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Optimisation or satiation, testing diet selection rules in goats

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Abstract

Several hypotheses have been formulated to explain diet selection by herbivores, focusing on the maximization of nutrient intake, the minimization of plant secondary compounds, or the satiety hypothesis. This research aimed at studying diet selection revealing which chemical characteristics of plants form the bases for dietary preferences of goats. This was done by setting up a feeding experiment with three different combinations of tree species *Acacia karroo*, *A. nilotica* and *A. sieberana*. The chemical characteristics of these three *Acacia* species were used to predict diet selection. To test the validity of the satiety hypothesis, goats were placed on a conditioning diet of one of the three species. We found a clear preference for *A. karroo* and an avoidance of *A. nilotica* when these two were offered to the goats. In trials where *A. nilotica* was present, tannin minimization was the best explaining diet selection rule. In trials where *A. nilotica* was not present, however, tannin minimization was not the best explanation. Our findings suggest that tannins are not avoided but kept below a certain threshold. Below this threshold, goats based their dietary choices on other chemical characteristics of the *Acacia* species. Acid detergent fibre (ADF) minimization could then best explain preferences in trials with *Acacia karroo* and *A. sieberana* that have generally low tannin content. Goats did not maximize nutrient intake or digestibility, and we found no support for the satiety hypothesis.

Keywords: Dietary preferences; Satiety hypothesis; *Acacia*; Tannin; Plant secondary compounds

1. Introduction

Two principal hypotheses have been formulated to explain diet selection by mammalian herbivores. The first one is based on the idea that herbivores are constrained in their capacity to detoxify PSC, and they minimize PSC intake (e.g. Freeland and Janzen, 1974). The second hypothesis states that herbivores aim at maximizing nutrient intake, while being limited by intake (e.g. Westoby, 1974, 1978). Diet optimisation is assumed under both hypotheses, either through nutrient maximization or minimization of plant secondary compounds (PSC). Numerous studies showed that, for example, ruminants selected diets richer in nutrients and poorer in PSC, than the average food availability (Atwood et al., 2001; Behmer et al., 2002; Bailey and Provenza, in press). Both hypotheses are related to the chemical characteristics of the forage. Many studies linked these forage chemical characteristics with diet selection, for example, the effects of tannins on browsing by giraffe (Furstenburg and Vanhoven, 1994), effects of the chemical composition of natural vegetation on diet selection of goats (Dube

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and Ndlovu, 1995; Nyamangara and Ndlovu, 1995), effects of tannins on browsing ruminants (Cooper and Owen-Smith, 1985), effects of proteins and tannins on diet selection (Bernays et al., 1989; Duncan and Gordon, 1999), effects of nutrients on patch selection (Langvatn and Hanley, 1993; Kronberg and Malechek, 1997), or effects of secondary metabolites on plant acceptance by ruminants (Cooper et al., 1988). However, a problem in many of these studies is that nutrients and PSC are often confounded, obscuring such diet selection rules. They assume either maximization of nutrient intake or minimization of PSC, and overlook the possible trade-off between these two alternative hypotheses (see for example Bryant et al., 1991; Behmer et al., 2002).

A relatively new theory to explain diet selection by herbivores is the satiety hypothesis. This hypothesis provides an alternative explanation for diet selection, taking both the avoidance of PSC and the intake of nutrients into account (Provenza, 1995, 1996; Bailey and Provenza, in press). A key concept in the satiety hypothesis is aversion, the decrease in preference for food just eaten (Provenza et al., 2003; Bailey and Provenza, in press). The aversion will be especially pronounced when food contains either high levels of toxins, rapidly digestible nutrients, or is lacking specific nutrients (Scott and Provenza, 1998). These aversions are the result of interactions between the various sensory systems (i.e. taste and smell) and the postingestive effects (i.e. nausea or satiation) (Provenza et al., 2003; Bailey and Provenza, in press). The satiety hypothesis could provide an explanation for the cases in which animals stop eating highly nutritious food and start seeking alternatives. In controlled environments, animals mostly selected food based on nutrients, but if several foods of the same quality are provided the animals are predicted to select for variety (e.g. Scott and Provenza, 1998; Atwood et al., 2001; Provenza et al., 2003).

The aim of this paper is to studying diet selection revealing which chemical characteristics of plants form the bases for dietary preferences of goats. As measures for nutrient content, we used crude protein (CP, i.e. a measure for nitrogen), phosphorus (P), and the digestibility (higher digestibility means higher nutrient availability). We chose P as one of the nutritional traits of the forage as it might sometimes be limiting (Bokdam and Wallis De Vries, 1992). As measures for PSC content, we used concentrations of tannin, phenols and of fibres, i.e. acid detergent fibre (ADF), acid detergent lignin (ADL) and neutral detergent fibre (NDF). We set-up a feeding experiment with goats in South Africa using *Acacia karroo*, *A. nilotica* and *A. sieberana* as forage species. These species vary in their nutrient and PSC contents and digestibility (Table 1), whereas the selection of three species of the same genus minimizes other differences existing between different plants that could compromise the experiments with confounding effects. Moreover in a separate experiment, we could not find differences in selection of these plant species by goats based on sensory characteristics (smell, taste and texture) (N. Sminia, F. van Langevelde and W.F. de Boer, unpublished data). The chemical characteristics of these three *Acacia* species were used to test whether maximizing nutrient intake, minimizing PSC intake, or the satiety hypothesis explains the diet selection in the goats (Tables 2 and 3).

By using two forage species per feeding trial, it was possible to determine which chemical characteristics goats used for their choices. Imagine, for example, a situation in which a goat is offered a combination of *A. kar-*

Table 1
Chemical characteristics of *Acacia karroo*, *A. nilotica* and *A. sieberana* (in %)

	A. karroo (%)	*A. nilotica* (%)	*A. sieberana* (%)
CP	14.8 b	14.9 b	21.8 a
P	0.2 b	0.21 b	0.29 a
ADF	21.5 b	17.1 a	26.7 c
ADL	16.2 b	12.4 a	18.0 b
NDF	32.6 b	21.4 a	36.9 b
Digestibility	62.3 c	80.0 a	73.5 b
Tannin	0.51 b	1.13 c	0.26 a
Phenols	0.0036 b	0.0041 b	0.0017 a

Species with similar letters (per chemical characteristic) are not significantly different ($P > 0.05$). See Section 2 for further explanation.

Table 2
Predicted diet choices in feeding trials were goats where offered two different forage species, based on (a) nutrient intake maximization and (b) intake minimization of plant secondary compounds

Feeding trial	When maximizing		
	CP	P	Digestibility
(a) Nutrient intake maximization			
Ak + An	n.p.	n.p.	An
Ak + As	As	As	As
An +As	As	As	n.p.

Feeding trial	When minimizing				
	Tannins	Phenols	ADF	ADL	NDF
(b) Intake minimization of plant secondary compounds					
Ak + An	Ak	n.p.	An	An	An
Ak + As	As	As	Ak	n.p.	n.p.
An + As	As	As	An	An	An

Chemical characteristics of the forage species are listed in Table 1. Ak = *A. karroo*, An = *A. nilotica*, As = *A. sieberana*, n.p. = no preference, CP = crude protein; P = phosphorus, ADF = acid detergent fibre, ADF = acid detergent lignin, and NDF = neutral detergent fibre.

Table 3
Predicted diet choices derived from the satiety hypothesis

Conditioning diet	Feeding trial offered		
	Ak + An	Ak + As	An + As
A. karroo	An	As	n.p.
A. nilotica	Ak	n.p.	As
A. sieberana	n.p.	Ak	An
Control	n.p.	n.p.	n.p.

The prediction depends on the conditioning diet. The feeding trials as the combination of offered forage species can be found in the columns. Ak = *A. karroo*, An = *A. nilotica* and As = *A. sieberana*; n.p. = no preference; control = no conditioning.

roo and *A. sieberana*. If the goat chooses *A. karroo*, one can conclude that the goat apparently minimized ADF in its diet, as ADF is the only chemical characteristic that can explain the preference for *A. karroo* (Table 1). If the goat would choose *A. sieberana*, then its choice is not as clear as it could be explained by minimizing tannins or phenols, or maximizing CP, P or digestibility. To test the satiety hypothesis, animals were placed on a conditioning diet of only one of the *Acacia* species. We predict that, for example, a goat would prefer *A. nilotica* in the *A. karroo* and *A. nilotica* feeding trials if the conditioning diet was *A. karroo*. In the trials where *A. karroo* was not present one would then expect no preference (Table 3).

2. Material and methods

2.1. Feeding trials

We did the experiments on the Ukulinga research farm of KwaZulu-Natal University, Pietermaritzburg, South Africa. Feeding trials took place in a period of 8 weeks between November 2004 and February 2005, where we used 12 indigenous goats. Goats were acclimatised to the research set-up in a pilot study 1 week prior to the research. The goats were divided into 4 groups of 3 goats. Each group received a different conditioning diet. The 4 different conditioning diets (Table 3) and the 3 different feeding trials (Table 2) yielded 12 different combinations that we tested each day. All goats were monitored twice under each combination. The order of the different diets and feeding trials was determined by a split-plot block design.

Each week, the conditioning started 2 days prior to 3 days with feeding trials. The goats were fed with *Acacia* branches cut on the farm. During conditioning, goats received such a quantity that forage was leftover when they stopped feeding. The conditioning diet was necessary to test the satiety hypothesis (see Table 3). Animals in the control group had the possibility to feed on all three *Acacia* species. On the days of conditioning, animals were fed in the early morning (around 8 a.m.), and on the days of the feeding trials, goats were fed when all trials for that day had been finished (around 12 a.m.) to ensure sufficient appetite during the trials. In addition to the *Acacia* branches, animals received approximately 200 g of hay per day to insure normal rumen function (Duncan and Young, 2002; Dziba et al., 2003). The hay was harvested on the research farm. On the end of the fifth day, goats were released from their individual pens after all feeding trials had been finished. Goats were released into a meadow where they could forage. The condition of the animals stayed stable over the experiment.

Approximately 1 h prior to the feeding trials each day, the animals received a branch of their conditioning diet to reduce differences in appetite (Dziba et al., 2003). During each feeding trial, the two different *Acacia* species were offered to the goats. Two branches of each of the two forage species were tied to the side of an individual pen, after which the goat was allowed into the pen. It was ensured that within every week each goat received every combination of the *Acacia* species and that a specific combination was only used once in a group. Diet observation recordings were started at the first bite. We recorded the number of bites per branch using counters, and calculated average bite weight (amount removed divided by number of bites). A goat was allowed to feed on the branches for 10 min or until one of the branches had been depleted to ensure that diet selection was based on plant characteristics and not on forage availability. We measured 10 min as maximum observation time since it gave a good indication of the initial diet choice. The majority of trials stopped before 10 min due to depletion of one of the species. The preferences during the feeding trials agreed with field observations.

Branches were weighted before and after the trial. Unbrowsed control branches were also weighted before and after the trials to estimate the weight loss due to transpiration. After the trials, branches were oven-dried at 48 °C for 48 h to avoid the effect of transpiration and/or moisture differences between days. Intake per forage species was calculated as the difference between start and end weight, corrected for transpiration.

Chemical characteristics of the leaves were determined in the same period and area as the feeding trials, using separate samples: crude protein CP (by the Kjeldahl method) and phosphorus P were determined by the Animal Science laboratory of KwaZulu-Natal University according to the methods described by Hambleton (1977). Digestibility was determined with nylon bag techniques with rumen fistulated cows. Digestibility was calculated as the dry weight loss divided by the initial dry weight. Acid detergent fibre ADF, acid detergent lignin ADF, and neutral detergent fibre NDF were determined by the procedure described by Goering and Van Soest (1970). The tannins were determined by the radial diffusion assay method (Hagerman, 1987, 1988, 2002). The phenols were determined by the modified Prussian blue assay for total phenols (Graham, 1992; Hagerman, 2002).

2.2. Statistical analysis

To test the diet selection in trials where each goat could only choose between two *Acacia* species, a binomial distribution was used. Preference was tested by calculating whether the proportion of bites for the selected forage species differed significantly from $P = 0.5$. Here, a normality approximation could be used, because in the majority of the trials the total number of bites exceeded 30 and the expected proportion was $P = 0.5$ (Zar, 1984). Because the bite-data are discrete, and the Z-distribution is continuous, a correction for continuity was applied. Only trials where more than five bites were taken were included in the analysis.

Further, a three-dimensional contingency table (i.e. forage species × conditioning diet × feeding trial) was analysed. Since the number of trials with a specific combination of conditioning diet × feeding trial was always smaller than 30, the normality approximation could not be applied (Zar, 1984). Therefore, a two-tailed binomial test was used (Zar, 1984) to determine the proportion of no preference (i.e. the proportion of trials that did not differ significantly from $P = 0.5$). The expected proportions for the forage species were calculated as 0.5 × (1-proportion no preference). If a significant effect was found, the table was partitioned. Because the order of this partitioning was determined a posteriori, the χ^2 critical value for each partition was based on $\alpha = 0.05/n$ where n = the number of partitions (Siegel and Castellan, 1988).

The predictions (Tables 2 and 3) suggest that goats eat one *Acacia* species per feeding trial, but in reality goats can also take some bites from the other species as well during a feeding trial. This can be seen as deviation from the perfect agreement with the predicted preference. To calculate which hypothesis gave the best explanation for the distribution of observed preferences, a Kappa measurement of agreement was calculated. The Kappa measurement of agreement is based on the calculation of K_{hat} (Bishop et al., 1975), which gives an overview of the correctly classified and miss-classified trials. K_{hat} varies between 0 and 1 (=perfect agreement); a value of e.g. 0.140 could be thought of as a 14% better agreement than just by chance. The classification of K_{hat} values as suggested by Monserud and Leemans (1992) was used in this study. Significant differences between K_{hat} values were calculated using a pair wise test (Congalton, 1991). The critical value for significance was corrected for the number of partitions. Only the predictions with a $K_{hat} > 0.05$ were included in the analysis, resulting in $\alpha = 0.05/15 \approx 0.0033$.

3. Results

3.1. Feeding trials

We found a significant difference between the bite weights of goats consuming the *Acacia* species, with a larger average bite weight for goats feeding on *A. sieberana* (Kruskal–Wallis $\chi^2 = 10.263$; d.f. = 2; $P < 0.001$; Fig. 1). There was no significant difference between the trials with preferences calculated based on the number of bites versus based on the bite weights ($\chi^2 = 29.795$; d.f. = 36; $P < 0.001$). In the remainder of the analysis, we used only the number of bites.

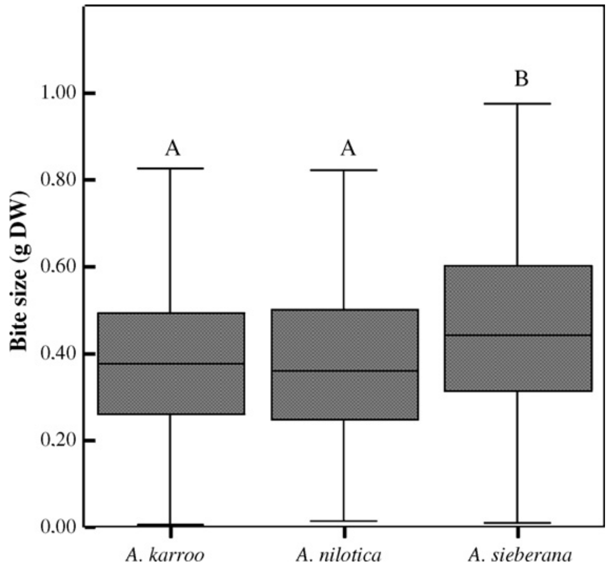

Fig. 1. Median bite weight (g DW) plus quartiles of goats foraging on three *Acacia* species.

In 14 trials, goats took <5 bites and the data of 1 additional trial were lost, so that 273 trials were available for analysis. We found that the preference of goats for one of the *Acacia* species was depending on both the conditioning diet and the combination of forage species ($\chi^2 = 453.928$; d.f. = 24; $P < 0.001$; Fig. 2), as both the conditioning diet ($\chi^2 = 351.495$; d.f. = 21; $P < 0.001$) and the forage species combination ($\chi^2 = 461.265$; d.f. = 21; $P < 0.001$) had a significant effect on the forage species that was selected. The number of trials with no preference was far less than expected under a binomial distribution ($\chi^2 = 88.442$; d.f. = 3; $P < 0.001$). In contrast, preference for *A. karroo* and *A. sieberana* was found significantly more often than expected based on a binomial distribution (respectively $\chi^2 = 228.093$; d.f. = 3; $P < 0.001$, and $\chi^2 = 109.021$; d.f. = 3; $P < 0.001$), and *A. nilotica* was significantly avoided ($\chi^2 = 28.371$; d.f. = 3; $P < 0.001$).

3.2. Predictions

None of the predictions (Tables 2 and 3) was able to fully explain the distribution of forage species preference (Table 4). Tannin minimization seems to yield the best explanation. However, in the *A. karroo* and *A. sieberana* trials, the tannin minimization cannot explain the recorded 71 out of 98 trials with a preference for *A. karroo*. Based on the significantly lower tannin content in *A. sieberana* than in *A. karroo* (Table 1), one would expect a preference for *A. sieberana* if tannin intake was minimized. In order to improve our explanation of the observed preference, we combined several

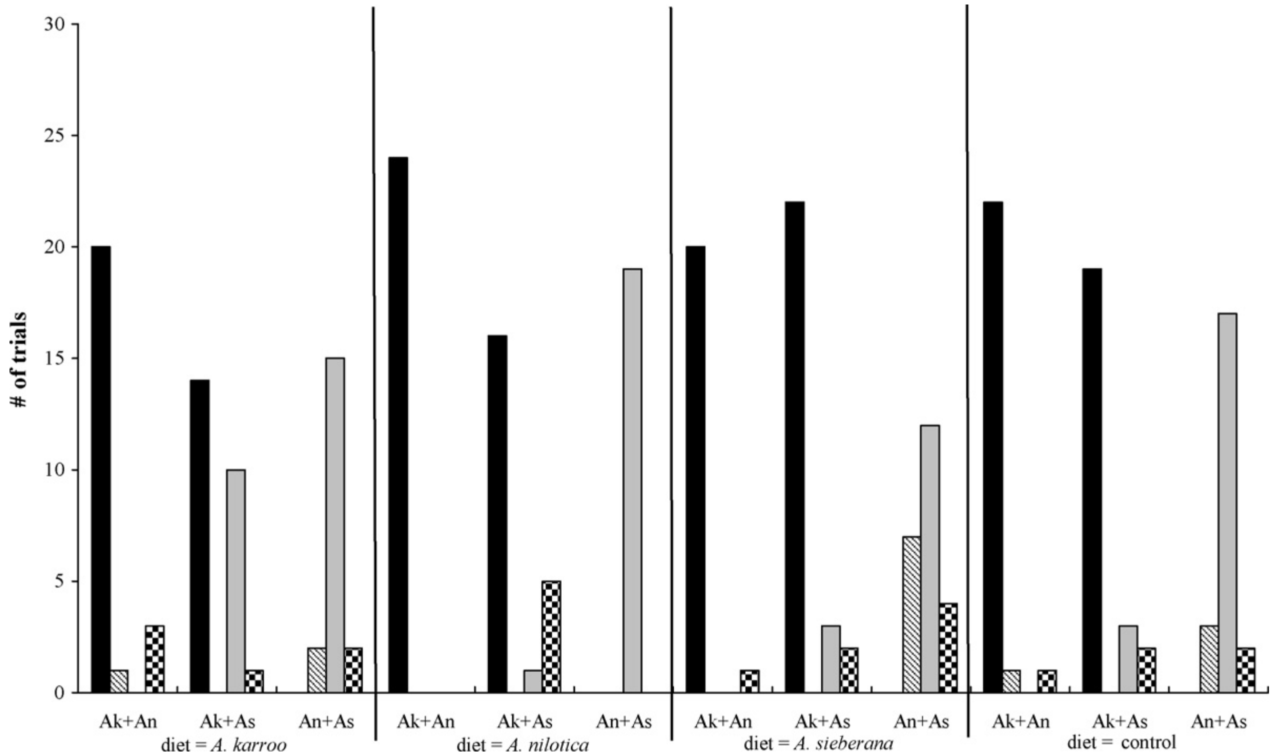

Fig. 2. Number of feeding trials where either one of the two offered *Acacia* species was preferred by goats or where no preference was found. Preference for *A. karroo* = black, *A. nilotica* = striped, *A. sieberana* = grey, and no preference = blocked. Ak = *A. karroo*, An = *A. nilotica*, As = *A. sieberana*. Combinations of species (e.g. Ak + An) are the feeding trials and diets are conditioning diet (e.g. diet = *A. karroo*) (see Tables 2 and 3).

predictions (denoted as combination in Tables 4 and 5) as we expected that tannin minimization could explain the results in the trials with *A. nilotica*, and that ADF minimization could explain the findings in trials with *A. karroo* and *A. sieberana*. For the latter, we selected ADF because it was the only chemical characteristic that could explain preference for *A. karroo* when fed both *A. karroo* and *A. sieberana* (Tables 1 and 2). This combination hypothesis gives a relatively high K_{hat}, 0.62, indicating a very good fit. Table 5 shows the results of the pair wise comparison for the different hypotheses. As can be seen, the combination hypothesis has a significant better fit, with the exception of the tannin minimization, than the other hypotheses. The satiety hypothesis did not explain the diet choices of the goats.

Table 4
Overview of the level of agreement between predictions and observations with K_{hat} values and corresponding variances for the various hypotheses based on nutrient intake maximization and intake minimization of plant secondary compounds (Table 2), and the satiety hypothesis (Table 3), and the combination hypothesis (see text)

Hypothesis	Level of agreement		
	K_{hat}	Variance	Fit[a]
CP/P maximization	0.11	0.002	Poor
Digestibility maximization	−0.06	0.003	No
ADF minimization	0.10	0.004	Poor
ADL/NDF minimization	0.03	<0.001	Very poor
Tannin minimization	0.36	<0.001	Fair
Phenols minimization	0.11	<0.001	Poor
Satiety hypothesis	0.19	0.003	Poor
Combination	0.62	0.004	Very good

[a] Fit is based on the following interpretation of K_{hat} values: >0.75 = very good-excellent agreement; 0.4–0.75 = fair-good; <0.4 = poor agreement; 0.05–0.0 = very poor or not better than would be expected based on chance (Monserud and Leemans, 1992).

4. Discussion

4.1. Dietary preference and chemical characteristics

We found that the goats showed an overall avoidance of *A. nilotica*. Tannin minimization is the only explanation for this preference in the trials with *A. karroo* and *A. nilotica*. In the feeding trials with *A. nilotica* and *A. sieberana*, several other possibilities for the avoidance of *A. nilotica* than tannin minimization could be valid. As the difference in tannin content between *A. karroo* and *A. nilotica* is smaller than the difference between *A. nilotica* and *A. sieberana*, we advocate that tannin avoidance is the most important feature in diet selection. It appears that the ingestion of *A. nilotica*, with

Table 5
P-values of the pair wise multi comparison test between the K_{hat} values for the different hypotheses (Table 4)

Hypothesis	CP/P maximizing	ADF minimizing	Tannins minimizing	Phenols minimizing	Satiety hypothesis	Combination
CP/P maximizing						
ADF minimizing	0.402					
Tannins minimizing	0.002*	0.003*				
Phenols minimizing	0.500	0.415	0.006			
Satiety hypothesis	0.153	0.131	0.028	0.196		
Combination	<0.001*	<0.001*	0.004	<0.001*	<0.001*	

CP/P maximization, ADF, tannin or phenol minimization, the satiety hypothesis, and the combination hypothesis (see text); *P*-values with * are significant. Only predictions with $K_{hat} > 0.05$ were included.

the exception of the pods, is generally considered not to be harmful (Kellerman et al., 1988), which suggests that the avoidance of *A. nilotica* by the goats is related to the high tannin content. The importance of tannin minimization is also illustrated in Table 5, as tannin minimization is the best explaining single factor. However, the explanatory power of tannin minimizing appeared to be limited, especially in the feeding trials with *A. karroo* and *A. sieberana*. The only factor that could explain the preference for *A. karroo* in these trials was the difference in ADF content. ADF primarily consists of cellulose, lignin, silica, soluble proteins, and ash, which are the least digestible parts of the plant. These fibre-related components are found to have a negative effect on food selection for kudu (*Tragelaphus strepsiceros*) and impala (*Aepyceros melampus*) (Cooper et al., 1988). The conclusion that goats minimize tannins (below a certain threshold) and then minimize ADF was supported by the combination hypothesis of tannin minimization and ADF minimization. The K_{hat} of this combination hypothesis was the highest found and indicates a very good agreement between observed and predicted values (Table 4). Caution is needed when results of this experiment has to be extrapolated to free-range situations, where goats appear to select a mixed diet. By adopting this strategy, they reduce the risk of toxicity but the opportunity to learn about novel food is excluded (Duncan and Young, 2002).

4.2. *Effect of PSC*

By minimizing both tannins (or keeping below a certain threshold) and ADF, goats seem to minimize PSC. Tannin minimization is well-established as it can be toxic and reduces the digestibility of nutrients (Bernays et al., 1989; Fahey Jr. and Jung, 1989; Meyer and Karasov, 1991; McSweeney et al., 2001; Hagerman, 2002). Previous research on, for example, goats (Dziba et al., 2003) and kudu (Cooper and Owen-Smith, 1985) showed that tannins can have a significant effect on diet selection. ADF can, at least partly, be seen as an index for fibre-related PSC, since the amount of lignin is incorporated in this ADF measurement (Goering and Van Soest, 1970; Cooper et al., 1988).

Most herbivores have to cope with a wide range of PSC (Freeland and Janzen, 1974; Cooper and Owen-Smith, 1985; Cooper et al., 1988; Bernays et al., 1989; Bryant et al., 1991; Dube and Ndlovu, 1995; Duncan and Gordon, 1999; Behmer et al., 2002). Some of these can be highly toxic or even lethal, some can affect the food digestibility (e.g. lignin), and others can affect the digestive system. Tannins are an example of the latter type of PSC and are found in leaves and seeds of most plants species. In this study, especially the effect on the protein precipitating capacity of tannins was analysed, due to the method used for the determination of the tannin content (Hagerman, 1987, 1988, 2002). Martin and Martin (1982) argued that this is the best method to analyse the effect of tannins on herbivores, since it provides a measure of the effect that tannins have.

Ruminants are often consuming plants that contain tannins even when alternative plants (with less or even no tannins) are available. This was, for example, the case in the trials with *A. karroo* and *A. sieberana*. Three explanations can be given for these observations. The first is that animals cannot distinguish between plants with or without tannins, i.e. they do not have sensors or mechanism to detect tannins (Provenza, 1995). This seems to be invalid for this study since the goats seem to be able to distinguish tannins in *A. nilotica*. The second explanation is that the animals wilfully consume these plants. This could be the case because tannins also possess some beneficial characteristics. They, for example, increase the uptake of certain nutrients, promoting the utilisation of endogenous nitrogen (Ebong, 1995), reduce bloat (Fuller and Benevenga, 2004), and can reduce the parasite load (Kahiya et al., 2003). In the latter examples, tannin intake was often recorded at isolated cases under a specific physical condition of the herbivores. However, this does not seem to be a valid explanation for our study, since the goats showed similar behaviour over an 8 weeks period. The third, and most likely, explanation for our study is that herbivores can cope with a certain level (i.e. threshold) of tannins in their diet (Cooper and Owen-Smith, 1985), as the effects of PSC and nutrients tend to interact. Villalba et al. (2002), for example, showed that small quantities of tannin in the diet enhanced food intake while higher doses depressed it. Moreover, they showed that lambs consistently preferred food with a high energy value, but that the degree to which this preference was manifested depended on the toxins in that food.

4.3. Nutrient maximization

No evidence was found for the hypothesis of nutrient intake maximization in this study, since the predictions for CP, P, or digestibility maximization gave poor to even no agreement with the observations (Table 4). Even if one takes into account that errors can occur due to difficulties of discriminating between alternatives (Illius et al., 1999) or sampling of plants to cope with temporal or spatial variation (Westoby, 1974), the distribution of the preferences found is far off of what was expected (Table 2a).

4.4. PSC minimization

Both of the diet selection rules we found (i.e. tannin and ADF minimization) suggest PSC minimization. Our study thus supports the PSC minimization hypothesis. One should, however, take into account that this tannin minimization is probably only valid under a certain range of nutrient levels. It is found to be depending on season (Nyamangara and Ndlovu, 1995; Dziba et al., 2003). The exact effect of tannins is found to depend on the quantity and quality of the plant's nutrients content (Behmer et al., 2002; Villalba et al., 2002). Many studies have shown that food is selected based on protein levels (Bernays et al., 1989; Nyamangara and Ndlovu, 1995; Dziba et al., 2003). The minimal level of, for example, CP in the diet is around 7–11% (Prins, 1996 and reference therein). The CP contents of the *Acacia* species used in this study are all above this threshold. When proteins are not limiting, tannins may be an important factor in food selection (Bernays et al., 1989 and reference therein). This could be an issue in our study, since there is a possibility that the nutrient contents (CP and P) are sufficient in all three *Acacia* species, and that therefore selection is made on the basis of tannin minimization. The minimization of secondary compounds is often used to explain variation in diet selection that cannot be explained by nutrient maximization (Duncan and Gordon, 1999), so further studies are required to investigate this interaction effect.

4.5. Satiety hypothesis

No proof has been found to support the satiety hypothesis. The K_{hat} value indicated a poor fit for this hypothesis. In our study, the nutrient contents (CP and P) are above the threshold for maintenance, and in the case of *A. karroo* and *A. nilotica*, there is no significant difference in the contents of CP and P. So, in feeding trials with *A. karroo* and *A. nilotica*, one could expect feeding preferences derived from the satiety hypothesis. However, this is certainly not the case, since in 66 out of 93 trials the recorded preferences do not agree with the predictions (Table 3).

We tested the satiety hypothesis under natural conditions without artificially adding of stimuli, which could be related to the postingestive effect. In previous studies working with the satiety hypothesis, these artificial stimuli have been used (Duncan and Young, 2002; Villalba et al., 2002; Ginane et al., 2005). Scott and Provenza (1998), for example, argued that if the nutrient content was constant, the satiety hypothesis worked based on (artificial) variation in flavours. Our results suggest that the evidence of the satiety hypothesis found in previous studies could partly be the result of the unnatural variation offered.

5. Conclusion

We show that diet selection within the 'realm of possibilities' (Provenza et al., 2003) is not about maximizing nutrient intake (Westoby, 1974, 1978) nor having a varied diet (Provenza, 1995). Our results suggest that in a situation where the nutritional demands (i.e. CP and P) are satisfied, diet selection focuses on minimizing PSC. This study provided additional support for the idea that rather than avoiding tannins, herbivores keep tannins below a certain threshold. Below this threshold, goats based their dietary choices on other chemical characteristics. Acid detergent fibre (ADF) minimization could best explain preferences in trials with *Acacia karroo* and *A. sieberana* that have generally low tannin content. Further research will have to show if similar selection choices are made if the nutritional quality of available forage is lower or if a wider range of choices are present.

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