



Hedmark University College

Faculty of applied ecology and agriculture

BRAGE

Hedmark University College's Open Research Archive

<http://brage.bibsys.no/hhe/>

This is the author's version of the article published in

African Journal of Range and Forage Science

The article has been peer-reviewed, but does not include the publisher's layout, page numbers and proof-corrections

Citation for the published paper:

Skarpe, C., Bergström, R., Danell, K., Eriksson, H., & Kunz, C. (2012).
Of goats and spines - a feeding experiment. *African Journal of
Range and Forage Science*, 29(1), 37-41.

doi: 10.2989/10220119.2012.687075

1 Of goats and spines - A feeding experiment

2

3 Christina Skarpe¹ (Corresponding author), Roger Bergström², Kjell Danell³, Helena
4 Eriksson⁴, Camilla Kunz⁵

5

6 ¹ Department of Forestry and Wildlife Management, Hedmark University College, NO-
7 2480 Koppang, Norway and Norwegian Institute of Nature Research, Tungasletta 2, NO-
8 7485 Trondheim, Norway. E-mail: christina.skarpe@hihm.no

9

10 ² Department of Wildlife, Fish and Environmental Studies, Swedish University of
11 Agricultural Sciences, SE-901 83 Umeå, Sweden, and Forestry Research Institute of
12 Sweden, Uppsala Science Park, SE-751 83 Uppsala, Sweden, E-mail:
13 roger.bergstrom@skogforsk.se

14

15 ³ Department of Wildlife, Fish and Environmental Studies, Swedish University of
16 Agricultural Sciences, SE-901 83 Umeå, Sweden, E-mail: kjell.danell@slu.se

17

18 ⁴ FAO, Viale delle Terme di Caracalla 00153 Rome, Italy, E-mail:
19 Helena.Eriksson@fao.org

20

21 ⁵ Fågelsångsgatan 4, SE-26 877 Kågeröd, Sweden, E-mail: camilla.kunz@telia.com

22

23 Key-words: *Acacia tortilis*; browsing; feeding rate; functional response, plant defence;

24

25

26

27 *Running headline:* Of goats and spines

28

29 Abstract

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

34

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

39

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

48

49

50

51

52

53

54

55

56

57

58

59

60 Introduction

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

72

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

86

87 Many woody species in the African savanna are spiny and some species have both long
88 straight and short hooked spines on the same branches (Timberlake 1980; Cooper and
89 Owen-Smith 1986; Coates-Palgrave 2002). This provides an opportunity to

90 experimentally test the differential function of the two types of spines on twig browsing
91 mammals.

92

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

102

103 Material and Methods

104 Data collection

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

110

111 The feeding trial included 5 goats: 4 adult females and 1 sub-adult female. Goats were of
112 the traditional Tswana breed with a live weight (females) of ca 20 kg (Nsoso *et al.*,
113 2003). We used three paddocks, two 3 x 3 m (test paddocks), and one 3 x 6 m (resting
114 paddock). In the larger one, which was shaded, the goats were kept between trials and
115 during nights. The fence was a veldspan fence, 1.2 m high, on which we hung a black
116 plastic cover to prevent the goats from getting stuck with their horns in the fence and to
117 limit interference between the goats during trials. In the test paddocks the plastic was set
118 up on three sides only to facilitate observations. Between trials, goats were fed twice
119 daily with lucern, grass and branches of the studied species. In the resting paddock water

120 was always available. In each test paddock an iron tube was placed and used to fasten
121 bundles of test branches.

122

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

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

141

142 At the time of the experiment, the trees were basically leafless, and any leaves remaining
143 were removed before the trials. The whole experiment was done during 18-24 September
144 1997.

145

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

150

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

156

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

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

168

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

178

179 Data handling and statistics

180 Bite diameter was calculated as a mean per bundle and total intake was calculated as
181 mass loss during the trial minus mass loss due to drying. Mass removed per biting action

182 and per bite were calculated as total mass loss divided by number of biting actions and by
183 number of bites, respectively. Utilisation was expressed as total intake*100 divided by
184 bundle weight before trial.

185

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

199

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

202

203 Results

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

209

210 The number of bites varied among groups, and was 30-45 % lower than the number of
211 biting actions (Table 1). Number of bites was highest on the bundles without both spines
212 and hooks, but there was no difference in feeding rate (bites per minute) among treatment

213 groups. Bite diameter and mass per bite were larger on bundles without spines and hooks
214 than on those fully armed (Table 1). The mean bite diameter (1.76-2.27 mm depending
215 on treatment) corresponded to the twig diameter (2.10-2.23 mm) at the position of the
216 first long spine seen from the twig apex.

217

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

226

227 Mean total intake (g per bundle) was more than two times higher on the no spines/hooks
228 group than on controls (Table 1). The utilisation of biomass was considerably higher on
229 treated bundles than on control bundles (Table 1). A higher total mass loss in
230 combination with a tendency to lower pre-trial biomass, due to biomass reduction with
231 treatment, resulted in more than 3 times higher utilisation of the no spines/hooks group
232 (20 %) than of the control group (6 %; Table 1).

233

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

238

239 Discussion

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

244

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

254

255 The bundles without spines and hooks had no larger maximum bite diameter than those
256 of the other treatments, but a considerably larger proportion of the bites was in the upper
257 range of the diameter frequency distribution (Figure 1; cf Belovsky *et al.* 1991). The
258 strong influence of spines on bite diameter and bite size (table 2) suggests that when not
259 restricted by spines the goats utilise more twigs closer to their maximum bite diameter,
260 probably determined by factors, such as trade-off between positive and negative twig
261 characteristics (Palo *et al.*, 1992). Also bite mass changed in response to the treatments.
262 In the present study mean bite mass varied between 0.64-1.10 g among groups. That
263 corresponds to data reported by Gowda (1996) who found that mean bite mass of goats
264 feeding on *A. tortilis* was 0.7 and 1.5 g of twig and leaves from spiny and spineless
265 shoots, respectively. Mass per biting action did not vary among treatments, suggesting
266 that it depended on other factors than the twig, such as mouth size of the goats (Gordon,
267 2003).

268

269 It is doubtful whether the small hooks (usually a few mm long) prevent pruning, but they
270 may increase handling time and possibly search time or deter the goats with their floppy
271 ears (Cooper and Owen-Smith, 1986), resulting in the observed relationship between
272 hooks and number of biting actions and of bites. Spines, on the other hand, may act more
273 as a barrier against biting, as suggested by the relationship between spines and bite
274 diameter and bite size. This pattern is further supported by the fairly good

275 correspondence between bite diameter and twig diameter at the position of the first spine,
276 seen from the twig apex. The only group mean bite diameter that exceeded the twig
277 diameter at point of first spine was the diameter of the no spines or hooks group.

278

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

290

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

305

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

312

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

320

321 Acknowledgements

322 We acknowledge the permission by The Office of the President of Botswana to do
323 research in the country. We thank Neil Fitt for kindly permitting us to use a piece of his
324 land for tree plantations and goat pens and Gavin Edwards, for lending us the goats.
325 Maxwell Moyo was a skilled technician and helped us with field-work and taking care of
326 the goats. We also thank Frank Taylor, whose land we used for raising tree seedlings and
327 André de Jongh, for arranging the goat feed supply. The study was financed by
328 Sida/SAREC.

329

330

331

332

333

334

335

336

337 References

- 338 Belovsky, GE Schmitz OJ, Slade JB, Dawson TJ. 1991. Effects of spines and thorns on
339 Australian arid zone herbivores of different body masses. *Oecologia*, 88, 521-528.
- 340 Brooks R, Owen-Smith N. 1994. Plant defenses against mammalian herbivores: Are
341 juvenile *Acacia* more heavily defended than mature trees? *Bothalia*, 24, 211-215.
- 342 Campbell BM. 1986. Plant spinescence in a nutrient poor ecosystem. *Oikos*, 47:168-172.
- 343 Coates Palgrave K. 2002. *Trees of Southern Africa*. Struik Publishers, Cape
344 Town, South Africa.
- 345 Cooper SM & OWEN-SMITH, N. (1986) Effects of plant spinescence on large
346 mammalian herbivores. *Oecologia* 68, 446-455.
- 347 Dangerfield JM, Perkins JS, Kaunda SK. 1996. Shoot characteristics of *Acacia tortilis*
348 (Forsk.) in wildlife and rangeland habitats of Botswana. *African Journal of*
349 *Ecology*, 34, 167-176.
- 350 Gordon IJ. 2003. Browsing and grazing ruminants: are they different beasts? *Forest*
351 *Ecology and Management*, 181, 13-21
- 352 Gowda JH, Albrechtsen BR, Ball JP, Sjöberg M, Palo RT. 2003. Spines as mechanical
353 defence: The effects of fertilizer treatment on juvenile *Acacia tortilis* plants. *Acta*
354 *Oecologica*, 24, 1-4.
- 355 Gowda JH. 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos*, 77,
356 279-284.
- 357 Gowda JH. 1997. Physical and chemical response to juvenile *Acacia tortilis* trees to
358 browsing: Experimental evidence. *Functional Ecology*, 11, 106-111.
- 359 Gross JE, Thompson Hobbs N, Wunder BA. 1993. Independent variables for predicting
360 intake rate of mammalian herbivores: biomass density, plant density, or bite size?
361 *Oikos*, 68, 75-81.
- 362 Grubb PJ. 1992. A positive distrust in simplicity - lessons from plant defenses and
363 from competition among plants and among animals. *Journal of Ecology*, 80, 585-
364 610.
- 365 Milewski AV, Young TP, Madden D. 1991. Thorns as induced defenses: experimental
366 evidence. *Oecologia*, 86, 70-76.
- 367 Nsoso SJ, Aganga AA, Moganetsi BP, Tshwenyane SO. 2003. Body weight, body

- 368 condition score and heart girth in indigenous Tswana goats during the dry and wet
369 seasons in southeast Botswana. *Livestock Research for Rural Development* (15) 4.
370 Retrieved July 21, 2009, from <http://www.lrrd.org/lrrd15/4/nsos154.htm>.
- 371 Obeso JR. 1997. The induction of spinescence in European holly leaves by browsing
372 ungulates. *Plant Ecology*, 129, 149-156.
- 373 Palo T, Bergström R, Danell K. 1992. Digestibility, distribution of phenols, and fiber at
374 different twig diameters of birch in winter. Implication for browsers. *Oikos*, 65,
375 450-454.
- 376 Rooke T. 1998. *Responses to simulated browsing in five savanna shrubs*. Honor
377 thesis in Animal Ecology, Swedish University of Agricultural Sciences, Umeå,
378 Sweden.
- 379 Rosenthal JP, Kotanen PM. 1994. Terrestrial plant tolerance to herbivory. *Trends in*
380 *Ecology and Evolution*, 9, 145-148.
- 381 Searle KR, Shipley LA. 2008. The comparative feeding behaviour of large browsing and
382 grazing herbivores. In: Gordon IJ, Prins HHT (eds), *The ecology of browsing and*
383 *grazing*. Berlin: Springer Verlag. pp 117-148.
- 384 Sebata A, Ndlovu LR. 2010. Effect of leaf size, thorn density and leaf accessibility on
385 instantaneous intake rates of five woody species browsed by Matabele goats
386 (*Capra hircus* L) in a semi-arid savanna, Zimbabwe. *Journal of Arid*
387 *Environments*, 74, 1281-1286.
- 388 Skarpe C, Bergström R, Bråten A-L, Danell K. 2000). Browsing in a heterogenous
389 savanna *Ecography*, 23, 632-640.
- 390 Theimer TC, Bateman GC. 1992. Patterns of prickly-pear herbivory by collared
391 peccaries. *Journal of Wildlife Management*, 56, 234-240.
- 392 Timberlake JR. 1980. *Handbook of Botswana Acacias*. Ministry of Agriculture,
393 Gaborone, Botswana.
- 394 Wilson SL, Kerley GIH. 2002. The effect of plant spinescence on the foraging efficiency
395 of bushbuck and boergoats: browsers of similar body size. *Journal of Arid*
396 *Environments*, 55, 150-158
- 397 Wilson SL, Kerley GIH. 2003. Bite diameter selection by thicket browsers: The effect of

398 body size and plant morphology on forage intake and quality. *Forest Ecology and*
399 *Management*, 181, 51-65.

400 Young TP. 1987. Increased thorn length in *Acacia drepanolobium* - an induced response
401 to browsing. *Oecologia*, 71, 436-438.

402

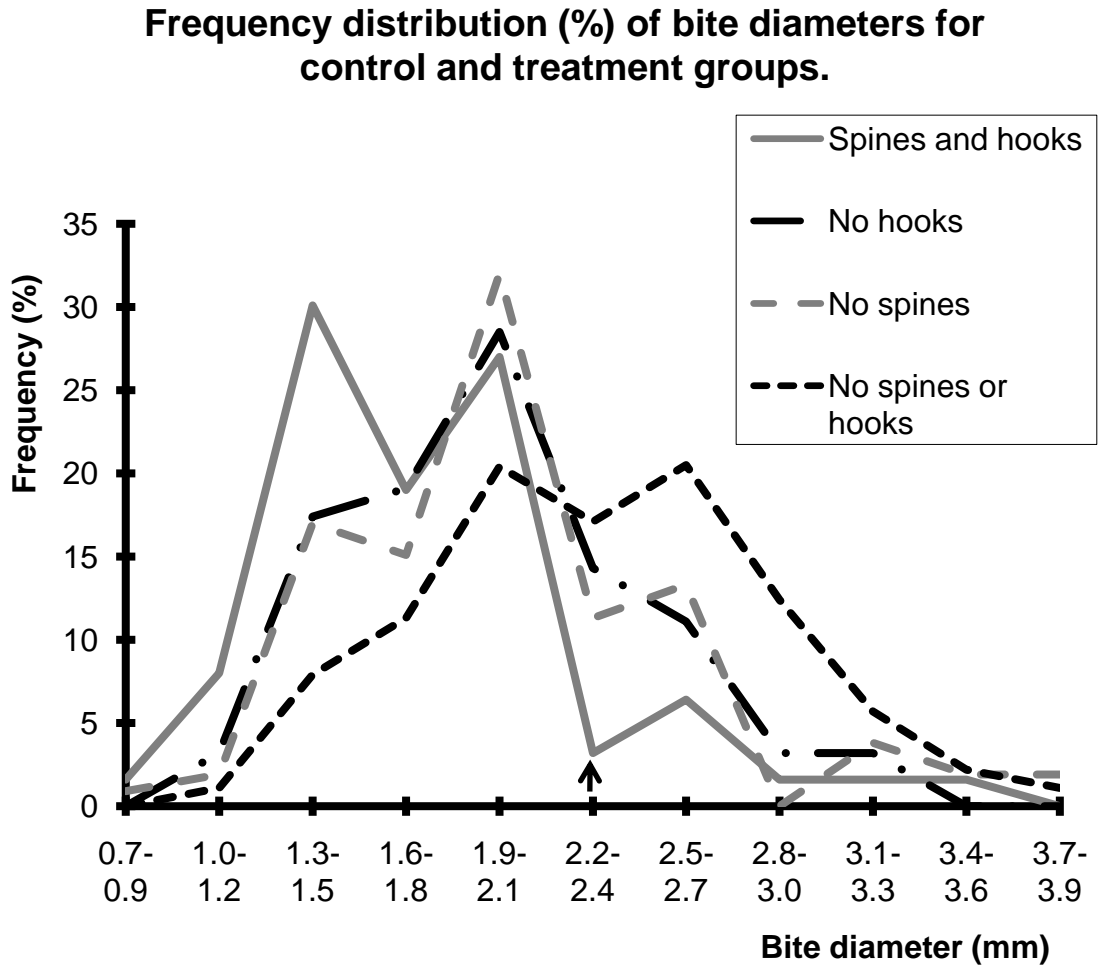
403 Table 1. Browsing characteristics in relation to experimental removal of spines and/or
 404 hooks. Values are means per treatment (\pm Standard Error of the mean (SE)). “Twig
 405 diam.” refers to twig diameter at the position of the most distal straight spine. Significant
 406 differences ($p < 0.007$; after Bonferroni correction) within rows are indicated by different
 407 letters.

Twig characteristics	With spines		No spines	No spines &		F	p
	& hooks	No hooks		hooks			
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	

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

df	Corrected Model		Spines		Hooks		Spines * hooks	
	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

411 Fig. 1. Frequency distribution (%) of bite diameters of the three treatment groups and the
 412 control group (with spines and hooks). Arrow shows the twig diamet



413
 414 (2.2 mm) at the position of the first long spine seen from the apex of the twig.
 415

416
 417
 418
 419