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Resource selection by impala (*Aepyceros melampus*) in savanna systems, South Africa: which factors govern forage selection in a mixed feeder?

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Master of Science

Johannesburg, 2010

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 the Witwatersrand, Johannesburg. It has not been submitted before for any degree of examination at any other university.



(Signature of candidate)

24 August 2010

Abstract

Herbivores can be divided into three general groups: grazers, browsers and mixed feeders. Mixed feeders switch between grazing and browsing throughout the year, mostly due to changes in environmental conditions. I investigated fine scale resource selection in a mixed feeder, impala (*Aepyceros melampus*), as well as how their diet changed across seasons and which factors drove a change in diet. The study was conducted in two savanna reserves in South Africa, where I located foraging impala herds on a daily basis. At each feeding area I collected data at three spatial scales: species level, feeding station level and patch level. Some of the data included species identification, greenness, biomass (of the feeding station) and type of cover (in the patch). I also sampled an unused patch located 40 m away. I found that impala preferred grazing and especially grazing on *Panicum maximum* and *Urochloa mosambicensis*. Impala browsed infrequently and even though I expected them to make a switch from a grass dominated diet to a browse dominated diet, I only saw an expansion of their diet. Impala included more forbs, seed pods and grass stems in their diet during the late dry season. Greenness (of the species, feeding station and patch), biomass and type of cover were all important in driving selection. Because of their smaller bite sizes impala were able to select for single green stems located within mostly dry tufts of grass. Contrary to previous suggestions, impala did not switch from predominantly grazing to browsing when the 2 monthly running mean of rainfall fell below 30mm.

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CHAPTER 1 – GENERAL INTRODUCTION

Literature review

Resource selection in herbivores is not only influenced by the presence of secondary compounds or the potential nutritional content of forage (Heady 1964; Cooper et al. 1988; Du Toit et al. 1990; Seagle and McNaughton 1992; Murray 1995) but also by the quality and quantity of available resources at any given time (Owen-Smith 1994; Wilmshurst et al. 1999). Structural deterrents such as spines on trees (Cooper and Owen-Smith 1986) and silica in grass (McNaughton et al. 1985; Massey et al. 2009) also impact on how much feeding a herbivore would do on a specific food source. Exactly how all these factors influence resource selection in large herbivores remains an important question in herbivore ecology (Heady 1964; Owen-Smith 2005).

Plant cell walls are mostly made up of cellulose, which is partially digestible, and lignin, which is indigestible (Short et al. 1974; McNaughton and Georgiadis 1986). The contents of plant cells are composed of proteins, minerals and soluble carbohydrates, which vary in quantities between plant species (Jarman 1974) and plant parts (Demment and Van Soest 1985). The nutritional quality of plants is determined by a combination of the ratio of cell walls to cell contents (Owen-Smith 2005), and the concentration of nutrients constituting the cell contents (McNaughton and Georgiadis 1986), and also varies between plant parts (McNaughton and Georgiadis 1986; Arzani et al. 2004). Changes in light, water, and soil content (Van Soest 1994), as well as maturation of plant cells (Van Soest 1994; Arzani et al. 2004) influence the nutritional content of plant cells.

Nutritional content not only differs between plant types, but also varies between plant parts, with fruits, stems and seed pods all having variable nutritional qualities (Heady 1964). Generally fleshy fruits are considered highly nutritious, but some might contain indigestible carbohydrates, which could outweigh the nutritional benefits (Demment and Van Soest 1985). Grass stems are generally high in fiber and low in nutrition and thus not favoured by herbivores (Murray and Illius 2000; Arzani et al. 2004), while some seed pods are good sources of nutrition during the dry season, when other food sources are scarce, and are consumed by both domestic and wild herbivores (Coppock et al. 1986; McNaughton and Georgiadis 1986; Miller 1994; Miller 1996). Hence, it would be most advantageous to a mixed feeder to select for the most nutritious plant parts available at a given time. I expect impala to switch to alternative plant parts when their preferred forage becomes unavailable or declines in quality.

There also exists a negative relationship between forage maturity and digestibility, with grasses increasing in fiber content (Van Soest 1994; Arzani et al. 2004), and tree foliage increasing in oils and resins, with age (Jarman 1974). 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 and Owen-Smith 1996). Both grass and non-grass species experience physical changes across seasons (Jarman 1974), but even though grasses keep growing for a long time, even after being grazed, they tend to produce most of their foliage immediately following the onset of rain and only last for a short period (Jarman 1974). Leaves from non-grass species on the other hand stop growing when they reach maturity, but tend to produce clusters of leaves at various times. Hence, when no nutritious grass is available there might be leaves from dicots present (Jarman 1974).

However, even if plant species are nutritionally acceptable, the presence of physical structures (e.g., thorns and spines on twigs and stems, prickles on leaves) also influence selection

by limiting herbivore bite size and bite rates (Cooper and Owen-Smith 1986), or influencing the twig size that is selected by herbivores (Belovsky et al. 1991), and thus influencing diet composition. The presence of spines prevents kudu from eating small leaves and decreases food intake rate; whereas, smaller antelope (e.g. impala), having smaller bite sizes, are less limited by leaf size and the presence of spines (Cooper and Owen-Smith 1986).

Similar to spinescence on woody species, grasses contain silica bodies that act as herbivore deterrents and differ in concentrations between species and plant parts (McNaughton et al. 1985; Massey et al. 2009). This variability in nutritional quality and physical properties of forage affect herbivore distribution at a local and regional scale (Seagle and McNaughton 1992), and force herbivores to switch to alternative species when favoured species are insufficiently available (Albon and Langvatn 1992; Wilmshurst et al. 1999; Mysterud et al. 2001).

Herbivores can be divided into three general groups: browsers, grazers and mixed feeders (Hofmann 1989). Of the 44 large herbivores that occur in Africa, 10 are considered to be mixed feeders (Owen-Smith 1982). Herbivores that almost exclusively graze include sable antelope (*Hippotragus niger*), buffalo (*Syncerus caffer*) and white rhino (*Ceratotherium simum*), with those that predominantly browse being kudu (*Tragelaphus strepsiceros*), black rhino (*Diceros bicornis*) and giraffe (*Giraffa camelopardalis*) (Skinner and Chimimba 2005). Intermediate feeders, or mixed feeders, are herbivores that feed on a combination of grasses and non-grass species throughout the year (Jarman 1974; McNaughton and Georgiadis 1986), and can be broadly classified into two groups: mixed feeders preferring grass, and mixed feeders preferring browse (McNaughton and Georgiadis 1986).

Various factors have been put forward to explain the grazer/browser continuum among herbivores, some of which include anatomical differences between the animals belonging to the different groups (McNaughton and Georgiadis 1986; Hofmann 1989). Gordon and Illius

(1994) and Robbins et al. (1995) performed detailed investigations examining differences between grazers and browsers, but even though theses studies aimed at finding anatomical differences to explain the browser/grazer dichotomy, none of them attempted to explain how and why mixed feeders change between diets. Even though kudu are browsers, studies have shown that they prefer certain species to others (Owen-Smith and Cooper 1987a) and that their diet changes between seasons. Unpalatable evergreen dicot species become more acceptable as the dry season progresses and palatable deciduous species decrease in abundance (Owen-Smith and Cooper 1987b; Owen-Smith 1994). Resource switching has been shown in various large mammal species, including eland (*Taurotragus oryx*), which switch between diets during resource limiting periods (Nge'The and Box 1976; Watson and Owen-Smith 2000; Skinner and Chimimba 2005) and nyala (*Tragelaphus angasii*) switch from predominantly browsing to incorporating grass in their diet in the dry season (Van Rooyen 1992).

Impala are intermediate feeders that prefer to graze, but their diet include grasses, browse, forbs, seeds and fruit (Jarman 1974; McNaughton and Georgiadis 1986; Skinner and Chimimba 2005) and they switch between forage types in response to fluctuating environmental factors such as decreased rainfall (Du Toit1988; Van Rooyen 1992; Meissner et al. 1996; Skinner and Chimimba 2005). My first objective for this study was to identify the resources impala use to make up their diet and which factors influence that selection, and to classify resources used by impala into three classes; preferred resources, reserve resources, and buffer resources. My second objective was to investigate the feeding patterns of impala, and how that changes between seasons.

Together with investigating the feeding patters I will aim to classify the resources used by impala into preferred, reserve and buffer resources. Preferred resources are plant species that are highly palatable and most readily eaten by herbivores whenever available and

nutritionally acceptable (Owen-Smith 2005). Reserve resources are used to supplement the diet when preferred resources are declining in availability and nutrition, and buffer resources are used only to help sustain herbivores through the dry season when very little other forage is available or palatable (Owen-Smith 2005). Preferred resources are likely to be key resources, which are essential to determining or influencing survival over resource limiting periods (Varley and Gradwell 1960; Illius and O'Connor 2000). I expect to show that certain plant species (Bailey et al. 1996) and plant species characteristics (Wilmshurst et al. 1999) are important for determining habitat selection at fine or broad scales for mixed feeders and I expect to find impala choosing the greenest forage available at a given time.

Even though I expect greenness to be a driving factor in selection at a broader scale, larger scale selection is also influenced by various factors including shrub and tree cover in a feeding patch, and the biomass of patches and feeding stations. Canopy cover of especially *Acacia* spp. increases the nutritional value of sub-canopy grasses (Belsky 1994; Ludwig et al. 2004; Treydte et al. 2007), and the need for vigilance in some large mammals (Underwood 1982; Bednekoff and Ritter 1994; Hunter and Skinner 1998) increases the tendency for some prey species to select more open areas (Underwood 1982; Martella et al. 1995; Mysterud and Ostbye 1999). However, because of the relatively small body size of impala, it has high energy requirements (McNaughton and Georgiadis 1986), and therefore needs high quality foods (Illius and Gordon 1992; Van Soest 1994). High biomass areas are generally high in fiber and low in nutrition, and accordingly, herbivores should prefer to feed from low biomass areas that have intermediate height grasses; this should maximise digestibility and energy intake (Demment and Van Soest 1985; Wilmshurst et al. 1999; Wilmshurst et al. 2000; Mutanga et al. 2004). Thus, although cover influences large scale selection in many herbivores (Underwood 1982; Mysterud

and Ostbye 1999; Martella et al. 1995) I expect larger-scale selection in impala to be driven by forage quality, rather than by cover.

Study design

Study area

The study was conducted on the border of the Mpumalanga and Limpopo Provinces in South Africa in two reserves situated in the savanna biome of South Africa (Figure 1.1). The savanna biome is the largest biome in Southern Africa, covering almost 50% of its area, and is widely known as a vegetation type where there is a well-established grass layer occurring beneath a woody layer. Savanna covers vast areas in the northern and eastern parts of South Africa and also stretches into Namibia, Botswana and Zimbabwe, where it makes up the dominant vegetation type (Scholes 1997; Schmidt et al. 2002). In South Africa the savanna biome is well conserved mainly due to the presence of Kruger National Park and Kalahari Gemsbok Park within the biome, as well as many smaller reserves (Rutherford and Westfall 1996). Savannas are often referred to as bushveld and can be sub-divided into bushveld classes, including sour bushveld, usually occurring on nutrient poor soils and generally avoided by herbivores, and sweet bushveld that is usually associated with nutrient rich soils and is preferred by herbivores (Schmidt et al. 2002). Both of the reserves used for this study were located in the lowveld bushveld, which again can be classified as being sour or sweet. The lowveld bushveld is characterised by "open tree savanna" in the low land areas, dense upland areas and river banks dominated by woodland vegetation (Van Rooyen and Bredenkamp 1996). The dominant tree species in the lowveld bushveld include, among others, *Combretum* spp, *Acacia* spp, *Terminalia*

spp, *Euclea* spp. and *Ziziphus mucronata* (Van Rooyen and Bredenkamp 1996; Schmidt et al. 2002). This veld type also has a moderately developed shrub layer with species such as *Dichrostachys cinerea* being common. The grassy layer is poor to moderately developed and dominant grasses species include *Aristida* spp, *Eragrostis* spp, *Panicum* spp, *Digitaria* spp, *Urochloa* spp, and *Themeda triandra* (Van Rooyen and Bredenkamp 1996; Van Oudtshoorn 2004).

Study animal

Impala occur in open woodland in northeastern South Africa, southwest Zimbabwe, Mozambique, Botswana and Namibia. They are medium sized mammals (40-55 kg), feed on a variety of plant species and occur in areas where water is available (Skinner and Chimimba 2005). Males and females are distinct, with males carrying horns. Impala are fairly common antelope and therefore easy to locate and observe from a vehicle without the need for radio collars. They are mixed feeders, consuming a wide variety of plant species and plant parts throughout the year, including fallen leaves from some tree species (Du Toit 1988, Skinner and Chimimba 2005). However, very few studies on the diet composition of impala (either by isotope analysis, gut contents analysis, or observational studies) have been consistent in either predicting or showing species preference for impala (Du Toit 1988, Van Rooyen 1996, Sponheimer 2003). Although most studies find impala to feed more on grass during certain times of the year, these percentages vary from 60- 90% during the wet season (Du Toit 1988, Sponheimer 2003) dropping down to anything from 10-75% (Du Toit 1988; Skinner and Chimimba 2005) during the dry season . The biggest lack in many studies is the failure to report adequate rainfall or climatic data during and prior to the study period, which might be a key factor behind impala

resource selection. I aim to produce a better understanding of the dynamics revolving around resource selection by impala and how that relates to changes in weather patterns throughout a season.

Data collection

I sampled data at three spatial scales: plant species level, feeding station level and feeding patch level. I sampled each study area three times a week on alternating days. In each area I searched for feeding impala herds by vehicle. At each feeding area I search for fresh bites, fresh bites could be clearly seen as bites that had no dried rim (Macandza 2009). Plants with fresh bites were classified as used, feeding stations that had used plant species present were classified as used, and feeding patches with used feedings stations were classified as being used.

I recorded different attributes at the various scales: plant species scale, involved identifying used and unused species, ranking their greenness and measuring their height. At feeding station level I estimated biomass, and ranked the percentage of basal cover of a species within the feeding station, and at the feeding patch level I ranked each patch according the amount and type of cover present (i.e. short grass, tall grass or shrubs, tree canopy cover, and shrubs and tree canopy). I sampled an unused patch for each used patch, which was located 40m away in a random compass direction (Matson et al. 2005). Greenness should be an important factor in driving impala movements and resource selection (Skinner and Chimimba 2005) and because they feed on such big variety of plant parts, the presence of seedpods, fruits and fresh foliage might increase selection of a feeding station or patch.

Microhistology

To better discern feeding patterns I did microhistology analysis on impala faeces collected at feeding sites. Microscopic inspection of faecal samples is known to have variable accuracy with estimating diet content (Sparks and Malechek 1968; Dearden et al. 1975; Vavra and Holechek 1980). The accuracy of these analyses is dependent on many factors including the duration of digestion within the ruminant and the sample preparation procedure (Vavra and Holechek 1980). However, despite these factors it has been shown that microhistology is a useful method to estimate herbivore diet (Alipayo et al. 1992; Carrière 2002). I used microhistology on impala faecal samples to distinguish monocot and dicot plant material and to determine the proportion of samples that contained seeds during each season.

Data analysis

Using multi-model inference (Anderson 2008) I developed models that would enable me to address the hypotheses associated with each of my objectives. I compared candidate models using Akaike's Information Criterion, corrected for small sample bias (AICc). The model with the lowest AICc, out of all the candidate models, was considered most parsimonious and therefore the best model (Anderson 2008). I estimated selection by calculating log odds ratios (± 95% confidence intervals) for all the explanatory variables present within the best models

I also investigated the change in selection of grass species with a variation in environmental conditions brought on by a change in season. I calculated the proportion of grasses in impala's faeces (from microhistology results) over a two weekly period, and compared that to mean two-weekly greenness. I used the forb and grass selection data to calculate mean weekly proportions of grass and forbs within the diet. I also compared the mean proportions

(±95% confidence interval) of forage (selected grass and forbs, and grass in faeces) within each season. Lastly I averaged grass, browse and forb consumption for each month to get an idea of how the contribution of various forage types changed in each study area throughout the dry season.

I calculated the proportion of faecal samples that contained seeds for every season and compared that between seasons and study areas. I also calculated the percentage of times that *Eucleas* were fed on when encountered, during each season for each study area. I used the stem selection data and calculated mean weekly proportions of stems within the diet. These proportions of plant parts were compared to mean weekly greenness number across the study period. All statistical modeling was done in R version 2.10.1 (R development Core Team, 2008) using the lmer function with binomial errors, with Matrix and lattice packages for mixed effect models. I used the glm function for fixed effect models, and the lm function for linear regression.

Thesis structure

The two data chapters (chapter 2 and chapter 3) are written up in article format each with separate introduction, methods, results and discussion sections. A detailed description of the study design is given in the general introduction (chapter 1) and I elaborate on the methods, including data analyses, relevant to each particular chapter in the text of that chapter. 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 focuses on resource selection at three spatial scales: plant species level, feeding station level, and patch selection level. Additionally chapter 2 classifies resources used

by impala into preferred, reserve and buffer resources based on when and to what extend the species were used. Lastly chapter 2 investigates which species are key to the survival of impala during resource limiting times. The main objective for chapter 2 is: to investigate which resources impala select for at different spatial scales, and which factors influence that selection. I expected 1) to see impala choose the greenest forage available at a given time, and 2) to see greenness of vegetation to drive larger scale selection.

Chapter 3 investigates the change in resource use between seasons. Specifically I focus on the potential switch from a grass dominated diet to a browse dominated diet late in the dry season and potential expansion of diet by consumption of other plant parts during the dry season. My main objective for chapter 3 is: to investigate if there is a switch between resources across seasons, and which factors influence this switch. I expect 1) impala to switch from a grass dominated diet to a browse dominated diet towards the end of the dry season, and 2) impala to use alternative plant parts to supplement their diet when their preferred resources are unavailable. Again, because impala are mixed feeders I expect greenness to be a driving factor behind them switching between diets. A decrease in greenness of their preferred resources should have them utilizing alternate sources.

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Figures

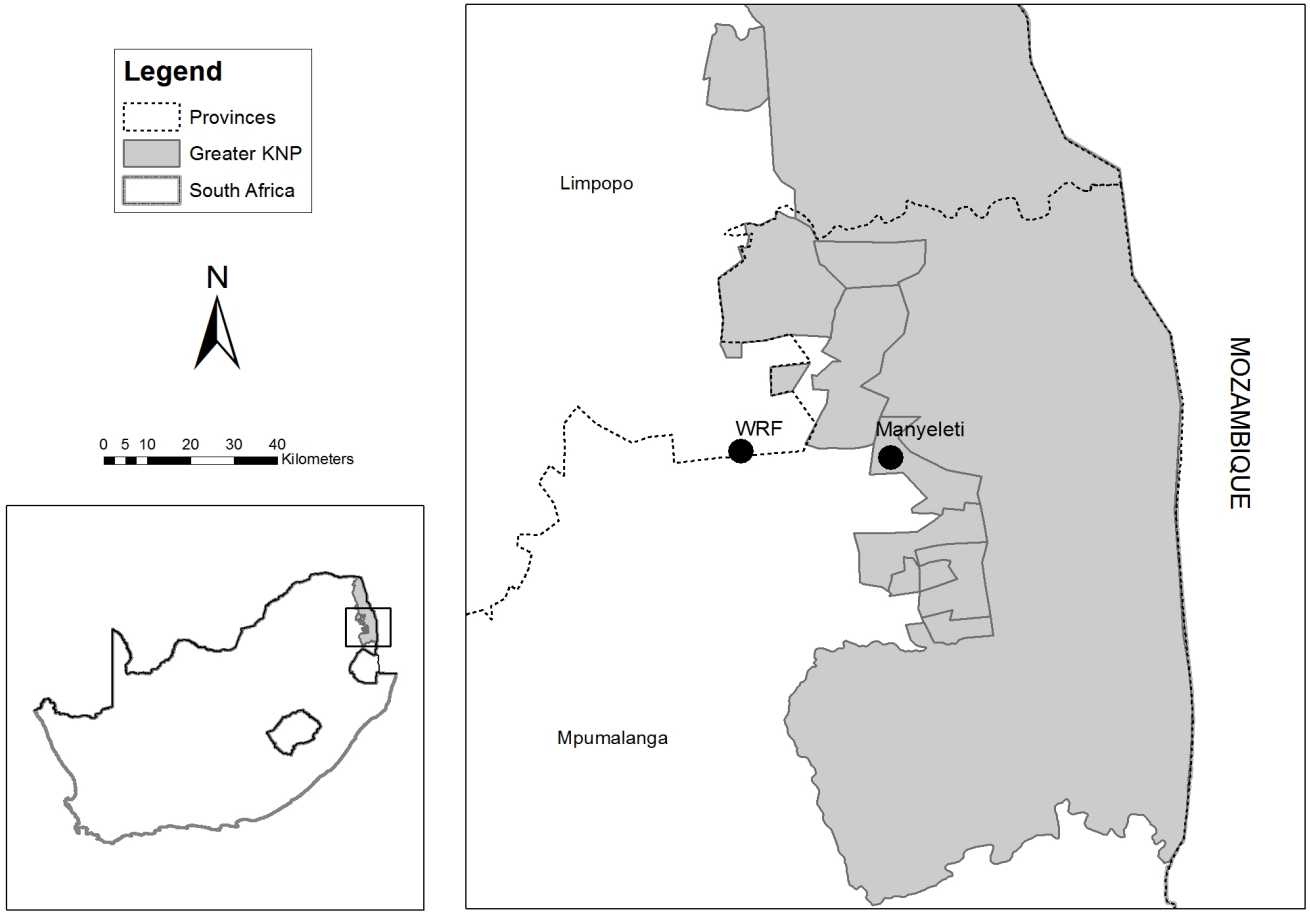


Figure 1.1. Map of South Africa, showing the locations of the two study areas, Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), adjacent to Greater Kruger National Park (Greater KNP). Both reserves are located close to the border of the Mpumalanga and Limpopo provinces of South Africa.

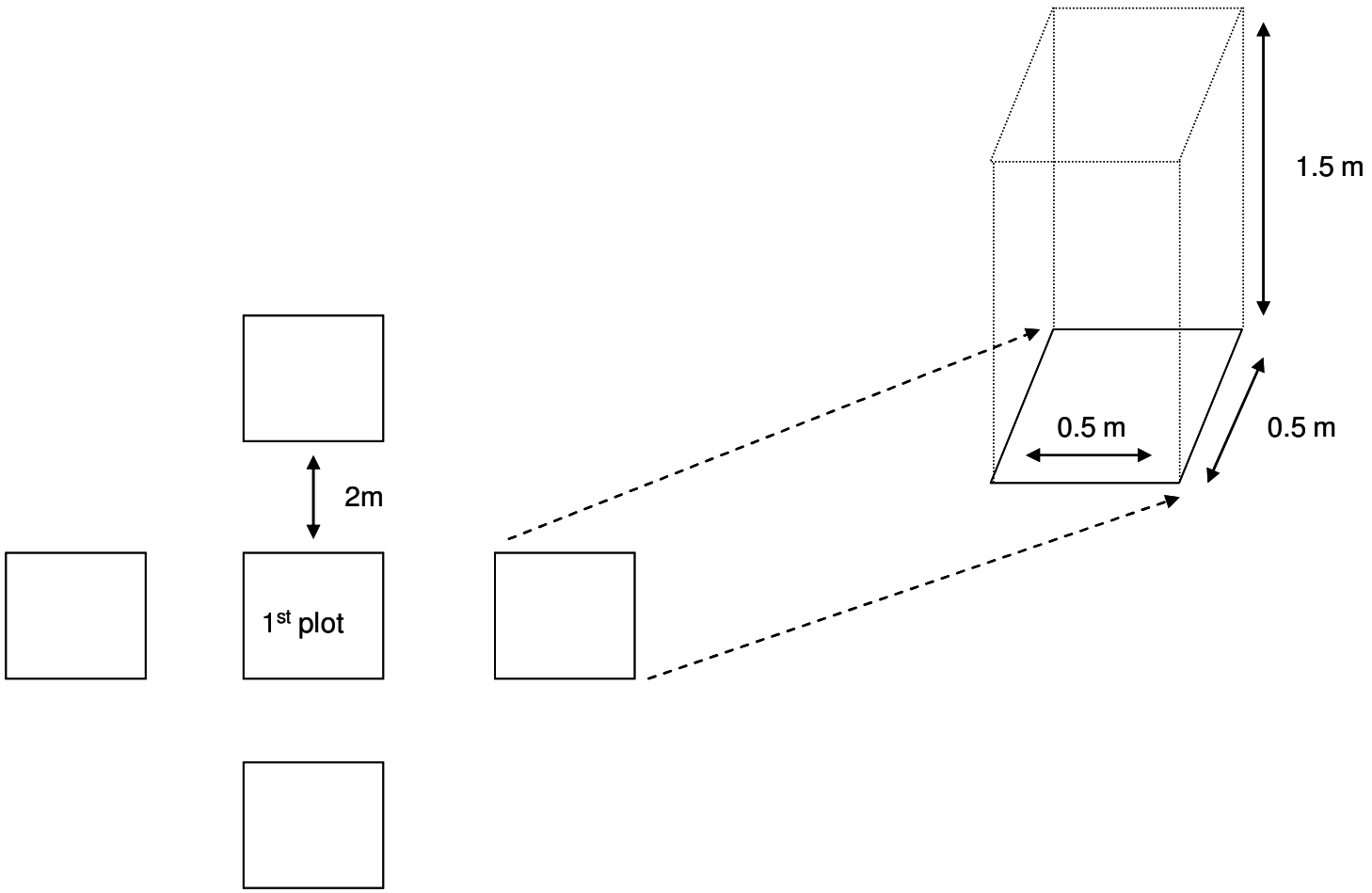


Figure 1.2. Sampling regime, with plot placements in the four cardinal directions, 2 m from the first plot. If on inspection a clear feeding path was recognized, plots would be placed 2 m apart down the feeding path. Each plot was virtually extended to a height of 1.5 m and thus represented a 3 dimensional area of 0.5 m × 0.5 m × 1.5 m.

CHAPTER 2 - FINE SCALE RESOURCE SELECTION BY IMPALA IN SOUTH AFRICAN SAVANNA SYSTEMS

Abstract

An important question in large herbivore ecology is why an animal selects to eat from certain plant species and not others. Many factors influence how mammalian herbivores select and use forage resources, some of these include the presence of secondary compounds and nutrient content. These factors vary between plant species and change with variability in environmental conditions, which in turn influence herbivore movements at various scales. Herbivores can be divided into three feeding groups: grazers, browsers and intermediate (or mixed) feeders. Impala (*Aepyceros melampus*) is an intermediate feeder that feeds on grasses, dicots and various plant parts. This study investigated the fine scale resource selection of impala in two savanna reserves in South Africa. My main objectives were to determine which factors drive selection at different scales, to classify species into preferred, reserve and buffer resources and to identify the species that comprise key resources for impala. Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF) are located 30km apart, near the Orpen gate of the Kruger National Park. I recorded data at three spatial scales, species level, feeding station level, and feeding patch level. Specifically I recorded which species impala fed from, and the physical attributes of the species and areas that they occur in. I found that greenness was an important factor at all spatial scales and that biomass and type of cover were important at large scales. I identified *Panicum maximum* as a preferred species and key resource driving impala movements, with various dicots making up reserve and buffer resources. Potential nutritional benefit was most important in governing

resource selection in impala, with impala selecting forage that was highest in quality and digestibility at all scales.

Introduction

An important question in large herbivore ecology is why an animal selects to eat from certain plant species and which factors influence that selection (Owen-Smith 2005). These questions become more important for herbivores that switch between browsing and grazing, because those mixed feeders not only choose within forage types but also between them (Jarman 1974; McNaughton and Georgiadis 1986). Preferred resources are plant species that are highly palatable and most readily eaten by herbivores whenever available and nutritionally acceptable (Owen-Smith 2005). Reserve resources are used to supplement the diet when preferred resources are declining in availability and nutrition, and buffer resources are used only to sustain a herbivore through the dry season when very little other forage is available or palatable (Owen-Smith 2005). Key resources are essential to influencing survival of herbivores during resource limiting periods (Varley and Gradwell 1960; Illius and O'Connor 2000), and could comprise of species present within any of the above feeding groups. I aim to show that certain plant species (Bailey et al. 1996) and plant species characteristics (Wilmshurst et al. 1999) are important for determining habitat selection at fine or broad scales for mixed feeders.

Some factors that influence selection of forage include variability in secondary compounds (Freeland and Janzen 1974; Cooper and Owen-Smith 1985; Du Toit et al. 1990; Vicari and Bazely 1993) and nutrients (Cooper et al. 1988; Du Toit et al. 1990; Seagle and McNaughton 1992; Murray 1995), the presence of structural deterrents such as thorns on trees

(Cooper and Owen-Smith 1986) or silica bodies in grass (McNaughton et al. 1985; Massey et al. 2009), and the quality and quantity of available resources at a given time (Owen-Smith 1994; Wilmshurst et al. 1999). Herbivores feed from a variety of plants to prevent overdosing on certain toxins and prefer familiar species that offer nutritional benefits (Freeland and Janzen 1974). However, seasonal and temporal variability in water availability, temperature, and light induce changes in nutrient content of preferred forage (Van Soest 1994). This variability in nutritional quality of forage affect herbivore distribution at a local and regional scale (Seagle and McNaughton 1992) and force herbivores to switch to alternative species when favoured species are insufficiently available (Albon and Langvatn 1992; Wilmshurst et al. 1999; Mysterud et al. 2001).

Herbivores can be divided into three general groups: browsers, grazers and mixed feeders (Hofmann 1989). Mixed feeders, or intermediate feeders, can be broadly classified into two additional groups: mixed feeders preferring grass, and mixed feeders preferring browse (McNaughton and Georgiadis 1986). Of the 30 large herbivores that occur in Kruger National Park, South Africa, there are 14 grazers, 11 browsers and 4 mixed feeders (Du Toit 2003). Impala (*Aepyceros melampus*) are intermediate feeders that prefer grass. They switch between forage types in response to fluctuating environmental factors such as decreased rainfall (Du Toit 1988; Van Rooyen 1992; Skinner and Chimimba 2005). My main objective for this study was to identify the resources that make up impala's diet, how this varies with changes in environmental conditions, and to classify resources used by impala into three classes: preferred resources, reserve resources, and buffer resources.

Nutritional quality of plants is determined both by the ratio of cell walls to cell contents and by the concentration of nutrients (e.g. protein, minerals, and soluble carbohydrates)

of the cell contents (Owen-Smith 2005; Codron et al. 2007). The ratios and concentrations differ between plant species and plant parts (Arzani et al. 2004; Codron et al. 2007), change with season, differs considerably between grass and browse, and ultimately influence palatability (Jarman 1974; McNaughton and Georgiadis 1986; Cooper et al. 1988). For example, there is a negative correlation between total fiber content and the selection of old leaves by kudu (*Tragelaphus strepsiceros*), between total fiber content and the selection of new and mature leaves by impala, and a positive correlation between selection of old leaves by kudu and impala and the magnesium content (Cooper et al. 1988). 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 fiber content (Van Soest 1994); therefore, I expected (1) impala to select the greenest and youngest forage available to obtain the most nutritious forage.

Larger scale selection is influenced by tree canopy cover in a patch, with canopy cover of especially *Acacia* spp. increasing the nutritional value of sub-canopy grasses (Belsky 1994; Ludwig et al. 2004; Treydte et al. 2007). Tree and shrub cover also influences vigilance (Underwood 1982; Bednekoff and Ritter 1994; Hunter and Skinner 1998), which increases the tendency for some prey species to select more open areas (Underwood 1982; Mysterud and Ostbye 1999; Martella et al. 1995). However, because of their relatively small body size, 45 - 55 kg (Walker 1996), impala have high energy requirements (McNaughton and Georgiadis 1986), and therefore need high quality foods (Illius and Gordon 1992; Van Soest 1994). Thus, although cover influences habitat selection in many herbivores (Underwood 1982; Mysterud and Ostbye 1999; Martella et al. 1995), I expected (2) to find larger scale selection driven by potential nutritional value of the station or patch, indicating that impala prioritize forage quality over other factors.

Predictions at species level:

1.1 The selection of a plant species is only dependent on the specific species

1.2. The selection of a plant species is dependent on the greenness of that species

1.3 The selection of a plan species is dependent on the basal cover of the species

1.4 The selection of a plant species is dependent on the height of the leaves of the plant species

1.5 The selection of a plant species is dependent on the season that the species is available as well as on any of the above factors (greenness, basal cover, height of leaves.

Predictions at feeding station level:

2.1 The presence of certain plant species increase the selection of a feeding station

2.2 The presence of certain plant species together with the greenness of the feeding station during a specific season increase selection of a feeding station

2.3 The presence of certain plant species together with biomass of the feeding station during a specific season increase the selection of a feeding station, and

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

Predictions at feeding patch level:

3.1 The presence of certain species increase the selection of a patch

3.2 The presence of certain species and the greenness of the patch during a specific season increase the selection of a patch,

3.3 The presence of certain species in a patch and the type of cover present within the site during a specific season increase the selection of the patch, and

3.4 The presence of certain plant species in a patch, the greenness of the patch during a specific season, and the type of cover present in a patch during a specific season increase the selection of a patch.

Methods

Study Areas

The study was conducted in two reserves bordering the Limpopo and Mpumalanga provinces of South Africa, and sampling took place from May to October 2009. I focused on the dry season, when resources were becoming scarce and patterns in selection were more apparent. I divided the dry season into two periods, the early dry and late dry seasons, by comparing the greenness levels of vegetation on a week-by-week basis and assigning the next season when there was a sudden drop in greenness levels (Fig 2.1). Based on that, the early dry season was from middle of May to end of July, and the late dry season was from beginning of August to middle of October.

The first study area was at Wits Rural Facility (WRF), which is 350 ha in size and is located 30 km from the Orpen gate of the Kruger National Park. Mean annual rainfall in WRF is 670 mm, and the wet season is from October to April. Dominant tree species occurring in WRF include *Terminalia sericea, Acacia* spp. and *Combretum* spp. Dominant grasses include *Panicum maximum*, *Aristida* spp*, Urochloa mosambicensis, Pogonathria squarrosa*, *Bothriochloa insculpta*, *Heteropogon contortus*, *Eragrostis* spp, and *Cynodon dactylon* (Shackleton 1993).

Large mammals occurring on the property include impala, kudu, common duiker (*Sylvicapra grimmia*), reed buck (*Redunca fulvorufula*), water buck (*Kobus ellipsiprymnus*), bushbuck (*Tragelaphus scriptus*) and warthog (*Phacochoerus aethiopicus*). Hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*) are occasionally observed passing through WRF from neighbouring reserves.

The second study area was located 30 km from WRF, in Manyeleti Game Reserve (hereafter Manyeleti). 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 long term mean annual rainfall for Manyeleti is 507 mm, with the wet season spanning October to April. Kruger National Park occupies an area of approximately 2 million ha in the North-eastern parts of South Africa, bordering Zimbabwe and Mozambique. Kruger National Park has approximately 147 mammal species and roughly 1980 plant species (Mbunda 2003).

Impala occur in open woodland in northeastern South Africa, southwest Zimbabwe, Mozambique, Botswana and Namibia.They are mixed feeders and feed on a variety monocot and dicot plant species (Skinner and Chimimba 2005). A few studies have quantified the percentage of grasses that make up their diet, either via gut contents analysis (Van Rooyen 1996) or with isotope analysis (Sponheimer 2003), while others identified individual species eaten by examining faecal and eusophagal samples (Meissner 1996). Some of these studies were either performed under high stress situations (drought) or lack a description of climatic conditions. I aim to identify the species used by impala, while taking seasonal conditions into consideration and thus to form a better understanding of the feeding patterns of impala. Impala are fairly common antelope and therefore easy to locate and observe from a vehicle without the need for radio collars.

Data collection

I sampled each study area three times a week on alternating days. I drove through most of each study area each day, searching for feeding impala herds. 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. A feeding area, where impala spent 1-30 minutes feeding was identified as a feeding patch (Bailey et al. 1996). Once the herd had moved away from the patch I continued on foot and searched for plants that showed fresh bites. Fresh bites could be clearly seen as bites that had no dried rim (Parrini 2006; Macandza 2009). Plants with fresh bites were classified as used, feeding stations that had used plant species present were classified as used, and feeding patches with used feedings stations were classified as being used.

I placed a 0.5 m × 0.5 m plot square over the vegetation where I found the fresh bites, and extended the plot square to approximately 1.5m high. This was to include any possible browsed vegetation that was within reach of impala. Each 0.5 m × 0.5 m × 1.5 m plot was classified as a feeding station (i.e. the area that can be used by a herbivore without moving its feet; Novellie 1978). At each patch I sampled 5 feeding stations, 2 m apart. The plots were placed in the four cardinal directions, from where the first one was placed. However, if on inspection it was clear that a distinct feeding path was followed, then the plots were placed 2 m apart down the feeding path.

Within each feeding station I recorded all the plant species present, scored the species as being used or unused, ranked greenness and basal cover for each species, and estimated biomass for the feeding station. I measured the midpoint of sward height of each species and the

height that bites were taken. I ranked species greenness and basal cover according to an 8 point scale (Walker 1976), where 0 = 0%, 1 = 1-10%, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-90%, 6 = 91-99%, and 7 = 100%. I measured biomass by modifying the comparative yield method (Haydock and Shaw 1975). I ranked each plot from 0-5 according to the percentage of edible forage present within the plot, where 0 = 0% (bare plot, or plot with no edible forage), 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-99%, and 5 = 100% (a plot filled with grass up to 1.5m). To convert the ranks into biomass, I clipped 20 plots of each rank, dried the clippings at 60°C for 2 days and weighed the clippings. I used linear regression to find the relationship between plot ranks and biomass and converted the ranked numbers into biomass ($g.m^{-2}$).

For each patch used by impala, I also sampled an unused patch. I located the unused patch by walking 40 m in a randomly-selected compass direction and collected the same data that was collected for the used patch (Matson et al. 2005). Both used and unused patches were ranked according to the dominant cover type present: short grass, tall grass (>1m high) and shrubs, only canopy cover, and patches with tall grass and tree canopy cover.

Data analysis

I investigated three levels of selection (use versus non-use): patch selection, feeding station selection, and plant species selection (Bailey et al. 1996). A species was scored as being used if it had fresh bites. A feeding station was used when any species present within the feeding station had been used, and patches were used when impala fed on any species within that patch. Selection of species and feeding stations were calculated using data from both used and unused patches.

Using multi-model inference (Anderson 2008) I developed four to eight models for each of the levels of selection in each of the study areas, representing each of the hypotheses. Separate models were developed or individual species. The models had plant species selection, feeding station selection and patch selection respectively as binary response variables. I used mixed-effect models with feeding station number and patch number as nested random effects for the species selection models and patch number as a random effect for the feeding station selection models. The fact that the selection of species and the use feeding stations within feeding patches are not independent of each other necessitates the use of nested random variables (Crawley 2007). The models for patch selection had only fixed effects. Prior to fitting any of the models I tested for collinearity between the various explanatory variables and no collinearity was found.

For species selection models I analysed grass and dicot species separately. Explanatory variables included in these full models were individual species, species basal cover (categorical), season (early dry and late dry), height of leaves (continuous) and greenness of the species (categorical). Because I wanted to investigate which species were eaten and which factors influence the selection of these species, the models contained various interactions between some of the explanatory variables and species. Differences in species selection estimates might allow me to classify species as preferred species.

For both feeding station selection and patch selection I was interested in determining if the presence of any species influences the selection of a feeding station or patch, compared to other factors such as the mean greenness of the station or patch, biomass of the feeding station (continuous), and type of cover present within a patch (short grass, tall grasses and shrubs, canopy cover, and tall grasses and canopy cover) and how selection at these spatial scales

changed with season (early dry and late dry). If the presence of certain species increased selection of feeding stations and patches, regardless of the season, it would allow me to classify plant species into preferred, reserve and buffer resources.

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 (w_i) where a higher number indicates a higher probability that the model is closest to reality, of all the candidate models. I calculated evidence ratios ($E_{i,j}$) using the relative likelihoods (w_i/w_j). 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).

I calculated log odds ratios (± 95% confidence interval) for the explanatory variables from each of the best models. Accordingly, I could not derive exact probabilities, but calculated log odds ratios relative to a reference, or baseline, category (Godvik et al. 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. All analyses were done in R version 2.10.1 (R development Core Team 2008). Statistical modeling was done using the lmer function for mixed effects models, with binomial errors and Matrix and lattice packages. The glm function with binomial errors was used for models with only fixed effects.

Results

I recorded 80 different plant species, 52 used and 29 unused by impala. Impala fed from 26 of the 46 grass species that I identified (Table I.I, Appendix I), and of the 34 woody species I identified, impala fed from 26 (Table I.II, Appendix I).

Species selection

Some species were only occasionally fed on, such as flowers and leaves from *Euclea*s, and seed pods from *Acacia*s and *D. cinerea* that were mostly fed on during the late dry season. Because impala fed on these plant parts so infrequently and only during one season, I could not quantify selection. All dicots were only selected when >75% green (Table 2.1). In both Manyeleti and WRF >80% of their grass diet was made up of *P. maximum* and *U. mosambicensis*, and the bulk of their non-grass diet in WRF was made up of *D. cinerea* and forb species, whereas in Manyeleti the bulk of their non-grass diet was made up of *Acacia* spp. and forb species. I used these species for subsequent analyses, and grouped all other grass species and all remaining non-grass species into two additional classes: "other grasses" and "other dicots" (i.e., forbs and other non-grass species that was not analysed as a separate category). When the model fitting functions fail to converge on a maximum likelihood estimate, false convergence errors occur. This happens when there are too few data points within a level of a categorical variable, i.e. when there are no or few data points within greenness of 0% during the early dry season, then that category can't be compared with the same level during the late dry season. Because of false convergence errors during analysis, I combined all the greenness ranks above 75% into one rank of >75% green.

The best model for dicot species selection in Manyeleti (w_i= 0.76) included only species as an explanatory variable. Thus greenness and season did not significantly influence the selection of dicot species; it was merely the individual species themselves that influenced selection. Compared to the selection of *Acacias*, forbs were more selected (log-odds = 2.966 ± 0.54) and *Euclea*s were more avoided (log-odds = -3.392 ± 0.74). The second ranked model had an interaction between species and season (Table 2.1), which suggested that species selection was dependent on the season, but evidence ratios indicate little support for this model ($E_{1,2}$ = 7.7). In WRF selection of dicots was influenced by the change in species, which was brought on by the different seasons (Table 2.2). Compared to the selection of other dicots in the early dry season, the selection of *D. cinerea* was higher during the early dry season (log-odds = -5.17 ± 3.04) and selection of other dicots during the late dry season was lower (log-odds = -3.94 ± 3.2). The model ranked second ($E_{1,2}$ = 1.6) included only species, which indicated a high plausibility for selection in WRF to be influenced only by specific dicot species.

Grass species selection in Manyeleti and WRF was influenced most by the greenness of individual species and the changes in individual species which were brought on by changes in season (Table 2.2). For both the best models the reference category was the selection of *P. maximum* in the early dry season. During both seasons in Manyeleti the highest selection was for *P. maximum*, followed by *Urochloa mosambicensis.* Other grasses were avoided more than either of the other two species. During the late dry season *U. mosambicensis* was avoided less than during the early dry season and other grasses were selected no different (Fig 2.2). In WRF impala selected *P. maximum* more during the late dry season than in the early dry season. The likelihood of *U. mosambicensis* being selected during the early dry was lower than selection during the late dry season and lower than selection of any of the other species. The likelihood of

impala selecting other grasses remained mostly unchanged regardless of season (Fig 2.2). Thus, in resource limiting periods (late dry season), impala selected *P. maximum* more.

In Manyeleti there was an increase in selection of grasses with an increase in grass greenness, which was more pronounced in the lower greenness classes (Fig 2.3). Across all greenness classes there was more selection for *P. maximum*, followed by *U. mosambicensis* and then other grasses species (Fig 2.3). In WRF selection for all three species remained mostly unchanged with an increase in greenness, but similar to Manyeleti, *P. maximum* was least avoided, followed by *U. mosambicensis* and then other grass species (Fig 2.3). The reference category for both study areas was the selection of *P. maximum* with a greenness of 0%.

Grass species selection models that contained only species as an explanatory variable had low model probabilities for both Manyeleti ($w_i = 0.00$) and WRF ($w_i = 0.00$). This suggests that those models were highly unlikely to be close to reality, and thus that specific grass species 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 impala select for the most nutritious forage available, not necessarily only for specific species.

Feeding station selection

The presence of some species, especially some of the grass species, greatly influenced whether impala used a feeding a station or not. The change in the mean greenness of a feeding station that was brought on by a change in season also played a role in determining whether a feeding station was used. The best model included the individual species and an interaction between season and mean greenness of the feeding station (Table 2.3). The nearest ranking model ($E_{1,2} = 1.6$), had an

additional interaction between season and biomass of the feeding station, which showed higher avoidance with an increase in biomass (Table 2.3). The best model for feeding station selection in WRF ($w_i = 0.95$) included variables for all the species (forbs, other dicots, *D. cinerea*, *P. maximum*, *U. mosambicensis*, and other grass species), an interaction between season and greenness, and an interaction between season and biomass of the feeding station (Table 2.3).

In Manyeleti the presence of all dicot species increased the likelihood of a feeding station being selected. Forbs increased selection most, followed by *Acacias* and other dicots (Fig 2.4). The only grass species that increased the likelihood of feeding station selection was *P. maximum*. There was no difference in selection with the presence *U. mosambicensis*. The presence of other grasses, and even more so the presence of *D. eriantha,* increased avoidance of a feeding station (Fig 2.4). In WRF selection of a feeding station was no different with the presence of any dicots. The presence of *P. maximum*, followed by *U. mosambicensis*, increased the likelihood of a feeding station being selected, while there was no difference in selection with the presence of other grasses (Fig 2.4).

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. These estimates were in comparison with the selection of feeding stations with a mean greenness of 0% during the early dry season (Fig 2.5). During the early dry season selection estimates were mostly unchanged with an increase in greenness, with impala greener feeding stations being selected more during the late dry season. Similar trends were visible in WRF (Fig 2.5). During the early dry season selection was slightly more for greener feeding stations and during the late dry season impala selected greener feeding stations more.

The best model in WRF contained an interaction between season and biomass, which indicated that the likelihood of a feeding station being selected was lower with an increase in biomass during the late dry season (log-odds = -3.956 ± 0.001) in comparison with the reference category, which was selection of feeding stations in the early dry season.

Patch selection

At the patch selection level species presence only influenced selection in Manyeleti, with greenness and the dominant cover type in each feeding patch were important drivers for selection at both study areas. Because of false convergence errors I only used two greenness ranks, <25% green and > 25% green for.

The model that best described patch selection in Manyeleti (w_i= 0.99) included species (*Acacias,* forbs, other dicots, *P. maximum*, *U. mosambicensis*, other grasses and *D. eriantha*) and interactions between mean greenness of a patch and season, and type of cover and season (Table 2.4). For patch selection in WRF, the best model included interactions between greenness and season, and cover and season (w_i= 0.99; Table 3). In addition to these interactions the second ranked model in WRF ($E_{1,2}$ = 77) included forbs, other dicots, *D. cinerea*, *P. maximum*, *U. mosambicensis* and other grasses as explanatory variables.

Compared to patches with no species, the likelihood of a patch being selected in Manyeleti was higher with the presence of *Acacias*, forbs and other dicots (in descending order). The only grass species that increased the likelihood of a patch being selected was *P. maximum*. Selection of patches were no different with presence of *U. mosambicensis* than with its absence, and patches that had *D. eriantha* or other grasses present were more likely to be avoided (Fig

2.6). In WRF the presence of a species in a patch made no difference to impala selecting the patch (Fig 2.6).

The presence of greenness in the best models for both study areas, indicated the importance of greenness in selection, but because I only had two greenness classes (>25% and <25%) for patch selection, it was harder to discern the influence of greenness on patch selection. I did find that during the early dry season there was no difference in selection of patches >25% green, compared to those <25% in the early dry season. During the late dry season there was no difference in selection of patches <25% green, but impala did select patches >25% green more (Fig 2.7). This indicates that impala were driven more to greener areas during periods when resources were most limiting. In WRF all estimates overlapped with the reference class, indicating that impala did not select any patches more or less than patches of <25% green in the early dry season.

Compared to patches dominated by short grasses in the early dry season, impala showed no difference in selection of patches dominated by any other type of cover, during either season in Manyeleti (Fig 2.8). However, in the early dry season in WRF all cover classes were avoided more than short grass patches in the early dry season, with those patches dominated by tall grasses and shrubs being avoided more than any of the other cover classes. There was no difference in selection estimates across all cover types during the late dry season (Fig 2.8).

Discussion

Species selection

I have demonstrated that impala use a range of both grasses and dicots throughout the dry season, and that selection of these species is influenced by season and greenness. Season was retained as an interactive variable in all but one of the species selection models, and even though greenness was not present as an explanatory variable in the dicot species selection models, I only observed impala to feed from dicots that were more than 50% green. Green vegetation indicates high nutrition forage (Van Soest 1994; O'Reagain and Owen-Smith 1996), with younger grasses being greener and most nutritious, and mature grasses being higher in fiber and thus browner (Jarman 1974; Short et al. 1974; Van Soest 1994). Young foliage have less resins and oils (Jarman 1974), and it is likely that impala only chose leaves from trees or forbs when they were most palatable (i.e., only more than 50% green). It is also likely for the same reason that selection of dicot species and grass species were seasonal, with impala only feeding on forage when either secondary compounds and resins, or fiber were least (Jarman 1974; Short et al. 1974; Van Soest 1994).

Even though impala fed from 58 plant species, the bulk of their diet was made up of *P. maximum* and *U. mosambicensis*. In Manyeleti >80% of their diet comprised of *P. maximum* and *U. mosambicensis*, and in WRF >85% of their diet was made up of *P. maximum*. In a study on impala during drought conditions Meissner and Pieters (1996) found that impala did not necessarily use only one grass species to make up the bulk of their diet, but rather used a few species moderately (5-15%), while dicots made up about 20% of their diet. In this study dicots comprised only a small portion of their diet, but important dicots included *Acacias* and forbs in Manyeleti, and *D. cinerea* and forbs in WRF. *Panicum maximum* was the species most selected for during low-quality forage conditions (greenness <10%, and late dry season). Forbs have been shown to contribute largely to their diet during the dry season (Du Toit 1988), likely because

forbs remain greener for longer than most grasses (Kallah et al. 2000). *Panicum maximum* is a nutritious grass (Ben-Shahar 1992; Murray and Illius 2000; Van Oudtshoorn 2004; Codron et al. 2007; Van Niekerk and Hassen 2009), but its greatest asset is that it stays green for longer (Grant et al. 2000) and is therefore favoured by most herbivores (Van Oudtshoorn 2004) 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. In Manyeleti selection of *P. maximum* was closely followed by selection of *U. mosambicensis*, which is also a nutritious grass species (Mutanga et al. 2004; Codron et al. 2007). It tends to grow in disturbed places, but is readily eaten by herbivores throughout the year (Van Oudtshoorn 2004). These findings confirm my expectation that impala should select for the nutritious forage available at a given time. It also agrees with factors that have been suggested for influencing selection at the species level, such as secondary compounds, nutritional value and toxin concentrations (Bailey et al 1996).

Feeding station selection

My results showed that feeding station selection indeed increased with the presence of *Acacias*, forbs, other dicots and *P. maximum* in Manyeleti, and with the presence of *P. maximum* and *U. mosambicensis* in WRF. With the two grass species being highly nutritious and fairly abundant it follows that impala would select feeding stations with them present. The presence of large trees influence the nutritional composition of sub-canopy grasses (Belsky et al. 1993; Belsky 1994; Treydte et al. 2007), with *Acacias* increasing the nutrient content of vegetation most (Ludwig et al. 2004). It is likely that the increase in feeding station selection with the presence of other

dicots, and especially *Acacias,* was because of an increased nutritional value in the vegetation growing underneath the trees. Because many forb species have nutritional values close to that of many grasses (Arthun et al. 1992; Kallah et al. 2000; Codron et al. 2007) impala might select feeding stations where forbs are present to supplement their diet, especially during the late dry season, similar to findings by (Du Toit 1988).

Feeding stations can also potentially be influenced by overall forage quality (Bailey et al. 1996). This was confirmed by my findings that greenness, influenced by season, was present as an explanatory variable in the feeding station models. The effect of greenness varied between seasons, with impala selecting for higher nutrition (greener) feeding stations during the late dry season (in Manyeleti), and during the early dry season only avoiding stations in the lower greenness classes. Because of their smaller size, impala have faster digestive rates (Demment and Van Soest 1985; McNaughton and Georgiadis 1986) and thus limit their fiber intake to gain the most nutrition from their diet (Demment and Van Soest 1985; McNaughton and Georgiadis 1986). During the early dry season acquiring a low fiber diet should be relatively easy with a fair amount of green forage still available (mostly >50%). During the late dry season grasses have matured and fiber content is higher (Short et al. 1974; Van Soest 1994), and leaves from dicots have increased in oils and resins (Jarman 1974), consequently good quality forage is less prevalent. During these times any forage that is greener than the bulk available, should be highly sought after and selected for.

The best model for feeding station selection in WRF, and the second ranked model in Manyeleti, both indicated a decrease in selection of feeding stations with an increase in biomass. Because of the positive relationship between fiber content and grass biomass (Demment and Van Soest 1985) ruminants should prefer to feed from intermediate biomass grasses, which would

maximize nutritional intake and digestibility (Wilmshurst et al. 2000). For example Thompson's gazelle (*Gazella thompsonii*) prefer areas of short grasses and intermediate biomass, which ensures a higher quality forage and increased digestibility (Wilmshurst et al. 1999). This negative relationship becomes more apparent during the late dry season, when grass maturation causes an increase in plant fiber content (Van Soest 1994). The negative relationship between biomass and the nitrogen content of grasses (Mutanga et al. 2004) could account for the decreased selection of feeding stations, especially during the late dry season when high nutrition forage is scarcer.

Patch selection

Most of the factors that could influence feeding station selection, could potentially influence herbivore patch selection, including the presence of plant species, forage quality and forage abundance (Bailey et al. 1996). The presence of specific species was not important in influencing patch selection in WRF. However, in Manyeleti patch selection was influenced by the same species that influenced feeding station selection, again indicating that *P. maximum* was the only grass species important in larger scale selection. Dicot species likely influenced patch selection for the same reasons as put forward for feeding station selection. Trees are known to alter sub-canopy grass nutrient content (Belsky et al. 1993; Belsky 1994; Ludwig et al. 2004; Treydte et al. 2007), and the relatively high nutritional values of forbs and their general longevity (Arthun et al. 1992; Kallah et al. 2000; Codron et al. 2007) are likely to increase the selection of patches by impala. Greenness interactions also showed the same trends as for finer scale selection levels. During the late dry season in Manyeleti, there was an increase in selection of patches with

greenness >25%, which again points to the importance of greenness of vegetation during resource limiting periods. Apart from the influence that seasonal change in greenness had on the selection of patches, I also found that impala avoided patches with tall grasses and shrubs, during the early dry season in WRF. Higher cover can decrease vigilance, and possibly increase predation risk (Jarman 1974; Underwood 1982; Fitzgibbon, Lazarus 1995; Hunter and Skinner 1998; Mysterud and Ostbye 1999), and short grasses necessarily mean lower biomass and thus increased nutrition and digestibility (Demment and Van Soest 1985; Wilmshurst et al. 2000; Mutanga et al. 2004). Because I did not measure vigilance, or predation risk I can not infer any relationship between type of cover and the risk of predation. However, it is possible that the positive relationship between selection of a patch and short grass cover can be because shorter grasses ensure a higher quality diet (Wilmshurst et al. 1999), or due to predator avoidance. Because the strongest trends in patch selection based on cover were seen in WRF (where there are no permanent predators), the avoidance of patches with tall grasses and high biomass, might be to increase energy intake, rather than to increase vigilance. These findings confirm my expectation (2) that impala would select areas that maximize forage quality.

Palatability classes

It would seem that *P. maximum* and *U. mosambicensis* were most palatable and are preferred forage species for impala, being selected for when overall forage quality is low. Because *P. maximum* was the species contributing most to impala's diet at both study areas, and also the species that increased feeding station selection at both study areas, and patch selection in Manyeleti, I suggest that *P. maximum* is a key resource for impala. Thus, it influences habitat

selection, especially during the resource limited season, and should ultimately influence survival (Varley and Gradwell 1960; Illius and O'Connor 2000).

Reserve resources are eaten less often than preferred sources and are used to supplement the diet when preferred resources are unavailable or insufficient to satisfy nutritional requirements (Owen-Smith 2005). Leaves from *Acacias* and forbs in Manyeleti, and *D. cinerea* in WRF, made up the reserve resources for impala. *Acacias* and forbs increased selection of patches and feeding stations, but selection of these species were mostly confined to the late dry season. *Dichrostachys cinerea* was also only selected during the late dry season. Mixed feeders not only select for plant types but also for plant parts (Jarman 1974; McNaughton and Georgiadis 1986), and from what I recorded it seemed that not only the aforementioned dicot species, but also specific parts from these species contributed to the reserve diet of impala. In both study areas impala fed on fallen or hanging seed pods. The bulk of seed pods eaten in WRF were from *D. cinerea*, but impala frequently ate *Acacia* seed pods in Manyeleti. Seed pods are a good source of nutrition during the dry season, when other food sources are scarce, and are consumed quite generously by browsers and mixed feeders, both domestic and wild (Coppock et al. 1986; McNaughton and Georgiadis 1986; Miller 1994; Miller 1996). Seed pods from *Acacias* have been shown to be the most common seeds consumed and dispersed by impala, and makes up a great part of their diet during the dry season (Miller 1996). Hence, although impala are preferential grazers (Skinner and Chimimba 2005), their reserve resources were made up of various parts of dicot species.

Unpalatable evergreen species are consumed by browsers and mixed feeders towards the end of the dry season when more palatable deciduous woody species and nutritious grasses become unavailable (Owen-Smith and Cooper 1987; Owen-Smith 1994). These species make up

buffer resources for herbivores (Owen-Smith 2005). The only species that I identified as a buffer resource was *Euclea* spp. These species were abundant at both study areas (present at 10% of patches in WRF and 30% of patches in Manyeleti), yet it was only towards the very end of the dry season that any of the leaves, and plenty of flowers, of these species were consumed. It is likely that there are more species making up this specific foraging category for impala; however, because of a higher than average rainfall in the preceding wet season, many grasses still showed green parts toward the end of the dry season. It was only in areas where alternative resources were depleted that impala used reserve resources. Thus, although impala fed from a variety of forage, their preferred, reserve and buffer resources were made up of only a few species.

Conclusion

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 impala fed on a wide variety of species, only a few species influenced selection at all spatial scales, with *P. maximum* being a key resource driving impala movements. This study showed that greenness was crucial in shaping impala selection patterns, with cover and biomass also important in influencing forage and habitat selection in impala. Overall, season seemed to influence the effect that most of these factors had on selection. At the patch selection level significant trends were only seen in Manyeleti. This is likely because WRF has fewer predators and smaller impala herds (maximum 20 animals versus up to 100 in Manyeleti). Hence, there is less competition within impala herds for resources, which will have impala herds reacting differently to changing foraging conditions. Despite these differences, the study showed that

mixed feeders such as impala, selected very specific plant parts and species, which allowed them to use the highest quality forage available at any given time.

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Tables

Table 2.1. Percentage of dicot species that impala selected for within each greenness category, in Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), over a five month period from Many to October 2009.

Study area	Species	Percentage eaten within each greenness class		
		<50% green	> 50% green	>75% green
Manyeleti	*Acacias*	0	0	100
	Other dicots	0	0	100
	Forbs	0	0	100
	Eucleas	0	0	100
WRF	*D. cinerea*	0	0	100
	Other dicots	0	0	100
	Forbs	0	0	100
	Eucleas	0	0	100

Table 2.2. Some candidate high ranking, and low ranking mixed-effect models, and their coefficients, describing species selection (dicots and grasses), in Manyeleti and WRF, showing various explanatory variables and interactions (×) included in models.

Model Name	Model Rank	Explanatory variables	AICc	ΔAICc	k	w_i
Manyeleti Species Selection - Dicots	1	Species	260.3	0.00	4	0.76
	2	Species× Season	264.4	4.1	8	0.1
	5	Species × Season Species × Greenness	269.8	9.5	16	0.01
WRF Species Selection - Dicots	1	Species × Season	117.0	0.0	2	0.44
	2	Species	118.0	1	4	0.27
	3	Species × Season Species × Greenness	119.3	1.3	6	0.14
	4	Species × Season Species × Basal.Cover	120.1	2.1	6	0.09
Manyeleti Species Selection -Grass	1	Species × Season Species × Greenness	3933	0.00	21	0.99
	2	Species × Greenness Species × Basal.Cover	3967	34	24	0.00
	8	Species	4499	566	3	0.00
WRF Species selection - Grass	1	Species × Season Species × Greenness	1846	0.0	21	0.99
	2	Species × Greenness	1979	133	12	0.00
	6	Species	1986	140	6	0.00
	7	Species × Season	1989	143	8	0.00

Table 2.3. Some candidate high ranking, and low ranking mixed-effect models, and their coefficients, describing feeding station selection in Manyeleti and WRF, showing various explanatory variables and interactions (×) included in models. P. max = *Panicum maximum*, U. mos = *Urochloa mosambicensis*, forbs = all forb species, dicots = other dicot species, grass = other grass species

Model Name	Model Rank	Explanatory variables	AICc	ΔAICc	k	w_i
Manyeleti Feeding Station Selection	1	Acacia spp + P.max + U.mos + Grass + Dicots + Forb + D.eriantha Greenness × Season	2864	0.00	19	0.62
	2	Acacia spp + P.max + U.mos + Grass + Dictos + Forb + D.eriantha Greenness × Season Biomass × Season	2865	1.0	21	0.38
	3	Acacia spp + P.max + U.mos + Grass + Dicots + Forb + D.eriantha Biomass× Season	3142	278	11	0.00
	4	Acacia spp + P.max + U.mos + Grass + Browse + Forb + D.eriantha	3152	288	8	0.00
WRF Feeding Station Selection	1	P.max + U.mos + Grass +Dicots + Forb + D.cinerea Greenness × Season Biomass × Season	1494	0.00	20	0.95
	2	P.max + U.mos + Grass +Dicots + Forb + D.cinerea Greenness × Season	1500	6	18	0.05
	3	P.max + U.mos + Grass +Dicots + Forb + D.cinerea Biomass × Season	1601	107	10	0.00
	4	P.max + U.mos + Grass + Dicots + Forb + D.cinerea	1602	108	7	0.00

Table 2.4. Some candidate high ranking, and low ranking fixed-effect models describing patch selection in Manyeleti and WRF, showing various explanatory variables and interactions (×) included in models. P. max = *Panicum maximum*, U. mos = *Urochloa Mosambicensis*, forbs = all forb species, dicots = other dicot species, grass = other grass species.

Model Name	Model Rank	Explanatory variables	AICc	ΔAICc	k	w_i
Manyeleti Patch Selection	1	Acacias + P.max + U.mos + Grass + Dicots + Forbs + D.eriantha Greenness × Season Cover × Season	537.77	0.00	8	0.99
	2	Acacias + P.max + U.mos + Grass + Dicots + Forbs + D.eriantha Greenness × Season	554.51	16.74	11	0.00
	4	Acacias + P.max + U.mos + Grass + Dicots + Forbs + D.eriantha Cover × Season	582.45	44.68	8	0.00
WRF Patch Selection						
	1	Greenness × Season Cover × Season	321.7	0.00	16	0.98
	2	P.max + U.mos + Grass +Dicots + Forbs + D.cinerea Greenness × Season Cover × Season	330.25	8.55	16	0.01
	5	P.max + U.mos + Grass +Dicots +Forbs + D.cinerea	371.18	49.48	7	0.00

Figures

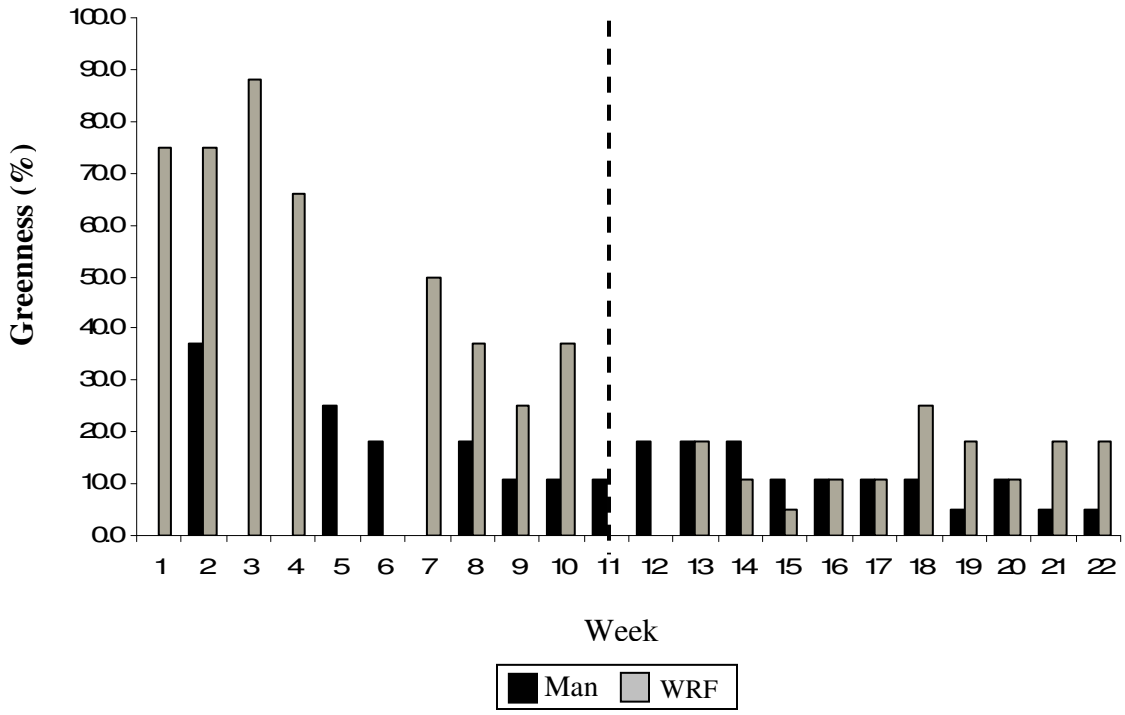


Figure 2.1. Mean weekly greenness for Manyeleti and WRF, with the broken bar indicating the split between the early dry and late dry seasons, from data collected over a five month period from May to October 2009.

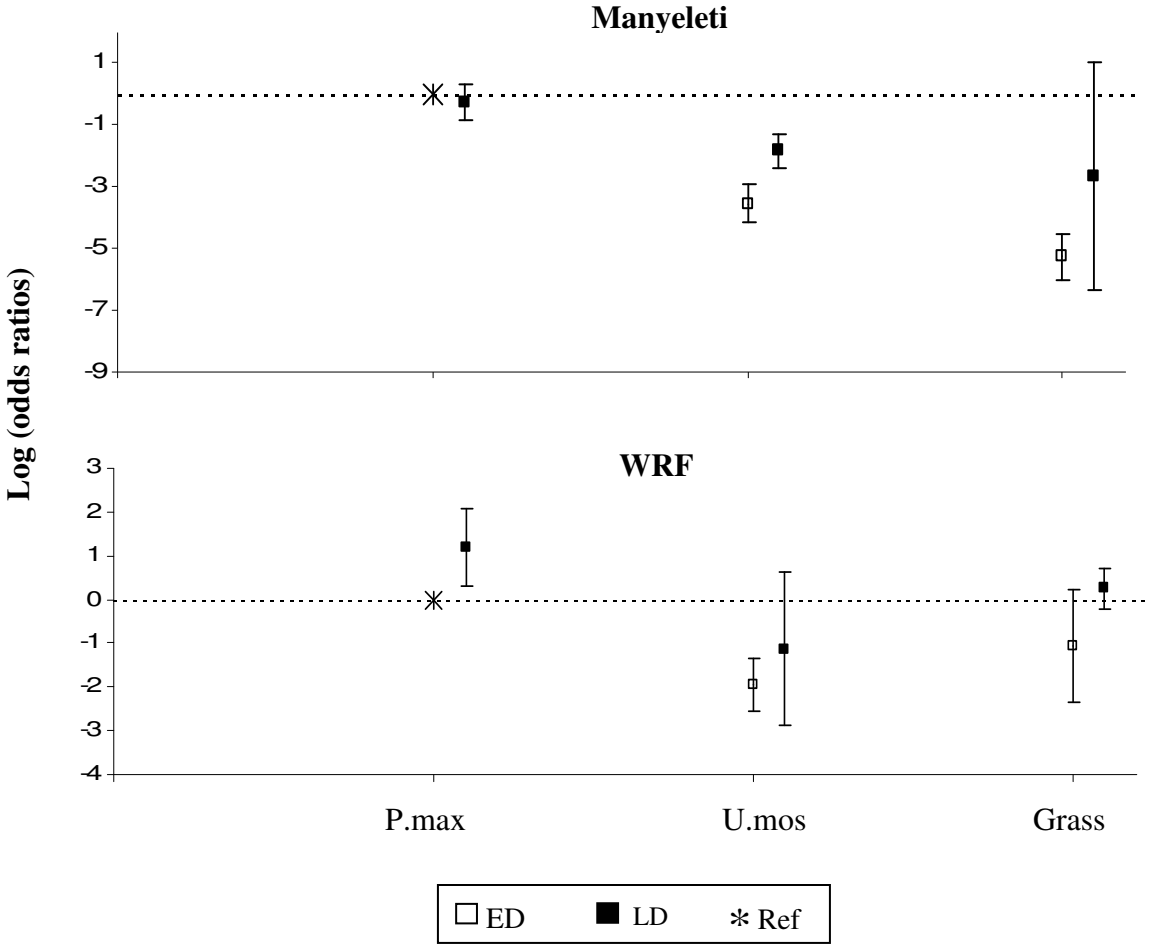


Figure 2.2.Grass species selection estimates (± 95% confidence interval), during the early dry season (ED) and late dry season (LD) for Manyeleti and WRF. The broken line indicates the reference level for the reference category (*), which is *P. maximum* in the early dry season. P.max = *Panicum maximum,* U.mos = *Urochloa mosamibicensis*, Grass = all other grasses. From data collected over a five month period between May and October 2009.

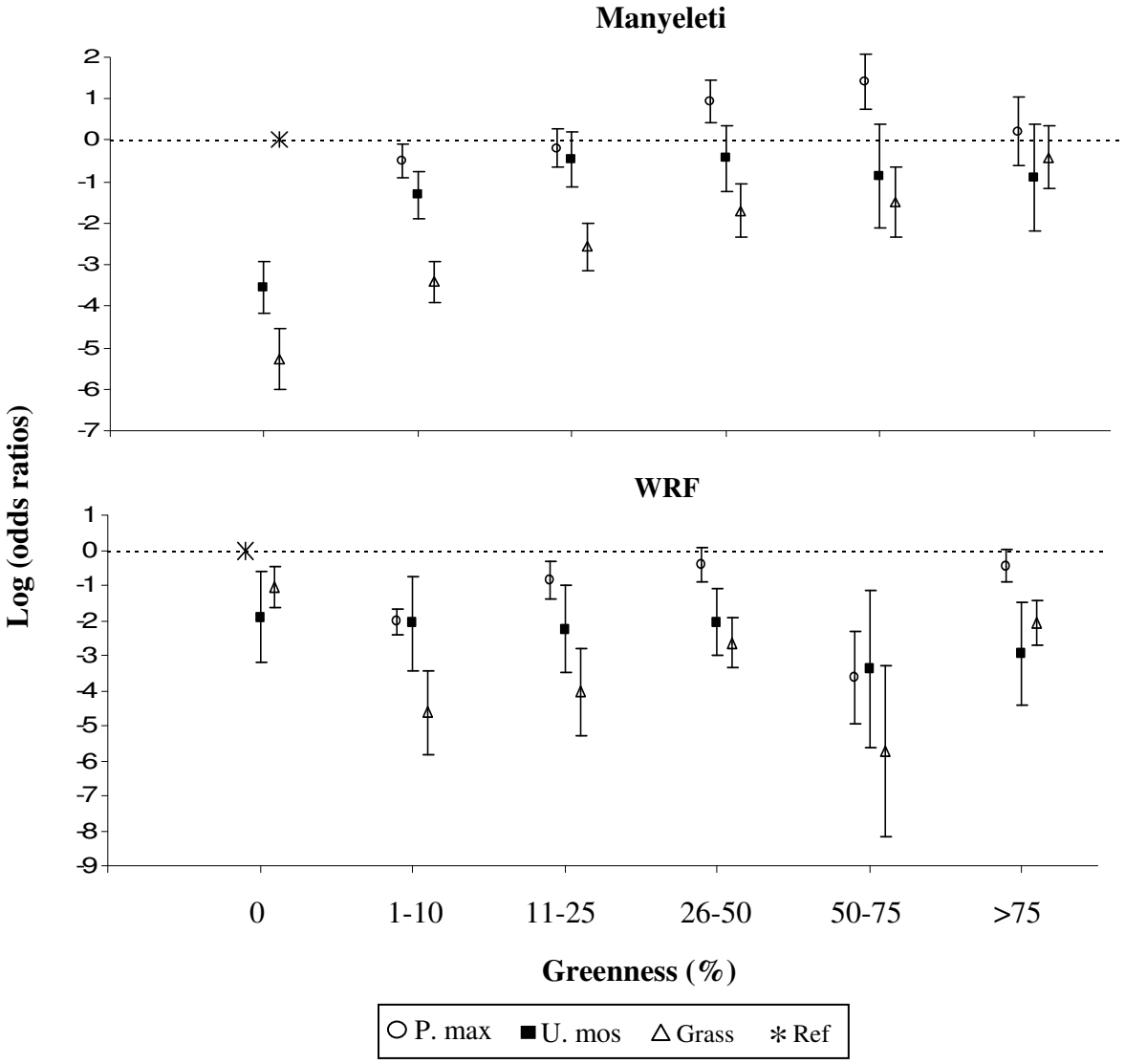


Figure 2.3. Species selection estimates (± 95% Confidence interval), of *P. maximum* (P. max), *U. mosambicensis* (U. mos), and other grass (Grass), based on greenness for Manyeleti and WRF. Reference category (Ref) is *P. maximum* with greenness of 0%. From data collected over a five month period between May and October 2009.

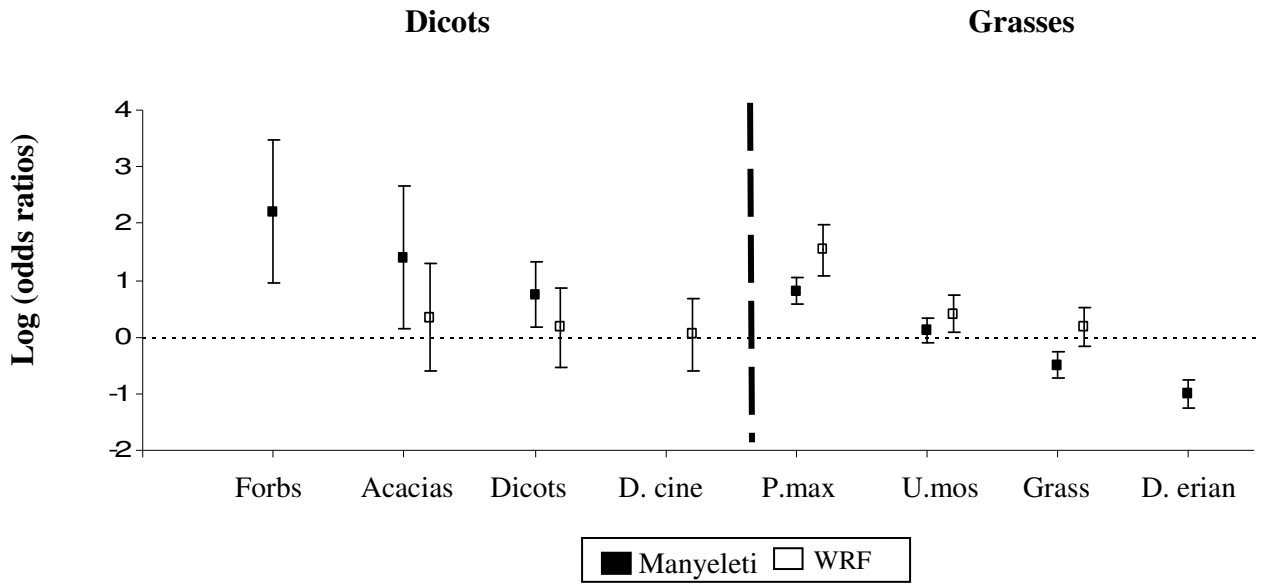


Figure 2.4. Feeding station selection estimates (± 95% confidence interval) based on the presence of species in Manyeleti and WRF. Reference category is the absence of species (horizontal broken line). Vertical broken line represents division between dicots and grasses. Forbs = all forb species, Acacias = *Acacia* species, Dicots = other dicot species, D.cine = *Dichrostachys cinerea*, P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis,* grass = other grass species, D.erian = *Digitaria eriantha*. From data collected over a five month period between May and October 2009.

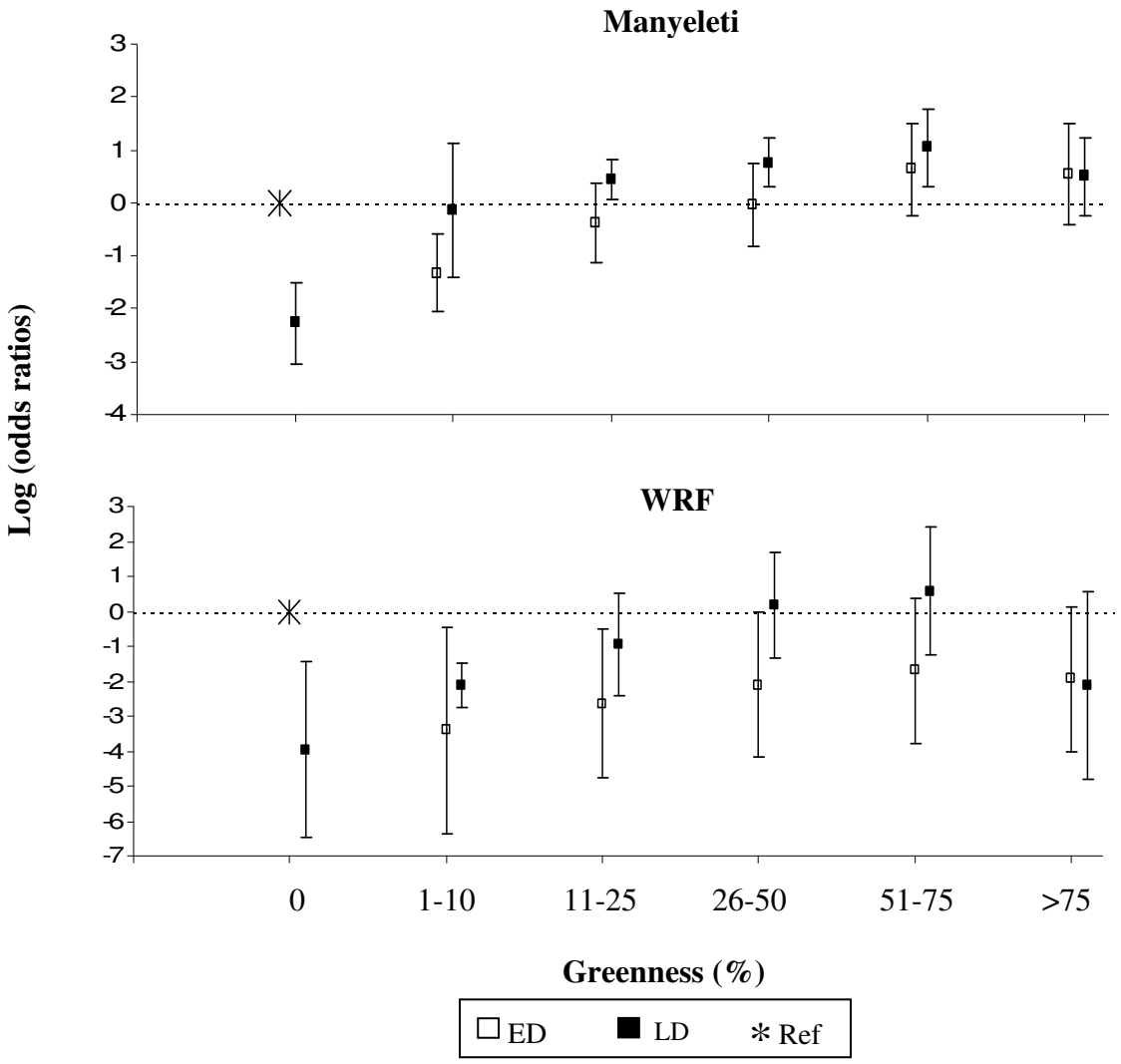


Figure 2.5. Feeding station selection estimates (± 95% confidence interval), based on the mean greenness of a feeding station in the early dry (ED) and late dry (LD) for Manyeleti and WRF. Reference category (Ref) is feeding stations with greenness of 0% in the early dry season. From data collected over a five month period between May and October 2009.

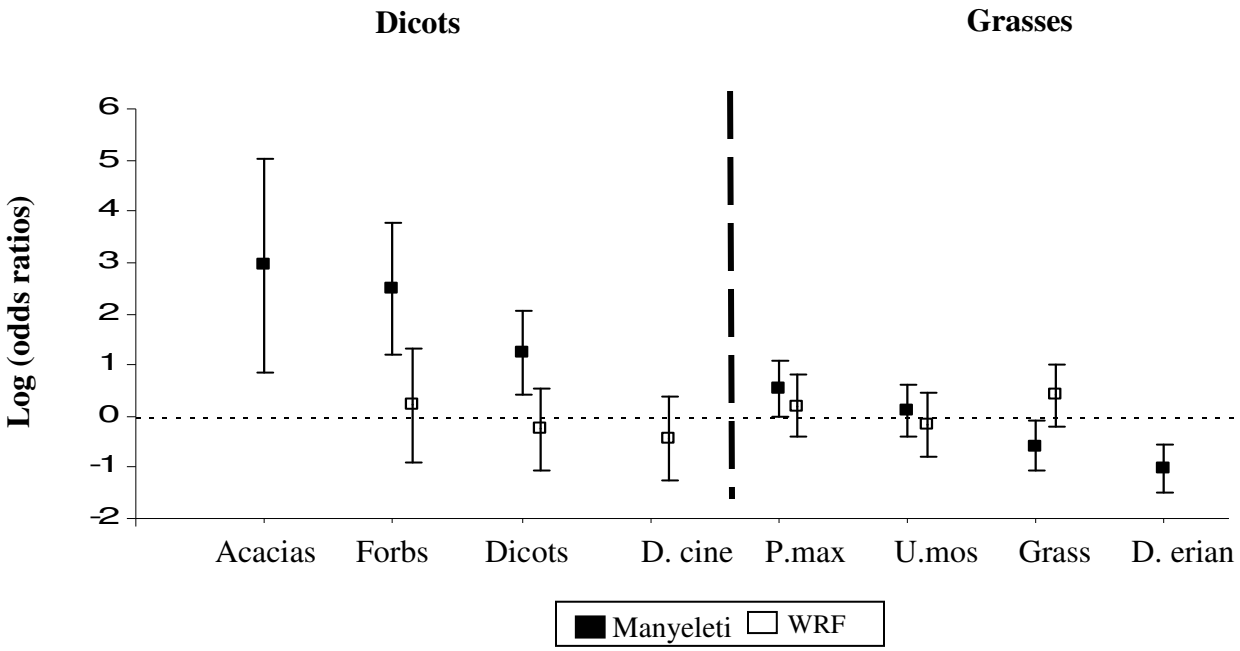


Figure 2.6. Patch selection estimates (± 95% confidence interval) based on the presence of species in Manyeleti and WRF. Reference category is the absence of species (horizontal broken line). Vertical broken line represents division between dicots and grasses. Acacias = *Acacia* species, Forbs = all forbs, Dicots = other dicot species, D.cine = *Dichrostachys cinerea*, P.max = *Panicum maximum*, U.mos = *Urochloa mosambicensis,* Grass = other grass species, D.erian = *Digitaria eriantha*,. From data collected over a five month period between May and October 2009.

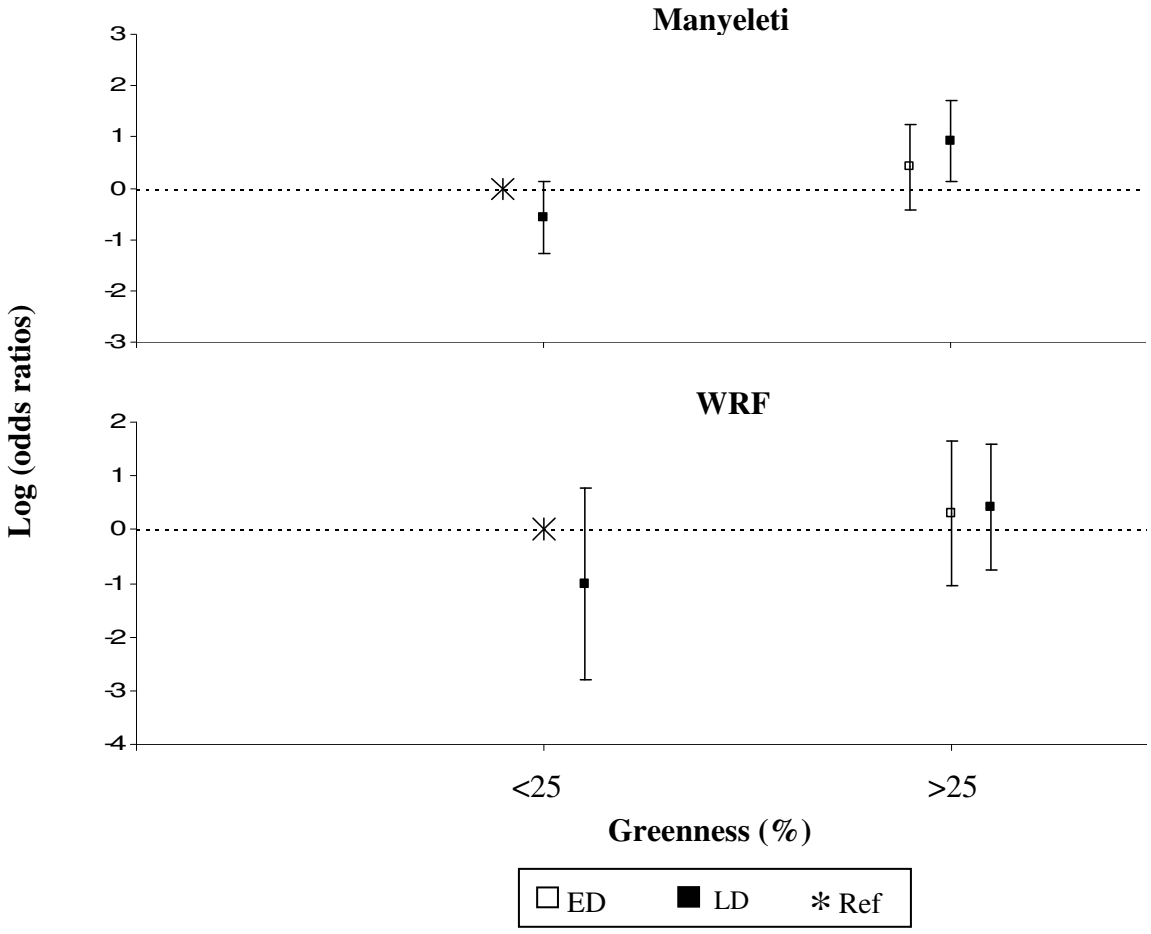


Figure 2.7. Patch selection estimates (± 95% confidence interval) based on greenness during the early dry (ED) and late dry (LD) seasons for Manyeleti and WRF. Reference category (Ref) is patches with 0% greenness in the early dry season. From data collected over a five month period between May and October 2009.

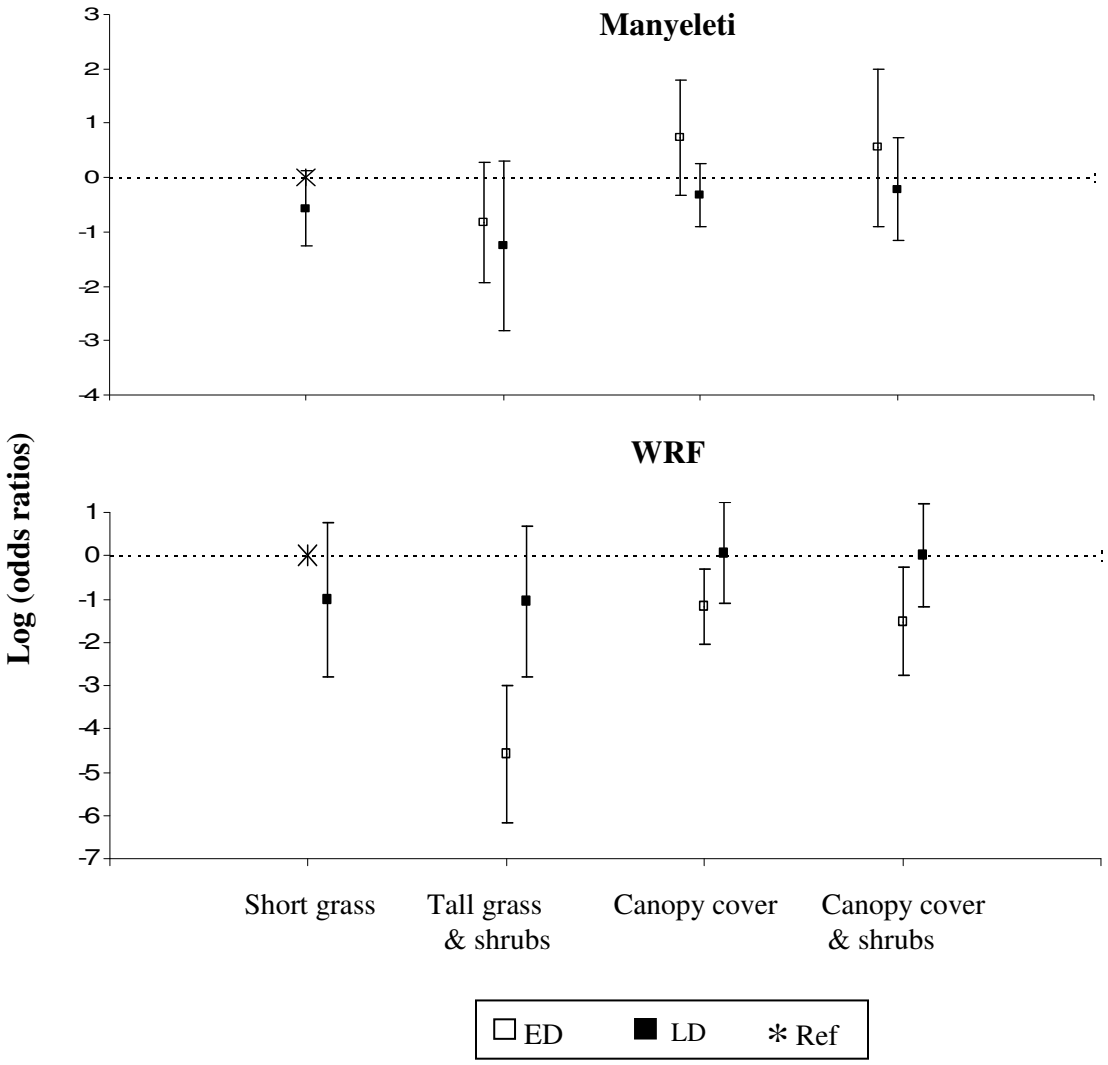


Figure 2.8. Patch selection estimates (± 95% confidence interval) based on dominate type of cover present during early dry (ED) and late dry (LD) seasons, for Manyeleti and WRF. Reference category (Ref) is patches with short grasses in the early dry season. From data collected over a five month period between May and October 2009.

CHAPTER 3 - RESOURCE SELECTION IN A MIXED FEEDER: WHICH FACTORS DRIVE SWITCHING BETWEEN DIETS?

Abstract

Various studies have investigated resource partitioning and the browser/grazer continuum in mammalian herbivores, with most focusing on possible digestive differences between grazers and browsers, but none of these studies investigated resource switching in intermediate feeders. Impala (*Aepyceros melampus*) is an intermediate feeder that eats a variety of grasses, dicots and plant parts. My main objective for this study was to investigate whether the diet of impala changed across seasons and which factors influenced that change. I conducted the study in two savanna reserves in South Africa, Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), over a five-month period from May to October 2009, during which I located and observed impala in feeding areas. I recorded greenness, estimated the biomass, and ranked basal cover of each plant species. I collected fresh faeces where available to assess diet composition through microhistology. Using mixed effect models and linear regression, I established that a decrease in greenness decreased selection of grasses, and increased selection of grass stems and forbs. There was also a positive relationship between greenness and grass in faeces. Additional factors that influenced selection of grasses included biomass and the change in species basal cover between seasons. I demonstrated that despite a drastic drop in rainfall, impala did not switch from a grass dominated diet to a browse dominated diet, but there was an overall expansion of diet.

Introduction

Much research has been done on the grazer/browser continuum and resource partitioning among herbivores (Hofmann 1989; Gordon and Illius 1994; Robbins et al. 1995), but an important question remains: why do some herbivores switch between grazing and browsing? Herbivores can be divided into three general groups: browsers, grazers and mixed, or intermediate, feeders (Hofmann 1989). Of the 44 large herbivores that occur in Africa, 10 are considered to be mixed or intermediate feeders (Owen-Smith 1982). Herbivores that predominantly browse include kudu (*Tragelaphus strepsiceros*), dik-dik (*Madoqua kirkii*) and giraffe (*Giraffa camelopardalis*), and those that only graze include wildebeest (*Connochaetes taurinus*), buffalo (*Syncerus caffer*) and waterbuck (*Kobus ellipsiprymnus*). Intermediate feeders consist of a few herbivores that feed on a combination of grasses and dicot species and alter their diets throughout the year. Intermediate feeders include those that prefer grass such as impala (*Aepyceros melampus*), and eland (*Taurotragus oryx*) is an example of those that prefer to browse (Hofmann and Stewart 1972; Jarman 1974; McNaughton and Georgiadis 1986; Skinner and Chimimba 2005). Intermediate feeders vary their diets in response to variation in resources, resulting from a change in habitat or seasons (Hofmann and Stewart 1972; Jarman 1974).

Although intermediate feeders use a combination of plant types, much of their diets are dominated by either grass or browse at specific times of the year (Jarman 1974). Eland is an intermediate feeder that prefers to browse (Skinner and Chimimba 2005) and only uses grass when no palatable browse is available (Watson and Owen-Smith 2000), and nyala (*Tragelaphus angasii*) spends most of its time browsing, but would use grasses during the late dry season (Van Rooyen 1992). Impala is an intermediate feeder that prefers to graze, but its diet includes grasses,

browse, forbs, seeds and fruit (Jarman 1974; McNaughton and Georgiadis 1986; Skinner and Chimimba 2005). Impala switches between forage types, and plant parts, in response to fluctuating environmental factors such as change in rainfall (Du Toit 1988; Van Rooyen 1992; Skinner and Chimimba 2005).

It has been suggested that differences in feeding patterns in herbivores are due to anatomical differences between grazers and browsers, most of which include differences digestive tract and salivary glands (McNaughton and Georgiadis 1986; Hofmann 1989). However, further investigations showed that with allometric corrections there are no anatomical differences between grazers and browsers (Gordon and Illius 1994; Robbins et al. 1995). Hence, there are only a few suggestions for the browser/grazer continuum, and even less work has been done investigating mixed feeders and why some herbivores switch between diets. My main objective for this study was to investigate if impala switch from a grass dominated to a browse dominated diet during the dry season, and which factors drive this switch.

Nutritional content of plant cells, and fiber content of cell walls, differ between monocots and dicot species (Jarman 1974; Codron et al. 2007). Non-grass species have higher soluble cell contents than grasses, but also have higher lignin concentrations in the cell wall that lowers digestibility (Demment and Van Soest 1985; Codron et al. 2007), and grasses have silica bodies that vary in concentration between species and deter herbivores (McNaughton et al. 1985; Massey et al. 2009).

Furthermore, not only does nutritional content vary between grasses and dicots, but the quality of forage also varies with season, soil content, rainfall, etc. (Van Soest 1994). There is a strong positive relationship between forage maturity and the fiber content of grasses and leaves on trees (Van Soest 1994), and between oils and resins in leaves and age of leaves

(Jarman 1974). While both grasses and non-grass species change across seasons, grasses keep growing for a long time even after being grazed, but foliage stop growing when they reach maturity (Jarman 1974). However, grass foliage tend to be most nutritious immediately following the onset of rain, but with all the foliage produced almost at once, it matures and declines in nutritional value roughly at the same time. Consequently, at any one time, most grasses are in the same state of maturity. Dicots on the other hand also produce leaves after the first rains, but tend to produce clusters of leaves continuously throughout the growing season (Jarman 1974). Hence, leaves from dicots might be available at times when there is no nutritious grass present. These changes in forage across a temporal scale affect herbivore distribution (Seagle and McNaughton 1992) and cause herbivores to use alternative species when their preferred forage becomes nutritionally unfavourable (Albon and Langvatn 1992; Wilmshurst et al. 1999; Mysterud et al. 2001). Accordingly, I expect (1) to see impala to switch from a grass dominated diet to a browse dominated diet during the late dry season when grass quality diminishes.

Quality of forage also varies between plant parts with fruits, grass stems, and seed pods all differing in digestibility and nutrient content (Arzani et al. 2004; Codron et al. 2007). Even though fleshy fruits have fairly high nitrogen concentrations (Codron et al. 2007), fruits can contain a high percentage of structural carbohydrates which will lower digestibility, and might even outweigh any nutritional benefits (Demment and Van Soest 1985; Codron et al. 2007). Grass stems are generally high in fiber and low in nutrition and accordingly not favoured by herbivores (Murray and Illius 2000; Arzani et al. 2004). Unlike stems, seed pods are good sources of nutrition during the dry season, when other food sources are scarce, and are consumed by many browsers and mixed feeders, both domestic and wild (Coppock et al. 1986;

McNaughton and Georgiadis 1986; Miller 1994; Miller 1996). Moreover, impala is a relatively small ruminant, with high energy demands, and accordingly requires high quality, good nutrition forage to satisfy its nutritional demands (Demment and Van Soest 1985; McNaughton and Georgiadis 1986). Hence, it would be most advantageous for impala to select the most nutritious plant parts available at a given time. I therefore expect (2) impala to switch to alternative plant parts, i.e. various seed pods, fruits and grass stems, which would provide higher nutrition forage when their preferred forage, grass leaves, becomes unavailable or declines in quality.

Thus the hypotheses I want to test are, for both Manyeleti and WRF:

1.1 The selection of a grass species changes with a change in greenness of the species during a specific season

1.2 The selection of a grass species changes with a change in the basal cover of the species during a specific season

1.3 The selection of a grass species with changes in biomass of a plot during a specific season

1.4. The selection of a grass species changes with changes in the height of leaves of the species during a specific season

1.5-1.8 The selection of a grass species changes with changes in both greenness and basal cover during a specific season

1.6. The selection of a grass species changes with changes in both greenness and biomass during a specific season

1.7 The selection of a grass species changes with changes in both greenness and height of leaves during a specific season, and

1.8 The selection of a grass species changes in greenness, biomass and basal cover during a specific season.

Methods

Study Areas

The study was conducted in two savanna reserves on the border of the Limpopo and Mpumalanga provinces of South Africa, and sampling took place during the dry season, from May to October 2009. I focused on the dry season, because that is generally the time when mixed feeders, switch between resources (Mcnaughton 1986; Du Toit 1988; Van Rooyen 1992; Hulbert et al. 2001). I divided the dry season into two periods, the early dry and late dry seasons, by comparing the greenness levels of vegetation on a week-by-week basis and assigning the next season when there was a sudden drop in greenness levels (Fig 3.1). The early dry season was from middle of May to end of July, and the late dry season from beginning of August to middle of October.

The first study area was at Wits Rural Facility (WRF), which is located 30 km from the Orpen gate of the Kruger National Park. Wits Rural Facility is 350 ha in size and the mean annual temperature is 22°C, with mean annual rainfall being 670 mm. The wet season is from October to April. Dominant grasses occurring on the property include *Panicum maximum*, *Aristida* spp*, Urochloa mosambicensis, Pogonathria squarrosa*, *Bothriochloa insculpta*, *Heteropogon contortus*, *Eragrostis* spp, and *Cynodon dactylon.* Some of the dominant tree species are *Terminalia sericea, Acacia* spp. and *Combretum* spp. (Shackleton 1993). Large

mammals occurring on the property include impala, kudu, common duiker (*Sylvicapra grimmia*), reed buck (*Redunca fulvorufula*), water buck (*Kobus ellipsiprymnus*), bushbuck (*Tragelaphus scriptus*) and warthog (*Phacochoerus aethiopicus*). Hyaena (*Crocuta crocuta*) and leopard (*Panthera pardus*) are occasionally observed passing through WRF from neighbouring reserves.

The second study area was located 5 km from the Orpen gate of Kruger National Park, in Manyeleti Game Reserve (hereafter Manyeleti). Because there are no fences between Manyeleti and Kruger National Park, Manyeleti forms part of the Greater Kruger National Park, and all animals are free to move about the whole area. The main gate of Manyeleti is located 30 km from WRF. The long term mean annual rainfall for Manyeleti is 507 mm, with the bulk of rainfall occurring from October to April. Kruger National Park occupies an area of approximately 2 million ha in the North-eastern parts of South Africa, bordering Zimbabwe and Mozambique. It has approximately 147 mammal species and roughly 1980 plant species (Mbunda 2003).

I chose to study impala because they are fairly common antelope in southern Africa and thus easy to locate and observe from a vehicle without the need for radio collars. They occur in open woodland in northeastern South Africa, southwest Zimbabwe, Mozambique, Botswana and Namibia (Skinner and Chimimba 2005). They eat a variety of plant species and plant parts and occur near water (Skinner and Chimimba 2005).

Data collection

I sampled each study area three times a week on alternating days. I drove through most of each study area each day, without crossing back to the same area within the same day. In each study

area I searched for feeding impala herds. Once I located feeding herds, I observed them from the vehicle until they moved away from the feeding area. I then proceeded to the area on foot and searched for plants that showed fresh bites. Fresh bites could be clearly seen as bites that had no dried rim (Parrini 2006; Macandza 2009). I classified areas that showed fresh bites as used.

I placed a 0.5 m × 0.5 m plot square over the vegetation where I found the fresh bites, and extended the plot square 1.5 m. This was to include any browsed vegetation that was within reach of impala. In each feeding area I sampled 5 plots, 2 m apart. The plots were placed in the four cardinal directions, from where the first one was placed. However, if on inspection it was clear that a distinct feeding path was followed, then the plots were placed 2 m apart down the feeding path.

Within each plot I identified all the used and unused grass, browse and forb species. I also recorded which plant part was used, i.e., leaves, stems, fruit, or flowers. Plant species were grouped together into three categories "grass", "browse", and "forbs", but I also kept a record of any specific species that was clearly only used during a specific season. I recorded the greenness and basal cover for each species, estimated biomass for the plot, and measured the midpoint of sward height of each grass species. I used an eight point scale (Walker 1976) to rank species greenness and basal cover, where 0 = 0%, 1 = 1-10%, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-90%, 6 = 91-99%, and 7 = 100%. I estimated biomass by modifying the comparative yield method (Haydock and Shaw 1975). I ranked each plot form 0-5 based on the presence of edible forage, where 0 = 0% (a bare plot, or a plot with no edible plant parts), 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-99%, and 5 = 100% (a plot full of grass up to the height of 1.5m). I randomly clipped 20 plots of each rank, dried the clippings at 60°C for 2 days and weighed the clippings. I

used linear regression to determine the relationship between plot ranks and biomass and converted the ranked numbers into biomass ($g.m^{-2}$).

To compare species in areas used by impala with those not used by impala, I also sampled an unused area. This area was located by walking 40 m in a randomly-selected compass direction. I collected the same data in the unused area that I collected at the used area (Matson et al. 2005). Analyses on used and unused species were done on the data collected from used and unused areas.

Microhistology

At each used patch I searched for, and collected, fresh impala faeces (i.e., faeces still wet and warm to the touch). After collection the faeces were oven dried at 60°C. I crushed the dried samples to a powder, boiled it in 5 ml of Nitric acid for 2 minutes and for another 5 minutes in water (MacLeod and Kerly 1996). I washed each sample through a sieve with a 1 mm mesh size. The fragments that passed through were then washed through a 0.25 mm sieve and I inspected the remaining fragments under a binocular light microscope at 40 × magnification. The purpose of the microhistology was to distinguish between monocot and dicot species (Carrière 2002). Starting in the top left corner of the slide and moving downwards, I followed a grid system to identify 50 fragments in each sample. This allowed me to estimate the percentage of monocots and dicots in impala's diet on a monthly basis at both study areas.

Data analysis

Grass selection

I investigated the change in selection of grass species with a variation in environmental conditions brought on by a change in season. Using multi-model inference (Anderson 2008) I developed up to eight mixed-effect models for each study area to find the model best describing grass species selection. The models had grass species selection (use versus non-use) as binary response variables, with greenness (categorical), height of leaves (continuous), species basal cover (categorical) and plot biomass (continuous) as explanatory variables in the full models. Season was added as an interaction with the other variables, to determine how the influence of change of season on the other variables affects the selection of grass species. The models had plot number nested within feeding area number as random effects. The fact that the selection of species and the use feeding stations within feeding patches are not independent of each other necessitates the use of nested random variables (Crawley 2007).

I compared the models using Akaike's Information Criterion, corrected for small sample bias (AICc). These models were based on the hypotheses that I developed. Prior to fitting any of the models I tested for collinearity between the various explanatory variables and no collinearity was found. The model with the lowest AICc, out of all the candidate models, was considered most parsimonious and therefore the best model (Arsenault and Owen-Smith 2008). For each of the models I calculated relative likelihoods (w_i), which indicate the probability of a model representing reality, with a higher number indicating the model in the candidate set that is closer to reality. Further model comparison was done by calculating evidence ratios ($E_{i,j}$), these are used to compare the weights of evidence (w_i/w_j) between candidate models. A higher evidence ratio indicates better support for model *i* over model *j* (Anderson 2008).

I estimated grass species selection by calculating log odds ratios (± 95% confidence intervals) for all the explanatory variables present within the best models. Log odds ratios are measures of likelihood, calculated in relation to a reference category. Values above 0 indicate more selection and values below 0 indicates more avoidance than the reference category (Godvik et al. 2009; Zuur et al.2009; Van Beest et al. 2010). Selection estimates equal to, or overlapping with, the reference category, indicates no difference in selection compared to the reference category.

Dietary contribution

To further investigate diet composition, and how it changed between seasons, I calculated the proportion of grasses in impala's faeces (from microhistology results) over a two weekly period. I also used the recorded selection data on feeding patterns of impala and calculated mean weekly proportions of grass and forbs within the diet. Together with the proportional data I calculated mean weekly greenness for both study areas (for use with the microhistology data I calculated mean 2-weekly greenness). I transformed the proportions of forage into odds and log transformed the odds. To find the change in proportions of forage in diet which was brought on by a change in greenness, I performed linear regression on the proportions of grass in impala's faeces and greenness, as well as the change in proportion of grasses and forbs in impala's diet due to a change in greenness. In addition to the above mentioned regression analyses, I also calculated mean proportions of forage (grass and forbs selected, and grass in faeces) for each season at each study area. Lastly I averaged grass, browse and forb

consumption for each month to show how the contribution of various forage types changed in each study area throughout the dry season.

Plant parts

I used the presence of seeds in faecal samples to quantify the proportion of samples containing seeds during each season. *Eucleas* were present in many of the feeding patches, but were rarely fed on by impala. I used this data to calculate the percentage of occurrences of feeding on *Eucleas*.

To investigate grass stem selection, and how it changed between seasons, I used the stem selection data and calculated mean weekly proportions of stems within the diet. I also calculated the mean weekly greenness at both study areas. I transformed the proportions of stems eaten into odds and log transformed the odds. This allowed me to do linear regression on the change in proportions of stems in impala's diet due to a change in greenness. In addition to the regression analyses, I calculated mean proportions of stems selected during each season for each study area.

All statistical modeling was done in R version 2.10.1 (R development Core Team, 2008) using the lmer function with binomial errors, with Matrix and lattice packages for mixed effect models. The lm function was used for linear regression analyses.

Results

Grass selection

A change in season, from early dry to late dry, brought on changes in greenness and basal cover of plant species, and these changes influenced the selection of grasses. The models that best described grass species selection in Manyeleti ($w_i = 0.99$) and WRF ($w_i = 0.98$) both contained interactions between season and greenness, season and biomass, and season and species basal cover. This indicated that the effect of greenness, biomass and basal cover on grass selection changed with a change in season (Table 3.1).

Greenness varied between study areas and decreased from May to October in a response to changes in rainfall (Fig 3.2). This variation in greenness brought on changes in grass species selection across the dry season (Fig 3.3). During the early dry season selection of grasses remained mostly unchanged across all greenness classes. Thus, in the early dry season impala fed on grasses regardless of greenness. During the late dry season, however, there was an increase in grass selection with an increase in greenness. Accordingly, when forage was least nutritious (low greenness classes in the late dry season), impala avoided grasses more.

Differences in basal cover of grasses between seasons influenced selection of grasses at both study areas (Fig 3.4). In both study areas there was a decrease in selection of grasses with an increase in basal cover during the early dry season. In the late dry season selection remained mostly unchanged across all basal cover classes.

The areas that impala used in the late dry season had higher biomass than the areas used during the early dry season. However, there was almost no difference in biomass between used and unused areas (Fig. 3.5). Selection estimates showed that compared to the selection of grasses in the early dry season, impala avoided grasses in higher biomass plot more during the late dry season in Manyeleti (log-odds = -2.4 ± 0.0004) and WRF (log-odds = -3.2 ± 0.0013).

Thus, even though impala used plots with higher biomass during the late dry season, they avoided grasses in these higher biomass plots more.

Dietary contribution

Regression analysis did not show a relationship between proportion of grass present in faeces and 2-weekly greenness in either Manyeleti (log-odds = -0.016 ± 0.278) or WRF (log-odds = -0.011 ± 0.032). This is confirmed with a comparison between early dry and late dry seasons that showed proportions of grass in faeces remaining mostly unchanged (Fig 3.6). I expected a decrease in grass selected with a decrease in greenness, but in Manyeleti (log-odds = 0.346 ± 0.572) there was no difference in selection of greenness with an increase in greenness. In WRF grass selection was negatively related to greenness (log-odds = -0.468 ± 0.448). Seasonal comparisons reveal another pattern, with grass selection being lower in Manyeleti in the late dry season, but very little difference in selection between seasons in WRF (Fig 3.7).

There was a negative relationship between the selection of forbs and greenness in Manyeleti (log-odds = -0.043 ± 0.024), but no difference in selection of forbs with a change in greenness in WRF (log-odds = 0.010 ± 0.035). A comparison between early dry and late dry season forb proportions showed an increase in forb consumption for both study areas, but larger confidence intervals in WRF show high variation during the late dry season (Fig 3.7). These results indicated that late in the dry season impala adjusted their diet to some degree.

Notwithstanding a decrease in greenness throughout the dry season, the bulk of impala's diet comprised grasses. In Manyeleti forb selection increased during the late dry season, and apart from a higher browse selection between May and June, the contribution of browse to

the diet remained mostly unchanged. In WRF there was an increase in forbs in the diet during the late dry season and browse oscillated from fairly little to almost nothing and back to very little, from early dry to late dry season (Fig 3.8).

Plant parts

Impala frequently fed on fallen seed pods from *D. cinerea* and *Acacias* throughout the dry season. In Manyeleti there was a clear increase in seed present in faeces in the late dry season, but in WRF there was a slight decrease in seeds during the late dry season (Table 3.4). *Euclea*s were often encountered during both seasons, but were only fed on during the late dry season (Table 3.4).

During the late dry season when vegetation was mostly between 1-10% green, impala avoided eating any grass leaves. They sought out single grass stems to feed on. These single green stems were mostly situated well inside a tuft of brown grass, where impala would find the stems and feed on them. There was a marked increase in stem use transitioning from the early dry to the late dry season. In Manyeleti stem consumption increased from 16% during the early dry season to 35% during the late dry season, and in WRF from 9% to 74% (Fig 3.9). Regression analysis showed a negative relationship between stem consumption and greenness in Manyeleti (log-odds = -0.306 ± 0.057) and WRF (log-odds = -0.493 ± 0.261), which was consistent with my expectations.

To summarize, I found that there was an increase in the contribution that stems and forbs made to the diet. I also found that various factors, including, greenness, basal cover and biomass, influenced grass selection, and that the effect of those factors change between seasons.

Discussion

Grass selection

My results provide evidence that a change in season brought on changes in greenness, biomass and basal cover of grass species, which led to a change in the relationship between grass species selection and each of those variables. Impala went from feeding on grasses of all greenness categories in the early dry season, to avoiding browner grasses in the late dry season. This indicates that when their preferred forage declined in quality, due to a change in season, impala switched to different sources. Green vegetation indicates high-nutrition forage (O'Reagain and Owen-Smith 1996; Van Soest 1994), with greener grass being more nutritious, and browner grass being higher in fiber and secondary compounds (Jarman 1974; Short et al. 1974; Van Soest 1994). Consequently greenness is important in driving herbivore movements, and influencing selection of areas and forage (Wilmshurst et al. 1999; Chapter 2). Du Toit (1988) suggested that impala switch from a grass dominated diet to a browse dominated diet when the 2-month running mean of rainfall (2-MRMR) drops below 30 mm; hence a major change in diet should occur toward the end of the dry season. Similarly, Van Rooyen (1992) and Meissner et al. (1996) found impala switching between diets in the late dry season, when resources are limited. I did see a drop in rainfall, with the 2-MRMR far below 30 mm, but contrary to my expectations I did not see impala make a switch from a grass dominated diet to a browse dominated diet late in the dry season. I contribute this to the fact that the preceding wet season had an above average rainfall

(150 mm above average in Manyeleti, and 250 mm above average in WRF) and thus even with almost no rainfall during the dry season, mean weekly greenness never fell to 0%.

During the early dry season selection was lower for higher basal cover grass, whereas during the late dry season basal cover did not influence selection of grasses. This suggests that during the early dry season, when highly palatable green grass leaves are readily available, impala might avoid higher basal cover tufts to feed from tufts with fewer stems present. In the late dry season, when most forage is of low quality, impala might be indifferent to basal cover of grasses because all grass parts are of similar quality or because they feed from additional sources. Some studies suggest that grass basal cover is not significantly influenced by rainfall or grazing pressure (Jacobs and Schloeder 2003) and others showed that precipitation has a direct positive effect on basal cover (O'Connor et al. 2001). Good condition lands have grasses with high basal cover, because these retained water, decreased soil loss and decreased evapotranspiration from soils (O'Connor et al. 2001). I found no studies that investigated the benefits of specific basal coverage to mammalian herbivores, but I suspect that basal cover is linked to number of stems in a tuft, and it has been shown that increased in number of stems of a tuft, and consequent fiber increase, deter herbivores (Heady 1964; Parrini 2006).

During the late dry season impala used areas with higher biomass than during the early dry season, with hardly any difference between used and unused areas during either season. It was also evident that grass species selection was lower during the late dry season, in areas with higher biomass. Accordingly, although impala moved into areas with higher biomass, they did not select grasses more. A possible explanation for these trends is that impala avoided grasses with high biomass because of potential high fiber and low nutrition associated with high-biomass grasses (Demment and Van Soest 1985; Wilmshurst et al. 2000). This positive relationship

between biomass and fiber becomes more apparent during the late dry season, when grass maturation causes an increase in plant fiber content (Short et al. 1974; Van Soest 1994). There also exists a negative relationship between biomass and the nitrogen content of grasses (Mutanga et al. 2004). For example Thompson's gazelle (*Gazella thompsonii*) prefer areas of short grasses and intermediate biomass, which maximizes digestibility (Wilmshurst et al. 1999), and impala generally avoid areas of high biomass (see Chapter 2). In general impala avoid high biomass areas more (see Chapter 2), but the movement into areas with higher biomass in the late dry season was likely because of the incorporation of browse in their diet. The presence of trees and forbs will increase the overall biomass of plots. I sampled unused areas 40 m away from used areas, but the fact that unused areas also had a higher biomass during the early dry season, might demonstrate that a distance of 40 m is not large enough to incorporate differences between used and unused areas larger than patch size.

Following these explanations, my expectation of a switch in diet is at least partially satisfied, with impala using alternative resources during the late dry season, even if not making a complete switch from grass to browse.

Diet contribution

Because of various factors contributing to inaccuracies surrounding the estimation of diet composition with microhistology analysis (Vavra and Holechek 1980), a certain amount of caution is needed when interpreting microhistology results. However, because I did not identify individual plant species, but only distinguished monocots and dicots, much uncertainty was excluded. Even though I expected less grass in faeces with a decrease in greenness, there was no

evidence of this in either study area, but there was a slight drop in grass selection in the lat dry season. Impala also increased their selection of forbs towards during the late dry season by almost 6% in Manyeleti and 4% in WRF. These results are supported by Du Toit (1988), who also showed that a large portion of impala's dry season diet consists of forbs. Various forb species have nutritional values that meet, or even exceed, those of some grasses (Arthun et al. 1992; Kallah et al. 2000; Codron et al. 2007), and forbs tend to still be green when most grasses have dried up (Kallah et al. 2000). The fact that impala fed from forbs during the early dry season, but increased the consumption during the late dry season, suggests that forbs might always be nutritionally acceptable, but because grasses are the favoured resources of impala, they only feed from forbs either when grasses are not available or only when forbs are present. Although impala did not switch from a grass dominated diet to a browse dominated diet during the dry season, they did change their diet to incorporate a high proportion of forbs.

Plant parts

Dichrostachys cinerea made up 30% of impala's browse intake in WRF, which included the consumption of seed pods throughout the dry season. In both study areas impala fed on fallen, or hanging, seed pods. Although the bulk of seed pods eaten in WRF came from *D. cinerea* impala frequently ate *Acacia* seed pods which made up the bulk of their seed diet in Manyeleti (personal observation). Seed pods from *Acacia*s have been shown to be the most common seeds consumed and dispersed by impala, and constitutes a great part of their diet during the dry season (Du Toit 1988; Miller 1996). Because of high protein concentrations and high digestibility (Hashim 1990), seed pods are good sources of nutrition during the dry season, when other food sources are

scarce and high in fiber, and are consumed quite generously by browsers and mixed feeders, both domestic and wild (Coppock et al. 1986; McNaughton and Georgiadis 1986; Hashim 1990; Miller 1994; Miller 1996). From this it follows that impala should actively search for and consume seed pods, especially in resource limiting periods.

Unlike the consumption of seed pods, which were eaten because they are high in protein and valuable food sources, I suspect it is only when very little other nutritional forage was available that impala fed on the flowers and leaves of *Euclea*s. *Euclea*s are evergreen trees, and generally rejected by browsing herbivores for most of the year, but become more acceptable during the dry season (Owen-Smith and Cooper 1987). It has been shown that phenolic compounds vary in concentrations and vary between seasons within some *Eucleas* (Bapela et al. 2008), and Cooper and Owen-Smith (1985) also found evergreen species in general, but specifically *Eucleas,* to have high concentrations of condensed tannins. They did however also find that most evergreen species were avoided in the wet season, but some of them were foraged on during the dry season when deciduous species had few or no leaves available to browse from. Goats regularly fed from *Eucleas* despite their high tannin content (Cooper and Owen-Smith 1985) and low nitrogen values (Codron et al. 2007), which suggests that there has to be additional features to *Eucleas* which makes them palatable, at least at certain times of the year. Du Toit (1988) also observed, but not quantified, impala feeding on fallen flowers from some trees, and it would be of great interest to perform a more detailed investigation of the quantities of flowers and leaves that comprise impala's diet during the late dry season, especially those coming from evergreen species.

Plant parts differ in digestibility and nutritional content (Short et al. 1974; Codron et al. 2007), and grass stems are generally considered to be a poor source of nutrition, because of

high fiber and low digestibility (Demment and Van Soest 1985; Arzani et al. 2004; Murray and Illius 2000). Contrary to these findings, I found impala to consume a considerable amount of stems. My results showed that impala increased stem consumption with a decrease in mean weekly greenness, which suggests that they use stems to supplement their diet in resource limiting periods. Because of their smaller incisor arcade, which is also scaled to body size (Gordon and Illius 1988), impala are able to take more selective bites than herbivores of larger size (Jarman 1974; Gordon and Illius 1988). Accordingly, if a tuft of grass comprises mostly dry, unpalatable stems and leaves, impala might be able to select single green stems hidden well inside. Thus, even though stems are considered a poor source of nutrition compared to the nutritional value of leaves, if there are single stems available that are greener than the surrounding tuft, it might be the highest nutrition forage available for impala to select. Meissner et al. (1996) also found impala to increase grass stem consumption during the dry season, and topi, which also have a small bite size, are also able to select single green swards from large tufts of grass (Murray and Illius 2000). These results, together with consumption of seed pods, support the idea that impala use alternative plant parts towards the end of the dry season when forage is declining in nutritional quality.

Conclusion

Because of the decrease in high quality forage during the dry season, it becomes increasingly difficult for smaller herbivores to satisfy their energy requirements (Demment and Van Soest 1985), and it is during these resource limiting periods that intermediate feeders switch to alternative resources (Du Toit1988; Van Rooyen 1992; Meissner et al. 1996). My main objective was to investigate a possible change in resource use by impala across the dry season. I

demonstrated that impala do not necessarily switch from a grass dominated to a browse dominated diet during every dry season, but they did alter their diet composition. Contrary to my expectations, the only discernible change in diet was an increase in forb and grass stem consumption toward the end of the dry season. This was likely because of the above average rainfall of the preceding wet season, and therefore changes in resource selection were less obvious. Hence, it would seem that grasses are impala's preferred food source and that plant parts and forbs are high quality forage providing sustenance during the dry season. I suggest that future studies should focus on years with average preceding wet seasons, to formulate a better understanding of what the norm is for resource switching in impala.

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Tables

Table 3.1. All candidate mixed-effect models, with their respective coefficients, describing grass species selection in Manyeleti. From data collected from May to October 2009.

Model	Rank	Variables	AICc	ΔAICc	k	w_i
Manyeleti - Grass Species Selection	1	Season × Greenness Season × Biomass Season × Basal.Cover	4443	0.00	18	0.99
	2	Season × Greenness Season × Basal.Cover	4453	10	16	0.00
	3	Season × Greenness Season × Biomass	4512	69	14	0.00
	4	Season × Greenness	4520	77	12	0.00
	5	Season × Greenness Season × Height.Leaves	4521	78	13	0.00
	6	Season × Biomass	5129	587	4	0.00
	7	Season × Basal.Cover	5030	686	6	0.00
	8	Season × Height.Leaves	5138	695	4	0.00

Table 3.2. All candidate mixed-effect models, with their respective coefficients, describing grass species selection in WRF. From data collected from May to October 2009.

Model	Rank	Variables	AICc	ΔAICc	k	w_i
WRF - Grass species Selection	1	Season × Greenness Season × Biomass Season × Basal.Cover	2056	0.00	18	0.98
	2	Season × Greenness Season × Basal.Cover	2064	8	16	0.01
	3	Season × Greenness Season × Biomass	2091	35	14	0.00
	4	Season × Greenness Season × Height.Leaves	2095	39	14	0.00
	5	Season × Greenness	2100	44	12	0.00
	6	Season × Basal.Cover	2251	195	6	0.00
	7	Season × Biomass	2283	227	4	0.00
	8	Season × HeightLeaves	2287	231	4	0.00

Table 3.3. Percentage of *Euclea* usage (leaves or flowers), calculated by comparing the number of occurrences of Eucleas with the number of occurrences of feeding during the early dry season and late dry seasons in Manyeleti and WRF. Data collected over a five month period from May-October 2009.

	Early Dry Season	**Late Dry Season**
Manyeleti	0%	24%
WRF	0%	14%

Table 3.4. Percentage of faecal samples that contained seeds during the early dry and late dry seasons in Manyeleti and WRF, numbers in brackets show number of actual faecal samples used for analysis. Data collected over a five month period from May to October 2009.

	Early Dry Season	**Late Dry Season**
Manyeleti	21% (n=19)	33% (n=31)
WRF	22% (n=15)	15% (n=16)

Figures

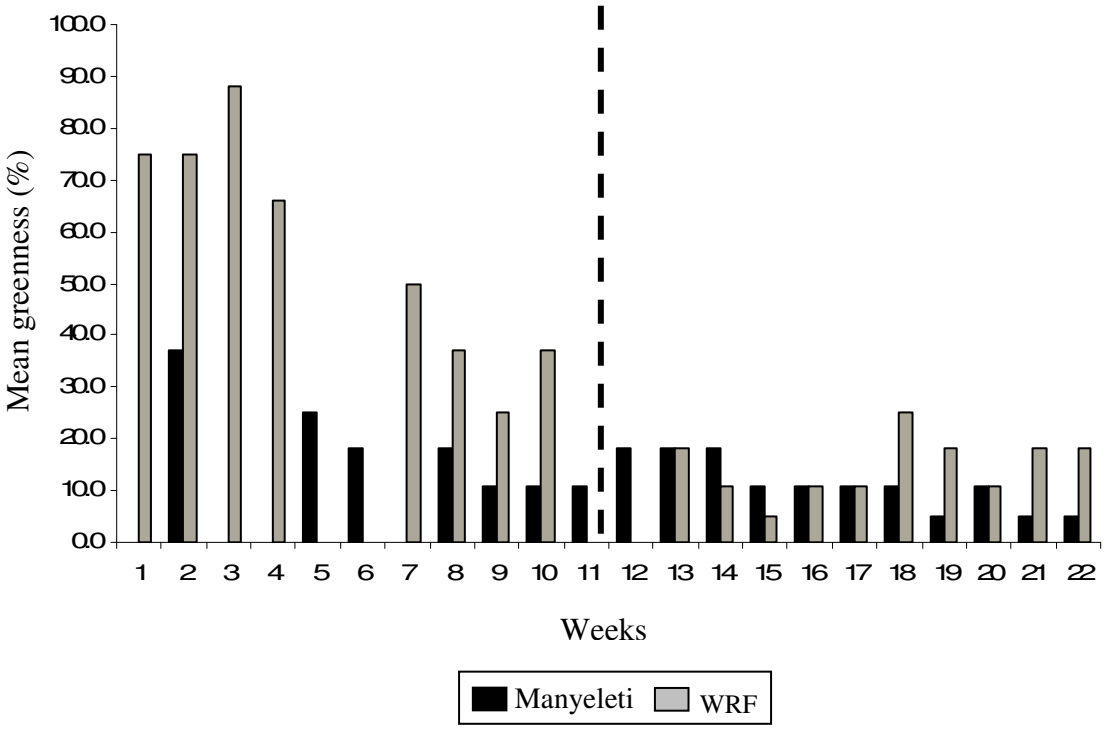


Figure 3.1. Mean weekly greenness for Manyeleti and WRF, over a five moth period between May and October 2009. Broken vertical bar indicates division between early dry season and late dry season.

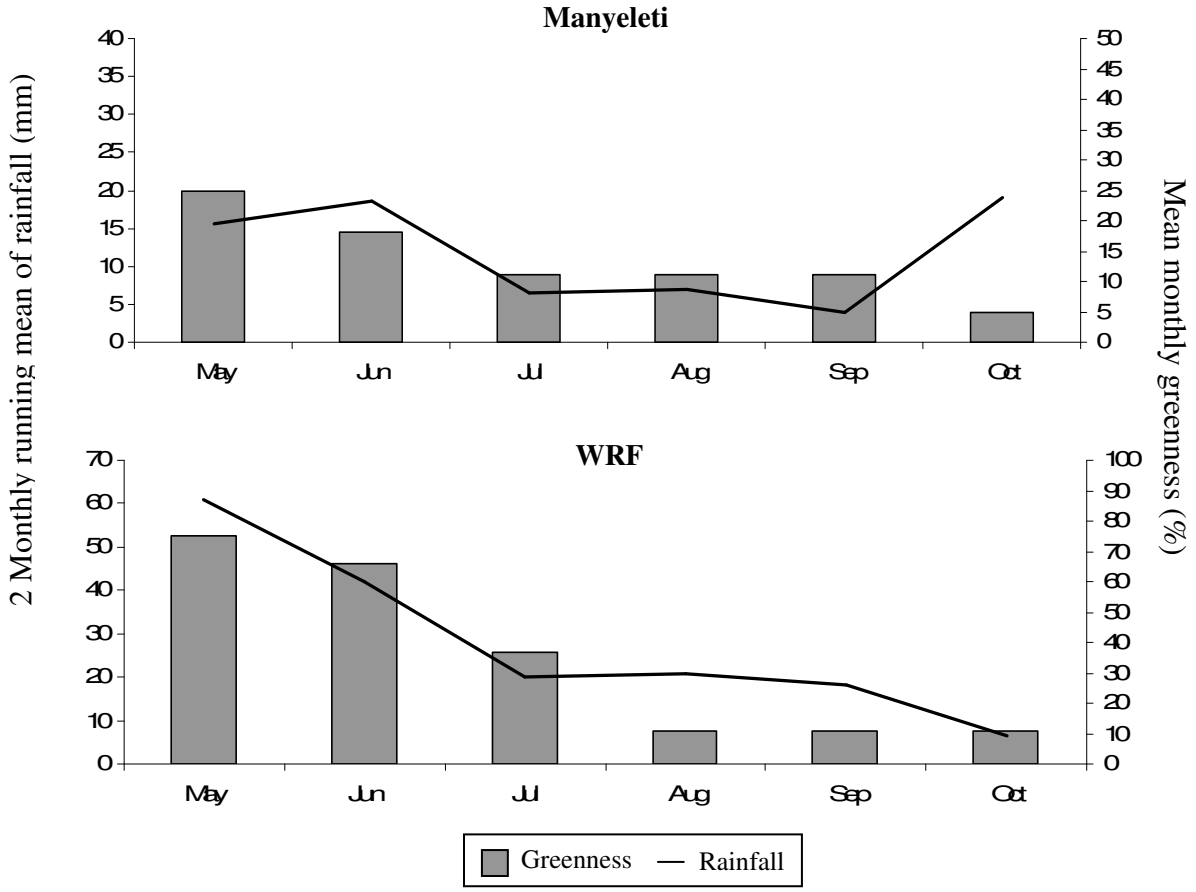


Figure 3.2. The 2- monthly running mean of rainfall and mean monthly greenness for Manyeleti and WRF, measured over a five month period from May to October 2009.

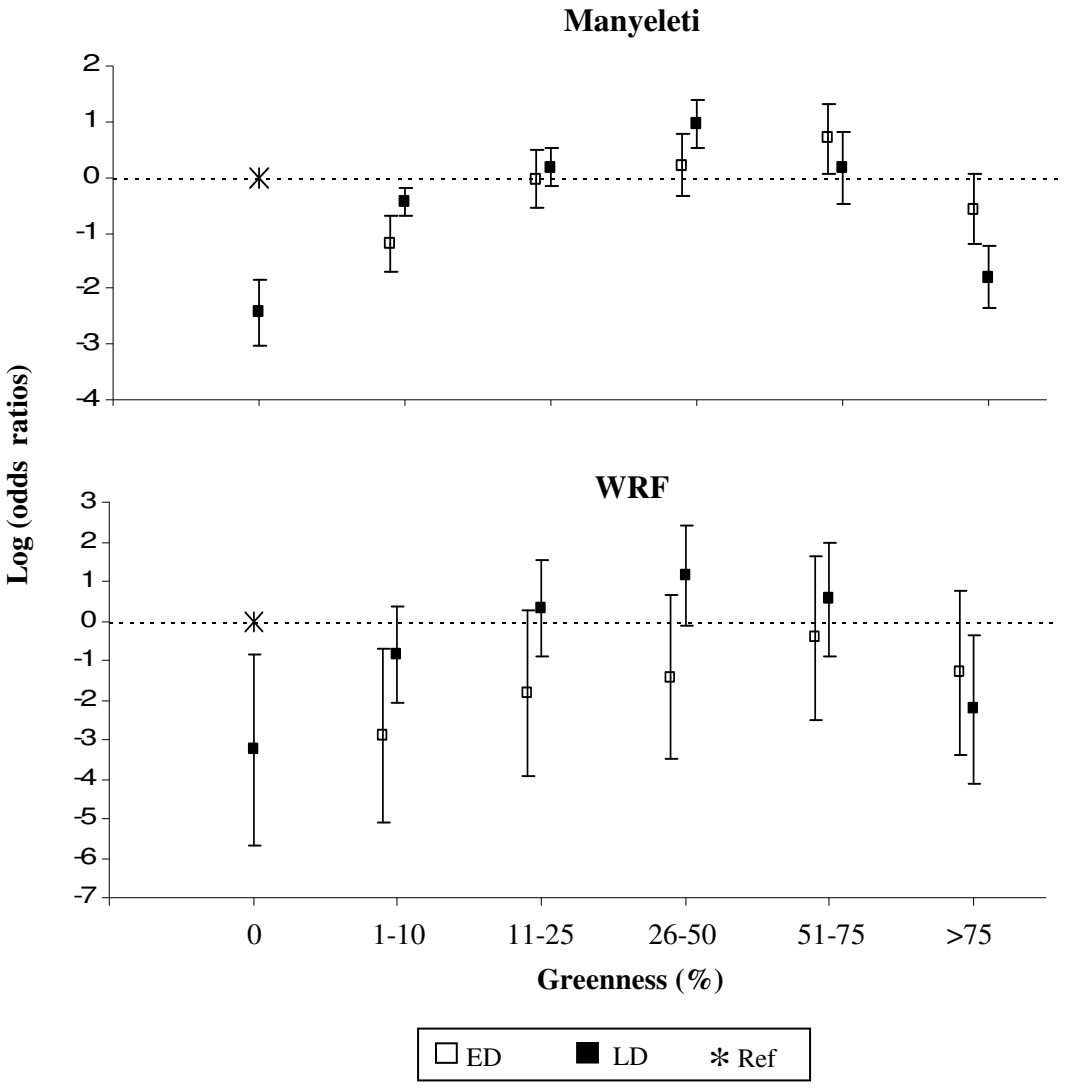


Figure 3.3. Grass species selection estimates (± 95% confidence interval) based on greenness during the early dry (ED) and late dry (LD) seasons for Manyeleti and WRF. Reference category (Ref) is grasses with a greenness of 0% in the early dry season. From data collected over a five month period form May – Oct 2009.

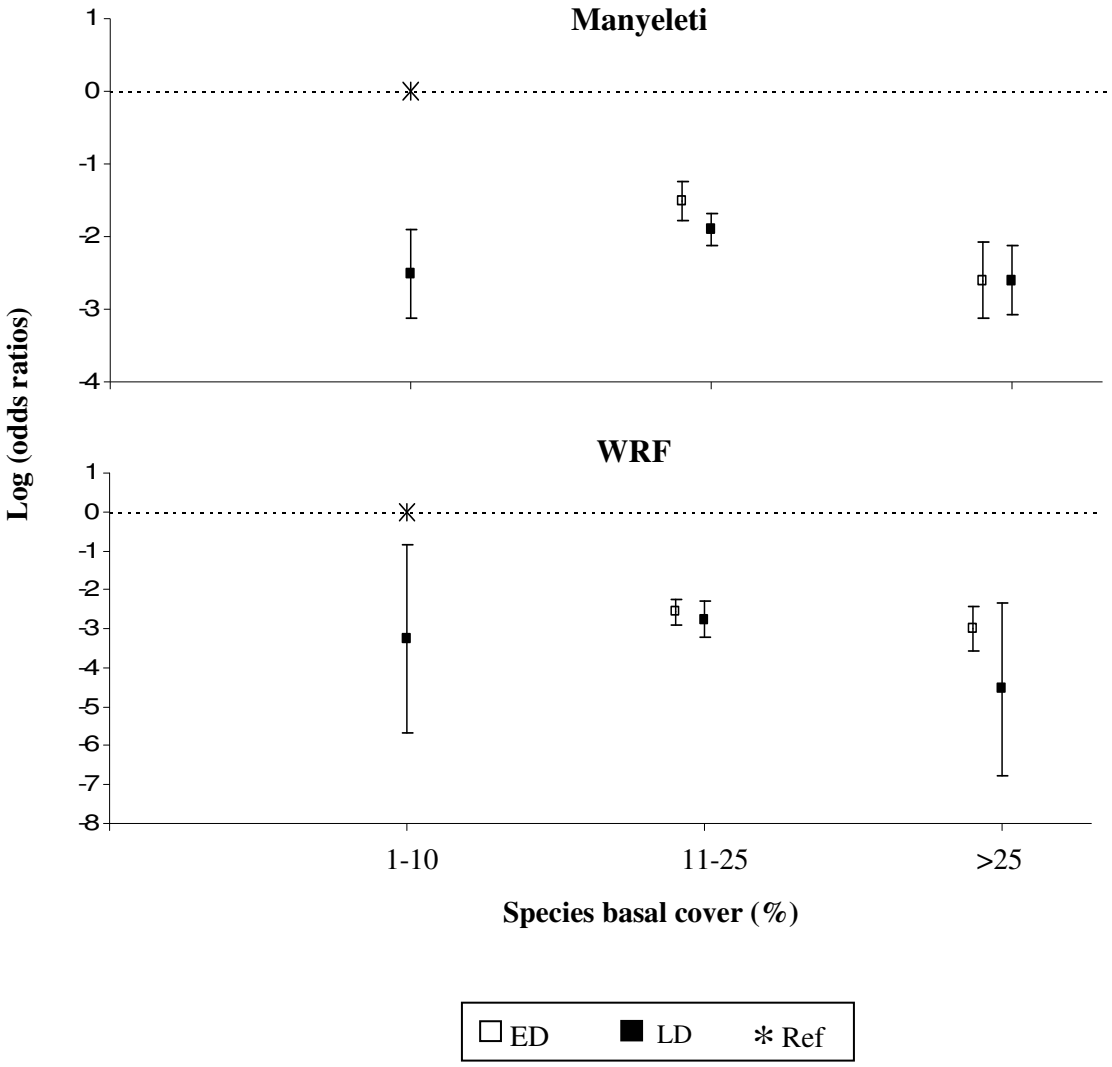


Figure 3.4. Grass species selection estimates (log odd ratios ± 95% CI) based on the percentage of species basal cover during the early dry (ED) and late dry (LD) seasons, for Manyeleti and WRF. Reference category (Ref) is grass species with basal cover of 1-10% during the early dry season. Data collected over a five month period from May to October 2009.

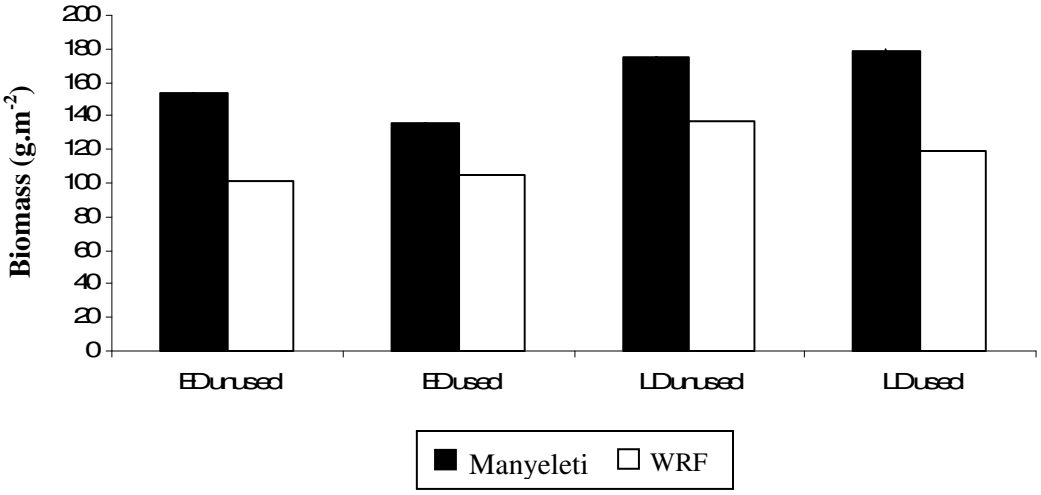


Figure 3.5. Mean monthly biomass for used and unused areas in Manyeleti and WRF, during the early dry (ED) and late dry (LD) seasons. Data collected over a five month period from May – October 2009.

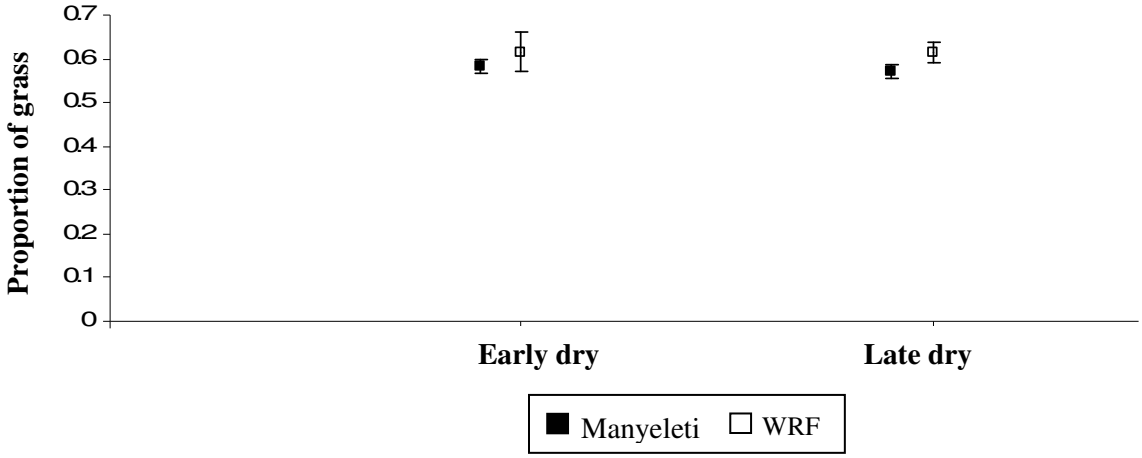


Figure 3.6. Mean (± 95% confidence interval) proportions of grasses present in impala faeces, during the early dry) and late dry seasons, in Manyeleti and WRF. Data recorded over a five month period between May and October 2009.

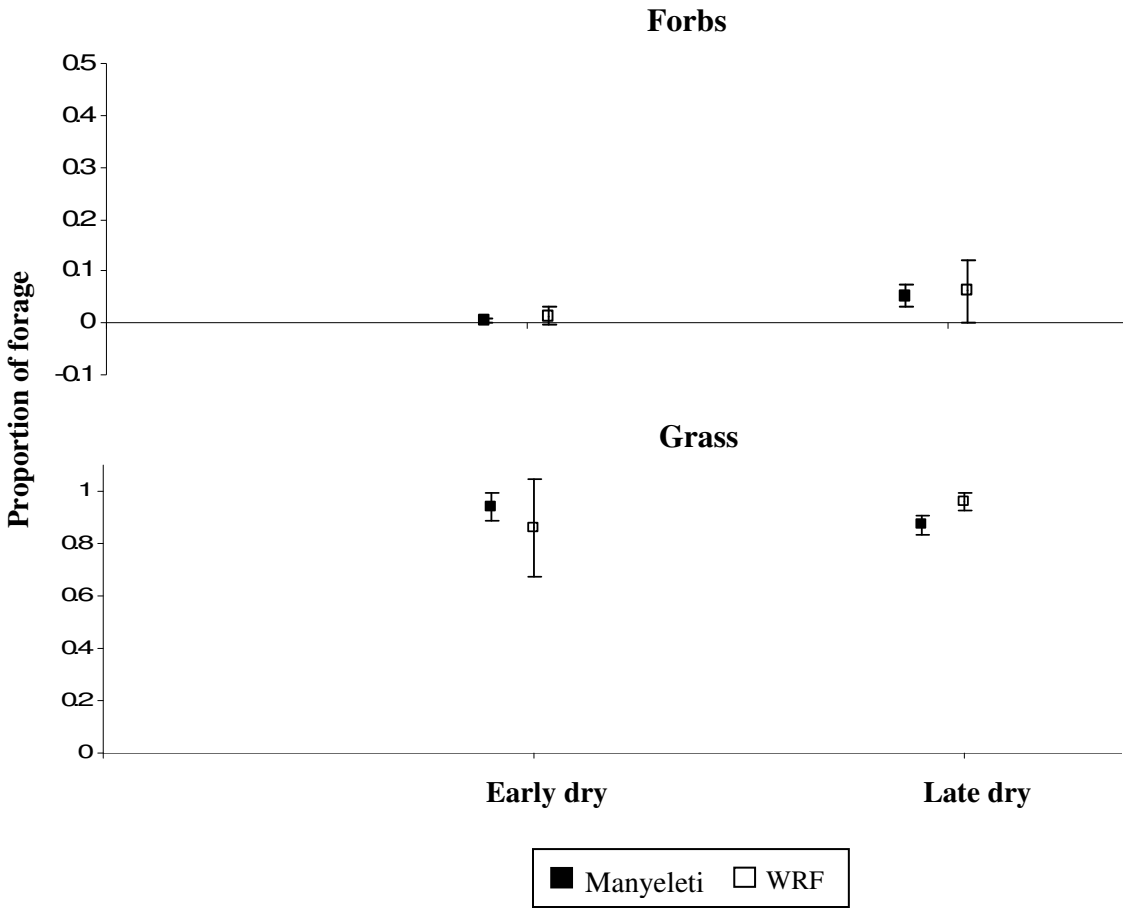


Figure 3.7. Mean (± 95% confidence interval) weekly proportions of forbs and grass selected during the early dry and late dry seasons, in Manyeleti and WRF. Data recorded over a five month period between May and October 2009.

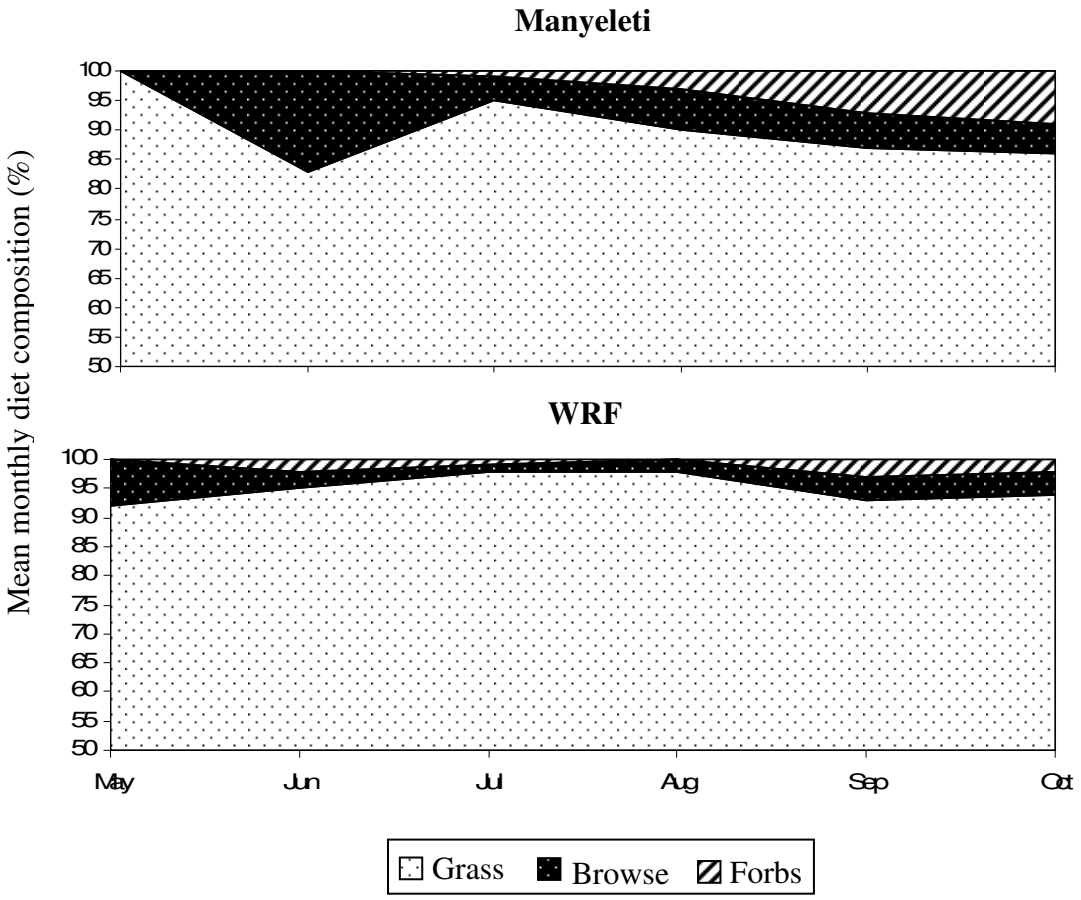


Figure 3.8. Mean monthly composition of grass, browse and forbs in the diet of impala in Manyeleti and WRF. From data collected between May and October 2009

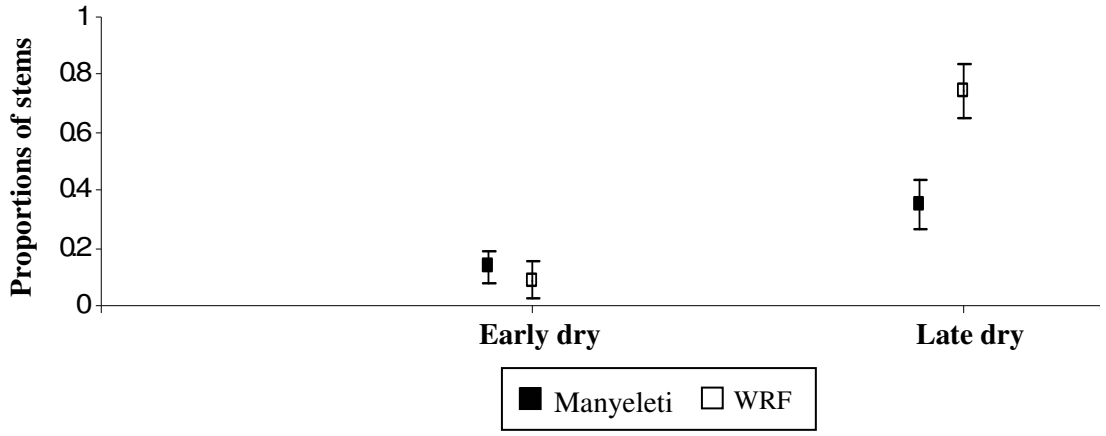


Figure 3.9. Mean (± 95% confidence interval) weekly proportions of stems selected by impala during the early dry (ED) and late dry (LD) season in Manyeleti and WRF. From data collected over a five month period (May to October 2009).

CHAPTER 4 - SYNTHESIS

I set out to investigate resource selection in a mixed feeder. This was broken down into two main components: studying the factors that might influence selection at three different spatial scales (Chapter 2), and how selection of grass species changes across seasons (Chapter 3). As an example of a mixed feeder I investigated the selection patterns of impala.

I studied forage selection at three spatial scales: species level, feeding station level and patch selection level (Chapter 2). The variables included in the study included greenness, species basal cover, height of grass leaves, biomass of a feeding station, and type of cover present in a feeding patch. I found that there are many factors contributing to whether a plant species, feeding station or feeding patch is being selected. At all the three of these levels I found greenness to influence selection, with the influence of greenness being more pronounced in the late dry season. Biomass was an additional variable influencing the selection of feeding stations, and type of cover influenced feeding patches. Species basal cover and height of leaves did not influence selection at any of the spatial scales, but the change in species basal cover across season did influence grass species selection (Chapter 3). Greenness and season were also major driving factors behind diet swtiching. Although I did not see a significant swtich between diets, there was an overall shift to using different resources in drier periods (chapter 3). To summarize my findings I will be comparing my results with work done previously on other large mammalian herbivores, mixed feeders and specifically impala.

High greenness indicates higher nutrition forage (Demment and Van Soest 1985; O'Reagain and Owen-Smith 1996) and younger, greener forage is lower in fiber and higher in digestibility (Demment and Van Soest 1985; Van Soest 1994). Impala only consumed dicots that

were >75% green, this suggests that those species were less preferred than grasses, which were grazed even when <10% green. Macandza (2009) found that sable antelope (*Hippotragus niger*), although feeding mostly from the greenest forage, also fed on brown grasses and only avoided grasses <30% green. Similarly Parrini (2006) showed sable antelope to avoid patches that were <10% green. Impala, which is relatively smaller than sable, should be more selective to obtain the best quality food to fulfill their dietary requirements (McNaughton and Georgiadis 1986). Yet, I found impala to feed from grasses <10% green, but I also showed impala to select single green stems in tufts dominated by dry grasses. Accordingly, impala was selective for greenness at plant level as well as at a larger scale. This is opposite to what Heitkönig and Owen-Smith (1988) found on roan antelope (*Hippotragus equinus*). Roan antelope, during the dry season, was not selective for greenness at a plant level, but rather for a low stem:leave ratio. Similarly Parrini (2006) could not determine whether sable antelope was selecting for single green swards or whether they accepted browner forage during the dry season. Hence, the smaller bite sizes of impala allow them to be selective for greenness at plant level.

Following these findings, the change in greenness between seasons was again important in governing resource selection (Chapter 3). I expected impala to make a switch from a grass dominated diet to a browse dominated diet late in the dry season, when their preferred forage decreases in nutritional quality an increases in fiber (Du Toit 1988; Van Rooyen 1992; Meissner et al. 1996). Yet, despite a notable change in greenness, I did not see an obvious switch between plant types. However, even though impala did not make a clear switch between diets, I did see a change in the contribution that forbs, grass stems and seed pods made to their diet. Du Toit (1988) performed a detailed study on the feeding patterns of impala, and similar to what I found, he showed that their diet was dominated by grasses. He did however find that impala used

a large proportion of dicots during the dry season. These results are echoed by those of Van Rooyen (1992) and Meissner et al. (1996), who also showed impala to make a discernible switch between forage types during the dry season. Although it has been suggested that impala switch between resources when 2-month running mean of rainfall falls below 30 mm (Du Toit 1988), in the present study impala did not follow this pattern. Despite the lack of diet switching, there was an overall expansion of dietary diversity for impala during the late dry season, supporting ungulate foraging theory (Owen-Smith and Novellie 1982) and the diet expansion of sable antelope during the dry season (Macandza 2009).

Because *P. maximum* drove impala movements and selection at a larger scale, this grass species was identified as a key resource for impala. *Panicum maximum* was also identified as a key species for sable antelope (Parrini 2006). *Panicum maximum* has been shown to be vital as a grazing grass to wild herbivores (Van Oudtshoorn 2004) and because of its high nutrition content it is able to sustain herbivores for a long period through the dry season. Impala fed from this species during times when overall greenness was low and resources limited, unlike buffalo (*Syncerus caffer*) which resorts to feeding on otherwise unpalatable *Bothriochloa* spp. to sustain them throughout the late dry (Macandza et al. 2004). The difference in plant species selected by impala and buffalo is likely due to differences in bite sizes and the ability of impala to select single green stems from a tuft. Buffalo needs to acquire larger volumes of forage than impala, because of their relative larger size (McNaughton and Georgiadis 1986). Thus if there is a grass that is generally unpalatable, but retains certain high quality characteristics later in the dry season, herbivores that are less able to select single green stems from more palatable grasses, will necessarily be driven to feed on alternatives.

Not only did estimated biomass contribute greatly to selection of feeding stations (Chapter 2), but impala selected against grasses in high biomass areas (Chapter 3). Biomass is positively related to fiber content of grass, and thus negatively related to digestibility (Wilmshurst et al. 2000; Wilmshurst et al. 1999). Herbivores should aim to acquire forage low in fiber with high digestibility and proteins. This has been shown in Thompson's gazelle (Wilmshurst et al. 1999), which feeds from low biomass grasses. Notwithstanding, avoidance of low quality forage is not always possible for larger herbivores that need to ingest large quantities of food to sustain them. Sable antelope has been shown to feed on grasses taller than 10 cm (Parrini 2006), with the heights of selected grasses changing between seasons. In addition larger scale selection by sable was influenced by the height of swards, and varied between seasons. Bradbury et al. (1996) showed sward height to be positively related to protein densities in grasses, and showed a high variability in grass protein contents between seasons. Height of grasses was not retained as an explanatory variable in any of my models but impala had a wide tolerance of grass height, and used patches with grasses varying in height from 1 cm to 160 cm (Fig II.I, Appendix II) and fed on grasses varying from 1 cm – 1 m in height (Fig II.II, Apendix II). For a smaller antelope, such an impala that require a high quality forage, it would be highly beneficial to feed on grasses low on fiber, and that is likely the main reason for impala avoiding high biomass areas. Bison (*Bison bison athabascae*) graze at varying heights, but decrease their bite depth when grazing on tall grasses (Bergman et al. 2000). They suggested that bison aimed at avoiding stems, which are higher in fiber for more mature (i.e. taller) grasses. Impala are not constrained by large bite sizes which will cause them to ingest high quantities of highly fibrous material when grazing at tall heights, they can take selective bites aimed at specific nutritious swards or stems without having to adjust their bite sizes. I also suggest that it is for the same

reasons that impala avoided patches with tall grasses more, to enhance diet quality rather than to increase vigilance.

Lastly species basal cover was retained as a variable in the models best describing the change in grass species selection between seasons. The results showed that higher basal cover classes are more avoided. Because of the fairly broad basal cover classes used and the lack of literature on herbivore species preference, it was hard to attribute the trends to a specific characteristic associated with an increase in species basal cover. A possibility is that an increase in basal cover is related to an increase in the number of stems per tuft, which again will increase potential fiber intake from stems, which generally deter herbivores (Heady 1964; Parrini 2006).

Conclusions and recommendations for future work

This study showed that impala are true mixed feeders, not being constrained by available plant types, but using any available high quality forage. I found that they do not make a definite switch between diets every dry season, even if rainfall is low, but that a decrease in greenness is a main driver in the change in selection between and within seasons and at various spatial scales. Eland is a mixed feeder, but different studies have shown great variability in the proportion of grasses and browse in their diet, with some suggesting that they predominantly browse but switch to grasses in the dry season (Watson and Owen-Smith 2000), and others suggesting that they predominantly graze but use browse in dry months (Nge'The and Box 1976). Accordingly, changes in the diet of impala might be dependent on the availability of good quality forage, and not necessarily be the same each year. Interestingly I found that unlike many other herbivores impala feed regularly from grass stems in the dry season, likely because of their smaller bite

sizes and again the search for green forage. None of the studies on resource selection in impala have found the same results, many showed similar trends, but there seem to be no definite patterns. Future research should aim to investigate at which greenness levels impala switch to a browse dominated diet, since 2 monthly running mean of rainfall does not seem to be the determining factor. This would require research over longer periods, throughout wet and dry seasons, as well as nutritional analysis on plant species throughout the study periods. This will allow a better perception of the seasonal dynamics within plant species and how that impacts on impala resource selection. Moreover, research aimed at addressing the influence of predation and vigilance behaviour in impala will be invaluable in determining which factors drive larger scale selection.

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APPENDIX I – USED AND UNUSED SPECIES

Table I.I. Used and unused grass species recorded at both study areas

	Used	Unused
1	*Arundinella nepalensis*	*Aristida adscensionis*
2	*Bothirochloa insculpta*	*Aristida congesta*
3	*Chloris virgata*	*Aristida stipitata*
4	*Cynodon dactylon*	*Chloris gayana*
5	*Dactyloctenium giganteum*	*Cymbopogon excavatus*
6	*Digitaria eriantha*	*Cymbopogon validus*
7	*Eleusine coracana*	*Dactyloctenium geminatum*
8	*Enteropogon macrostachyus*	*Digitaria diagonalis*
9	*Eragrostis aspera*	*Digitaria longiflora*
10	*Eragrostis ciliaris*	*Digitaria monodactyla*
11	*Eragrostis rigidior*	*Eragrostis biflora*
12	*Eragrostis superba*	*Eragrostis chapelieri*
13	*Eragrostis trichophora*	*Eragrostis gummiflua*
14	*Heteropogon contortus*	*Eragrostis lehmanniana*
15	*Hyperthelia dissoluta*	*Melinis repens*
16	*Panicum deustum*	*Pennisetum macrourum*
17	*Panicum maximum*	*Schizachyrium sanguineum*
18	*Panicum coloratum*	*Sporobolus africanus*
19	*Perotis patens*	*Sporobolus festivus*
20	*Pogonarthria squarrosa*	*Sporobolus fimbriatus*
21	*Schmidtia pappophoroides*	*Trichoneura grandiglumis*
22	*Setaria incrassata*	
23	*Sporobolus nitens*	
24	*Themeda triandra*	
25	*Tricholaena monachne*	
26	*Urochloa mosambicensis*	

Table I.II. Used and unused dicot species recorded at both study areas, those indicated with "spp." were not identified up to species level, but merely to the genus

	Used	Unused
1	*Acacia karroo*	*Acacia exuvialis*
2	*Acacia grandicornuta*	*Capparis* spp.
3	*Acacia mellifera*	*Ciccus cornifolia*
4	*Acacia nigrescens*	*Dalbergia melanoxylon*
5	*Acacia nilotica*	*Diospyros mespiliformis*
6	*Albizia harveyi*	*Dombeya rotundifolia*
7	*Azima tetracantha*	*Ptaeroxylon obliquum*
8	*Combretum apiculatum*	*Pyrostria hystrix*
9	*Combretum hereroense*	
10	*Combretum zeyheri*	
11	*Dichrostachys cinerea*	
12	*Ehretia amoena*	
13	*Euclea* spp.	
14	*Flueggea* spp.	
15	Forb spp.	
16	*Gardenia* spp	
17	*Grewia* spp.	
18	*Gymnosporia* spp.	
19	*Ormocarpum trichocarpum*	
20	*Pavetta gardeniifolia*	
21	*Philenoptera violacea*	
22	*Schotia capitata*	
23	*Spirostachys africana*	
24	*Strychnos* spp.	
25	*Terminalia sericea*	
26	*Ziziphus mucronata*	

APPENDIX II – GRASS HEIGHTS

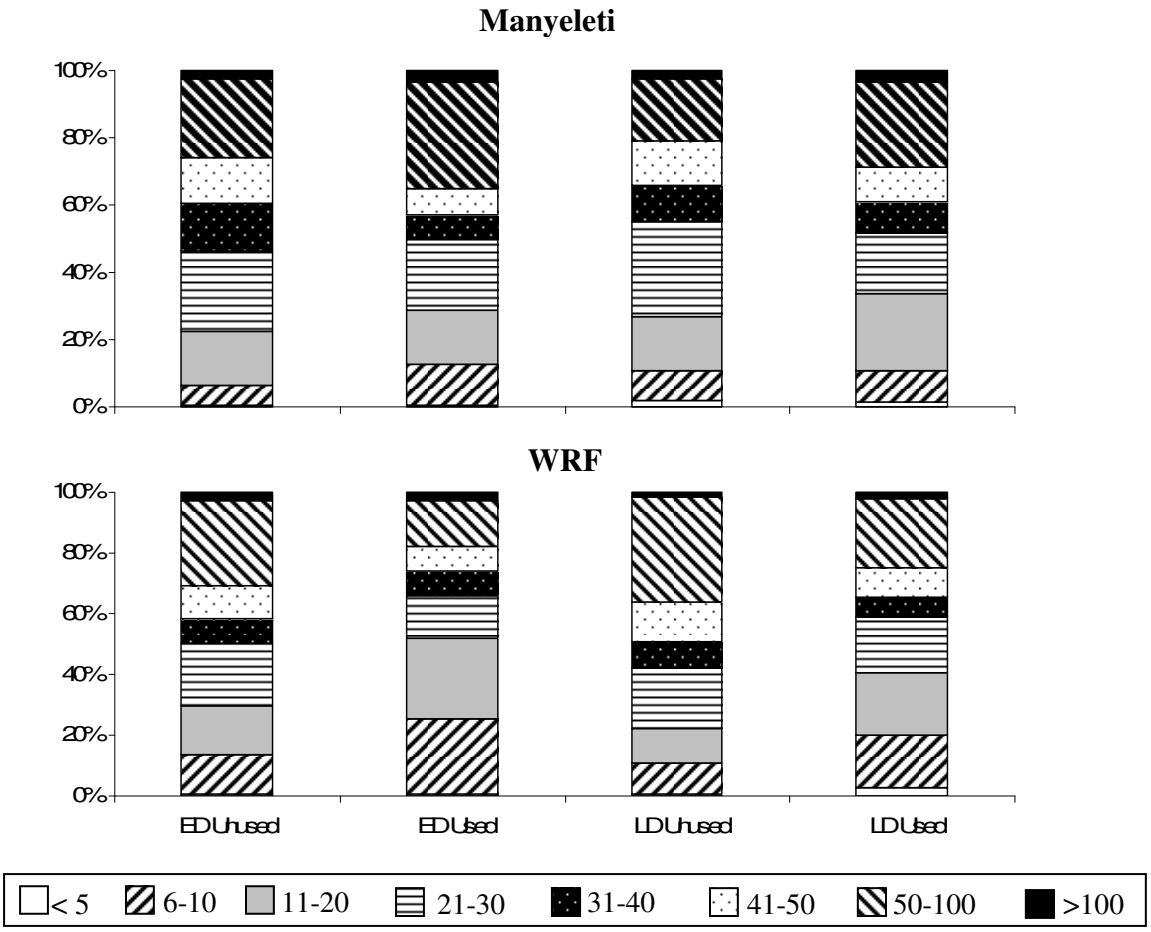


Figure II.I. Percentage of grass within certain height categories (cm) in Manyeleti and WRF in used and unused patches with the early dry (ED) and late dry (LD) season. Data collected over a five month period from May to October 2009.

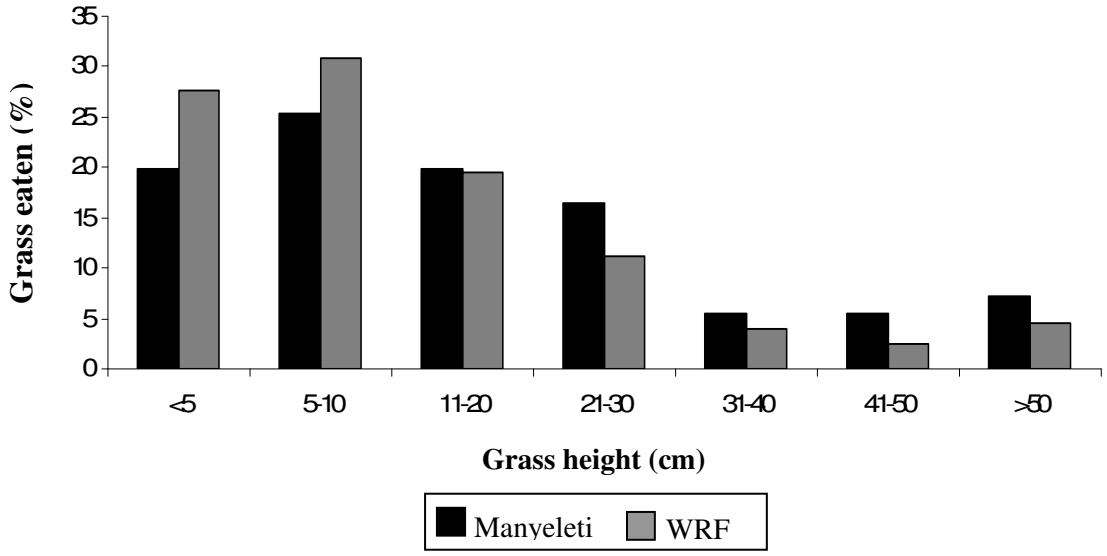


Figure II.II. Percentage of grass eaten within each height category, in Manyeleti and WRF over a period of five months from May to October 2009