# The diet of kudus in a mopane dominated area, South Africa

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The composition of the plant species eaten by kudu (*Tragelaphus strepsiceros*) determines the diet quality, which impacts on kudu condition and mortality levels. The year-round diet composition of kudus in the Limpopo Province, a mopane (*Colophospermum mopane*) dominated area, was determined by faecal analysis. The most important dietary plant species were *Colophospermum mopane*, *Grewia bicolor, Terminalia prunioides, Tinnea rhodesiana, Boscia albitrunca* and *Combretum apiculatum*, with *C. mopane* comprising on average 39.2 % of diet per month. Small amounts of herbs, grasses and seeds made up the remaining part of the diet. The contribution of *C. mopane* in the diet was negatively correlated with precipitation. *Colophospermum mopane* was consumed, irrespective of its high condensed tannin load (5.2–9.8 % DW) for the majority of the months. No seasonally significant differences were detected for modelled kudu diet crude protein, tannin or phenol concentrations. *Colophospermum mopane* showed significant seasonal differences with lowest values of protein, tannin and phenols in the late wet season. Surprisingly, crude protein concentrations were positively correlated with high levels of tannins and phenols for *C. mopane*. The diet of kudus comprised of significantly more species during the wet season compared to the dry season. Diet diversification, instead of protein maximization, seems a potential tool to satisfy protein requirements while reducing potential toxic effects associated with a high intake of secondary compounds. A significant positive correlation was therefore detected between the tannin concentration of *C. mopane* leaves and the number of plant species in the diet.

Key words: bushveld, condition, condensed tannin, crude protein, preference, habitat use.

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## Introduction

Due to large-scale kudu mortalities during the drought of 2002, kudu populations decreased critically in different nature areas and game ranches in northern South Africa. Mass mortality among kudus frequently occurs, and from 1981–1986 kudu mortalities were reported from numerous ranches in the dry winter months between July and September (Van Hoven 1991). Kudu population crashes commonly occur in game fenced areas in the Arid Sweet Bushveld of the Limpopo Province (Van der Waal & Smit 2001). Previous research (Owen-Smith 1982; Owen-Smith & Cooper 1989) showed that the dietary quality and quantity of the vegetation in kudu habitats can differ strongly per season. This variation is mainly related to rainfall and consequently forage availability. Owen-Smith & Cooper (1989) showed that food quality and availability decrease in the dry season (May-October), and that the estimated metabolisable energy intake falls below the nutritional requirements of the kudu during this period. The nutritional gain can be reduced by the amount of secondary plant compounds like poly-phenols which includes condensed tannins. Diet quality in deciduous savannas is expected to differ significantly between the wet and the dry season, and might therefore offer an explanation for the observed mass mortality kudus suffered, rather than simple lack of food. The first hypothesis that will be tested in this study is that kudu diet quality (measured by crude protein, tannin, and phenol concentrations) is lower in the dry season compared to the wet season; do kudus maximise protein or minimise secondary compounds?

The study area is situated in the Mopani veld (Acocks 1988), of the northern part of the Limpopo Province. Mopani veld is generally regarded as valuable browse (Walker 1980). *Colophospermum mopane*, a winter deciduous tree species, has a variable leaf carriage period that may continue through the dry season into the next wet season. Due to its dominance, *C. mopane* is expected to play an important role in the kudu diet. *Colophospermum mopane* is known for its antifeedants, like polyphenolic compounds, e.g. condensed tannins (Macala *et al.* 1992). Tannins bind with dietary, enzymatic and microbial protein to form insoluble complexes that are not degraded in the rumen, resulting in a reduced digestibility and intake. Information on the fate of tannin-protein complexes post-rumen varies and kidney, liver and gastrointestinal tract damage in animals consuming tanniferous forage has been reported (Bailey 1978). Cooper & Owen-Smith (1985) found that plant species with condensed tannin content of > 5 % leaf dry weight are preferably avoided by kudu in a non-mopane area. Van Hoven (1991) investigated kudu mortalities during winter in savanna areas of South Africa, covering drought conditions, and revealed significant correlations between kudu mortality, kudu density, and tannin content of the browse. It is therefore expected that in the rainy season, when forage availability is high, deciduous *C. mopane* is avoided by kudus due to its high tannin content. The high forage availability during the rainy season enables the kudu to select for high quality alternative browse. The kudu diet composition is therefore expected to consist only of high quality species. Subsequently, species with a tannin content >5 % are not expected in the rainy season diet. Rainfall influences forage availability, and diet choices, and thereby stocking rates (Bothma *et al.* 2004). Due to the high availability of *C. mopane* during the dry season, we hypothesise that the contribution of *C. mopane* to the kudu diet increases in the dry season, resulting in a negative relation between rainfall and percentage *C. mopane* material in the kudu faeces.

In this study, the year-round diet of kudus in a mopane (*Colophospermum mopane*) dominated area is analysed through faecal analysis. This microhistological examination of herbivore droppings provides an estimate of the ingested biomass per plant taxon (Stewart 1967; Sparks & Malechek 1968; Cid & Brizuela 1990; Bartolome *et al.* 1995). To this end, epidermis fragments of ingested plants in the faeces are compared to photomicrographs of epidermis fragments on reference slides. This is possible because the plant cuticle, an indigestible layer covering the epidermis, bears a specific pattern of underlying epidermal cells and hairs along with structures of its own (Stace 1965). This pattern can be identified down to genus or species level, even after passage through the herbivore gut.

## Study area

The study was conducted on the Messina Experimental Farm, situated along the Limpopo River (22º12'S and 29º50'E), within the central zone of the Limpopo Belt. The study area covers 6991 ha, and is divided by a game-proof fence into a northern game section (4605 ha) and a southern cattle section (2386 ha), with kudu occurring in both sections. The mean annual rainfall is 357 mm (measured over a 66-year period from 1927/1928 to 1993/1994). The coefficient of variation for the total annual rainfall is 36 %, indicating a high frequency of droughts. Of the total annual rainfall, 75 % is recorded during the period November–March. The mean daily maximum temperature varies from 25 ºC in July to 34 ºC in January; winter temperatures can be regarded as moderate (Dekker & Van Rooyen 1995).

The study area falls within the northern block of the Mopani veld or *Colophospermum mopane-Acacia nigrescens* Savanna type, where *C. mopane* is the dominant tree species (Dekker & Van Rooyen 1995). The vegetation in the study area is relatively homogeneous. In total, 183 plant species were recorded in eight distinct plant communities (Dekker & Van Rooyen 1995). The browse availability on the Messina Experimental Farm was determined by Dekker & Smit (1996) in both the northern and southern section. The total leaf DM ranged between 1224 kg/ha and 2672 kg/ha (Dekker & Smit 1996). *Colophospermum mopane* contributed substantially to the total leaf DM in all communities.

The kudu population size in the game section, determined by a helicopter game count in 2002, approached a hundred. No major off-takes or mortalities occurred since then (Cornelis van der Waal *pers. comm*. 2005).

## Materials and Methods

### *Faecal analyses*

The leaves of over a 100 species of potential food plants occurring on the Messina Experimental Farm were sampled for a reference collection. Pieces of relevant parts (foliage, seeds and fruits) were cleaned in household bleach overnight, washed in water, and fragments of epidermis stripped off and mounted in glycerol. Photographs of these slides were used to identify the fragments of cuticle observed in samples of kudu faeces. The magnification ranged from 200–400 times, depending on cell, hair or stomata size of the epidermis fragment. The cuticles on mature green plant parts show the pattern of the epidermis cells they cover. Very young undeveloped cuticles present in the dung samples may show no imprints of the epidermis cells in which case no identification was possible. Also, soft cuticles may get crinkled beyond recognition. However, often hairs, glands or specific patterns were present on the cuticle itself which allowed identification of a given species. Digestibility of plant parts as such bore no relation to recognition of cuticle or epidermis fragments. Due to its chemical composition, plant cuticle is indigestible in any animal's guts (Stace 1965). This applies to the leaves of trees and grasses as much as to forbs.

The faecal analysis was carried out on monthly collected mixed faecal samples of kudu droppings from June 2003 to May 2004. Individual pellet groups are not independent samples of the diet of a single animal (Lewis 1994); the availability of food items changes with increasing consumption, thereby influencing diet composition. Also, herbivores vary their choice of food plants between meals in order to maintain a varied diet, and to limit consumption of secondary chemicals (Freeland 1991, McArthur and others 1991); McArthur *et al.* 1991). Each mixed sample consisted of three or more sub-samples, which were randomly collected in the study area. Every sub-sample consisted of five fresh (< 24 hours old) kudu pellets. All collected sub-samples from the same month were pooled and thoroughly mixed. The mixed pellet samples were heated under pressure to 115 ºC in water for ± 2 hours, and left to soak overnight. A sub-sample was washed in a blender, and strained over a plankton sieve, then preserved in 70 % ethanol. The samples were analysed by using a microscope, and at least 100 cuticle or epidermis fragments in each sample were identified by comparison with the reference collection. The surface area of individual fragments was estimated by counting the obstructed grid cells (0.01 mm² per cell) in the microscopic field of view (De Jong *et al.* 2004). The abundance of each species was calculated as a percentage of the total area of the fragments measured (De Jong *et al.* 2004). Encountered grass species in the faeces were placed into one category as the amount of consumed grasses was relatively low and their nutritional value assumed to be similar.

### *Diet quality*

Foliage samples of the most important dietary plant species ($n = 5$; comprising 66 % of the kudu diet) were collected in the field for quality analysis by the University of Limpopo from December 2002 till June 2004. Seven fresh leaves were randomly collected at kudu browse height from the canopies of 40 randomly selected trees, in each sample cycle of 55 days. The bias of this hand-sampling method is unknown. Samples were transported in plastic bags to the laboratory in a cooler box where they were dried in plant presses in the shade at room temperature (Mueller-Harvey 2001; Hagerman 2002). The dried leaves were thoroughly mixed, and a pooled sample of 10 g per treatment per sample cycle (55 days) was sent to the Botany Department, University of Cape Town, for the determination of total phenolics, condensed tannins and crude protein. All parameter values were measured in %DW, phenol content was based on GAE (Gallic acid equivalents) and condensed tannin content on STE (Sorghum tannin equivalents) as described by Hagerman (2002). Additional nutritional data ($n = 5$; comprising 24 % of the kudu diet) were obtained from other sources (Aganga & Adolga-Bessa 1999; Aganga & Mosase 2001; Fustenburg & van Hoven 1994; Lagendijk 2003) or retrieved from the Animal Feed Recourses Information System (AFRIS) (FAO 2004). Dietary species were classified into four groups: deciduous woody, evergreen woody, forbs and others. A monthly class average per nutritional parameter was used for species for which no nutritional data was available (9 % of the kudu diet). The diet quality, in terms of condensed tannins crude protein, and total phenolics was calculated using $\sum(x_i * perc_i)$ with $x_i$ as the bi-monthly average value of the quality parameter (condensed tannin, crude protein, or phenol) per plant species $i$ and $perc_i$ as the mean monthly percentage of occurrence of a plant species $i$ in the diet, similar to Owen-Smith & Cooper (1989). Climatic data were obtained from the South African Weather Service which were measured at the Macuville weather station (No. 0809706X), situated on the Messina Experimental Farm.

### *Statistical analysis*

Anovas were carried out using as dependent variables, the mean values recorded per month for species richness (averaged from the different samples) or the monthly mean diet quality parameters. As dependent variables did not violate basic assumption for normality (Kolmogorov-Smirnov test) and equality of variances (Levene's test), Anovas were carried out to test for seasonal difference, using SPSS (v12), followed by a Tukey multiple comparison test (Zar 1984).

## Results

### *Kudu diet: species composition*

The fragments of 20 dicotyledonous species contributed 82 % of the analysed kudu faecal samples and, together with the grass species, comprised 96.6 % of a full year's samples (Table 1). The remaining 3.4 % consisted of species which were only encountered once and were therefore not included in the diet quality analyses. *Colophospermum mopane* was the most prominent in the faecal samples; it was consumed each month in relatively large amounts, with an annual average

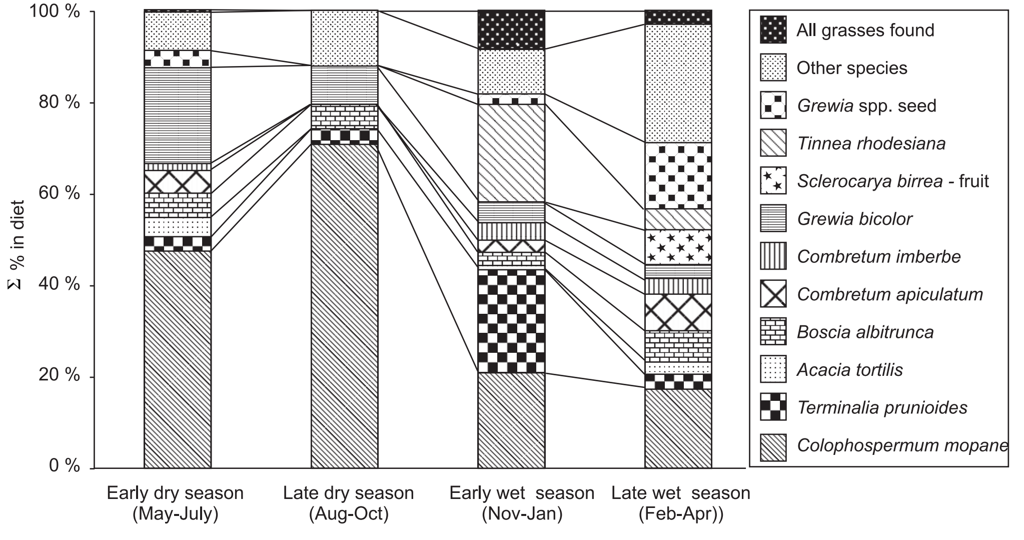


Fig. 1. Seasonal differences of kudu diet composition for the main (annual > 1.9 %) dietary species.

Table 1

*Annual percentage of species occurrence in the kudu diet and their average seasonal nutritional component value (EW=Early Wet; LW=Late Wet; ED=Early Dry, LD=Late Dry)*

| Classification | Species | % annual diet | crude protein % DW | | | | condensed tannin % DW | | | | phenol % DW | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | EW | LW | ED | LD | EW | LW | ED | LD | EW | LW | ED | LD |
| Deciduous woody | *Acacia nigrescens* | 0.9 | 13.3* | 12.9* | 11.5* | 12.0* | 3.3** | 3.3** | 3.3** | 3.3** | 10.3* | 9.5* | 9.8* | 9.6* |
| | *Acacia tortilis* | 1.9 | 11.6** | 11.6** | 11.6** | 11.6** | 3.8** | 4.6** | 5.0** | 4.5** | 2.6** | 3.0** | 3.3** | 3.0** |
| | *Colophospermum mopane* | 39.2 | 11.8 | 12.3 | 9.9 | 7.1 | 9.4 | 7.7 | 7.4 | 4.3 | 8.2 | 6.4 | 6.7 | 5.3 |
| | *Combretum apiculatum* | 4.0 | 13.2 | 12.6 | 9.6 | 11.8 | 0.9 | 0.6 | 0.5 | 0.7 | 14.3 | 13.1 | 13.6 | 13.7 |
| | *Combretum imberbe* | 2.0 | 14.2** | 14.2** | 14.2** | 14.2** | 3.1** | 3.1** | 3.1** | 3.1** | 13.3** | 13.3** | 13.3** | 13.3** |
| | *Combretum mossambicense* | 0.6 | 13.3* | 12.9* | 11.5* | 12.0* | 3.6* | 3.5* | 3.5* | 3.0 * | 10.3* | 9.5* | 9.8* | 9.6* |
| | *Gardenia resiniflua* | 1.3 | 13.3* | 12.9* | 11.5* | 12.0* | 3.6* | 3.5* | 3.5* | 3.0 * | 10.3* | 9.5* | 9.8* | 9.6* |
| | *Grewia bicolor* | 9.4 | 16.2 | 14.5 | 12.8 | 14.5 | 4.8 | 5.2 | 5.1 | 5.0 | 3.9 | 3.5 | 3.7 | 3.7 |
| | *Sclerocarya birrea* | 0.9 | 13.3* | 12.9* | 11.5* | 12.0* | 3.6* | 3.5* | 3.5* | 3.0 * | 10.3* | 9.5* | 9.8* | 9.6* |
| | *Terminalia prunioides* | 7.8 | 11.6 | 11.0 | 8.2 | 10.3 | 3.6* | 3.5* | 3.5* | 3.0 * | 19.8 | 17.9 | 18.2 | 18.6 |
| | *Tinnea rhodesiana* | 6.5 | 13.3* | 12.9* | 11.5* | 12.0* | 3.6* | 3.5* | 3.5* | 3.0 * | 10.3* | 9.5* | 9.8* | 9.6* |
| | *Ziziphus mucronata* | 0.8 | 14.3** | 14.3** | 14.3** | 14.3** | 0.2** | 0.2** | 0.2** | 0.2** | 10.3* | 9.5* | 9.8* | 9.6* |
| Evergreen | *Boscia albitrunca* | 5.1 | 15.6 | 14.2 | 14.6 | 12.8 | 0.4 | 0.4 | 0.4 | 0.4 | 0.6 | 0.6 | 1.0 | 1.0 |
| | *Schotia brachypetala* | 0.7 | 15.6* | 14.2* | 14.6* | 12.8* | 10.3** | 10.3** | 10.3** | 10.3** | 0.6* | 0.6* | 1.0* | 1.0* |
| Forbs | *Hibiscus micranthus* | 0.9 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| | *Indigofera heterotricha* | 0.7 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| Others | *Kyllinga alba* | 1.3 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| | *Sclerocarya birrea* - fruit | 1.9 | 6.2** | 6.2** | 6.2** | 6.2** | 2.6** | 2.6** | 2.6** | 2.6** | n.a. | n.a. | n.a. | n.a. |
| | *Grewia* spp. Seed | 5.1 | 19.0** | 19.0** | 19.0** | 19.0** | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| | Unknown 1 | 1.5 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| | Unknown 5 | 1.2 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |
| | Grass species (all) | 2.9 | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. | n.a. |

*Class average **Data retrieved from literature or FAO database (annual value) of almost 40 %. The percentage of mopane in the diet was the highest during the late dry season (August–November) (Fig 1.), reaching a peak of 91 % in September. The contribution of *C. mopane* to the diet was always >16 %, except for March when it dropped to 3 % and was replaced by *Combretum apiculatum*. Besides *C. mopane*, only six species comprised >5 % of the kudu diet when averaged over the year; these were *Grewia bicolor* (9.4 %), *Terminalia prunioides* (7.8 %), *Tinnea rhodesiana* (6.5 %), *Boscia albitrunca*, and *Grewia* spp. seeds (5.1 %). Grass species were only eaten at the beginning of the wet season, with a maximum contribution of 13.5 % in samples in December. The percentage of grasses in samples declined as the wet season progressed. In February, when the fruits of *Sclerocarya birrea* (marula) ripened (late wet season), large quantities were found in the dung samples which peaked at 16 % contribution in this month's samples.

The contribution of *C. mopane* in the kudu faecal samples could be best explained by a quadratic regression model in which the

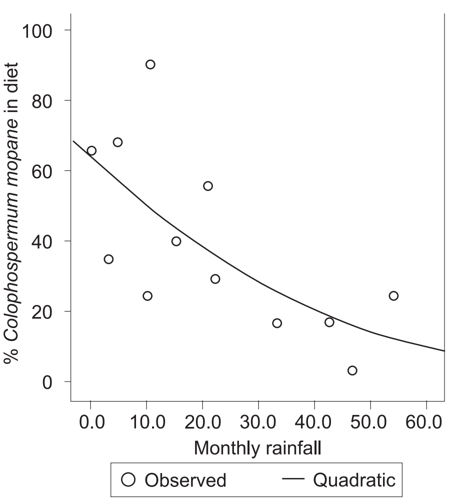


Fig 2. Relationship between monthly amount of rainfall (mm) and % of *Colophospermum mopane* leaf material in the diet of kudus.

monthly percentage of *C. mopane* in the diet was significantly related to the monthly precipitation records ($n = 12$; $F = 4.03$; $P < 0.05$; $r^2 = 0,472$; Fig. 2).

The number of dietary species during the dry season was relatively stable and ranged from eight to 13 between months. During the wet season, the contribution of other species gradually increased from 15 species in December to 25 in April, including the species encountered only once. The average number of different species recorded in the faecal samples in the dry season was 10.8, which is significantly lower than the 18.2 consumed during the wet season (Anova, $F_{1,10} = 8.417$; $P < 0.02$).

*Diet quality*

The calculated crude protein content declined in the late dry season and reached its minimum (6.2 % DW) in October. In the late wet season (May 2004), the maximum crude protein values recorded were 12.6 % DW, corresponding to the month with the highest number of species found in the diet (Table 1). Surprisingly, no significant differences (Anova, $F_{3,8} < 3.583$; $P > 5$ %) could be found in average CP, tannin or phenol concentrations between the wet and dry season, probably because high diet CP persisted quite long into the dry season, as shown in Table 2. However, when the analysis was repeated for the dominant diet species (*C. mopane*) only, significant differences were detected, with significantly lower values of CP, tannins, and phenols in the late dry season compared to the wet seasons (Anova, $F_{3,8} > 6.664$; $P < 0.03$; with a Tukey post hoc test at 5 %).

Condensed tannin content, projected for the diet, generally followed the same trend as crude protein levels with low levels in the late wet and late dry seasons (Table 2). No significant seasonal difference could be detected for average tannin levels. Measured condensed tannin levels in *C. mopane* were only 3.8 % DW in October/November (annual lowest), but the tannin values more than doubled in December/January to 9.8 % DW,

Table 2
*Diet quality estimates in terms of crude protein, condensed tannins and phenol*

| Season | Month | Nutritional component (%) | | |
|---|---|---|---|---|
| | | Crude protein | Condensed tannin | Phenol |
| Early wet | January | 11.1 | 4.9 | 8.0 |
| Early wet | February | 10.1 | 3.7 | 3.5 |
| Late wet | March | 10.0 | 2.0 | 4.2 |
| Late wet | April | 10.6 | 3.3 | 5.2 |
| Late wet | May | 12.6 | 4.2 | 6.0 |
| Early dry | June | 11.0 | 5.8 | 5.6 |
| Early dry | July | 10.5 | 7.0 | 6.8 |
| Early dry | August | 10.6 | 4.7 | 6.3 |
| Late dry | September | 9.5 | 4.9 | 5.8 |
| Late dry | October | 6.2 | 2.5 | 3.6 |
| Late dry | November | 9.4 | 3.0 | 13.0 |
| Early wet | December | 11.3 | 3.7 | 7.5 |

when the percentage of *C. mopane* in the diet declined to 16 %. Condensed tannin levels in mopane leaves were between 7.2–9.8 % for the entire period between December and July.

The other species were lower in tannin levels than *C. mopane*, normally < 5 % (Table 1), except for *Schotia brachypetala*, with estimated levels around 10 %. Mopane tannin content increased significantly concomitant with crude protein levels (Spearman-r = 0.657; $P < 0.05$; $n$ =12). However, no significant correlation between tannin and crude protein, comprising all species, could be detected (Spearman-r = 0.399; $P > 0.05$; $n = 12$).

Phenol content varied over the season; in November the estimated dietary phenol content reached a peak of 13.0 % DW, caused by a large amount of *Terminalia prunioides* (62.7 %) in the diet. *Terminalia prunioides* and *Combretum apiculatum* had higher phenol levels than *C. mopane* throughout the year. Lowest dietary phenol levels were recorded in February at 3.5 %. The phenol content of only *C. mopane* increased significantly with CP levels (Spearman-r = 0.600; $P < 0.05$; $n = 12$). No significant correlation could be found between the percentage occurrence of *C. mopane* foliage in the diet of kudu and any of the other three parameters of *C. mopane* foliage quality (Spearman test).

## Discussion

Owen-Smith & Cooper (1987) stated that the local soil nutrient status is an important factor in influencing plant defence mechanisms against herbivory. The majority of our forage quality estimates was obtained from field samples, but some literature data were used as well, which may not be representative for the quality of the species occurring in the study area. Hence, it is possible that the results of the diet quality estimates might deviate from actual values. Another point of discussion is the availability of the different forage species, which was not measured in this study, and could also influence kudu diet selection. So, further research is needed to support the general validity of our findings.

We found that the diet quality between the wet season and dry season was not significant in terms of CP, tannin or phenol content. Dekker & Smit (1995) revealed that browse availability in the study area is lowest from September to November (late dry season). During the same period, estimated dietary crude protein levels reached a minimum with CP levels varying between 6.2–9.5 % between months. As was hypothesised, the contribution of *C. mopane* to the kudu diet peaked during this period of limited forage availability. The large contribution to the kudu diet and the long leaf carriage period of *C. mopane*, which often appears as early as September with leaf senescence starting as late as June (Dekker & Smit 1995), illustrates that *C. mopane* is the most important species in the kudu diet. Dekker & Smit (1995) also noticed that the long leaf carriage period of *C. mopane*, relative to other tree species, underlies its potential value as a fodder resource in the study area. The expected correlation between increased intake of *C. mopane* foliage and decreasing rainfall was confirmed in this study, and followed a quadratic relationship. Several parallels with research on kudu of the Nylsvley Nature Reserve, where *Burkea africana* and *Ochna pulchra* are dominant tree/shrub species (Owen-Smith & Cooper 1988), could be noticed. Their study, conducted at the Nylsvley Nature Reserve showed that during the late wet season forbs comprised circa half the diet, but during the course of the dry season, foliage of palatable evergreen species became the most important dietary component. Our study also revealed that the species that were generally favoured became more important during the course of the dry season, forbs however showed to be less favoured in comparison to the Nylsvley study. Both studies showed that fruits and seeds were often eaten/selected, but comprised a minor part of the diet. Grass consumption also revealed a similar pattern; grasses were only consumed at the beginning of the wet seasons, and grass intake decreased as the season progressed.

Kudu browse not only on foliage, but also on the supporting twigs and shoots. Histological faecal analyses can only identify foliage, fruit and seed fragments with certainty. The woody twig material in the diet was therefore not considered. Stems and twigs are of a lower quality than foliage and, as our diet quality calculations were based on leaf quality data only, we might have over-estimated the diet quality. Other determinants such as trace elements, not included in this study, might also influence the browsing behaviour and nutritional gain of kudu in the Mopani veld of the Limpopo Province.

However, the quality of *C. mopane* was significantly different in the late dry period, with lowest values of CP, tannins and phenols. Measured condensed tannin levels of *C. mopane* were above 7.2 % DW except between September and November (3.8–5.2 % DW). These findings do not match the results of Cooper & Owen Smith (1985), who found in their study at Nylsvley that plant species with condensed tannin contents > 5 % of leaf dry mass are preferentially avoided by kudu, except in periods when little other food was available. At the onset of the wet season the contribution of *C. mopane* declined as expected but still formed a substantial part of the diet. Apparently kudus do not reject *C. mopane* foliage due to high tannin concentrations. The question is of course, do they have a choice; is the forage availability sufficiently large to enable to switch diet to species with a lower tannin content? The fact that *C. mopane* formed a substantial part of the kudu diet during the wet season proves that tannin-rich species are not avoided when food availability is sufficiently large. High condensed tannin levels do not seem to pose a threshold limiting browse consumption by kudu in the study area. In fact, the coupling between crude protein levels and secondary compounds is remarkable, and the tannin content does not increase with the building-up of structural carbohydrates in the dry season. This atypical pattern in mopane is confirmed in recent studies (Wessels *et al.*, *in prep.*).

Sinclair (1975) and Owen-Smith (1982) showed that during the season of active vegetation growth, herbivores are surrounded by an abundance of potential food in the form of plant foliage. We found that the number of species comprising the kudu diet increased at the beginning of the wet season. Kudus seem to select for diet quality, but are restricted in their choices by the availability of species in their habitat. However, during the dry or cold season when many deciduous plants are dormant, food availability decreases drastically in both quantity and quality. Against a background of low forage availability and quality the timing of leaf flushes and the ripening of fruits therefore have an important influence on dietary composition, as could be seen in this study by the increased intake of *Grewia* seeds, *Sclerocarya birrea* fruits, and *Terminalia prunioides* leaves the moment they became available. Owen Smith & Novellie (1982) found that kudu exhibited a tendency to widen their diet as the dry season advanced. They suggested that kudus were limited more by the availability of food than by the effects of food quality on digestive rates. However, our study showed that the number of species in the kudu diet increases significantly during the wet season compared to the dry season. Hence, we can conclude that kudus do not restrict their diet to quality-rich species only in times of high forage availability. This pattern of a broad diet in times of plenty and a restricted diet when the food availability and quality is reduced, is not a pattern predicted by the optimal foraging theory in terms of nutrient or energy maximisation (Stephens & Krebs 1986), but seem to follow the idea, also illustrated in Owen-Smith & Cooper (1987), that dietary thresholds are more important than optimisation. However, forage availability and quality are confounded in this study, and therefore calls for controlled feeding experiments in order to be able to separate the unique effect of forage availability and forage quality on kudu diet selection. Except for the low forage availability, and therefore limited potential of alternative forage species in the dry season, an alternative hypothesis might be found in the positive correlation between protein levels and tannin and phenol concentration. Choosing for high protein forage automatically increases the concentration of the secondary compounds in the diet. In order to avoid toxic effects, kudus seem to follow the satiety hypothesis (Provenza *et al*. 2003), and diversify their diet in the wet season, leading to an increased number of species in the period that secondary compound concentrations are at its highest. Owen Smith & Novellie (1982) also suggested that large herbivores need to restrict their intakes of various potential toxins below certain maximum thresholds, and that this could be an important factor promoting varied diets. In fact, we found a significant positive correlation between the condensed tannin concentration of *C. mopane* leaves and the total number of species in the diet ($r_s = 0.701$, $P < 0.01$, $n = 12$); the higher the tannin concentration, the more forage species the kudus consumed. This diversification could also be an alternative explanation for the fact that the average diet crude protein concentration was not larger during the wet season. A diverse diet, spreading the risk of an excessive intake of secondary compounds, seems more important than maximising protein intake.

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