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Do zebra (Equus quagga) select for greener grass within the foraging area?

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DO ZEBRA (*EQUUS QUAGGA*) SELECT FOR GREENER GRASS WITHIN THE FORAGING AREA?

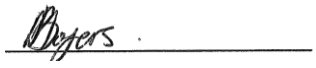
Melinda Boyers

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

Johannesburg, 2011

DECLARATION

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



(Signature of candidate)

5th October 2011

ABSTRACT

Spatial patterns in topography and forage distribution clearly determine large herbivore movements but our understanding of the foraging strategies that free-grazing herbivores adopt at different temporal and spatial scales is limited. Different foraging response patterns are displayed at different scales. Here fine-scale foraging strategies of Zebra (*Equus quagga*) were investigated by studying their selection for vegetation greenness in a Southern African savanna. Zebras have high-energy requirements thus the primary productivity and condition of the habitat plays an important role on their movements. Grass greenness was measured by Normalized Difference Vegetation Index (NDVI), a proxy for vegetation productivity and quality. Finer-scale studies are needed to understand the processes leading to a correlation between NDVI and herbivores performance. Data was collected at two different spatial scales, foraging area and feeding station. Food selection was recorded in relation to grass species and grass tuft greenness. Within the foraging area, grass species and greenness within zebra feeding stations were compared with random non-used stations. Within the feeding station, species and greenness of grasses eaten by zebra were compared with those of grasses available but not eaten. Zebra selection was not consistent across scales. Although greenness was a factor in selection at feeding station levels and grass tuft levels; feeding station selection was limited to greenness due to season, and selection for species occurred only at the grass tuft level. However, zebra did select for the greener grass tufts within the feeding station even if it meant to eat 'less palatable' species (i.e. *Eragrostis rigidior*) instead of 'very palatable' species (i.e. *Panicum maximum*).

ACKNOWLEDGEMENTS

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CHAPTER 1

GENERAL INTRODUCTION

This study was designed as part of a 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 understand foraging strategies of zebra (*Equus quagga*) at the fine scales according to greenness and species.

THE NEED FOR THE STUDY

Climate change is already happening and represents one of the greatest environmental, social and economic threats facing the planet. Understanding how climate influences ecosystems represents a challenge in ecology and natural resource management. The majority of the evidence of climate change points to changes in plant phenology and species distribution (Craine *et al.* 2009).Thus, understanding mechanisms such as foraging strategies that free-grazing herbivores adopt at different spatial and temporal scales is central to animal ecology (Fryxell *et al.* 2004; Prins & Van Langevelde 2008) and ecosystem management (Bailey *et al.* 1996, Senft *et al.* 1987), allowing scientists to understand the impact of climate change.

The phenology of plants used by herbivores is directly linked to climate, and the reproductive timing of herbivores matches vegetation dynamics (Berteaux *et al.* 2006). In an African savanna system, rainfall after a dry spell generates substantial soil respiration activity and soil respiratory carbon losses (Veenendaal *et al.* 2004), suggesting that savanna ecosystems are strongly sensitive to rainfall variability (Parry 2007). Precipitation and nutrient limitations represent associated constraints that affect vegetation production at various spatial and temporal scales (Chamaille-Jammes & Fritz 2009). Tools, such as the Normalized Difference Vegetation Index (NDVI), may be used to measure the greenness associated with rainfall patterns (Pettorelli *et al.* 2005). However, such indices are meant to build forecasting models at large temporal and spatial scales, whereas finer-scale studies are needed to understand the processes leading to a correlation between greenness, such as NDVI, and herbivore performance (Berteaux *et al.* 2006).

Recent studies have tied vegetation dynamics, as assessed by the NDVI, with animal species distribution and the movement pattern of animals (Boone*et al.* 2006, Bro-Jorgensen *et al.* 2008, Mueller *et al.* 2007, Musiega & Kazadi 2004, Vina *et al.* 2008). Large herbivore grazing patterns are largely affected by abiotic factors such as slope and distance to water and by biotic factors such as forage quantity and quality. Although abiotic factors are the primary determinants of large-scale

distribution patterns and act as constraints within which mechanisms involving biotic factors operate (Bailey *et al.* 1996), the distance moved and the direction taken by herbivores is largely determined by forage distribution and quality. Herbivores have evolved to adjust their foraging strategies, in relation to the spatial distribution and availability of plants, to maximise food intake (Gordon & Lindsay 1990). Grass height, grass species composition, woody canopy cover (Sinclair 1985, Ben-Shahar 1991, Owen-Smith 2002) and grass greenness (McNaughton 1985, Sinclair 1985) influence resources and/or habitat conditions for large grazers. Groom and Harris (2009) found that grass greenness can be considered a proxy for grass quality, and may be a better predictor than percentage crude protein.

Senft *et al.* (1987), McNaughton (1991) and Bailey *et al.* (1996) suggested that large herbivore grazing distribution patterns are hierarchical in nature, and thus animals have varying scales of forage selection. Broadly stated, selection begins at a landscape level, progressively getting to a finer scale through the feeding patch, feeding station and finally, plant part or bite (Bowers 2006). Feeding patch choice and forage selection by ungulates are positively associated with plant quality (Pettorelli *et al.* 2007, Wilmshurst *et al.* 1995). However, different herbivores have different trade-offs between forage quality (greenness and species) and quantity (mass). As zebras are a high-density non-ruminant herbivore, they have a hind-gut digestive system that allows them to process their food at relatively faster rates than foregut ruminants, which may allow zebras to exploit a greater range in grass quality and quantity(Hack *et al.* 2002), ultimately portraying them as bulk feeders. Zebra's selection preferences are currently inconclusive. Thus in this study, I analyze zebra's forage selection for greenness of vegetation and species composition at the feeding station and grass tuft level within foraging areas in Manyeleti Game Reserve. The main objective of this study, addressed in detail in chapter 2 is to investigate whether greenness influences zebra feeding behaviour at different spatial scales. I expect to see zebra choose the greenest forage available at any given time independently of grass species.

LITERATURE REVIEW

SPATIAL SCALES AND FORAGING HIERARCHIES

Spatial patterns in topography and forage distribution clearly determine large herbivore movements but our understanding of the relative importance of landscape elements that occur at different spatial scales is limited. Ungulates interact with their forage through a series of nested processes such as ingestion and chewing, searching and walking, digestion and rumination, resting, etc. These processes and the associated behaviours define potential scales of interest (Laca, 2008). Different foraging response patterns are displayed at different scales defining different hierarchies (Senft *et al.* 1987, Bailey *et al.* 1996, Bowers 2006) which may begin at the landscape scale and progressively decreases to a finer scale through the feeding patch, feeding station and finally, plant part or bite (Bowers, 2006). The following forage hierarchies are defined according to Bailey *et al.* (1996):

a. Grass tuft

The smallest scale is a bite and is clearly defined by a sequence of herbage prehensive jaw and tongue movements, and severance by head movement (Laca*et al.* 1994).

b. Feeding station:

A feeding station is the spatial area that is available to the animal without moving its front feet (Novellie, 1978). It is regarded as an area where an animal starts to forage and continues as forage diminishes until it starts to move to another station to repeat the process (Bailey*et al.* 1996). Factors that may influence selection of a feeding station are forage availability and plant species composition, structure and quality.

c. Feeding patch:

A feeding patch is a collection of feeding stations. A feeding patch is separated from another when animals break a foraging sequence when they reorient to a new location (Bailey*et al.* 1996). Factors that may have an effect in selection of a feeding patch are forage availability, plant species and topography.

d. Foraging area:

A foraging area is a collection of feeding patches the animal makes use of during a foraging bout. Foraging bouts are defined by a change in behaviour such as from foraging to resting (Bailey *et al.* 1996). Foraging area selection criteria may be influenced by topography, distance to water, forage quality, forage abundance and phenology.

FACTORS INFLUENCING FORAGE SELECTION

1. SPECIES COMPOSITION

In the course of the year the leaf to stem ratio, greenness and growth stage of the grasses change with consequent seasonal variation in grass quality (Owen- Smith 2002). As grass quality changes so do the preference for particular plant species and this preference vary among herbivores (O'Reagain & Schwarz 1995, Meissner *et al.* 1999, Parrini 2006). The most utilized grasses in the zebra and wildebeest's diet in a study done by Bodenstein *et al.* (2000) were *Panicum maximum*, *Heteropogon contortus*, *Urochloa mosambicensis* and *Themeda triandra*. In another study done by Ben-Shahar (1991), the species that contributed most to the zebra diet was *Panicum maximum* (approximately 30%), while *Aristida congesta*, *Dactyloctenium aegyptium* and *Themeda triandra* had a lesser share (approximately 20% and less for each species).However, zebra moved seasonally between grass communities containing a high proportion of nutritious species rather than by selecting particularly nutritious species within communities (Ben-Shahar & Coe 1992).

2. PHYSICAL CHARACTERISTICS OF THE GRASSES

The physical properties and structure of the grass influences its acceptability (O'Reagain 1993). Many animals show a clear preference for green material as compared with dry material (e.g. sheep and cattle, O'Reagain 2001). Because greenness is negatively related to grass maturity (Van Soest 1994), younger vegetation is often greener and in general an indication of higher quality forage (O'Reagain & Owen-Smith 1996). Grass greenness can be considered a proxy for grass quality, and may be a better predictor than percentage crude protein (%CP) (Groom & Harris 2009). A similar preference for greenness has been observed in wild herbivores. The plant species acceptance was mainly correlated with greenness, for both wildebeest (Wilmshurst *et al.* 1999) and zebra (Winkler 1992). During the late growth period sable antelope had a preference for *Panicum maximum* with a selection for greenness (Parrini, 2006). *Panicum maximum* grows underneath the trees and remains green for longer compared to other grasses (Magome 1991).

During the wet season grazers such as zebra (*Equus quagga*, Boddaert 1785), wildebeest (*Connochaetes taurinus*, Burchell 1823), Thomson's gazelle (*Eudorcas thomsonii*, Günther 1884), Coke's hartebeest (*Alcelaphus buselaphus* ssp. *cokii*, Günther 1884) and oryx (*Oryx beisa*ssp. *callotis*, Thomas 1892) located in the Amboseli-Tsavo ecosystem in southern Kenya were positively associated with areas of higher grass biomass and greener grass (Groom & Harris 2009). Groom & Harris (2009) found that in the wet season, wild grazers were selecting areas, which had both high

quantity and quality of grass, and grass characteristics were more important than abiotic or human-related variables in explaining the observed distribution of wild grazers.

3. FORAGING STRATEGIES

Herbivore foraging strategies may differ at various scales and foraging decisions proceed from coarse to fine and from fine to coarse scales. Although information may be perceived at multiple scales, attention to one scale may constrain other scales thus the relationship between grazers and forage resources depend on the scale of analysis (Laca 2000). Herbivores must perceive differences among plant parts, plants, and feeding stations so that they can discriminate and select among alternatives. While it is known that grazing animals can perceive differences among feeding stations and small patches, it is not clear whether they are able to directly perceive large units of spatial selection (Bailey *et al.* 1996). For example, ability to see distant patches is diminished while the animal obtains information about a bite by touch or smell, because the range of visibility declines as the head is lowered (Laca 2000). Conversely, if attention is on assessing the landscape within which the animal is moving, details of bites and feeding stations that fall within the search path are missed (Laca, 2000). Decisions made at larger temporal and spatial scales (e.g., where to begin grazing) can constrain behaviours that occur at smaller scales. Consequences of decisions made at small scales may be integrated and used to make decisions at higher levels. During the dry seasons, herbivores are faced with a reduction in forage quantity and quality thus the intake rate of forage would decrease thus increasing the movement rate across scales. Selection of patches and feeding stations, which occur at larger scales, may also affect grazing distribution patterns. Larger herbivores may be forced to select lower quality diets to maintain intake when forage is limited (Bailey *et al.* 1996). Diet selection, movement rates, and other mechanisms that occur at small scales can at least partially explain grazing patterns observed across landscapes and regions. The selection of food items however, occurs on many levels and it is difficult to say whether the animals are feeding selectively without defining the scale of measurements that controls the dispersion of food items (Ben-Shahar, 1991).

NDVI

Normalized Difference Vegetation Index (NDVI) is an index of vegetation greenness, which can be considered a proxy for grass quality (Groom & Harris 2009). Green plants have high reflectivity in the near-infrared wavelengths and absorb red wavelengths for photosynthesis. NDVI is defined by the equation: NDVI = (NIR–VIS) / (NIR + VIS), where NIR is the reflectance of the Earth's surface in the

near-infrared channel and VIS is the reflectance in the visible portion of the spectrum or the red channel (Tucker & Sellers 1986). Chlorophyll level, indicative of the greenness of the vegetation, and Leaf Area Index (LAI) indicating the vertical thickness of the vegetation, largely determine NDVI values (van Bommel *et al.* 2006). Generally, LAI will increase with the thickness of the green layer or with the number of green layers. High NDVI values are usually associated with well-developed green vegetation such as closed canopy in woodland or a continuous green grass layer, whereas low NDVI values are generally associated with a noncontinuous vegetation cover or a non-green cover like exposed bare soil, water or plant senescence (van Bommel *et al.* 2006).

While there is general agreement among researchers working in semi-arid areas of southern Africa that many wildlife species select green areas, there is a lack of unbiased parameters to compare greenness among seasons or different areas (Verlinden & Masogo 1997). Satellite remote sensing data fulfill most of the methodological conditions and most NDVI time series are commonly obtained from the MODIS data source, but it is not always clear if the remotely sensed environmental parameters are focused at determining the NDVI at the foraging levels (Verlinden & Masogo 1997). Numerous studies have used NDVI to indicate animal movement patterns at large spatial scales (e.g. Osborne *et al.* 2001; Vina *et al.* 2008). NDVI also has been used as direct measure of plant phenology to investigate the impact of seasonality and predictability in plant phenology for breeding synchrony of red deer (Loe *et al.* 2005) and to detect key periods of plant productivity determining animal performance (Pettorelli *et al.* 2006). Young *et al.* (2009) proposed the use of MODIS NDVI to indicate elephant spatial use in wet and dry savannas. Vina *et al.* (2008) used MODIS NDVI for mapping habitat distribution of pandas. However at large spatial resolutions NDVI measures are susceptible to inaccuracies through soil surface reflectance and high vegetation densities (Pettorelli *et al.* 2005) and that the spatial resolution of the analysis determines whether or not patterns are detected (Bro-Jorgensen *et al.* 2008).A recent study was able to detect differences in seasonal feeding station greenness within buffalo foraging areas using a handheld NDVI sensor (SpectroSense 2+) (Macindoe, unpublished). Macindoe noted that NDVI and visual estimates of greenness follow the same trend. Such a comparison will help to determine if satellite-derived NDVI measures are sufficiently sensitive to detect fine-level determinants of herbivore response to greenness. Therefore proposing that studies should conduct analyses of animal distributions at multiple spatial scales is important since this affects whether or not only patterns are detected, but it may also shed light on the causal factors behind observed distribution patterns.

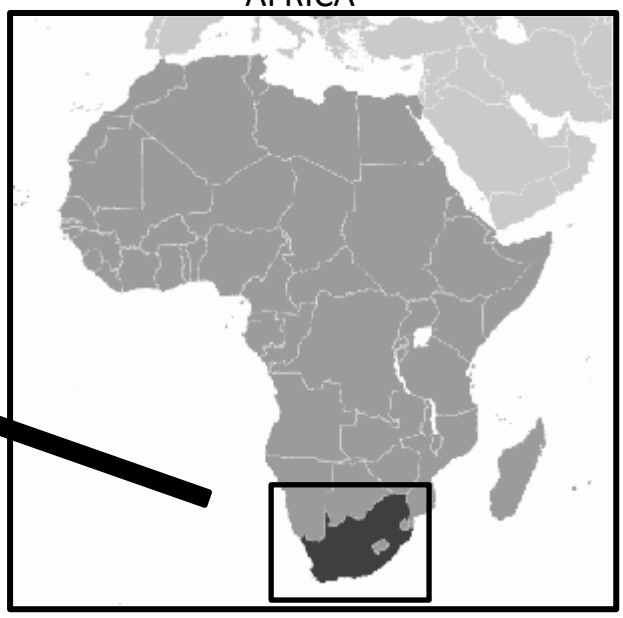
STUDY AREA

The study area is in Manyeleti Game Reserve, which runs along the western boundary of the Kruger National Park from Orpen gate southwards (Figure 1.1). The area is characterized by high mean temperatures in summer, mild, generally frost-free winters, and rainfall strongly concentrated between October and April. The long-term average annual rainfall for the Orpen region is 550 mm (Gertenbach 1980). Rainfall is largely confined to the summer months with very little to no rain experienced over winter (Bowers 2006). December, January and February are on average the wettest months of the year, while August and September are the driest (Gertenbach 1980).

The landscape located in the triangle formed by the Olifants River, Timbavati River and the western boundary of KNP (which included Manyeleti) was classified as *Combretum* spp./*Colophospermum* mopane Woodland of the Timbavati area (Gertenbach 1983). The substratum of this area is mainly granite and gneiss intersected by numerous intrusions of dolerite. The underlying geological formation of this area is gabbro, which forms an intrusion into granite rock (Gertenbach 1983). The Timbavati gabbro consists of quartz gabbro, gabbro and olivine gabbro and occurs as large plates, which are intrusive in the basement complex. Soils originating from gabbro are rich in dark coloured minerals such as Fe and Mg. The parent rock of these soil formations erode easily to deep fertile soils with a good water-holding capacity but slow absorption (Bodenstein *et al.* 2000).

The veld type is known as Granite Lowveld (Mucina & Rutherford 2006).It falls within the savanna biome (Rutherford & Westfall 1994), which is defined as having a discontinuous over story of woody plants and an herbaceous layer dominated by C_4 grasses (Venter*et al.* 2003). The dominant tree species are *Acacia nigrescens* and *Sclerocarya birrea*. The most dominant shrubs are several *Grewia* spp*, Ziziphus mucronata, Flueggia virosa* and *Ormocarpum trichocarpum*. The grass stratum is dominated by *Heteropogon contortus, Themeda triandra, Panicum maximum* and *Enneapogon spp*. Various forbs are also present (Bodenstein *et al.* 2000).

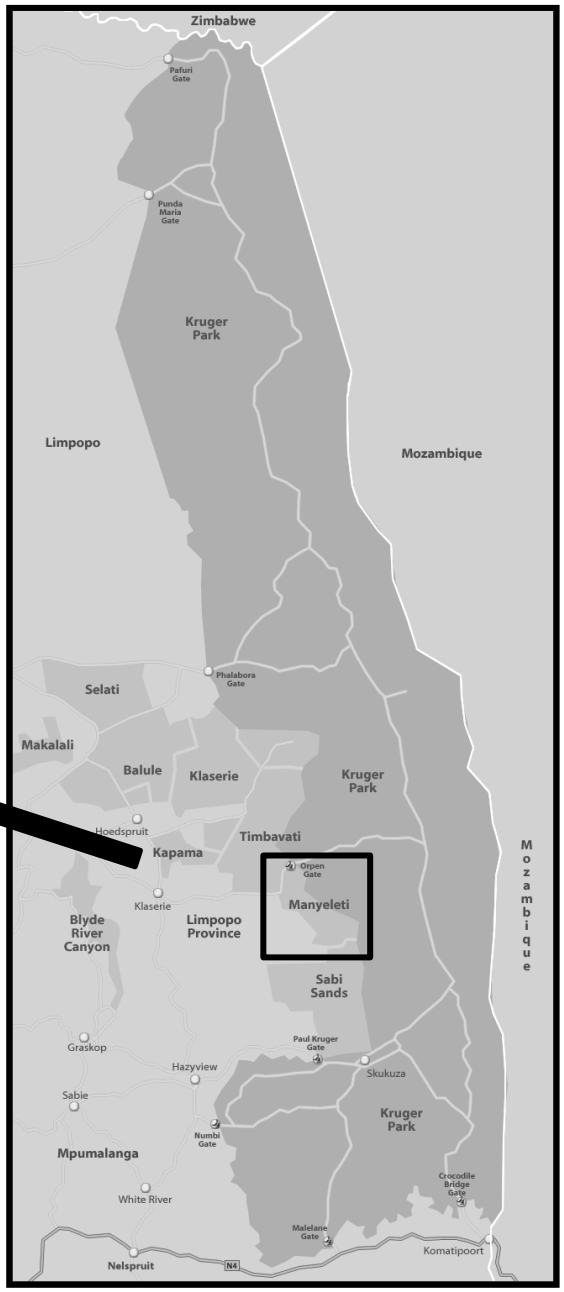
AFRICA



SOUTHERN AFRICA



GREATER KRUGER PARK



MANYELETI GAME RESERVE

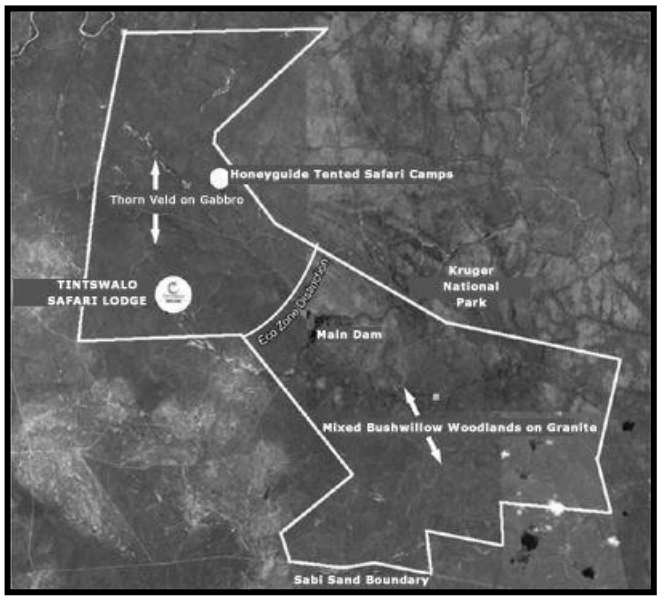


Figure 1.1: Map of Southern Africa, showing the location of the study area, Manyeleti Game Reserve, adjacent to Kruger National Park. The reserve is located close to the border of the Mpumalanga and Limpopo provinces of South Africa.

STUDY DESIGN

I sampled data at two spatial scales: grass tuft within a feeding station and feeding station within a foraging area. The data was collected over one dry season, which transitioned through, to the early wet season. For the data analysis I broke down the field season into three periods according to rainfall and greenness (Figure 1.2). Monday to Friday I searched for feeding zebra herds by vehicle. In the early morning and late afternoon (predominant feeding time of ungulates) I drove throughout the reserve and searched for grazing individuals or groups within 100 m off the road. Once an individual or group was sighted feeding, detailed observations of the exact location where bites were taken were made (this observation was classified as a feeding observation). After the animal left the foraging area, I, the observer, approached the area on foot and searched for the freshly grazed grass i.e. individual bite points. Freshly grazed grass is identifiable as the bitten leaf/stem remains white and has no dried rim while older grazed grass turns brown quickly (Macandza 2009, Kleynhans*et al.* 2011). At the first identified sign of fresh feeding I placed a 0.5 m x 0.5 m quadrat to represent a feeding station (Figure 1.3). When fresh footprints or/and signs of cropping identified a foraging path, I placed nine additional quadrats starting from a random point along the path. If a foraging path could not be identified I placed nine or more quadrats surrounding the central quadrat. Grass tufts with fresh bites were classified as used and feeding stations that had used grass tufts present were classified as used. I recorded different attributes at the various scales: grass tuft level involved identifying used and unused species and ranking their greenness according to Walker's (1976) eight-point scale. Greenness of vegetation is generally an indication of high quality forage (O'Reagain and Owen-Smith 1996), and is negatively related to grass maturity, digestibility, and fibre content (Van Soest 1994). At feeding station level, I measured NDVI, and identifying all species present within the feeding station. For every used feeding station sampled, I sampled an unused feeding station identified by grass tufts that have not been grazed. These were placed randomly around the used feeding stations (at least 2 m apart).

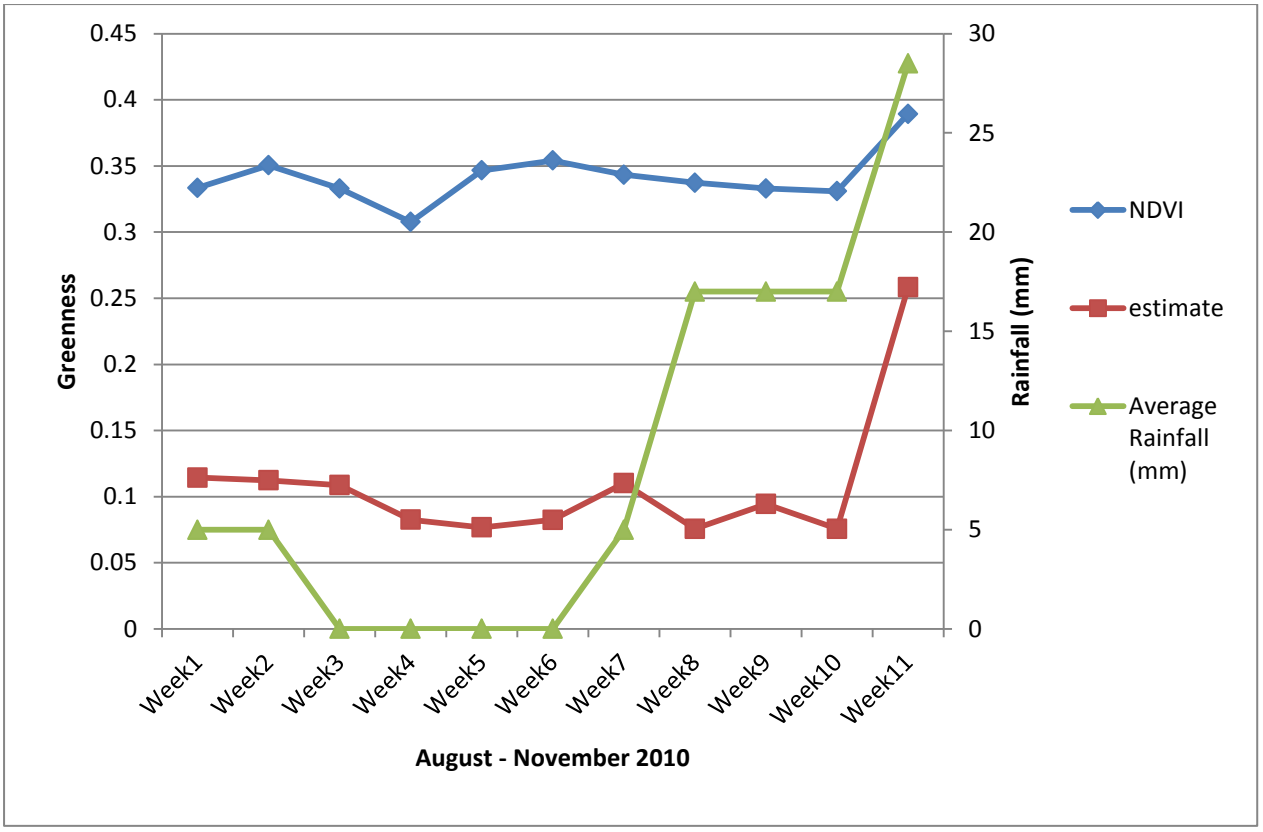


Figure 1.2: The relationship between the estimated greenness values, NDVI and average rainfall.

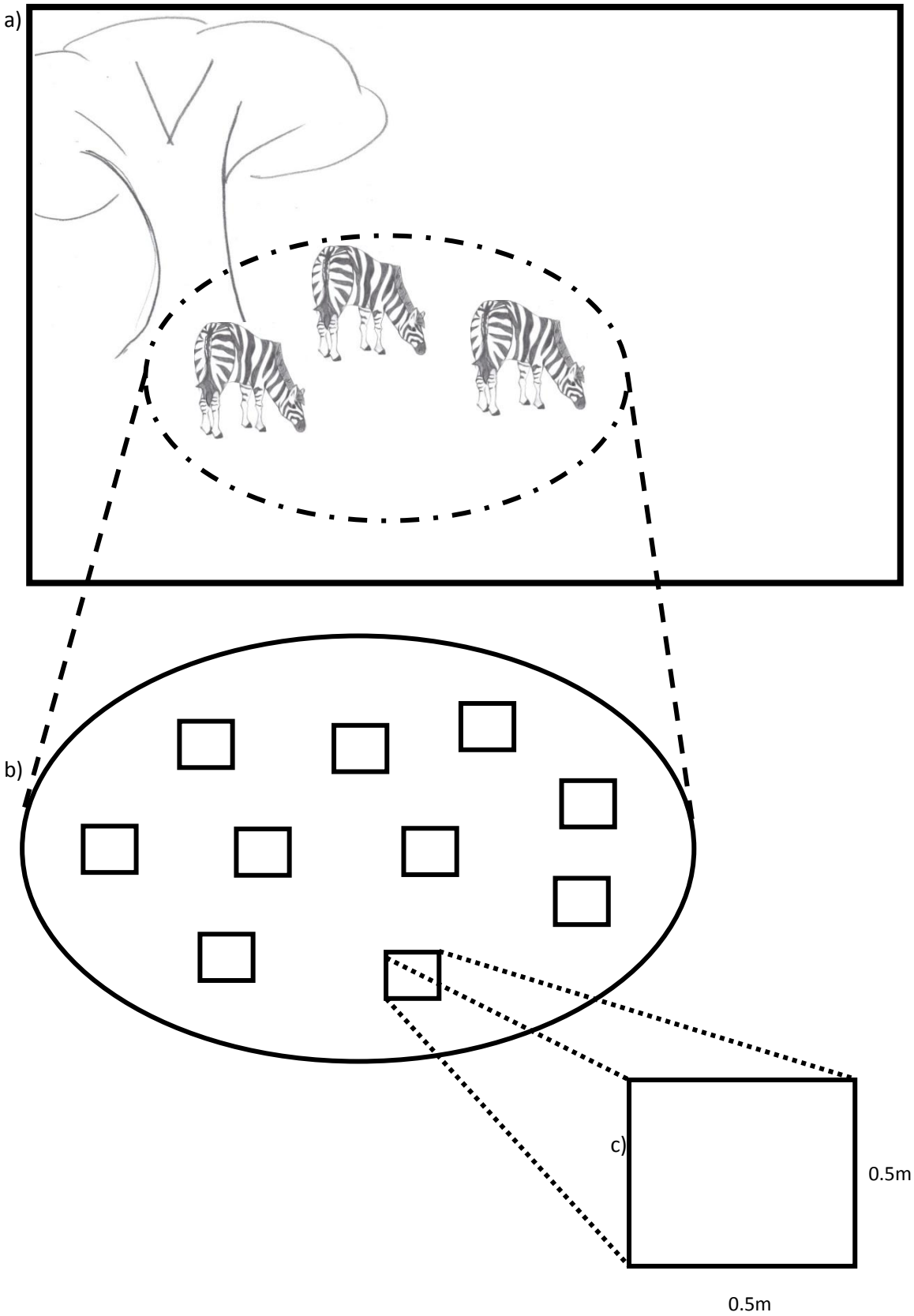


Figure 1.3: Sampling regime, a) a foraging area was determined, b) fresh bites were identified and quadrats were placed surrounding the central quadrat if a foraging path was not determined. c) Each quadrat was 0.5m x 0.5m identifying a feeding station. Both used and non-used feeding stations were sampled

THESIS OUTLINE

The purpose of Chapter 1 is to serve as a general introduction to the topic dealt with in more detail in Chapter 2, where I elaborate on the methods, including data analyses. The references used within each chapter are reported at the end of each particular chapter. Supplementary information and results that are not directly relevant to the chapters yet are necessary background information are reported as appendices.

Chapter 2 is written in article format with separate introduction, methods, results and discussion sections. Its focus is on resource selection at two spatial scales: grass tuft within a feeding station, and feeding stations within a foraging area. The main objective of this study is to investigate how greenness influences zebra feeding behaviour at different spatial scales. The aim is to 1) determine whether zebra select for the greenest grass tufts within feeding stations and 2) to determine whether the zebra select for the greener feeding stations within the foraging area. The key questions addressed are:

1. Predictions at grass tuft level within a feeding station:
    1.1 The selection of a grass tuft is only dependent on the greenness
    1.2 The selection of a grass tuft is only dependent on the specific species
    1.3 The selection of a grass tuft is dependent on the greenness of that species
    1.4 The selection of a grass tuft is dependent on the season that the species is available as well as greenness.
2. Predictions at feeding station level:
    2.1. The selection of a feeding station is only dependent on the greenness of that feeding station
    2.2. The presence of certain plant species increase the selection of a feeding station
    2.3. The presence of certain plant species together with the greenness of the feeding station during a specific season increase selection of a feeding station
    2.4. The presence of specific species together with greenness of the station during a specific season as well as the biomass of the feedings station during a specific season increases the selection of the feeding station

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CHAPTER 2

DO ZEBRA (*EQUUS QUAGGA*) SELECT FOR GREENER GRASS WITHIN THE FORAGING AREA?

INTRODUCTION

Resource distribution is a fundamental factor governing the movement and distribution of herbivores (Muya & Oguge 2000). Predicting the distribution of large herbivore species, either for the purpose of conservation or management, requires an understanding of the mechanisms of resource use by these species. Thus, understanding foraging strategies that free-grazing herbivores adopt is central to animal ecology (Fryxell*et al.* 2004, Prins & Van Langevelde 2008) and is critical for ecosystem management (Senft *et al.* 1987, Bailey *et al.* 1996).

However it is imporant to consider that selection for foraging components ranges from the fine scale of individual plants within communities to the large scale of landscape within regions (Senft *et al.* 1987, Bailey *et al.* 1996, Ritchie & Olff 1999). Accordingly recognizing the differences in foraging behaviours that occur along spatial and temporal scales is critical for understanding the mechanisms that result in grazing distribution patterns (Bailey & Provenza 2008). Hence, for example, decisions made at larger temporal and spatial scales (e.g., where to begin grazing) can constrain behaviours that occur at smaller scales and a consequence of the decision made at small scales may be integrated and used to make decisions at higher levels(Bailey *et al.* 1996).Thus herbivores must integrate information from lower level behaviours (bites, feeding stations, and patches) if they are to use those experiences to evaluate spatial alternatives at higher levels (foraging areas, camps, and home ranges) (Bailey *et al.* 1996). Nonetheless resource heterogeneity occur at all spatial scales in the environment and we cannot say upfront at which spatial scale resource selection by grazers might occur (Senft *et al.* 1987).

Crude protein can usually be regarded as a reliable indicator of both the overall nutrient status and palatability of forage (Bodenstein*et al.* 2000), whereas Groom and Harris (2009) found that grass greenness can be considered a proxy for grass quality, and may be a better predictor than percentage crude protein. Forage quality is also related to plant species. The preference for particular plant species varies between herbivores (Lawler *et al.* 1998, Bos 2002).

The Burchell zebra was used in this study to determine a large herbivore's foraging selection at the finer scales. As zebras are a high-density non-ruminant herbivore, with a mean adult female weight of about 310 kg occurring in social units averaging 6-7 animals (Grubb, 1981), they have a

hind-gut digestive system that allows them to process their food at relatively faster rates than foregut ruminants, which may allow zebras to exploit a greater range in grass quality(Hack*et al.*2002). In the southwestern part of the Greater Kruger National Park, Ben-Shahar (1991) in Sabi-Sands game reserve and Bodenstein *et al.* (2000) in Timbavati game reserve have both studied zebra's diet and found that grass height and grass greenness were positively associated with the acceptance of grass. Whereas in Punda Maria in Kruger National Park, zebra accepted grass within a wider range of grass greenness, including brown grass during both the early and late dry seasons (Macandza, 2009). A study done in Makgadikgadi Pans National Park in Botswana, found that at larger scales zebra direct their movement to patches of high-quality resources within a large, natural landscape (Brooks & Harris 2008).

Many researchers working in the semi-arid areas of southern Africa are in agreement that many wildlife species select green areas for foraging. Yet there is a lack of unbiased parameters to compare greenness among seasons or different areas (Verlinden & Masogo 1997). Tools, such as Normalized Difference Vegetation Index (NDVI), could fulfill those requirements (Pettorelli *et al.* 2005). NDVI is a good indicator of leaf area, especially in open systems like savannas where it never reaches saturation values (Skidmore & Ferwerda 2008). The NDVI thus represents the first useful tool with which to couple climate, vegetation and animal distribution and performance at large spatial and temporal scales (Pettorelli *et al.* 2005). Recent studies have tied vegetation dynamics, as assessed by the NDVI, with animal species distribution and the movement pattern of animals (Musiega & Kazadi 2004, Boone *et al.* 2006, Mueller *et al.* 2007, Bro-Jorgensen *et al.* 2008, Vina *et al.* 2008), however It is not always clear if the remotely sensed NDVI are focused at determining the NDVI at the foraging levels (Verlinden & Masogo 1997). Therefore, finer-scale studies are needed to understand the processes leading to a correlation between NDVI and herbivore foraging selection (Berteaux *et al.* 2006).

Therefore, I aim to fill the gap concerning the foraging strategies of free-grazing herbivores at small spatial scales by determining if greenness is a factor governing grazing within foraging areas. This study focuses on resource selection at two spatial scales: grass tuft within a feeding station, and feeding stations within a foraging area. The main objective is to investigate whether greenness or plant species or a combination of both influences zebra feeding behaviour at the two spatial scales. For both feeding station selection and grass tuft selection I was interested in determining if the presence of any species influences the selection of a feeding station within a foraging area or a grass tuft within a feeding station respectively, compared to other factors such as the greenness of the feeding station or grass tuft, and how selection at these spatial scales changed with season (mid dry, late dry and early wet). I expect to see within a foraging area that1) zebra do not select feeding

stations randomly but select feeding station that are greener than random locations, and 2) select feeding stations where a certain species is present. Within a feeding station, I expect that1) zebra are selective for greener tufts of grass but 2) they do not select for a certain species. Thus, zebra will prioritize forage quality over other factors.

METHODS

STUDY AREA

The study was done in Manyeleti Game Reserve, which is situated in Mpumalanga province close to the Limpopo province border in South Africa. Manyeleti Game Reserve (hereafter Manyeleti) runs along the western boundary of the Kruger National Park from Orpen gate southwards. There are no fences between Manyeleti and Kruger National Park and it forms part of the Greater Kruger Park, with the main gate located 5 km from Orpen gate. The Greater Kruger National Park has approximately 147 mammal species and roughly 1980 plant species (Mabunda 2003).

Manyeleti falls within the savanna biome, defined as having a discontinuous over story of woody plants and a herbaceous layer dominated by C_4 grasses (Venter*et al.* 2003). Manyeleti is located in the veld type known as Mixed Lowveld Bushveld (van der Merwe, 2009). The vegetation in this area is an open tree savanna with the dominant tree species being *Acacia nigrescens* and *Sclerocaryabirrea*. The most dominant shrubs are *Grewia spp, Ziziphus mucronata, Flueggia virosa* and *Ormocarpum trichocarpum*. The grass stratum is dominated by *Heteropogon contortus, Themeda triandra, Panicum maximum* and *Enneapogon spp*. Various forms are also present (Bodenstein *et al.* 2000).

The area is characterized by high mean temperatures in summer (32.4˚C), mild, generally frost-free winters (17.8˚C), and rainfall strongly concentrated between October and April. The rainfall in the area is 500-700 mm (Kingfisherspruit: annual long term average = 572 mm, collected over 41 years, KNP Scientific Services) and a potential evaporation of 6 mm/day in October.

The substratum of this area is mainly granite and gneiss intersected by numerous intrusions of dolerite. The underlying geological formation of this area is gabbro, which forms an intrusion into granite rock (Gertenbach 1983). The Timbavati gabbro consists of quartz gabbro, gabbro and olivine gabbro and occurs as large plates, which are intrusive in the basement complex. Soils originating from gabbro are rich in dark coloured minerals such as iron and magnesium. The parent rock of these soil formations erode easily to deep fertile soils with a good water-holding capacity but slow absorption (Bodenstein *et al.* 2000).

FIELD DATA COLLECTION

The dry season is a critical period for African ungulates: the low rainfall causes the quality of the food to decline during this part of the year, therefore data collection spanned over one dry season (August-October 2010) and transition period to the beginning of the wet season (November 2010). The dry season was further divided into two periods, namely mid dry (August-September) and late dry (October) based on the monthly rainfall and greenness values.

I sampled the study area every week from Monday till Friday. By vehicle, I drove through the reserve searching for feeding zebra herds. Overall, I sampled as many feeding herds as possible, not returning to the same area on the same day thus avoiding re-sampling the same herd on the same day. Once located, I observed them foraging and only approached the foraging area once zebra had moved on. The location of the foraging area was confirmed by the presence of fresh bites, identified by a lighter and brighter colour at the surface of the broken grass leaves and stems than old bites (Macandza 2009). Within the foraging area, I sampled data at two spatial scales: feeding station and grass tuft level.

At the first identified sign of fresh feeding, I placed a 0.5 m x 0.5 m quadrat to represent a feeding station. According to Novellie (1978), the feeding station is the area that a foraging animal can harvest food resources from without moving its front feet. All feeding stations with fresh bites were recorded as 'used'. For each feeding station used by zebra, I also located and sampled an 'unused' feeding station by randomly selecting feeding stations that did not show any grazing (van der Merwe, 2009). These were placed randomly around the used feeding stations (at least 2 m apart). For both used and unused feeding stations, I recorded the grass species composition and the average greenness of the station with a hand held NDVI measuring tool (SpectroSense 2+). Within the used feeding stations, I recorded all the plant species present, scored the species as being 'used' (by identifying fresh bites as explained above)or 'unused' and I estimated greenness for each species according to an 8 point scale proposed by Walker (1976): 0%, 1-10%, 11-25%, 26-50%, 51-75%, 76-90%, 91-99%, 100%. I followed van Oudtshoorn (1999) for the identification and nomenclature of grass species.

To calculate the NDVI greenness I used the SpectroSense 2+ tool. The SpectroSense 2+ hand-held meter with 8-channel sensors is produced by Skye Instruments who are specialist manufacturers of light and radiation sensors. Sensors were mounted on the top of an adjustable pole at 1.25m high for the measurement of a ground area of 0.5m x 0.5m block which represents a feeding station. The meter fits on a bracket at hand height with a spirit level to indicate the correct angle of measurement. I took one reading of each feeding station and between 10 to 12 feeding stations

within a foraging area. I then calculated the means and standard error of each foraging area to determine the variance among the samples.

DATA ANALYSIS

I investigated use versus non-use at two levels of selection: grass tufts within a feeding station and feeding station within a foraging area. A species was scored as being used if it had fresh bites. A feeding station was scored as being used when any species present within the feeding station had been used. I defined seasons for data analysis based on rainfall patterns and mean NDVI greenness of the grass: mid dry season of 2010 (Season 1), late dry season of 2010 (Season 2) and early wet season of 2010 (Season 3).

For data analysis, I only included the four most abundant grass species that were present in at least 10 feeding sites used by zebra per season. I did this to secure large sample size and reliable comparison of acceptability of grass species. At the grass tuft level, I calculated grass tuft availability and acceptability for each grass species for each season following Owen-Smith and Cooper (1987). Grass tuft availability was calculated by dividing the number of grass tufts of a particular species by the total number of grass tufts recorded. Grass tuft acceptability was calculated by dividing the number of grass tufts of a particular species that has been grazed by the total number of grass tufts of that species. To assess the effect of grass greenness on grass tuft acceptability I averaged the midpoints of the greenness categories recorded for each grass species during a specific season. At the feeding station level, I calculated the site-based availability and site-based acceptability of each species per season. Site-based availability of each grass species was calculated by dividing the number of feeding stations that had a certain species present by the total number of feeding stations recorded. Site-based acceptability of each grass species was calculated by dividing the number of feeding stations where a particular grass species was grazed by the total number of feeding stations where that same grass species was present.

Various logistic models were fitted to the data to test the research hypothesis regarding the relationship between the likelihood that feeding station or tuft was grazed and availability of species and greenness. I used the Generalized Linear Mixed Effects Models procedure in R version 2.10.1 (R Development Core Team 2010) using the 'lme4 package' (Bates *et al.* 2011). The statistical software uses a reference cell coding where one group of a categorical predictor is used as a reference and the effects of the other groups are relative to that reference group. Because of false convergence errors during analysis, when the model fitting functions fail to converge on a maximum likelihood estimate, which happens when there are too few data points within a level of a categorical variable, I combined the greenness ranks 50-75% and 76-90% into one rank of 50-90% green.

For grass tuft selection models, explanatory variables included were availability of individual species (categorical), season (mid dry, late dry and early wet (categorical)), and greenness of the species (categorical) as fixed effects and foraging area number and feeding station number as nested random effects. The reference cell used in the grass tuft models was greenness category 1-10% *P. maximum* species and mid dry season.

For feeding station selection, the explanatory variables used in the model were individual species availability (categorical), season (mid dry, late dry and early wet (categorical)), and the NDVI values (continuous) of each feeding station as fixed effects and foraging area number as a nested random effect. The reference cell used in the feeding station models was absence of the individual species and mid dry season. Prior to fitting any of the models I tested for collinearity between the various explanatory variables and collinearity was found between the species basal cover and the NDVI measurement. As expected, the leaf area index increases with the thickness of the green layer or with the number of green layers (van Bommel *et al.* 2006). This showed that as the cover increased so did the NDVI measurement. Thus, cover as a variable was removed from the model.

Models were compared using Akaike's Information Criterion, corrected for small sample bias (AICc). Of all the candidate models, the one with the lowest AICc value was considered the best model (Anderson 2008). Further model comparison was done by calculating the relative likelihoods of all the candidate models (wi) where a higher number indicates a higher probability that the model is closest to reality, of all the candidate models. I calculated evidence ratios (Ei,j) using the relative likelihoods (wi/wj). Evidence ratios are used to compare weights of evidence between models of the same set, where a higher evidence ratio indicates better support for model i over model j (Anderson 2008).

To assess the soundness of the logistic regression model against actual outcomes, I tested the goodness-of-fit of the best model. Logistic regression predicts the logit of an event outcome from a set of predictors. Because the logit is the natural log of the odds (or probability/[1–probability]), it can be transformed back to the probability scale. The resultant predicted probabilities can then be revalidated with the actual outcome to determine if high probabilities are indeed associated with events and low probabilities with nonevents. The degree to which predicted probabilities agree with actual outcomes is expressed as a measure of association. I used the Ĉ statistic as the measurement of association. The Ĉ statistic represents the proportion of pairs with different observed outcomes for which the model correctly predicts a higher probability for observations with the event outcome than the probability for nonevent observations. The Ĉ statistic ranges from 0.5 to 1. A 0.5 value means that the model is no better than assigning observations randomly into outcome categories. A

value of 1 means that the model assigns higher probabilities to all observations with the event outcome compared with nonevent observations (Peng*et al.* 2002).

To assess the foraging strategies of zebra I looked at each variable independently as well as the interaction between species and greenness and the interaction between species and season. I calculated the log odd ratios from the model coefficients and calculated the 95% confidence intervals from the variances and covariances of the estimated parameters in the model. Accordingly, I could not derive exact probabilities, but calculated log odds ratios relative to a reference, or baseline, category (Godvik *et al.* 2009, van der Merwe 2009, Van Beest *et al.* 2010). This indicated how levels of a category differed from a baseline (Zuur *et al.* 2009). Values above 0 indicate higher selection relative to the reference category, and values below 0 indicate lower selection relative to the reference category (Godvik *et al.* 2009). Confident intervals overlapping with the reference category indicate selection estimates no different than that of the reference category.

RESULTS

I sampled 94 foraging areas over 11 weeks. The total number of feeding stations (grazed and non-grazed distributed equally) amounted to 1120 and within the grazed feeding stations, I recorded 4860 grass tufts (2223 grazed and 2637 non-grazed). I recorded 33 different grass species, 27 used and 6 unused by zebra (Appendix I). Of the 27 different grass species grazed, I selected the 4 most abundant species (45% *Panicum maximum, 11% Urochloa mosambicensis, 7% Digitaria eriantha, 8% Themeda triandra*, Figure 2.1) and grouped all the other species into one group, namely 'Other' for data analysis.

For both feeding station selection and grass tuft selection I was interested in determining if the presence of any species compared to the mean greenness influenced the selection of a feeding station or tuft respectively, and how selection at these spatial scales changed over season (mid dry, late dry and early wet).

GRASS TUFTS WITHIN A FEEDING STATION

Observations of free-grazing zebra in Manyeleti show that zebra adapt their foraging strategies according to greenness and species. Out of 13 different models the best model was Model 1, with a ranking of 1 (Table 1). This model included an interaction between species (*P. maximum*, *U. mosambicensis*, *D. eriantha*, *T. triandra* and 'others') and greenness and an interaction between species (*P. maximum*, *U. mosambicensis*, *D. eriantha*, *T. triandra* and 'others') and season (Table 1), which suggests that grass species selection in Manyeleti was influenced mostly by the greenness of individual species and the changes in individual species which were brought on by changes in

season. The model fitted the data well and with a high probability that the model predicted actual outcomes (C = 0.859, Figure2.2). The estimated logistic regression coefficients of the best model used to calculate the log odds are given in Appendix II. The best model reference category was the selection of *P. maximum* species with a greenness category of 1-10%, in the mid dry season.

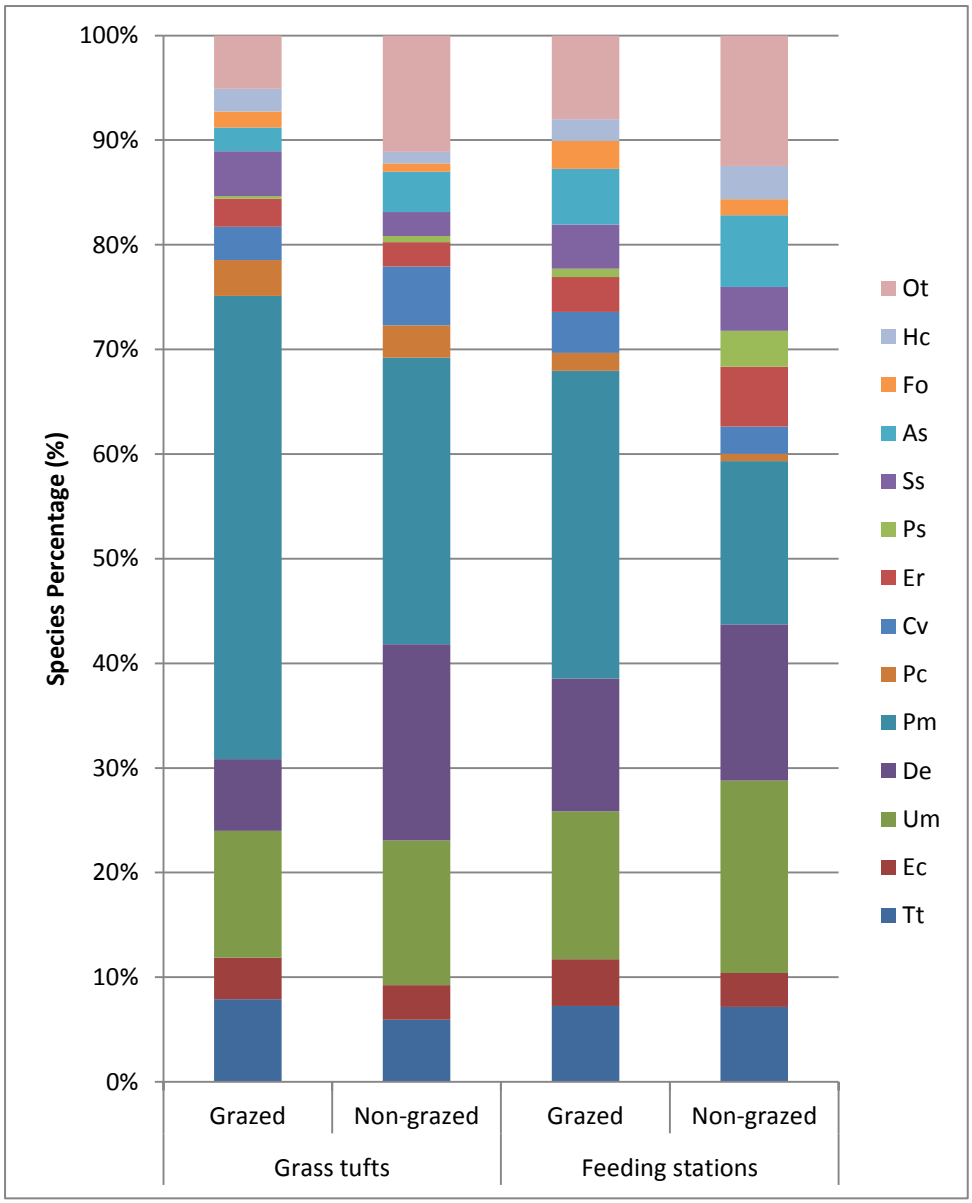


Figure 2.1: Grazed and non-grazed grass species of grass tufts found within used feeding stations and grass species found within used and non-used feeding stations. Ot – Other, Hc – *Heteropogon contortus*, Fo – Forbs, As – *Aristida* sp, Ss – *Setaria sphacelata*, Ps - *Pogonarthria squarrosa*, Er – *Eragrostis rigdior*, Cv – *Chloris virgata*, Pc – *Panicum coloratum*, Pm – *Panicum maximum,* De – *Digitaria eriantha*, Um –*Urochloa mosambicensis*, Ec – *Eragrostis chloromelas*, Tt – *Themeda triandra*

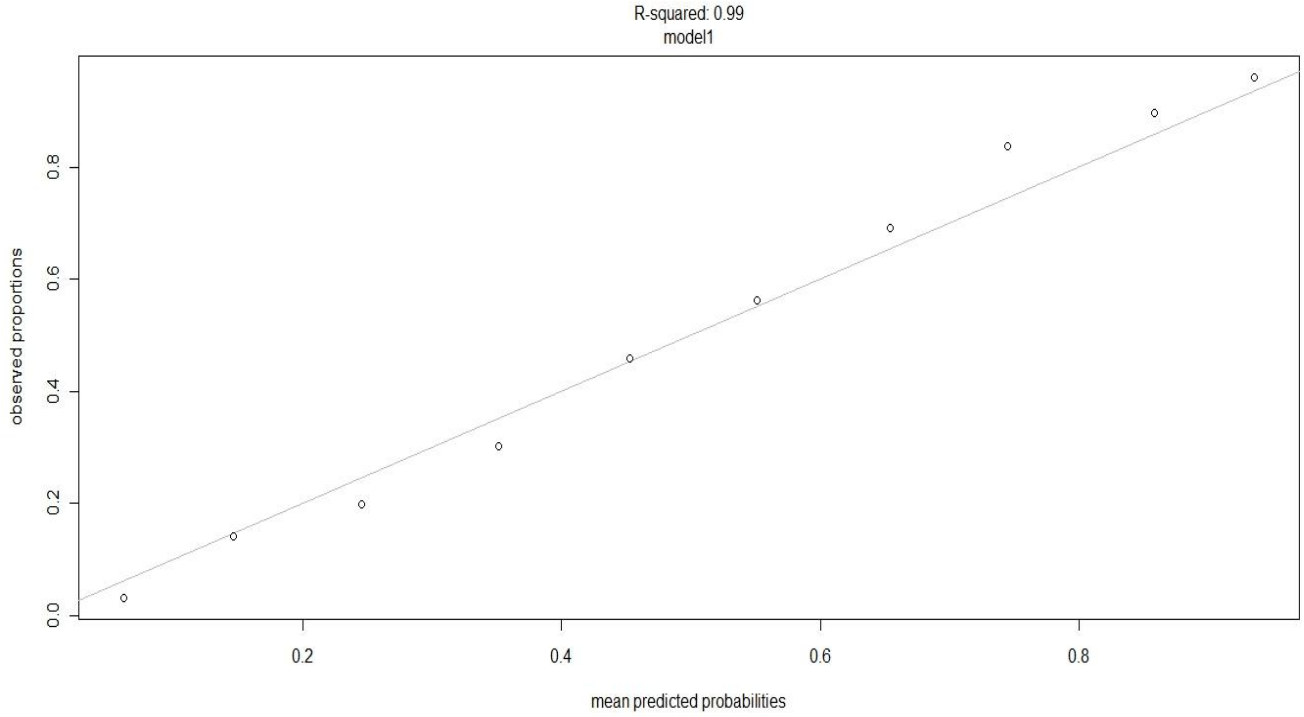


Figure 2.2: Graphical representation of the goodness of fit of the best model at grass tuft level (Model 1) indicating how well the model fits the data.

There was an increase in selection of grasses with an increase in grass greenness, which was more pronounced in the lower greenness classes. Compared to a greenness value of 1-10%, greenness categories 11-25% (log-odds = 2.43 ± 0.195), 26-50% (log-odds = 4.09 ± 0.411) and 51-90% (log-odds = 3.95 ± 0.670)were more selected (Figure2.3). In the mid dry season, most of the grass tufts where below 10% green but the few grass tufts that were in the higher greenness categories were almost 100% grazed when available (Figure 2.4a). The same results were found in the late dry season (Figure 2.4b). Thus, as the tuft greenness increased, the probability of being selected would increase. The early wet season has a higher number of grass tufts within the 11-25% and 26-50% greenness category and the number of grass tufts grazed increased as the greenness of the tuft increased similarly to the previous two periods however zebra did not select tufts with 1-10% greenness (Figure 2.4c). Hence, zebra would prefer to eat grass that is in the higher category of greenness.

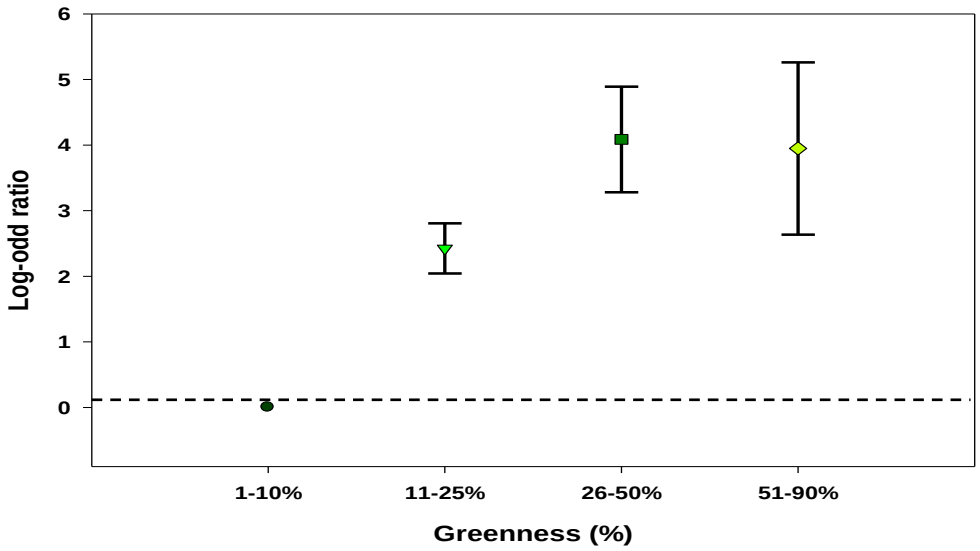
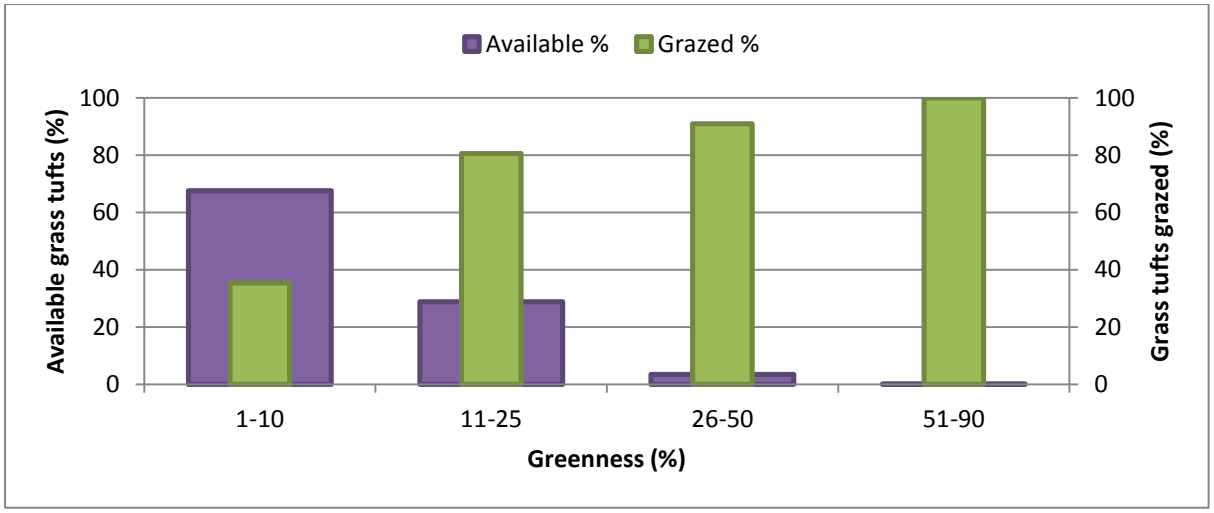
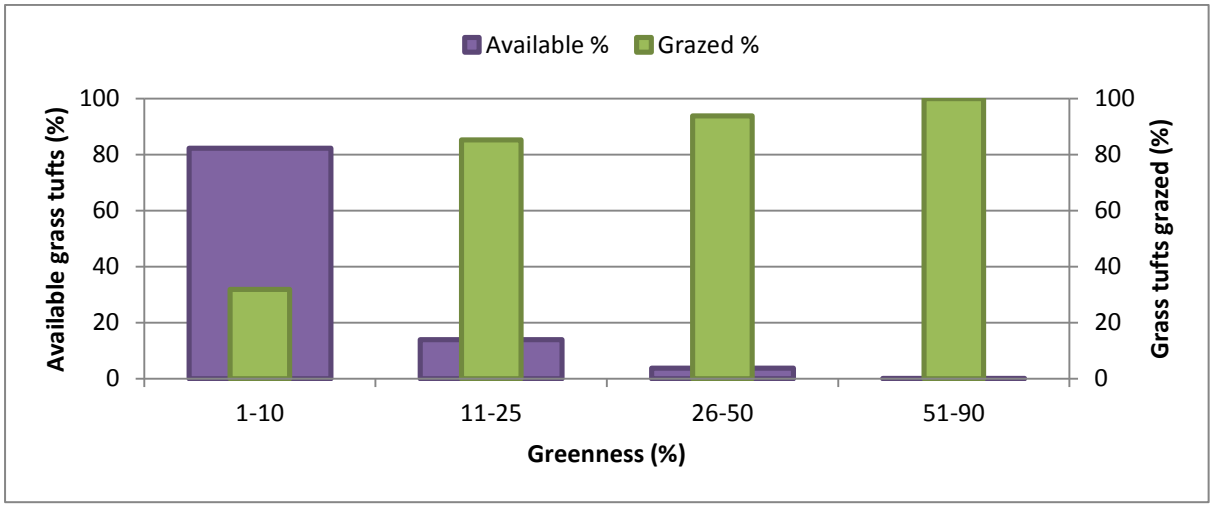


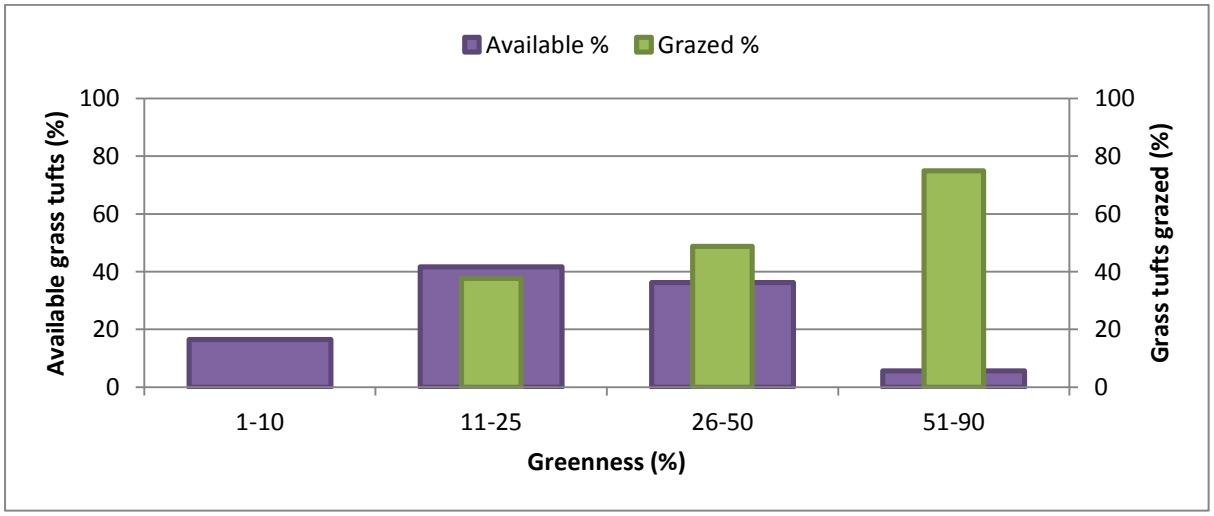
Figure 2.3: Grass tuft greenness selection estimates (± 95% confidence interval) for Manyeleti from data collected over a three month period between August and November 2010. The broken line indicates the reference level for the reference category, which is greenness category 1-10%.



a) Mid dry season



b) Late dry season



c) Early wet season

Figure 2.4: Percentage of available grass tufts (primary x axis) compared to the percentage of the grass tufts that are grazed within each greenness category (secondary x axis) in the three different seasons: a) Mid dry season, b) Late dry season and c) Early wet season.

Across all greenness classes there was more selection for *P. maximum*, except when the grass tufts were over 51% green (Figure 2.5). During the late dry season *P. maximum* was sought after but during the mid-dry season the other grasses were selected no different(Figure 2.6). *D. eriantha* (Log odds = -2.602 ± -3.15) and *U. mosambicensis*(Log odds = -1.993 ± -2.47)were more avoided by zebra across all seasons (Figure 2.7).The likelihood of zebra selecting other grasses remained mostly unchanged regardless of season, except for when 'other'(log-odds = 0.505 ± 2.689) had a higher value of greenness than *P. maximum* (reference) (Figure 2.5). There is a higher probability that zebra would select towards the greener grass.

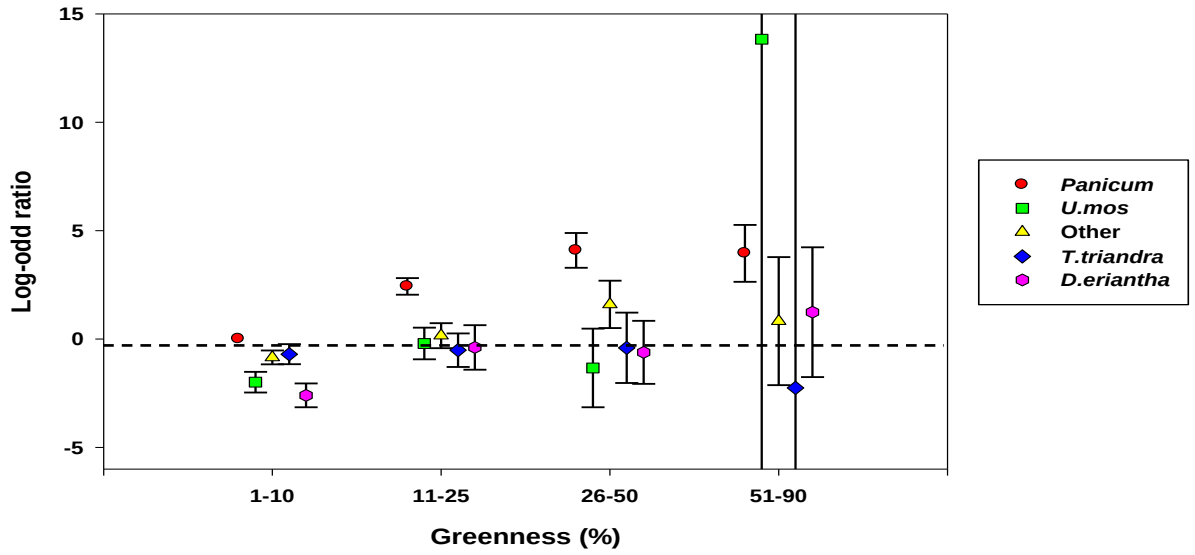


Figure 2.5: Grass species selection estimates per greenness category (± 95% confidence interval) for Manyeleti. The broken line indicates the reference level for the reference category, which is *P. maximum* at the 1-10% greenness category. Panicum = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Other = all other grasses, T.triandra = *Themeda triandra*, D.eriantha = *Digitaria eriantha*. From data collected over a three month period between August and November 2010

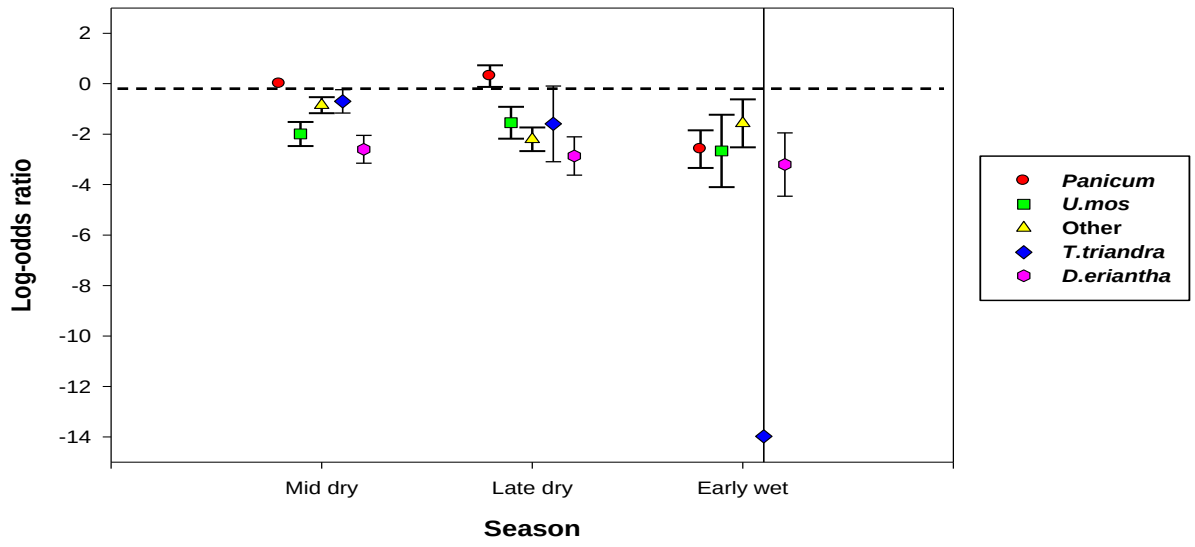


Figure 2.6: Grass species selection estimates per season (± 95% confidence interval) for Manyeleti. The broken line indicates the reference level for the reference category, which is *P. maximum*. P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Other = all other grasses, T.triandra = *Themeda triandra*, D.eriantha = *Digitaria eriantha*. From data collected over a three month period between August and November 2010.

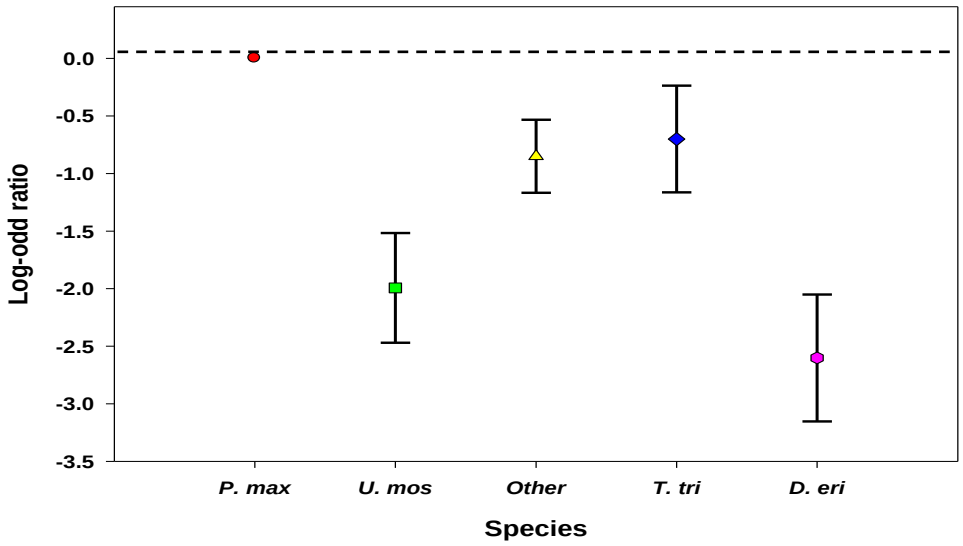


Figure 2.7: Grass species selection estimates (± 95% confidence interval) for Manyeleti. The broken line indicates the reference level for the reference category, which is *P. maximum*. P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Other = all other grasses, T.tri = *Themeda triandra*, D.eri = *Digitaria eriantha*. From data collected over a three month period between August and November 2010

Grass species selection models that contained only species or only greenness as an explanatory variable had low model probabilities (only species $w_i = 0.00$; only greenness $w_i = 0.00$; Table 1). This suggests that those models were highly unlikely to be close to reality and that specific grass species alone or grass greenness alone did not influence selection. Accordingly, this indicates that selection of a grass species is influenced by other factors, including the greenness of that species and season, and that zebra select for the most nutritious forage available, not necessarily only for specific species or greenness. Consequently I found that zebra selected more for *P. maximum* later in the dry season than any other species and have a general preference for *P. maximum* except in the early wet season or when the other species were green.

Table 1: Candidate mixed-effect models, and their coefficients, describing grass tuft selection in Manyeleti, showing various explanatory variables and interactions (×) included in models listed from higher to lower ranked.

Model selection based on AICc :							
Model #	Fixed effects:	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
mod1	Species X Greenness + Species X Season	32	5137.73	0	1	1	-2536.65
mod13	Greenness X Species+Season	24	5176.73	39	0	1	-2564.24
mod2	Species X Greenness + Season X Greenness	30	5180.43	42.7	0	1	-2560.02
mod9	Species + Greenness + Season	12	5222.86	85.12	0	1	-2599.4
mod3	Species X Greenness	22	5242.23	104.5	0	1	-2599.01
mod10	Species + Greenness	10	5284.7	146.97	0	1	-2632.33
mod12	Greenness + Season	8	5503.43	365.7	0	1	-2743.7
mod4	Greenness X Season	14	5507.87	370.14	0	1	-2739.89
mod7	Greenness	6	5570.58	432.85	0	1	-2779.28
mod5	Species X Season	17	6148.88	1011.14	0	1	-3057.37
mod11	Species + Season	9	6218.93	1081.2	0	1	-3100.45
mod6	Species	7	6229.62	1091.88	0	1	-3107.8
mod8	Season	5	6593.67	1455.93	0	1	-3291.83

FEEDING STATION SELECTION WITHIN A FORAGING AREA

Overall the observations showed that species did not influence feeding station select. However the change in the mean greenness of a feeding station that was brought on by a change in season may influence whether a feeding station was used. The best model (Model 9, ranking of 0.71; Table 2) for feeding station selection included an interaction between greenness of the station and presence of species (*P. maximum*, *U. mosambicensis*, *D. eriantha*, *T. triandra* and 'others') and an interaction between seasons and presence of species (*P. maximum*, *U. mosambicensis*, *D. eriantha*, *T. triandra* and 'others')(Table 2). The nearest ranking model (Model 7, $w_i = 0.29$) had only the

interaction between seasons and individual species (Table 2), which suggested that species selection was dependent on the season, but this model had a low probability (w_i = 0.29)indicating that it does not give actual outcomes. Both models fitted the data well(R^2 = 0.99; Figure 2.8). The best model reference category used in the feeding station models was absence of the individual species in the mid dry season. The estimated logistic regression coefficients of the best model are given in Appendix III.

Table 2: Some candidate high ranking, and low ranking mixed-effect models, and their coefficients, describing feeding station selection in Manyeleti, showing various explanatory variables and interactions (×) included in models.

Model selection based on AICc :							
Model #	Fixed effects:	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
mod9	NDVI X (T.triandra+U.mos+D.eriantha+P.max+Other) + Season X (T.triandra+U.mos+D.eriantha+P.max+Other)	25	3093.46	0	0.71	0.71	-1521.45
mod7	Season X (T.triandra+U.mos+D.eriantha+P.max+Other)	19	3095.27	1.82	0.29	1	-1528.47
mod10	NDVI X Season + NDVI X (T.triandra+U.mos+D.eriantha+P.max+Other)	17	3115.88	22.43	0	1	-1540.81
mod1	NDVI + Cover + Season + T.triandra + U.mos + D.eriantha + P.max + Other	13	3127.14	33.68	0	1	-1550.49
mod8	Cover X (T.triandra+U.mos+D.eriantha+P.max+Other)	25	3133.17	39.71	0	1	-1541.3
mod6	NDVI X (T.triandra+U.mos+D.eriantha+P.max+Other)	13	3135.94	42.48	0	1	-1554.89
mod5	T.triandra + U.mos + D.eriantha + P.max + Other	7	3136.27	42.82	0	1	-1561.11
mod2	NDVI	3	3244.03	150.57	0	1	-1619.01
mod3	Cover	5	3246.16	152.71	0	1	-1618.07
mod11	Intercept only	2	3259.01	165.55	0	1	-1627.5
mod4	Season	4	3263.01	169.55	0	1	-1627.5

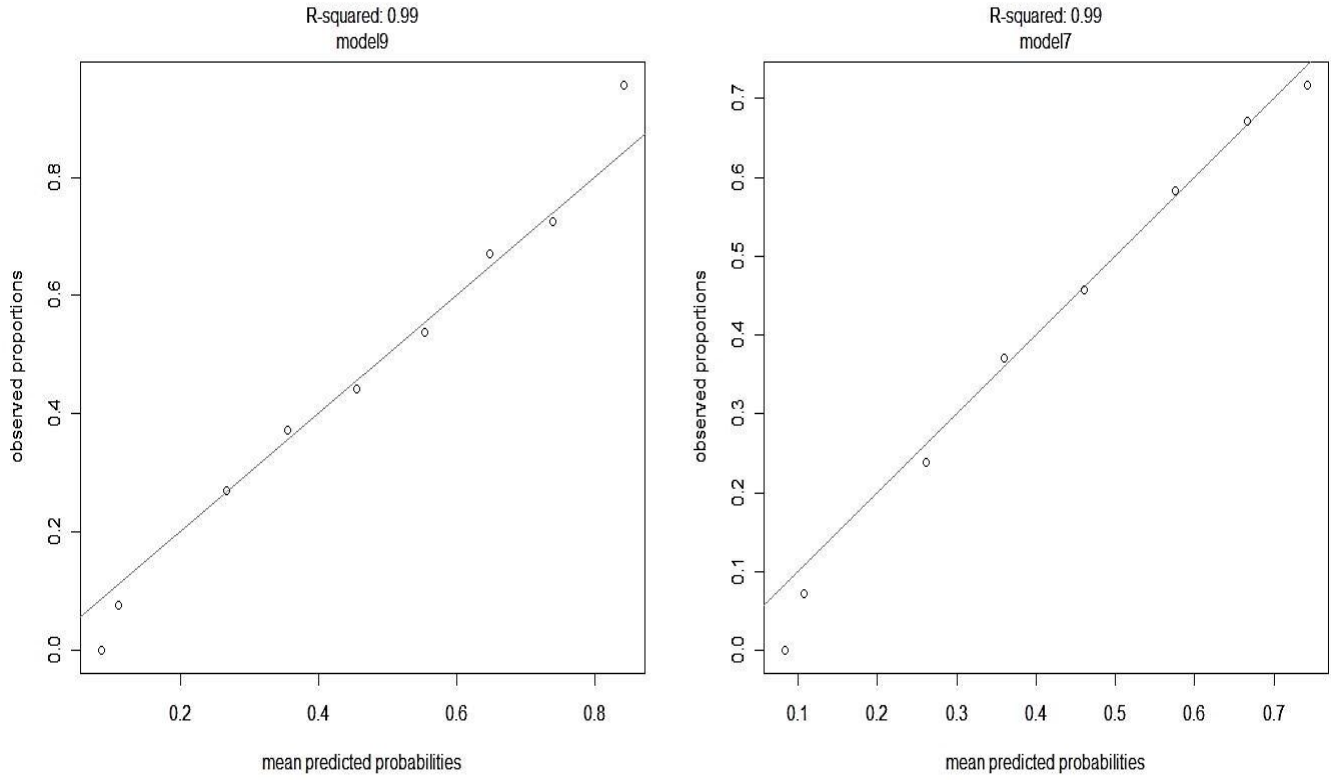


Figure 2.8: Goodness of fit graphically represented to indicate how well the best model (model 9) and the next ranked model (model 7) at the feeding station level fits the data.

Compared to the reference, the likelihood of a feeding station being selected was higher with the presence of *U. mosambicensis* with an average NDVI above 0.4 (Log-odds = 4.05 ± 2.64).Selection of feeding stations were no different with presence of *T. triandra* (log-odds = -1.13 ± 1.40), *D. eriantha* (log-odds = 0.475 ± 0.877) or other grasses (log-odds = -0.718 ± 0.800) present than with its absence, however feeding stations that had *P. maximum* (log-odds = 0.2032 ± 0.845) present showed an avoidance in selection as the mean greenness increased (Figure 9). Conversely there was no difference in feeding stations with no species and feeding stations with a species within a specific season (Figure 2.10).

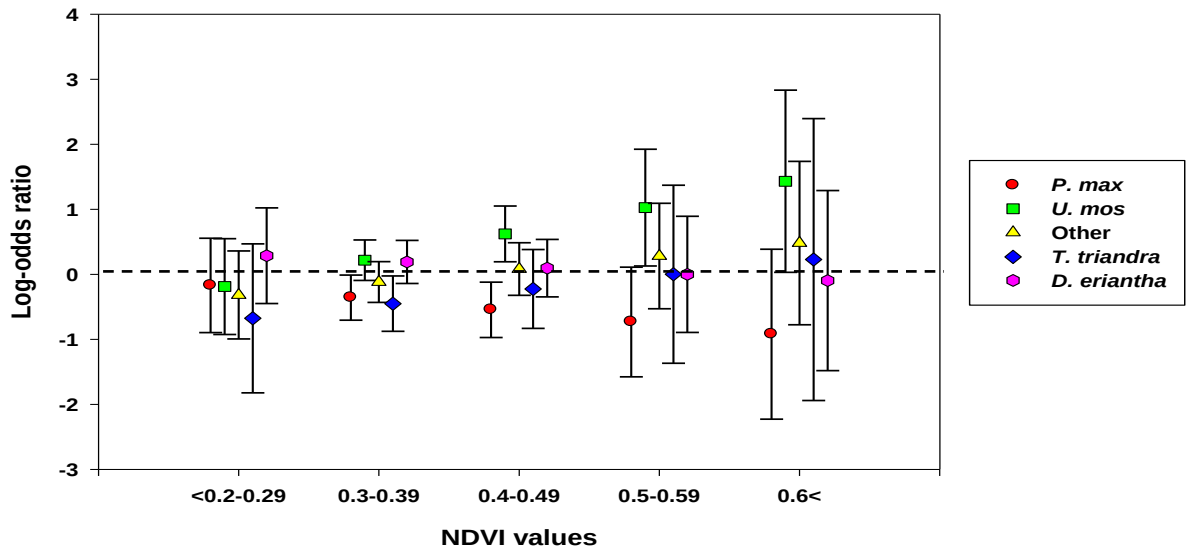


Figure 2.9: Feeding station selection estimates within NDVI categories (± 95% confidence interval) for Manyeleti. The broken line indicates the reference level for the reference category, which is the absence of species. P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Other = all other grasses, *T.triandra* = *Themeda triandra*, *D.eriantha* = *Digitaria eriantha*. From data collected over a three month period between August and November 2010

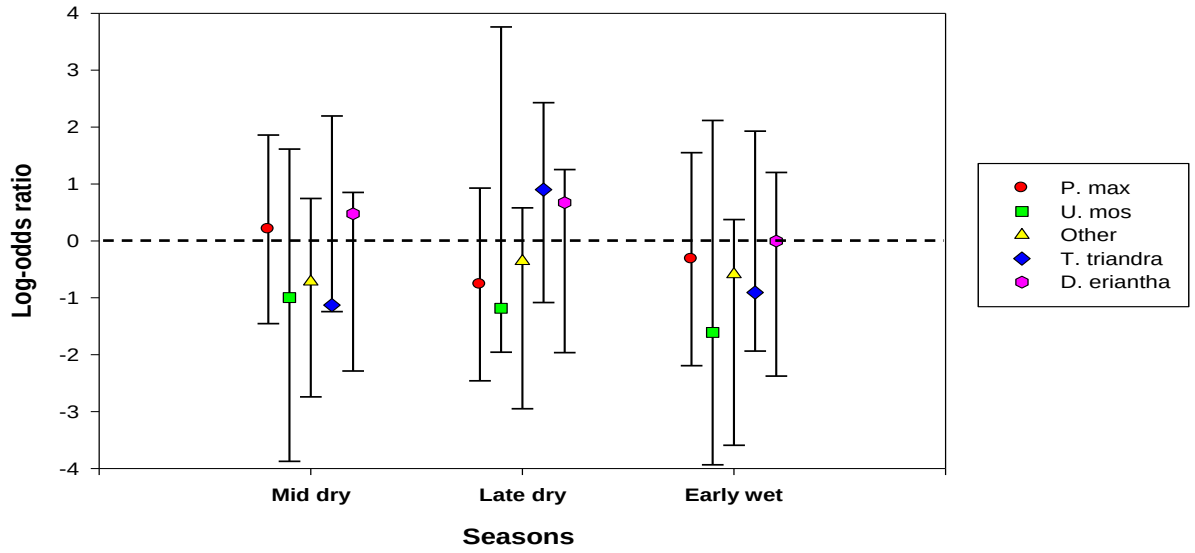
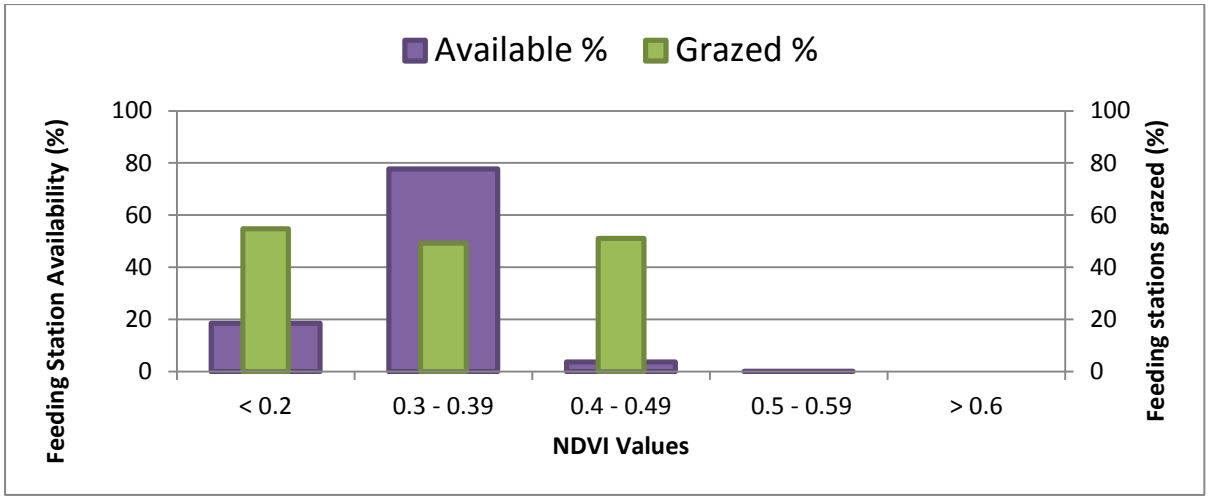
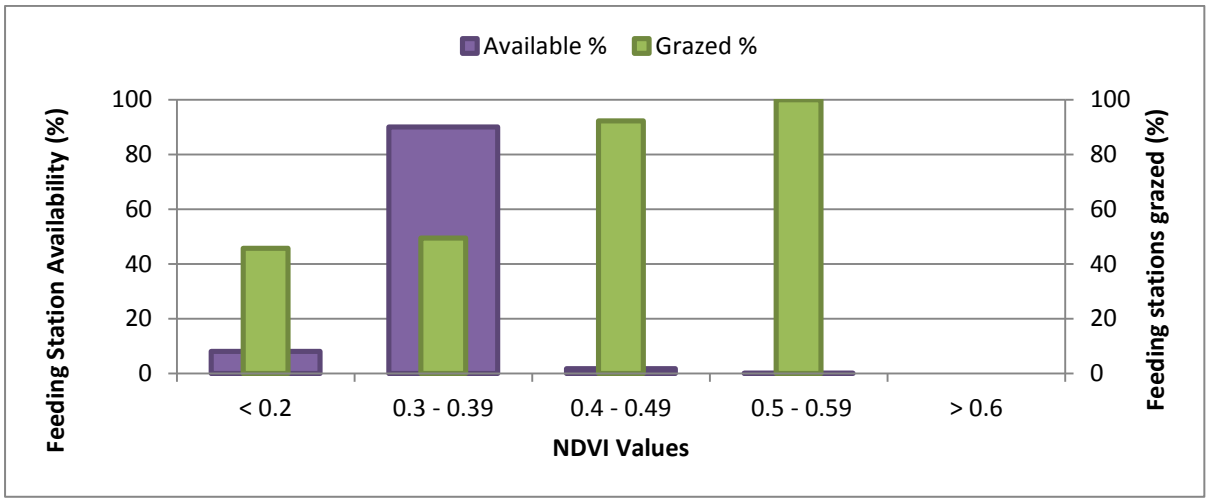


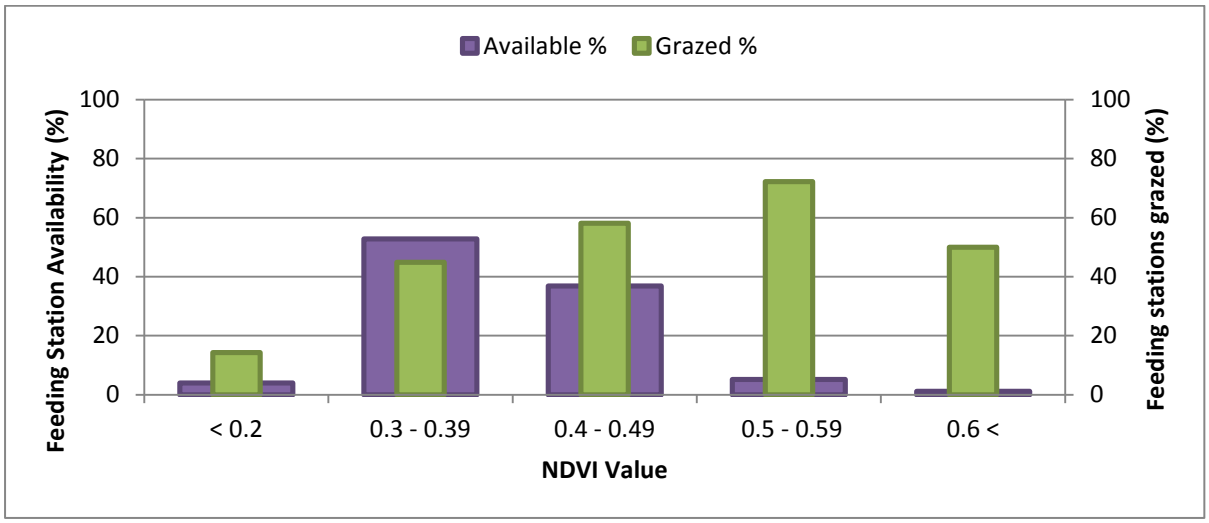
Figure 2.10: Feeding station selection estimates per season (± 95% confidence interval) for Manyeleti. The broken line indicates the reference level for the reference category, which is the absence of a species. P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis*, Other = all other grasses, T.tri = *Themeda triandra*, D.eri = *Digitaria eriantha*. From data collected over a three month period between August and November 2010.



a) Mid dry season



b) Late dry season



c) Early dry season

Figure 2.11: Percentage of available feeding stations (primary x axis) compared to the percentage of the feeding stations that are grazed within each greenness category (secondary x axis) in the three different seasons: a) Mid dry season, b) Late dry season and c) Early wet season.

The presence of greenness in the best model, indicated the importance of greenness in selection. Similar to species selection there was a general increase in the likelihood of a feeding station being selected with an increase in mean greenness of the feeding station (Figure 2.11). During the mid-dry season selection estimates were mostly unchanged with an increase in greenness (Figure 2.11a), however with zebra greener feeding stations were being selected more during the late dry season (Figure2.11b). During the early wet season selection for greener feeding stations were prominent but there was more feeding stations in that greenness category available compared to previous seasons (Figure 2.11c).

Feeding station selection models that contained only an interaction between greenness and season as an explanatory variable had low model probabilities (w_i = 0.00; Table 2). This suggests that those models were highly unlikely to be close to reality, and that change in grass greenness according to season did not have a significant effect in selection. However, zebra did have a slight preference for greener feeding stations in the late dry season.

DISCUSSION

Of the two hypotheses on grass tuft selection mentioned, only one was largely confirmed by this study. Grass tuft selection was aimed at the tuft with the highest quality of grass (greenness) however the second hypothesis was not supported as zebra were selective towards a certain species. But selectivity increased when there was a combination of preferred species and greenness. However, at the feeding station level both hypotheses were confirmed but with limitations. Firstly, zebra did select a feeding station based on greenness but only during the late dry season whereas the other seasons did not show selection. Secondly, more feeding stations were selected where *U. mosambicensis* was present but only when the feeding station greenness was above 40% green.

At the smallest scale, animals are confronted with spatial variability among the grass canopy, due to inherent differences in the nutrient content of different species, but because zebra are 'non' selective feeders (Macandza 2009) spatial resource heterogeneity should not influence selection. However this study's observations of free-grazing zebra in Manyeleti show that zebra adapt their foraging strategies according to greenness and species at the very fine scales, specifically during the late dry season, and less so in the wet season.

In the late dry season selection for greenness occurs at the feeding station level as well as the grass tuft level. However feeding station selection was limited to greenness due to season, selection for species occurred largely at the grass tuft level. In a study done by Ben-Shahar (1991), zebras were found to have some selectivity but the levels of selection were comparatively low compared to wildebeest. However Ben-Shahar and Coe (1992) found that zebra moved seasonally between grass

communities containing a high proportion of nutritious species rather than by selecting particularly nutritious species within communities. Whereas this study does show that zebra are indeed selective towards a certain species but only during the drier months. This is supported by Kleynhans *et al.* (2011) and Bodenstein *et al.* (2000) where their results show that *P. maximum* is the nucleus of the total diet and makes up at least 30% of that diet. *P. maximum* is a nutritious grass (Ben-Shahar & Coe 1992; Murray & Illius 2000; van Oudtshoorn 2009; Codron *et al.* 2007; Van Niekerk & Hassen 2009) and an indicator of good veld conditions (van Oudtshoorn 2009), but its greatest asset is that it stays green for longer (Grant *et al.* 2000) and is therefore favoured by most herbivores (van der Merwe 2009, van Oudtshoorn 2009) well into the dry season (Mutanga *et al.* 2004). This would explain why *P. maximum* made up the bulk of the diet and why it is selected for during resource-limiting times.

Even though grass tufts were selected according to species there was a higher probability that zebra would graze the grass tuft that was greener even if it was a lesser palatable species. For example, zebra selected *E. rigidior* with greenness above 26% compared to *P. maximum* with greenness less than 10%. In other studies, the most palatable plants or plant parts that are within reach were selected until palatability of remaining forage within the feeding station decreased to a threshold value (Bailey *et al.* 1996). The patterns of selectivity seen at the grass tuft level may be a means of compensating for variations in local conditions (Ben-Shahar 1991). Consequently, zebras will ultimately select for the more nutritious forage available at a given time.

I found that at the grass tuft level zebra selected towards a combination of both species and greenness but this trend did not follow through to the next hierarchal level which was the feeding station. Selectivity at the feeding station seems limited to the late dry season. This may be a consequence of what was noticed at the grass tuft level. Although zebra showed a limited feeding station selection, I did notice two trends with *P. maximum* and *U. mosambicensis*. As the feeding stations became greener, there was a lower probability that zebra would select a feeding station that had *P. maximum* present. This observation could be a consequence of what was observed at the grass tuft level, that when there was an overall increase in palatability of the general grass sward, the variety of accepted plants increased. On the other hand, zebra showed a tendency to select feeding stations that displayed *U. mosambicensis* as greenness increased above 40%. During the dry season, I did observe various ages of dung present within foraging areas giving an indication that zebra had a tendency to return to areas previously grazed. *U. mosambicensis* grows in disturbed and overgrazed areas which may be the reason for 'inadvertently' selecting feeding stations that presented this species.

Each scale is functionally defined based on characteristic behaviours that occur at different rates (Bailey *et al.* 1996). These levels are associated with different units of space that vary in absolute dimension with the body size and foraging strategy of the herbivore (Bailey *et al.* 1996). Despite this definition the hierarchical approach to describe foraging behaviour followed in this study reveals that the selection of feeding stations and the feeding at feeding stations are fundamentally different processes (Wallis De Vries *et al.* 1999). This indicates that there is a possibility that zebra may not select at this level because this hierarchal scale is ultimately a man-made entity defined by humans and that zebra do not view a 0.5 by 0.5 m quadrat as a feeding station. Ultimately it is the animal's perceptions and foraging responses that must define the boundaries between the subunits within hierarchical scales (Senft *et al.* 1987). Ben-Shahar (1991) proposed that zebra can be selective but it all depends on which scale you are looking at whether they are selective or not. This study did not look at the patch level, thus there may be a chance that zebra may select towards greenness at this level or even a higher hierarchal level such as landscape.

The major sources of greenness measures are either satellite images (e.g. NDVI, Osborne *et al.* (2001); Vina *et al.* (2008)) or field-based studies (i.e. Macandza 2009; Parrini & Owen-Smith 2010) that take visual greenness estimates using Walker's (1976) eight-point scale. A recent study was able to detect differences in seasonal feeding station greenness within buffalo foraging areas using a handheld NDVI sensor (SpectroSense 2+) (Macindoe, unpublished). This study enhances the notion that NDVI can be used at small scales too as it is able to detect greenness at which animals respond. Analyses at multiple spatial scales are important as a study done at one spatial scale may not detect all the patterns. Therefore the causal factors behind these observed distribution patterns may be incorrectly looked upon or not detected at all (Bro-Jorgensen, Brown, & Pettorelli, 2008). Overall zebra may or may not be selective depending on the scale of selection, and studies that have used NDVI, have mainly looked at the landscape scale to track animal movement. However this study has indicated that multiple hierarchal levels need to be studied before an assumption can be made at the landscape levels.

These results support my expectations that (1) greenness is an important factor in governing resource selection, and (2) that forage quality is a driving factor in larger scale selection. Although the highest quality of grass (greenness) was selected, zebra were selective towards a certain species. Indicating that, depending on scale and season, zebra adapt their foraging strategies according to greenness and species. The results detected some selectivity, so that the distinction of zebra as generalists or selectors depends on the scale of definition. Even though the feeding station concept is a useful structural concept, it has little support as a scale of selection in this study. Thus, the dimensions of measurements (study area) are important in defining selectivity. Although the promise

remote sensing technology offers to ecology is to provide data at large and synoptic scales, small scale foraging decisions by herbivores have been shown to significantly alter their large scale distribution patterns (Pretorius, 2009). Thus landscape level foraging selection may not represent the true forage selection that occurs at all levels. To further our understanding of the foraging strategies of large herbivores, future research will have to focus on comparing the levels of selection, seasonal variation. I suggest for future studies to look at the effects of seasonal variation of preferred forage in Manyeleti and how forage selection would compare to other regions, such as the Serengeti plains.

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APPENDICES

Appendix I

Used species	Unused species
Panicum maximum	*Cymbopogon* sp
Panicum coloratum	*Perotis patens*
Urochloa mosambicensis	*Cenchrus ciliaris*
Digitaria eriantha	*Aristida* sp
Themeda triandra	*Aristida scabrivalvis*
Heteropogon contortus	*Sporobulus festivus*
Setaria sphacelata var. *Sphacelata*	*Sporobulus nitens*
Eragrostis superb	*Pogonarthria squarrosa*
Eragrostis trichophora	*Sporobulus fimbriatus*
Eragrostis rigidior	
Eragrostis ciliaris	
Panicum ecklonii	
Tricholaena monachne	
Eragrostis lehmanniana	
Eragrostis chloromelas	
Cynodon dactylon	
Chloris virgata	
Dactyloctenium giganteum	
Bothrio chloaradicans	

APPENDIX II: GENERALIZED LINEAR MIXED MODEL REPRESENTING THE COEFFICIENTS THAT ARE USED TO DETERMINE THE LOG-ODD RATIOS FOR GRASS TUFT SELECTION

Generalized linear mixed model fit by the Laplace approximation					
Formula: Eaten ~ Species.Treatment * Greenness + Species.Treatment * Season + (1 | Foraging.Area/Feeding.site)					
Data: g8					
	AIC	BIC	logLik	deviance	
	5137	5345	-2537	5073	
Random effects:					
Groups	Name	Variance	Std.Dev.		
Feeding.site:Foraging.Area	(Intercept)	0.27538	0.52477		
Foraging.Area	(Intercept)	0.44454	0.66674		
Number of obs: 4860, groups: Feeding.site:Foraging.Area, 1120; Foraging.Area, 93					
Fixed effects:					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	-8.99E-03	1.50E-01	-0.06	0.952125	
Species.TreatmentU.mos	-1.99E+00	2.43E-01	-8.2	2.40E-16	***
Species.TreatmentOth	-8.50E-01	1.62E-01	-5.25	1.52E-07	***
Species.TreatmentT.triandra	-7.00E-01	2.37E-01	-2.96	0.003075	**
Species.TreatmentD.eriantha	-2.60E+00	2.81E-01	-9.261	< 2e-16	***
Greeness11-25%	2.43E+00	1.95E-01	12.447	< 2e-16	***
Greeness26-50%	4.09E+00	4.11E-01	9.949	< 2e-16	***
Greeness51-90%	3.95E+00	6.70E-01	5.891	3.85E-09	***
Season2	2.99E-01	2.19E-01	1.362	0.173346	
Season3	-2.60E+00	3.80E-01	-6.827	8.65E-12	***
Species.TreatmentU.mos:Greeness11-25%	1.79E+00	3.54E-01	5.043	4.59E-07	***
Species.TreatmentOth:Greeness11-25%	1.00E+00	2.71E-01	3.705	0.000211	***
Species.TreatmentT.triandra:Greeness11-25%	1.80E-01	3.72E-01	0.485	0.627499	
Species.TreatmentD.eriantha:Greeness11-25%	2.21E+00	4.98E-01	4.449	8.63E-06	***
Species.TreatmentU.mos:Greeness26-50%	6.56E-01	9.17E-01	0.716	0.473939	
Species.TreatmentOth:Greeness26-50%	2.45E-01	5.45E-01	0.449	0.65327	
Species.TreatmentT.triandra:Greeness26-50%	2.93E-01	8.17E-01	0.359	0.719539	
Species.TreatmentD.eriantha:Greeness26-50%	1.99E+00	7.24E-01	2.74	0.006147	**
Species.TreatmentU.mos:Greeness51-90%	1.58E+01	6.10E+02	0.026	0.979288	
Species.TreatmentOth:Greeness51-90%	1.68E+00	1.50E+00	1.115	0.26482	
Species.TreatmentT.triandra:Greeness51-90%	-1.56E+00	1.25E+03	-0.001	0.999006	
Species.TreatmentD.eriantha:Greeness51-90%	3.84E+00	1.52E+00	2.526	0.011523	*
Species.TreatmentU.mos:Season2	4.45E-01	3.20E-01	1.394	0.16334	
Species.TreatmentOth:Season2	-1.35E+00	2.35E-01	-5.755	8.69E-09	***
Species.TreatmentT.triandra:Season2	-8.94E-01	7.61E-01	-1.175	0.240159	
Species.TreatmentD.eriantha:Season2	-2.65E-01	3.81E-01	-0.696	0.486552	
Species.TreatmentU.mos:Season3	-6.71E-01	7.01E-01	-0.958	0.338181	

Species.TreatmentOth:Season3	-7.20E-01	4.72E-01	-1.524	0.127579	
Species.TreatmentT.triandra:Season3	-1.33E+01	2.85E+02	-0.047	0.962792	
Species.TreatmentD.eriantha:Season3	-6.02E-01	5.98E-01	-1.007	0.313706	

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					

APPENDIX III: GENERALIZED LINEAR MIXED MODEL REPRESENTING THE COEFFICIENTS THAT ARE USED TO DETERMINE THE LOG-ODD RATIOS FOR FEEDING STATION SELECTION

Generalized linear mixed model fit by the Laplace approximation					
Formula: Grazed ~ NDVI * (T.triandra + U.mos + D.eriantha + P.max + Other) + Season * (T.triandra + U.mos + D.eriantha + P.max + Other) + (1 | Foraging.area)					
Data: n6					
	AIC	BIC	logLik	deviance	
	3093	3237	-1521	3043	
Random effects:					
Groups	Name	Variance	Std.Dev.		
Foraging.area	(Intercept)	5.29E-13	7.27E-07		
Number of obs: 2348, groups: Foraging.area, 94					
Fixed effects:					
	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	0.6389	1.9209	0.333	0.739442	
NDVI	-1.2551	5.6415	-0.222	0.823948	
T.triandraPresent	-1.1297	1.4004	-0.807	0.419815	
U.mosPresent	-0.9979	0.8894	-1.122	0.261835	
D.erianthaPresent	0.4755	0.8774	0.542	0.587862	
P.maxPresent	0.2032	0.8456	0.24	0.810112	
OtherPresent	-0.7176	0.8004	-0.897	0.369959	
Season2	-1.6295	0.6312	-2.581	0.009838	**
Season3	0.7243	0.7239	1.001	0.317059	
NDVI:T.triandraPresent	2.2607	4.1429	0.546	0.585289	
NDVI:U.mosPresent	4.0482	2.6371	1.535	0.124755	
NDVI:D.erianthaPresent	-0.9525	2.5946	-0.367	0.713533	
NDVI:P.maxPresent	-1.873	2.4692	-0.759	0.448135	
NDVI:OtherPresent	1.9966	2.3576	0.847	0.397065	
T.triandraPresent:Season2	2.031	0.4595	4.42	9.85E-06	***
T.triandraPresent:Season3	0.2209	0.4679	0.472	0.636883	
U.mosPresent:Season2	-0.1881	0.2278	-0.826	0.409042	
U.mosPresent:Season3	-0.6112	0.354	-1.727	0.084222	.
D.erianthaPresent:Season2	0.1975	0.2459	0.803	0.421836	
D.erianthaPresent:Season3	-0.4787	0.3134	-1.528	0.12658	
P.maxPresent:Season2	-0.9684	0.2538	-3.815	0.000136	***
P.maxPresent:Season3	-0.5237	0.3281	-1.596	0.110465	
OtherPresent:Season2	0.3619	0.2395	1.511	0.130702	
OtherPresent:Season3	0.1303	0.3101	0.42	0.67424	

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1					