bailey *et al.*, 1996; Redfern *et al.*, 2003), especially considering that herbivory, vegetation and their interactions shape the environment (Bailey *et al.*, 1996; Adler *et al.*, 2001; Bergman *et al.*, 2001; Kie *et al.*, 2002). Many studies have investigated factors affecting ungulate distribution and dynamics (Sinclair *et al.*, 1985; Seagle & McNaughton, 1992; Ottichilo *et al.*, 2000; Ogutu & Owen-Smith, 2003; Redfern *et al.*, 2003; Kröger & Rogers, 2005; van Bommel *et al.*, 2006; Winnie *et al.*, 2008; Ogutu *et al.*, 2009; Mordecai, 2016), but few have estimated the relative importance of these factors across seasons and landscape of different heterogeneity (Kie *et al.*, 2002; Groom & Harris, 2009).

Literature review

In order to survive and grow, populations of large herbivores need to occupy a suitable habitat, containing three fundamental characteristics: food, shelter and security (Owen-Smith, 2003). Variations in food quality, quantity and distribution (Bailey *et al.*, 1996; Bergman *et al.*, 2001; Kie *et al.*, 2002), the distribution and availability of shelter from atmospheric factors (Owen-Smith, 2003) and predation intensity (Creel *et al.*, 2014) shape both herbivore activity and distribution. The study focuses on ungulate resource selection, which is principally shaped by the food aspect of the suitable habitat. As no large predator is hosted at TENR, and the search for shelter mainly affects ungulate activity and thermoregulation patterns (Owen-Smith, 2003), these two aspects of habitat suitability are not considered here. In this study, I investigated how forage quality, quantity and distribution affect ungulate resource selection, and the potential influence of elevation and burning regime on their distribution.

Spatial hierarchy nature of resource selection

Ungulate resource selection differs at different spatial scales defining different hierarchies (Senft *et al.*, 1987; Bailey *et al.*, 1996), ranging from the bite to the home range (Bailey *et al.*, 1996). It is critical to define the spatial scale under consideration, because not only does a decision made at one scale have consequences on decisions at other scales, but also different factors can affect resource selection at different scales. For example, Wilmshurst *et al.* (1999) found that blue wildebeest resource selection was affected by both grass height and greenness when looking at the ecosystem scale, but only by grass greenness at landscape scale.

Every ungulate feeding session starts with a crucial decision made at the feeding patch level: from which plant, or part of it, to take the first bite (diet selection; Senft *et al.*, 1987). Different parts of a plant supply different quantities of energy (Owen-Smith, 2002). For example, green growing leaves are rich in protein, which makes them desirable for ungulates, while stems have high levels of fibre, being more difficult to digest (Murray & Illius, 1996; Owen-Smith, 2002). In addition, some plant parts are more easily accessible than others (O'Reagain & Schwarz, 1995). To maximise their energy intake, ungulates start a feeding session on the plant that is the easiest one to reach and of the highest quality within the feeding patch. After a while, they will have to choose where to forage next (location selection) (Senft *et al.*, 1987; O'Reagain & Schwarz, 1995; Bailey *et al.*, 1996). The decision to leave a feeding patch depends on its forage intake rate, on the expected rate intake of other patches and on the energetic cost of travelling from patch to patch (Charnov, 1976). Ungulates will leave a patch for another one when the forage intake rate of the former falls below the intake rate of the surrounding feeding patches (Charnov, 1976; O'Reagain & Schwarz, 1995). From a broader point of view, when the average forage intake of an area is too low to sustain an individual, the individual will move to a different area, because it will now be worth to start a possibly long and energetically expensive research for better forage (O'Reagain & Schwarz, 1995; Owen-Smith, 2002). Therefore, decisions made at the feeding patch scale can shape ungulate distribution at the landscape scale and determine the size of their home range (Bailey *et al.*, 1996). In the same way, selection performed at the landscape scale affects distribution at the feeding patch scale. Indeed, when an ungulate starts a feeding session in an area with a low average forage intake, but sufficient to sustain it, it will continue exploiting that area rather than investing energy in searching for a better one. This would eventually prevent the ungulate from discovering better but further feeding patches during the same foraging session (Bailey *et al.*, 1996).

Heterogeneity (forage distribution)

Landscape heterogeneity is a crucial factor in maintaining animal diversity and is one of the main drivers of ungulate distribution (Kie *et al.*, 2002; Owen-Smith, 2004). A heterogeneous landscape can, for example, offer both high and low quality forage. The former allows populations to grow, while the latter acts as a buffer, sustaining populations when favoured resources have been depleted (Owen-Smith, 2004). By sustaining a high biodiversity, heterogeneous landscapes can compensate for restrictions in animal geographical range and for the lack of migration (Cromsigt *et al.*, 2009), while mitigating landscape temporal variability, even as extreme as climate change and droughts (Du Toit & Cumming, 1999; Illius & O'Connor, 2000; Prins & Fritz, 2008). This makes heterogeneity an essential aspect that management should protect and improve in order to maintain a high biodiversity within a protected area. Moreover, several studies have demonstrated that landscape homogenization, caused by the provision of artificial waterholes or inappropriate fire programmes, has led to the decline in the diversity of ungulate species in Africa (Owen-Smith, 1996; Adler *et al.*, 2001; Ogutu & Owen-Smith, 2003). An example is the Kruger National Park, where the introduction of permanent waterholes where water seldom occurred naturally (Thrash & Derry, 1999), caused a critical decline in the number of roan antelope (*Hippotragus equinus*) (Harrington *et al.*, 1999).

Heterogeneity levels do not only affect the number of ungulates that an area can sustain, but also their distribution within the area (Kie *et al.*, 2002; Owen-Smith, 2004; Prins & Fritz, 2008; Cromsigt *et al.*, 2009). Indeed, in heterogeneous landscapes, ungulates would concentrate on the scattered high quality areas, thus having a clumped distribution (Bailey *et al.*, 1996). On the other hand, ungulates would forage on what is available in a homogenous landscape, resulting in a more random distribution (Bailey *et al.*, 1996).

Niche differentiation

The realized niche is the totality of resources and environmental factors composing the spatial area used by a species (Day & Young, 2004). Based on the competitive exclusion principle, different species cannot coexist in the same realized niche, as this would raise an unsustainable level of competition (MacArthur & Levins, 1964). The more similar the resource requirements of two species, the more intense the competition among them and the more likely that one will be excluded from the niche (Day & Young, 2004). Sympatric species can reduce competition by occupying niches offering different forage, in order to decrease their diet overlap (Schwartz & Ellis, 1981). This behaviour results in different species having different distributions based on their physiological, behavioural and ecological characteristics. Indeed, the use of different niches by different species of sympatric large herbivores has been explained as the result of digestive adaptations, differences in metabolic requirements and differences in muzzle morphology allowing the exploitation of different heights of grass (Macandza *et al.*, 2012).

A good example of sympatric species having both different digestive adaptations and metabolic requirements are ruminant and non-ruminant herbivores. The former tend to select higher quality grass than the latter, due to their digestive mechanisms. Indeed, ruminants have a more efficient digestion but, because they chew and regurgitate the same bite of grass repeatedly, they are unable to handle large amounts of forage (Demment & Van Soest, 1985; Duncan *et al.*, 1990). Therefore, ruminats are usually considered to be specialists, i.e. they seek forage of higher quality than what is available on average. On the other hand, non-ruminant grazers can fulfil their energy requirements by ingesting high quantities of lower quality grass, as their faster digestion allows them to compensate quality for quantity and to be generalists (Demment & Van Soest, 1985; Duncan *et al.*, 1990).

An example of sympatric ungulates having different realized niches based on their muzzle shape is represented by long and short grass specialists (Arsenault & Owen-Smith, 2008). Ungulates with a wide muzzle, like black and blue wildebeest (*Connochates gnu* and *C. taurinos*), will have a realized niche prevalently composed of short grass (Wilson & Hirst, 1977; Janis & Ehrhardt, 1988), while the niche used by narrow muzzled ungulates, like sable antelope (*Hippotragus niger*) and red hartebeest (*Alcelaphus buselaphus*), would be composed by tall grass (Janis & Ehrhardt, 1988; Murray & Brown, 1993; Harrington *et al.*, 1999).

Relationship between sympatric species

Ungulate distribution is also affected by the presence of other sympatric species. Interspecific relationships include competition for resources, facilitation and predation. These relationships affect ungulate distribution in relation to both the environment (Kröger & Rogers, 2005; Odadi *et al.*, 2011), and other species distribution (Sinclair, 1985). Ungulates compete for a resource when the resource is limiting and it is simultaneously used by more species, resulting in a decrease in the fitness of at least one of the species (Odadi *et al.*, 2011). Competition usually leads to the exclusion of one of the species from the niche (Day & Young, 2004), which can have different consequences. For example, if competing species are able to diversify the use of the same plant, by foraging on different parts of it or on different heights, the species will be able to use the same areas and even the same feeding patches (Macandza *et al.*, 2012). On the other hand, if one of the species uses completely different foraging resources, the competing species will usually be widely separated (Sinclair, 1985). Facilitation occurs when one species modifies the environment, usually increasing the quality of available forage, to the advantage of a second species, whose fitness increases (Arsenault & Owen-Smith, 2002; Odadi *et al.*, 2011). The consequence of facilitation between sympatric species is the creation of a foraging succession in which the facilitator and the facilitated species use the same areas at consecutive times (Arsenault & Owen-Smith, 2002). An additional interaction among sympatric species is predation. Ungulates can modify their behaviour and/or distribution to lower their exposure to predation risk (Bonnot *et al.*, 2013). For example, ungulates can group (Creel *et al.*, 2014), and form mixed-species assemblages, where sympatric species are geographically closer to each other than expected (Sinclair, 1985). The formation of large groups of herbivores increases the chances of sighting a predator from distance by increasing the number of vigilant individuals in the herd (detection effect). At the same time, it decreases the probability of an individual being predated upon (dilution effect) (Sinclair, 1985; Kie, 1999). Alternatively, ungulates can avoid high predation risk areas. This could possibly create a trade-off between areas of high quality forage and areas of low predation risk (Hernández & Laundré, 2005). For example, red deer (*Cervus elaphus*) in Europe are known to exploit the cover offered by trees by foraging in forested areas during the day, while selecting open grasslands, where forage is of higher quality, during the night (Godvik *et al.*, 2009; Bonnot *et al.*, 2013). All these sympatric relationships take place at the same time, at different spatial scales and between different ungulate species, contributing to shaping herbivore behaviour and distribution.

Seasonal variations

Grass quality and quantity vary with season. In the late dry season, after months without precipitations, all the available grass is old and dry, with a high fibre and low protein content (Meissner, 1997). As animals keep foraging and new grass cannot grow without water supply, both forage quality and quantity reach their lowest in the dry season (Owen-Smith, 2002). To survive until the beginning of the wet season, ungulates rely on key resource areas (areas offering forage of high quality during limiting periods), such as wetlands/bottomlands and burnt areas (Owen-Smith, 2002). Both burnt areas and wetlands offer the highest quality of grass available in this period, thus attracting several ungulate species (Moe *et al.*, 1990; Archibald & Bond, 2004; Parrini & Owen-Smith, 2010; Macandza *et al.*, 2012).

Fire is an integral part of African savannas and grasslands and, being an effective management tool, it has been used by many reserves (Gureja & Owen-Smith, 2002; Archibald *et al.*, 2005; Parrini & Owen-Smith, 2010). Burning is usually performed during the late dry season, as it improves forage quality by removing moribund grass layers and stimulating the sprouting of new nutritious grasses (McNaughton, 1985; Hobbs *et al.*, 1991). However, the early dry season could be a better time for burning, as it gives grass more time to regrow, provided there is enough moisture in the soil, and thus provides grazers with green grass during the dry season (Parrini & Owen-Smith, 2010). The use of burnt areas by ungulates has been proved to increase the protein content of their diet, acting as an important resource in reducing stress caused by forage restriction during the dry season (Hobbs & Spowart, 1984; Parrini & Owen-Smith, 2010). The presence of burnt areas affects ungulate distribution in different ways at different spatial scales. At the landscape scale, burnt areas attract ungulates (Archibald & Bond, 2004). If fire is managed in a patchy way, it contributes in creating a heterogeneous environment, where grazers can interchange between burnt areas, offering small quantities of high quality grass, and un-burnt areas, having higher quantities of poor quality grass (Fuhlendorf & Engle, 2001; Vermeire *et al.*, 2004). At a narrower spatial scale, burnt areas are more homogeneous than un-burnt ones, as fire resets the vegetation and the regrowth consists of a uniform layer of short sprouting grasses (Archibald & Bond, 2004). As grasses in burnt areas are all equally palatable to grazers, ungulates are more uniformly dispersed in burnt than in un-burnt areas (Hobbs *et al.*, 1991; Archibald & Bond, 2004).

Distance from water, slope and elevation

Forage characteristics are not the only important factors in shaping ungulate resource selection and distribution. Geographical factors contribute to shaping ungulate distribution especially at the landscape scale, the most important of them being distance from water and slope (Western, 1975; Thrash & Derry, 1999; Illius & O'Connor, 2000; Helm, 2007; Groom & Harris, 2009). Distance from water is particularly important for water dependent species, like zebra (*Equus quagga*) and both wildebeest (Estes, 1991), which have to drink often. These species are expected to be closer to water than water independent species, and this trend is accentuated in the late dry season, when water content of forage is at its lowest (Owen-Smith, 2002). At this time, obligate drinkers face a trade-off between their water and foraging needs (Owen-Smith, 1982; Illius & O'Connor, 2000; Redfern *et al.*, 2003; Cromsigt *et al.*, 2009). These species feed close to a water source, in order to minimise their movements between feeding patches and water sources. Given this, locations close to water usually suffer from high level of grazing and trampling, leading to a decrease in both quantity and quality of available forage (Lange, 1969; Thrash & Derry, 1999). Water independent species, on the other hand, can graze on higher quality grass far from water, but this means investing energy in travelling to water (Thrash & Derry, 1999; Redfern *et al.*, 2003; Groom & Harris, 2009). In this study, distance from water was not considered because of the high abundance of water sources within the study area.

Slope is another important constraint in ungulate grazing distribution (Bailey *et al.*, 1996; Helm, 2007). Ungulates perceive changes in altitude and they prefer to forage at a constant altitude during a feeding bout (Bailey *et al.*, 1996). Helm (2007) found that both wildebeest species at TENR avoided grazing on steep slopes. Therefore, these species would avoid certain locations because of their physical inaccessibility due to slope presence, regardless of grass quantity or quality at the site. In her study, Helm (2007) visually identified slope degree. I found this method very subjective, and therefore I identified slopes in the study area from a Digital Elevation Model. The steepest slope was only 20° and the study area was clearly mainly flat. Slope was therefore not considered in this study.

Elevation can indirectly affect ungulate resource use, as quality of forage varies with elevation. Wilmshrust *et al.*, (1999) explain grassland and montane ungulate elevation migration with the maturation hypothesis. Bell (1971) explains the same phenomenon as driven by water accumulation. Merging the two ideas, it seems that ungulates use location at higher altitudes during the wet season, and move to lower areas in the dry season, due to grass quantity being the strongest driver in landscape use. In the wet season, higher altitudes receive rain first; rain that then runs downhill and accumulates at bottomlands. Because of it, grass emerges sooner at higher altitudes and it is thus favoured by ungulates. When the dry season starts, grass at higher altitudes gets depleted first, while grass at bottomlands have had water for longer time and have been used less, being so more abundant; consequently, ungulates, such as blue wildebeest, use areas at different altitudes through the year. The effect of elevation on ungulate resource use has been seldom studied in South Africa (Bell, 1971; Wilmshurst *et al.*, 1999), therefore I believed it would be an important factor to add to the study.

Study area

The study was conducted at Telperion and Ezemvelo nature reserves, a complex of natural reserves covering 13,000 ha in total (Coetzee, 2012). The study area is located on the boundary of Gauteng and Mpumalanga provinces, on the edge of the central inland plateau of the northern part of South Africa (latitude 25˚38' S - 25˚45' S, longitude 28˚55' E- 29˚03' E; Figure 1, APPENDIX) (Coetzee, 2012). Though the Wilge River represents the only big source of water, water provision is ensured throughout the reserves by the occurrence of many dams and temporary rivers.

The vegetation in the study area has been defined as Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina *et al.*, 2005). Many plant communities form a mosaic of woodlands, grasslands and wetlands (Swanepoel, 2006). The most common grass species are *Elionurus muticus, Eragrostis curvula* and *Setaria sphacelata*, while *Themeda triandra* and *Eragrostis gummiflua* are present but not so common (Swanepoel, 2006). The study area hosts a variety of animals, including about 250 species of birds. Among mammals, there are blesbuck (*Damaliscus pygargus phillipsi*), eland (*Taurotragus oryx*), giraffe (*Giraffa* *camelopardalis),* impala (*Aepyceros melampus*) and my focal species black and blue wildebeest, red hartebeest and plains zebra. Though the reserves do not host any large carnivore, leopard (*Panthera pardus*) have been camera trapped inside the area, and small predators, such as aardwolf (*Protetes cristata*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) are commonly seen.

The reserves experience a wet and a dry season, from November to March (≈ 462 mm of rain on average) and from April to October (≈ 163 mm of rain on average) respectively (Swanepoel, 2006). The mean annual rainfall is of about 625 mm (Swanepoel, 2006). However, the study was conducted during a drought, and thus the seasonal rainfall was lower than the average: about 105 mm of rain fell in the wet season 2017-2018, and about 50 mm in the dry season 2018 (Table 1, APPENDIX. Source: Ezemvelo Nature Reserve weather station). Daily temperatures are the highest in January and February, reaching a daily mean maximum of 26˚C, while the lowest daily mean temperatures of about 4-5˚C are reached in June and July (Swanepoel, 2006).

The Wilge River runs from south to north, dividing the study area into a West and an East sections. The two sections (from now on referred to as the West and the East section respectively) are composed of three different reserves: Ezemvelo Nature Reserve and Boholokwa lying on the West section, and Telperion Nature Reserve covering the East section of the reserves. The sections differ in both topography and management. The West section is principally made of flat open grassland, presenting abundant wetlands along the water sources, while the East section has a more savanna-like aspect, being more wooded (Helm, 2007) (Figure 2, APPENDIX). In addition, managers of the West section apply an annual burning plan, according to which they burn a different area every year. On the other hand, the East section managers do not to implement fire, but perform controlled fire breaks along the roads to prevent big natural fires to spread. Ungulates have been observed crossing the river and are free to move through the whole study area, although movements across the two sections have not been quantified.

Aim and objectives

The aim of the study was to understand how resources and constraints might shape ungulate distribution and interspecific resource overlap, possible cause of competition, at TENR, a transitional zone between grassland and savanna situated in the eastern Highveld in South Africa. To do it, the study investigated specialist and generalist ungulate landscape use at different spatial scales, across seasons and landscape having different forage distribution and fire regimes

Objective 1: To compare the role of grass greenness, heterogeneity, burnt landscape, elevation and competition on landscape use by generalist and specialist grazer ungulates, and to analyse how it varied across different seasons and sections having different forage distribution and fire regimes.

Objective 2: To investigate the role of forage quality, quantity, height and feeding patch status (un-burnt, burnt or wetland) on feeding patch selection by specialist and generalist grazer ungulates, and to analyse how it varied across different seasons and sections having different forage distribution and fire regimes.

Predictions

For objective 1, I hypothesised that generalists and specialists would select resources in different ways. The ruminant species, red hartebeest, and black and blue wildebeest, would favour grass of the highest available quality. Therefore, they would prefer burnt over un-burnt areas, especially during the dry season. Due to the presence of large burnt areas only in the West section, ruminants would also prefer the West section of the reserves. Greenness (measured in the form of Normalised Difference Vegetation Index - NDVI) and heterogeneity would positively influence their resource selection. In addition, I expected ruminants to prefer foraging at different altitudes through the year: at higher altitudes during the wet season and at lower during the dry season, when the short high quality grass presents at high altitudes is depleted. Finally, I expected ruminants to have a narrow distribution, concentrated on areas of high quality forage. I expected the generalist zebra to use a wider variety of areas, as they can rely on a wider quality of forage. Consequently, zebra distribution would be the widest. I expected black and blue wildebeest to use different areas as, being very similar in physiology and morphology, they would use very similar foraging niches, and thus compete for resources. I also predicted red hartebeest to use different areas than zebra in order to decrease potential competition with them, as both species prefer tall grasses.

For objective 2, I expected specialist and generalist species to select feeding patches with different characteristics. Red hartebeest, being ruminant and tall grass specialists, would select feeding patches with tall grass (taller than 11 cm) of high quality. During the late dry season, due to the overall decrease of grass quality and the fact that it is impossible for red hartebeest to reach short grass such as on burnt areas, they would preferentially select feeding patches in wetlands.

I expected the two wildebeest species to use very similar niches, but not the same. They are both ruminant and short grass specialists, so they would select feeding patches having short grass (shorter than 11 cm) of high quality. However, as blue wildebeest are adapted to a larger variety of habitats, I expected blue wildebeest to be less selective than black wildebeest. In addition, during the limiting late dry season, I expected both species to increase their use of burnt feeding patches. I expected the generalist zebra to select feeding patches based on their availability through the year, while, during the late dry season, zebra would select feeding patches with more biomass than in the other seasons. Being non-ruminant, zebra can ingest a higher quantity of forage than ruminants and would compensate the low quality of forage available in the late dry season by foraging at a higher quantity.

Study species

Wildebeest

Wildebeest are ruminant antelopes of the family Bovidae, with broad muzzle and cowlike horns (Estes, 1991). There are two species of wildebeest: the blue, or common, wildebeest which is distributed through eastern and southern Africa, and the black wildebeest which is endemic to South Africa (Codron & Brink, 2007). Blue wildebeest are bigger than black wildebeest and morphologically they differ mainly in horn shape and tail colour (Helm, 2007). Blue wildebeest can use a variety of savanna habitats, while black wildebeest are confined to open grasslands (Codron & Brink, 2007). Both species are grazers and considered to be short grass specialists (Janis & Ehrhardt, 1988), as their muzzle morphology also suggests (Janis & Ehrhardt, 1988; Murray & Brown, 1993; Codron & Brink, 2007). Being specialized ruminants, both the species rely on high quality forage to supply their feeding requirements. In addition, wildebeest are considered to be water dependent grazers which need to drink every day (Estes, 1991).

Red hartebeest

Red hartebeest is a large ruminant antelope of the Alcelaphinae subfamily. It has high shoulders, elongated forehead and heart shaped curved horns (Estes, 1991). Being ruminants, they have a slow and highly efficient digestion (Owen-Smith *et al.*, 2013) and they need to ingest high quality grass (McNaughton & Georgiadis, 1986). Red hartebeest also have a narrow muzzle which allows them to graze selectively (Janis & Ehrhardt, 1988; Murray & Brown, 1993). Red hartebeest have a preference for tall grass (Murray & Brown, 1993) and drink on average 3.2 litres of water daily (Price, 1978), less than the other species of the Alcelaphinae subfamily (Jarman, 1974; Estes, 1991). This species is known to be susceptible to competition with other tall grass grazers, such as plains zebra and cattle, and even with smaller ones such as blesbuck (*Damaliscus pygargus phillipsi*) (Estes, 1991; Odadi *et al.*, 2011).

Plains zebra

The plains zebra, also known as Burchell´s zebra, is the most numerous of the zebra species, occurring throughout eastern and southern Africa (Estes, 1991; Groom & Harris, 2009). It is usually found in open savanna environments or open woodlands. Zebra belong to the family Equidae and they are hindgut fermenters non-ruminant grazers. Zebra are able to compensate for their less efficient digestive system by feeding on larger quantities of low quality grass compared to ruminants (Estes, 1991). They have strong upper and lower incisors, which enable them to forage on both tall and short grass, making them generalist feeders. However, their sensitive mobile lips allow them to perform a certain level of selection on forage, especially when the quantity of available grass becomes a constraint (Estes, 1991; Cromsigt *et al.*, 2009). Plains zebra are considered to be highly water dependent, as they need to drink every day. The result is that their distribution is strongly influenced by distance from water and forage quantity and quality (Estes, 1991; Redfern *et al.*, 2003; Groom & Harris, 2009).

Study design

Data collection took place over a total of 80 days, spreading over four seasons, between September 2017 and August 2018. I identified four seasons based on NDVI (a proxy for vegetation quality and primary productivity) and rainfall yearly patterns (Figure 3, APPENDIX): late dry season (September-October 2017), wet season (February 2018), early dry season (May 2018) and mid dry season (August 2018). Every season spanned a three weeks period of data collection. I collected data at two spatial scales: the landscape and the feeding patch scale. I defined a feeding patch as a cluster of feeding stations close enough for an ungulate to use them in a single feeding bout (Bailey *et al.*, 1996).

For the landscape scale, I drove around the study area, travelling all the available roads, from dawn to sunset twice per season. I mainly collected data in the early and late hours of the day, when ungulate foraging is more intense (Gureja & Owen-Smith, 2002). Every time I encountered a foraging individual or a group of the study species, I stopped the vehicle and I recorded the season, section of the reserves and species. I considered a group as one sighting. I recorded my GPS position, and the angle and distance between the foraging individual or the most central foraging individual in a group and myself in order to triangulate the animal‘s location.

For the feeding patch scale, I walked to the observed foraging location recorded the previous day and collected data on both the used feeding patches and a correspondent available non-used one. I placed a 0.5 m^2 quadrat in the centre of the used feeding patch, identified by the triangulated GPS position, and 4 quadrats, spaced 4 meters apart along each cardinal direction, for a total of 5 quadrats per feeding patch (adapted from Owen-Smith *et al.*, 2013) (Figure 4, APPENDIX). I then repeated the same operation 100 meters from the central quadrat in a random direction, recording data as an available feeding patch. For each quadrat of used and available feeding patches I recorded: grass height and greenness by visual estimation (Walker, 1976), grass biomass as the value obtained with a disc pasture meter (Zambatis *et al.*, 2006; Arena *et al.*, 2015) and the feeding patch status as burnt, un-burnt or wetland.

Dissertation outline

The first chapter of this dissertation is a general introduction to the study itself, which is explored in details in chapters 2 and 3. The references used in each chapter can be found at the end of the chapter in which they have been used. Chapter 2 and 3 are both written in article format, with their own introduction, methods, results and discussion. This writing choice involves some repetitions, which have however been kept to a minimum. Figures and tables are presented at the end of the relevant chapter. Figures and tables that are referred to in more than one chapter have been placed in an appendix at the end of the dissertation. Chapter 2 focuses on ungulate resource selection and distribution at landscape scale, while chapter 3 is focused on forage selection at feeding patch scale. Chapter 4 represents the general conclusion of the study, synthesising the findings of the two chapters.

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CHAPTER TWO: *Ungulate landscape selection based on resources and constraints at Telperion and Ezemvelo nature reserves, South Africa*

Abstract

Understanding the role of resources and constraints on ungulate landscape use and distribution provides crucial information for fenced reserves management. The role of resources, constraints and interspecific relationships on the landscape use of specialist and generalist ungulate grazers was investigated across seasons and areas with different topography and management in a grassland-savanna transition zone in the eastern Highveld, South Africa. Results indicate that under the existing conditions during the study, interspecific relationships, in the form of distance between species of ungulates, are important in shaping ungulate landscape use and suggest the presence of competition between black and blue wildebeest. The most important resource for black and blue wildebeest appeared to be the presence of large burnt areas, available only in the West section of the study area. This would partly explain the almost exclusive use of this section by black wildebeest. However, red hartebeest were also usually seen in the West section, while zebra preferred the East section, suggesting that forage available in the East section of the study area might be of too low quality for ruminants. Blue wildebeest distribution and resource use was in between zebra and black wildebeest, suggesting that blue wildebeest may not be pure specialists. The restriction of red hartebeest and black wildebeest to the West section could represent a problem for the survival of these species, thus it should been taken into consideration by the management.

Introduction

The majority of large wild ungulates in South Africa are found in fenced protected areas, implying that available resources are limited in space and time. Species with similar morphology and physiology tend to use similar resources (Day & Young, 2004), but different species cannot survive having the same realized niches (i.e. the set of environmental factors and resources used by a species) (Schwartz & Ellis, 1981; Day & Young, 2004). Moreover, ungulate resource selection varies with spatial and temporal scale, with decisions made at broader spatial scales being less frequent and having a stronger impact on ungulate distribution than decisions made at narrower scales (Bailey *et al.*, 1996). As herbivory, vegetation and the interaction between the two contribute to shaping the environment (Bailey *et al.*, 1996; Adler *et al.*, 2001; Bergman *et al.*, 2001), it is crucial to understand ungulate landscape use and distribution in relation to resources and constraints in order to implement effective management strategies of enclosed areas (Senft *et al.*, 1987; Bailey *et al.*, 1996; Redfern *et al.*, 2003).

Ungulate distribution is primarily driven by availability of resources and presence of constraints. Resources are usually related to forage characteristics that attract ungulates, while constraints are mainly physical traits within the environment (Bailey *et al.*, 1996; Redfern *et al.*, 2003). The strongest constraints in ungulate distribution are thought to be distance from water (Western, 1975; Illius & O'Connor, 2000; Redfern *et al.*, 2003; Groom & Harris, 2009) and slope (Bailey *et al.*, 1996; Helm, 2007). Distance from water mostly affects water dependent herbivores such as zebra (*Equus quagga*) and black and blue wildebeest (*Connochaetes gnu* and *C. taurinus*). These species face a trade-off between their water and energy needs, especially during the dry season. Indeed, in the dry season, the moisture content of forage is extremely low (Owen-Smith, 2002), so more animals obtain water from permanent water sources (Lange, 1969). Trampling and grazing by a large number of herbivores cause the quality and quantity of grass in close vicinity to water sources to decline (Thrash & Derry, 1999). Therefore, obligate drinkers have to choose whether to satisfy their energy requirements by foraging on good quality grass far from water, thus investing energy in travelling, or to forage on lower quality grass closer to water, at the expense of obtained energy (Thrash & Derry, 1999). On the other hand, slope represents a constraint for several ungulates. Ungulates can perceive changes in slope and they tend to start and finish a forage bout minimizing changes in elevation (Bailey *et al.*, 1996). Large ungulates, such as cattle, generally avoid slopes over 10° (Cook, 1966), and both wildebeest species in particular have been observed avoiding steep slopes (Helm, 2007). Cook (1966) suggested that ungulates avoid slopes because they are physically too steep, or either because distance from water increases while on slopes.

Among forage characteristics acting as resources for ungulates, grass quality and distribution are thought to be the most important (Owen-Smith, 2004; Cromsigt *et al.*, 2009). Kie *et al.* (2002) found that heterogeneity in forage distribution explained 57% of variance of mule deer (*Odocoileus hemionus*) home range use in California. A landscape with a heterogeneous forage distribution offers many niches, and can thus sustain a higher biodiversity (Owen-Smith, 2004) than a homogeneous landscape, which offers a smaller variability of resources (Owen-Smith, 1996; Harrington *et al.*, 1999). When forage quantity is not limiting, ungulates tend to select the highest quality of forage available. Consequently, in a heterogeneous landscape, ungulates will spend more time searching for areas of high quality grass and will be more concentrated in such areas (Bailey *et al.*, 1996). However, when grasses of high quality are depleted, a heterogeneous landscape may still offer grass of lower quality, that ungulate can use to sustain themselves (Owen-Smith, 2004). On the other hand, when foraging in homogenous landscapes, with grasses of similar quality, ungulates will spend less time searching for grass and will be randomly distributed. If all grass is depleted in homogeneous landscapes, herbivores will be unable to sustain themselves (Owen-Smith, 2004).

Grass quality and distribution vary over the year with changes in temperature and rain patterns (Owen-Smith, 2002) and ungulate distribution varies accordingly. Grass greenness declines to low levels during the dry season, when most of the grasses are high in fibre and low in protein content (Meissner, 1997; Illius & O'Connor, 2000; Owen-Smith, 2002). To cope with the latter, grazers can increase the use of high quality areas, like recently burnt ones (Moe *et al.*, 1990; Parrini & Owen-Smith, 2010), or move to areas of low quality grass that were previously avoided (Casebeer & Koss, 1970; Owen-Smith, 1994). Burnt areas not only offer a layer of new high quality grasses which attracts ungulates (Moe *et al.*, 1990; Gureja & Owen-Smith, 2002; Archibald & Bond, 2004), but foraging in these areas also increases the quality of grazers' diet, especially during the dry season (Hobbs & Spowart, 1984; Parrini & Owen-Smith, 2010). Many reserves have used fire as a management tool with the aim of relieving ungulate nutritional stress (Gureja & Owen-Smith, 2002; Parrini & Owen-Smith, 2010).

Ungulates select resources based on their digestive system, energy requirement and preference for grass, all considered species-specific characteristics. Thus, for example, ruminants select high quality grass more consistently than non-ruminants. This is due to the different digestion mechanism, which allows non-ruminants to sustain themselves with high quantity of grass with protein content that is too low to maintain ruminants (Owaga, 1975). Because of the broader dietary tolerance, non-ruminant species can use a larger variety of resources than ruminants (Du Toit & Cumming, 1999). Consequently, non-ruminants tend to have a wider distribution than ruminants (Du Toit & Cumming, 1999). Among ruminants, some species, such as black and blue wildebeest, are considered short grass specialists. These species would find burnt areas particularly attractive. On the other hand, long grass specialist, like red hartebeest (*Alcelaphus buselaphus*), may not be able to exploit the very short regrowth of burnt areas (Gureja & Owen-Smith, 2002). Indeed, red hartebeest have a narrow muzzle allowing them to be very selective on tall grass but preventing them to reach short tufts (Janis & Ehrhardt, 1988).

Finally, some species of ungulates prefer to use areas at different elevation during the year. Wilmshurst *et al.* (1999) observed blue wildebeest in the Serengeti at higher altitudes during the wet season and migrating to low-lying grasslands in the limiting dry season. Bell (1971) explained this ungulate migration in the Serengeti with a succession of grass created by the rain and the hypothesis that grass quantity would be the main driver for ungulate landscape use. According to the author, rain reaches higher areas first, to then run downhill and accumulate at bottomlands. Thus, in the wet season, grass emerges sooner at higher altitudes than at bottomlands, being selected by ungulates. At the beginning of the dry season, grass at higher altitudes would be depleted, while grass at lower altitudes would be more abundant, as it has had water for longer (Bell, 1971; Wilmshurst *et al.*, 1999). Consequently, ungulates would move to bottomlands during the dry season.

Ungulate distribution is also affected by relationships with other species. Interactions such as competition, facilitation and predation, not only affect ungulate distribution (Kröger & Rogers, 2005; Odadi *et al.*, 2011), but also affect distances between different ungulates species (Sinclair, 1985). For example, when sympatric ungulates compete for a resource, i.e. when they simultaneously use a limiting resource and the fitness of at least one species decreases (Odadi *et al.*, 2011), one of the species will eventually modify its resource use, to relieve competition (Day & Young, 2004). In so doing, the species will use different areas, usually being more distant from each other than expected (Sinclair, 1985). Facilitation, on the contrary, occurs when a species modifies one or more resources of the environment to the advantage of another species, whose fitness increases (Odadi *et al.*, 2011). Foraging facilitation commonly consists in grazing by one species increasing the quality of forage available also to other species through the stimulation of grass regrowth (Arsenault & Owen-Smith, 2002). When two species facilitate each other, they generally use the same areas but at different times, creating a grazing succession (Sinclair, 1985; Arsenault & Owen-Smith, 2002). In addition, different species of sympatric ungulates are known to group and forage closer to each other than expected by chance, in order to avoid predation (Sinclair, 1985). Indeed, the presence of more individuals in the same area increases the possibility of sighting a predator (detection effect) while decreasing the probability of an individual to be chosen by a predator (dilution effect) (Sinclair, 1985; Kie, 1999).

Telperion and Ezemvelo nature reserves (TENR) are a complex of nature reserves enclosed by a fence and situated in South Africa. The reserves are divided into a West and an East section, differing both topographically and in management strategies. Large burnt areas are provided every year by the managers in the large flat open grasslands composing the West section, while in the more mountainous and wooded East section, managers only burn fire breaks to prevent the spreading of natural fires. This implies that the different sections of the reserves have different resource availability and distribution. In addition, among the grazing ungulates inhabiting the reserves, there are the generalist non-ruminant zebra, the ruminant tall grass specialist red hartebeest and both black and blue wildebeest, two ruminant short grass specialists morphologically very similar, but differing in dimensions and habitat use. Blue wildebeest are bigger and adapted to several environments, from savanna to grassland, while black wildebeest are smaller, and are grassland specialists (Janis & Ehrhardt, 1988; Codron & Brink, 2007). These characteristics made TENR a suitable area to investigate the effect of different management regimes and heterogeneity on seasonal landscape use by generalist and specialist grazing species.

Specifically, I investigated the role of vegetation greenness, heterogeneity, elevation, burnt areas and ungulate interspecific competition on distribution and landscape use by black and blue wildebeest, red hartebeest and plains zebra, and how it varied with seasons and sections of the reserves. Distance from water and slope were not considered in this study because of the numerous water sources scattered throughout the study area and the presence of only few steep slopes.

I expected ungulate landscape use to be affected by both resources and constraints. I predicted (1) all ruminants to select areas based on greeneness and heterogeneity, due to their need of high quality forage, with black and blue wildeebest being also positively associated with burnt areas (resources). In addition, (2) both species of wildebeest would rather avoid areas with a high elevation, as previously observed in the same reserves (Helm, 2007), or use them only during the wet season. On the other hand, (3) the generalist zebra would have a looser selection of resources than ruminants, due to the their ability to use a wider variety of resources (Du Toit & Cumming, 1999). (4) Ruminant distribution would be smaller and more clumped than non-ruminant's, due to their requirement for high quality grass (Du Toit &

Cumming, 1999). In addition, I expected (5) blue wildebeest to have a wider distribution than black wildebeest due to their larger size and more diversified diet (Codron & Brink, 2007).

As per interspecific competition, I expected (6) the two wildebeest species to compete for resources due to their similar physiology and morphology, thus to be further from each other than it would be if they were not influencing each other. I also expected (7) red hartebeest and zebra to compete for forage, as they both prefer medium to tall grass, but to a lesser degree than wildebeest, as zebra should be able to lower competition by foraging on grass of quality that would be too low for ruminants. I expected (8) seasons to interact with grass greenness and heterogeneity in affecting ruminant resource selection. In particular, during the late dry season, ruminant species would select greener and more heterogeneous areas than in the other seasons, due to the scarcity of high quality forage. Instead, non-ruminant zebra would not be affected by seasons. I expected (9) the section of the reserves to have a strong impact on the species distribution, due to both the different topography and management of the sections.

Methods

Study area

The study took place at Telperion and Ezemvelo nature reserves. The reserves are located on the edge of the central inland plateau of the northern part of South Africa (latitude 25˚38’ S - 25˚45’ S, longitude 28˚55’ E- 29˚03’ E; Figure 1, APPENDIX) (Coetzee, 2012). Several temporary rivers and dams, and few perennial rivers ensure water provision to the reserves throughout the year. The Wilge River is the largest water source in the reserves, running from south to north and dividing the study area into the West and the East sections. The West section mainly consists of large flat open grasslands interspersed with several wetlands along the rivers, while the East section is composed of grassland with scattered trees (Helm, 2007). The reserves experience a wet season from November to March (≈ 462 mm of rain on average) and a dry season from April to October (≈ 163 mm of rain on average) (Swanepoel, 2006). The mean annual rainfall is of about 625 mm (Swanepoel, 2006). The seasonal rainfall during the study period was lower than the average: about 105 mm of rain in the wet season 2017-2018, and about 50 mm in the dry season 2018 (Table 1, APPENDIX. Source: Ezemvelo Nature Reserve weather station). Therefore, the study was conducted during a drought. Daily temperatures are the highest in January and February, reaching a daily mean maximum of 26˚C, while the lowest daily mean temperatures of about 4-5˚C are reached in June and July (Swanepoel, 2006).

The main vegetation types in the study area are Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina *et al.*, 2005). Plant communities form a mosaic of woodlands and grasslands (Swanepoel, 2006). The most common grass species throughout the reserves are *Elionurus muticus, Eragrostis curvula* and *Setaria sphacelata*. *Themeda triandra* and *Eragrostis gummiflua* are also widely present (Swanepoel, 2006). The reserves house over 20 herbivores species, including blesbuck (*Damaliscus pygargus phillipsi*), eland (*Taurotragus oryx*), giraffe (*Giraffa camelopardalis),* impala (*Aepyceros melampus*) and my focal species black and blue wildebeest, red hartebeest and plains zebra. Some small carnivores, such as aardwolf (*Protetes cristata*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) are also present and leopards (Panthera pardus) have been observed crossing the reserves.

Data collection

Field data collection

I collected data over one year, from September 2017 to August 2018, covering four seasons: the late dry season (September-October 2017), the wet season (February 2018), the early dry season (May 2018) and the mid dry season (August 2018). The four seasons were identified from rainfall and Normalized Difference Vegetation Index (NDVI, a proxy for vegetation quality and primary productivity) patterns (Figure 3, APPENDIX).

I searched for black and blue wildebeest, red hartebeest and zebra during peak grazing times in the early morning and late afternoon (Gureja & Owen-Smith, 2002). The survey was conducted from the access roads of the reserves, driving them twice during a three weeks period in each season. Each time I encountered a foraging individual or group of the study species, I stopped the vehicle and recorded the distance and bearing from the ungulates using a laser range finder (Leica Rangemaster 1600B 7.0X) and a military compass. I recorded my position with a GPS (Montana 600 GPS Garmin) together with the species of the observed ungulates, the season and the section of the reserves. Using my GPS position, distance and bearing from the focal species, I triangulated the locations of the focal species using equation (1). Testing this method in the field, I calculated that it had an uncertainty of about 20 meters. Herds of single species were considered as one sighting and data were collected for the most central foraging individual, in order to minimize the risk of taking a location outside the herd due to the uncertainty of the triangulation method.

$$\begin{cases} \varphi_2 = asin\ (sin\ \varphi_1 \cdot cos\ \delta + cos\ \varphi_1 \cdot sin\ \delta \cdot cos\ \theta) \\ \lambda_2 = \lambda_1 + atan2\ (sin\ \theta \cdot sin\ \delta \cdot cos\ \varphi_1,\ cos\ \delta - sin\ \varphi_1 \cdot sin\ \varphi_2) \\ \text{where } \varphi \text{ is latitude, } \lambda \text{ is longitude, } \theta \text{ is the bearing (clockwise from north), } \delta \text{ is the angular} \\ \text{distance } d/R\text{; } d \text{ being the distance travelled, } R \text{ the earth's radius.} \end{cases} \quad (1)$$

Data manipulation

All the collected GPS locations of the focal species were imported into QGIS 2.18. I created a buffer of 500 m along all the accessible roads, in order to delineate only the visible areas. Then, using QGIS tool ‘Random points in layer bounds’, I generated ten random locations for each used position within the visibility buffer. I gave each location a status attribute (‘burnt’ if it was in a burnt area, or ‘un-burnt)’, and a section attribute (‘West’ or ‘East’), based on the section of the reserves in which it lay. The shapefile representing burnt areas of the West section was provided by the staff of Ezemvelo Nature Reserve and represented the area that was burnt as part of their management duties in July 2017. The only burnt areas present in the East section were long narrow fire breaks, covering a too small surface to be considered as burnt areas at this spatial scale.

I downloaded an elevation raster covering the whole study area with a resolution of 7.5 arc-secs from the Global Multi-resolution Terrain Elevation Data 2010 database. I downloaded four NDVI rasters, one per season, from the Moderate Resolution Imaging Spectroradiometer (MODIS) database. It is common to use MODIS NDVI in animal movement studies at large landscape scales as a proxy for vegetation quality and primary productivity (Pettorelli *et al.*, 2005; Winnie *et al.*, 2008). Pictures provided by MODIS NDVI represent 16 days composite images with a 250 m spatial resolution. One MODIS NDVI image was chosen per season, the only image falling within the three weeks of data collection, or the last one. I imported the elevation and NDVI rasters into QGIS, where an elevation and an NDVI value were assigned to each real and random animal location. I created four heterogeneity rasters, one per season, with a spatial resolution of 250 m. Heterogeneity was obtained by computing the average difference in absolute values between the NDVI value of each pixel and the NDVI values of the eight pixels surrounding it. The higher the heterogeneity value, the more heterogeneous the pixel. In order to analyse relationships between the species, I calculated the distance from each real and random location to the closest real individual of a different study species.

Data analysis

I conducted the data analysis in R version 3.5.1 (R Development Core Team, 2018), by fitting 22 generalized linear models (GLM) with a binomial error distribution through the Generalized Linear Effect Models procedure using the 'stats package'. The response variable was 'used' versus 'random' location. I tested seven independent factors, three categorical (landscape status, section of the reserves and season) and four continuous (NDVI, heterogeneity, elevation and distance from the closest individuals of other species). The effect of season and section was also included in interaction with NDVI and heterogeneity.

To make them comparable, I scaled all the continuous variables in order to have a mean of zero (Burnham & Anderson, 2003). I conducted model selection through the 'AICcmodavg package' (Mazerolle & Mazerolle, 2017) applying the Akaike's Information Criterion corrected for small sample bias (AICc) (Anderson, 2008). The model with the smallest AICc value was taken as the best model (Anderson, 2008). From this model, I calculated the predicted logit and associated 95% confidence intervals for categorical variables, and the predicted degree of use expressed in probability and its associated 95% confidence intervals for continuous variables. Predictions and plots were made using the 'jtools' package (Long, 2018). Results for categorical variables are shown in relation to the reference category of the variable. If the confidence interval of a category and the reference category do not overlap, there is a significant difference between the two categories of the variable (Godvik *et al.*, 2009).

<u>Results</u>

I collected 719 used ungulate locations across the study period, 92 in the late dry season, 228 in the wet season, 205 in the early dry season and 194 during the mid dry season. Sightings amounted to 141 for black wildebeest, 253 for blue wildebeest, 52 for red hartebeest and 273 for zebra.

Black wildebeest

Many of the tested variables appeared to influence black wildebeest landscape use: landscape burnt status, section of the reserves, elevation, distance from all the other species, NDVI and heterogeneity. Out of 22 models, the most parsimonious generalized linear model for landscape selection by black wildebeest was *m1* with a ranking of 0.97 (Table 2.1). This was the most general model containing all the investigated variables without interactions (Table 2.2). Black wildebeest favoured burnt areas more than un-burnt areas (log-odds = 1.26 ± 0.74) (Fig 2.1a) and they avoided the East section of the reserves (log odds = -4.24 ± 2) (Fig 2.1b). In addition, black wildebeest were preferentially found in low laying areas and closer than expected to the other focal species (Fig 2.2). Although NDVI and heterogeneity were part of the best model, their effect on landscape selection by black wildebeest was extremely low (Table 2.2). Compared to the other species, black wildebeest used the smallest portion of the reserves, being concentrated in the burnt area of the West section (Fig 2.3).

Blue wildebeest

The model best describing landscape use by blue wildebeest was *m15*, with a rank of 0.89 (Table 2.3). This model contained landscape burnt status, distance from all the other species, NDVI and an interaction between heterogeneity and the section (Table 2.4). Blue wildebeest favoured burnt areas over un-burnt areas (log-odds = 1.02 ± 0.35). In addition, the probability of locating blue wildebeest increased with the presence of zebra (Fig 2.4b) and the absence of black wildebeest (Fig 2.4c), while the presence of red hartebeest slightly increased the probabilities of sighting a blue wildebeest (Table 4). Moreover, blue wildebeest preferred areas having a higher heterogeneity value than what was available on average when in the West section, while they favoured more homogeneous areas than what was available on average in the East section of the reserves (Fig 2.5). The best model also contained NDVI, but it did not have a significant effect on landscape selection by blue wildebeest (Table 2.4). Though blue wildebeest favoured the West section slightly more than the East (Table 2.4), they used both sections of the reserves, having thus a wide distribution (Fig 2.3).

Red hartebeest

The most parsimonious generalized linear model for landscape selection by red hartebeest was *m14b*, with a rank of 0.51 (Table 2.5). The best model contained landscape burnt status, heterogeneity, distance from zebra and an interaction between NDVI and the section of the reserves (Table 2.6). Red hartebeest selected the East section of the reserves less than the West section (log-odds = -3.25 ± 1.41) (Fig 2.6a). The effect of NDVI on landscape use depended on the section of the reserves. Indeed, red hartebeest favoured areas with higher NDVI than what was available on average when in the West section, while preferring areas with lower NDVI compared to what available when in the East section (Fig 2.6b). Distance from zebra had a negative effect on the probability of sighting a red hartebeest, as red hartebeest used areas close to where zebra were foraging (Fig 2.7). Burnt landscape status and heterogeneity, the other variables contained in the best model, had a slight negative effect on the probabilities of sighting red hartebeest (Table 2.6). Red hartebeest distribution was mainly based in the West section of the reserves and appeared to be slightly wider than black wildebeest one, as red hartebeest were not concentrated in the burnt area (Fig 2.3).

Zebra

The best model representing zebra landscape use was *m13* with a rank of 0.39 (Table 2.7). This was the weakest best model of the study. It contained the variables NDVI, heterogeneity, distance from the other species, landscape burnt status and the section of the reserves (Table 2.8). Zebra strongly preferred the East section of the reserves compared to the West one (log-odds = 0.72 ± 0.23) (Fig 2.8). In addition, zebra used areas close to both black and blue wildebeest, but far from red hartebeest (Fig 2.9a,b,c). Zebra also preferred areas having a lower NDVI value than what was available on average (Fig 2.9d). Heterogeneous and burnt areas were slightly preferred by zebra, but these variables did not have a big impact on zebra landscape use (Table 2.8). Though favouring the East section of the study area, zebra used both sections of the reserves, having the widest distribution (Fig 2.3).

Discussion

This study indicates that ruminants at TENR preferred to forage in open grasslands, which are mainly situated in the West section of the reserves, with both species of wildebeest making an extensive use of the burnt landscape, when available. Black wildebeest distribution was the narrowest and differed greatly from the distribution of blue wildebeest, suggesting that blue wildebeest have a more generalist behaviour than black wildebeest, allowing them to use a larger variety of habitats (Ben-Shahar, 1991; Brink *et al.*, 1999). A similar result was also found at the feeding patch level (Chapter 3). Zebra was the only species that selected for the East section of the reserves. This suggests that quality of grass in that section was less suitable for ruminants, as only the non-ruminant species favoured it.

Although, landscapes in the East section had a slightly higher mean NDVI value than on the West section, this is confounded by the denser tree layer, which increases the mean NDVI, and thus grass quality may be lower on that side.

Both black and blue wildebeest used burnt areas located in the West section of the reserves more than expected if they had been foraging randomly. This result follows expectations, as many studies have shown that recently burnt landscapes attract ungulates (Gureja & Owen-Smith, 2002; Tomor & Owen-Smith, 2002; Archibald & Bond, 2004; Parrini & Owen-Smith, 2010). Being short grass specialists, wildebeest are expected to prefer short high quality forage such as recently burnt grass, especially during the dry season (Tomor & Owen-Smith, 2002; Archibald & Bond, 2004). The result is also supported by Helm (2007), who found that both wildebeest species favoured heavily utilized grass and recently burnt areas in every season in open plains in a previous study at TENR.

The section of the reserves had a strong effect on landscape selection by all the species but blue wildebeest. Both red hartebeest and black wildebeest preferred to forage in the West section of the reserves, which offered burnt areas throughout the year and is composed of flat open grasslands. Across the whole study period, black wildebeest and red hartebeest were seen foraging in the East section of the reserves only once and six times respectively (Fig 2.3). On the other hand, zebra preferred the East section of the reserves, which had no burnt areas of relevant size and more trees than the West section. Blue wildebeest used both sections almost equally, having a different distribution compared to black wildebeest. These results are consistent with the distribution of the four species described in the same study area by Deliberato (2017) based on sightings between 2010 and 2016. Differences in black and blue wildebeest landscape use have also been observed by Helm (2007), who found that black wildebeest preferred open grass habitats while blue wildebeest tended to stay closer to trees and exploit the shade (and possibly the better grass found under trees (Treydte *et al.*, 2009)). It is also known that blue wildebeest can forage more flexibly than black wildebeest because of their wider tolerance for different environments (Codron & Brink, 2007), while black wildebeest need an open landscape, which restricts their choices in the study area (Helm, 2007).

Grass greenness was a driving factor for zebra and hartebeest landscape use. Zebra were sighted in areas with a lower NDVI value than what was available on average. Being non-ruminants, zebra are limited by grass quantity, while the quality of grass they can accept may vary widely (Jarman, 1974; Owaga, 1975). Zebra were thus expected to select areas regardless of the NDVI value. The negative effect of NDVI on zebra landscape use could have been biased by the presence of trees in the East section of the reserves. Indeed, NDVI is a proxy for both vegetation greenness and biomass (Winnie *et al.*, 2008) and therefore areas containing trees have a higher NDVI value than grasslands alone. Therefore, when zebra use grasslands rather than woodlands, they appear to favour areas having a lower NDVI than the average, regardless of the grass quality on which they are foraging. On the other hand, the effect of grass greenness on red hartebeest landscape use depended on the section of TENR in which they were foraging. They preferred areas with a higher NDVI value than what was available on average when foraging in the West section of the reserves, while doing the opposite in the East section. Being ruminants, red hartebeest need to ingest grass of high quality (Demment & Van Soest, 1985; Duncan *et al.*, 1990), which can explain why they selected areas having higher NDVI value than the average when in the West section which is predominantly open grassland. On the other hand, red hartebeest were sighted on the East section only six times over the study period (Fig 2.3). This number of sightings is too small to draw any conclusion, thus it can only be said that, on the few occasions that red hartebeest were seen foraging on the East section of the reserves, they were using grasslands, which had a lower NDVI value than the East section average wooded area.

Blue wildebeest was the only species whose landscape use was affected by heterogeneity. They favoured more heterogeneous areas when in the West and more homogeneous areas when in the East section of the reserves. In this case, the higher presence of trees in the East section conferred wooded areas a higher heterogeneity value than grasslands. Thus, the use of more homogeneous locations in the East section indicates that blue wildebeest favoured open grasslands far from trees. This is supported by Helm (2007) who found that blue wildebeest benefit from environments offering some cover, but this is not a necessity for this species, which is well adapted to both savanna and grassland environment (Codron & Brink, 2007). On the other hand, the use of more heterogeneous areas in the West section indicates that blue wildebeest preferred to forage at the limit of burnt areas or in wetlands close to water sources (Chapter 3), as these were the areas with the highest heterogeneity values.

Distance from the closest individual of another ungulate species was the only factor affecting landscape selection by all the species. Black wildebeest foraged closer to all the other species than expected if they had foraged randomly, while all three ruminants were found closer to zebra than expected. The proximity between ruminants and the non-ruminant species supports the facilitation theory proposed by many authors (McNaughton, 1976; Illius & Gordon, 1987; Arsenault & Owen-Smith, 2002). In addition, these results indicate that black wildebeest had the smallest and most compact distribution, while zebra had the most widespread distribution (Fig 2.3). Red hartebeest had a slightly wider distribution than black wildebeest, but both species mainly used the West section of the reserves, with black wildebeest limited to the burnt area. On the other hand, blue wildebeest had a widespread distribution, similar to zebra. The same distributions were observed for all the species at TENR by Helm (2007) and by Deliberato (2017), indicating that the drought experienced during the study period did not modify the species distribution. The wide distribution of zebra could depend on the fact that non-ruminant species can use a wider set of resources than ruminants, like black wildebeest and red hartebeest (Du Toit & Cumming, 1999). Possibly due to their different energy requirements and diet tolerance, zebra were able to exploit the entire reserves, while ruminants were confined to a smaller area offering high quality forage. Blue wildebeest distribution was unexpectedly wider than both red hartebeest and black wildebeest distribution (Fig 2.3). Probably, the ability of blue wildebeest to use more habitats and to have a more flexible diet than both black wildebeest and red hartebeest (Codron & Brink, 2007), enabled them to exploit a wider part of the reserve, acting similarly to zebra. Ben-Shahar (1991) observed that blue wildebeest consumed grass species based on their availability in a South African reserve, suggesting that blue wildebeest could be more generalist than specialist, depending on the spatial scale of investigation.

Though black wildebeest were closer to blue wildebeest than expected, blue wildebeest were seen further from black wildebeest than expected. The incremented distance between species could suggest interspecific competition between the two species (Sinclair, 1985; Arsenault & Owen-Smith, 2002). This result was expected, as blue and black wildebeest have very similar forage preferences and are known to compete (Codron & Brink, 2007). When two species that select similar resources coexist, a differentiation in realized niche is necessary, with the result of the species being further from each other then expected if they were not interacting (Sinclair, 1985; Churchfield *et al.*, 1999). Similarly, zebra foraged further than expected from red hartebeest, while red hartebeest were closer to zebra than expected. Competition between the two species is a possibility, indeed their resource use overlapped in this study (both mostly used forage taller than 11 cm, see chapter 3), and they are known to compete for resources (Estes, 1991). However, this result is more probably due to the different population size and distribution of the two species. Being more abundant and having a wider distribution, many of the zebra found in the East section were far from the closest red hartebeest. Conversely, being less in number and highly concentrated in the West section, every observed red hartebeest was in close proximity to a zebra. Therefore, this result is more a consequence of other choices, such as forage selection, rather than a proxy for competition.

Against predictions, season did not have an effect on landscape selection by any species, meaning that all the species selected areas with the same characteristics, regardless of the season. Season affects ungulate selection through changes in grass quantity, quality and water content (Groom & Harris, 2009). The scarcity of grass and water during the dry season can force ungulates to move to areas that were less suitable before (Sinclair, 1985; Helm, 2007; Treydte *et al.*, 2009). The effect of season was relevant at a patch spatial scale, and thus it is discussed in Chapter 3.

Bailey *et al.* (1996) believed abiotic factors to be the main drivers of ungulate resource use at landscape scale. Redfern *et al.* (2003) however, stated that abiotic constraints must be combined with biotic factors to study herbivores distribution. This study, along with others (Sinclair, 1985; Groom & Harris, 2009; Gandiwa, 2013; Deliberato, 2017), demonstrates that biotic factors, such as grass quality and distribution, and interspecific competition, must be considered when investigating ungulate landscape use. Actually, elevation, the constraint analysed in this study, affected only black wildebeest landscape use, while forage resources and interactions between different species affected the landscape use of each grazer species.

This study had some limitations, the first one being the impossibility of discriminating between NDVI values of grass and tree canopies. In future studies, trees should be mapped and pixels that mainly contain trees should be excluded from the NDVI map. A second limitation lays in the calculation of heterogeneity. Indeed, although heterogeneity was present in each species best model, it significantly influenced only blue wildebeest landscape use. According to Owen-Smith (2004), the functional heterogeneity of a landscape depends on how animals perceive and respond to the landscape, rather than what a scientist perceives as heterogeneous. In this study, heterogeneity was based on differences in NDVI between neighbouring pixels at 250 m resolution. Possibly, ungulates do not perceive or value differences in grass greenness at such spatial resolution. Future studies should investigate landscape heterogeneity in terms of variations in grass cover, as done by others (Watson *et al.*, 2005; Gandiwa, 2013).

The virtual confinement of red hartebeest and black wildebeest to the West section of the reserves could represent a risk for these species. Indeed, this section is used by all the study species and there are signs of competition between the two wildebeest species. High levels of competition and an overuse of resources can lead to a species decline and eventually disappearance from an area (Sinclair & Norton-Griffiths, 1982). An obvious, though not easy, way of relieving competition for black wildebeest would be the removal of some blue wildebeest. Otherwise, the creation of dispersed large burnt areas in the East section of the reserves, especially at the beginning of the dry season, would increase the environment heterogeneity while contributing to increasing the overall grass quality of the East section, possibly making it suitable also for red hartebeest and black wildebeest. However, this study pictures a short amount of time, and thus the creation of a long-term monitoring program embedded in a management plan is recommended. In conclusion, this study highlights the importance of biotic factors, in particular interspecies interactions, in driving ungulate landscape use and distribution, while offering a good starting point for managing the present situation at TENR.

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Tables and figures

Table 2.1: Selection at landscape level: candidate models to test the importance of Normalised Difference Vegetation Index, heterogeneity, burnt status, distance from other species, elevation, reserves section and season on **black wildebeest** resource selection at landscape level, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects:	K	AICc	ΔAICc	w_i
Black wildebeest *n*(1551)					
m1	Status + NDVI + heterogeneity+ distance from other species + elevation + section	9	672.38	0	0.97
m13	NDVI + heterogeneity + distance from other species + status + section	8	681.21	8.84	0.01
m15	Status + NDVI + distance from other species + heterogeneity*section	9	682.23	9.85	0.01
m14	Status + heterogeneity + distance from other species + NDVI*section	9	682.95	10.57	<0.01
m1b	Status + NDVI + heterogeneity+ distance from blue w + elevation + section	7	684.53	12.16	<0.01
m13b	NDVI + heterogeneity + distance from blue w + status + section	6	690.94	18.56	<0.01
m15b	Status + NDVI + distance from blue w + heterogeneity*section	7	691.71	19.33	<0.01
m14b	Status + heterogeneity + distance from blue w + NDVI*section	7	692.36	19.98	<0.01
m7	Distance from other species + elevation + section	6	697.68	25.3	<0.01
m8	NDVI + heterogeneity + elevation + status + section	6	707.2	34.82	<0.01
m10	Status + NDVI + elevation + heterogeneity*section	7	707.51	35.13	<0.01
m9	Status + Heterogeneity + elevation + NDVI*section	7	708.41	36.03	<0.01
m7b	Distance from blue w + elevation + section	4	710.18	37.8	<0.01
m2	Status + NDVI + heterogeneity + section	5	716.57	44.2	<0.01
m6	Elevation + section	3	737.78	65.41	<0.01
m5	Distance from other species + elevation	5	778.09	105.71	<0.01
m4	Distance from other species	4	791.86	119.48	<0.01
m11	Status + heterogeneity + elevation + NDVI*season	11	799.92	127.55	<0.01
m12	Status + NDVI + elevation + heterogeneity*season	11	800.68	128.3	<0.01
m3	Status + NDVI + heterogeneity,	4	864.56	192.18	<0.01
m5b	Distance from blue w + elevation	3	871.16	198.78	<0.01
m4b	Distance from blue w	2	926.86	254.49	<0.01

* = interaction; *n*, no. observation; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 2.2: The most parsimonious generalized linear model representing the coefficients that are used to determine the log-odd ratios for landscape selection by **black wildebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-2.724	0.366	-7.451	<0.001
Burnt-Yes	1.265	0.250	5.059	<0.001
NDVI	-0.259	0.176	-1.472	0.141
Heterogeneity	-0.001	0.148	-0.009	0.992
Distance from blue wildebeest	-0.481	0.136	-3.525	<0.001
Distance from red hartebeest	-0.956	0.465	-2.054	0.040
Distance from zebra	-0.304	0.112	-2.707	0.007
Elevation	-0.551	0.170	-3.251	0.001
Section-East	-4.238	1.033	-4.101	<0.001

Table 2.3: Selection at landscape level: candidate models to test the importance of Normalised Difference Vegetation Index, heterogeneity, burnt status, distance from other species, elevation, reserves section and season on **blue wildebeest** resource selection at landscape level, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects:	K	AICc	ΔAICc	w_i
Blue wildebeest *n*(2783)					
m15	Status + NDVI + distance from other species + heterogeneity*section	9	1519.92	0	0.89
m14	Status + heterogeneity + distance from other species + NDVI*section	9	1524.17	4.25	0.11
m13	NDVI + heterogeneity + distance from other species + status + section	8	1529.81	9.89	0.01
m1	Status + NDVI + heterogeneity + distance from other species + elevation + section	9	1531.3	11.38	<0.01
m4	Distance from other species	4	1545.71	25.79	<0.01
m5	Distance from other species + elevation	5	1547.32	27.4	<0.01
m7	Distance from other species + elevation + section	6	1547.9	27.98	<0.01
m15b	Status + NDVI + distance from black w + heterogeneity*section	7	1653.74	133.83	<0.01
m10	Status + NDVI + elevation + heterogeneity*section	7	1656.95	137.03	<0.01
m14b	Status + heterogeneity + distance from black w + NDVI*section	7	1661.22	141.3	<0.01
m9	Status + Heterogeneity + elevation + NDVI*section	7	1663.67	143.75	<0.01
m2	Status + NDVI + heterogeneity + section	5	1668.24	148.32	<0.01
m13b	NDVI + heterogeneity + distance from black w + status + section	6	1668.62	148.7	<0.01
m1b	Status + NDVI + heterogeneity+ distance from black w + elevation + section	7	1670.09	150.17	<0.01
m12	Status + NDVI + elevation + heterogeneity*season	11	1670.13	150.21	<0.01
m8	NDVI + heterogeneity + elevation + status + section	6	1670.24	150.32	<0.01
m3	Status + NDVI + heterogeneity	4	1677.36	157.44	<0.01
m11	Status + heterogeneity + elevation + NDVI*season	11	1677.46	157.54	<0.01
m4b	Distance from black w	2	1697.22	177.3	<0.01
m6	Elevation + section	3	1698.59	178.67	<0.01
m5b	Distance from black w + elevation	3	1698.94	179.02	<0.01
m7b	Distance from black w + elevation + section	4	1700.57	180.65	<0.01

* = interaction; *n*, no. observation; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 2.4: The most parsimonious generalized linear model representing the coefficients that are used to determine the log-odd ratios for landscape selection by **blue wildebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Coefficients:	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	-2.625	0.176	-14.918	<0.001
Burnt-Yes	1.028	0.251	4.093	<0.001
NDVI	-0.003	0.130	-0.026	0.979
Distance from black wildebeest	0.297	0.118	2.507	0.012
Distance from red hartebeest	-0.119	0.111	-1.071	0.284
Distance from zebra	-1.158	0.118	-9.831	<0.001
Heterogeneity	0.090	0.131	0.691	0.490
Section-East	-0.403	0.262	-1.538	0.124
Heterogeneity:section-East	-0.549	0.162	-3.400	<0.001

Table 2.5: Selection at landscape level: candidate models to test the importance of Normalised Difference Vegetation Index, heterogeneity, burnt status, distance from other species, elevation, reserve section and season on **red hartebeest** resource selection at landscape level, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects:	K	AICc	ΔAICc	w_i
Red hartebeest n(572)					
m14b	Status + heterogeneity + distance from zebra + NDVI*section	7	291.6	0	0.51
m15b	Status + NDVI + distance from zebra + heterogeneity*section	7	293.94	2.34	0.16
m7b	Distance from zebra + elevation + section	4	294.81	3.21	0.10
m14	Status + heterogeneity + distance from other species + NDVI*section	9	294.94	3.34	0.10
m13b	NDVI + heterogeneity + distance from zebra + status + section	6	296.25	4.65	0.05
m15	Status + NDVI + distance from other species + heterogeneity*section	9	297.16	5.57	0.03
m7	Distance from other species + elevation + section	6	297.95	6.35	0.02
m1b	Status + NDVI + heterogeneity+ distance from zebra+ elevation + section	7	298.23	6.63	0.02
m13	NDVI + heterogeneity + distance from other species + status + section	8	298.64	7.04	0.01
m1	Status + NDVI + heterogeneity+ distance from other species + elevation + section	9	300.7	9.1	0.01
m4	Distance from other species	4	307.83	16.23	<0.01
m5	Distance from other species + elevation	5	309.69	18.09	<0.01
m6	Elevation + section	3	312.55	20.95	<0.01
m9	Status + Heterogeneity + elevation + NDVI*section	7	314.1	22.51	<0.01
m10	Status + NDVI + elevation + heterogeneity*section	7	315.51	23.92	<0.01
m2	Status + NDVI + heterogeneity + section	5	315.55	23.95	<0.01
m8	NDVI + heterogeneity + elevation + status + section	6	317.53	25.93	<0.01
m5b	Distance from zebra + elevation	3	333.22	41.62	<0.01
m4b	Distance from zebra	2	342.36	50.76	<0.01
m11	Status + heterogeneity + elevation + NDVI*season	11	351.34	59.74	<0.01
m3	Status + NDVI + heterogeneity,	4	355.43	63.83	<0.01
m12	Status + NDVI + elevation + heterogeneity*season	11	355.84	64.24	<0.01

* = interaction; *n*, no. observation; *k*, number of parameters in the model; AICc, Akaike's Information criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 2.6: The most parsimonious generalized linear model representing the coefficients that are used to determine the log-odd ratios for landscape selection by **red hartebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Coefficients:	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	-1.542	0.185	-8.319	<0.01
Burnt-Yes	-0.898	0.581	-1.546	0.122
Heterogeneity	-0.089	0.237	-0.377	0.706
Distance from zebra	-0.866	0.210	-4.132	<0.001
NDVI	0.348	0.270	1.287	0.198
Section-East	-3.244	0.731	-4.44	<0.001
NDVI:section-East	-1.563	0.811	-1.926	0.054

Table 2.7: Selection at landscape level: candidate models to test the importance of Normalised Difference Vegetation Index, heterogeneity, burnt status, distance from other species, elevation, reserve section and season on **zebra** resource selection at landscape level, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects:	K	AICc	ΔAICc	w_i
Zebra n(3003)					
m13	NDVI + heterogeneity + distance from other species + status + section	8	1702.37	0	0.39
m1	Status + NDVI + heterogeneity+ distance from other species + elevation + section	9	1703.4	1.03	0.23
m14	Status + heterogeneity + distance from other species + NDVI*section	9	1703.51	1.14	0.22
m15	Status + NDVI + distance from other species + heterogeneity*section	9	1704.36	1.99	0.14
m7	Distance from other species + elevation + section	6	1708.05	5.69	0.02
m4	Distance from other species	4	1722.9	20.53	<0.01
m5	Distance from other species + elevation	5	1723.03	20.66	<0.01
m8	NDVI + heterogeneity + elevation + status + section	6	1798.06	95.7	<0.01
m2	Status + NDVI + heterogeneity + section	5	1798.26	95.9	<0.01
m10	Status + NDVI + elevation + heterogeneity*section	7	1799.1	96.74	<0.01
m1b	Status + NDVI + heterogeneity+ distance from red hartebeest + elevation + section	7	1799.32	96.95	<0.01
m9	Status + Heterogeneity + elevation + NDVI*section	7	1800.01	97.64	<0.01
m13b	NDVI + heterogeneity + distance from red hartebeest + status + section	6	1800.15	97.78	<0.01
m6	Elevation + section	3	1800.23	97.87	<0.01
m15b	Status + NDVI + distance from red hartebeest + heterogeneity*section	7	1800.88	98.52	<0.01
m14b	Status + heterogeneity + distance from red hartebeest + NDVI*section	7	1802.15	99.79	<0.01
m7b	Distance from red hartebeest + elevation + section	4	1802.17	99.81	<0.01
m4b	Distance from red hartebeest	2	1825.33	122.97	<0.01
m5b	Distance from red hartebeest + elevation	3	1827.22	124.85	<0.01
m11	Status + heterogeneity + elevation + NDVI*season	11	1835.3	132.94	<0.01
m3	Status + NDVI + heterogeneity,	4	1835.4	133.04	<0.01
m12	Status + NDVI + elevation + heterogeneity*season	11	1840.9	138.53	<0.01

* = interaction; *n*, no. observation; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 2.8: The most parsimonious generalized linear model representing the coefficients that are used to determine the log-odd ratios for landscape selection by **zebra** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Coefficients:

	Estimate	Std. Error	Z value	Pr(>|z|)
(Intercept)	-3.031	0.164	-18.455	<0.001
NDVI	-0.331	0.116	-2.856	0.004
Heterogeneity	0.109	0.107	1.017	0.309
Distance from blue wildebeest	-0.955	0.113	-8.445	<0.001
Distance from red hartebeest	0.320	0.109	2.947	0.003
Distance from black wildebeest	-0.313	0.114	-2.741	0.006
Burnt-Yes	0.008	0.293	0.029	0.977
Section-East	0.725	0.220	3.302	<0.001

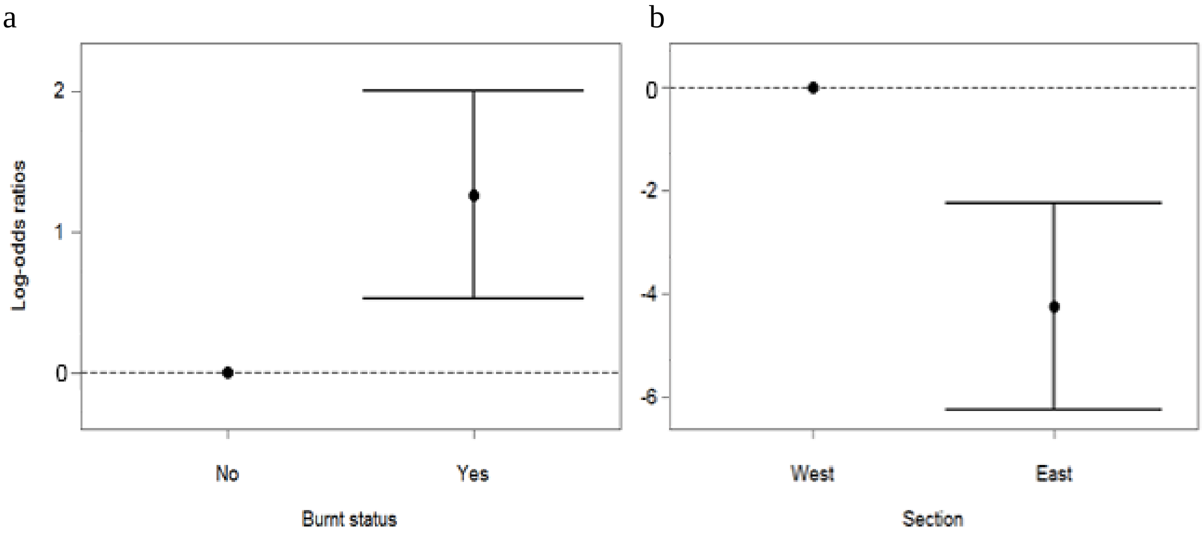

Figure 2.1: Predicted estimates (± 95% confidence interval) for landscape selection by black wildebeest for (a) landscape burnt status ’No’ and ‘Yes’, (b) section of the reserves ‘West’ and ‘East’ at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: (a) ‘No’, (b) ‘West’.

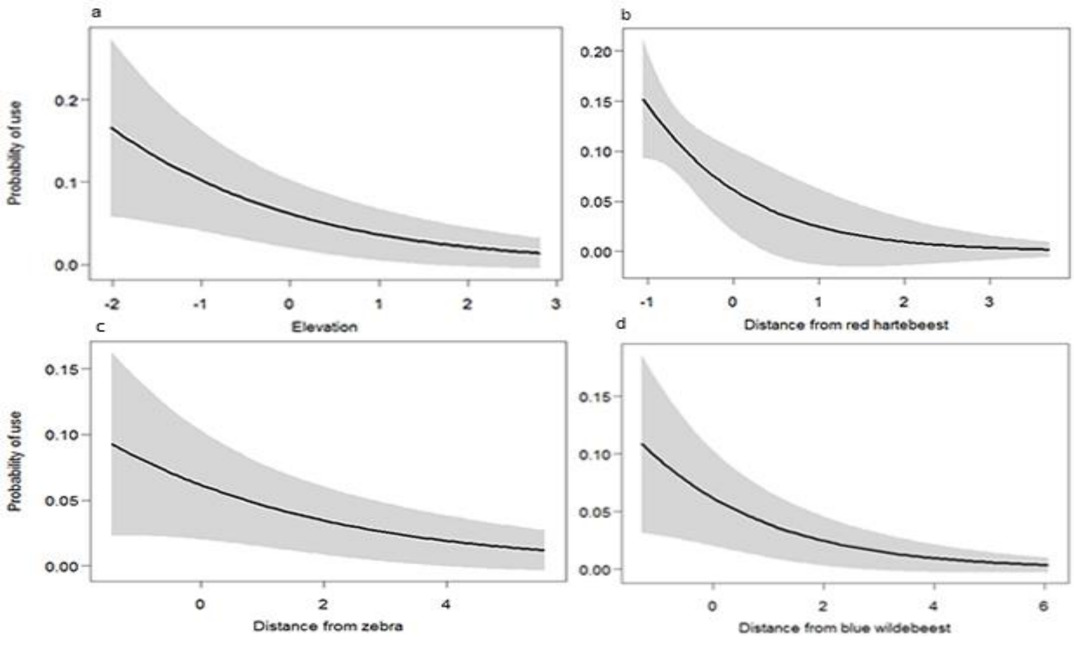

Figure 2.2: Predicted probabilities (± 95% confidence interval) for landscape selection by black wildebeest for (a) elevation, (b) distance from red hartebeest, (c) distance from zebra and (d) distance from blue wildebeest, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

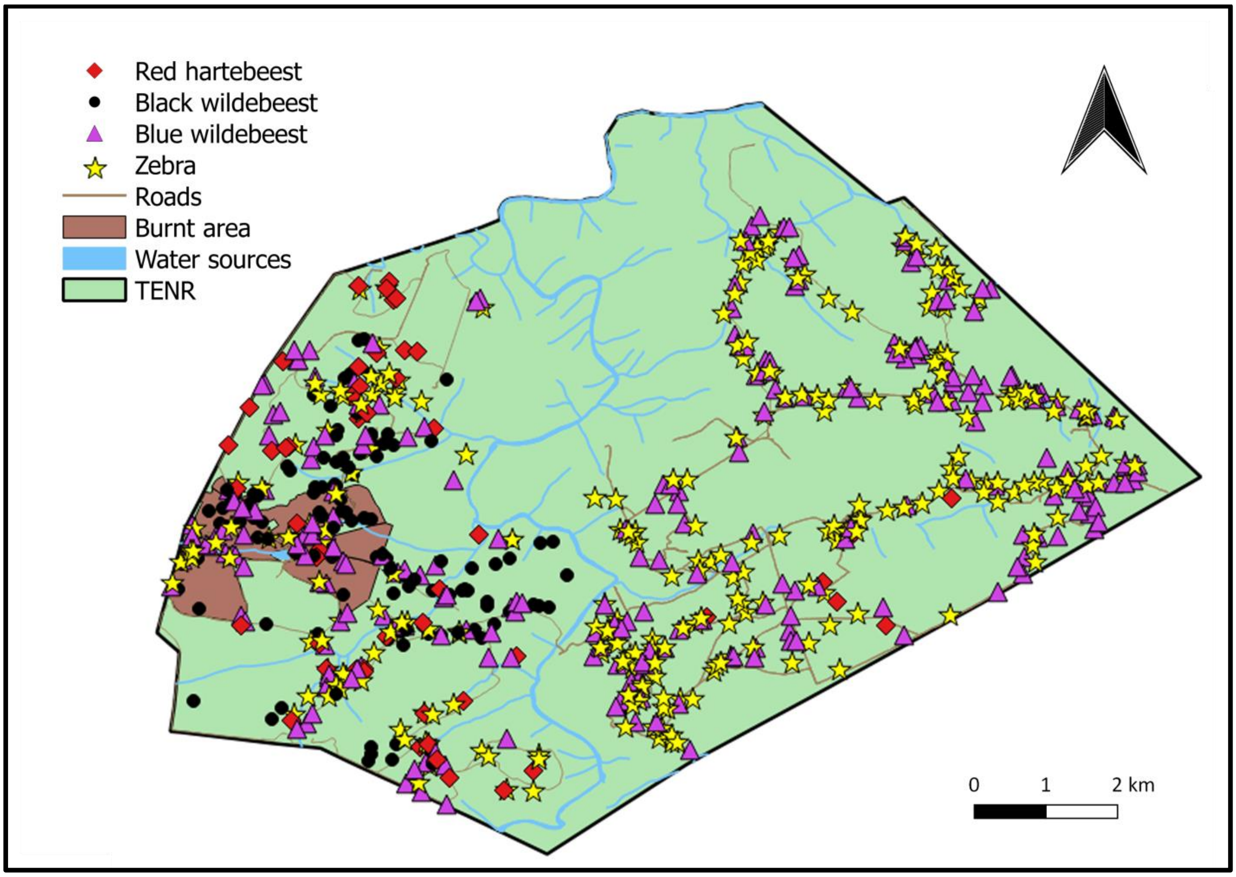

Figure 2.3: All the sightings collected between September 2017 and August 2018 at Telperion and Ezemvelo nature reserves, South Africa.

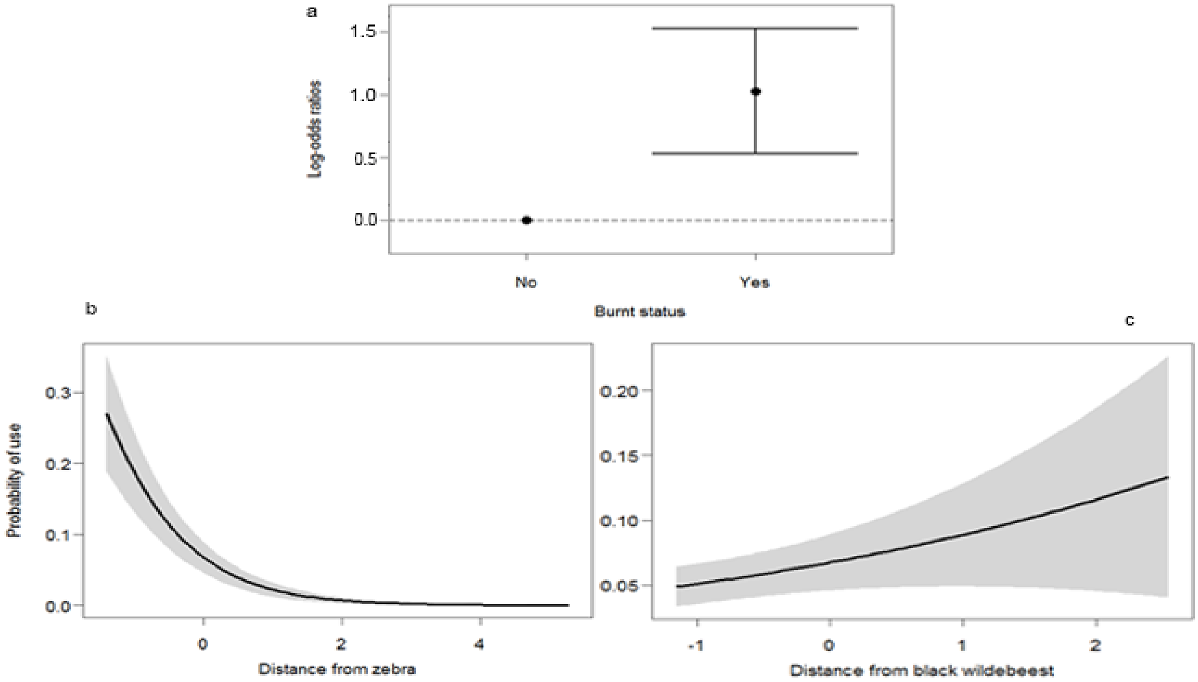

Figure 2.4: Predicted estimate and probabilities (± 95% confidence interval) for landscape selection by blue wildebeest for (a) burnt landscape status, (b) distance from zebra and (c) distance from black wildebeest at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line in figure (a) represents the reference level 'No'.

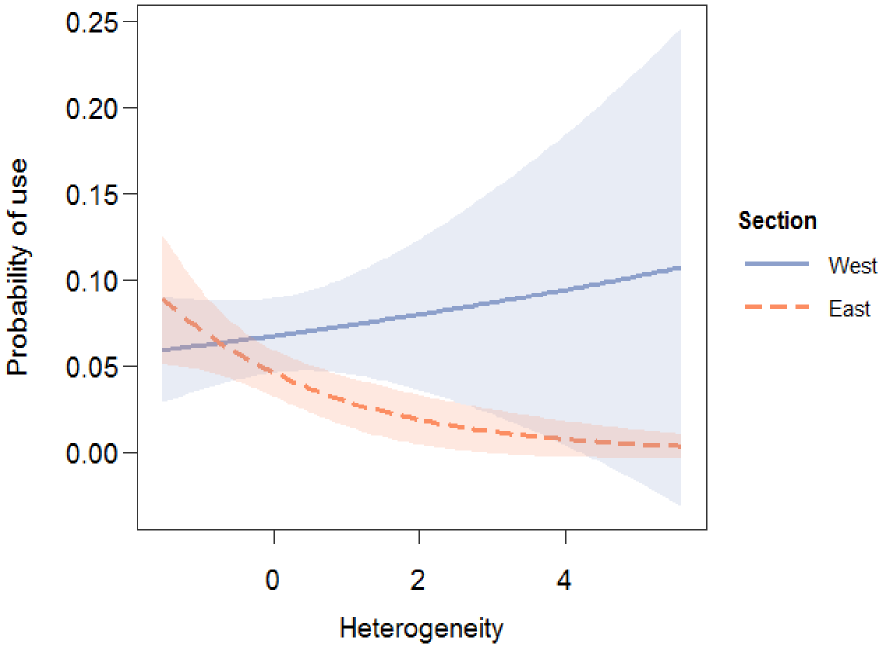

Figure 2.5: Predicted probabilities (± 95% confidence interval) for landscape selection by blue wildebeest for heterogeneity over section of the reserves 'West' or 'East' at Telperion and Ezemvelo nature reserves, South Africa, 2018.

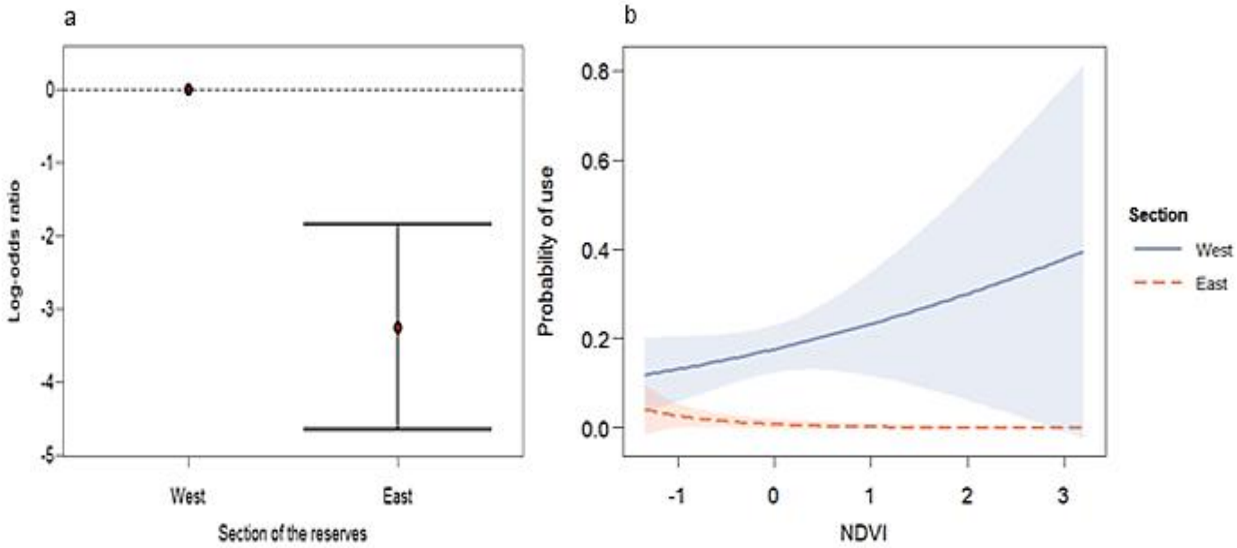

Figure 2.6: Predicted estimates and predicted probabilities (± 95% confidence interval) for landscape selection by red hartebeest for section (a) and Normalized Difference Vegetation Index over section of the reserves (b) 'West' or 'East' at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line in picture (a) represents the reference level 'West'.

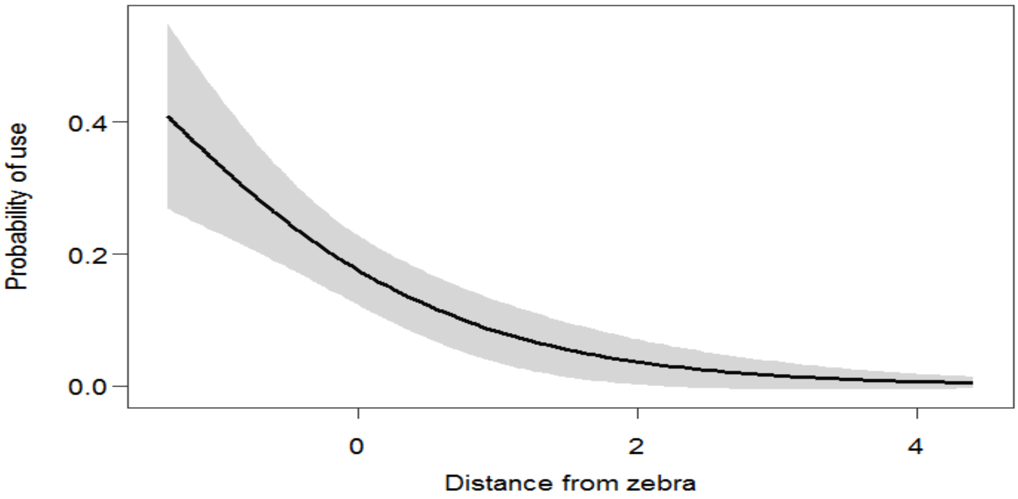

Figure 2.7: Predicted probabilities (± 95% confidence interval) for landscape selection by red hartebeest for distance from zebra at Telperion and Ezemvelo nature reserves, South Africa, 2018.

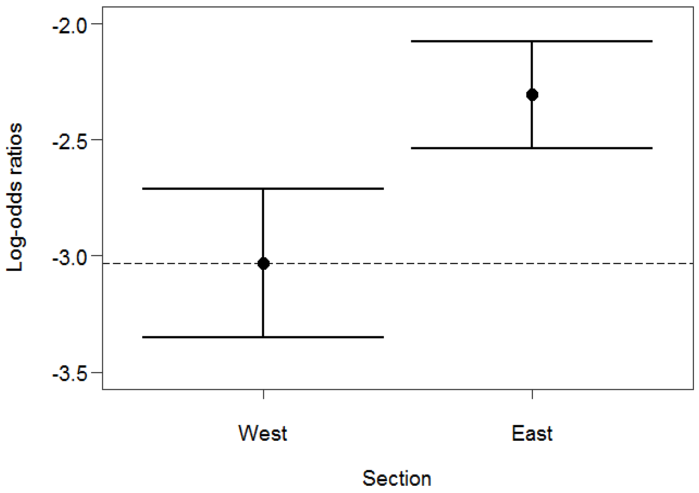

Figure 2.8: Predicted estimates (± 95% confidence interval) for landscape selection by zebra for section of the reserves 'West' and 'East' at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: 'West'.

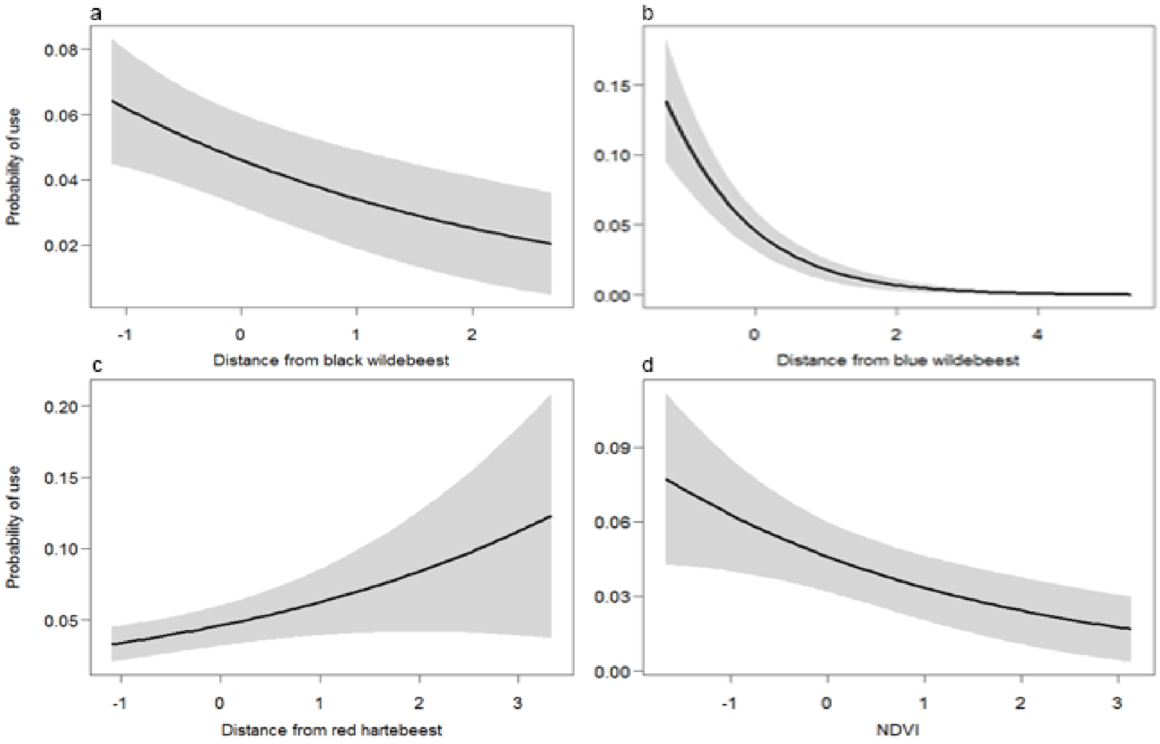

Figure 2.9: Predicted probabilities (± 95% confidence interval) for landscape selection by zebra for (a) distance from black wildebeest, (b) distance from blue wildebeest, (c) distance from red hartebeest and (d) Normalised Difference Vegetation Index (NDVI), at Telperion and Ezemvelo nature reserves, South Africa, 2018.

CHAPTER THREE: *Ungulate resource selection at feeding patch scale at Telperion and Ezemvelo nature reserves, South Africa.*

Abstract

It is important to know how ungulates select for resources at feeding patch scale, as an overlap in resource use by sympatric species might cause an unsustainable level of competition and eventually drive the local disappearance of one of the species. The role of grass greenness, height, biomass and feeding patch status (un-burnt, burnt or wetland) on generalist and specialist ungulate grazer feeding patch use was investigated in a fenced grassland-savanna transition zone in the eastern Highveld, South Africa, in order to understand factors shaping ungulate resource use. Results indicate the presence of an overlap in resource use by different species. Ruminants were all driven by grass greenness and their preferred grass height, short (< 10 cm) for black and blue wildebeest, and long (> 11 cm) for red hartebeest. The non-ruminant zebra applied a looser selection but preferred wetlands in any season, as did red hartebeest and blue wildebeest. Each species modified their behaviour during the late dry season, searching for more biomass or accepting less green or longer grass. Surprisingly, the presence of burnt feeding patches, both man-made and naturally occurring, did not affect any of the species feeding patch selection. This study points out the critical impact of seasons on ungulate resource use, and highlights the importance of wetlands in sustaining ungulates, suggesting that preserving this vegetation type should be a priority for enclosed reserves management. In addition, it describes resource use of sympatric black and blue wildebeest, species that seldom coexist in an enclosed area.

Introduction

Large ungulate dynamics and resource use are affected by several environmental characteristics, such as forage quality, biomass and distribution (Sinclair *et al.*, 1985; Bailey *et al.*, 1996). Wildlife is nowadays mainly found in reserves and enclosed areas, where a limited set of resources is available. As two species of ungulates cannot use the same set of resources at the same time (competitive exclusion principle, Schwartz & Ellis, 1981; Day & Young, 2004), a protected area must be heterogeneous to host different species of ungulates (Owen-Smith, 2004). Otherwise, competition over resources could lead to a decline and eventually the disappearance of one or more competing species (Sinclair & Norton-Griffiths, 1982). Competition is present at broad spatial scales as well as at fine ones, such as the feeding patch scale (i.e. a cluster of feeding stations close enough to be reached by an ungulate during a feeding bout; Bailey *et al.*, 1996). It is critical to understand how ungulate grazers use resources at feeding patch scale in order to perform effective management strategies (Senft *et al.*, 1987; Bailey *et al.*, 1996; Redfern *et al.*, 2003).

Forage quality, biomass and distribution interact to shaping ungulates resource selection at feeding patch scale. Indeed, grazers obtain the maximum quantity of energy they can by foraging on high quality grass and retain as much energy as possible by limiting movements while searching for food (Senft *et al.*, 1987; Kie, 1999). Consequently, ungulates start a feeding bout by selecting the best plant, or part of it, from a feeding patch readily available to them (Senft *et al.*, 1987; O'Reagain & Schwarz, 1995; Bailey *et al.*, 1996). They exploit it until its forage intake rate, which depends on both quality and biomass of forage present in the feeding patch, decreases below the level of the surrounding feeding patches (Charnov, 1976). At this point, ungulates would move to the closest feeding patch offering the highest forage intake rate (Senft *et al.*, 1987, O'Reagain & Schwarz, 1995).

Forage quality and biomass, and consequent ungulate behavioural responses vary seasonally. As grasses mature, the cell walls of leaves lignify and increase in fibre content, while decreasing in protein content (Meissner, 1997). In the late dry season, grass quality is at its lowest and most of the available grass is senescent or dead (Owen-Smith, 2002). In this period, the scarcity of proteins in forage may represent a serious constraint to ungulates survival, thus ungulates have to adapt their foraging behaviour in order to maximise forage intake (Moe *et al.*, 1990). To do so, herbivores need to forage for longer to compensate for the decreased grass quality (Demment & Van Soest, 1985; Duncan *et al.*, 1990; Parrini & Owen-Smith, 2010), widen their acceptance for grass species by including less palatable species and/or grasses of lower quality (Casebeer & Koss, 1970; Owen-Smith, 1994), or increase the use of bridging resources, i.e. higher quality resources available during a limiting period that can contribute to sustaining herbivore populations (Owen-Smith, 2002), such as burnt areas and wetlands (Moe *et al.*, 1990; Fynn *et al.*, 2015). The adoption of different foraging adaptations leads to different species selecting different resources in different seasons.

As forage quality is particularly low during the dry season, fire has often been used to alleviate nutritional stress for ungulates in this period (Moe *et al.*, 1990; Gureja & Owen-

Smith, 2002; Parrini & Owen-Smith, 2010). Indeed, grass quality in burnt areas is higher than in un-burnt areas (Moe *et al.*, 1990; Gureja & Owen-Smith, 2002; Archibald & Bond, 2004), because fire destroys layers of low quality grass and stimulates the sprouting of new high quality grass (Moe *et al.*, 1990; Hobbs *et al.*, 1991). Lemon (1968) recorded the protein content in grass leaves sprouting after a fire being up to 75-100% higher than in un-burnt leaves. Due to such increase in grass quality, many ungulates (e.g. blue wildebeest (*Connochaetes taurinos*), buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), zebra (*Equus quagga*) and warthog (*Phacochoerus aethiopicus*)) prevalently use burnt areas when available (Tomor & Owen-Smith, 2002; Archibald & Bond, 2004), improving the quality of their diet (as estimated by faecal crude protein content) (Hobbs & Spowart, 1984; Parrini & Owen-Smith, 2010).

However, the presence of burnt areas in the dry season may not be enough to sustain all the ungulate species present in an area. Indeed, some ungulates, such as red hartebeest (*Alcelaphus buselaphus*), have a narrow muzzle which allows them to be selective on tall grass but also prevents them from using short grass (Janis & Ehrhardt, 1988). As many species are simultaneously attracted to burnt feeding patches (Archibald & Bond, 2004), competition can arise in the form of broad muzzled short grass specialists, like blue and black wildebeest (*Connochaetes gnu*) keeping the regrowth too short for tall grass specialists to be able to exploit the burnt area (Gureja & Owen-Smith, 2002). However, tall grass specialists may rely on bridging resources offering taller grass, for example wetlands.

Wetlands have higher plant productivity than drylands and offer water and nutrients in abundance (Thompson & Polet, 2000). In addition, greenness and water content of drylands vegetation declines considerably during the dry season, while remaining relatively constant in wetlands (Fynn *et al.*, 2015), making them the best available source of tall grass of high quality by the late dry season (Thompson & Polet, 2000). Many ungulate species use dry habitats (i.e. grasslands, woodlands) during the wet season and gradually increase the use of wetlands as the dry season progresses (Bell, 1971; Parrini & Owen-Smith, 2010; Macandza *et al.*, 2012).

Ungulate resource selection does not only vary with seasons, but also depends on their digestive adaptations. Non-ruminants have a fast passage rate of forage through the gut, allowing them to forage on high quantities of low quality grass and to be more generalist (Demment & Van Soest, 1985; Duncan *et al.*, 1990). On the other hand, ruminants rely on grass of high quality, due to the longer digestive process, which prevents them to ingest high quantities of forage (Demment & Van Soest, 1985; Duncan *et al.*, 1990). Thus, ruminants and non-ruminants can avoid competition by using different niches, because of different selection patterns.

Telperion and Ezemvelo nature reserves, South Africa, are a cluster of reserves forming a fenced protected area. They host a variety of grazing ungulates, including the generalist non-ruminant zebra and the specialist ruminant red hartebeest, black and blue wildebeest. The reserves are under different management regimes: the West section implements more frequent controlled burns than the East section, with the result that the sections differ in terms of grass quality, biomass and heterogeneity of grass distribution across the year. These characteristics allowed me to test the effect of different management regimes on seasonal feeding patch selection by generalist and specialist grazing species. Specifically, I investigated the role of grass quality, biomass, height and feeding patch status (burnt, un-burnt or wetland) and how it varied with season and management strategy on feeding patch selection by red hartebeest, plains zebra, and black and blue wildebeest.

Because different species cannot coexist if there is a complete overlap in their resource use and based on species-specific digestive adaptations and preferences (Janis & Ehrhardt, 1988; Day & Young, 2004), I expected each species to use different selection criteria at feeding patch scale. Being ruminants, both the species of wildebeest and red hartebeest would use feeding patches offering high quality grass, but different grass height: both species of wildebeest would select short to very short grass (< 10 cm) due to their broad muzzle, while red hartebeest would prefer medium to tall grass (> 11 cm) because of their narrow muzzle (Janis & Ehrhardt, 1988); black and blue wildebeest would select very similar feeding patches, due to their very similar morphology; zebra would accept a wider variety of feeding patches, due to them being generalist and non-ruminant.

I predicted season to interact with grass quality, biomass and feeding patch status in shaping feeding patch selection of each species. During the wet season, when available grass should be abundant and of high quality, I expected specialists to select un-burnt feeding patches with high quality grass, based on their height preferences. In the same season, the generalist zebra was expected to select feeding patches based on their availability, as both quality and biomass of grass should not be limiting. During the dry season, when both grass quality and biomass of grass become limiting, I expected specialists to increase their use of bridging resources. In particular, based on grass height preferences, red hartebeest would select wetlands, while wildebeest would select burnt feeding patches. Being generalists, zebra would be the only species able to gain the energy they need from un-burnt feeding patches, but they would compensate for the scarce grass quality by ingesting more forage (Demment & Van Soest, 1985; Duncan *et al.*, 1990). Therefore, in this season, I expected zebra to select feeding patches offering more biomass than in the wet season, including wetlands, that would be suitable for quality, quantity and height of grass (Fynn *et al.*, 2015). I did not expect the section of the reserves to play an important role on feeding patch selection by any species. The main difference between the sections at feeding patch spatial scale is fire regime, but even if large burnt areas are provided in the West section, natural fires and fire breaks are present in the East section. Thus, as burnt feeding patches are available in both sections, I did not expect any species to favour different feeding patches based on the section they were in.

Methods

Study area

The study was conducted at Telperion and Ezemvelo nature reserves. They form a single fenced area that lies on the edge of the central inland plateau of northern South Africa between latitude 25˚38' S - 25˚45' S and longitude 28˚55' E- 29˚03' E (Figure 1, APPENDIX) (Coetzee, 2012). The reserves are supplied with water by several perennial rivers and by the occurrence of several temporary dams and streams created by the rain. The Wilge River is the biggest water source; it runs from south to north dividing the study area into two parts: the West and the East sections. The mean annual rainfall is of about 625 mm (Swanepoel, 2006), with a wet season extending from November to March (≈ 462 mm of rain on average), and a dry season from April to October (≈ 163 mm of rain on average) (Swanepoel, 2006). The study was conducted during a drought: the reserves received about 105 mm of rain in the wet season 2017-2018, and about 50 mm in the dry season 2018 (Table 1, APPENDIX. Source: Ezemvelo Nature Reserve weather station). The daily temperatures vary from a minimum daily average of 4-5°C recorded in June and July to a maximum daily average of 26˚C in January and February (Swanepoel, 2006).

The vegetation in the area is classified as Rand Highveld Grassland and Loskop Mountain Bushveld (Mucina *et al.*, 2005). The West section is mainly composed of large flat open grasslands with interspersed wetlands in proximity to rivers, while the East section represents a wooded grassland environment (Helm, 2007) (Figure 2, APPENDIX). The most abundant and conspicuous grass species throughout the reserves are *Eragrostis curvula, Elionurus muticus* and *Setaria sphacelata*. Furthermore, there is a strong presence of *Eragrostis gummiflua* and *Themeda triandra* (Swanepoel, 2006). The wetland is dominated by *Aristida junciformis, Eragrostis nindensis, Imperata cylindrica* and *Paspalum urvillei* (Helm, 2007).

The reserves host more than 20 herbivores species, including large mammals such as blesbuck (*Damaliscus pygargus phillipsi*), common eland (*Taurotragus oryx*), kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), and my focal species red hartebeest, plains zebra, black and blue wildebeest. Several small carnivores inhabit the reserves, for example aardwolf (*Protetes cristata*), African civet (*Civettictis civetta*), black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) (Helm, 2007). Leopard (*Panthera pardus*) has been seen moving through the reserves, but no large carnivore is permanent in the area.

Data collection

Data were collected from September 2017 to August 2018. I identified four seasons based on the Normalized Difference Vegetation Index (NDVI, a proxy for vegetation quality and primary productivity) and rainfall patterns (Figure 3, APPENDIX): the late dry season (September-October 2017), the wet season (February 2018), the early dry season (May 2018) and the mid dry season (August 2018). In each season, I collected data over a period of three weeks.

I searched for black and blue wildebeest, red hartebeest and zebra in the early morning and late afternoon, during peak grazing times (Gureja & Owen-Smith, 2002). I drove all the available roads in the reserves looking for ungulates, twice per season. Each time I encountered an individual or a group of the study species foraging, I recorded the species, the season, the section of the reserves and my position by GPS (Montana 600 GPS Garmin). I also noted the angle and the distance between the animals and my position, using a military compass and a laser range finder (Leica Rangemaster 1600B 7.0X). Herds of single species were considered as one sighting and data were collected for the foraging individual closest to the centre of the group.

The day after collecting ungulate locations, I reached these locations on foot using the GPS and compass, in order to collect data on feeding patch use. This method had an uncertainty of about 5 m, as tested in the field using a known fixed landmark. For each used feeding patch, I identified an available feeding patch 100 meters away from the used one, in a random direction. When the used feeding patch was on a slope, I took the available feeding patch on the same slope. For each used and available feeding patch, I placed five 0.5 m^2 quadrats: one at the used GPS location and four around it, one per cardinal direction, spaced 4 meters from the central quadrat (adapted from Owen-Smith *et al.*, 2013) (Figure 4, APPENDIX).

In each quadrat I recorded: 1) grass height divided in 4 classes, namely: very short (grass shorter than 5 cm), short (grass between 6 and 10 cm), medium (grass between 11 and 30 cm) and tall (grass taller than 30 cm); 2) the proportion of leaves that were green using Walker (1976) eight-point scale (0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99% and 100% green); 3) standing crop biomass using a disk pasture meter (Zambatis *et al.*, 2006; Arena *et al.*, 2015); 4) the feeding patch status as ‘Un-burnt’, ‘Burnt’ or ‘Wetland’.

The disc pasture meter is an instrument that measures compressed grass height. It consists of a graduated pole and a circular aluminium disc. The pole is positioned in the centre of the quadrat and the disc is dropped from a constant height. The grass will stop the aluminium disc at a certain height, legible on the pole (Arena *et al.*, 2015). The disc settling heights are then used to calculate grass standing crop biomass through the calibration equation (2) (Zambatis *et al.*, 2006) determined for grassland and savanna systems in southern and east Africa (Trollope & Potgieter, 1986). The equation is based on the fact that there is a linear relationship between the settling height and the standing crop of grass (Arena *et al.*, 2015), therefore the higher the disc settles in the quadrat, the more crop biomass is present in the feeding patch.

$$\{\textit{Grass standing crop (kg/ha)} = -3019 + 2260 \surd \textit{ mean disc height (cm)} \qquad (2)$$

Data analysis

To analyse feeding patch selection by the different ungulate species I fitted 19 generalized linear mixed models (GLMM) with a binomial error distribution. The response variable was 'used' versus 'available', with the mixed effect being represented by the five quadrats in each feeding patch. I conducted the analysis using the Generalized Linear Mixed Effect Models procedure in the 'lme4 package' (Bates *et al.*, 2011) in R version 3.5.1 (R Development Core Team, 2018). I tested six independent factors, five of which were categorical (grass greenness, grass height, feeding patch status, reserves section and season) and one continuous (standing crop biomass). Interactions of season and section with all the other variables were also tested. When there was multicollinearity between different levels of a categorical variable, I merged them to create a new combined level. Thus, grass greenness in black and blue wildebeest analyses had four classes: <10%, 11-50%, 51-90% and 91-100%, while grass height in red hartebeest and zebra analyses had three classes: <5 cm, 6-10 cm and >11cm.

I conducted model selection using Akaike's Information Criterion, corrected for small sample bias (AICc) (Anderson, 2008), using the 'AICcmodavg package' (Mazerolle & Mazerolle, 2017). The model with the smallest AICc value was considered as the best model (Anderson, 2008). For the best model, I calculated the predicted logit and associated 95% confidence intervals for single categorical factors and the predicted degree of use expressed as a probability and associated 95% confidence intervals for interactions and the continuous variable. Predictions allow for the calculation of accurate confidence intervals for interactions and have been previously used with binomial linear regressions (Anderson, 2008; Brotons *et al.*, 2004). Results of categorical variables are presented as referred to the smallest category level of each variable. In plots of categorical variables, if confidence intervals of a category did not cross the reference category level, there was a significant difference between the two levels (Godvik *et al.*, 2009). A category was considered to be preferred more than the reference category if its lower confidence interval was higher than the reference level. Predictions and plots were made with the 'jtools' package (Long, 2018).

<u>Results</u>

I sampled 1544 feeding patches over four seasons, 328 in the late dry season, 416 in the wet season, 392 in the early dry season and 408 in the mid dry season. The total number of quadrats, from both used and available feeding patches, amounted to 1230 for black wildebeest, 2900 for blue wildebeest, 580 for red hartebeest and 3010 for zebra.

Black wildebeest

Selection of feeding patches by black wildebeest was mainly affected by grass greenness, height and biomass. Out of 19 models, the best was *m14* with a ranking of 0.73 (Table 3.1). The model contained the categorical variables grass greenness, height and feeding patch status and an interaction between the continuous variable grass biomass and season (Table 3.2). Black wildebeest selection for feeding patches was positively related to feeding patch greenness, with a preference for the greenest class (91-100%) over the least green one (log-odds = 1.19 ± 0.54) (Fig 3.1a). Black wildebeest avoided long grass and favoured grasses below 10 cm (Fig 3.1b). In general, I observed black wildebeest to use burnt feeding patches in a higher proportion than what was available (Fig 3.2). However, after accounting for the other factors, they favoured burnt feeding patches less than the reference category ‘un-burnt’ (log-odds = -1 ± 0.64) (Fig 3.1c). The effect of grass biomass on feeding patch selection by black wildebeest depended on season. Indeed, black wildebeest preferred feeding patches offering more biomass than what was available on average during the late dry and wet seasons, while they selected less biomass during the early dry and mid dry seasons (Fig 3.3).

Blue wildebeest

The best model for blue wildebeest was *m17*, with a weight of 1 (Table 3.3). It included the variables greenness, feeding patch status, grass biomass and an interaction between grass height and season (Table 3.4). Similar to black wildebeest, blue wildebeest preference for feeding patches increased with the greenness of the feeding patch (Fig 3.4a). Blue wildebeest used burnt feeding patches in a higher proportion than what was available (Fig 3.5). However, after accounting for the other factors, they favoured burnt feeding patches less than un-burnt ones (log-odds = -0.71 ± 0.52) and favoured wetlands significantly more than un-burnt feeding patches (log-odds = 2.06 ± 0.93) (Fig 3.4b). Moreover, the probability of a feeding patch being used by blue wildebeest was negatively related to its standing crop biomass (Fig 3.6). The effect of grass height on feeding patch selection by blue wildebeest depended on season. Indeed, in the late dry and wet seasons, blue wildebeest did not favour grass of any height class (Fig 3.7). On the other hand, during the early dry and mid dry seasons, they favoured very short and short grass much more than both medium and long grass, and more than any height class in the other seasons (Fig 3.7).

Red hartebeest

The best model describing feeding patch selection by red hartebeest was *m14*, the same as black wildebeest, with a rank of 0.98 (Table 3.5). The model contained grass greenness and height, the feeding patch status and an interaction between standing crop biomass and season (Table 3.6). Red hartebeest selected feeding patches with a wide range of greenness and long grass. In particular, they avoided feeding patches with a greenness value lower than 10% (Fig 3.8a) and they favoured grass longer than 11 cm more than grass shorter than 5 cm (log-odds = 1.29 ± 0.64) (Fig 3.8b). Red hartebeest slightly preferred wetlands more than un-burnt feeding patches and did not show any preference between burnt and un-burnt feeding patches (Fig 3.8c). The effect of standing crop biomass depended on season. During the late dry season, red hartebeest selected feeding patches having more biomass than what was available on average more than they did in any other season (Fig 3.9).

Zebra

Zebra selected feeding patches based on grass greenness, biomass and feeding patch status. The best model describing feeding patch selection by zebra was *m13* with a rank of 1 (Table 3.7). The model contained the variables grass height and biomass, feeding patch status and an interaction between greenness and season (Table 3.8). Grass height was included in the best model, but zebra did not select any particular height class of grass (Fig 3.10a). On the other hand, zebra preferred wetlands significantly more than both burnt and un-burnt feeding patches (log-odds = 1.72 ± 0.77) (Fig 3.10b). The probability of a feeding patch being selected by zebra was negatively related to the feeding patch biomass (Fig 3.11). Therefore, zebra selected feeding patches offering less grass biomass than what was available on average. In addition, zebra preference for grass greenness depended on season. They did not show any preference for greenness during the late dry and wet seasons (Fig 3.12). On the other hand, in the early dry season, zebra preferred the greenest grass classes over the two least green (Fig 3.12), while during the mid dry season, they selected grass of intermediate greenness (between 11 and 90%) more than both the greenest and the least green classes (Fig 3.12).

Discussion

The aim of the study was to investigate resource selection effect on community interactions of specialist and generalist grazer ungulates at TENR, across seasons and reserves sections with different fire regimes. As predicted from the focal grazing species physiology and known grass preferences, red hartebeest and black wildebeest selected feeding patches with high greenness and longer and shorter grass respectively. Surprisingly, red hartebeest preferred wetlands in every season and not only during the dry season, and black and blue wildebeest did not favour burnt feeding patches throughout the year. Unexpectedly, selection for feeding patches by blue wildebeest was very different from black wildebeest selection, appearing to be more similar to generalist species selection. As expected, zebra showed to be less selective than the ruminant species at feeding patch scale. However, zebra favoured wetlands and feeding patches offering less biomass than what was available, regardless of grass height, and they selected very green grass at the beginning of the dry season to accept all greenness classes by the late dry season.

As expected from digestive adaptation and supported by other studies (Bergman *et al.*, 2001; Odadi *et al.*, 2011), ruminant species selected feeding patches with high greenness, with the only surprising result being the wide variety of greenness preferred by red hartebeest (> 10%). Moreover, as predicted from muzzle morphology (Janis & Ehrhardt, 1988) and confirmed by several studies (Owaga, 1975; Wilmshurst *et al.*, 1999; Helm, 2007; Arsenault & Owen-Smith, 2008; Hamunyela, 2017), red hartebeest selected grass taller than 11 cm, black wildebeest selected grass shorter than 10 cm and zebra did not select any height of grass in particular, but mostly fed on grass taller than 11 cm.

Both blue wildebeest and zebra selected feeding patches having less biomass than what was available on average throughout the year. Helm (2007) findings support this, as the author also describes blue wildebeest preferring less biomass during the wet season than during the rest of the year. On the other hand, the fact that zebra selected less biomass than what was available and increased the acceptance for less green grass in the late dry season indicates that the overall quality of available grass was adequate to sustain them, and so zebra did not have to compensate the low quality of forage by foraging on a higher quantity of grass.

Surprisingly, none of the species favoured burnt feeding patches in any season. Even more surprisingly, once all the studied characteristics of a feeding patch were taken into account, black and blue wildebeest appeared to even avoid burnt feeding patches. This does not mean that wildebeest did not use burnt feeding patches per se, but rather that, at the feeding patch scale, other forage characteristics had more weight on feeding patch selection by wildebeest than being burnt. Indeed, both black and blue wildebeest favoured large burnt areas at a broader spatial level (Chapter 2). Probably, the burnt feeding patches selected by wildebeest were usually further than 100 meters form the closest un-burnt feeding patch. If so, due to the data collection methodology, both the used and the available feeding patches recorded would have been ‘burnt’. Moreover, wildebeest probably frequently foraged in un-burnt feeding patches close to burnt ones, in which case I could have taken the available feeding patch inside the burnt area, resulting in wildebeest avoiding burnt feeding patches.

Zebra, blue wildebeest and red hartebeest favoured wetlands in every season. Wetlands represent a unique source of high quality grass and water, and because of it, they are known to attract ungulates (Fynn *et al.*, 2015). In addition, wetlands could have been favoured even more because of fire management in the study period. Indeed, burning took place in the West section of the reserves in July 2017 and August 2018. The burning of 2017 was performed two months before the beginning of the wet season (Figure 2, APPENDIX), possibly delaying grass regrowth, while fire of 2018 was performed during the last data collection period. Because of unfortunate timing and the possible overgrazing of burnt areas by other ungulate species, grass regrowth on burnt areas was very short during the whole study period (personal observation). The regrowth may have been too short for red hartebeest to be able to exploit it, pushing even more red hartebeest to use wetlands.

The section of the reserves and season were considered in interaction with grass quality, quantity, height and feeding patch status. As predicted, the reserves section was not an important factor in shaping feeding patch selection by any of the species, and therefore species selected feeding patches with the same characteristics in both sections of the reserves. On the other hand, season had an important effect on the resource selection of all species, with the most interesting results being the different, and somewhat unexpected, ways in which each species behaved during the late dry season. All the species modified their resource selection presumably in order to cope with the low quality of grass available in this season, and each species did it by widening their acceptance criteria, though in different ways.

During the late dry season, red hartebeest and black wildebeest selected feeding patches offering more biomass than in the other seasons. Possibly, due to the low quality and quantity of grass available in this season, these species increased their acceptance for grass of lower quality in order to satisfy their energetic needs (Casebeer & Koss, 1970; Owen-Smith, 1994), with the result of selecting feeding patches having a higher biomass of forage. Groom and Harris (2009) found that Coke’s hartebeest (*Alcelaphus buselaphus cokii*), zebra and blue wildebeest preferred grass of both high biomass and greenness in the wet season, while selecting only for forage quantity in the dry season. The authors concluded that forage quantity is more important than forage quality in sustaining ungulates in a resource-stressed environment, as was observed for red hartebeest and black wildebeest in this study.

Blue wildebeest and zebra applied a different strategy in the late dry season: they became less selective for certain forage characteristics. Blue wildebeest selected grass shorter than 10 cm during the early and the mid dry season, but showed no selection for height in the late dry season. Therefore, blue wildebeest also accepted medium to tall grass when the quality of forage was limiting. Arsenault and Owen-Smith (2008) found the same trend, with blue wildebeest making higher use of medium to tall grassland in the late dry season than in the rest of the year at Hluhluwe-iMfolozi Park, South Africa. Zebra, on the other hand, selected feeding patches of medium to high greenness during the early and the mid dry season, but not during the late dry season. As the quality of grass decreased, zebra became less selective for greenness and eventually started to forage randomly on what was available. This result is not common in literature. Sinclair (1985) found that zebra preferred tall grass in the dry season and short grass in the wet season and Bell (1971) observed the same pattern in both blue wildebeest and zebra in the Serengeti. The uncommon behaviour of zebra in this study could be explained by the abundance of long grass that was available in each season. Indeed, at least 66% of grass available in each season was longer than 11 cm. Thus, zebra were probably selecting areas of long grass inside the study area, but this was not visible from the feeding patch scale. At this scale, zebra accepted any class of greenness, increasing their acceptance for lower quality grass.

Blue wildebeest selection for feeding patches appeared to be in between black wildebeest and zebra selection. Indeed, blue wildebeest selected feeding patches with high greenness and short grass, like black wildebeest, but also with less biomass and wetlands, like zebra. Being morphologically, physiologically and phylogenetically very similar, black and blue wildebeest should use very similar niches (Day & Young, 2004). Such unexpected differences in feeding patch selection may be caused by a cascading multispecies interaction due to the coexistence of multiple species of the same guild. It could also suggest the presence of competition between black and blue wildebeest, mitigated by the ability of blue wildebeest to use wider set of resources. Indeed, black wildebeest are grassland specialists while blue wildebeest are able to exploit a wide variety of habitats (Codron & Brink, 2007). Thus, blue wildebeest diet is more malleable, making them able to act more similarly to generalists than black wildebeest. Actually, the definition of blue wildebeest as specialist may not be a perfect fit. Ben-Shahar (1991) found that blue wildebeest consumed grass species according to their availability, the same as the generalist zebra did, in a South African reserve. The only difference the author found between these two ungulate species was a shift in grass species acceptance between the dry and the wet seasons by blue wildebeest that was not present in zebra. He concluded that the definition of a species as generalist or specialist is highly influenced by the considered spatial and temporal scale of investigation.

In order to deepen our knowledge on ungulate resource selection and improve the management of the study area, further studies should consider grass species preference, faecal protein content as a proxy for chosen grass quality, and foraging behaviour. This information would give us a better understanding of competition between the wildebeest species at TENR and contribute to improve management. Actually, grass species preference and faecal protein content were to be part of this study, but in the end, I did not have enough data to include these variables in the study.

The biggest limitation of this study was the necessity of staying close to roads to observe foraging individuals. Indeed, it was not feasible to place GPS collars on individuals inside the reserves and it was extremely difficult not to chase ungulates away by walking close to them. Therefore, I chose to collect ungulates feeding locations from roads, with the disadvantage of covering only about 500 meters on each side of the road. Nevertheless, this method allowed me to collect relative accurate locations of animals and, because of the extensive road network, results at feeding patch level can be extrapolated to the entire area covered by the reserves. In conclusion, this study describes resource use of sympatric ungulates at feeding patch level, including black and blue wildebeest, which have seldom been studied together (Codron & Brink, 2007; Helm, 2007), and highlights the critical importance of wetlands, a resource which was selected by three out of four species in every season. Management should be informed and take the importance of wetlands into consideration when managing these areas.

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Tables and figures

Table 3.1: Feeding patch selection: candidate models to test the importance of grass greenness, biomass and height, patch status, reserve section and season on **black wildebeest** feeding patch selection, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects:	K	AICc	ΔAICc	w_i
Black wildebeest *n*(1230)					
m14	Greenness + height + status + biomass*season	18	1477.92	0	0.73
m17	Greenness + status + biomass + height*season	24	1479.89	1.97	0.27
m13	Height + biomass + status + greenness*season	24	1492.29	14.37	<0.01
m18	Greenness + status + biomass + height*section	15	1498.18	20.25	<0.01
m12	Greenness + height + status + biomass*section	14	1500.11	22.19	<0.01
m15	Greenness + height + biomass + status*season	20	1501.18	23.26	<0.01
m16	Greenness + height + biomass + status*section	13	1501.51	23.58	<0.01
m19	Status + biomass + height + greenness*section	16	1501.79	23.87	<0.01
m8	Greenness + height + status	11	1502.57	24.64	<0.01
m11	Greenness + height + biomass + status	12	1502.98	25.05	<0.01
m10	Height + biomass + status	9	1527.26	49.33	<0.01
m5	Height + status	8	1528.77	50.85	<0.01
m1	Greenness + height	9	1532.23	54.31	<0.01
m7	Greenness + height + biomass	10	1532.75	54.82	<0.01
m4	Height + biomass	7	1533.1	55.18	<0.01
m9	Greenness + biomass + status	9	1557.78	79.86	<0.01
m2	Greenness + biomass	7	1579.47	101.55	<0.01
m6	Biomass + status	6	1598.09	120.17	<0.01
m3	Greenness + status	8	1620.62	142.69	<0.01

* = interaction; *n*, no. quadrats; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 3.2: The most parsimonious generalized linear mixed model representing the coefficients that are used to determine the log-odd ratios for feeding patch selection by **black wildebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.226	0.268	-0.845	0.398
greenness1 11-50%	0.245	0.224	1.093	0.275
greenness1 51-90%	0.521	0.274	1.901	0.057
greenness1 91-100%	1.188	0.284	4.182	<0.001
Height6-10 cm	0.028	0.173	0.159	0.874
height11-30 cm	-1.543	0.256	-6.038	<0.001
height> 30cm	-1.339	0.440	-3.04	0.002
Burnt-Yes	-1.000	0.225	-4.444	<0.001
Burnt-Wetland	-0.255	0.586	-0.436	0.663
Biomass	0.103	0.039	2.663	0.008
seasonEndOfWet	0.413	0.298	1.387	0.165
seasonEarlyDry	0.833	0.234	3.561	<0.001
seasonMidDry	0.870	0.232	3.756	<0.001
biomass:seasonEndOfWet	-0.063	0.048	-1.309	0.190
biomass:seasonEarlyDry	-0.195	0.042	-4.626	<0.001
biomass:seasonMidDry	-0.181	0.043	-4.224	<0.001

Table 3.3: Feeding patch selection: candidate models to test the importance of grass greenness, biomass and height, patch status, reserve section and season on **blue wildebeest** feeding patch selection, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects	K	AICc	ΔAICc	w_i
Blue wildebeest n(2900)					
m17	Greenness + status + biomass + height*season	24	3044.21	0	1
m14	Greenness + height + status + biomass*season	18	3079.62	35.41	<0.01
m13	Height + biomass + status + greenness*season	24	3227.89	183.68	<0.01
m15	Greenness + height + biomass + status*season	21	3287.9	243.7	<0.01
m18	Greenness + status + biomass + height*section	16	3315.16	270.95	<0.01
m16	Greenness + height + biomass + status*section	15	3331.07	286.87	<0.01
m19	Status + biomass + height + greenness*section	16	3337.36	293.15	<0.01
m12	Greenness + height + status + biomass*section	14	3338.22	294.02	<0.01
m11	Greenness + height + biomass + status	12	3347.34	303.14	<0.01
m8	Greenness + height + status	11	3358.58	314.37	<0.01
m10	Height + biomass + status	9	3412.27	368.06	<0.01
m5	Height + status	8	3428.61	384.4	<0.01
m7	Greenness + height + biomass	10	3436.38	392.17	<0.01
m1	Greenness + height	9	3440.58	396.37	<0.01
m9	Greenness + biomass + status	9	3474.21	430	<0.01
m4	Height + biomass	7	3478.9	434.69	<0.01
m2	Greenness + biomass	7	3550.22	506.01	<0.01
m6	Biomass + status	6	3595.9	551.69	<0.01
m3	Greenness + status	8	3690.4	646.2	<0.01

* = interaction; *n*, no. quadrats; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 3.4: The most parsimonious generalized linear mixed model representing the coefficients that are used to determine the log-odd ratios for feeding patch selection by **blue wildebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.172	0.215	-0.797	0.425
greenness1 11-50%	0.373	0.146	2.566	0.010
greenness1 51-90%	0.728	0.178	4.083	<0.001
greenness1 91-100%	1.252	0.198	6.316	<0.001
Burnt-Yes	-0.719	0.157	-4.567	<0.001
Burnt-Wetland	2.052	0.413	4.965	<0.001
Biomass	-0.028	0.014	-2.031	0.042
height6-10 cm	-0.042	0.229	-0.184	0.854
height11-30 cm	-0.075	0.258	-0.29	0.772
height> 30 cm	-0.135	0.367	-0.368	0.713
seasonEndOfWet	-0.136	0.240	-0.567	0.571
seasonEarlyDry	1.601	0.282	5.678	<0.001
seasonMidDry	1.152	0.227	5.08	<0.001
height6-10 cm:seasonEndOfWet	0.096	0.331	0.29	0.772
height11-30 cm:seasonEndOfWet	-0.032	0.311	-0.103	0.918
height> 30 cm:seasonEndOfWet	-0.107	0.386	-0.278	0.781
height6-10 cm:seasonEarlyDry	-0.269	0.396	-0.679	0.497
height11-30 cm:seasonEarlyDry	-3.452	0.361	-9.551	<0.001
height> 30 cm:seasonEarlyDry	-5.589	0.830	-6.734	<0.001
height6-10 cm:seasonMidDry	-0.319	0.330	-0.967	0.334
height11-30 cm:seasonMidDry	-2.614	0.330	-7.931	<0.001
height> 30 cm:seasonMidDry	-19.717	746.736	-0.026	0.979

Table 3.5: Feeding patch selection: candidate models to test the importance of grass greenness, biomass and height, patch status, reserve section and season on **red hartebeest** feeding patch selection, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects	K	AICc	ΔAICc	w_i
Red hartebeest *n*(580)					
m14	Greenness + height + status + biomass*season	19	774.11	0	0.98
m15	Greenness + height + biomass + status*season	19	781.66	7.54	0.02
m17	Greenness + status + biomass + height*season	22	790.02	15.9	<0.01
m3	Greenness + status	10	794.2	20.08	<0.01
m8	Greenness + height + status	12	794.52	20.41	<0.01
m5	Height + status	7	795.96	21.84	<0.01
m9	Greenness + biomass + status	11	796.01	21.89	<0.01
m11	Greenness + height + biomass + status	13	796.51	22.4	<0.01
m10	Height + biomass + status	8	797.93	23.82	<0.01
m16	Greenness + height + biomass + status*section	14	798.3	24.19	<0.01
m6	Biomass + status	6	799.73	25.62	<0.01
m12	Greenness + height + status + biomass*section	16	801.55	27.44	<0.01
m1	Greenness + height	10	802.26	28.14	<0.01
m18	Greenness + status + biomass + height*section	16	802.45	28.33	<0.01
m19	Status + biomass + height + greenness*section	18	802.49	28.38	<0.01
m2	Greenness + biomass	9	803.66	29.55	<0.01
m7	Greenness + height + biomass	11	803.81	29.7	<0.01
m13	Height + biomass + status + greenness*season	31	808.6	34.49	<0.01
m4	Height + biomass	6	808.97	34.86	<0.01

* = interaction; *n*, no. quadrats; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 3.6: The most parsimonious generalized linear mixed model representing the coefficients that are used to determine the log-odd ratios for feeding patch selection by **red hartebeest** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-3.431	0.650	-5.279	<0.001
greenness1 11-25%	1.037	0.307	3.381	<0.001
greenness1 26-50%	1.398	0.341	4.098	<0.001
greenness1 51-75%	1.348	0.399	3.377	<0.001
greenness1 76-90%	1.349	0.418	3.227	0.001
greenness1 91-100%	1.376	0.440	3.129	0.002
height1 6-10cm	0.721	0.411	1.752	0.080
height1 >11cm	1.287	0.419	3.074	0.002
Burnt-Yes	0.385	0.533	0.721	0.471
Burnt-Wetland	1.583	0.667	2.373	0.018
Biomass	0.126	0.044	2.844	0.004
seasonEndOfWet	0.880	0.576	1.529	0.126
seasonEarlyDry	1.390	0.526	2.643	0.008
seasonMidDry	2.578	0.548	4.705	<0.001
biomass:seasonEndOfWet	-0.113	0.050	-2.262	0.0234
biomass:seasonEarlyDry	-0.164	0.050	-3.274	0.001
biomass:seasonMidDry	-0.218	0.052	-4.179	<0.001

Table 3.7: Feeding patch selection: candidate models to test the importance of grass greenness, biomass and height, patch status, reserve section and season on **zebra** feeding patch selection, at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Model #	Fixed effects	K	AICc	ΔAICc	w_i
Zebra *n*(3010)					
m13	Height + biomass + status + greenness*season	23	3998.13	0	1
m14	Greenness + height + status + biomass*season	17	4027.11	28.97	<0.01
m16	Greenness + height + biomass + status*section	14	4027.17	29.04	<0.01
m15	Greenness + height + biomass + status*season	20	4032.59	34.46	<0.01
m17	Greenness + status + biomass + height*season	20	4037.36	39.23	<0.01
m18	Greenness + status + biomass + height*section	16	4046.55	48.42	<0.01
m11	Greenness + height + biomass + status	11	4050.14	52.01	<0.01
m12	Greenness + height + status + biomass*section	14	4053.11	54.97	<0.01
m9	Greenness + biomass + status	9	4053.22	55.09	<0.01
m19	Status + biomass + height + greenness*section	16	4055.42	57.29	<0.01
m10	Height + biomass + status	8	4063.95	65.82	<0.01
m8	Greenness + height + status	10	4071.07	72.94	<0.01
m6	Biomass + status	6	4071.84	73.7	<0.01
m5	Height + status	7	4088.35	90.22	<0.01
m3	Greenness + status	8	4102.57	104.44	<0.01
m7	Greenness + height + biomass	9	4102.99	104.86	<0.01
m2	Greenness + biomass	7	4104.63	106.5	<0.01
m1	Greenness + height	8	4110.27	112.14	<0.01
m4	Height + biomass	6	4126.39	128.25	<0.01

* = interaction; *n*, no. quadrats; *k*, number of parameters in the model; AICc, Akaike's Information Criterion corrected for small-sample bias; ΔAICc, difference between model AICc and that of the lowest model; *wi*, model probability (Akaike weight).

Table 3.8: The most parsimonious generalized linear mixed model representing the coefficients that are used to determine the log-odd ratios for feeding patch selection by **zebra** at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Fixed effects:				
	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	0.288	0.176	1.631	0.103
height1 6-10cm	0.094	0.135	0.692	0.489
height1 >11cm	-0.119	0.144	-0.827	0.408
Biomass	-0.037	0.008	-4.479	<0.001
Burnt-Yes	-0.314	0.175	-1.791	0.073
Burnt-Wetland	1.720	0.340	5.064	<0.001
greenness1 11-50%	0.132	0.180	0.730	0.466
greenness1 51-90%	0.073	0.272	0.270	0.787
greenness1 91-100%	0.155	0.289	0.536	0.592
seasonEndOfWet	-0.113	0.288	-0.391	0.696
seasonEarlyDry	-0.632	0.631	-1.002	0.317
seasonMidDry	-0.192	0.159	-1.205	0.228
greenness1 11-50%:seasonEndOfWet	-0.015	0.330	-0.047	0.963
greenness1 51-90%:seasonEndOfWet	0.099	0.393	0.252	0.801
greenness1 91-100%:seasonEndOfWet	0.052	0.390	0.132	0.895
greenness1 11-50%:seasonEarlyDry	-0.130	0.655	-0.198	0.843
greenness1 51-90%:seasonEarlyDry	1.492	0.701	2.13	0.033
greenness1 91-100%:seasonEarlyDry	1.557	0.713	2.183	0.029
greenness1 11-50%:seasonMidDry	0.560	0.259	2.158	0.031
greenness1 51-90%:seasonMidDry	1.355	0.628	2.159	0.031
greenness1 91-100%:seasonMidDry	-0.094	0.364	-0.257	0.797

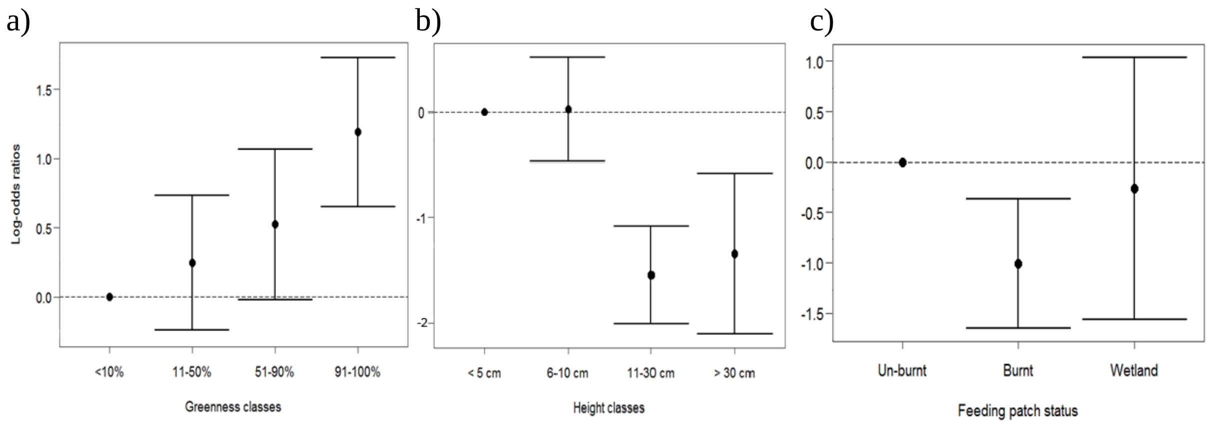

Figure 3. 1: Predicted estimates (± 95% confidence interval) for feeding patch selection by black wildebeest for (a) grass greenness '<10%', '11-50%', '51-90%' and '91-100%', (b) grass height '< 5 cm', '6-10 cm', '11-30 cm' and '> 30 cm', (c) feeding patch status 'Un-burnt', 'Burnt' and 'Wetland' at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: (a) '<10%', (b) '< 5 cm', (c) 'Un-burnt'.

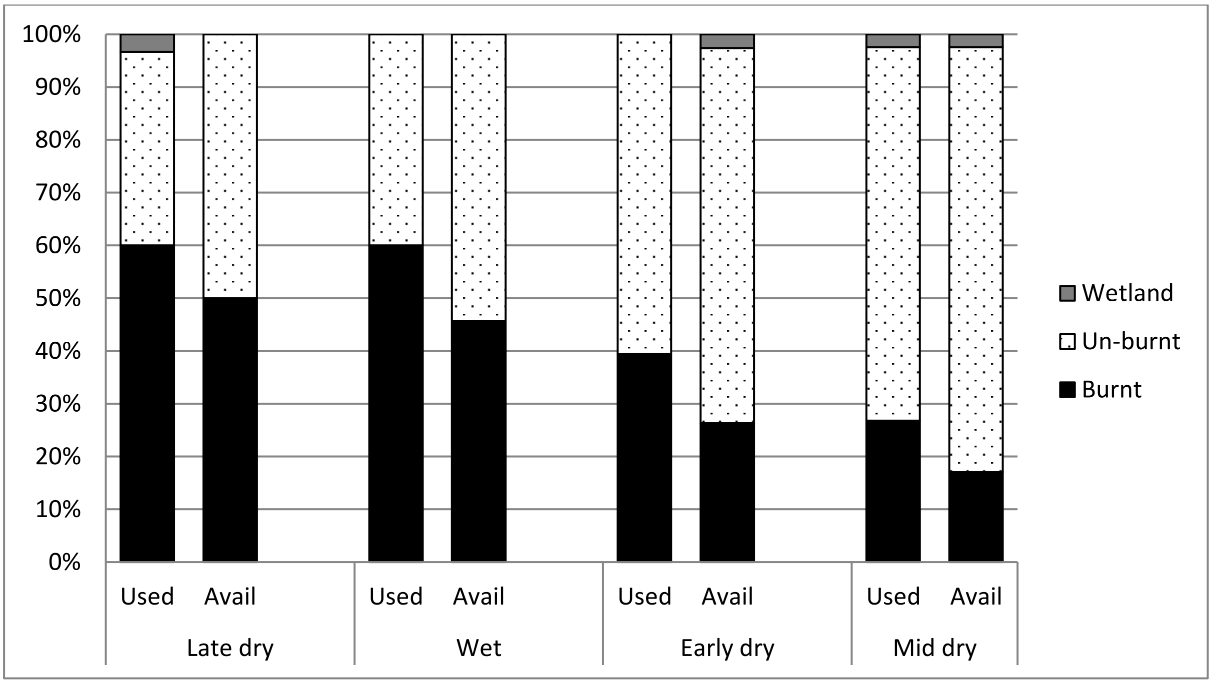

Figure 3. 2: Black wildebeest proportion of used and available feeding patch burnt status (Burnt, Un-burnt and Wetland) in each season (late dry, end of wet, early dry and mid dry) at Telperion and Ezemvelo nature reserves, South Africa, 2018.

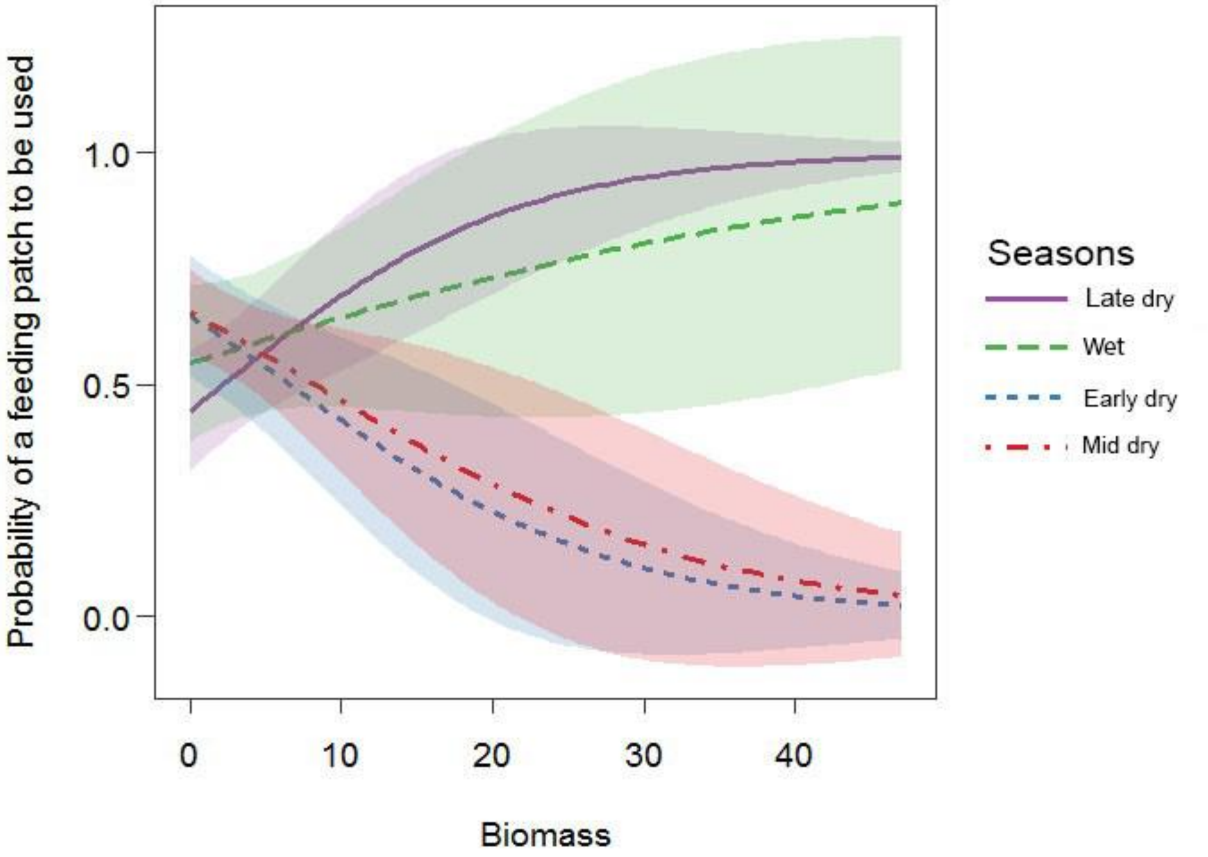

Figure 3. 3: Predicted probability (± 95% confidence interval) for feeding patch selection by black wildebeest for biomass over seasons at Telperion and Ezemvelo nature reserves, South Africa, 2018.

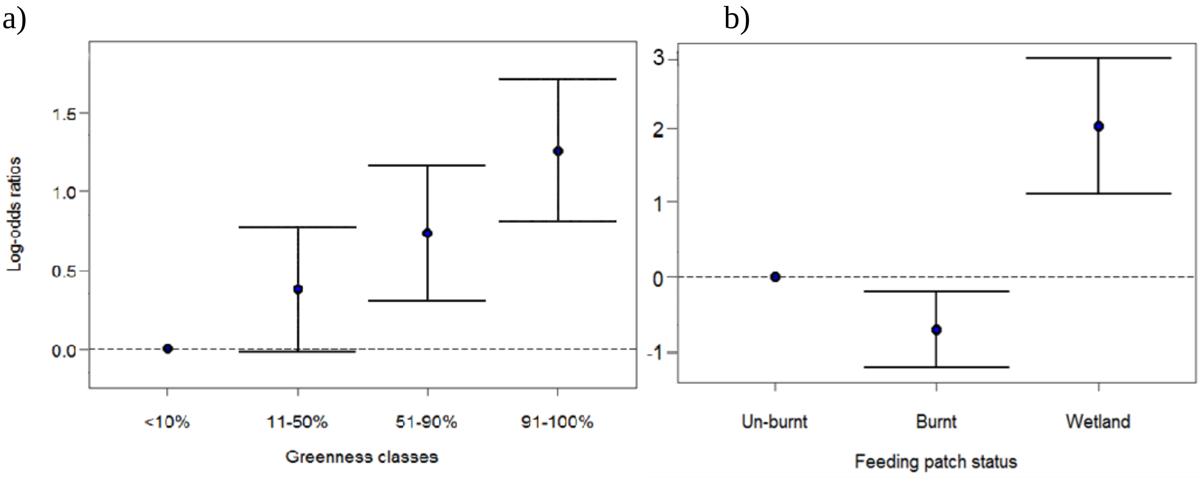

Figure 3. 4: Predicted estimates (± 95% confidence interval) for feeding patch selection by blue wildebeest for (a) grass greenness ‘<10%’, ’11-50%’, ’51-90%’ and ’91-100%’, (b) feeding patch status ‘Un-burnt’, ‘Burnt’ and ‘Wetland’ at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: (a) ‘<10%’, (b) ‘Un-burnt’.

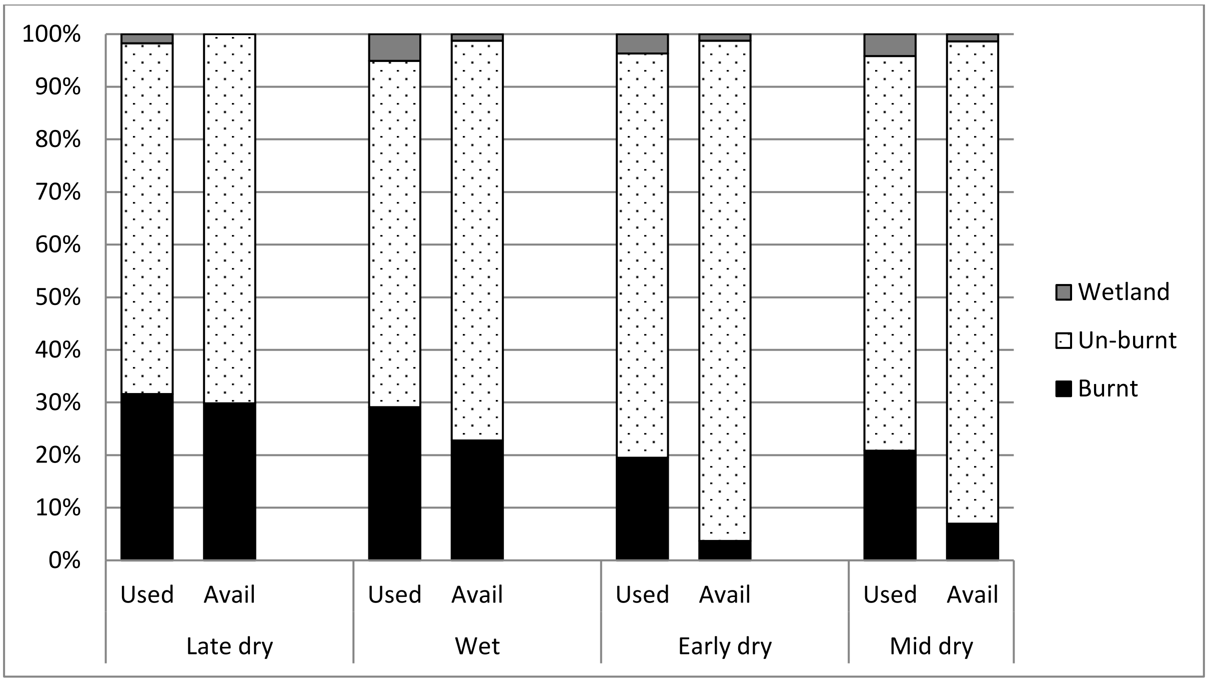

Figure 3. 5: Blue wildebeest proportion of used and available feeding patch burnt status (Burnt, Un-burnt and Wetland) in each season (late dry, end of wet, early dry and mid dry) at Telperion and Ezemvelo nature reserves, South Africa, 2018.

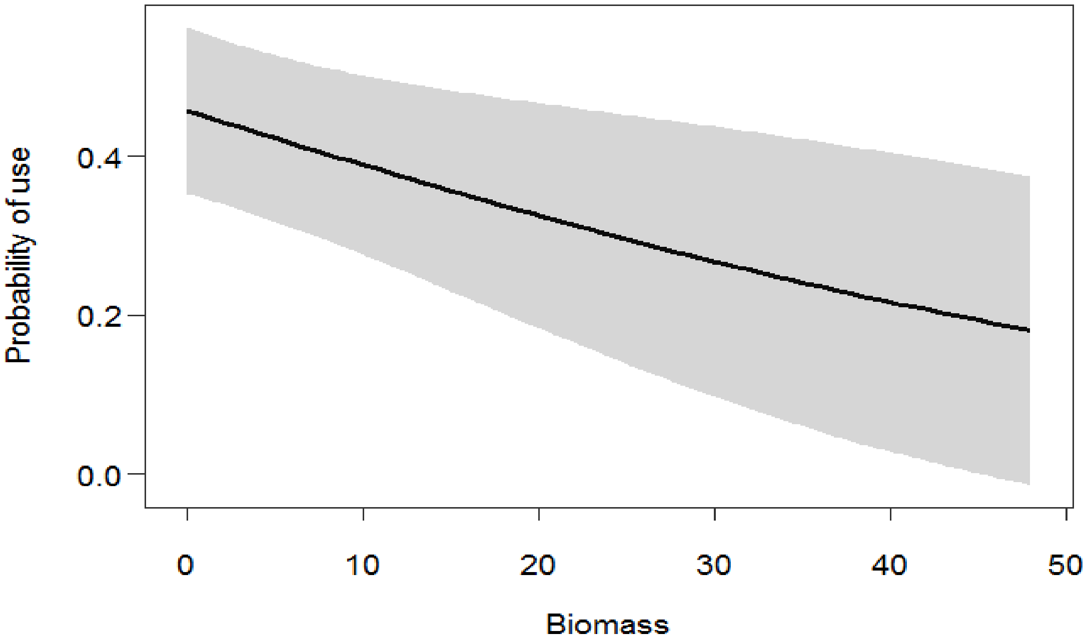

Figure 3. 6: Predicted probability (± 95% confidence interval) for feeding patch selection by blue wildebeest for biomass at Telperion and Ezemvelo nature reserves, South Africa, 2018.

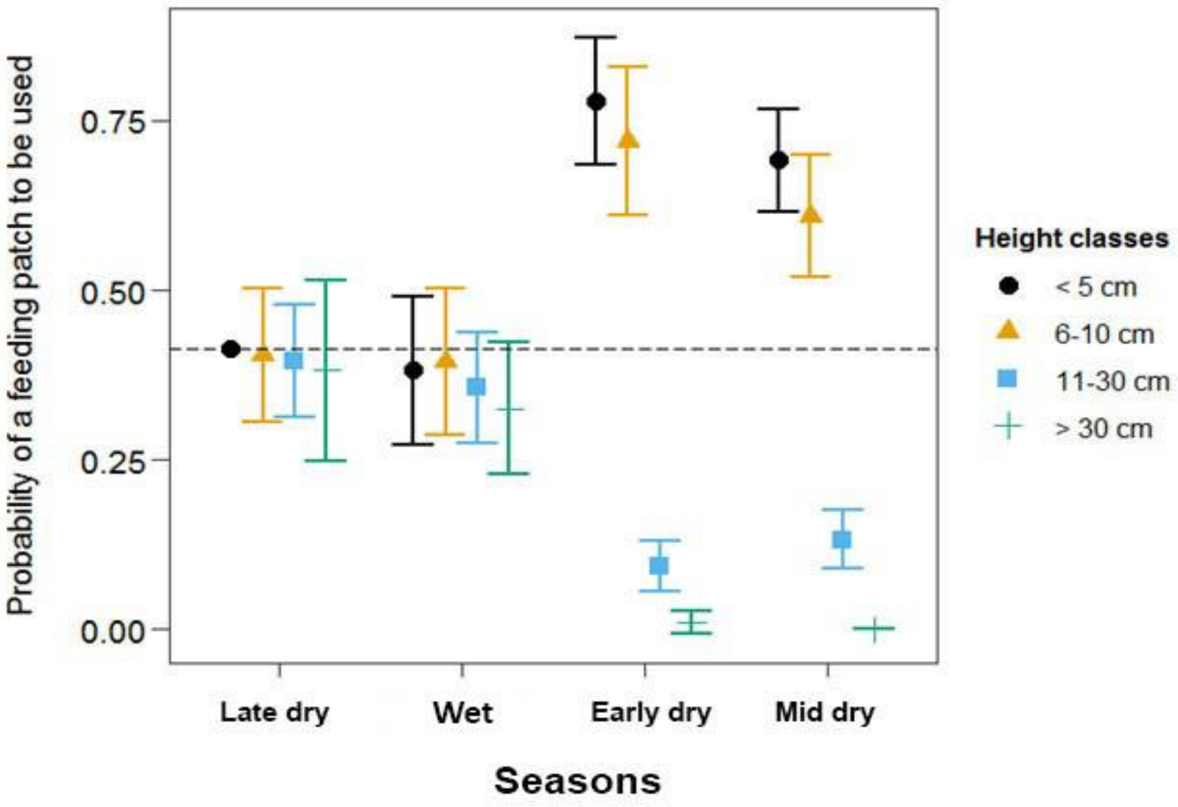

Figure 3. 7: Predicted probability (± 95% confidence interval) for feeding patch selection by blue wildebeest for grass height '< 5 cm', '6-10 cm', '11-30 cm' and '> 30 cm' based on seasons (late dry, end of wet, early dry and mid dry) at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: '< 5 cm' in late dry season.

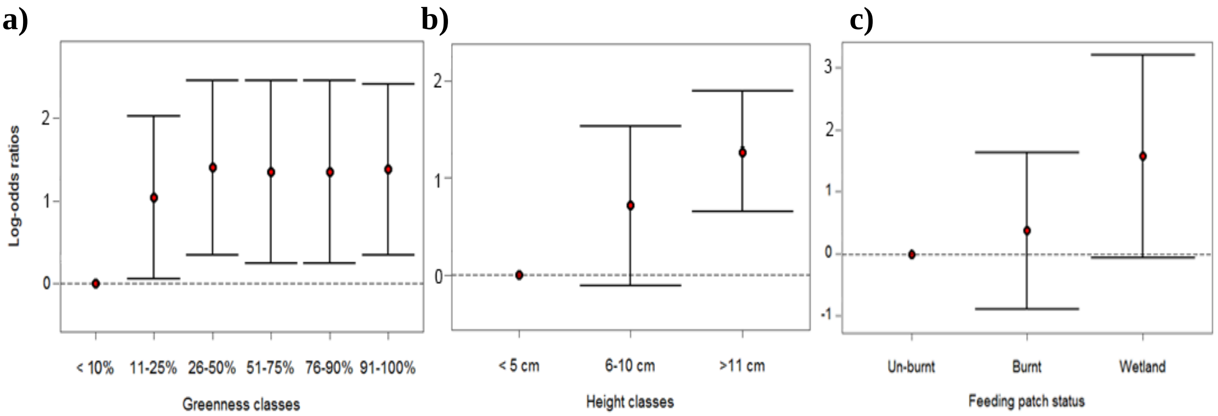

Figure 3. 8: Predicted estimates (± 95% confidence interval) for feeding patch selection by red hartebeest for (a) grass greenness '< 10%', '11-25%', '26-50%', '51-75%', '76-90%' and '91-100%', (b) grass height '< 5 cm', '6-10 cm' and '> 11 cm', (c) feeding patch burnt status 'Un-burnt', 'Burnt' and 'Wetland' at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed lines indicate the reference level: (a) '< 10%', (b) '< 5 cm', (c) 'Un-burnt'.

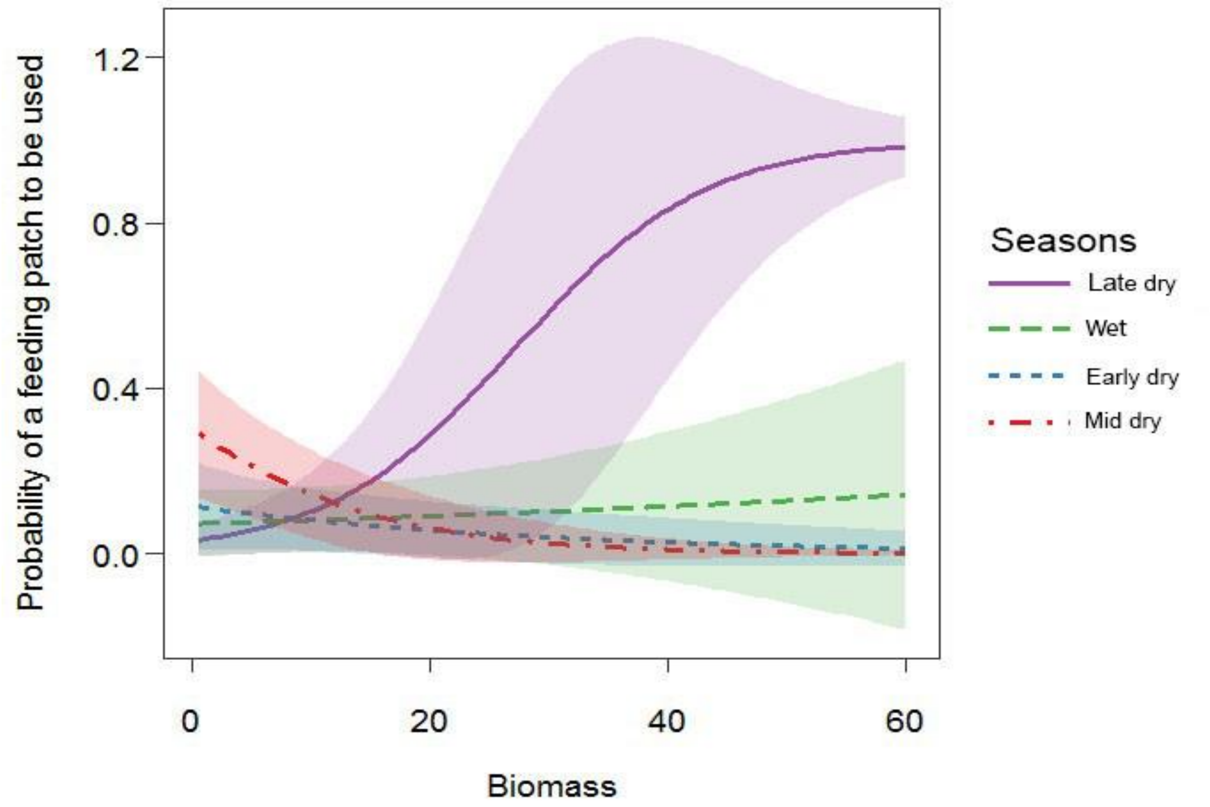

Figure 3. 9: Predicted probability (± 95% confidence interval) for feeding patch selection by red hartebeest for biomass over seasons (late dry, end of wet, early dry and mid dry) at Telperion and Ezemvelo nature reserves, South Africa, 2018.

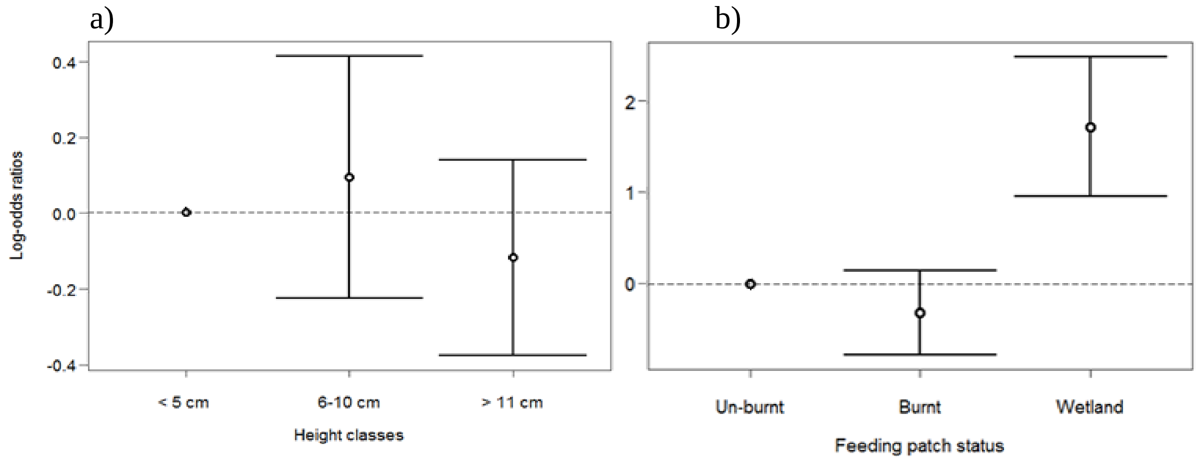

Figure 3. 10: Predicted estimates (± 95% confidence interval) for feeding patch selection by zebra for (a) grass height '< 5 cm', '6-10 cm' and '> 11 cm' and (b) feeding patch burnt status 'Un-burnt', 'Burnt' and 'Wetland' at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed lines indicate the reference levels: (a) '< 5 cm', (b) 'Un-burnt'.

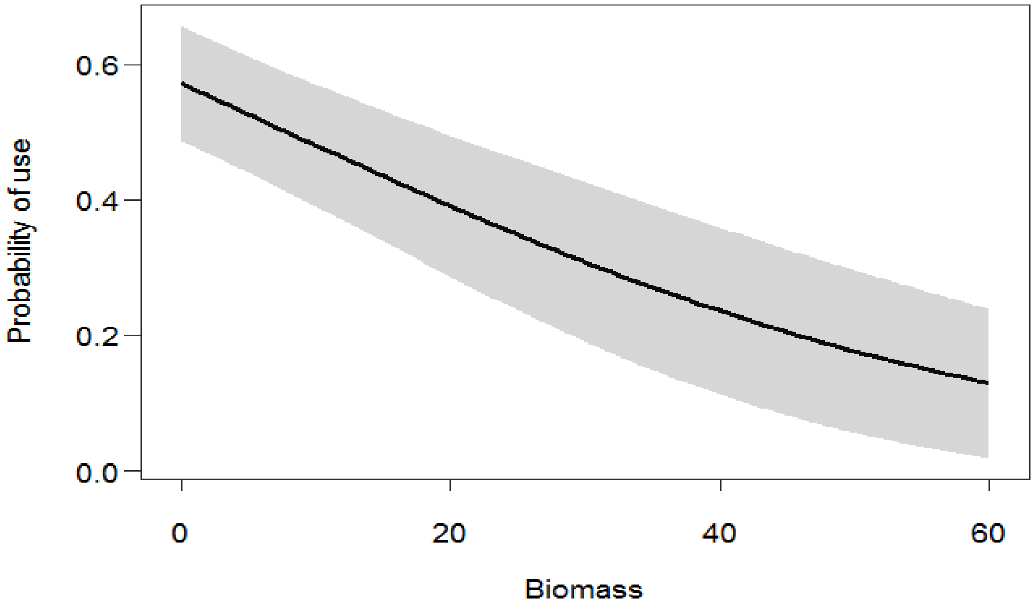

Figure 3. 11: Predicted probability (± 95% confidence interval) for feeding patch selection by zebra for standing crop biomass at Telperion and Ezemvelo nature reserves, South Africa, 2018.

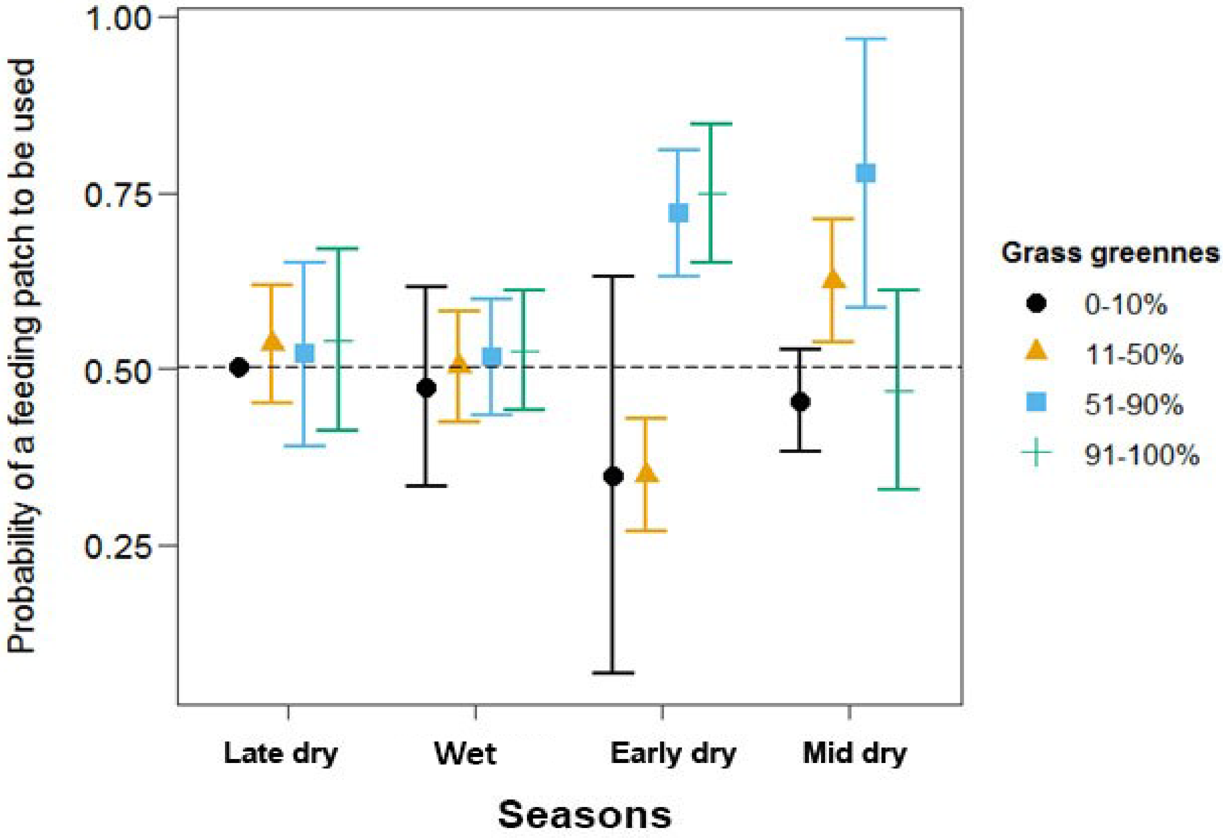

Figure 3. 12: Predicted probability (± 95% confidence interval) for feeding patch selection by zebra for grass greenness ‘0-10%’, ’11-50%’, ‘51-90%’ and ’91-100%’ based on seasons (late dry, end of wet, early dry and mid dry) at Telperion and Ezemvelo nature reserves, South Africa, 2018. The dashed line indicates the reference level: ‘0-10%’ in late dry season.

CHAPTER FOUR: *General conclusion*

The aim of the study was to investigate the role of resources and constraints in shaping seasonal resource use, distribution and interspecific relationships of both specialist and generalist grazer ungulates, at different spatial scales across two areas having a different topography and fire regime.

The most interesting results obtained in the study were probably those for the blue wildebeest. This species selected features, at both landscape and feeding patch scales, that were at times more similar to black wildebeest and at times more similar to zebra. Indeed, both wildebeest species selected burnt landscape, avoided burnt feeding patches, favoured grass of high quality and preferred grass shorter than 10 cm in the early and mid dry seasons. On the other hand, blue wildebeest selected feeding patches offering less biomass than what was available on average and wetlands in every season, similar to zebra. If similarities in resource use by black and blue wildebeest were expected, due the morphology and physiology of the species being almost the same (Day & Young, 2004; Codron & Brink, 2007), they were not expected with zebra. Indeed, blue wildebeest and zebra have different digestive systems, energy requirement and foraging height preferences (Estes, 1991; Groom & Harris, 2009). However some previous studies that found some similarities include Ben-Shahar (1991) who showed that grass species comprising the diet of blue wildebeest and zebra overlapped considerably in Sabi-Sand Wiltuin, a South African reserve, and thus blue wildebeest appeared to be as generalist as zebra. The author suggested that blue wildebeest can be defined as both specialist and generalist, depending on the spatial scale of investigation. The definition of specialist and generalist grazers should be revised to become either more specific and precise, or more flexible, including behaviours in between the two terms. For example, blue wildebeest and other species with a similar behaviour, could be defined as 'intermedialist'.

Another interesting result of the study is the probable presence of competition between the two species of wildebeest at TENR. It is suggested by the fact that blue wildebeest foraged further from black wildebeest than expected if they were foraging randomly, and it is confirmed, at feeding patch scale, by the exploitation of some similar resources. Competition is not the only issue for wildebeest; indeed sympatric black and blue wildebeest can interbreed and give birth to fertile hybrids (Fabricius *et al.*, 1988; Grobler *et al.*, 2011). Hybridization perpetuated for several generations could eventually bring to the extinction of one of the two species (Fabricius *et al.*, 1988). This would more probably be the endemic black wildebeest, being the species with the most restricted range and having a limited genetic pool caused by two bottleneck events (Codron & Brink, 2007; Grobler *et al.*, 2011). The signs of competition between the two species of wildebeest showed in this study should be further investigated as it might have important management repercussions. This study also shows the importance of comparing resource selection at different spatial scales, exemplified particularly by the resource use of red hartebeest and both species of wildebeest. Indeed, red hartebeest selection for a wide variety of grass greenness at feeding patch level was a surprising result (Chapter 3) since, being ruminant, they were expected to use the greenest grass available (Demment & Van Soest, 1985; Duncan *et al.*, 1990), as wildebeest did. However, the comparison of the two spatial scales shows that red hartebeest selected areas having a higher NDVI value, and thus a higher quality of vegetation, than what was available at the landscape spatial scale. Once areas of high quality grass were selected, red hartebeest could probably afford to forage on feeding patches of various quality, avoiding only those being less than 10% green. Therefore, in this study, grass quality had a bigger impact on red hartebeest resource selection at landscape than at feeding patch scale.

Similarly, both black and blue wildebeest favoured burnt areas at landscape scale, but avoided burnt feeding patches. Analysing the two spatial scales together, I can suggest that both wildebeest favoured the large burnt area, and foraged often in un-burnt feeding patches in proximity to burnt ones. In addition, blue wildebeest had a clear preference for wetlands and for highly heterogeneous areas in the West section of the reserves. These areas are represented by wetlands and the transitional zone between burnt and un-burnt grass, supporting the idea that wildebeest used the edge of burnt areas, foraging on feeding patches sometimes inside and sometimes outside of the burns. A possible reason for it could be the overall low quality of grass around the reserves, which would force wildebeest to forage mostly on burnt grass throughout the year, and using un-burnt feeding patches only in close vicinity to burnt feeding patches. In addition, being able to exploit more resources (Codron & Brink, 2007), blue wildebeest would also integrate their diet by foraging in wetlands. Indeed, even if there was only one large burnt area at the landscape scale, there were many long fire breaks and small burnt areas throughout the reserves. Thus, the comparison between both the spatial scales allows seeing how wildebeest interact with burnt areas, in a way that would have been impossible studying only one spatial scale.

Other similar studies have found that different resources are selected at different spatial scales. For example, Wilmshurst *et al.* (1999) observed that in the Serengeti, Tanzania, grass greenness was an important driver for wildebeest resource selection at different spatial scales, while grass height influenced resource selection only at the narrowest investigated scale. In the same way, Boyers (2011) found that zebra selected for grass species only at the grass tuft scale, while grass greenness was more important at the feeding station selection, while Parrini (2008) observed sable antelope (*Hippotragus niger*) avoiding stems at feeding patch scale but foraging on what was available at grass tuft scale. This study confirms that ungulate resource selection depends on the spatial scale of investigation, adding to the current knowledge about this guild.

Another important result of the study is the somewhat unexpected distribution of the species, with red hartebeest and black wildebeest almost exclusively using the West section of the study area. As ruminants need to ingest grass of high quality (Demment & Van Soest, 1985; Duncan *et al.*, 1990), the use of only one part of the reserves by these species could suggest the presence of grass of lower quality in the East section. Indeed, zebra and blue wildebeest were the only species making an extensive use of the East section and they are the species with the most flexible diet in the study (Estes, 1991; Codron & Brink, 2007). This suggests that black wildebeest and red hartebeest, the most specialist species, are forced to forage in the West section by the high quality of grass present there.

Although zebra favoured the East section of the reserve, they were not confined there. Actually, all four ungulate species foraged in the West section while only two used the East. Unfortunately, due to the higher abundance of trees on the East section, it was impossible to compare grassland greenness between the two sections through NDVI. However, the mean NDVI value of the sections was very similar (Table 2, APPENDIX), supporting the idea that grasslands in the East section were of a lower quality than the West section ones. Another clue indicating that the East section offered grass of poorer quality, could be the abundance of tall grass in this section. Indeed, long grass usually contains less protein than shorter grass, being of lower quality (Owen-Smith, 2002). Only 23% of grass available in the East section was shorter than 10 cm, against the 41% in the West section (Figure 5, APPENDIX).

In conclusion, although TENR represent a unique situation, because of its topography, different management across the area and the presence of both black and blue wildebeest, results of this study can apply to different fenced areas in Southern Africa. Indeed, the virtual confinement of ungulate species, represented in this study by red hartebeest and black wildebeest, to a possibly overused area, represented by the West section of the reserves, coupled with probable competition, here between black and blue wildebeest, could represent a threat for such species at TENR as well as in any other fenced protected area. To try to reduce the overlap in resource use and possible competition, fire could be used as a tool for moving grazers from an overused area to an underused one (Archibald & Bond, 2004). Indeed, large burnt areas are known to attract ungulates and, in this study, were favoured by both wildebeest species, and slightly selected by zebra. Thus, the provision of large burnt surfaces in underutilised areas, in this case the East section of the reserves, could help in increasing the overall quality of grass of the area while attracting some of the ungulates. In addition, if burning is managed in a patchy way, it can also contribute in increasing the heterogeneity of the area (Fuhlendorf & Engle, 2001; Vermeire *et al.*, 2004). The decreased competition, in between wildebeest, joined by the increased number of areas offering grass of high quality, would help specialist species in sustaining themselves and growing in population size. At the same time, the health of wetlands should be strictly maintained, as this environment contributes to regulating ecosystem functions, and represents the main source of high quality forage and water for large grazers during the dry season (Fynn *et al.*, 2015).

This study deepens the knowledge of ungulate resource selection and its effect on ungulate distribution. It also confirms the importance of conducting resource selection studies at different spatial scales as the importance, and sometimes the role, of resources changes with a change in spatial scale. In addition, it highlights the relationship between sympatric black and blue wildebeest, which has been seldom studied, showing how the sympatry of these species could potentially be detrimental for black wildebeest. However, more research is needed on these topics to better understand ungulate resource selection and dynamics in fenced areas. Future studies should remove the effect of trees from NDVI comparisons of grassland quality and should consider heterogeneity as a difference in grass cover and quantity rather than quality. In addition, ungulate preferences for grass species should be investigated and nitrogen and phosphorus faecal content should be evaluated to compare the diet quality of different ungulates.

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APPENDIX

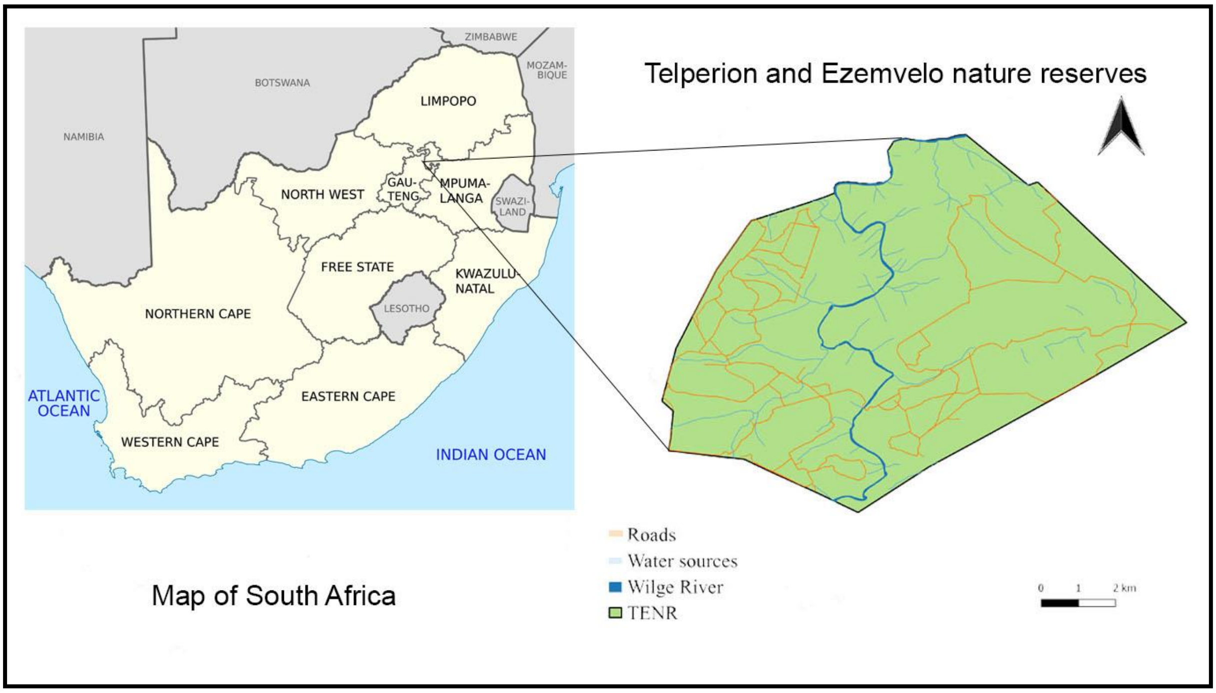

Figure 1: Telperion and Ezemvelo nature reserves, located on the border of Gauteng and Mpumalanga, South Africa.

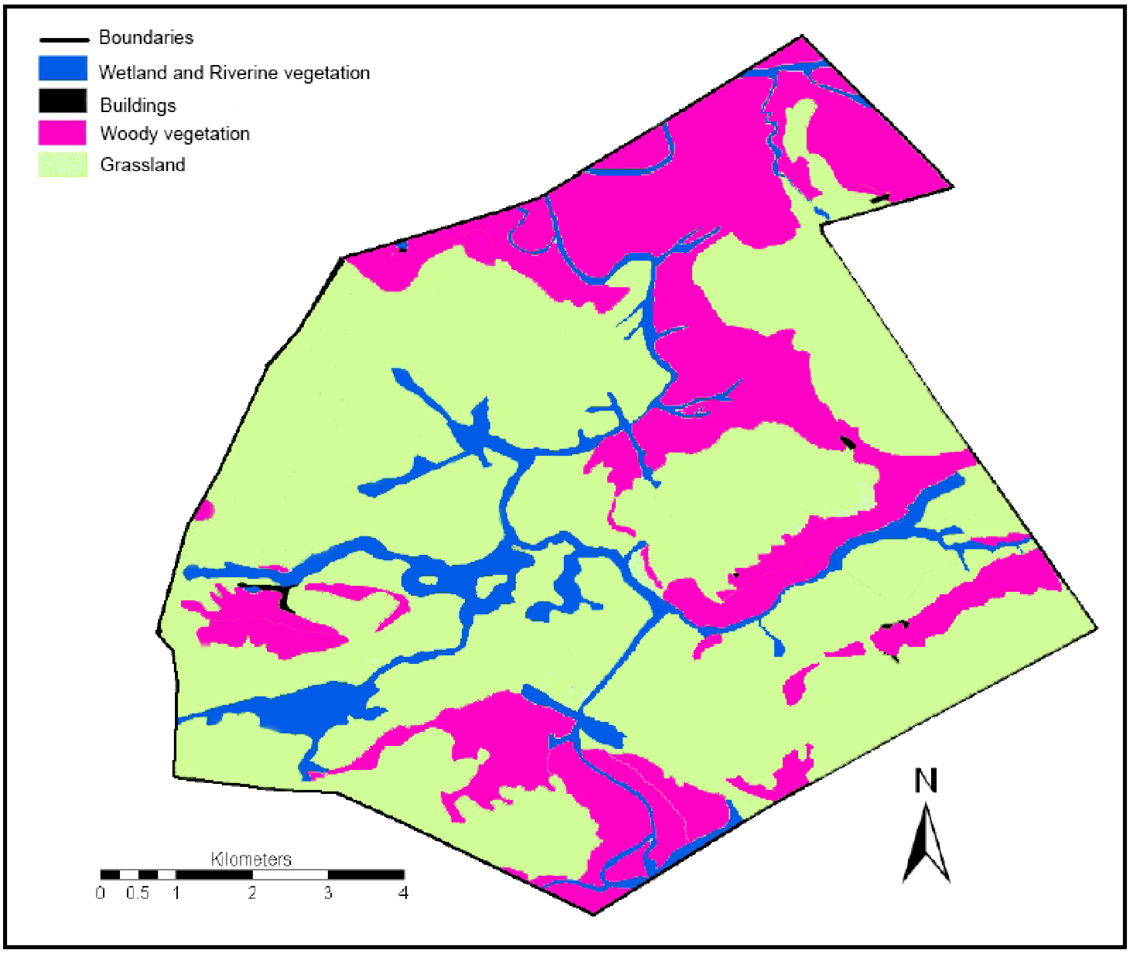

Figure 2: Vegetation types at Telperion and Ezemvelo nature reserves, South Africa. Adapted from (Swanepoel, 2006).

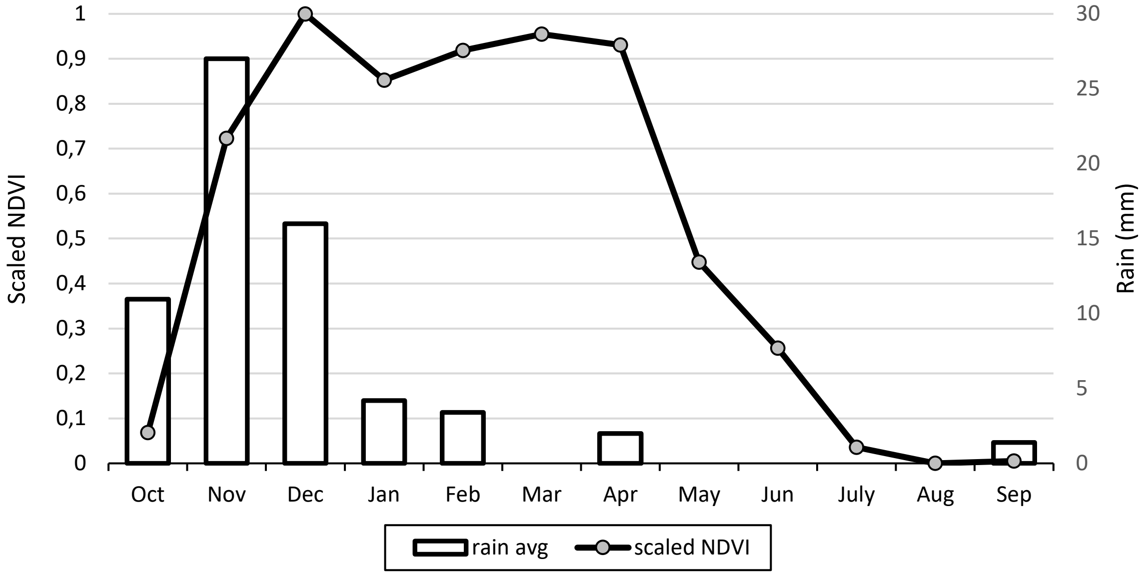

Figure 3: Rain and Normalized Difference Vegetation Index trends from September 2017 to October 2018 at Telperion and Ezemvelo nature reserves, South Africa.

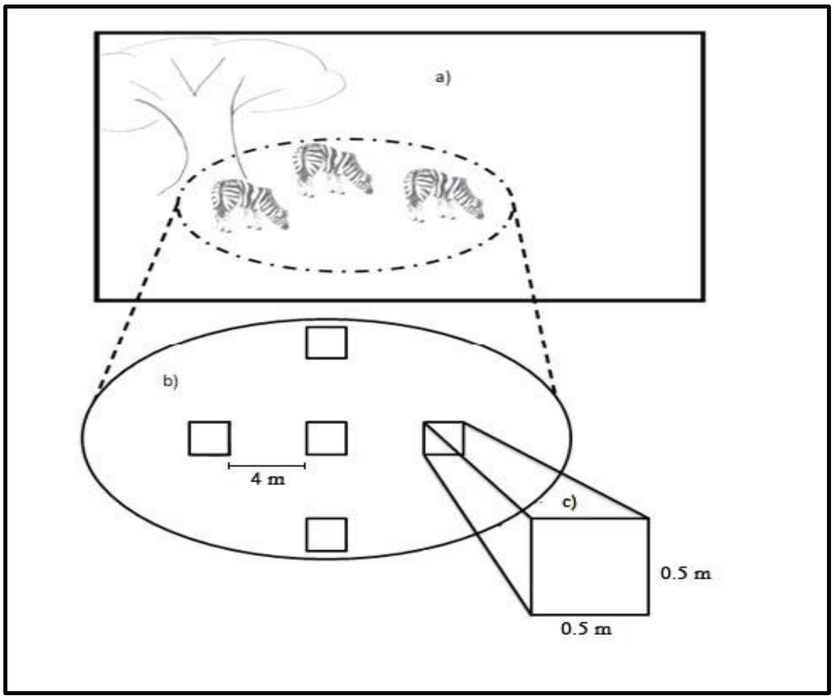

Figure 4: Quadrats disposition for feeding patch level data analysis. a) feeding area, b) feeding patch and c) feeding station. Adapted from (Boyers, 2011).

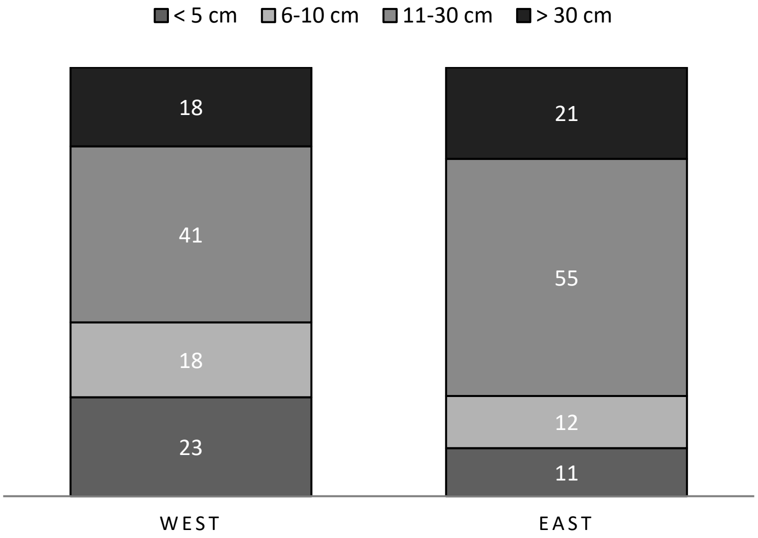

Figure 5: Percentage of availability of each class of grass height at Telperion and Ezemvelo nature reserves, South Africa, 2018, accounting for every season and every species.

Table 1: Rainfall average (mm) in 2017 and 2018 at Ezemvelo Nature Reserve, South Africa. Data collected by the weather station in situ.

Month	**AVG (mm) 2017**	**AVG (mm) 2018**
January	NA	13
February	159	20
March	0	0
April	121	2
May	50	0
June	0	0
July	0	0
August	0	0
September	4	3
October	99	47
November	54	NA
December	16	NA

Avg = average rainfall; NA = Not Available Data.

Table 2: Summary statistics (means ± SE) of the variables included in the GLMs for resource selection at landscape level by the four ungulate species at Telperion and Ezemvelo nature reserves, South Africa, 2018.

Species	**Section**		**Elevation (m)**	**NDVI**	**Het**	**Dist red h. (m)**	**Dist black w. (m)**	**Dist blue w. (m)**	**Dist zebra (m)**
Black wildebeest	West	Used	1350 ± 3	0.30 ± 0.01	0.26 ± 0.01	774 ± 36	\	519 ± 35	607 ± 35
		Random	1354 ± 1	0.32 ± 0.01	0.26 ± 0.01	959 ± 24	\	786 ± 24	801 ± 21
	East	Random	1401 ± 2	0.34 ± 0.01	0.23 ± 0.01	3517 ± 82	\	674 ± 19	582 ± 14
Blue wildebeest	West	Used	1375 ± 5	0.32 ± 0.02	0.26 ± 0.01	789 ± 49	389 ± 33	\	515 ± 39
		Random	1353 ± 1	0.29 ± 0.01	0.23 ± 0.005	986 ± 19	688 ± 16	\	801 ± 15
	East	Used	1392 ± 4	0.26 ± 0.01	0.16 ± 0.01	3517 ± 200	4990 ± 187	\	260 ± 20
		Random	1402 ± 1	0.32 ± 0.01	0.21 ± 0.004	3728 ± 64	4701 ± 55	\	570 ± 11
Red hartebeest	West	Used	1354 ± 4	0.31 ± 0.03	0.30 ± 0.03	\	555 ± 59	627 ± 83	488 ± 64
		Random	1352 ± 2	0.28 ± 0.01	0.28 ± 0.01	\	692 ± 36	809 ± 40	825 ± 34
	East	Used	1370 ± 14	0.14 ± 0.04	0.14 ± 0.03	\	4251 ± 594	503 ± 224	448 ± 194
		Random	1398 ± 3	0.31 ± 0.01	0.25 ± 0.01	\	4516 ± 125	665 ± 35	588 ± 27
Zebra	West	Used	1372 ± 6	0.31 ± 0.02	0.22 ± 0.01	636 ± 52	494 ± 50	603 ± 66	\
		Random	1354 ± 1	0.33 ± 0.01	0.20 ± 0.004	980 ± 18	691 ± 15	812 ± 16	\
	East	Used	1387 ± 4	0.33 ± 0.01	0.17 ± 0.01	4033 ± 189	4498 ± 166	349 ± 24	\
		Random	1401 ± 1	0.36 ± 0.01	0.19 ± 0.03	4014 ± 64	4615 ± 55	673 ± 14	\

Abbreviations: Het = Heterogeneity; Dist red h. = Distance from the closest red hartebeest; Dist black w. = Distance from the closest black wildebeest; Dist blue w. = Distance from the closest blue wildebeest; Dist zebra = Distance from the closest zebra