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ORIGINAL PAPER

Seasonal diet changes in elephant and impala in mopane woodland

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Abstract Elephant and impala as intermediate feeders, having a mixed diet of grass and browse, respond to seasonal fluctuations of forage quality by changing their diet composition. We tested the hypotheses that (1) the decrease in forage quality is accompanied by a change in diet from more monocots in the wet season to more dicots in the dry season and that that change is more pronounced and faster in impala than in elephant; (2) mopane (*Colophospermum mopane*), the most abundant dicot species, is the most important species in the elephant diet in mopane woodland, whereas impala feed relatively less on mopane due to the high condensed tannin concentration; and (3) impala on nutrient-rich soils have a diet consisting of more grass and change later to diet of more browse than impala on nutrient-poor soils. The phosphorus content and in vitro digestibility of monocots decreased and the NDF content increased significantly towards the end of the wet season, whereas in dicots no significant trend could be detected. We argue that this decreasing monocot quality caused elephant and impala to consume more dicots in the dry season. Elephant changed their diet gradually over a 16-week period from 70% to 25% monocots, whereas impala changed diets rapidly (2–4 weeks) from 95% to 70% monocots. For both elephants and impala, there was a positive correlation between percentage of monocots and dicots in the diet and the in vitro digestibility of these forage items. Mopane was the most important dicot species in the elephant diet and its contribution to the diet increased significantly in the dry season, whereas impala selected other dicot species. On nutrient-rich gabbroic soils, impala ate significantly more monocots than impala from nutrient-poor granitic soils, which was related to the higher in vitro digestibility of the monocots on gabbroic soil. Digestibility of food items appears to be an important determinant of diet change from the wet to the dry season in impala and elephants.

Keywords *Colophospermum mopane* · Diet choice · Digestibility · Intermediate feeders · South Africa

Introduction

Within herbivores, intermediate feeders have a mixed diet of grass and browse. They respond to seasonal fluctuations of forage quality and quantity by changing their diet composition (Hofmann 1989), in contrast to species that are either grazers or browsers. Grass usually contains more cell wall than browse, and the amount of lignified fibre increases as the dry season progresses, which decreases the

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quality of grass (Van Soest 1994). On the other hand, grass generally has higher digestibility than browse (Van Wieren and Van Langevelde 2008), which is mainly due to the lower content of lignified fibre in grass (Hummel et al. 2006). Browse contains more secondary compounds than grass, which reduce intake by herbivores (Jansen et al. 2007; Duncan and Poppi 2008). For example, tannins are pervasive in browse but almost absent in grass (Ellis et al. 1990).

Two contrasting African herbivores, impala (*Aepyceros melampus*; a medium-sized ruminant) and African elephant (*Loxodonta africana*; a megaherbivore with hindgut fermentation), are both mixed feeders. Elephant and impala have different strategies to cope with changing forage conditions over the seasons. Elephants have a diet dominated by browse in the dry season, but they mainly feed on green, nutritious grasses in the early wet season (Hansen et al. 1985; Beekman and Prins 1989; Cerling et al. 2006). Relative to their body mass, elephants have a short mean gut retention time, and they can include food items of low digestibility in their diet (Owen-Smith 1988). These larger herbivores have generally lower relative nutrient requirements and can survive on a lower-quality diet (Bell 1971; Jarman 1974; Clauss et al. 2003).

Because of their small body mass, impalas have relatively high nutrient requirements; they feed on higher-quality forage. As ruminants, they probably have long gut retention time and hence digestion efficiency is high (Hofmann 1989; Clauss et al. 2003). Meeting these high nutrient requirements becomes more difficult when condensed tannins and forages with high concentrations of fibre are consumed because digestion in ruminants is assumed to be limited at high tannin concentration (Duncan and Poppi 2008). It has been suggested that small animals are less able to process high-fibre diets than large animals (Bell 1971; Jarman 1974; Clauss et al. 2003), although other studies could not find evidence for this (Pérez-Barbería et al. 2004; Clauss et al. 2009). However, ruminants are better at digesting fibres than non-ruminants (Van Soest 1996). Impalas mainly feed on grasses (Wronski 2002) but switch to more browse in the dry season (Meissner et al. 1996; Sponheimer et al. 2003a). They change their gut physiology in response to this changing diet (Hofmann 1989). Changes in rumen surface area through the increase or decrease in papillae surface and number may require 3–4 weeks for impala in response to these dietary changes (Klein and Fairall 1986). As far as we know, there is no literature on whether changing forage quality leads to physiological or morphological changes in the digestive tract of elephants, although this could be expected.

Due to their physiological differences, we can expect differences in dietary changes between these two herbivores. We studied dietary changes in impala and elephant in mopane-dominated woodland. For impala, we compared dietary changes on both nutrient-rich and -poor soils because we expect that both grass and browse are higher in quality on nutrient-rich than on nutrient-poor soils. Mopane (*Colophospermum mopane*) is a single-stemmed, medium-sized tree or shrub with distinctive, butterfly-shaped leaves. It is common in southern Africa and often forms a dense, monospecific stand. Mopane is an important food source for elephants (Styles and Skinner 2000; Ben-Shahar and Macdonald 2002; Holdo 2003). It has high forage quality as its leaves are nutritious even when dry and fallen (Lagendijk et al. 2005). However, mopane contains high levels of condensed tannins and other secondary compounds compared to other plant species. This condensed tannin concentration fluctuates between seasons (Ferwerda et al. 2005; Codron et al. 2006; Wessels et al. 2007). Mopane maintains its foliage well into the dry season, providing an important food source for browsers and intermediate feeders both in the wet season (summer) and dry season (winter).

In this paper, we test the hypotheses that the decrease in forage quality is accompanied by a change in diet in both impala and elephant and that this change differs between the said species. We expect that both species will react to a strong increase in fibre content in the grass at the end of the dry season by switching to a more browse-dominated diet because the increase in fibre content in dicots is expected to be less than that in grass (Van Wieren and Van Langevelde 2008). When the grass quality becomes too low, it pays to increase the exploitation of the relatively large cell content that characterizes many dicot species (Van Wieren and Van Langevelde 2008). We also expect that the switch will be more pronounced in impala when compared to elephant where we expect that the switch will be more gradual. Both species will be more or less similarly affected in their digestive capability with an increase in dietary fibre but the elephant is expected to be able to compensate better for a high-fibre diet by the ability to increase its intake which is made possible by decreasing the gut retention time. In the impala, a ruminant and thus adapted to longer retention times, such compensation is more limited. We further test whether mopane, the most abundant dicot species in the area, is the most important species in elephant diet in mopane woodland, whereas impalas feed relatively less on mopane due to the high condensed tannin concentration. Mopane can provide the bulk for elephants, particularly in the dry season. In contrast, impalas need relatively high-quality forage and are assumed to be more limited by high amounts of condensed tannins than elephant (Duncan and Poppi 2008). Finally, we tested whether impalas on nutrient-rich soils have a diet consisting of more grass and change later to a diet of more browse than impalas on nutrient-poor soils. This latter prediction could not be tested for elephants as the area with nutrient-rich soils was too small to sustain an elephant herd.

Materials and methods

Study site

The study was conducted in mopane woodland in the Associated Private Nature Reserves (APNR) (185,000 ha, 24°14′ S and 31°24′ E), located on the western border of the Kruger National Park (KNP), South Africa. The borders with the KNP are unfenced and animals can move freely between reserves. The estimated number of impala in the APNR in 2005 was over 16,000 while the number of elephants was estimated at almost 1,200. The mean annual rainfall in the study area is 431 mm, with most rain falling from October through March. The mean annual minimum temperature is 17°C and the mean annual maximum temperature is 29°C (APNR, unpublished data).

To study the effect of soil nutrient status, the study area was stratified between granite-derived soil (representative of nutrient-poor soils) and gabbro-derived soil (representative of nutrient-rich soils). The vegetation on the gabbroic soil was burned in November 2005, at the onset of the growing season. Gabbroic soils are fertile with good water-holding capacity but slow absorption (Meissner et al. 1996). Gabbroic soils are dark-coloured, caused by a high concentration of iron (Fe) and magnesium (Mg). Granitic soils are sandy and often nutrient-poor; they are lighter-coloured, caused by quartz-like minerals. Their water-holding capacity is poorer than gabbroic soils (Meissner et al. 1996). The tree foliage/grass biomass ratio at the end of the growing season is about equal in granitic areas but tends to be more grassy in gabbro area (Pretorius, unpublished data).

Forage plants

The five most abundant browse species available for elephant and impala were: *C. mopane* (60–80% of available tree biomass), *Combretum apiculatum* (10–15%), *Acacia nigrescens* (5–10%), *Grewia bicolour* and *Grewia monticola* (5–10% together). The *Grewia* spp. were pooled in the plant analysis. Bi-weekly, from the beginning of February (end of the wet summer period) to the end of May (mid dry winter period) 2006, leaf samples of these five species and leaf samples of three dominant grass species (*Panicum maximum*, *Digitaria eriantha* and *Urochloa mosambicensis*, which comprise >55% of available grass biomass) were collected on both soil types. Sampling was done at three different sites within the same soil type, and within these sites three different trees and three different grass patches were sampled, yielding one sample per soil type per species for each bi-weekly period. Browse was collected at a height between 0.5 and 1.5 m because both impala and elephant browse from this height, although elephant will also browse at higher levels (95% of their bites are taken at a height <2 m; Smallie and O’Connor 2000).

The plant samples were dried at 70°C in a stove for 48 h. The dried samples were thoroughly mixed, ground and analysed for the following parameters: nitrogen (N), phosphorus (P), neutral detergent fibre (NDF), condensed tannin (CT) and in vitro digestibility. N and P were measured after destruction with a mixture of sulfuric acid, Se and salicylic acid with a Skalar San-plus autoanalyzer (Novozamsky et al. 1983). NDF was determined using the ANKOM filter bag procedure (ANKOM Technology, Macedon, NY, USA), with omission of the sodium sulphite and the heat-resistant α-amylase, and expressed as a percentage of organic matter by subtracting the residual ash weight. Neutral detergent solution was prepared following Goering and Van Soest (1970). In vitro digestibility of organic matter was measured according to Tilley and Terry (1963), using microbial fermentation (donor inoculum: fistulated cattle rumen fluids) followed by vertebrate enzymes (Pepsin, HCl). The in vitro digestibility was also expressed as percentage of organic matter by subtracting the ash weight of the samples. Condensed tannins were measured using the proanthocyanidin method and standardized by purified quebracho tannin (Waterman and Mole 1994). The reactivity of tannins to acid butanol assay is species specific; hence, the concentrations are relative measures of mopane tannin concentration and are reported in terms of weight of quebracho tannin (Waterman and Mole 1994).

Herbivore diet

To determine diet, leaves and twigs of the five browse species were sampled for an epidermis reference collection. Plant parts were cleaned in household bleach for 24 h and rinsed in water. Leaf epidermis fragments were stripped off and mounted in glycerol on slides. Plant species were identified from epidermis and cuticle fragments present in the faeces.

On granitic soils, ten fresh (less than 12 h old) elephant dung samples and ten fresh impala dung samples were collected bi-weekly starting from the beginning of February (end of the wet summer period) until the end of May (mid dry winter period). Each pooled impala dung sample originated from several individuals, probably of one herd. On gabbroic soils, at least five fresh impala dung samples were collected (at the same frequency as on granitic soil) because the extent of this vegetation type was less than that of the granitic area, and herds were thus much rarer. It is unlikely that the same animals visited both sites because impalas are territorial and family herds have a fixed home range. Samples were heated in a high-pressure cooker (115°C to 125°C) in water for at least 2 h and left to soak overnight. To separate inner tissue from epidermis and cuticle, a 5-g subsample was washed in a blender with tap water, strained over a plankton sieve (0.01 mm) and stored in 70% ethanol. The subsample was transferred into a Petri dish and allowed to settle. Ten random grab samples of the residue were taken with a Pasteur pipette and mounted on a slide. Ten epidermis fragments were identified on each slide using our reference material, and their surface areas were measured using a 0.01-mm^2 graticule (De Jong et al. 2004). To avoid pseudoreplication, the results of the ten grab samples were pooled for each dung sample. The five browse species were identified separately (*Grewia* spp. were pooled). Unidentified browse and other dicot species were pooled in the category 'other dicots'. The grasses and other monocot species were pooled in the category 'monocots'. The abundance of each forage type (monocots and the five browse species) was represented as a percentage of the total measured fragment area (De Jong et al. 2004). Using the plant composition in the faeces, we refer to diet composition in the text.

Statistical methods

All tests were carried out in SPSS for Windows (15th edition, Chicago, IL, USA).

Percentages were arcsine square root transformed before analysis.

Changes in forage quality parameters (N, P, in vitro digestibility, NDF and CT) of monocots and dicots over time were analysed by linear regression.

Structured repeated-measurements mixed models with an autoregressive structure of the first order, AR (1), were carried out to test for changes in diet composition (percentage of monocots, mopane and other dicot species) of elephants and impala over time, followed by Bonferroni multiple-comparison tests. The mixed model structure offers the possibility to test whether there were statistically significant differences between the 2-week sample periods.

For each period, we calculated the average value per forage quality parameter for monocots and dicots, as well as the average percentage of monocots and dicots in the diet of elephants and impala. Correlations between the forage quality parameters and the herbivore diet composition were analysed by Pearson correlation tests.

Differences in forage quality parameters of the selected monocot and dicot species between gabbroic soil and granitic soil were analysed with a Wilcoxon paired-sample test as assumptions of normality were violated. A paired samples *t*-test was performed to test for differences in the percentage of monocots between impala diet on granitic and gabbroic soil.

Results

Forage quality

The dicot species had low in vitro digestibility compared to the monocots. Monocots also had higher P content and lower condensed tannin concentration. However, the N concentration of monocots was relatively low and the NDF concentration was high compared to the dicots (Table 1). Mopane had the highest P concentration, the highest in vitro digestibility and the lowest NDF of all dicot species. This makes mopane a high-quality forage species among dicots. However, mopane also contained high condensed tannin concentration.

In monocots, P (linear regression, $t=-2.261$, $P<0.05$, $n=18$, $R^2=0.24$) and in vitro digestibility (linear regression, $t=-3.653$, $P<0.01$, $n=18$, $R^2=0.45$) declined over time. NDF increased over time (linear regression, $t=2.372$, $P<0.05$, $n=18$, $R^2=0.26$). Both N and CT did not change significantly over time (linear regression, $P>0.05$ for both analyses). In dicots, no significant trend in N, P, in vitro digestibility, NDF or CT over time could be detected (linear regression, $P>0.05$ for all analyses).

Herbivore diet

The proportion of monocots in the diet of elephant decreased significantly over time (repeated-measurements mixed model, $F_{7,\ 41.990}=19.013$, $P<0.001$). At the beginning of February, the mean percentage of monocots in the diet was 70% and this decreased to 25% by the end of May. The decrease in the percentage of monocots in the diet was gradual as there were no significant differences between any two subsequent periods (Fig. 1a). The contribution of mopane in the elephant diet ranged between 20% and 65%. The contributions of *A. nigrescens*, *C. apiculatum* and the *Grewia* spp. in the diet were relatively small, ranging 1.5–7%, 0–2% and 0–5%, respectively (Fig. 1a).

The proportion of monocots in the impala diet on granitic soil decreased significantly over time (repeated-measurements mixed model, $F_{7,\ 42.633}=37.077$, $P<0.001$). There was a steep decrease in the proportion of monocots in the impala diet between March and April, whereas the differences between the other subsequent study periods were not significant (Fig. 1b). At the beginning of February, the average percentage of monocots in the diet was 96% and this decreased to 70% by the end of May. The proportions of the dicot species in the impala diet were small, ranging 0–7% for *C. mopane* and 0–5% for *A.*

Table 1 Mean values of the different quality parameters (% organic mass, OM) for the sampled species on granitic soil as averaged over the sample periods

Forage type	Species	Mean				
		N	P	Digestibility	NDF	CT
Monocots	*Digitaria eriantha*	1.00	0.19	55.2	74.1	0.016
	Panicum maximum	1.65	0.26	58.3	73.3	0.007
	Urochloa mosambicensis	1.24	0.25	53.7	73.8	0.007
Dicots	*Acacia nigrescens*	2.81	0.10	44.3	56.0	0.118
	Combretum apiculatum	1.79	0.09	42.7	49.2	0.062
	Grewia spp.	2.17	0.11	33.6	61.7	0.162
	Colophospermum mopane	1.90	0.11	46.7	48.9	0.144

N nitrogen, *P* phosphorus, *Digestibility* in vitro digestibility, *NDF* neutral detergent fibre, *CT* condensed tannins

nigrescens. *C. apiculatum* and *Grewia* spp. were hardly eaten (maximum=0.8% in the diet; Fig. 1b). Impala did not concentrate their diet choices on the five most abundant woody browse species but selected other dicot species.

Correlation between forage quality and herbivore diet composition

For both elephants and impala, there was a positive correlation between the percentage of monocots in the diet and the in vitro digestibility of the monocots (Pearson correlation, elephant: $r=0.847$, $P<0.05$, $n=6$; impala: $r=0.927$, $P<0.01$, $n=6$; Fig. 2). None of the other monocot quality parameters (N, P, NDF and CT) was correlated with the percentage of monocots in the diet of the herbivores (Pearson correlation, $P>0.05$ for each correlation). The same positive correlation was observed for the percentage of dicots in the diet and the in vitro digestibility of dicots (Pearson correlation, elephant: $r=0.829$, $P<0.05$, $n=6$; impala: $r=0.834$, $P<0.05$, $n=6$; Fig. 2). Similar to monocots, none of the other plant quality parameters correlated with the contribution of dicots to the diet.

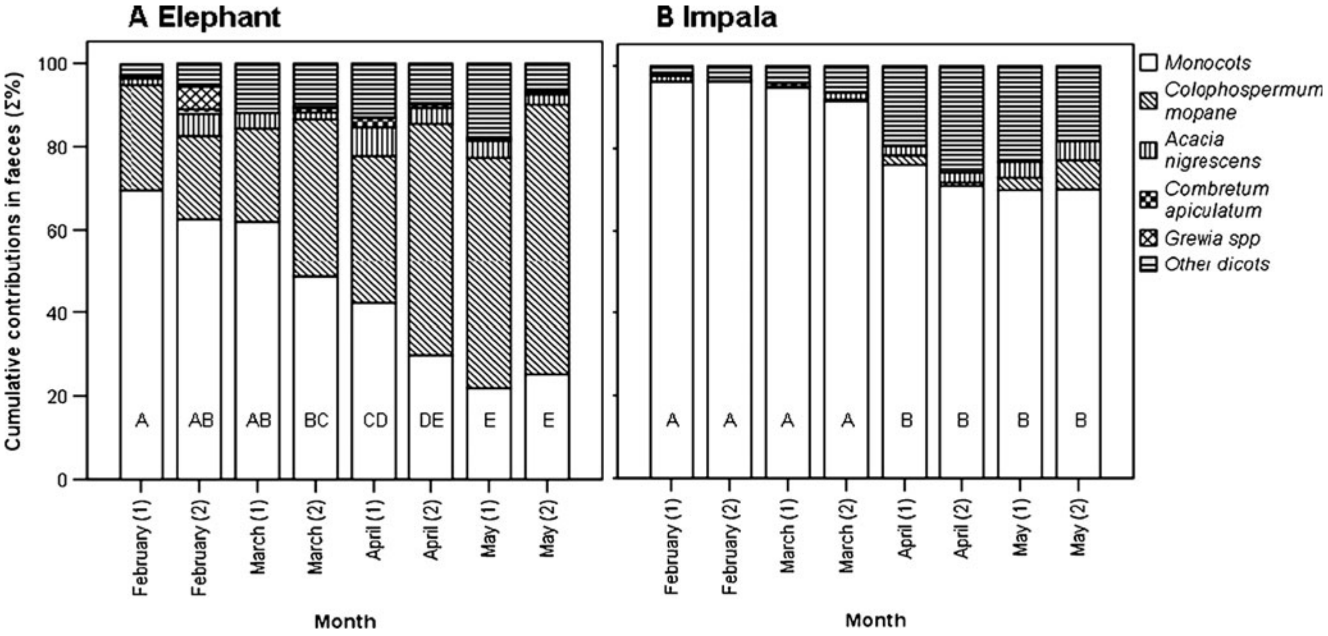

Fig. 1 Cumulative mean contribution (Σ%) of monocots, the four dicot species and other dicots in the faeces of elephant (**a**) and impala (**b**) over time. On the *x*-axis, the eight sample periods from the beginning of February (end of the wet summer period) until the end of May (mid dry winter period) are displayed: *1* means the first 2 weeks of the month and *2* the last 2 weeks. *Letters* indicate statistical differences between identical subsets ($P<0.05$) in terms of the percentage of monocots in the diet between the sample periods as calculated from Bonferroni multiple-comparison test

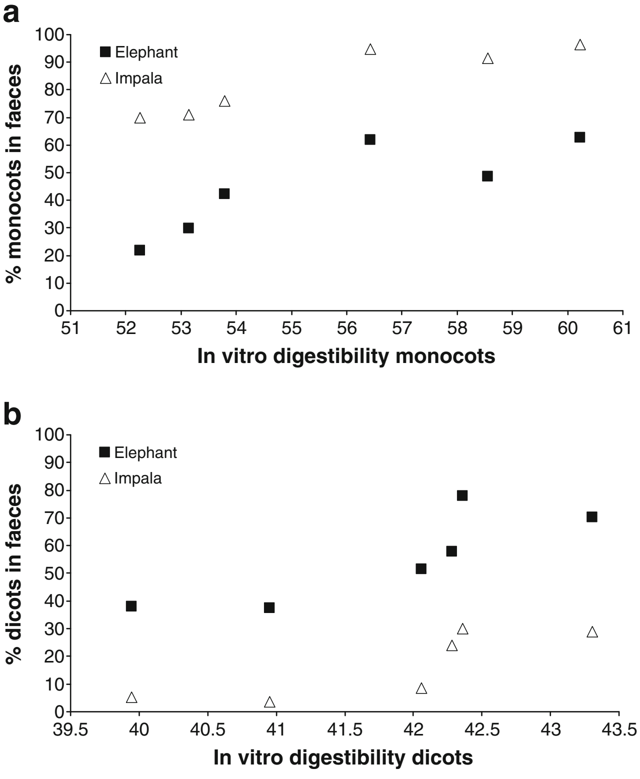

Fig. 2 Correlation between in vitro digestibility (% organic mass) of monocots (**a**) and dicots (**b**) and mean percentage of these forage items in the faeces of elephants and impala per biweekly period

Forage quality and impala diet on nutrient-rich and -poor soil

Forage quality was different between the vegetation on gabbroic soils (nutrient-rich) and on granitic soil (nutrient-poor). In monocots, there were significant differences in three quality parameters (Table 2), as in vitro digestibility and NDF were higher and P content was lower on gabbroic soil compared to granitic soil. For dicots, there were also significant differences in three forage quality parameters (Table 2), N and P were higher on gabroic soil, but also NDF was higher there.

Similarly as on granitic soil, the percentage of monocots in the diet of impala on gabbroic soil decreased significantly over time (repeated-measurements mixed model, $F_{7,\ 23.673}$=26.222, P<0.001), with a steep decrease between March and April. The percentage of monocots in the diet of impala on gabbroic soil changed from 97% to 75%, as compared to 96% to 70% on granitic soil (Fig. 3). The percentage of monocots in the diet of impala was higher on gabbroic soil than on granitic soil (paired samples *t*-test, t=−2.510, P=0.040).

Discussion

Diet switch of elephants and impala from wet to dry season

Elephants and impala changed their diet composition from the wet to the dry season. The contribution of monocots in the diet of both herbivores decreased during this period. We found a significant decrease in the quality of monocots over time (indicated by a decrease in P and in vitro digestibility and an increase in NDF), but the quality of dicots did not change over time. For both elephants and impala, there was a positive correlation between percentage of monocots and dicots in the diet and the in vitro digestibility of these forage items. We therefore suggest that the decrease in in vitro digestibility of monocots over time is the main cause for elephants and impala to decrease the contribution of monocots in their diet. We can however not rule out the effect of forage availability as we did not include this in our study. Our findings are supported by the

Table 2 Differences in quality parameters (% organic mass, OM) of the selected monocot and dicot species between gabbroic soil (nutrient-rich) and granitic soil (nutrient-poor) according to the Wilcoxon paired sample test

Forage type		Mean (% OM) poor	Mean (% OM) rich	*Z*-value	Number, *n*	*P*-value	Significance
Monocots	N	1.22	1.25	0.000	15	1.000	ns
	P	0.21	0.15	−3.010	15	0.003	**
	Digestibility	54.8	59.1	−2.726	15	0.006	**
	NDF	74.4	71.7	−2.442	15	0.015	*
	CT	0.009	0.008	−0.140	15	0.889	ns
Dicots	N	2.15	2.30	−2.240	20	0.025	*
	P	0.10	0.11	−2.725	20	0.006	**
	Digestibility	42.0	43.3	−1.008	20	0.313	ns
	NDF	54.0	55.5	−2.016	20	0.044	*
	CT	0.12	0.13	−0.261	20	0.794	ns

N nitrogen, *P* phosphorus, *Digestibility* in vitro digestibility, *NDF* neutral detergent fibre, *CT* condensed tannins, *ns* not significant

**P*<0.05; ***P*<0.01

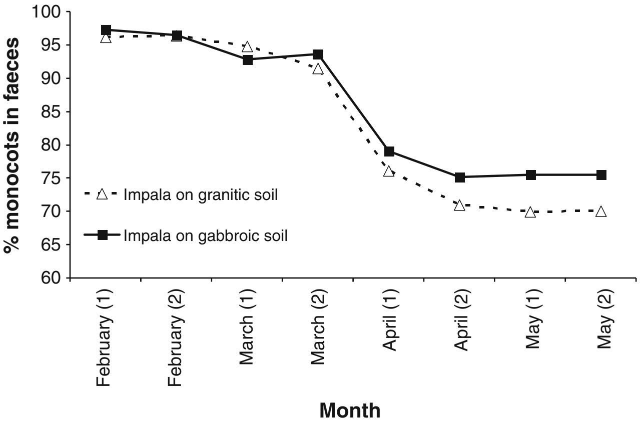

Fig. 3 Comparison of the mean percentage of monocots in the faeces of impala on granitic and gabbroic soil over time. On the *x*-axis, the eight sample periods from the beginning of February (end of the wet summer period) until the end of May (mid dry winter period) are displayed: *1* means the first 2 weeks of the month and *2* the last 2 weeks

research of Hadjigeorgiou et al. (2003) who suggested that in goats and sheep, digestibility and not N content was correlated with diet selection of forage items with N content >1.1.%. In ruminants, the N threshold is predicted at 1.1% N because rumen microbes cannot be maintained below this threshold without an additional source of N (Van Es and Boekholt 1976; Lloyd et al. 1978; Van Soest 1994; Prins 1996). The N concentration of monocots in our study never dropped below 1.13% OM. We hypothesize that, where N contents are above 1.1% OM, in vitro digestibility in monocots, and therefore energy, is the most important quality parameter for diet composition and changes in in vitro digestibility trigger diet changes. We expect that the influence of digestibility also operates in other similarly sized animals with a comparable digestive strategy in similar vegetation types. For instance, Owen-Smith and Novellie (1982) also suggested that N intake remains well in excess of maintenance requirements and is therefore not the limiting factor at least for browsing ungulates.

Difference in diet switch between elephants and impala

Intermediate feeders with different body masses and differences in digestive physiology employ different diet selection strategies. We observed that the diet switch was different for elephant and impala. Elephants gradually changed their diet over time. The reduction in monocots in the diet of elephant lasted for the full 16 weeks. Impala changed their diet over a shorter period of time than that of elephant. The rapid change in diet composition of impala in 2 to 4 weeks corresponds to the findings of Klein and Fairall (1986). The elephant is expected to be able to compensate better for a high-fibre diet by its ability to decrease the gut retention time and thereby increase the total intake. In the impala, such compensation is more limited, which could explain the more sudden diet switch of impala. The percentage of monocots in impala diet after this change (70%) was high compared to the elephant diet (25%). In total, the decrease in the contribution of monocots in the diet was larger for elephant than for impala. Although the change in diet in impala is relatively small, it could have an effect on their survival and fecundity. For example, Prins et al. (2006) show that small differences in diet can have large consequences for diet breadth, diet overlap and segregation between species and hence influence interspecific competition. Our finding that elephant changed their diet to more dicots in the dry season is supported by other studies (Hansen et al. 1985; Cerling et al. 2006; Codron et al. 2006; 2011). Impalas are mainly grazers in the wet season and only change their diet to a higher percentage of dicots (while maintaining their monocot-dominated diet) when the monocots are of such low quality that it is more profitable to eat more dicots.

We cannot fully understand why grasses still dominate the diet of impala in the dry season, but elephants switch to a mopane-dominated diet. The trade-off between costs and benefits for feeding on either monocots or dicots is made differently between the two species. This different trade-off could be influenced by differences in digestion efficiency between the species, as Sponheimer et al. (2003b) for instance showed that ruminants have a higher digestion efficiency than hindgut fermenters on C_3 and C_4 grasses, but this is probably also higher on other forage types. These differences in digestion efficiency could partly explain the higher contribution of monocots in the impala diet. However, other factors might also play a role here, such as differences in sensitivity to secondary compounds between impala and elephant or differences in forage availability in relation to species-specific energy requirements (Pretorius 2009).

Importance of mopane in the diet of elephants and impala

We showed that elephant in mopane woodland changed their diet to predominantly mopane in the dry season. The diet change in elephant was specifically between monocots and mopane. The contribution of mopane in the elephant diet was large, ranging from 20% to 65%, whereas it was small in the impala diet (0–7%). The diet change in elephant to predominantly mopane can be explained by the high abundance of mopane in the area, as well as by forage quality parameters as mopane has relatively high P content, high in vitro digestibility and low NDF content compared to the other dicot species, although mopane also has high condensed tannin content. The high condensed tannin concentration could be the reason that impala did not feed on mopane to a large extent but selected other dicot species. Apparently, the high condensed tannin concentrations did not greatly influence elephant diet composition, although digestion of especially hindgut fermenters is assumed to be negatively affected under high concentrations of condensed tannins (Duncan and Poppi 2008). It has been suggested that elephant can tolerate condensed tannins (Lagendijk et al. 2005; Wessels et al. 2007). Styles and Skinner (2000) and Rooke et al. (2004) suggested that browsers can produce salivary tannin-binding proteins as an adaptation to tannin-rich forage. Also, in other studies, mopane has been suggested to be an important food source for elephants due to its high quality and abundance (Styles and Skinner 2000; Ben-Shahar and Macdonald 2002; Holdo 2003). The importance of mopane in the diet of elephant in this study is in contrast with the findings of Codron et al. (2006) and Codron et al. (2011). In the first study, the authors suggested that mopane may deter feeding as a result of high percentages of secondary compounds and force elephant to forage on grasses (Codron et al. 2006). In the second study, the authors suggested that in a mopane-dominated area, where diversity of browse species is low, elephants need to maintain dietary diversity and therefore feed less on mopane (Codron et al. 2011). However, our data indicate that mopane is indeed the most important browse species in the diet of elephants and that this species constitutes 65% of the diet after the diet switch. The differences in our studies could be due to differences in the vegetation between the study areas. Even though both areas were mopane-dominated, differences in abundance of mopane and other dicot species are possible.

Difference in forage quality and impala diet on nutrient-rich and -poor soil

Contrary to expectations, impala on nutrient-rich soils changed diets at the same time as impala on nutrient-poor soils. As predicted, however, impala on nutrient-rich soils ate significantly more monocots than impala on nutrient-poor soils, although this difference was small. Differences in forage quality parameters were not consistent between nutrient-rich and -poor soils (Table 2). However, in monocots, in vitro digestibility was higher on the nutrient rich soil, where impalas foraged on more monocots. This is in line with our suggestion that forage digestibility is the most important determinant of diet choice when forage nitrogen content is above critical threshold (Van Es and Boekholt 1976; Lloyd et al. 1978; Van Soest 1994; Prins 1996).

Conclusion

We argue that forage nutrient content and in vitro digestibility determine herbivore diet changes from the wet to the dry season, showing this for two herbivore species of considerably different body mass and digestive system. Hence, forage quality parameters, partly determined by soil properties, can be used to predict diet composition and changes therein.

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