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Seasonal variations in diet selection of Nguni goats: effects of physical and chemical traits of browse

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Goats select some browse species more than others, given options. Seasonal trends of diet selection of Nguni goats indexed by intake were investigated in cafeteria-style experiments. The relationships between diet selection and plant chemical/physical traits of Vachellia nilotica, Vachellia robusta, Dichrostachys cinerea, Euclea crispa, Rhus lancea and Ziziphus mucronata, representing abundant species were studied in the dry and rainy seasons. Seasonal changes in browses affected diet selection. Selection of long shoot species, which were concomitantly broad-leafed, was higher than species with short shoots. Selection was higher for spineless than spinescent species. Diet selection correlated positively with increased leaf mass. In the rainy season, cellulose positively correlated with intake, number of bites and browsing time, whereas in the dry season, cellulose correlated with bite size. Diet selection tended to be driven more by shoot morphology and leaf mass than by either spinescence or plant chemistry. Plant chemical influence on diet selection was diverse in both seasons and showed no definite trend, whereas spinescence had no significant effect on short-term intake. The results represent important input to goat production and range forage species management.

Keywords: browse species, chemical components condensed tannins, intake, leaf mass

Introduction

Browse forages in African savannas are an essential dietary resource for mammalian herbivores (Ben Salem and Smith 2008; Sebata and Ndlovu 2012), supplying vital nutrients for growth and reproduction (Assefa et al. 2008; Estell 2010). In semi-arid and arid environments where herbage is seasonal or absent, it is the most important available forage resource (Ben Salem and Smith 2008). Browse has the advantage of maintaining a sufficient nutritional level of protein, digestible fibre and minerals during critical periods of the year relative to herbaceous plants (Decandia et al. 2008). On the other hand, certain browse species have chemical and physical defence mechanisms to protect them from mammalian herbivores (Kaitho 1997; Rogosic et al. 2008; Estell 2010). Browse is heterogeneous in nutrient content, secondary metabolites, morphological traits and flavours (Skarpe et al. 2007; Wang et al. 2011), conferring different levels of defence and nutrition. In addition, seasonal variations in nutrients and plant secondary compounds (Duncan et al. 2008) are potential drivers of diverse specific and intraspecific selection trends.

It is imperative to understand why herbivores select some browse species relative to others, and the underlying mechanisms influencing selection. This knowledge is fundamental to developing predictive models for effective rangeland management (Ungar 1996) and improved animal productivity. Efficient production demands that mammalian herbivores select and constitute a diet minimal in herbivory deterring plant secondary metabolites (PSMs) (Provenza et al. 2003; Sebata and Ndlovu 2012), but adequate in proteins, carbohydrates, minerals and vitamins (Skarpe et al. 2007). Plant secondary metabolites are chemical compounds that do not serve any primary role in plant metabolism, but deter herbivory and enhance plant defence/survival against pathogens (Solaiman 2010). Common PSMs in forages include tannins, alkaloids, saponins, terpenes and lignin, amongst which condensed tannins (CTs) are the most prevalent.

Condensed tannins bind proteins, carbohydrates and minerals, reducing forage nutrient value and utility (Ben Salem et al. 2005; Dove 2010; Estell 2010). However, minimal concentrations improve protein use efficiency by tentatively binding and increasing supply to the abomasum and small intestine for enzymatic digestion and absorption (Nsahlai et al. 1998; McAllister et al. 2005; Solaiman and Owens 2010). Condensed tannins in browse of hot and arid environments are potentially always detrimental to ruminants because of their high concentration relative to those in browse of temperate regions (Waghor 2008). Lignin is a polyphenolic plant secondary metabolite in the cell wall that prevents fibrolytic microbial activity (Solaiman and Owens 2010) and reduces ruminal roughage degradation.

Goats select plants and plant parts rich in protein (Dziba et al. 2003; Provenza et al. 2003; Avondo et al.
2008). Browse protein supplies the rumen microflora with essential nitrogen for microbial protein synthesis, multiplication and growth, thus enhancing fibrolytic activity (rumen function). Microflora that flow alongside rumen digesta to the small intestine provide well over 50% of essential metabolisable protein (Rappetti and Bava 2008). Browse morphology and phenology are widely known to affect herbivore forage selection and intake (Papachristou et al. 2003; Wilson and Kerley 2003; Scogings et al. 2004; Sebata and Ndlovu 2010).

Browse shoot morphology affects ungulate herbivory (Dziba et al. 2003; Scogings et al. 2004). Browse is either characterised by growth of new leaves on new succulent long shoots or growth of new leaves on old short shoots (Scogings et al. 2004). Spines/thorns are other morphological features that influence foraging behaviour of herbivores (Dziba et al. 2003; Papachristou et al. 2003; Wilson and Kerley 2003). Spinescent plants are expected to deter mammalian herbivory relative to spineless plants that have no physical defence. Spines render access to foliage difficult and ungulates, specifically goats, manoeuvre their tongue and lips to pluck them (Sebata and Ndlovu 2010). Given various levels of spinescence, different browse species are expected to offer different levels of deterrence. The number of thorns per unit length of branch bearing foliar material and volume of foliage potentially will affect forage accessibility and ease of harvesting by ungulates. In addition, plant phenology and leaf morphology are browse traits that affect forage selection and intake (Papachristou et al. 2003; Sebata and Ndlovu 2010). Loss of foliage by deciduous browse species in the dry season and the growth of new leaves in the rainy season lead to abundant forage sources, eliciting behavioural adjustments in goat diet selection (Sanon et al. 2008; Sebata and Ndlovu 2010).

The main aim of this study was to determine the trends of diet selection by Nguni goats indexed by intake in the dry season in July (dormant season) and rainy season in December (growing season). Interaction of plant structural components such as spines/thorns, shoot morphology, leaf phenology, and plant chemical components including proteins, fibre and tannins with browse selection within and between the dry and rainy seasons was evaluated. The study investigated the factors affecting diet selection of Nguni goats served six common browse species in a semi-arid savanna in Gauteng province, South Africa. These species consisted of Vachellia nilotica (L.) P.J.H.Hurter & Mabb. (Acacia nilotica), Vachellia robusta (Burch.) Kyal. & Boatwr. (Acacia robusta), Dichrostachys cinerea (L.) Wight & Arn., Euclea crispa (Thunb.) Gürke, Rhus lancea L. and Ziziphus mucronata Willd. fed collectively in a cafeteria-style.

It was hypothesised that (1) deciduous and evergreen species will be selected differently within and between seasons (Papachristou et al. 2003), (2) spinescence will negatively affect selection (Wilson and Kerley 2003; Skarpe et al. 2012), (3) species that produce new leaves on new long-shoots will be selected more than those that produce most of their leaves on old lignified short-shoots (not requiring new shoot extension to support new leaves) (Scogings et al. 2004), (4) fine-leaved species will be less selected than broad-leaved species (Sebata and Ndlovu 2010) and (5) tannins and fibre will negatively affect intake (Papachristou et al. 2003) but protein will positively affect intake (Dziba et al. 2003; Provenza et al. 2003).

Materials and methods

Study site and vegetation

The study was conducted in Roodeplaat, 30 km north-east of Pretoria, South Africa (25°20’ to 25°40’ S, 28°17’ to 28°25’ E). The average annual rainfall of this area is 646 mm, while the average temperature range is 20–29 °C in January and 2–16 °C in July. Mucina and Rutherford (2006) classify the vegetation as Bushveld Savanna.

Study plants

The study was based on plants that are representative of the most abundant species in the study area and have various combinations of shoot morphology, leaf size, leaf life span and physical defence. Vachellia nilotica is characterised by bipinnate leaves with tiny leaflets mainly on old shoots; it is deciduous and armed with long straight thorns. Vachellia robusta has bipinnate leaves with leaflets that are bigger than those of V. nilotica. It is also deciduous with long straight thorns. Dichrostachys cinerea has bipinnate leaves that are borne on both new and old shoots. These leaves are tiny and shed at the approach of winter or drought. Dichrostachys cinerea carries long straight thorns of relatively low density. Euclea crispa is spineless with broad, tough, evergreen leaves borne on new shoots. Rhus lancea is an evergreen species that has broad leaves and grows new leaves on new shoots; the shoots are spineless. Ziziphus mucronata has broad leaves borne mainly on new shoots and is deciduous. It carries both hooked and straight thorns at close intervals on young twigs, rendering prehensibility by goats difficult. Details of these species can be found in van Wyk and van Wyk (2001) and von Breitenbach (1995).

Study goats

Nguni goats were used as model browsers. They are indigenous goats of small-framed bodies with a short coat. Nguni goats are one of the dominant indigenous breeds in South Africa (Rumosa Gwaze et al. 2009) and are very hardy, prolific and adapted to all agro-ecological zones (Nyamukanza and Scogings 2008). They have coat colours ranging from brown, black and white to variegated combinations of the three.

Conditioning and adaptation of goats

Six two-year old ewes of mean weight 22.46 ± 2.14 kg were used for this trial. Prior to the trial during each season, the animals were allowed two weeks of adaptation to the experimental procedure. They were placed individually in pens 3 m × 1.5 m under shelter that was open to one side with three solid walls raised to the roof. Buckets were provided for pellets, hay and water. Buckets for pellets and hay were fixed and held in place with wire rings to prevent goats from throwing out the contents while eating. Goats were maintained on lamb/ewe rations from Epolt (a division of Rainbow Farms (Pty) Ltd, South Africa) and 100 g daily allowance of lucerne hay. The lamb/ewe pelleted rations
contained 13% crude protein, 12% moisture, 14% fibre, 2.5% fat, 1.5% calcium, 0.2% phosphorus, 1% urea, 0.5% other non-protein nitrogen sources and 10 000 IU/IE kg$^{-1}$ vitamin A. These goats were subsequently served various randomised arrangements of freshly cut branches of different browse each morning as part of the experimental diet and later the maintenance diet for each day. Baseline maintenance ration intake data were collected and calculated to ensure that animals received sufficient feed to meet their daily requirements. Apart from the hay, goats were fed 500 g of pellets that was incrementally adjusted by 10% per day in the event of total consumption or reduced by the same proportion, if the pelleted diet was not entirely consumed.

**Diet selection experiment**

The diet selection experiment was conducted over six days in July and December; the design followed Dziba et al. (2003). Thirty-nine freshly cut branches of each of the six browse species with a mean length of 53.5 cm (SEM 0.55) were cut in the morning of each experimental day. Cut ends of branches were placed into buckets containing fresh water and kept under shade to minimise transpiration loss. Thirty-six branches of each species were used for the experiment and three reserved for chemical sampling. The trial was conducted with six goats per day and six consecutive randomised treatments for each one of them.

The experiment was run between 08:00 and 13:00 on each of the six experimental days. Individual branches of all six species were offered clamped in holes on a foraging board (Dziba et al. 2003) and spaced to minimise searching time as well as overlapping. The foraging board was placed in a 3 m $\times$ 3 m pen to which each goat was introduced individually. To control for ordering effects, branches of each browse species were placed equally in the first, second and third order across individual animals during the experiment. A 6 $\times$ 6 latin square design was applied to obtain six unique arrangements as treatments per goat. The arrangement on the board was such that no branch of a given species appeared in the same position more than once for each goat nor did it occur next to the same species more than twice in the entire trial. This design ensured that there was an equal opportunity for goats to select from all available options with very little movement. In addition, adequate caution was taken in the design of the foraging device to keep all branches within view of the browsing animal.

Each branch was weighed before serving and after foraging. These branches were respectively packaged in marked paper bags, oven dried and weighed to obtain dry mass. From the conditioning phase, a maximum of 3 min was allotted to each goat to forage granted that no branch was depleted and the goat did not stop foraging either. Bites per species were counted using a tally counter. Bite size was calculated as the difference in mass between served specific branches and the left over, divided by number of bites taken. Fresh weights of branches were subsequently converted to dry matter (DM) to determine intake (g DM) as an index of diet selection (Haschick and Kerley 1997). Video footage of each bout was recorded in view of determining browsing time for the respective branches in the entire experiment. Bite rate and intake rate of different branches were calculated from number of bites, bite size, intake and browsing time. Prior to video recording, information relating to goat number, feeding bout and date were displayed to mark the transition from one bout to another. Actions of each goat as it browsed from one branch to another were matched with audio descriptions to enhance subsequent data collection and processing. Following audio identification of species by the video camera operator and visual confirmation from the footages, respective browsing times were taken using a stopwatch. Goats foraged from one species to another and sometimes switched intermittently. Cumulative browsing time per branch of each feeding bout were recorded, pausing the video at every transition to the next one and stopping the stopwatch to take stock of specific browsing time per branch.

**Sampling and chemical analyses**

Three branches of predetermined size for each browse species were weighed and put in a separate paper bag. Labelled samples were oven dried to constant mass for 3 d at 60 °C. The mean moisture content of the respective extra branches was subsequently used to convert fresh weight of served branches to dry weight. Dry leaves were pooled for all branches per day per species and each day was taken as a replicate. Dry mass of foliage and interthorn distances of spinescent species were measured. Pooled oven-dried leaf material of the three branches of each species was milled to pass through a 1 mm sieve and subsequently analysed for nitrogen, condensed tannins (CT), neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL). Hemicellulose and cellulose were determined by difference. All the chemical analyses were done in the animal science laboratory of the University of KwaZulu-Natal, Pietermaritzburg. Crude protein was determined by the AOAC (1997) using a LECO FP2000 nitrogen/protein analyser (LECO Corporation, St Joseph, MI, USA). Fibre fractions were determined according to van Soest et al. (1991) using an ANKOM060 fibre analyser (ANKOM Corporation® Technology, Fairport, NY, USA). The HCl–butanol proanthocyanidin assay (Porter et al. 1986) was used to determine condensed tannins as leucocyanidin equivalent (Makkar 1995) and absorbances read at a visible wavelength of 550 nm using a Beckman DU-640 spectrophotometer.

**Calculations and statistical analysis**

All data were analysed using SAS 9.1 (SAS Institute 2002). Data were tested for normality. Intake was square root transformed, whereas hemicellulose was log-transformed. All transformed data were back transformed for presentation in tables.

The data were subjected to analysis of variance using the general linear models (GLM) procedure of SAS 9.1 in a two season $\times$ six feeds design with six replicates (days). The model used was:

$$ Y_{ijk} = \mu + s_i + p_j + (SP)_{ij} + \varepsilon_{ijk} $$

where $Y_{ijk}$ is the observation, $\mu$ is the population mean, $s_i$ is the season effect ($i = 1–2$), $p_j$ is the plant species effect ($j = 1–6$), (SP)$_{ij}$ is the interaction between seasons and plant
species and $e_{ik}$ is the residual error. The Scheffé test was used for significant interactions because sample sizes were not balanced. The $t$-test was used to test the effect of plant traits including long shoots and short shoots, fine and broad leaves, deciduous and evergreen species, and spinescent and spineless species on intake and intake variables. Pearson correlation analysis was used to determine the relationships between selection, selection-related variables, leaf mass fraction, interthorn distance and chemical component variables. Significant associations were regressed to model the relationships. The level of significance was standardised at maximum probability difference $p < 0.05$ for all statistical tests.

Results

Diet selection of Nguni goats was significantly affected by the interaction of seasons and species ($F_{5,60} = 2.52; p = 0.04$; Figure 1). Selection in the dry season was split in three tiers; $R. lancea$ was the most selected species, followed by $V. robusta$, $Z. mucronata$ and $E. crispa$. The bottom tier of $D. cinerea$ and $V. nilotica$ was the most selected species, followed by $V. robusta$ and $E. crispa$ with improved intake from that of the dry season (Figure 1). They were followed by $Z. mucronata$ and $D. cinerea$, whereas $V. nilotica$ was least selected (Figure 1). Selection of deciduous species ($n = 48$; $V. nilotica$, $D. cinerea$ and $Z. mucronata$) was lower than that of evergreen species ($n = 24$; $R. lancea$ and $E. crispa$) ($t = 5.22; df = 34.02; p < 0.001$). Selection of browse species increased with increasing leaf mass (Figure 2, Table 1; $n = 6$; $r = 0.9; p = 0.025$), which was a trait of evergreen browses, notably $R. lancea$ and $E. crispa$, as opposed to most of the deciduous species ($V. nilotica$, $D. cinerea$ and $Z. mucronata$; Figure 2). $Vachellia robusta$, though deciduous, carried sufficient foliage and featured amongst the most selected in both seasons (Figure 1).

Regarding spinescence, selection of spineless species ($n = 24$; $E. crispa$ and $R. lancea$) was higher ($t = 5.22; df = 34.02; p < 0.001$) than spinescent species ($n = 48$; $V. nilotica$, $A. robusta$, $D. cinerea$ and $Z. mucronata$). Selection of browse species with new leaves mainly on long-shoots ($n = 36$; $E. crispa$, $R. lancea$ and $Z. mucronata$), which were simultaneously broad-leaved, was higher than species with new leaves mainly on short-shoots ($n = 36$; $t = -3.99; df = 65.80; p < 0.001$). Species with new leaves on short-shoots ($V. nilotica$, $D. cinerea$ and $A. robusta$) were typically fine-leaved in nature.

The correlation of leaf chemical components with selection and selection-related variables (Tables 2 and 3) showed no significant association of condensed tannins.
with diet selection in both seasons. In the rainy season, cellulose positively correlated with intake \((r = 0.85; \ n = 6; \ p = 0.031; \) Figure 3), bite number \((r = 0.98; \ n = 6; \ p = 0.001; \) Figure 4) and browsing time \((r = 0.93; \ n = 6; \ p = 0.007; \) Figure 5). In the dry season, cellulose also correlated with bite size \((r = 0.87; \ n = 6; \ p = 0.023; \) Figure 6).

**Discussion**

Congruent with our expectation, diet selection indexed by intake was significantly influenced by species, with the ranking: \(R. \ lancea > V. \ robusta > Z. \ mucronata > E. \ crispa > D. \ cinerea > V. \ nilotica\) in the dry season and \(R. \ lancea > V. \ robusta > E. \ crispa > Z. \ mucronata > D. \ cinerea > V. \ nilotica\) in the rainy season. Similar results, whereby species influenced intake, were observed in the Thornveld of the Eastern Cape (Dziba et al. 2003), the shrubs lands of the Mediterranean (Papachristou et al. 2003), the Zululand Thornveld (Mkhize 2008) and in recent studies in the semi-arid region of south-western Zimbabwe (Sebata and Ndlovu 2012). Browse species, by being either deciduous or evergreen, in part influence selection as a result of foliage biomass borne (Table 1) in

**Table 2:** Correlation coefficient with probability difference (in parentheses) for association of intake, time, bites and bite size with leaf chemical components and secondary compounds. ADF = acid detergent fibre, ADL = acid detergent lignin, CT = condensed tannins, HC = hemicellulose, NDF = neutral detergent fibre

<table>
<thead>
<tr>
<th>Compound</th>
<th>Time (s)</th>
<th>Intake (g DM)</th>
<th>Number of bites</th>
<th>Bite size (g DM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protein</td>
<td>0.09 (0.87)*</td>
<td>-0.28 (0.59)</td>
<td>0.27 (0.61)</td>
<td>0.73 (0.10)</td>
</tr>
<tr>
<td>NDF</td>
<td>0.10 (0.85)</td>
<td>0.43 (0.39)</td>
<td>0.10 (0.85)</td>
<td>0.49 (0.32)</td>
</tr>
<tr>
<td>ADF</td>
<td>0.08 (0.86)</td>
<td>0.44 (0.38)</td>
<td>-0.04 (0.95)</td>
<td>0.74 (0.09)</td>
</tr>
<tr>
<td>ADL</td>
<td>0.12 (0.83)</td>
<td>0.26 (0.61)</td>
<td>-0.21 (0.69)</td>
<td>0.63 (0.18)</td>
</tr>
<tr>
<td>HC</td>
<td>0.18 (0.73)</td>
<td>0.30 (0.56)</td>
<td>-0.37 (0.48)</td>
<td>-0.04 (0.94)</td>
</tr>
<tr>
<td>Cellulose</td>
<td>0.49 (0.31)</td>
<td>0.76 (0.08)</td>
<td>0.34 (0.51)</td>
<td>0.87 (0.02)*</td>
</tr>
<tr>
<td>CT</td>
<td>0.41 (0.42)</td>
<td>0.46 (0.36)</td>
<td>0.31 (0.55)</td>
<td>0.53 (0.28)</td>
</tr>
<tr>
<td>Rainy season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Protein</td>
<td>-0.19 (0.72)</td>
<td>-0.43 (0.39)</td>
<td>0.33 (0.95)</td>
<td>-0.64 (0.17)</td>
</tr>
<tr>
<td>NDF</td>
<td>0.37 (0.47)</td>
<td>0.56 (0.25)</td>
<td>0.66 (0.15)</td>
<td>0.42 (0.40)</td>
</tr>
<tr>
<td>ADF</td>
<td>0.59 (0.21)</td>
<td>0.70 (0.13)</td>
<td>0.76 (0.08)</td>
<td>0.54 (0.27)</td>
</tr>
<tr>
<td>ADL</td>
<td>0.30 (0.56)</td>
<td>0.50 (0.33)</td>
<td>0.51 (0.30)</td>
<td>0.40 (0.43)</td>
</tr>
<tr>
<td>HC</td>
<td>-0.04 (0.93)</td>
<td>0.83 (0.86)</td>
<td>0.24 (0.64)</td>
<td>-0.01 (0.98)</td>
</tr>
<tr>
<td>Cellulose</td>
<td>0.93 (0.01)*</td>
<td>0.85 (0.03)*</td>
<td>0.98 (0.01)*</td>
<td>0.61 (0.20)</td>
</tr>
<tr>
<td>CT</td>
<td>0.45 (0.37)</td>
<td>0.25 (0.63)</td>
<td>0.47 (0.34)</td>
<td>0.02 (0.97)</td>
</tr>
</tbody>
</table>

* \(p < 0.05\)

**Table 3:** Mean values (g kg\(^{-1}\); with SEM in parentheses) of plant leaf chemical components and secondary compounds of the different species for the dry and early rainy season. \(n\) = Species sample size, CP = crude protein, NDF = neutral detergent fibre, ADF = acid detergent fibre, HC = hemicellulose, ADL = acid detergent lignin, CT = condensed tannins

<table>
<thead>
<tr>
<th>Species</th>
<th>(n)</th>
<th>CP (g kg(^{-1}))</th>
<th>NDF (g kg(^{-1}))</th>
<th>ADF (g kg(^{-1}))</th>
<th>HC (g kg(^{-1}))</th>
<th>Cellulose (g kg(^{-1}))</th>
<th>ADL (g kg(^{-1}))</th>
<th>CT (g kg(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry season</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(D. \ cinerea)</td>
<td>1</td>
<td>142 (00.0)</td>
<td>414 (00.0)</td>
<td>232 (00.0)</td>
<td>182 (00.0)</td>
<td>101 (00.0)</td>
<td>131 (00.0)</td>
<td>67.4 (0.00)</td>
</tr>
<tr>
<td>(E. \ crispa)</td>
<td>7</td>
<td>99 (13.6)</td>
<td>413 (15.0)</td>
<td>313 (10.3)</td>
<td>100 (7.7)</td>
<td>125 (4.7)</td>
<td>188 (6.7)</td>
<td>57.5 (5.44)</td>
</tr>
<tr>
<td>(R. \ lancea)</td>
<td>10</td>
<td>120 (11.5)</td>
<td>375 (15.2)</td>
<td>242 (7.8)</td>
<td>133 (8.5)</td>
<td>135 (4.2)</td>
<td>107 (4.8)</td>
<td>66.3 (7.90)</td>
</tr>
<tr>
<td>(V. \ nilotica)</td>
<td>1</td>
<td>125 (00.0)</td>
<td>181 (00.0)</td>
<td>106 (00.0)</td>
<td>75 (00.0)</td>
<td>71 (00.0)</td>
<td>351 (30.0)</td>
<td>4.9 (0.00)</td>
</tr>
<tr>
<td>(V. \ robusta)</td>
<td>5</td>
<td>114 (15.5)</td>
<td>445 (17.3)</td>
<td>234 (4.8)</td>
<td>211 (15.3)</td>
<td>105 (3.7)</td>
<td>120 (3.7)</td>
<td>21.0 (1.05)</td>
</tr>
<tr>
<td>(Z. \ mucronata)</td>
<td>4</td>
<td>129 (3.1)</td>
<td>280 (19.0)</td>
<td>136 (3.7)</td>
<td>144 (11.9)</td>
<td>78 (1.9)</td>
<td>58 (1.9)</td>
<td>20.1 (3.29)</td>
</tr>
<tr>
<td>Rainy season</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(D. \ cinerea)</td>
<td>6</td>
<td>199 (10.8)</td>
<td>494 (11.0)</td>
<td>200 (17.6)</td>
<td>194 (17.0)</td>
<td>117 (4.3)</td>
<td>184 (16.2)</td>
<td>75.2 (16.68)</td>
</tr>
<tr>
<td>(E. \ crispa)</td>
<td>6</td>
<td>81 (6.6)</td>
<td>358 (21.2)</td>
<td>270 (16.8)</td>
<td>88 (8.0)</td>
<td>102 (9.2)</td>
<td>168 (9.0)</td>
<td>70.0 (8.85)</td>
</tr>
<tr>
<td>(R. \ lancea)</td>
<td>6</td>
<td>122 (6.1)</td>
<td>389 (13.4)</td>
<td>257 (11.3)</td>
<td>132 (7.7)</td>
<td>146 (7.5)</td>
<td>111 (11.7)</td>
<td>54.8 (11.54)</td>
</tr>
<tr>
<td>(V. \ nilotica)</td>
<td>6</td>
<td>140 (4.5)</td>
<td>220 (15.1)</td>
<td>103 (5.2)</td>
<td>117 (14.6)</td>
<td>55 (3.1)</td>
<td>48 (3.2)</td>
<td>5.6 (0.29)</td>
</tr>
<tr>
<td>(V. \ robusta)</td>
<td>6</td>
<td>143 (9.1)</td>
<td>517 (19.7)</td>
<td>256 (2.8)</td>
<td>262 (17.8)</td>
<td>109 (1.5)</td>
<td>147 (2.6)</td>
<td>12.8 (1.00)</td>
</tr>
<tr>
<td>(Z. \ mucronata)</td>
<td>6</td>
<td>173 (11.6)</td>
<td>377 (23.6)</td>
<td>169 (7.0)</td>
<td>208 (22.3)</td>
<td>81 (3.3)</td>
<td>88 (5.8)</td>
<td>58.6 (9.53)</td>
</tr>
</tbody>
</table>

**Figure 3:** Regression of percentage cellulose dry matter and short-term square root intake of Nguni goats from a pooled multi-species data set in the rainy season

\[ y = 0.2454x - 0.7069 \]
\[ R^2 = 0.7396 \]

**Figure 4:** Regression of percentage cellulose dry matter and mean number of bites cropped by Nguni goats from a pooled multi-species data set in the rainy season

\[ y = 1.7599x - 8.5696 \]
\[ R^2 = 0.9671 \]
In partial accord with our prediction that spinescense will negatively affect intake, whereas spinelessness will positively affect intake, spinescent *D. cinerea* and *V. nilotica* were the least selected in both dry and rainy seasons, whereas *V. robusta* and *Z. mucronata* were highly selected during the dry season. *Vachellia nilotica* was the least selected in the dry season and *D. cinerea* the least selected in the rainy season in the Zululand Thornveld (Mkhize 2008). Goats were found to forage more on spineless branches relative to spinescent ones (Skarpe et al. 2012). Low selection of *D. cinerea* in the current study contrasts with high selection that was observed in the wet season and low selection in the dry season in the Zululand Thornveld (Basha et al. 2012). Sanon et al. (2008) recorded very low intake of *D. cinerea* by goats, concurring with observations in the current study. Marked variation in the selection of *D. cinerea* in various ecological zones is suggestive of the effect of climate and soil on plant morphology and phenology (Grime 1977).

Generally, spinescent species experienced diverse levels of selection in both seasons, consistent with the structure and nature of spines/thorns. Long straight spines are observed to affect intake significantly (Mkhize 2008). Contrary to this observation, *V. robusta*, which was highly selected in both seasons, had straight thorns at close intervals, whereas *Ziziphus mucronata*, with straight and hooked thorns at relatively longer interthorn distances (Table 1), were less frequently selected. Spinescence has been observed to function in conjunction with the morphology of specific foliage to influence selection of both *V. robusta* and *Z. mucronata* (SWF pers. obs.). Spinescence was also observed to deter herbivory by influencing bite size of common duiker, bushbuck and Boer goats (Wilson and Kerley 2003). Spines/thorns confer different levels of deterrence, amongst other factors, to browsing by mammalian herbivores. Diverse thorn morphology was observed to present different levels and extents of deterrence to herbivory by mammalian herbivores (Shipley and Yanish 2001).

Shoot morphology tended to have a significant influence on diet selection by Nguni goats in the present study as has been observed in the arid savanna of the Eastern Cape (Dziba et al. 2003). Species with new leaves on long-shoots (*E. crispa*, *Z. mucronata* and *R. lancea*) featured amongst the most selected, including *A. robusta* that had a high foliar mass. Similar results were observed in the False Thornveld of the Eastern Cape (Bakare and Chimonyo 2011), in the Zululand Thornveld (Mkhize 2008) and in semi-arid south-western Zimbabwe (Sebata and Ndlovu 2010).

The morphology of *D. cinerea* is such that the presence of spines/thorns at close intervals inhibits intake. Selection of long straight thorns as opposed to hooked thorns in *Ziziphus mucronata* contributes to reduced intake. Moreover, spinescence is generally observed to deter herbivory by influencing bite size of common duiker, bushbuck and Boer goats (Wilson and Kerley 2003). Spines/thorns confer different levels of deterrence, amongst other factors, to browsing by mammalian herbivores. Diverse thorn morphology was observed to present different levels and extents of deterrence to herbivory by mammalian herbivores (Shipley and Yanish 2001).

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of *E. crispa* also occurred in the rainy season. Conversely, there was marginal decline in the selection of *R. lancea*, attributable to the presence of sufficient foliage on most browse species. *Ziziphus mucronata* also declined in intake from the dry to the rainy season, though with the growth of new long-shoots. Besides being spinescent, which partially deters mammalian herbivory (Skarpe et al. 2012), the growth of new long-shoots is expected to have enhanced the selection of *Z. mucronata*. The decline in intake of *Z. mucronata* is suggestive of factors other than foliage or shoot morphology that might not have been examined in the present study. Condensed tannins and lignin content of *Z. mucronata* increased significantly from the dry to the rainy season (Table 3). Increase in the lignin content of *Z. mucronata* increased significantly from the dry to the rainy season, though with the growth of new long-shoots. Besides being spinescent, which partially deters mammalian herbivory (Skarpe et al. 2012), the growth of new long-shoots is expected to have enhanced the selection of *Z. mucronata*. The decline in intake of *Z. mucronata* is suggestive of factors other than foliage or shoot morphology that might not have been examined in the present study. Condensed tannins and lignin content of *Z. mucronata* increased significantly from the dry to the rainy season (Table 3). Increase in the lignin content of *Diospyros lycoides* and *Scutia myrtina* might have depressed their consumption by goats (Scoogings et al. 2004).

Intake in relation to leaf morphology showed that broad-leaf species (*E. crispa*, *R. lancea* and *Z. mucronata*) featured amongst the most selected in both seasons. Incidentally, *V. robusta*, which has fine leaves, was consistently highly selected in both seasons. Its high selection by Nguni goats could be attributed to the high presence of foliar biomass and modest condensed tannins. Relative to *E. crispa* and *R. lancea*, which are spineless, *Z. mucronata* was less frequently selected in the rainy season, consistent with observations that Nguni goats will select more of spineless broad-leaf species relative to spinescent ones (Mkhize 2008; Skarpe et al. 2012). Selection patterns showed a strong inclination towards species with high foliar mass, which was a common characteristic of broad-leaved as opposed to most fine-leaved species.

Inconsistent with our prediction that crude protein will positively affect intake (Dziba et al. 2003; Provenza et al. 2003), there was no correlation between intake and crude protein in the current study in both the dry and rainy seasons. Conversely, Mkhize (2008) observed a very weak positive relationship between intake and crude protein in a similar study in the Zululand Thornveld in the dry season.

Crude protein content of the six browse species across seasons was within a narrow range, except for *E. crispa*, in which crude protein content was significantly lower in both the dry and rainy seasons. Given that intake was measured over a short period, specific selection would have been difficult if it were potentially dependent on crude protein content (Alonso-Díaz et al. 2008). Shoot and leaf morphology were observed earlier in the study to have an overbearing influence on selection, suggesting that goats’ primary objective function was intake maximisation and crude protein was secondary in the event of a lag. There is an empirical report of a positive association of intake and crude protein (Dziba et al. 2003; Ganqa et al. 2005).

Cellulose was positively correlated with bite size in the dry season, whereas there was a positive correlation between cellulose, intake and bite number in the rainy season. All of the other fibre components (NDF, ADF, hemicellulose and ADL) had no statistically discernable effect on intake and associated intake variables. These observed results differ from our prediction that fibre will negatively affect intake (Papachristou et al. 2003). In the dry season, cellulose was correlated with bite size given that the the largest bites were taken from species characterised by growth of new long-shoots relative to those with new growth on old short-shoots. Big bites culminated in high intake rates from these species, potentially increasing diet cellulose content. In the rainy season, dormancy ceded to active growth with an increase in cellulose as structural fibre. This may have led to increased intake from *V. robusta*, *E. crispa* and *R. lancea*, all of which presented goats the opportunity to crop both foliage and twigs. In ruminants, there is no data showing a discernable intake pattern where fibre ranges from zero to 40%, except for a positive trend in wild ruminants (Meyer et al. 2010). However, fermentable fibre at 19% enhances passage rate and also improves butter fat (Solaiman 2010). In terms of DM, forage fibre will become prohibitive to intake and passage rate at levels well above the 40% mark (Meyer et al. 2010), with no defined pattern below this range in domesticated ruminants. The cellulose content of plant species ranged between 5% and 18% and fibre between 18.1% and 49.4% in both the dry and early rainy seasons, potentially increasing instantaneous intake. In addition, browse condensed tannins bind and reduce available crude protein (Robbins et al. 1978) in those feeds that are otherwise rich in crude protein (8.1–19.9%), but cellulose intake supplies fermentable energy that supports microbial protein synthesis (Sniffen et al. 1992). These mechanisms may increase the available true protein delivered at the post-ruminal gut and thus would increase intake.

Inconsistent with our prediction that condensed tannins will negatively affect intake (Papachristou et al. 2003), there was no significant correlation of condensed tannins and intake in both dry and rainy seasons. Condensed tannins at concentrations higher than 5% in browse plants negatively affect intake (Dove 2010; Muir 2011). However, in the present study there was no discernable effect in contradiction to this widely observed trend. These observations are consistent to those found in the Zululand Thornveld (Mkhize 2008).

Close examination of the different browse species revealed that condensed tannin concentration of *D. cinerea*, *E. crispa* and *R. lancea*, which all exceeded 5% concentration, had no specific effect on their respective intake or selection relative to those with lower concentrations, namely *V. nilotica*, *V. robusta* and *Z. mucronata*. In the dry season, *E. crispa* was one of the least selected, whereas *R. lancea* featured amongst the most selected species and was consistent in the rainy season, and *D. cinerea* was one of the least selected in both seasons. It plausible that the threshold of 5% condensed tannins as a bar to effective intake and utilisation of tanniferous browse is not generally tenable in the present study, but applies to some species. Goats are tolerant to tanniferous browses (Dove 2010). The increase in importance of browse with aridity (Ben Salem et al. 2005) and associated goat husbandry (Assefa et al. 2008) is likely to have allowed goats to develop the ability to tolerate and efficiently utilise tannin-rich browses. In addition, goats consume a variety of browses and plant secondary compounds (Devendra and Burns 1983; Provenza et al. 2003; Iason and Villalba 2006), some of which may neutralise or dilute (Iason and Villalba 2006; Rogosic et al. 2006) the effects of condensed tannins on intake and utilisation of browses. Browses rich in condensed tannins were taken in low quantity when
fed to goats individually, but when fed collectively, more was consumed (Rogosic et al. 2006). The absence of any primary influence of condensed tannins on intake is suggestive of a secondary role in the current study. However, in cafeteria trials where animals have many options to choose from, the association of particular effects with specific plant species is apparently impossible (Alonso-Díaz et al. 2008), because all browse species in the current study contained condensed tannins. The ability of goats to consume and utilise tannin-rich browse reasserts their role as very important biological controllers of bush encroachment and invasive alien species (Scogings et al. 2004).

Conclusion

Diet selection of Nguni goats was significantly influenced by plant species and seasonality in the current study. Related factors included spinescence, which exerted a partial influence, and shoot/leaf morphology, which influenced diet selection significantly. Plant species with rich foliar biomass in both seasons also exerted a significant influence on diet selection. Cellulose influenced diet selection in the rainy season, whereas protein and condensed tannins had no significant influence on intake in both seasons. These results suggest that the influence of crude protein, condensed tannins and other leaf fibre components may be secondary to intake of browse by Nguni goats in the bushveld of Gauteng. The primary functional objective of goats must be the maximisation of intake, given the high intake of more leafy species (V. robusta and R. lancea).

Goat’s ability to consume and utilise tanniferous browse, in addition to selecting a wide range of species, will potentially promote conservation of a species-rich browse composition of rangeland. This is because cropping of above-ground browse by goats allows for subcanopy plant exposure to sunlight and enhances growth. In addition, it is imperative that these measures be adopted to conserve rangeland and enhance biodiversity, to achieve appropriate stocking to prevent over-grazing/browsing and range degeneration, for water conservation to ensure plant growth and survival, and implementation of controlled burning to regenerate palatable grasses and browse. Goats will serve as appropriate biological controllers of bush encroachment and invasive leafy alien browse species, coupled to their universally acclaimed socio-economic importance as animals and food of the poor.

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