



**FORAGING BEHAVIOUR OF RUMINANT AND NON-RUMINANT GRAZERS AS A
FUNCTION OF HABITAT HETEROGENEITY IN TELPERION AND EZEMELO
NATURE RESERVES (EZEMELO SECTION)**

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A research report submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in partial fulfillment of the requirements for the degree of Master of Science in Resource Conservation Biology.

DECLARATION

I Ndamonenghenda Hamunyela hereby declare that this research paper is my own unaided work. It is being submitted for the degree of Master of Science in Resource Conservation Biology at the University of the Witwatersrand, Johannesburg. It has not been submitted or presented before for examination to any University.

A handwritten signature in black ink, appearing to read 'H. Hamunyela', written over a horizontal line.

(Signature of candidate)

__29__ day of __May__ 2017 in Namibia

ABSTRACT

An understanding of animal foraging behaviour is key to proper management strategies that ensure the survival and species persistence within nature reserves. Here the foraging behaviour of ruminant (hartebeest and wildebeest) and non-ruminant (zebra) grazers were observed and compared between two areas with distinctively different vegetation structure, the natural vegetation (NL) and previously cultivated land (PCL), in Telperion and Ezemvelo Nature Reserves (TENR). Natural vegetation was dominated by tall grass of low greenness with patches of short to very short grass, while the PCL was dominated by areas of very short to short grass (grazing lawns) with patches of medium to tall grass. Step rate (SR) and foraging time spent per feeding station (FTFS) were used as indices of foraging behaviour. I also measured the characteristics of the grass sward (grass height and greenness) grazed on by the three species. Both ruminants had high SR and low FTFS. Despite having similar SR and FTFS, ruminants grazed on grass of different height. Hartebeest preferred tall grass with low greenness content (0-10%), while wildebeest preferred short to very short grass and were significantly selective of areas with relative high greenness (11-50%) on PCL, more so than any other species. Compared to ruminant grazers the non-ruminant (zebra) had low SR and high FTFS and like hartebeest they grazed on medium to tall grass of very low greenness content (0-10%). This study did not reveal any difference in feeding behaviour within species between the two study sites. The finding of this study confirms that ruminant and non-ruminant species have different foraging behaviour, and habitat heterogeneity is necessary for the reserve to support different grazing species.

Key words: digestive physiology, feeding station, step rate, wildebeest, hartebeest, zebra

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Chapter 1

1.1 MOTIVATION FOR THE STUDY

The key to proper wildlife management is based on gaining a good understanding of the strategies underlying large herbivores' survival in their habitats. This to a great extent comprises the appropriate understanding of the feeding behaviour of different herbivore species in a heterogeneous environment. Different herbivores species select for various habitats and landscapes based on their body mass (Du Toit & Owen-Smith, 1989; Cromsigt, Prins & Olf, 2009), but habitat selection and landscape use is also influenced by the digestive physiology of the different herbivores (Cromsigt, Prins & Olf, 2009). In other words, feeding behaviour does not only differ between herbivores of different sizes, but it also differs between ruminant and non-ruminant herbivores.

Large herbivore species characterise ecosystems on the African continent, and they are of ecological (Bell, 1971; McNaughton, 1985; Owen-Smith, 1988; Cromsigt & Olf, 2006) as well as economic importance (Prins *et al.*, 2000; Gordon *et al.*, 2004; Cromsigt & Olf, 2006). African savannas support the world's largest populations of grazers. Though savannas occupy extensive area of Africa, not all of it is available for wildlife use anymore. As elsewhere in the world, wild populations of African herbivores progressively depend on restricted (often fenced) protected conservation areas (Newmark, 1996; Cromsigt, 2006), of different sizes, vegetation types and environmental conditions. Thus, movements of these populations are restricted (Lamoot, 2004). This has compromised the utilisation of ecosystems at sufficiently large spatial scales (Hobbs *et al.*, 2008; Hobbs & Gordon, 2009) more especially during times of food scarcity.

The island biogeography theory of MacArthur and Wilson (1967) suggests species diversity to be related to area size. Therefore herbivore diversity and abundance can be considered a function of the reserve size (MacArthur & Wilson, 1967; Brashares *et al.*, 2001; Hansen & DeFries, 2007). However some studies suggest that wildlife diversity and abundance within fenced reserves is primarily driven by habitat heterogeneity and it is independent of reserve size (Cromsigt, Prins & Olf, 2009).

Habitat heterogeneity varies in time and space within reserves, the spatial variation of forage resources determines the distribution of different herbivores at different times of the year. This is mostly due to the variability in forage nutritive quality, and forage availability, with the highest quality and abundance in the wet season and a decrease in quality and availability in the dry season (Bokdam & WillisDeVies, 1992; Ducan, 1992; Lamoot, 2004). The spatial and temporal variation in forage resources has differential effects on herbivores depending on the digestive structure, and thus the degree of selectivity characterised by the species. The changes in resource availability and quality across seasons influences resource harvesting at the smallest level of foraging (grass tuft level) by the foraging herbivores, more specifically in grazers.

Many studies have highlighted the importance of habitat heterogeneity based on herbivores distribution within different habitat types in the landscape (Woodward, 1997; Bergan *et al.*, 2001). This distribution is influenced by the way animals acquire food at the grass tuft level, which makes up an integral part of foraging behaviour. The amount of forage herbivores consume per day depends on the daily rate of forage intake (Woodward, 1997; Bergan *et al.*, 2001) and the rate of digestion of the ingested feed in the gut (Owen-Smith & Novellie, 1982; Mertens, 1987; Illius & Gordon, 1991; Meissner & Paulsmeier, 1995; Bergan *et al.*, 2001). In other words, forage intake is influenced by the bite rate, bite size and time spent feeding which depends on whether the herbivore possesses a

ruminant or a non-ruminant digestive physiology and this is what leads to the observed herbivore distribution at a higher level.

As Festa-Bianchet and Apollonio (2003) indicated, studies of animal behaviour can provide a critical approach to wildlife conservation through examination of individual differences, to highlight the role of variability and to identify trade-offs between different behavioural strategies. Though many aspects of foraging behaviours have been studied, there is a need for more studies looking specifically at the lowest level (plant and leaf level) of feeding behaviours of ruminant and non-ruminant grazers regarding forage partitioning in heterogeneous habitats. More especially studies on the foraging behaviour of red hartebeest, for which most behavioural studies to my understanding are dated in the 1970-1990s (i.e. Price, 1978; Janis & Ehrhardt, 1988; Murray & Brown, 1993; Estes, 1995), and those past studies lacked the aspect of actual foraging behavioural observation in natural habitats. Therefore, the aim of this study was to investigate and compare the foraging behaviour of ruminant (hartebeest, black wildebeest) and non-ruminant (zebra) grazers in two distinctly different vegetation types, the natural vegetation (NL) and the previously cultivated land, in Telperion and Ezemvelo nature reserves (TENR). This might be critical for the development of improved adaptive management strategies in the reserve. It is very important to learn and understand how herbivores with different digestive physiology and mouth morphology utilise forage resources available in their habitat for proper resource management (Gordon, 1989).

1.2 LITERATURE REVIEW

Landscape heterogeneity

Habitat heterogeneity is described as an uneven spatial and temporal distribution of resources and conditions (Mikheev, Afonina, & Pavlov, 2010). Essential resources for plants are usually distributed unevenly in environments (Caldwell & Pearcy, 1994; Hutchings, John & Stewart, 2000) both in time and space. As a consequence plants have a heterogeneous distribution across landscapes and across seasons. The unpredictability of heterogeneity in natural habitats (Xiao, Yu & Wang, 2006) makes it more likely that animals will have evolved the flexibility to cope with, and perhaps even benefit from, heterogeneous habitats more so than from homogeneous habitats. Heterogeneity is scale dependent, ranging from fine-scale to landscape scale (Pinel Alloul, 1995 & Mikheev, Afonina & Pavlov, 2010). Depending on the scale of heterogeneity, plant features and the herbivore foraging behaviour, heterogeneous habitats can either favour foraging or make it more difficult (Mikheev, Afonina & Pavlov, 2010).

Savanna ecology and hence heterogeneity is shaped by disturbances. Fire and herbivore interactions are significant natural factors affecting vegetation succession and are major determinants of tree-grass dynamics in savanna environments (Carlsson, 2005). Novellie (1975) found that continuous grazing keeps the grass short throughout the year, and this is mostly observed in disturbed areas such as burned areas.

Patterns in vegetation change at different spatial and temporal scales in savannas are also driven by other factors such as climate, change in rainfall patterns, geology and soil nutrients availability (Gillson, 2004). Pre-historic, historic and recent human activities (Scholles and Archer, 1997) such as,

abandonment of cultivated land creates patches of land with different characteristics compared to the surrounding natural areas and thus identified as contributing factors to vegetation heterogeneity in savanna ecosystems.

African ungulates have different foraging behavioural adaptations, some of which increases vegetation heterogeneity. Herbivores' effects on vegetation establishment, growth and reproductive success are well documented (see McNaughton, 1984). For example, previous studies suggest some grazing ungulates have the ability to transform grassland communities, often creating grazing lawns with different vegetation structure and composition compared to adjacent plant communities (Lamprey, 1963; McNaughton, 1984). The effect of these forms of disturbances can be explained by the intermediate disturbance hypothesis. The intermediate disturbance hypothesis states that diversity is highest at an intermediate level of disturbance and that species may last the longest at that disturbance level (Carlsson, 2005).

Habitat heterogeneity is becoming more and more important in reserve management. The recognition of the importance of the role of resource heterogeneity in reserve conservation have been cemented by the adoption of the 'heterogeneity paradigm' in conservation of biodiversity (Du Toit & Cumming, 1999; Fuhlendorf & Engle, 2001; Du Toit *et al.*, 2003; Kröger & Rogers, 2005; Cromsigt, Prins & Olf, 2009). The paradigm emphasises that resource managers need to enhance resource heterogeneity in savanna reserves to increase wildlife species richness and abundance especially in small-sized reserves (Owen-Smith, 2004; Cromsigt, Prins & Olf, 2009). Increased resource heterogeneity in small reserves might help reduce the effect of reserve size and lack of migration ability on species richness and abundance (Owen-Smith, 2004; Cromsigt, Prins & Olf, 2009). According to Lamoot (2004), the foraging animal is confronted with more foraging decisions in heterogeneous habitats than in homogeneous ones.

Large herbivores foraging behaviour

Mammalian fauna has been progressively isolated and fragmented within nature reserves of different sizes, habitat diversity, and animal species diversity (McNaughton & Georgiadis, 1986). Protected areas support a large number of large grazing species which are presumed to graze the same grasses while the mechanism of resource partitioning is often unclear (Sinclair, 1985).

Foraging herbivores interact with vegetation at different ecological hierarchies, namely: regional scale, landscape scale, patch level scale and plant level scale (Senft *et al.*, 1987). Since wild animals in South Africa are mostly found in fenced protected areas (Newmark, 1996; Cromsigt, 2006), they are not confronted with decision-making at the highest ecological level, such as seasonal migrations (Lamoot, 2004). Rather, the highest level applicable to confined herbivores is the landscape level, in which they select among the different plant communities (Lamoot, 2004) found within the reserves. Within communities food items are found in patches made up of a tree, shrub or herbaceous swards (Owen-Smith, 2002). Each patch is structurally and compositionally different from other patches, and patches vary in the nutritional quality and quantity of forage available (Georgiadis & McNaughton, 1990; Laca, Shipley & Reid, 2001). For a foraging herbivore, a patch can be defined as a collection of bites in an area within which the herbivore maintains relative constant movement and intake rate over a limited period of time (Bailey *et al.*, 1996). Large herbivores feed within these forage patches selecting within a diversity of grass tufts and by doing so, they move through areas with poor or less acceptable forage (Bailey *et al.*, 1996; Owen-Smith, 2005; Prins, 1996; Venter, Nabe-Nielsen, Prins, & Slotow, 2014).

Since a forager encounters food in patches, it spends time travelling between these patches looking for the ones with the most acceptable forage, making

decisions as to which patch types it will visit, and when it should leave the patch (Charnov, 1976). Within patches, animals select where to take a bite while avoiding certain species and showing preference for others (Guerin *et al.*, 1988; Ayantunde *et al.*, 1999). Selection of food resources is also present between plant parts (leaves, stem, seed and fruit) (Stobbs, 1973; Diarra *et al.*, 1995; Manser & Brotherton, 1995; Ayantunde *et al.*, 1999). At the smaller scale, each grass tuft is distinct with a different composition of dry and fresh leaves, providing a very heterogeneous resource (Illius & Gordon, 1987; Wright & Illius, 1995; Brooks, 2005). The type of decision will depend on the physiology of the forager (e.g. ruminant vs. non ruminant) but also on the nutritional quality, availability and distribution of grass tufts.

Early studies by Hofmann and Stewart (1972) tried to explain resource partitioning by African large herbivores on the basis of digestive physiology differences, categorising them into grazers (diet dominated by grass), browsers (diet dominated by browse) and intermediate feeders (diet composed of both resources). These digestive adaptations were primarily independent of body size (Hofmann, 1989). On the other hand, McNaughton and Georgiadis (1986) divided feeding preference of African herbivores into four broad categories namely: grazers, mixed feeders preferring grass, mixed feeders preferring browse and browsers. Other studies further explained that body size and mouth structure influence the animal's ability to select high-quality forage among different parts of the grass and grass height, to enable resource partitioning and reduce inter-specific competition (McNaughton & Georgiadis, 1986; Illius & Gordon, 1987; Murray & Brown, 1993; Drescher, 2003; St-Louis & Côté, 2012).

It is widely accepted that the two primary determinants of foraging behaviour are the forage availability and forage quality (Ruckstuhl *et al.*, 2003; Lamoot, 2004). Nutritional quality of herbage consumed is governed by its composition, firstly in terms of the proportion of cell wall fibre relative to cell content and

secondly in terms of concentrations of protein, soluble carbohydrates, mineral elements and other nutrients in the plant cell (Owen-Smith, 2002). In most cases, the time spent foraging in one plant community is proportional to the quantity and quality of forage present in that community (Bailey *et al.*, 1996). Therefore, herbivores should spend more time in areas with abundant high-quality forage (Bailey *et al.*, 1996; Groom & Harris, 2009), and also move slowly through more rewarding plant communities and fast across the less rewarding ones (Senft *et al.*, 1987).

However, in times of limited forage quality, grazers may have no choice but to choose areas with the highest forage biomass to meet the nutritional requirements, suggesting that forage quality becomes less of concern in resource-stressed areas or periods (Groom & Harris, 2009). Non-ruminants adjust faster and better to poor quality forage than the ruminant grazers in resource-stressed areas or periods owing to differences in morpho-physiological structures. Apart from forage quality and availability, forage intake rate and selection by a grazing herbivore are also influenced by morpho-physiological characteristics differences among species such as the width and shape of their incisors, muzzle width, body size (Ruckstuhl *et al.*, 2003) and the nature of their gastrointestinal track. For example, Owen-Smith (1985) observed that selective feeders such as kudu (*Tragelaphus strepsiceros* and *Tragelaphus imberbis*) and impala (*Aepyceros melampus*) have narrow muzzles, roughage feeders such as wildebeest have wider muzzles, whereas fresh grass grazers such as waterbucks have intermediate sized muzzles.

All these adaptations account for differences in the extraction of forage resources in different animal species (Shiple, 1999). The major constraint in the digestive morphology is that mammalian herbivores' digestive enzymes cannot break down fibre; therefore, they rely on symbiotic microbes in the gastrointestinal track for fibre breakdown (Hofman, 1989; Shiple, 1999). Since

microbial food digestion requires a lot of time (Hummel *et al.*, 2006; Munn *et al.*, 2008), some species have evolved specialised compartments as part of the digestive system to accumulate all the fibrous material for slow fermentation (Munn *et al.*, 2008). Herbivores are categorised according to where fermentation occurs along the gastrointestinal tract; i.e. foregut and hindgut fermenters (Hofmann, 1989; Munn *et al.*, 2008).

Generally, apart from the differences in the location of fermentation chambers in the two groups of animals, the activity that takes place in the fermentation chambers are quite similar. Both ruminants and non-ruminants share digestive micro-organisms from similar taxonomic groups (Giesecke, 1969; Jannis, 1976), and they both produce volatile fatty acids as the product of cellulose fermentation in comparable rate and proportion (Barcroft *et al.*, 1944; Janis, 1976).

Despite the similarities in the general fermentation process, ruminants and non-ruminants digestive systems possess some differences which are mostly related to the positioning of the fermentation chambers in the digestion system. The fermentation chamber in ruminants (rumen) is located just before the stomach (Shipley, 1999). In ruminants, all food materials including soluble proteins and carbohydrates enter directly into the rumen for fermentation after ingestion, and the absorption of all nutrients happens in the small intestine which is located after the rumen (Shipley, 1999). During fermentation the fibrous content of the food floats on the rumen juice, is filtered out (Van Soest, 1996 & Clauss *et al.*, 2013) and returned to the mouth (a process called regurgitation) (Munn *et al.*, 2008). In the mouth further chewing reduces the food to a certain size, small enough to pass through the reticulum-omasum opening (Langer, 1988; Van Soest, 1994; Shipley, 1999) and to increase the surface area for absorption (Janis, 1976). Due to the regurgitation process all the energy locked up in cellulosic materials is released and absorbed (Van Soest, 1996 & Clauss *et al.*, 2013). The

process of cellulolysis requires a lot of time and thus prolongs the ingesta retention time (Hofmann, 1989 & Chivers, 1989), thus, ruminants avoid plant parts that take long to digest, such as grass stalks. The higher the cellulose content the slower the fermentation and intake rate (Chivers, 1989). Hence ruminants have a limit to the amount of cellulose content they can digest (Janis, 1976). Because of the high forage retention time and the need to feed on forage with limited cellulose content, ruminants tends to be selective and spent a lot of time searching for high-quality forage with acceptable cellulose content at times of limited quality food.

The ruminants' digestive system is said to be more efficient than the non-ruminants because the digestion happens before the food enters the nutrient absorption hotspot, the small intestine (Janis, 1976). The amount of forage that a ruminant consumes per day depends on the feeding time and its forage cropping rate (Hudson, 1985; Spalinger & Hobbs, 1992). The volume of the rumen is in direct proportion to body mass (Demment, 1982; Croomsigt, 2006). Ruminants' intake rate is constrained by forage availability at low forage biomass and by forage digestibility at high forage biomass, suggested by the quantitative model of the forage maturation hypothesis (Fryxell, 1991; Bergman *et al.*, 2001). Further constraints of the ruminant digestive system include the size of the rumen and reticulum, ingesta flow rate, and rumen cellulolytic bacteria activities that influence the forage retention time (Hoffman, 1989). In addition, ruminants chew the cud (ruminates) which is argued to take up part of grazing time, (see: Hofmann, 1989; Woodward, 1997; Hodgson, Cosgrove & Woodward, 1997).

In hindgut fermenters (non-ruminants), digestion occurs in the enlarged cecum (Janis, 1976), also referred to as the enlarged part of the lower intestinal tract or hind-gut (Shipley, 1999). The cecum is located at the end of the digestive system after the small intestine; hence a considerable amount of protein and carbohydrate gets absorbed in the small intestine before food reaches the

fermentation site (cecum) (Hintz *et al.*, 1971; Janis, 1976). In non-ruminants, the energy released through cellulose fermentation is absorbed in the fermentation site (the cecum) (Janis, 1976). Because non-ruminants are unable to re-chew the ingested food, their digestive system only digests cellulose to a certain degree, less than in ruminants, and thus they have a faster passage rate of food through the gastrointestinal track (Chivers, 1989 & Munn *et al.*, 2008). Food is only retained for about 29 hours in medium sized animals (St-Louis & Côté, 2012). Low forage retention time in non-ruminants and low efficiency in cellulose digestion allows for the high forage intake rate (Munn *et al.*, 2008) and enables them to subsist on forage with very high cellulose content (Janis, 1976; Duncan, 1992; St-Louis & Côté, 2012) to compensate for low quality diets (Bell, 1971; Janis, 1976; Foose, 1982; Duncan *et al.*, 1990; Munn *et al.*, 2008).

Study species

Zebra (Equus quagga)

Burchell's zebra (*Equus burchelli*) are the most numerous of the zebra species, occurring throughout eastern and southern Africa (Groom & Harris, 2009). Zebras are hindgut fermenters (Estes, 1995), non-ruminant grazers with a diet composed of 92% grass (Sponheimer *et al.*, 2003; Codron *et al.*, 2007; Turner & Getz, 2010). They forage more intensively in the wet season, consuming more bites of grass for each step taken than in the dry seasons (Havarua, Turner, & Mfunne, 2014).

The possession of the upper and lower incisor by zebra allows them to crop grass swards down to very short height, while their digestive physiology allows them to feed on a wide range of forage of different nutritional quality (Duncan *et al.*, 1990; Menard *et al.*, 2002; St-Louis & Côté, 2012). Zebras are known to adapt to diverse habitats, feeding on both short and tall grass (Trail, 2004; Croomsigt *et al.*,

2008; Treydte *et al.*, 2011). This dietary shift may represent a survival strategy for zebra to achieve their nutrient requirements in the dry seasons by consuming vegetation of high biomass but poor quality, as opposed to vegetation of higher quality but low biomass (Arsenault & Owen-Smith 2011; Havarua, Turner, & Mfunne, 2014). However, water availability can constrain the movement and distribution of water-dependent species within semi-arid environments, so that some areas may be unavailable for foraging (Western 1975; Redfern *et al.*, 2003; Bradley, 2012). Zebra are obligate drinkers, which require drinking daily and thus they are usually found no further than 10-12 km from surface-available water, although rarely extend up to 16 km (Western, 1975; Skinner & Smithers, 1990; Kingdon, 1997; Hack, East & Rubenstein, 2002; Groom & Harris, 2009).

The spatial dynamics of most zebra populations are unknown outside the Kruger National Park and Serengeti, while within these protected areas their resource acquisition strategies, patterns of spatial dispersion and regulatory factors are poorly understood (Hack, East & Rubenstein, 2002; Grange *et al.*, 2004).

Therefore, more studies on zebra are crucial in the understanding of the dynamic and strategies of their survival under different environmental conditions and different habitat types.

Black wildebeest (Connochaetes gnou)

Wildebeest (*Connochaetes*) is a large, high-shouldered, ruminant antelope with a broad muzzle and cow-like horns (Estes, 1995). There are two wildebeest species found in South Africa, the blue wildebeest (*Connochaetes taurinus*) and black wildebeest (Codron & Brink, 2007). Both species are grazers with a diet composed of 90% grass (Sponheimer *et al.*, 2003; Codron *et al.*, 2007; Turner & Getz, 2010). They prefer short, green grass, and both are known to supplement their diets with browse (trees, shrubs, forbs) when grasses are limited (Van Zyl, 1965; Skinner & Smithers, 1990; Gagnon & Chew, 2000; Codron & Brink, 2007).

This is however contradicted by the study by Von Richter (1971) that did not observe wildebeest browsing, and only occasionally making use of tall grass. Cromsigt (2006) referred to wildebeest as a short grass specialist. The wildebeest's feeding specialisations such as the possession of wide incisor breadth (Murray & Brown 1993; Arsenault & Owen-Smith, 2011) enable it to exploit short grasslands more efficiently than other ruminants (Estes, 1995). Based on the incisor and mouth anatomy wildebeest and zebras are classified as roughage grazers (Owen-Smith 1982; Ben-Shahar & Coe, 1992).

Black wildebeest herds tend to stay in the same area for prolonged periods and this presents a problem in conserving the grass cover, therefore giving grass no time to regenerate and recover (Estes, 1995). These effects can be exacerbated by the lack of migration due to the fencing of nature reserves (Estes, 1995). However in open ecosystems, like the Serengeti ecosystem, only blue wildebeest are found which migrate on regional-scale (Maddock, 1979; Fynn, Chase & Röder, 2013). Wildebeest are water dependent grazers (Estes, 1995). They drink water once every 24 hours during the dry months (Von Richter, 1971), while during the rainy season the species is less dependent on open water as they make use of the moisture content of fresh grass (Von Richter, 1971). Black wildebeest was chosen for this study and not blue wildebeest because it is endemic to Southern Africa.

Hartebeest (Alcelaphus buselaphus)

Hartebeest is a large ruminant antelope with high shoulders, elongated forehead and oddly shaped horns (Estes, 1995). Hartebeest are classified as roughage grazers (Estes, 1995), which can subsist on pastures of relatively poor quality partly because they are equipped with a narrow muzzle which allows them to graze more selectively than most bulk feeders (Janis & Ehrhardt, 1988). The comparative study done by Murray and Brown (1993), on the feeding behaviour

of alcelaphine species found that hartebeest were selective of leaves when feeding on swards with low percentage of green grass. The study suggested that among all the alcelaphine species hartebeest perform poorest in forage intake, having low bite weight and rate (Murray & Brown, 1993), and therefore had a relatively low intake of forage (Price, 1978). The reduced intake rate in hartebeest is believed to compensate for slow passage of ingesta in their digestive system (Price, 1977). This is particularly prevalent during the dry season when the intake rate drops by approximately 80 percent (Price, 1978).

In East Africa hartebeest is associated with areas of medium or tall, coarse grass swards (Kingdon, 1982; Murray & Brown, 1993). Hartebeest is also known to migrate between short, well-drained pastures during the rainy season and tall grass dominated grassland in the dry season (Estes, 1995). Their preference for tall grass suggests hartebeest would compete with other tall grass grazers. For example hartebeest and other tall grass specialists such as topi are known to compete with cattle for pasture (Ogutu *et al.*, 2014). Earlier studies suggest red hartebeest moves slower and spent more time in feeding patches compared to zebra (Venter *et al.*, 2014). This observation is most likely due to hartebeest being more selective than the zebra, owing to their ruminant digestive system. This ruminant drinks on average 3.2 litres of water daily (Price, 1978).

Report structure

This research report consists of two chapters. Chapter one of this report serves as a general introduction of the research, and it consists of the motivation for the study and the literature review. Chapter two is written in the format of an article, consisting of a title, an introduction, study objectives, hypothesis relevant to all the objectives, methods and material, study area, study design, statistical analysis, results, discussion, and conclusions. The list of references for chapter one and two are combined and given at the end of the report.

Chapter 2

Foraging behaviour of ruminant and non-ruminant grazers as a function of habitat heterogeneity in telperion and ezemvelo nature reserves (ezemelo section)

2.1 INTRODUCTION

Herbivores mostly feed in groups of different species. But species cannot co-exist if they utilise exactly the same resources (Schoener, 1974). Therefore different grazing species have evolved feeding strategies and mechanisms for resource partitioning to enable co-existence. These strategies include species selecting for the different parts of the plant, selecting for plants from different taxa, selecting for plants at different growth stages and occupying different sub-habitats (Lamprey, 1963; Vesey- Fitzgerald, 1960; Mackie, 1970; Janis, 1976). The mechanisms of resource partitioning are more pronounced and distinguishable during the resource stressed season “the dry season” (Janis, 1976; Voeten & Prins, 1999). During this time grazing animals may apply different strategies, not necessarily mutually exclusive: they might increase their forage intake, increase the range of acceptable forage, and migrate to find areas with better forage or prolong their daily feeding time (Beekman & Prins, 1989).

All these strategies of resource partitioning are governed by morpho-physiological differences among species (Voeten & Prins, 1999), and by food resource diversity and availability. This in turn has a bearing on ungulate diversity, with habitat heterogeneity and therefore resource diversity positively influencing species diversity (Owen-Smith, 2004).

Here the feeding behaviour of three grazing species; zebra, hartebeest and black wildebeest were studied and compared to determine the differences and the similarities in the feeding behaviour in terms of the time spent per feeding

station, step rate and the characteristics of the grass sward they feed on (grass height and greenness).

Objectives of the study

Objective 1: To compare step rate of ruminants and non-ruminant grazers within and between the previously cultivated land and natural land in Telperion and Ezemvelo nature reserve.

Objective 2: To compare the time spent at each feeding station by the ruminants and the non-ruminants within and between the previously cultivated land and natural land in Telperion and Ezemvelo nature reserve.

Objective 3: To determine the height and the proportion of greenness of grasses in the area grazed by ruminants and non-ruminants on the previously cultivated land and on the natural land.

Objective 4: To compare greenness and grass height selectivity by the ruminants and non-ruminants grazing species.

Hypotheses

Hypotheses to objective 1:

- (i) Ruminants would have similar step rate and they would have a low step rate on the previously cultivated land, and high step rate on the natural land.
- (ii) Non-ruminant would have low step rate on both study sites. Therefore, the step rate will not differ across the two sites.
- (iii) Non-ruminants would have lower step rate than ruminants on natural land while having similar step rate on previously cultivated land.

Hypotheses to objective 2:

- (i) Ruminants would have similar feeding time per feeding station and they would spend more time per feeding station on the previously cultivated land than on natural land.
- (ii) Ruminants would spend longer/shorter time per feeding station in the natural land, shorter if the animal decides to move on immediately when it realises that there is less acceptable food in the feeding station and longer if the animal decides to stay and search for food.
- (iii) Non-ruminants would spend more time per feeding station than ruminants on both the previously cultivated land and the natural land. Therefore, time spent per feeding station by the non-ruminant would not differ across the two sites.
- (iv) Non-ruminants would spend more time per feeding station than ruminants on natural land but not on the previously cultivated land.

Hypotheses to objective 3:

- (i) Hartebeest would feed on the short greenest grass on the previously cultivated land, while selectively feeding on the tall and short greenest grass on the natural land.
- (ii) Wildebeest would feed on the short greenest grass on the previously cultivated land, and they will feed off patches of short green grass in the natural land.
- (iii) Zebra would feed on the short green grass on the previously cultivated land while grazing non-selectively on the tall dry grass on the natural land.

Hypotheses to objective 4:

- (i) Hartebeest would select for tall grass with high greenness.
- (ii) Wildebeest will select short grass with high greenness.
- (iii) Zebra would select for tall grass with low greenness.

2.2 METHODS AND MATERIALS

2.2.1 Study area

The study was conducted in Telperion and Ezemvelo nature reserves (TENR), which is situated on the edge of the central inland plateau of northern South Africa, Gauteng Province (Mac Fadyen & Reilly, 2013). This area was classified by Acocks (1975), as a Rocky Highveld Grassland, a intermediate zone between the grassland and savanna biomes (Mac Fadyen & Reilly, 2013). A tributary of the Olifants River, the Wilge River (Swanepoel, 2006) cuts through the reserve and divides it into two sections; the Telperion section and the Ezemvelo section (Fig. 2.1). This study focused on the Ezemvelo section of the nature reserve, which is approximately 8468 ha in size (Helm, 2007).

The reserve is situated between the latitudes of 25°38'24" S and 25°44'24" S and the longitude of 28°55'48" E and 29°02'24" E (Swanepoel, 2006). The climate of the area is characterised by summer rainfall. The rainy season occur over the months of October to March (Swanepoel, 2006 & Helm, 2007), and the driest conditions are experienced during winter, from June to August (Swanepoel, 2006). The reserve receives a mean annual rainfall of 650 mm (Helm, 2007). January and February have the highest recorded temperature, with daily maximum temperatures of 26°C and daily minimum temperatures of 14 - 15°C (Swanepoel, 2006). July is characterised by the lowest recorded temperature with the maximum of 18°C and the minimum of 4°C (Swanepoel, 2006).

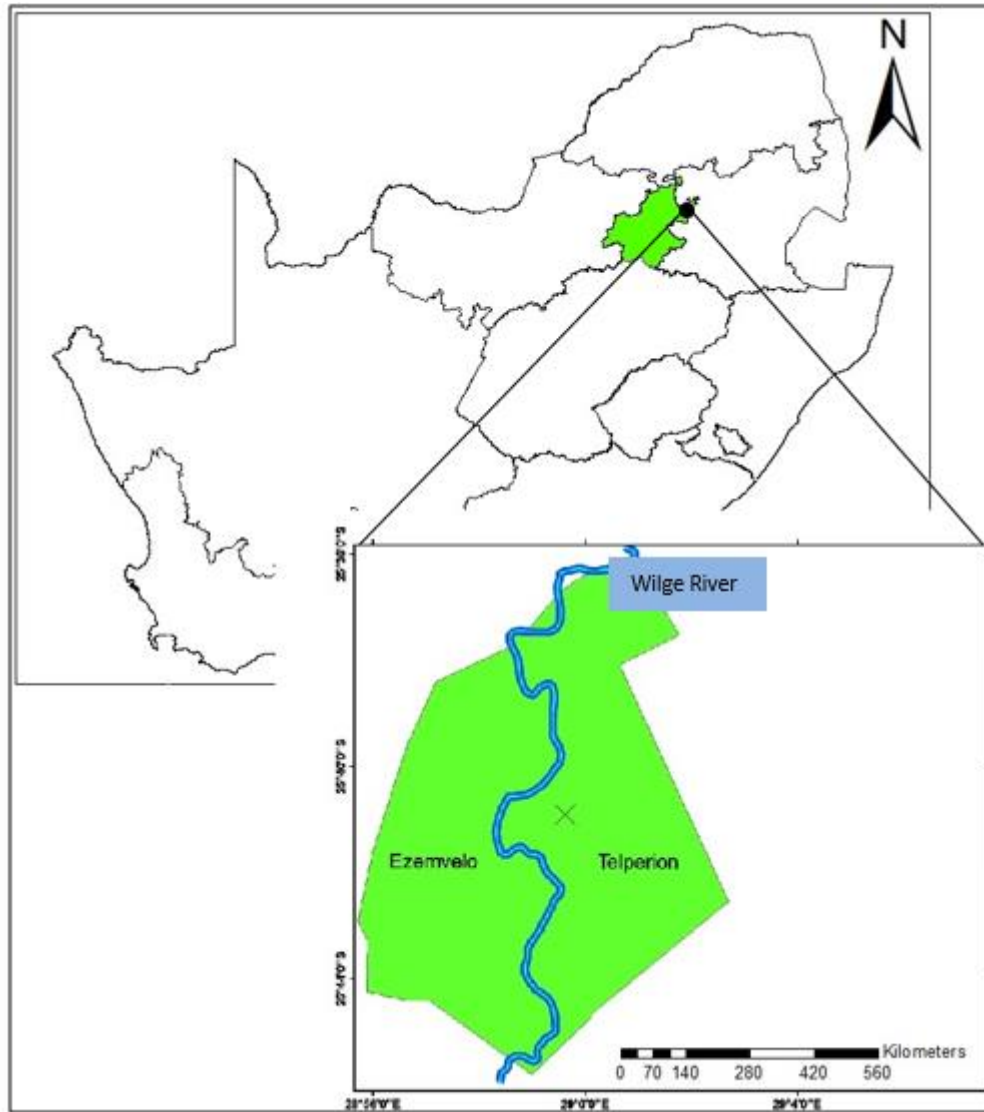


Figure 2.1: The location of the Telperion and Ezemvelo nature reserve (TENR) within Gauteng Province in South Africa.

A study by Swanepoel and Bredenkamp (2007) identified twenty-two major plant communities and four sub-communities, in Ezemvelo. Plant communities are distributed in a mosaic of woodlands, grasslands and wetlands based on the heterogeneous habitats created by the variations in topography, which is typical of Bankenveld vegetation (Swanepoel & Bredenkamp, 2007). Vegetation in the study area could be broadly separated into two distinct categories, those of natural vegetation (NL) only disturbed by fire and herbivory and the previously

cultivated land (old fields, PCL). The previously cultivated fields were formerly used for cultivation of crops, vegetables, groundnuts and fruit trees. These two areas are distinguishable by their apparent differences in the grass communities (Fig. 2.2).



Figure 2.2: Vegetation of the two study sites in Telperion and Ezemvelo nature reserve (TENR); natural land (NL) and previously cultivated land (PCL).

The NL of the Ezemvelo section is characterised by tall grass, on hilly and flat topography, the most dominating grass species include: *Themeda triandra*, *Elionurus muticas*, *Eragrostis gummiflua* and *Eragrostis curvula* (Swanepoel, 2006). Despite the prevalence of tall grasses, NL has a few flat areas of short grass, which hosts a large concentration of black wildebeest and blesbuck. PCL is characterised by almost flat areas dominated by grass grazed to very short height (*Cynodon dactylon*, *Eragrostis curvula*, *Pennisetum sphacelatum* and *Cymbopogon nardus*) typical of disturbed moist grassland (Swanepoel, 2006). Within the matrix of short grass there are patches of tall grass, dominated by *Hyparrhenia hirta* and other grass species such as *Eragrostis chrolomelas*, *Hyparrhenia filipendula*, *Imperata cylindrica*, *Andropogon chinensis* and *Cymbopogon excavatus*, most of which are pioneer species (Swanepoel, 2006). The Wilge River lies along the eastern part of the PCL and there is a belt of thick woody vegetation along the river.

Telperion and Ezemvelo nature reserves hosts a diversity of large mammal species, which include zebra, black and blue wildebeest, red hartebeest, blesbuck (*Damaliscus pygargus phillipsi*), kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), waterbuck (*Kobus ellipsiprymnus*), giraffe (*Giraffa camelopardalis*), amongst the large mammals with no large predator species.

2.2.2 Data collection

This study was carried out during the dry season of 2016 in the months of July, September and October. The observations were done during the morning and afternoon as these are the main feeding periods for large herbivores (Arsenault & Owen-Smith, 2008).

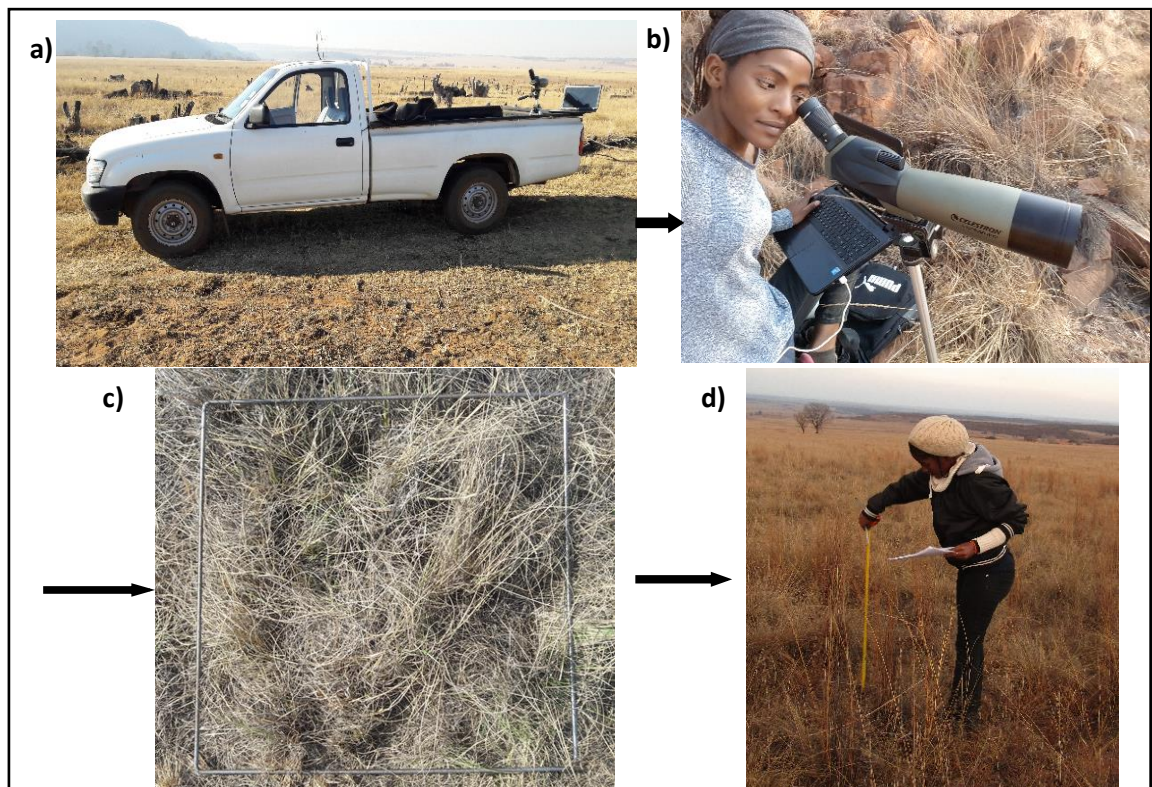


Figure 2.3: Data collection process, a) Animal herd location with a vehicle, b) Observation of step rate and feeding time per feeding station with a spotting scope, c) Random placing of quadrat at feeding areas, d) Collection of height and greenness data.

Animal foraging observations

Herds of grazing animals or individuals were located from a vehicle. Once the herd or individual had been located, one focal foraging adult in clear sight was selected for observation, from a safe distance to avoid disturbance. Observations were made with the aid of a pair of binoculars and a spotting scope and each focal observation lasted 3-8 minutes (Fig. 2.3 a, b). The same focal individual was not observed twice during the same sampling session (morning and afternoon). Focal observations were repeated with different individuals from all the three study species (zebra, hartebeest and black wildebeest) and on both vegetation types (NL and PCL) during the morning (sunrise – 9h00 am), and afternoon periods (16h00 - sunset).

During each focal observation session I recorded the number of steps taken (only steps taken with the head below the spine were counted, the steps taken with the head up were excluded, as I was interested in foraging steps), the time spent feeding in between steps and the time spent by the animal in non-foraging activities. The entire data recording was done with the Behavioural Observation Research Interactive Software (BORIS) (Friard & Gamba, 2016) at the time of observation with a laptop computer. BORIS is a freely available software designed for behavioural observations, and it has a function to record both point and state events. In this study, this software was used to record the number of steps (point events) taken over a certain time period and the duration of non-foraging bouts within the focal observation period (state event) (Fig. 2.4). From these observations I calculated two indices of feeding behaviour: step rate and feeding time per feeding station.

Step rate (SR) is the total number of steps taken per minute and it is used as an indication of the spatial distribution of acceptable forage items. This is based on the idea that the animal will take more steps per minute if the food items are

widely distributed (Novellie, 1975). In this study, a step was defined as a forward movement of either of the front legs (Ruckstuhl, Festa-Bianchet & Jorgenson, 2003).

Feeding time per feeding station (FTFS) is defined as the time spent taking sequence of bites between non-consecutive steps (Parrini & Owen-Smith, 2010). Feeding time per feeding station is also a measure of feeding efficiency (Parrini & Owen-Smith, 2010) and it is used as an estimate of quantitative food intake (Owen-Smith & Novellie, 1982). For this study, a feeding station is described as an area in which a grazing animal grazes without taking a step forward (as defined by Novellie, 1975), in other words, is the area between two non-consecutive steps (Fig. 2.4).

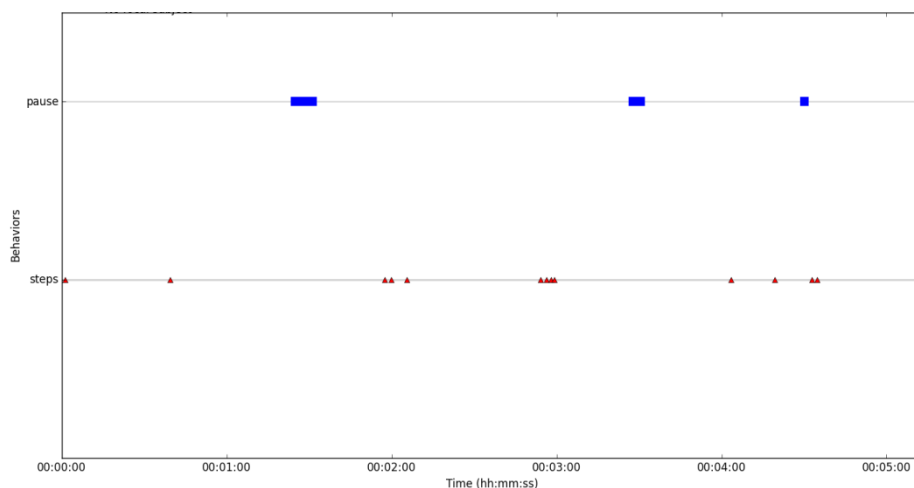


Figure 2.4: Sample graph generated with BORIS, showing the pattern of steps (triangles) taken over one observation period, time between non-consecutive steps (FTFS) (open spaces between the triangles), and time spent on non-feeding behaviours (pause- thick lines above the steps). This graph was generated for one of the observations on an individual zebra.

A total of 465 observations were made, 91 on hartebeest, 241 on black wildebeest, 133 on zebra. The number of observations varied between species due to the chances of encounter of species. Since there is no boundary between

the Telperion and the Ezemvelo sections of the reserve, animals move freely between the two sections. Zebra and hartebeest often migrate to Telperion, restricting opportunities of observing these two species. This resulted in the overall low number of observations for the two species and in particular for hartebeest that occur in relatively low numbers on the entire reserve.

Bite rate observations were originally planned as bite rate is used as a measure of feeding selectivity at the feeding station level (e.g. 30 seconds in a feeding station taking 10 bites is not the same as 30 seconds at the feeding station taking 30 bites) but it was not feasible because of the tall grass and windy conditions which made bite counting difficult and not reliable.

Vegetation sampling

Sward height and greenness were used to describe the grass available and selected by the different herbivore species. Grass height and greenness is also used to understand the resource partitioning by associations of grazing herbivores (Bodenstein, Meissner, & Van Hoven, 2000). Sward height and litter depth, representing the balance of vegetation growth and herbivory, are commonly used indicators of herbivore impact on grass-dominated communities (MacDonald *et al.*, 1998; Moore *et al.*, 2015).

After feeding observations, the foraging area was located on foot and confirmed by the presence of fresh foot tracks, fresh bites and presence of fresh faeces. A quadrat measuring 0.5 m² was placed randomly on the feeding area to represent a feeding station. The first quadrat was supplemented by two further quadrats in each cardinal direction spaced 2 m apart to make a total of nine feeding stations at each feeding area (Fig. 2.5), following the procedures by Owen-Smith, Le Roux and Macandza (2013). The height of grass within the quadrats was measured

with a measuring tape, extrapolated for the whole plot and recorded in the following grass height categories:

< 5cm -very short

6-10 cm -short

11-30 cm -medium

>30 cm -tall

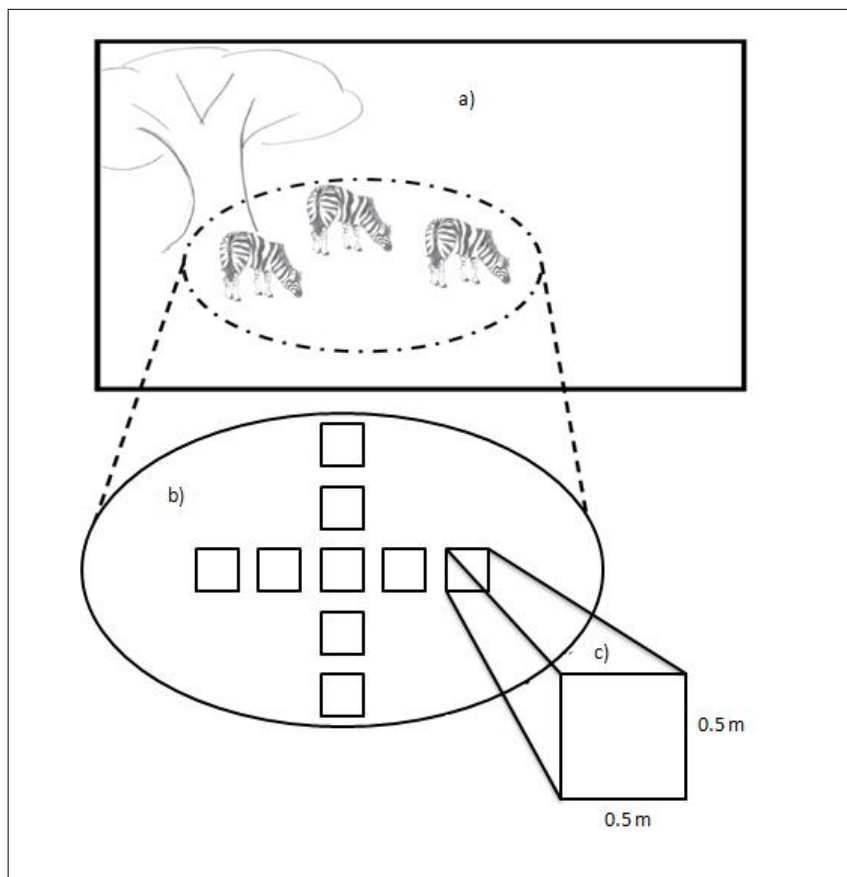


Figure 2.5: Vegetation inventory process, a) feeding area, b) feeding patch and c) feeding station, modified from Boyers (2011).

Within the quadrats, the proportion of green grass leaves compared to the dry brown leaves was visually estimated using Walker's (1976) eight-point scale: 0, 1-

10, 11-25, 26-50, 51-75, 76-90, 91-99 or 100% green. This procedure was repeated in the foraging areas of all observed herds of interest.

The inventory of the general vegetation characteristics (grass height and greenness) were done by walking transects measuring 1675 m (two per site). Vegetation sampling was done along each transect by placing a 0.5 m² quadrat at 20 m intervals. The height and greenness of the grass within the quadrats was measured and estimated as described above.

2.2.3 Statistical analysis

Each observation session (morning or afternoon) on the same herd, was considered as one sample and data from the observations pooled to provide a sample estimate. SR was calculated by dividing the total number of steps taken by the total feeding period (the total observation time – non-foraging time). FTFS was derived from BORIS as the time between non-consecutive foraging steps (Fig. 2.4) and the mean time spent feeding in each feeding station was then calculated as the total time spent feeding divided by the total number of feeding stations.

A Shapiro Wilk's test was used to test for normality. Step rate and FTFS data were log transformed to follow a normal distribution as required for parametric test. For SR and FTFS comparisons among the three animal species (zebra, hartebeest and wildebeest) on NL, one-way ANOVA was used, followed by the Tukey Post Hoc test when the one-way ANOVA test found a significant difference among the three species. A t-test was used to compare SR and FTFS between wildebeest and zebra on PCL. A t-test was also used to compare SR and FTFS for each species between the two vegetation types on the Ezemvelo section. Step rate and FTFS log transformed means and confidence intervals (CI) were then back transformed for result reporting.

Grass height and greenness use was compared among the three species with a Pearson Chi-square test. I also calculated grass height and greenness selection by the three species using Manly standardised resource selection Index following Desbiez & Bodmer (2009). The index is based on the W_i relationship which is given by the proportional resource use divided by the proportional resource available: $W_i = O_i/\pi_i$.

Where:

O_i = Proportion of the sample of used resource units in category i .

π_i = Proportion of available resource units in category i .

A W_i value >1 indicate positive resource selection, W_i value <1 indicates resource avoidance, and a W_i value around 1 indicate resource use in proportion to resource availability.

All statistical analysis were performed using STATISTICA software (StatSoft, 2001).

2.3 RESULTS

Although the study aimed to observe and compare the feeding behaviour of the three grazing species on both natural land (NL) and previously cultivated land (PCL), one species (hartebeest) was not observed grazing on the PCL during the time of the study, resulting in the comparison between two species (zebra and hartebeest) only on the PCL.

Indices of foraging behaviour

I collected a total of 110 samples which were pooled from 465 individual observations for SR and FTFS. Of these 73 were collected from natural vegetation

(27 zebra, 21 hartebeest and 25 wildebeest), and 37 from previously cultivated land (8 zebra and 29 wildebeest).

Step rate varied between ruminants and non-ruminant species (Fig. 2.6). On NL the ruminant species had similar SR, 9.7 steps/min (95% CI: 8.3-11.2) and 10 steps/min (95% CI: 8.7-11.5) for hartebeest and wildebeest respectively ($p=0.936$). Zebra had a mean SR of 4.8 steps/min (95% CI: 4.2-5.4) which is relatively lower than both ruminants mean step rate ($p=0.0001$). A similar pattern of SR was found for the PCL, whereby the mean SR for the ruminants (wildebeest) was 2.7 steps/min (95% CI: 1.7-4.0) higher than non-ruminants (zebra) mean step rate ($t\text{-value}= 4.602$, $df=35$, $p=0.0001$).

No statistical difference was detected in the mean SR of wildebeest and zebra between NL and PCL (zebra: $t\text{-value}=1.250$, $df=33$, $p=0.219$; wildebeest: $t\text{-value}=0.521$, $df=52$, $p=0.604$). Mean SR of zebra varied only by 1.3 steps/min (95% CI: 0.8-2) between NL and PCL. While wildebeest mean SR varied only by 1 steps/min (95% CI: 0.9-1.3).

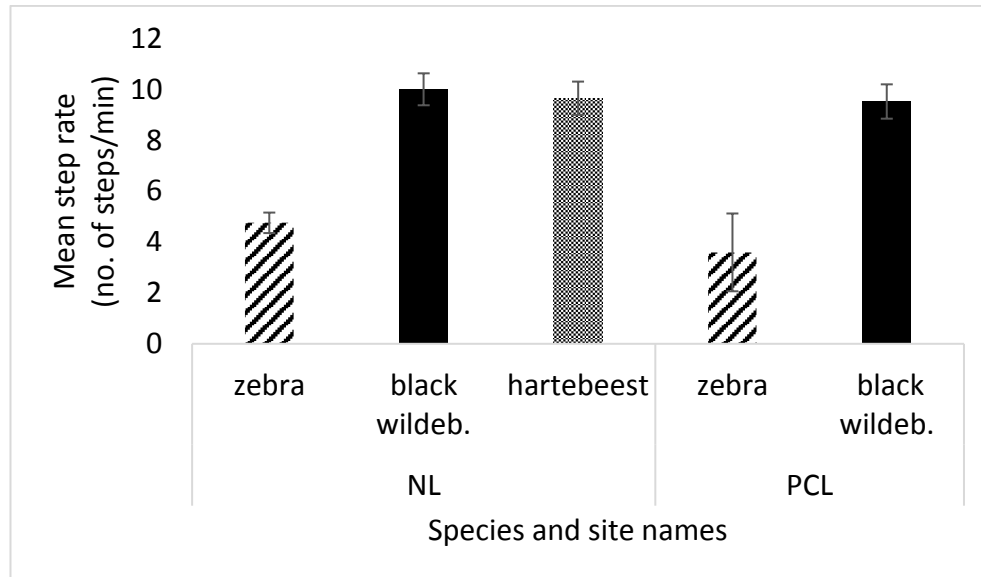


Figure 2.6: Comparison of mean step rate (SR) (the number of steps divided by feeding time (min)) (mean \pm S.E.) for zebra, black wildebeest and hartebeest on the two study sites (natural land (NL) and previously cultivated land (PCL)) in Telperion and Ezemvelo nature reserve (TENR).

Similarly ruminant and non-ruminant grazers FTFS varied on both vegetation types (Fig. 2.7). Ruminants had similar FTFS on NL ($p=0.440$) that was 7.0 sec (95% CI: 6.0-8.1) and 6.2 sec (95% CI: 5.3-7.1) for hartebeest and wildebeest respectively. Both ruminant species spent relatively less time per feeding station compared to non-ruminant zebra that had a mean FTFS of 13.4 sec (95% CI: 11.7-15.3) ($p=0.0001$). On PCL ruminant (wildebeest) had also a relatively lower mean FTFS than the non-ruminant, with a mean difference of 1.9 sec (95% CI: 1.4-2.6) ($t\text{-value}=-4.162$, $df=35$, $p=0.0002$).

The mean FTFS for both zebra and wildebeest was not found to differ between the two vegetation types (zebra: $t\text{-value}=0.028$, $df=33$, $p=0.977$; wildebeest: $t\text{-value}=-1.266$, $df=52$, $p=0.210$). Zebras' mean FTFS on NL was only 1.0 sec (95% CI: 0.7-1.5) higher than on PCL, while wildebeest mean FTFS on NL was only 1.1 sec (95% CI: 0.9-1.3) lower than on PCL.

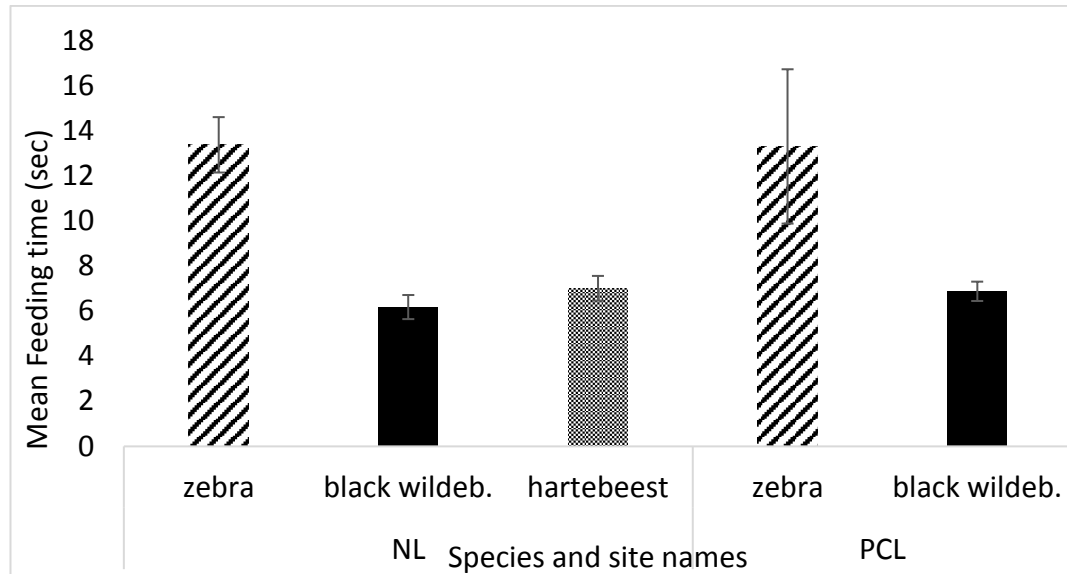


Figure 2.7: Comparison of mean feeding time per feeding station (FTFS)(feeding time (seconds) spent per feeding station) (mean+/- S.E) for zebra, black wildebeest and hartebeest on the natural land (NL) and previously cultivated land (PCL) in Telperion and Ezemvelo nature reserve (TENR).

Vegetation characteristic/selection

The two sites were characterised by a distinct difference in the available vegetation. The NL was dominated by tall (>30 cm) to medium (11-30 cm) grass height, while the PCL was dominated by short (6-10 cm) to very short (<5 cm) grass (Fig. 2.8 a). Both vegetation types were characterised by grasses of low greenness content with the highest observed greenness being 26-50%, present only in very low proportion (<10%) on NL (Fig. 2.8 b).

A total of 129 grass height and greenness samples were collected from the foraging areas, of these 78 came from NL (29 for zebra, 21 for hartebeest and 28 for wildebeest) and 51 from PCL (9 zebra and 42 wildebeest).

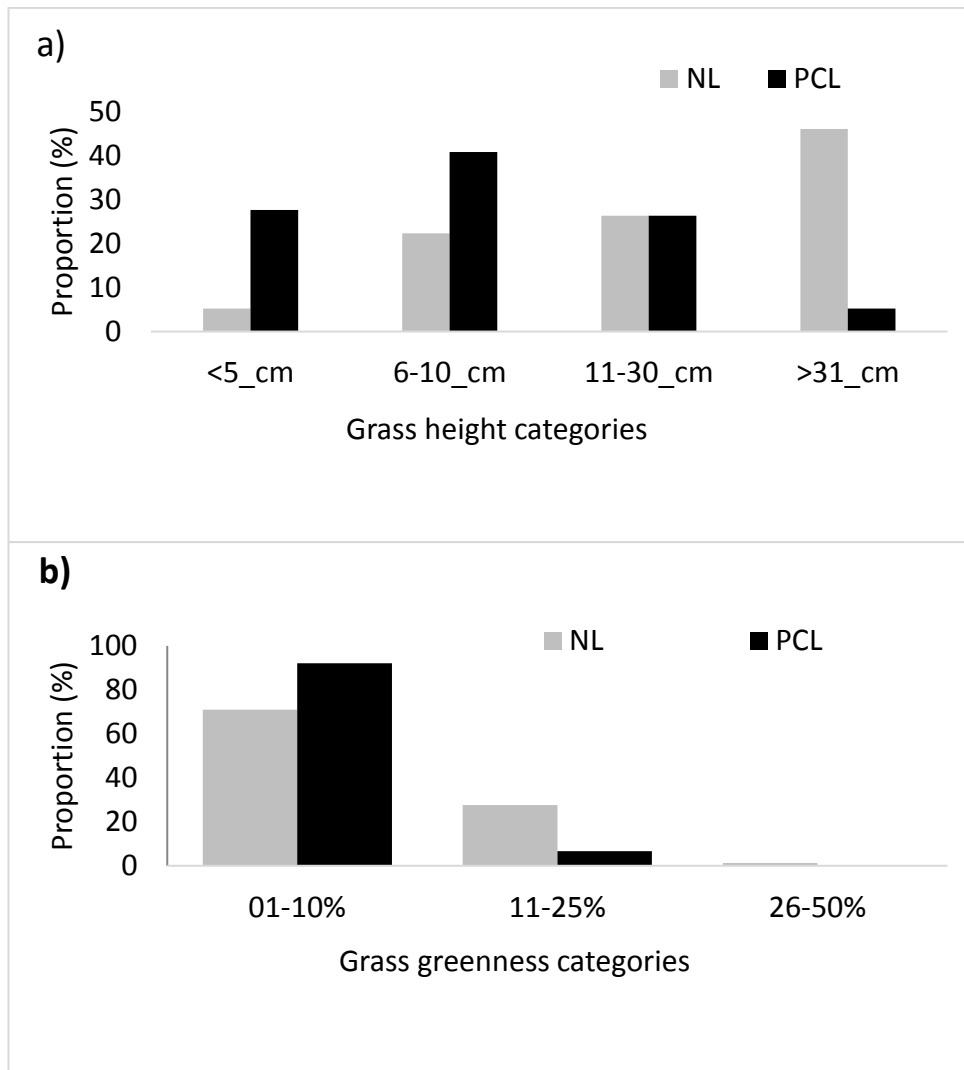


Figure 2.8: Available grass height and greenness, on natural land (NL) and previously cultivated land (PCL), a) Proportion of available grass height (cm), b) Proportion of available grass greenness (%).

The three grazing species utilised grass of different height on both vegetation types (NL: Chi-square=50.23, df=6, $p < 0.0001$; PCL: Chi-square=38, 5, df=3, $p < 0.0001$) (Fig. 2.9). Hartebeest and zebra utilised grass of similar height (Chi-square=4.98, df=2, $p = 0.82$) which is different from grass utilised by wildebeest (zebra and black wildebeest: Chi-square=29.56, df=3, $p < 0.0001$; hartebeest and black wildebeest: Chi-square=40.7, df=3, $p < 0.0001$). The highest proportion of hartebeest and zebra utilised medium height grass (hartebeest 80.9%, zebra 62%), and lower proportion utilised grass from other grass height classes but

none of the zebra or hartebeest grazed on very short (0-5 cm) grass (Fig. 2.9a). On the contrary wildebeest highest proportion grazed on short (53.5%) to very short grass (35.7%) and none of the wildebeest was found grazing on tall (>30 cm) grass (Fig. 2.9a). Similar patterns were found for zebra and wildebeest on the PCL (Fig. 2.9b). The highest proportion (77.8%) of zebra on PCL grazed on medium height grass and no zebra was found grazing on very short grass, while 62% of wildebeest grazed on very short grass and the proportional usage decreased with the increase in grass height (Fig. 2.9b).

The height of grass used by both zebra and wildebeest remained similar between NL and PCL (zebra: Chi-square=0.76, df= 2, p=0.68; black wildebeest: Chi-square=5.53, df=2, p=0.06).

The three species were found utilising grass of similar greenness content on NL as well as on PCL (Fig. 2.10). All species highest proportion (93 % zebra, 85% hartebeest and 84 % wildebeest) grazed on grass of very low greenness content of 1-10% on NL (Chi-square=4.1, df=6, p=0.65) (Fig. 2.10 a). Similarly on PCL, wildebeest and zebras' highest proportion grazed on grass with the greenness content of 0-10% (Chi-square=2.60, df = 2, p=0.27) (Fig. 2.10 b). Grass greenness of 1-10% was used in proportion to its availability by all species on NL and PCL except for wildebeest which avoided the 1-10% greenness and selected for 11-25% and 26-50% on PCL (Table 2.4). Wildebeest showed a level of positive selection for greener grass than the other species on PCL (Table 2.4).

Proportion grass greenness usage by both zebra and wildebeest was not found to differ between the two vegetation types, their highest proportion grazed on grass of 1-10% greenness on both NL and PCL (zebra: chi-square=0.58, df=1, p=0.44; black wildebeest: Chi-square=1.17, df=2, p=0.55) (Fig. 2.10).

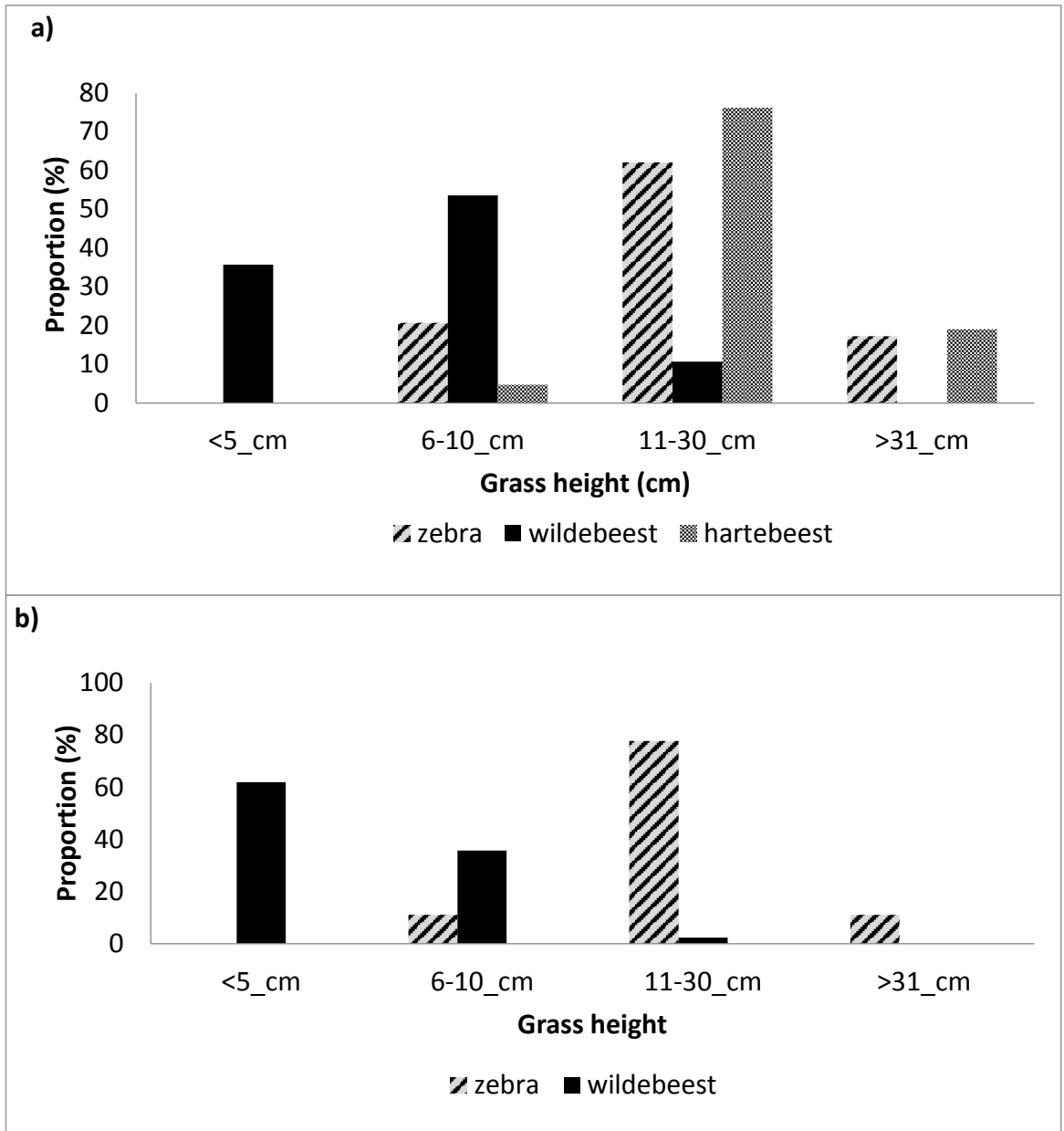


Figure 2.9: Comparison of the proportion of animals found feeding on the grass of different heights (cm) on (a) natural land (NL) and (b) previously cultivated land (PCL).

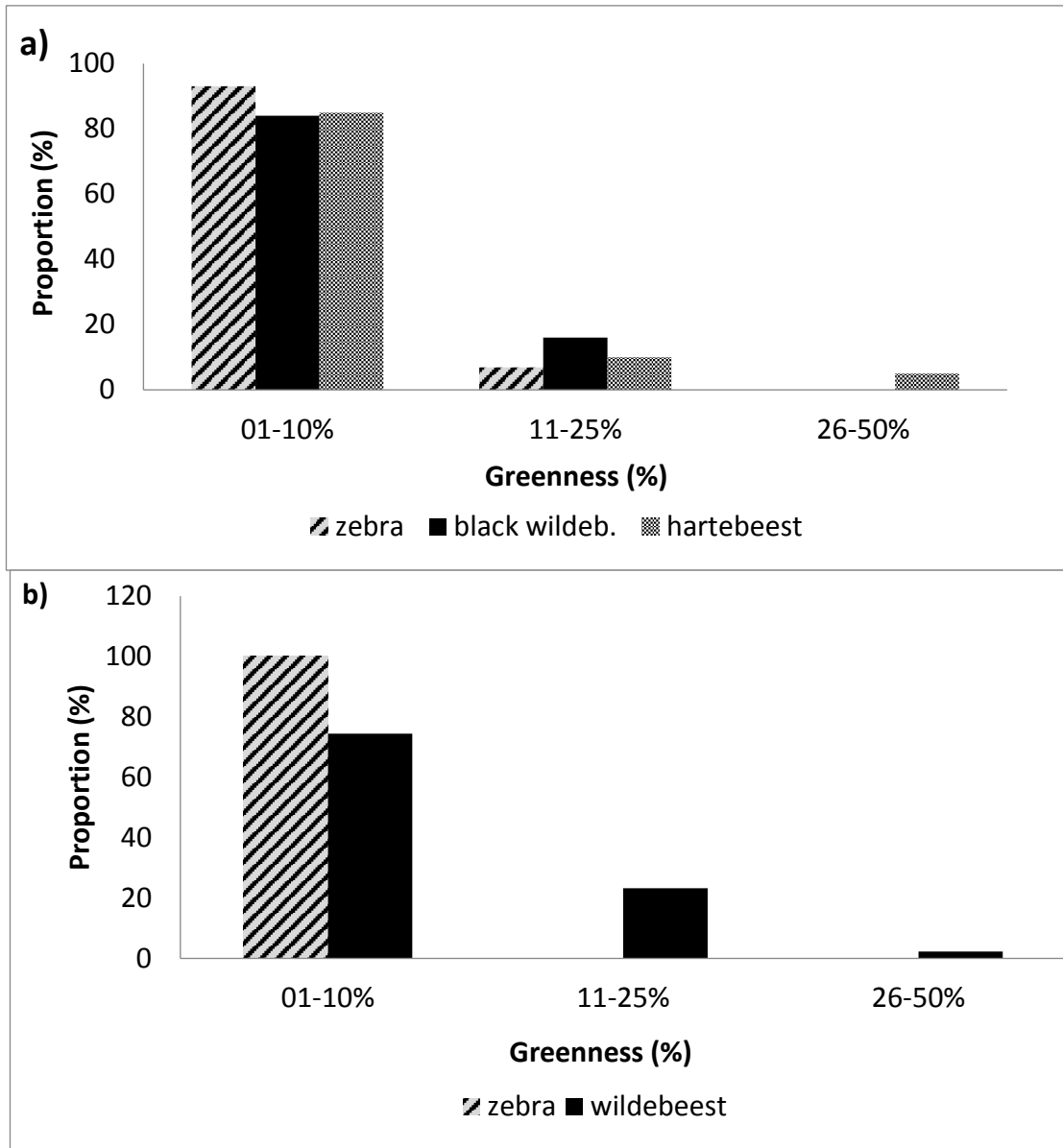


Figure 2.10: Comparison of proportion of animals of the different species (zebra, hartebeest and black wildebeest) found feeding on the grass of different greenness (%) on, (a) natural land (NL) and (b) previously cultivated land (PCL) in Telperion and Ezemvelo nature reserve (TENR).

Table 2.1: Height and greenness selection of the three grazing species within and across the two vegetation types (natural land (NL) and previously cultivated land (PCL)). The height or greenness category was considered selected for when: $W_i > 1$. Selected categories are marked with "+", avoided categories ($W_i < 1$) marked "-", and use in proportion to availability (W_i around 1) marked "=".

	NL			PCL	
Height categories	zebra	wildebeest	hartebeest	zebra	Wildebeest
<5_cm	-	+	-	-	+
6-10_cm	=	+	-	-	-
11-30_cm	+	-	+	+	-
>30_cm	-	-	-	+	=
Greenness categories					
01-10%	=	=	=	=	-
11-25%	-	-	-	-	+
26-50%	-	-	+	-	+

2.4 DISCUSSION

Ruminants and non-ruminants showed different feeding behaviour. Step rate, FTFS, selected grass height and greenness differed between the species within each site, but no difference in behaviour was observed for the same species between the two sites despite the different grass characteristics at each site. Although the two ruminant species (wildebeest and hartebeest) had similar

trends of SR and FTFS they showed selection for grasses of different height, supporting my 4th hypothesis.

The hartebeest and black wildebeest had similar SR and FTFS. As predicted, both species had high SR (on average = 9.7 steps/minute) and spent on average 6.7 sec per feeding station, despite grazing on grasses of different height. Hartebeest grazed mostly on medium height to tall grass (Fig. 2.9), and selected for medium height grass (Table 2.4), while wildebeest preferred to feed on short to very short grass and selected for both grass heights (Fig. 2.9 & Table 2.4). This, therefore, implies that they select for grass of different structural characteristics, which might be due to the adaptation in morpho-physiological characteristics for niche diversification and resource partitioning. Although all ruminants have evolved similar digestive physiology, each species has developed different foraging strategies to reduce competition and maximise its chances of survival (Meyer, Hummel & Clauss, 2010). Hence none of the ruminant species is exactly the same with regards to their food selection and foraging behaviour (Hofmann, 1989). St-Louis & Cote (2012) explained that adaptations in mouth morphology and differences in feeding style enable grazers to feed on different sward components thus allowing them to choose forage parts that are more suited to their digestive system. Hartebeest are tall grass grazers (Janis & Ehrhardt, 1988). Tall grass specialist grazers have narrow elongated faces, with narrower muzzles (Janis & Ehrhardt, 1988). This is likely an adaptation to allow for picking out desirable parts of plants, or desirable plants from stands of tall un-preferred or less preferred vegetation (Owen-Smith, 1982; Janis & Ehrhardt, 1988). Previous studies found that hartebeest searched and picked grass leaves (green or brown) from tall stands of high grass biomass, and their intake rate was lower than that of other alcelaphine antelopes (topi (*Damaliscus lunatus*) and wildebeest) (Murray & Brown, 1993). On the contrary, wildebeest has been described as short grass bulk feeders with a fast bite rate in areas mostly of low biomass with short highly nutritious forage (Murray & Brown, 1993), a behaviour made

possible by their wide muzzles (Janis & Ehrhardt, 1988) and wide incisor depth (Murray & Brown, 1993; Arsenault & Owen-Smith, 2011).

Whether the observed similarities in SR and FTFS are due to different foraging mechanisms, which is most likely the case since the species fed on grass of different height, could not be determined without bite rate observation. Bite rate might be important in revealing whether the ruminant that fed on the short grass takes more bites while at a feeding station as the animal walk around to eat everything which would not be much in terms of quantity. While, the tall grass grazer could spend that same time looking and selectively picking out the preferred part of the grass (green leaf) and hence should have a lower bite rate for a similar amount of time at the feeding station.

In contrast to the ruminants, zebra had a low SR and spent longer time at each feeding station (Fig. 2.6 & 2.7), proving hypothesis 1 and 2 correct. Zebra have been described in many studies as non-selective roughage grazers (Van Soest, 1994; Voeten & Prins, 1999), a feeding behaviour which might be responsible for low SR. Like the hartebeest, zebra fed on medium to tall grass. The evolutionary adaptation of the digestive system can explain the foraging behaviour of the two ruminant species compared to non-ruminants. Ruminant species are known to have evolved a very efficient digestive system (high digestibility of fibre) (Steuer *et al.*, 2013) which however comes at a cost. The highly efficient digestive system allows for high absorption of nutrients but causes a delay in the movement of food along the digestive track and thus results in longer forage retention time (Clauss *et al.*, 2013). Zebra are hindgut fermenters and unlike ruminants, their digestive system is less efficient in fibre digestion, with shorter forage retention time (Steuer *et al.*, 2013), and their forage passage rate is less affected by forage nutritional quality (Parra 1978; Owen-Smith & Novelli, 1982). Since the digestive systems of hindgut fermenters poorly digest fibre, the rate of forage digestion process is faster than in ruminants (Glover & Duthie, 1958; Duncan *et al.*, 1990;

Ben-Shahar & Coe, 1992). Hence a ruminant's digestive system remains full for a longer time compared to the non-ruminants (Van Soest, 1996), while non-ruminants have a high intake rate of forage per day (Glover & Duthie, 1958; Duncan *et al.*, 1990; Ben-Shahar & Coe, 1992) compared to ruminants. Food retention in the digestive system limits the intake of new food (Hofmann, 1989).

High SR and low FTFS in ruminants compared to non-ruminants can be further explained using a giving-up rule, which applies to animal feeding in feeding stations. The rule explains that an animal only stays in a feeding station until the remaining items are below a certain threshold and then they take a step forward and continue with the selection process (Senft *et al.*, 1987). Ruminants tend to reach the giving up threshold faster than the non-ruminants since they select for high-quality forage (owing to their digestive physiology), which is available in very low quantity in the dry season compared to the highly abundant less acceptable low-quality grass biomass. Hence, ruminants move faster between feeding stations and spend less time at each feeding station. Hofmann (1989) explained that for many of the ruminant species selectivity is a feeding strategy that helps the ruminant to cope at times of limited forage quality and availability. Perhaps the reason why zebra spent on average more time per feeding station and less time moving around searching for food, is because they utilise whatever is available at each feeding station to maximise forage intake and thus, reaching a giving-up threshold slower than ruminants. Non-ruminants employ foraging strategies for optimal diet selection which is directed toward maximisation of intake rate of critical nutrients over a wider range of forage qualities than would be the case for a ruminant.

The selection of different grass height by the three species might be influenced by the structural architecture of the grass. For instance hartebeest might have selected for medium height grass because it has softer and more nutritious leaves (younger growth stage) than tall grass, since hartebeest selects for leaves

against the stems (Murray & Brown, 1993). Grass at a younger growth stage is structurally softer than the tall mature grass (Bodenstein, Meissner & Van Hoven, 2000). This is also true for zebra, since despite the fact that zebra are roughage non-ruminant grazers, they select for grass of better structural and nutritional quality if presented with the opportunity (Bodenstein, Meissner & Van Hoven, 2000). This supports the idea that herbivores should use foraging strategies that favour selection of patches with better structure, growth stage and species composition (Janis & Ehrhardt, 1988). This helps grazers to maximise energy gain and reduce digestive constraints, by selecting a diet that enhances their digestive efficiency, and avoid structural tough and poor quality diets as it reduces nutrient uptake (Westoby, 1974, & Illius & Gordon, 1992).

The medium to tall grass usage by zebra (Fig. 2.9) has been observed and documented in several studies. Past studies, similarly suggested that zebra select for tall grass in non-growing seasons (Gwynne & Bell, 1968; Casebeer & Koss, 1970; Bell, 1971; Owaga, 1975; Skinner & Smithers, 1990; Ben-Shahar & Coe, 1992; Voeten & Prins, 1999). Despite the possession of the upper incisors in zebra, that allows them to graze on very short grass, during the dry seasons when the grass greenness is low (low forage quality), zebra select for areas of high biomass to meet their minimum daily nutrient requirement. Being a hindgut fermenter, non-ruminants have an advantage due to their ability to increase their intake rate on low-quality forage instead of selecting for high-quality forage (Ruckstuhl & Festa-Bianchet, 2003). This has also been supported by Senft *et al.* (1987), who explained that during critical times of low-quality forage, grazers have to make decisions on whether to select for quantity at the expense of quality and vice versa. While the non-ruminant grazers selects for quantity, ruminants are constrained by their digestive physiology and thus have to either select for grass parts (e.g. leaf) or grass at younger growth stage that are easily digestible.

Due to the lack of rainfall during the dry season and the high abundance of brown dry grass, zebra and hartebeest used grass of low greenness in proportion to its availability on both sites, contradicting my prediction. According to Owen-Smith and Novelli (1982), grazing ungulate might react to the decline in abundance of quality food by increasing the range of dietary acceptance, as long as there is adequate availability of low-quality forage. On the contrary areas grazed by wildebeest were found to have higher greenness, especially on the PCL compared to the greenness in the areas grazed by other species (Fig. 2.10), though the NL had generally relatively high greenness compared to the PCL (Fig. 2.8). Therefore there seems to be some kind of beneficial grazer-vegetation interaction resulting from cropping of grass to the shortest possible height. Grazing improves forage digestibility (Olubajo *et al.*, 1974; Misleavy *et al.*, 1982; McNaughton, 1984), and the resultant grazing lawn has forage of high nutritive value (McNaughton, 1984), plant biomass concentration, and thus, high yield to grazing herbivores (Stobbs 1973a, 1973b; McNaughton, 1984). The benefit of this grazer-vegetation interaction is dependent on the movement of the grazer to give the plants time to respond and re-grow (Senft *et al.*, 1987). This happens only after the animal has moved from the plant to the next, and significant plant response to re-growth occurs over a long period of time (Senft *et al.*, 1987). While moderate grazing may cause optimal rejuvenation of plant communities (Fox & Fox, 1986; Martinez-Fernan-Dez *et al.*, 1996; Cosmas, Gerontidis & Marathianou, 2000), overgrazing of such land can result in the decline in vegetation and the loss of herbaceous plant families which are critical in the structure of the grassland communities (Cosmas, Gerontidis & Marathianou, 2000). Therefore considering the findings of this study, black wildebeest feeding behaviour may facilitate vegetation re-growth in the short term but it can also graze the land to dis-function if the herds stay for too long in the same area. This might be exacerbated by overstocking of reserves.

Limitation of the study

Feeding behaviour comprises of different components and an elaborate study needs to use many indices of feeding behaviour. Foraging behaviour at the fine scale can be studied using a combination of different foraging behavioural indices. In addition to those used in this study, the following indices can be and have been used in many studies of foraging behaviour of grazers: bite rate (Parrini & Owen-Smith, 2010) and bite size, (see Cooper & Owen-Smith, 1986; Owen-Smith, 1976; Fleurance *et al.*, 2009; Edouard *et al.*, 2010), bite weight, bite depth, feeding time per feeding patch (Cooper & Owen-Smith, 1986), time spent travelling between feeding patches, feeding time (Owen-Smith, 1976), chew rate (Edouard *et al.*, 2010) and many more indices. The selection of the correct combination of indices to address specific objectives is very crucial to any foraging behaviour study. For this study the lack of bite rate observation posed limitations in the better understanding of the finding of other foraging behavioural indices. Although bite rate was included in the design of this study, field conditions did not allow for the reliable collection of bite rate data. Bite rate could have been useful in explaining the mechanisms underlying the similarities in SR and FTFS of the ruminant species.

Apart from the indices of foraging behaviour it is important to compare the foraging behaviour at different times of the year. Food resources vary among seasons and lack of comparisons between different season's results in the limited understanding of forage partitioning along the year. Wet season studies allows for possible identification of grass species which can be used in the analysis of grazing behaviour (Ben-Shahar & Coe, 1992), and thus might be important for improved understanding of forage usage and selection among different grazing species.

Furthermore, the focus of this study on one section of the reserve (Ezemvelo section) posed limitation on the full understanding of foraging behaviour and forage use by the grazing species over a larger area. More especially for the non-sedentary species such as zebra and hartebeest which migrated between the two sections of TENR that resulted in the limited observation of these species on Ezemvelo section compared to the more sedentary black wildebeest.

I therefore recommend more studies to be done on the foraging behaviour of the grazers of the TENR during the wet season, which include the examination of grass species composition in the diets of the different species. I further recommend the use of more foraging behaviour indices to better understand the trends of foraging behaviour of the different species. The use of the maximum possible area of observation is also necessary in the examination and better understanding of resource partitioning among different grazing species.

2.5 CONCLUSIONS

Understanding the basis of animal foraging behaviour is clearly complex. The animal feeding behaviour not only varies between animals with different digestive system but some aspects also differ between animals with similar digestive system. For instance ruminants have similar SR and FTFS but they forage on grass of different height. Ruminants SR and TFFS differ from non-ruminants, but the ruminant hartebeest forage on grass of similar height as a non-ruminant zebra.

Studies of animal foraging behaviour contribute to a better understanding of resource partitioning among different species and wildlife interactions that lead to improved wildlife and habitat management. The wildebeest population within the TENR needs to be controlled to prevent land degradation especially in the previously disturbed land, considering the wildebeest feeding behaviour of

cropping the vegetation to a very short height. Furthermore, over-stocking of zebra may lead to the decline in number of the tall grass leaf eating hartebeest.

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