Grass attributes and seasonal changes in foraging by a preferentially grazing savanna mixed feeder

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Jorista van der Merwe*, Jason P. Marshal

Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, 1 Jan Smuts Ave, Wits 2050, South Africa

ABSTRACT

Driven by metabolic requirements, large mammalian herbivores often become more selective to attain high-quality forage during dry times, especially in semi-arid habitats. Our main objective was to investigate which plant characteristics form the major drivers in the forage use of a mixed feeder during the dry season. The study was done in two savanna reserves in South Africa, Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), during the dry season from May to October 2009. We observed impala (*Aepyceros melampus*) and identified the grasses, dicots, and plant parts that they fed on. We recorded greenness, estimated biomass of feeding patches, ranked basal cover of each grass species, and measured the average height of used grasses. We collected fresh faeces to assess diet composition through microhistology. We found that location, season, greenness, basal cover, and height of grass influenced grass use. The probability of using grass increased with an increased in grass height and impala was more likely to use greener grass in the late dry season. We demonstrated that greenness is one of the key drivers in grass use and together with the indirect effect of rainfall play a major role in herbivore forage use in highly seasonal environments.

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1. Introduction

Large herbivores that inhabit semi-arid savannas face the challenge of acquiring adequate nutrition in highly seasonal environments emphasized by periods of food scarcity (Owen-Smith and Cooper, 1989; Rueda et al., 2008; Wilmshurst et al., 1999b). Driven by metabolic requirements, mammalian herbivores often become more selective in order to obtain high-quality forage during dry seasons (Belovsky, 1991; Demment and Van Soest, 1985; Wilmshurst et al., 2000), and as a result animals sometimes exhibit great behavioural changes in foraging coinciding with seasonal changes (Birkett et al., 2012). One strategy to meet this challenge is to shift diet from high-quality forage types that are available in times of resource-abundance to types that can sustain individuals during resource-limiting periods.

High-nutrient forage is often associated with high greenness (O'Reagain and Owen-Smith, 1996) and, with the exception of evergreen forage, is a major driver in the diet selection of herbivores (Codron et al., 2006). Changes in resource abundance and resource quality, because of seasonal fluctuations, affect herbivore

distribution (Seagle and McNaughton, 1992) and cause herbivores to use alternative resources when their preferred forage becomes nutritionally unfavourable (Albon and Langvatn, 1992; Wilmshurst et al., 1999a,b; Mysterud et al., 2001). Specifically these changes in forage quality drive intermediate feeding herbivores to switch from a diet dominated by one type of forage to another that is more readily available while avoiding as much fibre as possible (Hofmann, 1989).

Impala (*Aepyceros melampus*) are intermediate feeders that switch between grazing and browsing (Jarman, 1974; McNaughton and Georgiadis, 1986). The switch between dominant diet types is suggested as either a direct response to plant nutritional content (Jarman, 1974; Kos et al., 2012; Van Soest, 1994), or an indirect response to fluctuating environmental factors such as changes in rainfall that will influence plant nutritional value (Du Toit, 2003; Van Rooyen, 1992). Many studies indicate that impala include more grasses in their diet during the rainy season with a switch to browsing during the dry season (Du Toit, 2003; Kos et al., 2012; Meissner et al., 1996; Owen-Smith and Cooper, 1985; Van Rooyen, 1992). Although it is speculated that the major driver for this switch is the increased fibre and a decrease in nutrition of grasses, few studies have closely investigated which plant and environmental characteristics drive the use of grass.

Compared to larger herbivores, such as buffalo (*Syncerus caffer*) that feed on large amounts of low quality forage, impala, having

* Corresponding author. Present address: 1125 Lincoln Dr, Life Sciences II, Room 251, Southern Illinois University, Carbondale, IL 62901, USA. Tel.: +1 618 3050533.
 E-mail address: jvandermerwe@siu.edu (J. van der Merwe).

small body mass (40–55 kg), require lesser amounts of much higher quality forage to satisfy their high energy demands (Demment and Van Soest, 1985; Klein and Fairall, 1986; McNaughton and Georgiadis, 1986). This implies that when the quality of their favoured forage component (i.e., grass) decreases through the dry season a switch by impala away from that component should be highly pronounced, and the timing of the switch should be predictable according to the characteristics of the forage. Multiple previous studies have investigated the intermediate diets of herbivores (Meissner et al., 1996; Van Rooyen, 1992), with many focussing on the nutritional changes in vegetation associated with changes in seasons. Because greenness of grasses deteriorates as the season progresses and most grasses are brown by the end of the dry season, we expect that grass greenness will play a major role in impala resource use. In addition, other grass characteristics might influence grass use. O'Reagain and Owen-Smith (1996) showed that short, low-biomass grasses were grazed more often, and thus grass height and biomass should play a role in grass use. Our main objective was to investigate the grass characteristics that drive grass-use in impala. Although this study focused on a single dry season, incorporating the effect of the preceding wet season on forage conditions and herbivore responses, will contribute to a better understanding of diet switching by mix-feeding herbivores in semi-arid savannas.

2. Materials and methods

2.1. Study areas

The study was conducted in two reserves, comprising savanna habitat, on the border of the Limpopo and Mpumalanga provinces of South Africa. Sampling took place during the dry season, from May to October 2009. We focused on the dry season because limited resources during the dry season should force mixed feeders to switch between resource types (Du Toit, 2003; Hulbert et al., 2001; McNaughton and Georgiadis, 1986; Van Rooyen, 1992). Based on mean weekly greenness levels of vegetation we split the dry season into early dry (mid-May through July) and late dry seasons (August to mid-October).

We conducted fieldwork at Wits Rural Facility (WRF) and Manyeleti Game Reserve (Manyeleti), both located less than 30 km from the Orpen gate of the Kruger National Park. Wits Rural Facility is a 350 ha fenced property with mean annual rainfall of 670 mm (Shackleton, 1993). Large mammals occurring in WRF include impala, kudu (Tragelaphus strepsiceros), common duiker (Sylvicapra grimmia), reedbuck (Redunca fulvorufula), waterbuck (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. Manyeleti is a reserve of 22 750ha, contiguous with Kruger National Park, and forms part of the Greater Limpopo Transfrontier Park, which is over 3 million ha. Mean annual rainfall for Manyeleti is 507 mm. Dominant grasses in both sites include Panicum maximum, Aristida spp., Urochloa mosambicensis, Pogonarthria squarrosa, Bothriochloa insculpta, Heteropogon contortus, Eragrostis spp, and Cynodon dactylon. Some of the dominant browse species are Dichrostachys cinerea, Terminalia sericea, Vachellia spp. (formerly Acacia spp.), Combretum spp., and evergreen Euclea trees.

2.2. Field observations and vegetation measurements

We sampled each study area three days a week on alternating days, by driving through each study area and recording all encountered impala herds up to a distance of ~100 m from the road. Once we located feeding herds, we observed them through binoculars until they moved out of the area. We then searched the patch for plants that showed fresh bites (i.e., no dried leaf edge; Parrini, 2006). To ensure that bites were taken by impala we inspected the ground for tracks leading to plants where bites were observed. We classified areas that showed fresh bites as used.

If a patch was used, we placed a 0.5 m × 0.5 m plot square over the vegetation where we found the fresh bites. This 0.5 × 0.5 m plot was classified as the feeding station (an area that a herbivore can use without moving its feet; Bailey et al., 1996). Plants that showed fresh bites were classified as used. We then extended the plot square 1.5 m vertically, to include any browsed vegetation that was within reach of impala (Du Toit, 1990). In each feeding patch we sampled 5 plots, 2 m apart. The plots were placed in the four cardinal directions, from where the first one was placed.

Within each feeding station we identified all the used and unused grasses and dicots. Because it can be hard to successfully detect plucked browse leaves, we did not quantify the bites taken from browse and just recorded the species as used (many times we could observed impala feeding from a specific species through binoculars). Plants were identified to species level but because some species were only present, or used, a few times we grouped species together into three categories "grass", "browse" (i.e., woody dicots), and "forbs" (i.e., herbaceous dicots). Regrouping of plant species also aided in model parameterization. We recorded the greenness of each grass and browse species as well as the basal cover for each grass species. We estimated biomass for each feeding station, and measured the midpoint of sward height of each grass species.

We used an eight point scale (Walker, 1976) to rank all grass species based on greenness of the whole tuft and grass basal cover (of grass tufts), where $0 = 0\%$, $1 = 1–10\%$, $2 = 11–25\%$, $3 = 26–50\%$, $4 = 51–75\%$, $5 = 76–90\%$, $6 = 91–99\%$, and $7 = 100\%$. Classes were later reduced to 6 classes: $0 = 0\%$, $1 = 1–10\%$, $2 = 11–25\%$, $3 = 26–50\%$, $4 = 51–75\%$ and $5 = >75\%$ green. Basal cover was estimated as the total basal cover for all grasses of the same species occurring within the same plot, and re-grouped into 3 classes, $1–10\%$, $11–25\%$ and $>25\%$ cover. We estimated biomass by modifying the comparative yield method (Haydock and Shaw, 1975). Each plot was ranked from 0 to 5 based on the presence of forage, where $0 = 0\%$ (a bare plot, or a plot with no 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 1.5 m). We randomly clipped 20 plots of each rank and recorded the weight of each sample after drying clippings at 60 °C for two days. We used linear regression to determine the relationship between plot ranks and biomass and converted the ranked numbers into mean biomass (g/m^3).

2.3. Microhistology

At each used patch we searched for, and collected, fresh impala faeces (i.e., still wet and warm). After faeces were oven dried at 60 °C, we crushed the dried samples to a powder, boiled them in 5 ml of Nitric acid (55%) for 2 min and for another 5 min in water (MacLeod and Kerly, 1996). We washed each sample through a sieve with a 1 mm mesh, and then again through a 0.25 mm sieve. We inspected the remaining fragments under a binocular light microscope at 40 × magnification, with the purpose being to distinguish between monocot and dicot species (Carrière, 2002). Starting in the top left corner of the slide and moving downwards, we followed a grid system to identify the first 50 fragments in each sample. This allowed us to estimate the percentage of monocots and dicots in impala's diet on a 2-weekly basis at both study areas.

2.4. Data analysis

Using multi-model inference (Burnham and Anderson, 1998) we developed up to 15 mixed-effect models to find the model best describing *a priori* hypotheses on grass species use. The models had grass-use (yes or no) as response variables, season (early dry or late dry), location (Manyeleti or WRF), greenness (6 ranks, categorical), height of leaves (centimetre, continuous), species basal cover (3 ranks, categorical) and plot biomass (g m^{-3}, continuous) as explanatory variables in the full models. The models had plot number nested within feeding patch number as random effects. There was no collinearity among any of the variables.

We compared the models using Akaike's Information Criterion (AIC), corrected for small sample bias (AICc), where the best model is the one with the lowest AICc (Burnham and Anderson, 1998). For each of the models we calculated the Akaike weights (w_i), which provides the weight of evidence in favour of a model i, the closer the weight is to 1 the greater the weight of evidence supporting that model. We estimated grass species use 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 greater probability of grass being grazed and values below 0 indicate a lesser probability of grass being grazed than the reference category (Godvik et al., 2009; Van Beest et al., 2010; Zuur et al., 2009). Selection estimates equal to, or overlapping with, the reference category, indicates no difference in use compared to the reference category.

To further investigate diet contribution, we calculated the mean two-weekly proportions of grass in impala's faeces (from micro-histology results) and used linear regression to compare the proportions with the two-weekly greenness. *Diet* is defined within this manuscript as vegetation that is used, as determined through field observations or microhistology.

All statistical modelling was done in R version 2.15.2 (R Core Team, 2012) 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.

3. Results

3.1. Grass use

We sampled 263 feeding sites within Manyeleti (94 early dry sites, 169 late dry sites) and 130 within WRF (75 early dry sites, 55 late dry sites). During both seasons at both sites, *P. maximum* was the most common grass species (within impala feeding patches) and also the most used grass species. In Manyeleti 63% of the estimated total diet comprised of *P. maximum* in the early dry season, dropping in the late dry season to 44%, while in WRF *P. maximum* made up the bulk of the diet during both seasons (70% in the early dry and 76% in the late dry season). Woody and her-baceous dicots made up only a small portion of the diet at both sites. In Manyeleti dicots made up 14% of impala's diet during both seasons, with the most used dicot groups being *Vachellia* spp. and forbs (20 and 25% of dicot component respectively). In WRF 18% of their diet comprised of dicots in the early-dry season and 23% in the late dry season. *Dichrostachys cinerea* and forbs made up the bulk of their dicot diet (30 and 25% of dicot diet respectively).

The top model describing grass-use ($w_i = 0.99$) retained location, and interactions between greenness and season, height of grass and season, and basal cover and season as variables (Table 1).

Impala was less likely to use grasses in WRF than they were in Manyeleti (log odds = −1.069 ± 0.28 95% CI), but apart from differences in mean weekly greenness during the early dry season

Table 1
Estimated coefficients and 95% confidence intervals (CI) from logistic regression that were used in estimating the probability of impala grazing during the early dry (ED) and late dry (LD) seasons in Manyeleti Game Reserve (Manyeleti) and Wits Rural Facility (WRF), South Africa, Mar–Oct 2009. All estimates are in comparison to a reference category. [a–d]

Variable	Estimate	Upper 95% CI	Lower 95%CI
Intercept	−1.918	−1.237	−2.599
Location WRF[a]	−1.069	−0.787	−1.351
Season LD[b]	0.538	1.313	−0.237
Greenness 1-10%[c]	0.696	1.398	−0.005
Greenness 11−25%	1.663	2.387	0.940
Greenness 25−50%	1.735	2.442	1.027
Greenness 51−75%	2.471	3.210	1.733
Greenness 75%	2.298	3.038	1.558
Height of Leaves	0.020	0.028	0.013
Basal Cover 11-25%[d]	1.560	1.888	1.231
Basal Cover>25%	0.389	1.019	−0.240
LD × Greenness 1−10%	0.839	1.615	0.063
LD × Greenness 11−25%	0.854	1.682	0.025
LD × Greenness 26−50%	1.626	2.531	0.722
LD × Greenness 51−75%	0.669	1.792	−0.453
LD × Greenness>75%	0.636	1.850	−0.578
LD × Height of Leaves	−0.009	0.000	−0.018
LD × Basal Cover 11−25%	−0.749	−0.309	−1.189
LD × Basal Cover>25%	−0.424	0.600	−1.448

[a] Reference category − Manyeleti.
[b] Reference category − Early dry season.
[c] Reference category − 0% greenness.
[d] Reference category − 1−10% basal cover.

(Fig. 1), no other site differences were noted. Average weekly greenness decreased rapidly during the late dry season, with a more drastic change seen in WRF than in Manyeleti.

Compared to grasses that were completely brown during the early dry season (the reference category) all other grasses had a greater higher likelihood of being used. The probability of grass being grazed increased with greenness and was greater during the late dry season than the early dry season (Fig. 2).

The probability of impala grazing increased with an increase in grass height during both seasons (Fig. 3). Although wide confidence intervals show no difference between the 2 seasons, there does seem to be a change in estimates when grasses reach ∼60 cm. Very tall grasses (>60 cm) were less likely to be grazed in the late dry season than during the early dry season, while this pattern was reversed for grasses less than 60 cm.

Finally, in addition to grass height and location, the basal cover of a tuft of grass also influenced grass use. There was a clear seasonal difference in the use of feeding stations, with impala using
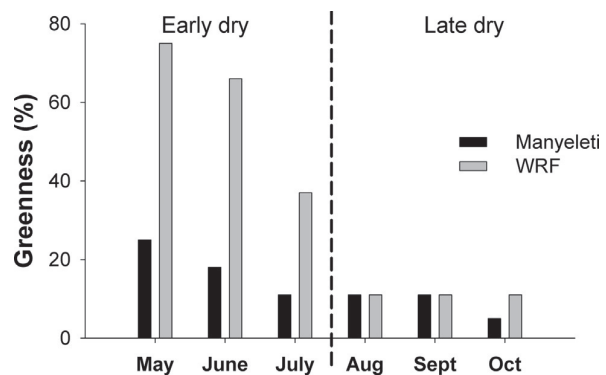

Fig. 1. Mean monthly greenness levels of vegetation during the early dry (May–Jul) and late dry (Aug–Oct) seasons in Manyeleti game reserve (Manyeleti) and Wits Rural Facility (WRF), May–Oct 2009.
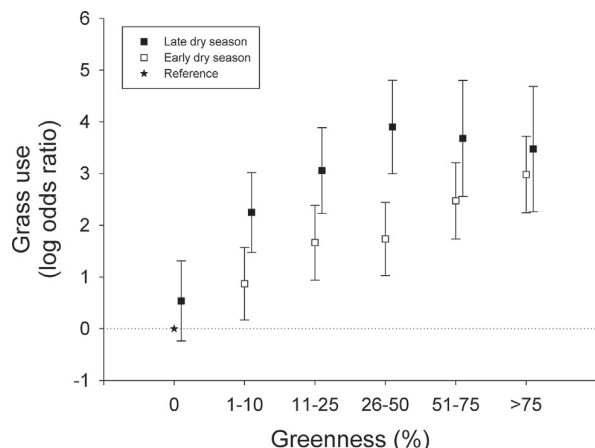
Fig. 2. Grass use estimates (±95% confidence intervals) based on grass greenness levels during the early dry and late dry season in Manyeleti Game Reserve and Wits Rural Facility (combined). All the estimates are in reference to grasses with 0% greenness in the early dry season (★). Estimates above the dashed reference line indicate greater likelihood of use than the reference class, while those below the reference line indicate lesser likelihood of being used compared to the reference class. From data collected May–Oct 2009.

grasses with intermediate cover (11–25%) more than others during the early dry season, but avoiding the same intermediate cover plants during the late dry season (Fig.4).

3.2. Dietary contribution

We found a general broadening of diet in the late dry season. From mean weekly proportions, we found that forb use increased in the late dry season in both Manyeleti and WRF by 3% and 5%, respectively, and even though overall grass use did not change dramatically at either location between the seasons, biting of stems increased 2-fold in Manyeleti and by more than 60% in WRF in the late dry season (Fig. 5).

A total of 31 faecal samples from WRF and 50 from Manyeleti were inspected. There was no evidence of a relationship between
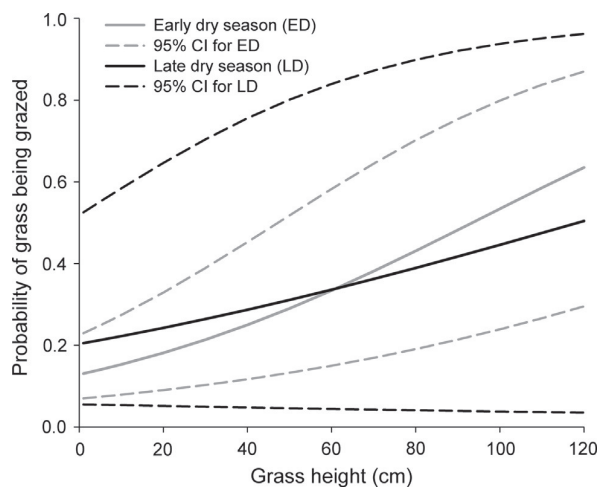

Fig. 3. Probability (solid lines) of grass being grazed (±95% confidence intervals; dashed lines) based on grass height during the early dry (grey lines) and late dry (black lines) seasons at both Manyeleti Game Reserve and Wits Rural Facility. From data collected May–Oct 2009.
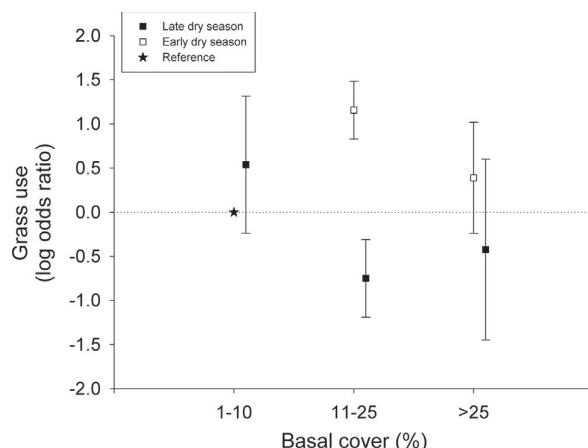

Fig. 4. Grass species use estimates (±95% confidence intervals) based on percentage basal cover in a feeding station during the early dry and late dry seasons in Manyeleti Game Reserve and Wits Rural Facility. All the estimates are in reference to grasses with 1–10% basal cover in the early dry season (★). Estimates above the dashed reference line indicate greater likelihood of use than the reference class, while those below the reference line indicate lesser likelihood of being used compared to the reference class. From data collected May–Oct 2009.

mean 2-weekly greenness and mean 2-weekly proportion of grass in faeces in both Manyeleti ($F_{1,9} = 1.65$, $P = 0.23$, $R^2 = 0.17$) and WRF ($F_{1,8} = 1.03$, 8, $P = 0.34$, $R^2 = 0.13$). In Manyeleti grass fragments made up 85% of faecal samples in the early dry season and 84% in the late dry season, compared to 93% and 88% for the same seasons
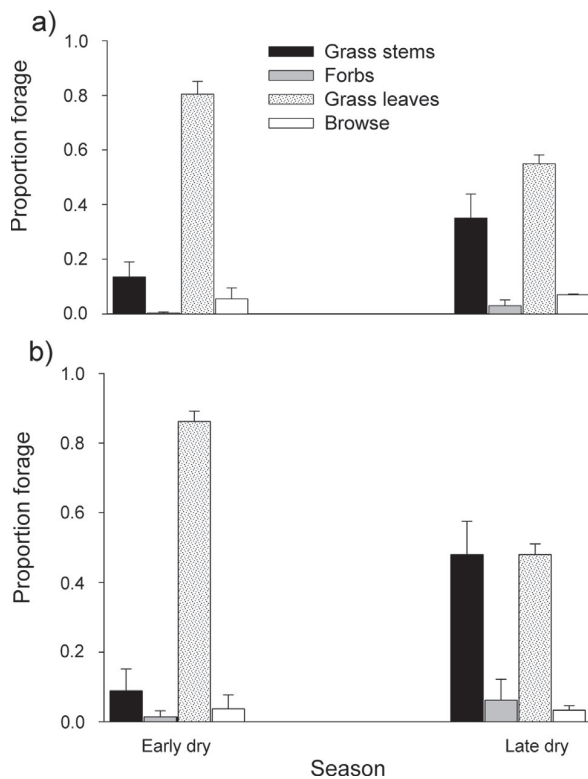

Fig. 5. Proportion of different types of forage types used by impala based on field observations during the early dry and late dry seasons in a) Manyeleti Game Reserve and b) Wits Rural facility. Proportion of "grass stems" refers to bites taken from stems and can include stems or other plant parts not visible to observer, while "Grass leaves" refers to bites that were taken only from grass leaves. From data collected May–Oct 2009.

from direct observations. Similarly, in WRF the majority of faecal samples comprised grass fragments during both seasons (81% in early dry and 76% in late dry), compared to 95% grass selected during both early and dry season from direct observations.

4. Discussion

Impala did not switch from a grass-dominated (>80% grass in diet) to a browse-dominated diet (>80% browse in diet) in the late dry season, actually impala was more likely to graze during the late dry season. The probability of grass being grazed was affected by season, height of grass, basal cover, and greenness.

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 fibre (Jarman, 1974; Short et al., 1974; Van Soest, 1994). Consequently greenness, and the change in greenness as a result of seasonal fluctuations, is a major factor driving herbivore movements by influencing selection of areas and forage (Wilmshurst et al., 1999a). Du Toit (2003) suggested that impala switch from a grass-dominated to a browse-dominated diet when the 2-month running mean of rainfall (2-MRMR) drops below 30 mm, hence decreasing the protein and energy content of forage. Similarly, Meissner et al. (1996) reported impala switching between diets in the late dry season when resources are limited. Rainfall dropped drastically in the late dry season during our study, with the 2-MRMR well below 30 mm, but contrary to our expectations we did not see impala make a switch from a grass-dominated diet to a browse-dominated diet late in the dry season. We attribute 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), which increased soil moisture and hence mean weekly greenness never fell to 0%. The study done by Meissner et al. (1996) took place during a drought period and hence a greater shift in diet should be expected (they found grass selection to decrease by almost 30% in the dry season), whereas a recent study by Kos et al. (2012) showed a decrease of 20% in grass selection from February–May, long before the expected dry-season change in forage quality. In comparison, the March–June period in our study area was considered the early dry season and grass greenness was near 100% with no limitation in forage quality, nor any expectation that impala would shift away from grazing.

Impala was more likely to select grasses in Manyeleti than they were in WRF. This behaviour might be attributed to the physical differences between the two locations. WRF had no permanent predators and a much denser arrangement of palatable tree species. The lack of predators might increase impala's willingness to move into denser areas dominated by trees and feed from these trees instead of grasses. Herbivores are often depicted as living in a "landscape of fear" whereby an animal trades-off quality or quantity of forage for safety (Brown and Kotler, 2004), and fear could play a major role in driving impala forage-selection patterns. We did not directly measure impala vigilance, but it is well-known that herbivores use more open areas to decrease predation risk (Riginos and Grace, 2008; Underwood, 1982). In Manyeleti an abundance of predators may have impala favouring more open areas dominated by grasses, leading to higher grass use than in WRF. The only other major difference between the 2 sites was that vegetation was almost 60% greener in WRF during the early dry season. We attribute this to the much higher-than-average rainfall in WRF. However, this increased greenness did not spill-over to the late dry season and could thus not explain any seasonal site differences in grass-use.

Apart from greenness and location grass-use was also influenced by the height of grasses and basal cover. Despite the potential high fibre and low nutrition associated with high-biomass grasses, and usual avoidance by ungulates (Demment and Van Soest, 1985; Mutanga et al., 2004; Wilmshurst et al., 1999a, 2000), use of grasses increased with grass height during both seasons. The steeper slope during the early dry season did however indicate that impala will use taller grasses in the early dry than in the late dry season. The use of shorter grasses is a strategy used by various antelope, for example Thompson's gazelle (*Gazella thompsonii*; Wilmshurst et al., 1999b) and wildebeest (*Connochaetes taurinus*; Wilmshurst et al., 1999a) to maximize digestibility, which makes it interesting that impala increased use of taller grasses. We suspect that impala's smaller incisor arcade, which is also scaled to body size (Gordon and Illius, 1988), allows them to take more selective bites than larger herbivores (Gordon and Illius, 1988; Jarman, 1974) and thus feed on the good parts of taller grasses that might be present.

Grass-use based on basal cover was only important at the intermediate level. It seemed likely that impala used intermediate basal cover plots more in the early dry season again because low basal cover plots were reflective of a sparsely vegetated area which forced impala to use different plots, while high basal plot might have more stems and hence more fibre. We are unsure why they would not have followed the same strategy in the late dry season, but perhaps during resource-limiting periods their strategy was to increase uptake of the proportion of leaves and hence the use of higher basal cover species is likely to ensure highest grass-leaf intake (Forbes and Coleman 1991).

Lastly, notwithstanding the high fibre and low digestibility associated with grass stems (Arzani et al., 2004; Demment and Van Soest, 1985; Murray and Illius, 2000), impala increased use of these many fold in the late dry season. Hence, similar to their use of taller grasses, impala might take a bite form a normally too-fibrous plant because of their ability to avoid the surrounding brown parts. It can also suggest that the top part of the stem contained a green shaft or leaf blade that was not visible to us. Regardless of which plant part was ingested it was clear that impala are able to select single green stems or any single green leaves within tufts of mostly dry grass (Meissner et al., 1996), much the same as topi (*Damaliscus lunatus*) who use their smaller incisor arcade to select single green swards from large tufts of grass (Murray and Illius, 2000).

We realize that field observations and faecal inspection do not necessarily provide a complete overview of the total diet of any animal (Holechek et al., 1982). Inaccuracies with identifying all the species that were eaten in the field, especially in the dry season when bites can be harder to see, together with variability in digestibility of food items make diet estimates complicated. We are however confident that our field observations and microhistology. complimented each other and although some biases may occur, the general trends remain.

As a result of lower 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 change their diet by switching to alternative resources (Codron et al., 2006; Du Toit, 2003; Klein and Fairall, 1986; Meissner et al., 1996; Van Rooyen, 1992). However, we showed that if conditions preceding the dry season are good then intermediate feeders do not necessarily need to switch between diets. Greenness, among others, is a clear driver in grass use and, together with the indirect effect of rainfall, plays a major role in highly seasonal environments.

Acknowledgements

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