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Goat preference for *Prosopis caldenia* and *Prosopis flexuosa*

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Prosopis caldenia and *P. flexuosa* are native woody plants in central Argentina. Circumstantial observations have shown that goats consistently select the first species and avoid the latter. The present study was designed to compare preference of goats for old and new branches of both species under controlled conditions. We ran choice tests that paired old and new branches of *P. caldenia* and *P. flexuosa* in all possible binary combinations. For each option a preference index was calculated by dividing the number of bites on the particular option by the total number of bites on both options. Goats showed the following preference order: old branches of *P. caldenia* > new branches of *P. caldenia* > old branches of *P. flexuosa* = new branches of *P. flexuosa*. Goat preference was positively correlated with total phenols and condensed tannins, whereas it was negatively correlated with neutral detergent fibre.

Keywords: goat preferences; diet selection; *Prosopis caldenia; Prosopis flexuosa*; semi-arid shrublands; Argentina

Introduction

Numerous evidence has pointed out the importance of chemical (reviewed by Bryant *et al.*, 1991*a*) and physical (reviewed by Myers & Bazely, 1991) defences on herbivore preference for woody plants. Although herbivores have morphological (Hofmann, 1988, 1989) and physiological (McArthur *et al.*, 1991) mechanisms to deal with anti-herbivore defences, these mechanisms present limitations. For example, detoxification of plant secondary compounds can represent high metabolic costs (Freeland & Janzen, 1974; McArthur *et al.*, 1991; Cheeke, 1994; Cheeke & Palo, 1995).Together, the mechanisms to counteract anti-herbivore defences, their limitations, and amount and type of anti-herbivore defences may explain why there is considerable variation in herbivore preference for woody plants.

In arid and semi-arid habitats, chemical defences of woody plants are mainly represented by phenols and terpeniods (Meyer & Karasov, 1991). Phenols can cause toxicity and/or inhibition of digestion (Robbins *et al.*, 1987; Lindroth, 1989; Hagerman *et al.*, 1992; Cheeke & Palo, 1995), which result in reduced acceptability by herbivores (Provenza, 1995; Provenza *et al.*, 1998). On the other hand, physical defences are

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represented by a variety of structural and morphological characteristics, such us hairs, prickles, spines, and thorns (Myers & Bazely, 1991). Spinescence has been show to reduce the feeding rate of mammalian herbivores (Cooper & Owen-Smith, 1986; Belovsky *et al.*, 1991). Moreover, intensive shoot damage of mature plants (e.g. burnt, topping) causes a reversion to a juvenile phase of growth (Kozlowski, 1971), which is frequently characterized by an increased allocation of carbon to chemical and/or physical defences (Bryant *et al.*, 1983, 1991*b*).

Prosopis caldenia and *P. flexuosa* are native, deciduous woody plants in central Argentina. Both species are high in leaf total phenols and posses a pair of straight long spines at each axillary bud (Pisani & Distel, 1998). However, circumstantial observations have shown that goats consistently select *P. caldenia* and avoid *P. flexuosa*. The present study was designed to compare preference of goats for old and new branches of both species under controlled conditions, and to relate preference to the level of nutrients, chemical defences, and physical defences.

Materials and methods

The study was conducted in an upland site located in the southern part of the Caldén District (Cabrera, 1976) (38° 45′ S; 63° 45′ W). The climate is temperate and semi-arid. Mean monthly air temperature ranges from a low of 7°C in July to a high of 24°C in January, with an annual mean of 15°C. Mean annual rainfall is 400 mm, with peaks in March (autumn) and October (spring). The more severe droughts occur in summer. Dominant soils are classified as Calciustolls. In uplands, they present a petrocalcic horizon at 60–80 cm depth. The physiognomy of the vegetation is shrubland. The most abundant woody species are *Prosopis caldenia*, *P. flexuosa*, *Larrea divaricata*, *Condalia microphylla*, and *Chuquiraga erinacea*, whereas herbaceous species are mainly represented by several species of the genus *Stipa*, *Poa ligularis*, *Piptochaetium napostaense*, *Medicago minima*, and *Erodium cicutarium*.

Prosopis caldenia and *P. flexuosa* are warm-season, leguminous trees native to Argentina (Burkart, 1976). They normally start producing leaves in October and lose their leaves in April (Distel & Peláez, 1985). Presently, both species are subjected to low levels of herbivory by wild and domestic animals, except for the pods, which are heavily eaten. Defensive traits such as phenols and spines might have resulted from evolutionary interactions with megafauna during the Pleistocene (Janzen & Martin, 1981; Bucher, 1987).

Five adult, female, crossbred Angora-Spanish goats and three replicates were used for each preference trial. Goats were tamed and familiarized with the vegetation of the study site. During trials they were restrained in a pen (10×10 m), located inside a 2-ha pasture representative of the upland shrublands. The rest of the time goats had free access to the pasture. The preference trials lasted 2 min each, and consisted of the individual offer of all possible binary combinations of old and new branches of *P. caldenia* and *P. flexuosa*. Old branches were harvested from intact plants, whereas new branches were harvested from plants that had been topped 10 months before starting the trials. Branches (8 mm basal diameter) were held erect in a wooden frame fixed on the ground (for details see Ortega-Reyes & Provenza, 1993). In each trial, the animal and the combination of branches (options) to offer were determined at random. The measured response variable was the number of bites on each of the two options. Finally, for each option a preference index was calculated by dividing the number of bites on the particular option by the total number of bites on both options. A preference index greater or smaller than 0·5 indicates preference for or rejection of an option, respectively.

During the preference trials, branches from five intact plants and five topped plants of *P. caldenia* and *P. flexuosa* were harvested for chemical analyses and spinescence assessment. In the lab, samples were sorted into leaves and stems, and air-dried. A low drying temperature (20–30°C) minimizes denaturing of carbon-based secondary metabolites

(Hagermann, 1988). Leaves were ground to pass a 1-mm sieve and analysed for total phenols (Folin-Denis Method; Swain & Hillis, 1959); condensed tannins (Vanillin-HCL Method; Broadhurst & Jones, 1978); neutral detergent fibre, acid detergent fiber, and lignin (Detergent System; Goering & Van Soest, 1970); nitrogen (semi-micro Kjeldahl); sodium, magnesium, calcium, and potassium (mass spectrophotometry, Hitachi Z6100); and phosphorous (Olsen & Dean, 1965). Branches were used to determine spine density (number of spines per cm of branch), and spine length (mm).

The statistical significance of the differences between the preference indices and 0·5 was determined by the *t*-test. The chemical composition and spinescence of old and new branches from *P. caldenia* and *P. flexuosa* were subjected to ANOVA and the statistical significance of the differences were established by the least significant difference test. Finally, the average preference indices for each option were correlated with the average chemical and spinescence variables of each option by Kendall Rank Correlation test (τ) (Sokal & Rohlf, 1995).

Results

Plucking of individual leaves was the exclusive feeding mode of goats on both species of *Prosopis*. When old branches of *P. caldenia* were paired either to new branches of the same species or to old or new branches of *P. flexuosa*, the preference indices were significantly greater ($p < 0{\cdot}01$) than 0·5 (Table 1). The same happened when new branches of *P. caldenia* were paired either to old branches or to new branches of *P. flexuosa*. Contrarily, when old branches of *P. flexuosa* were paired to new branches of the same species, the preference indices were not significantly greater ($p > 0{\cdot}05$) than 0·5. Together, goats showed the following preference order: old branches of *P. caldenia* > new branches of *P. caldenia* > old branches of *P. flexuosa* = new branches of *P. flexuosa*.

The chemical composition and spinescence of the branches are shown in Table 2. The correlations between the preference indices with either total phenols, condensed tannins, neutral detergent fibre or acid detergent fibre were the strongest (Table 3). Goats' preference was positively associated with total phenols and condensed tannins, but negatively associated with neutral and acid detergent fibre.

Discussion

The results were in agreement with circumstantial evidence showing that free-ranging goats consistently select *P. caldenia* and avoid *P. flexuosa*. The preferences of goats were

Table 1. *Preference of goats for old and new branches of* Prosopis caldenia *and* Prosopis flexuosa. *Each value represents the mean of five goats and three repetitions per goat. Values followed by an asterisk are significantly different (*$p < 0{\cdot}01$*) from 0·5 (value that indicates similar preference for both options). OB = old branches; NB = new branches*

Paired options	Preference index
OB *P. caldenia vs.* OB *P. flexuosa*	0·91 *vs.* 0·09*
OB *P. caldenia vs.* NB *P. caldenia*	0·70 *vs.* 0·30*
OB *P. caldenia vs.* NB *P. flexuosa*	0·92 *vs.* 0·08*
NB *P. caldenia vs.* OB *P. flexuosa*	0·80 *vs.* 0·20*
NB *P. caldenia vs.* NB *P. flexuosa*	0·78 *vs.* 0·22*
OB *P flexuosa vs.* NB *P. flexuosa*	0·45 *vs.* 0·55

Table 2. *Chemical composition and spinescence of old and new branches from* Prosopis caldenia *and* Prosopis flexuosa. *Values are means ± S.E. of five samples. Different letters in each row indicate significant (*$p < 0{\cdot}05$*) differences (LSD test). OB = old branches; NB = new branches*

	OB *P. caldenia*	NB *P. caldenia*	OB *P. Flexuosa*	NB *P. flexuosa*
Total phenols (A_{bs725}/60 mg DM)	$1{\cdot}1 \pm 0{\cdot}04^{a}$	$0{\cdot}8 \pm 0{\cdot}04^{b}$	$0{\cdot}6 \pm 0{\cdot}06^{c}$	$0{\cdot}4 \pm 0{\cdot}01^{d}$
Condensed tannins (A_{bs500}/60 mg DM)	$0{\cdot}18 \pm 0{\cdot}01^{a}$	$0{\cdot}16 \pm 0{\cdot}02^{a}$	$0{\cdot}15 \pm 0{\cdot}02^{a}$	$0{\cdot}14 \pm 0{\cdot}02^{a}$
Sodium (ppm)	137 ± 10^{a}	136 ± 37^{a}	208 ± 50^{a}	170 ± 26^{a}
Potassium (%)	$0{\cdot}96 \pm 0{\cdot}09^{a}$	$1{\cdot}34 \pm 0{\cdot}12^{b}$	$1{\cdot}18 \pm 0{\cdot}08^{ab}$	$1{\cdot}35 \pm 0{\cdot}11^{b}$
Magnesium (%)	$0{\cdot}30 \pm 0{\cdot}05^{a}$	$0{\cdot}17 \pm 0{\cdot}01^{b}$	$0{\cdot}36 \pm 0{\cdot}03^{a}$	$0{\cdot}19 \pm 0{\cdot}02^{b}$
Calcium (%)	$3{\cdot}8 \pm 0{\cdot}89^{a}$	$4{\cdot}8 \pm 0{\cdot}21^{a}$	$5{\cdot}5 \pm 0{\cdot}63^{a}$	$3{\cdot}7 \pm 0{\cdot}35^{a}$
Phosphorous (%)	$0{\cdot}13 \pm 0{\cdot}01^{a}$	$0{\cdot}10 \pm 0{\cdot}02^{ab}$	$0{\cdot}08 \pm 0{\cdot}01^{b}$	$0{\cdot}11 \pm 0{\cdot}01^{a}$
Protein (%)	$15{\cdot}8 \pm 0{\cdot}8^{a}$	$19.1 \pm 2{\cdot}5^{a}$	$15{\cdot}0 \pm 1{\cdot}2^{a}$	$18.2 \pm 0{\cdot}7^{a}$
Lignin (%)	$11{\cdot}6 \pm 0{\cdot}5^{a}$	$11{\cdot}3 \pm 0{\cdot}4^{a}$	$10{\cdot}5 \pm 0{\cdot}4^{a}$	$13{\cdot}0 \pm 0{\cdot}6^{a}$
Neutral detergent fibre (%)	$32{\cdot}8 \pm 1{\cdot}1^{a}$	$34{\cdot}5 \pm 1{\cdot}6^{ab}$	$36.3 \pm 2{\cdot}1^{ab}$	$38.3 \pm 0{\cdot}7^{b}$
Acid detergent fibre (%)	$20{\cdot}0 \pm 0{\cdot}7^{a}$	$22{\cdot}1 \pm 1{\cdot}0^{a}$	$22{\cdot}7 \pm 1{\cdot}5^{a}$	$25{\cdot}9 \pm 0{\cdot}6^{a}$
Spine density (spines per cm branch)	$0{\cdot}71 \pm 0{\cdot}07^{a}$	$1{\cdot}34 \pm 0{\cdot}09^{c}$	$0{\cdot}54 \pm 0{\cdot}04^{a}$	$1{\cdot}01 \pm 0{\cdot}07^{b}$
Spine length (mm)	$14{\cdot}5 \pm 1{\cdot}67^{a}$	$9.3 \pm 0{\cdot}96^{bc}$	$11{\cdot}8 \pm 1{\cdot}11^{ab}$	$7.2 \pm 0{\cdot}31^{c}$

Table 3. *Kendall Rank Correlation Coefficients (τ) between preference indices (n = 15) and chemical/spinescent variables (n = 5) of the different options*

	τ	p
Total phenols	1·00	0·04
Condensed tannins	1·00	0·04
Sodium	− 0·33	0·50
Potassium	− 0·67	0·17
Magnesium	< 0·0001	1·00
Calcium	< 0·0001	1·00
Phosphorous	0·33	0·50
Protein	< 0·0001	1·00
Lignin	< 0·0001	1·00
Neutral detergent fibre	− 1·00	0·04
Acid detergent fibre	− 1·00	0·04
Spine density	< 0·0001	1·00
Spine length	0·67	0·17

negatively related to the concentration of fibre, which is consistent with their relatively limited capacity to digest cell walls (Hofmann, 1988, 1989; Gordon, 1989). However, there were no significant differences in neutral detergent fibre among options (Table 3), which limits the importance of this factor as a possible determinant of goat preferences. Moreover, preference for woody species appears to be determined by anti-herbivore defences more than by nutrients derived from plant primary metabolism (Bryant *et al.*, 1992). Although in our study the preference indices were positively related to total phenols and condensed tannins, several factors may contribute to explain these results. The biological activity of phenols in general, and condensed tannins in particular, may vary according to their chemical structure (Zucker, 1983). For example, Clausen *et al.* (1990) clearly demonstrated that structurally different condensed tannins vary in their effectiveness as deterrents to browsing. Also, it has been shown that phenols with similar degrees of polymerization and capacity to bind proteins, but stereo-chemically different, can differentially influence the ingestive behaviour of mammalian herbivores (Butler, 1993). Alternatively, *P. caldenia* and *P. flexuosa* may differ either in the presence, structure or concentration of other secondary metabolites (e.g. alkaloids, terpens), which may be the main determinants of the rejection of *P. flexuosa*. Unfortunately, there is almost no information on the nature of the secondary chemistry in both species. On the other hand, the prehension abilities of goats may contribute to explain the lack of influence of either spine density or spine length on their preference (Table 3). The small mouth and agile lips and tongue enable goats to consume plant parts that are relatively inaccessible or protected by physical defences. When spine density is relatively high, plucking of individual leaves is the primary feeding mode of goats (Gowda, 1996).

Because woody plants represent an important part of goat diets in the study system, it has been argued that goats may be a possible species for biological control (J.M. Pisani, R.A. Distel, and E.E. Bontti, unpublished manuscript). However, the different preference of goats for woody species (as shown in the present study) may result in differential exploitation (and control) of woody species in a plant community.

Conclusions

When given a choice goats consistently select *P. caldenia* and reject *P. flexuosa*. There are two alternative hypotheses to explain the selective behaviour of goats: (1) that both

species differ in the chemical structure and, consequently, in the biological activity of phenols; and (2) that both species differ in the presence, amount and/or type of other secondary metabolites such as alkaloids and terpens.

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