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

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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

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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





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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 \times 0.5 m plot square over the vegetation where we found the fresh bites. This 0.5 \times 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 = 26-10%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.

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