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Of goats and spines - A feeding experiment

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Abstract

Spines in plants have evolved to reduce mammalian herbivory, and their main function may be to protect twigs more than photosynthetic tissue. Type and frequency of spines vary in different scales. We hypothesised that different types of spines affect animal foraging through different mechanisms.

We studied feeding behaviour by twig browsing goats in relation to two types of spines of *Acacia tortilis* using experimental manipulation of the occurrence of spines. Feeding time, number of biting actions, number and diameter of bites on trees (post-trial) and total intake were recorded.

The removal of either long straight spines or short hooked spines resulted in no feeding responses by goats. The removal of both types of spines tended to increase feeding time resulting in more and larger bites with larger bite diameters and in increased total intake and utilisation compared to control branches. The removal of spines gave no effects on feeding rate, expressed as biting actions/minute, number of twigs bitten/minute or intake rate (g/minute). Both types of spines reduced total intake and utilisation of browse, but the functional mechanisms were different with the long straight spines mainly influencing bite size and short hooked spines mainly affecting number of bites.

Introduction

Spines of different types constitute defense traits of plants against large mammalian herbivores (Cooper and Owen-Smith 1986; Grubb 1992; Obeso, 1997). The spinescence of plants shows variability on different scales (e.g. Campbell, 1986; Young, 1987; Belovsky *et al*. 1991; Milewski 1991; Grubb 1992; Theimer and Bateman, 1992; Gowda,1997, 2003; Skarpe *et al.* 2000). Contrary to many defense traits in plants, spines are believed to have evolved specifically to reduce herbivory by large mammalian browsers (Cooper and Owen-Smith 1986; Grubb 1992). Thus, spines of different type, size and spatial arrangements may be expected to differently affect mammalian foraging behaviour, including harvest rate (food items per time) which in turn depends on handling time (time required to chew a food item) and cropping time (time required to crop a food item) and bite size (mass of a food item).

Studies on within- and between plant variation in spinescence have revealed significant effects on the feeding behaviour in herbivores (Belovsky *et al.* 1991; Skarpe *et al.* 2000; Sebata and Ndlovu 2010). Experiments with removal of thorns have shown increased intake rate, bite rate and/or bite size/diameter on the thornless shoots compared to the thorny ones (Cooper and Owen-Smith 1986; Milewski 1991; Gowda 1996; Wilson and Kerley 2002, 2003). However, these experiments do not allow discriminating between the effects of different types of spines. Further, most studies have evaluated herbivore responses on twigs or branches in a leafy stage, and browsers such as domestic goats (*Capra hircus* L.) and bushbuck (*Tragelaphus scriptus* Pallas) have been found to swich from picking leaves between the thorns with the front of their mouth to twig biting using the molars with removal of the thorns (Gowda 1996; Wilson and Kerley 2002). Thus, the most important function of spines may be to protect twigs rather than leaves (Rosenthal and Kotanen 1994; Gowda 1996).

Many woody species in the African savanna are spiny and some species have both long straight and short hooked spines on the same branches (Timberlake 1980; Cooper and Owen-Smith 1986; Coates-Palgrave 2002). This provides an opportunity to experimentally test the differential function of the two types of spines on twig browsing mammals.

We used *Acacia tortilis* (Forssk.) Hayne as our study species. It carries both long straight and short hooked spines on the same branchlets. We studied the importance of spinescence on the feeding behavior of a medium-sized herbivore, the domestic goat (*Capra hircus*) L.. Through removal of either long straight spines, short hooked spines or both types on leafless twigs we could evaluate goat feeding behaviour in relation to spinescence and discriminate between the effect of the two types of spines. In feeding trials we tested the hypothesis that both types of spines reduce total intake of twig biomass by the goats, and predicted that this should be achieved by a reduction of feeding rate (items/time) and/or bite size (mass/bite).

Material and Methods

Data collection

The study was conducted in south-eastern Botswana (24°47'S, 25°50'E), an area with an annual rainfall of about 500 mm, mainly falling during the summer months, November to March (Botswana Department of Meteorological Services, unpublished). The vegetation is a savanna with mainly deciduous trees and shrubs of which many are spinescent (Skarpe *et al.* 2000).

The feeding trial included 5 goats: 4 adult females and 1 sub-adult female. Goats were of the traditional Tswana breed with a live weight (females) of ca 20 kg (Nsoso *et al.*, 2003). We used three paddocks, two 3 x 3 m (test paddocks), and one 3 x 6 m (resting paddock). In the larger one, which was shaded, the goats were kept between trials and during nights. The fence was a veldspan fence, 1.2 m high, on which we hung a black plastic cover to prevent the goats from getting stuck with their horns in the fence and to limit interference between the goats during trials. In the test paddocks the plastic was set up on three sides only to facilitate observations. Between trials, goats were fed twice daily with lucern, grass and branches of the studied species. In the resting paddock water was always available. In each test paddock an iron tube was placed and used to fasten bundles of test branches.

The goats were offered branches from unbrowsed, dormant, juvenile *Acacia tortilis*, which had been planted for other experimental purposes. *A. tortilis* has spinescent stipules, which can be long (up to 8 cm) and straight (hereafter called spines) or short (up to 0.5 cm) and hooked (hereafter called hooks; Coates-Palgrave 2002). These two types of stipules are mostly found on the same branchlet. The mean height of the trees was 1.0 m (SD: ±0.5; n=42) and all trees were 3 years old. The trees were planted two meters apart within a fenced area with virtually no other vegetation. Each feeding trial consisted of a presentation of a bundle of six branches, randomly selected from six randomly chosen trees. Each branch was 0.5 m long, and this roughly corresponded to mean length of the current annual shoots (Rooke 1998), which were produced the growing season ending ca 6 months before the trial. The bundles were separated randomly into 4 groups, which were treated as follows:

- control: no treatment (“with spines/hooks”)
- all hooks were removed; a hook was defined as a spiny stipule shorter than 1 cm (“no hooks”).
- all spines were removed; a spine was defined as a spiny stipule longer than 1 cm (“no spines”).
- all hooks and spines were removed (“no hooks/spines”).

At the time of the experiment, the trees were basically leafless, and any leaves remaining were removed before the trials. The whole experiment was done during 18-24 September 1997.

The different treatments were mixed in time to reduce possible systematic effects of induced changes of the trees initiated by branch clipping. The number of branches was large on each tree and the utilisation through our harvest was therefore considered to be small.

As many of the *Acacia* twigs lack spines (i.e. carry only hooks) on the apical part of the twig we also measured the twig diameter at the place of the first straight long spine seen from the apex of each twig. This was done before the trial. After these initial measurements, all bundles were weighed separately to the nearest 0.01 g. So was also an extra bundle, which was used for calculation of water loss during each trial.

One bundle (a control or a treated bundle) at a time was mounted in the iron tube in a test paddock and a goat was brought in. As we were interested in feeding behavioural responses by the goats, not in preferences between treatments, each trial consisted of only one bundle (treatment) at a time. Two persons carried out each trial, one observing the goat and one keeping the record. The following variables were recorded:

- number of biting actions, i.e., one action of food collection by the goat (cropping of a portion of a twig) as observed during the trials. Thus, several biting actions could target the same twig (rebrowsing; cf. definition of bite below).
- time from when a goat started to browse on a bundle until it ended. The clock was started when the goat had its nose less than 10 cm from a twig. The sum of seconds feeding on the bundle is hereafter called feeding time.

After 2 minutes the trial was stopped and the goat was removed from the test paddock. All bites (a bite is here defined as one bitten twig as observed after termination of the trial) were counted on the bundle and each bite diameter was measured to nearest 0.1 mm. The bundle was also weighed to nearest 0.01 g, as was the bundle used for water loss determination. This procedure was repeated between 16 and 20 times for each of the three treatments and the control. For various reasons a number of trials failed and we ended up with altogether 58 trials, 17 on control bundles, 13 on bundles with hooks clipped, 12 on bundles with spines clipped and 16 on bundles with both spines and hooks clipped.

<u>Data handling and statistics</u>

Bite diameter was calculated as a mean per bundle and total intake was calculated as mass loss during the trial minus mass loss due to drying. Mass removed per biting action and per bite were calculated as total mass loss divided by number of biting actions and by number of bites, respectively. Utilisation was expressed as total intake*100 divided by bundle weight before trial.

All variables were tested for normality and homogeneity of variances before analyses. If necessary, variables were log-transformed. One variable, utilisation, was arcsin-transformed before analyses. We regarded the presentation of each bundle within a treatment group as a replicate. Overall differences between treatment groups were tested with GLM-procedure (one-way ANOVA) and if significant a post-hoc mean separation test was done with Tukey. A Bonferroni correction was done with regard to the many related measurements (number of biting actions, number of bites, feeding time, total intake, mass of bundle, twig- and bite diameter). To explore the different effects of the two types of spines a two-factor ANOVA was run with spines and hooks as fixed factors. Initially a three-way analysis was done with spines, hooks and goats as fixed factors. Although there were often differences between individual goats, there was only in one case (bite diameter) a weak interaction with treatment, and subsequently goats were excluded from the analysis.

All analyses were performed with SPSS 17.0 2008 and differences were regarded as significant at $p<0.007$ (following Bonferroni correction).

Results

There was a tendency for goats to spend more time browsing from branches without spines and hooks than from control branches, although the difference was not significant ($p=0.016$; Table 1). The mean number of biting actions per bundle varied between 4.7 on control branches and 10.1 on branches with no spines. Mass per biting action and number of biting actions per minute did not differ among treatment groups (Table 1).

The number of bites varied among groups, and was 30-45 % lower than the number of biting actions (Table 1). Number of bites was highest on the bundles without both spines and hooks, but there was no difference in feeding rate (bites per minute) among treatment groups. Bite diameter and mass per bite were larger on bundles without spines and hooks than on those fully armed (Table 1). The mean bite diameter (1.76-2.27 mm depending on treatment) corresponded to the twig diameter (2.10-2.23 mm) at the position of the first long spine seen from the twig apex.

The frequency distributions of bite diameters were rather similar for the no hooks and no spines groups, but the control bundles and bundles with no spines and hooks deviated considerably (Figure 1). In the latter group, about 60 % of the bites were equal to or larger than the diameter at the position of the first spine (2.2 mm), while the corresponding values for the control group was 15 %. On the other hand, the control group, compared to the other three groups, had substantially more bites in the lower range of the frequency distribution. There was no difference in twig diameter at the most distal spine position between groups (pre-treatment; Table 1).

Mean total intake (g per bundle) was more than two times higher on the no spines/hooks group than on controls (Table 1). The utilisation of biomass was considerably higher on treated bundles than on control bundles (Table 1). A higher total mass loss in combination with a tendency to lower pre-trial biomass, due to biomass reduction with treatment, resulted in more than 3 times higher utilisation of the no spines/hooks group (20 %) than of the control group (6 %; Table 1).

Hooks and spines both impacted feeding behaviour by the goats, but showed no interaction (Table 2). Number of biting actions and number of bites were related to hooks, whereas bite diameter and mass per bite were related to spines. Both spines and hooks strongly influenced total intake and utilisation (Table 2).

Discussion

Goats changed feeding behaviour in response to our experimental removal of spines and/or hooks. We expected such responses to include an increase in feeding rate, and/or in bite size resulting in increased total intake and utilisation (Belovsky *et al.* 1991; Gross *et al.*1993; Gordon 2003; Searle and Shipley 2008).

In agreement with the prediction we found that removal of spines and hooks increased bite size (mass per bite; bite diameter).The separation in recording of biting actions and bites showed that rebrowsing on earlier browsed twigs was relatively common, even within a few minutes and in spite of ample availability of unbrowsed twigs (number of twigs on the bundles was much larger than the number of bites). This suggests that goats found a difference in palatability between twigs within each bundle, or that it was just most efficient to continue browsing on the selected twig as long as it provided good forage. The most intensive rebrowsing on earlier browsed twigs (number of biting actions per bite) was on the bundles without spines and hooks.

The bundles without spines and hooks had no larger maximum bite diameter than those of the other treatments, but a considerably larger proportion of the bites was in the upper range of the diameter frequency distribution (Figure 1; cf Belovsky *et al.* 1991). The strong influence of spines on bite diameter and bite size (table 2) suggests that when not restricted by spines the goats utilise more twigs closer to their maximum bite diameter, probably determined by factors, such as trade-off between positive and negative twig characteristics (Palo *et al.*, 1992). Also bite mass changed in response to the treatments. In the present study mean bite mass varied between 0.64-1.10 g among groups. That corresponds to data reported by Gowda (1996) who found that mean bite mass of goats feeding on *A. tortilis* was 0.7 and 1.5 g of twig and leaves from spiny and spineless shoots, respectively. Mass per biting action did not vary among treatments, suggesting that it depended on other factors than the twig, such as mouth size of the goats (Gordon, 2003).

It is doubtful whether the small hooks (usually a few mm long) prevent pruning, but they may increase handling time and possibly search time or deter the goats with their floppy ears (Cooper and Owen-Smith, 1986), resulting in the observed relationship between hooks and number of biting actions and of bites. Spines, on the other hand, may act more as a barrier against biting, as suggested by the relationship between spines and bite diameter and bite size. This pattern is further supported by the fairly good correspondence between bite diameter and twig diameter at the position of the first spine, seen from the twig apex. The only group mean bite diameter that exceeded the twig diameter at point of first spine was the diameter of the no spines or hooks group.

The removal of both types of spines resulted in more bites and more biting actions, but we detected no change in feeding time and feeding rate, expressed either as bites or biting actions per minute or intake rate (g/minute). Most likely there was an increase in feeding time, although not statistically significant ($p = 0.016$; Table 1), explaining the discrepancy seen. Thus, a long feeding time, leading to a large number of biting actions and bites, together with an increased bite diameter, seemed to be the major mechanisms in response to total removal of spines and hooks. Cooper and Owen-Smith (1986) found that biting rate (bites/minute) of goats was affected by removal of spines on *A. tortilis*, but not on four other studied plant species. Belovsky *et al.* (1991), found that the number of bites per minute was similar in a comparison between herbivory on several plant species.

A higher total intake together with lower initial weight of the treated bundles (due to removal of spines and/or hooks in treatment) resulted in a higher biomass utilisation of treated plants, especially unarmed ones. Although we can not perform a metabolic cost-benefit analysis of the mechanical defense, we see that by adding about 7 g extra weight of spines and hooks (Table 1) the plant reduced twig biomass loss in this single 2 minutes feeding bout with about 3 g (Table 1). Using for example nitrogen as the currency would probably reduce the difference. The proportion of spine biomass in our study, ca 20 %, was higher than that reported by Gowda (1997; 10 %) and Dangerfield *et al.* (1996; 6 %). As different from the two latter studies we used 3-yrs old, well spaced planted trees without much competing vegetation and protected from browsing, giving good growing conditions (Brooks and Owen-Smith 1994; Gowda, 1996, 2003). Grubb (1992) hypothesised that the well-developed spinescence of such small trees could be a way of protecting the relatively few shoot apices. Further, the length of the branches used in the different studies may influence the presented biomass figures.

Spines and hooks consist mostly of cellulose and lignin (Gowda, 1996) and are of low nutritional value. Therefore, from the herbivore point of view, the consumption of good food is even lower in the control group as about 15 % of the consumed mass consists of spines and hooks. Calculated in this way, i.e. excluding spines and hooks, the consumption was about 2.5 times higher in the no spines/hooks group compared with the control group.

The most striking pattern in our study was the intense browsing on and high utilisation of the bundles without both spines and hooks compared to other treatments. This was strongly related to both hooks and spines, but the functional mechanisms were different with the long straight spines mainly influencing bite size and the short hooked spines mainly affecting number of bites. The presence of spines reduced the direct damage on twigs of *A. tortilis*, a damage that, potentially, could be more serious than the loss of photosyntesising tissues.

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Table 1. Browsing characteristics in relation to experimental removal of spines and/or hooks. Values are means per treatment (± Standard Error of the mean (SE)). "Twig diam." refers to twig diameter at the position of the most distal straight spine. Significant differences (p < 0.007; after Bonferroni correction) within rows are indicted by different letters.

Twig characteristics	With spines & hooks	No hooks	No spines	No spines & hooks	F	p
Bundle weight before trial (g)	33.8 (2.06)	29.1 (1.95)	30.6 (1.98)	26.6 (1.72)	2.66	0.057
Twig diam. (mm)	2.20 (0.09)	2.22 (0.07)	2.19 (0.06)	2.18 (0.07)	0.08	0.972
Feeding time (sec.)	75.2 (8.36)	92.3 (10.05)	100.3 (7.72)	110.3 (6.00)	3.77	0.016
Number of biting actions	4.7^{a} (0.57)	6.8^{ab} (0.92)	5.8^{a} (0.74)	10.1^{b} (4.50)	5.84	0.002
Mass per biting action (g)	0.51 (0.07)	0.48 (0.08)	0.60 (0.08)	0.61 (0.06)	0.75	0.526
Biting action per minute	4.1 (0.48)	4.4 (0.25)	3.5 (0.44)	5.5 (0.53)	2.8	0.049
Number of bites	3.2^{a} (0.30)	4.8^{ab} (0.53)	4.3^{ab} (0.52)	5.5^{b} (0.41)	5.5	0.002
Bites per minute	3.2 (0.50)	3.3 (0.34)	2.6 (0.35)	3.2 (0.36)	0.43	0.730
Bite diameter (mm)	1.76^{a} (0.08)	1.90^{ab} (0.10)	2.00^{ab} (0.10)	2.27^{b} (0.12)	4.89	0.004
Mass per bite (g)	0.64^{a} (0.07)	0.64^{a} (0.08)	0.80^{ab} (0.10)	1.10^{b} (0.13)	4.67	0.006
Biting actions per bite	1.46 (0.16)	1.43 (0.12)	1.37 (0.09)	1.83 (0.16)	2.12	0.108
Total intake (g)	2.2^{a} (0.44)	2.9^{a} (0.44)	3.3^{a} (0.64)	5.7^{b} (0.63)	8.68	0.001
Intake rate (g/min)	2.2 (0.58)	2.1 (0.28)	2.1 (0.44)	3.0 (0.27)	2.54	0.066
Utilization (%)	6.3^{a} (0.90)	10.3^{a} (1.54)	11.3^{a} (2.14)	22.8^{b} (3.28)	12.47	<0.0001

Table 2. Effects of main factors (spines and hooks) and their interaction on browsing characteristics. “Twig diam.” refers to twig diameter at the position of the most distal straight spine. Significances (p < 0.007; after Bonferroni correction) are indicated in bold

	Corrected Model		Spines		Hooks		Spines * hooks	
df	3		1		1		1	
	F	p	F	p	F	p	F	p
Bundle weight before trial (g)	2.658	0.057	2.034	0.160	4.863	0.032	0.027	0.869
Twig diameter (mm)	0.077	0.972	0.202	0.655	0.101	0.922	0.049	0.826
Feeding time (sec)	3.774	0.016	6.919	0.011	2.752	0.103	0.190	0.665
No. of biting actions	5.836	**0.002**	4.618	0.036	10.189	**0.002**	0.627	0.432
Mass per biting action (g)	0.753	0.526	2.205	0.143	0.016	0.900	0.042	0.839
Biting actions per minute	2.798	0.049	0.023	0.879	6.212	0.016	2.176	0.146
No. of bites	5.495	**0.002**	4.012	0.050	10.207	**0.002**	0.106	0.746
Bites per minute	0.433	0.730	0.675	0.414	0.591	0.445	0.215	0.645
Bite diameter (mm)	4.890	**0.004**	9.040	**0.004**	3.874	0.540	0.403	0.528
Mass per bite (g)	4.674	**0.006**	9.137	**0.004**	1.895	0.174	1.685	0.200
Biting actions per bite	2.121	0.108	1.409	0.240	2.376	0.129	2.126	0.151
Total intake (g)	8.497	**< 0.0001**	12.222	**0.001**	9.020	**0.004**	1.045	0.311
Intake rate (g/min)	2.535	0.066	2.028	0.160	3.331	0.074	1.548	0.219
Utilisation (%)	12.401	**< 0.0001**	16.737	**< 0.0001**	13.862	**< 0.0001**	2.013	0.162

Fig. 1. Frequency distribution (%) of bite diameters of the three treatment groups and the control group (with spines and hooks). Arrow shows the twig diameter (2.2 mm) at the position of the first long spine seen from the apex of the twig.