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Selective behavior of Creole goats in response to the functional heterogeneity of native forage species in the central Monte desert, Argentina☆

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A R T I C L E   I N F O

A B S T R A C T

The changes in forage availability and the physicochemical variability of plants influence the diet selection by herbivores. In this study, the foraging behavior of Creole goats was studied in terms of botanical composition of the diet, food availability and physicochemical properties of vegetation. The study was performed in a desert rangeland in the northeast (NE) Mendoza region in Argentina. Experiments with grazing goats were made in dry (winter) and wet (summer) seasons and cafeteria experiments (feeding trial) were performed during the summer. Food availability was estimated from forage species cover. Botanical composition of the goat's diet was determined by microhistological analysis of fecal samples. Morphological parts of forage species consumed by goats were sampled and analyzed to determine chemical traits (plant nutrients and secondary metabolites) in both seasons. Also, during summer, the two morphological traits of browse species stem specific density (SSD) and specific leaf area (SLA) were evaluated. In the experiments with grazing goats, diet selection was evaluated based on Ivlev's electivity index ($\hat{I}$) and, in cafeteria experiments, preference was estimated based on the number of bites. Diet selection varied between the two seasons. Grazing goats showed differences in the patterns of diet selection related to changes in forage availability. The botanical composition of the diet had a greater ($p < 0.001$) participation of woody species in relation to grass species in both seasons, but the herbaceous stratum was more utilized by goats during the summer according to their higher availability. Correlations between diet and availability were positive in both seasons, but not significant in summer. The models including crude protein (CP), neutral detergent fiber (NDF) and total phenols (TP) had substantial support for predicting variation in diet selection in summer and winter. In both seasons the preference increased as the concentrations of CP, NDF and TP increased, but the effect of CP was significant only in winter. Thus, goats selected supplementary food mixtures (mixed diet) and tannins were not considered dissuasive but, rather, were maintained below a certain threshold. In summer, SSD was negatively and significantly related to diet selection by grazing goats. This morphological trait allowed explaining a greater percentage of the variation in $\hat{I}$ (36%) with regard to the variation explained by the chemical variables (16%). In cafeteria experiments,

in summer, the optimization of nutrient intake rate through consumption of species with low SSD values represented a best explanation for the preferences observed, whereas the hypotheses of minimization of secondary metabolites and maximization of nutrients were not able to fully explain the preferences observed in cafeteria experiments. To conclude, dietary decisions by goats in desert rangelands could be interpreted in terms of intake rate optimization and complementation of nutrients and secondary compounds, rather than by explanations involving the isolated effects of nutrient intake maximization or tannin intake minimization.

1. Introduction

Domestic goats (*Capra hircus*) possess diverse adaptations to harsh environments, where they face a complex food source dominated by woody plant species with marked variability in their morphological and chemical characteristics and heterogeneity in both spatial and temporal dimensions (Silanikove, 2000; Provenza, 2008; Waghorn, 2008). These adaptations involve integrated physiological and behavioral mechanisms that allow grazing goats to perceive the complexity of the food resource through chemosensory stimuli, in some cases detoxify and/or tolerate certain types of substances and finally, generate preference or aversion to certain foods (Hofmann, 1989; Villalba et al., 2002; Provenza, 2003; Glendinning, 2007).

Traditionally, chemical compounds that affect foraging decisions of mammalian herbivores have been classified into three major groups: nutrients, fiber and secondary metabolites (Cooper et al., 1988). In relation to secondary compounds (PSMs), numerous studies highlight the wide distribution and variability in the content and biological activity of polyphenolic compounds in woody plants, with special emphasis on tannins (Waterman and Mole, 1994; Hagerman, 2002; Makkar, 2010). For herbivores, this represents positive or negative effects depending on various factors such as the chemical nature and concentration of tannins in the plant, interaction with other metabolites, plant phenological stage or animal species (Baraza et al., 2009; Muir, 2011). The dissuasive power of these compounds would be mediated by their deleterious effects on palatability, intake and digestibility of forage species (Cheeke, 1988; Goel et al., 2005). However, tannins are not completely avoided by goats, but rather are tolerated under certain threshold (Jansen et al., 2007). This may be related to benefits provided by intake of small amounts of tannins, including supplying bypass protein (Makkar, 2010), reducing methane production (Muir, 2011) and anthelmintic and antitumor activities (De Bruyne et al., 1999; Min et al., 2003).

Some plant morphological traits such as specific leaf area (SLA), specific stem density (SSD), tensile strength and spines affect and/or restrict the food ingestion–digestion process (Cooper and Owen-Smith, 1986; Cornelissen et al., 2003; Sebata and Ndlovu, 2010). The dietary decisions performed by goats, based on the physical characteristics of forage, would have important implications for nutrient intake rate and the performance of these animals (Illius et al., 1999; Shipley et al., 1999).

The objective of this study was to investigate the foraging behavior of grazing goats in a desert ecosystem of Argentina in terms of botanical composition of the diet, availability and physicochemical properties of vegetation and forage selection in relation to seasonal variations. The hypotheses were tested in this study and their predictions are listed below:

(1) The dominant functional groups of plants in the diet and some morphophysiological adaptations of grazing herbivores are some of the criteria that allowed defining goats as opportunistic mixed feeders (Hofmann, 1989; Shipley, 1999; Dziba et al., 2003; Rogosic et al., 2008). Based on this hypothesis, we expect that grazing goats will show differences in the diet selection patterns related to changes in forage availability.
(2) Considering the learning model based on postingestive consequences diet selection behavior can be conceptualized as a functional behavioral response of grazing herbivores facing the dilemma of what and how much to eat (Provenza, 1995, 2003; Howery et al., 1998). The structural and chemical traits of forage plants address these behavioral responses because they can modify the internal state of the animal (Villalba and Provenza, 2009). According to this hypothesis, we expect that the dietary decisions of goats rather than maximize nutrients and minimize tannins, will enable them to eat complementary food mixtures (mix diets).
(3) The structural characteristics of plants primarily affect the rate at which herbivores can harvest food (Wright and Vincent, 1996). Considering that herbivores spend almost half of their daily time harvesting food (Owen-Smith, 1988), plants characteristics that increase the time to harvest enough food reduce the time available for other life requirements (Laca et al., 2001). Therefore, the effect of structural anti-quality traits on food selection may exceed the effect of chemical anti-quality properties (Spalinger et al., 1986; Shipley et al., 1999). We expect that the morphological traits of forage plants will provide a better explanation than their chemical traits for the selective behavior of goats.

2. Materials and methods

2.1. Study site

This study was conducted in the household "La Majada" (32°19′39′S, 67°54′36′W) situated in the northeast (NE) of Lavalle, Mendoza province (Argentina). This region is located on the plains at the Eastern foothills of

the Andes, formed by accumulation of Andean sediments during the upper Cenozoic and Quaternary periods (Guevara et al., 1997). Fluvial sediments were reworked by winds into an extensive dune system. The study area was classified as sub-desert according to Le Houérou (1999) Mean annual temperature is 18.3 °C and mean annual rainfall 159 mm (Villagra et al., 2005). Rainfall is mostly torrential and occurs primarily in the summer (wet season) and decreases in winter (dry season) (Villagra et al., 2005). Data were obtained from the Telteca Reserve weather station (32°20′S, 68°00′W). Soils in the study area are mainly sandy with undifferentiated horizons (Entisols and Aridisols).

The vegetation communities of greatest forage importance are semi-closed woodlands of *Prosopis flexuosa* DC. with *Atriplex lampa* Gillies ex Moq. in interdune valleys, and open woodlands of *P. flexuosa* with *A. lampa* and *Tricomaria usillo* Hook. & Arn. on dunes (Alvarez et al., 2006; Passera et al., 2004). The trees and shrubs most commonly found include *Prosopis flexuosa*, *Geoffroea decorticans* (Gillies. ex Hook. & Arn.) Burkart, *Bulnesia retama* (Gillies ex Hook. & Arn.) Burkart, *Capparis atamisquea* Kuntze, *Atriplex lampa*, *Tricomaria usillo* and *Mimosa ephedroides* Benth. The primary grass species include *Trichloris crinita* (Lag.) Parodi, *Pappophorum caespitosum* R. E. Fr. and *Panicum urvilleanum* Kunth.

2.2. Animals and management

Observational studies (experiments with grazing goats) were made in summer (February) and winter (August) and cafeteria experiments (feeding trials) were performed in summer (February). All experiments were carried out during 2009.

2.2.1. Grazing goats

Creole goats were selected from a commercial meat goat flock (*n* = 250). During each sampling period twelve dry goats (non-lactating and non-pregnant) were identified for collection of fecal samples. The animals traveled long distances (approximately 5 km daily). The most important forage species in the zone were present at the grazing site within a range of approximately 500 ha. This large area prevented overgrazing of vegetation and provided the goats with free dietary choices without any influence among animals. The goats grazed at the same site consisting of woodlands of *P. flexuosa* with *A. lampa* and *P. flexuosa* with *T. usillo* in both seasons. Goats grazed from 8.30 am to 5.00 pm and were penned near the household in the evening with access to water. Different animals were used for each sampling season. The selected goats were 36 ± 2.8 kg in body weight. Plant parts selected by the grazing goats in the same study area and in both sampling seasons were identified by Allegretti et al. (2012). To corroborate these observations, in the present study, two grazing animals were directly observed for 6 days in dry and wet seasons for 10-min periods every 30 min (Genin and Pijoan, 1993).

2.2.2. Feeding trials

For feeding trials, twelve dry Creole goats (non-lactating and non-pregnant) were selected in summer. Goats were allocated to individual pens, where they had free access to fresh water and trace mineral salt block. Goats were fed whit alfalfa hay and ground corn to meet their nutritional requirements (NRC, 2007). After adaptation period to the pens (10 days), the goats were blocked by live weight and body condition scores (Santucci et al., 1991) and assigned to three homogeneous groups of four goats. Each group received a different diet composed of a paired combination of the three most selected shrubs by grazing goats in summer, *C. atamisquea* (CA), *M. ephedroides* (ME) and *T. usillo* (TU). The three combined diets were: CA + ME, CA + TU and ME + TU. During a 3-day period, unbrowsed branches were collected from all three shrubs species in the morning and the animals received daily branches of the two species corresponding to each combination. The number of bites taken by the animal from the forage species offered was recorded for a maximum of 10 min. All goats were monitored twice under each combination (once in the morning and once in the afternoon). Preference was estimated on the basis of bites taken from each species (Illius et al., 1999; Jansen et al., 2007).

2.3. Forage availability

In both seasons, vegetation cover was used as an approximate measure of availability (Kufner et al., 2008). Forage species cover was estimated using the point quadrat method (Daget and Poissonet, 1971),

modified for the Monte area by Passera et al. (2007). At the grazing site, ten 50-m randomly distributed transects were established and 100 points (50 cm apart) were monitored per transect in each season. The species intercepting each point were recorded with a needle. The proportion of intercepts of each species was considered an estimate of cover. For each species consumed by goats, mean plant cover was calculated by season, and plant species were grouped into two categories: grasses and shrubs plus trees.

2.4. Diet analysis

To estimate botanical composition of the diet, five fecal samples were collected from each goat on five successive days during each sampling period. The samples were oven dried at 50 °C for 72 h. The feces were then ground in a Willey mill and passed through 1 mm screen. All five samples were mixed together, and one subsample per goat was analyzed. Botanical composition was determined using a microhistological technique (Holechek et al., 1982; Sparks and Malechek, 1968). Five microscope slides were prepared for each subsample and all epidermal fragments were censused on each slide at 100× magnification, the numbers of epidermal fragments of each species were converted to percentages. A reference plant collection was used for plant identification (Guevara et al., 2010; Monge, 1989).

2.5. Diet selection and preference

In the experiments with grazing goats, preference values were calculated for each species consumed based on Ivlev's electivity index ($\hat{I}$) as follows: (% species in diet − % species availability)/(% species in diet + % species availability) (Ivlev, 1961). Plants were classified according to this index into three categories: species eaten less than expected from its availability: Avoided (−1.0 to −0.3), species eaten in approximate proportion to its availability: Indifference (+0.3 to −0.3) and species eaten more than expected from its availability: Preferred (+1.0 to +0.3) (Puig et al., 2001). In cafeteria experiments, where each goat could choose between two forage species, preference was estimated on the basis of number of bites, according to Jansen et al. (2007). The advantage of using number of bites is that these represent a clear decision by the animal and can be counted easily by the researcher (Illius et al., 1999). The Kappa index (K_{hat}) was estimated to determine which chemical or morphological traits of native forage species explained the observed preferences (Hanley, 1987). This index allowed relating the observed preferences with the expected preference according to predictions (Jansen et al., 2007). Predictions were as follows: if the animals maximize nutrients, they will prefer species with higher nutrient content; if the animals minimize PMSs, they will prefer species with low levels of tannin and fiber, and if the animals maximize food intake rate, they will prefer species whose morphological traits allow higher food intake.

2.6. Chemical and morphological traits of forage species

On the basis of information obtained by visual observation of grazing goats (Section 2.2.1) and diet analysis (Section 2.4), morphological parts of forage species, which were accepted by goats, were sampled in both seasons. Samples were taken from 10 ungrazed plants of each species and one composite sample was made for each species. Plant samples were kept in paper bags and air dried prior to oven drying at 60 °C for 48 h. Samples were analyzed for chemical composition on a dry matter basis. Crude protein (CP) was calculated using nitrogen concentration which was determined according to AOAC (1990). Organic matter digestibility (OMD), neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin and cellulose were determined following Van Soest et al. (1991) in the Laboratory of Nutrition and Forage Quality Assessment, EEA INTA Balcare. Determinations of TP, TT and CT were completed based on Makkar (2010). Acid-butanol proanthocyanidin assay was used to determine condensed tannins (CT), Folin-Ciocalteu method was used to determine total phenols (TP) and total tannins (TT) were obtained by the difference of TP before and after treatment with polyvinylpolypyrrolidone. Also the biological activity was assessed by the radial diffusion method (BARD) (Hagerman, 1987). Specific leaf area (SLA) was determined on fresh leaves using a leaf-area meter (LiCor Area Meter Li-3100, Lincoln, NA, USA) and stem specific density (SSD) was determined on the terminal end of fresh stems in state of growth by dimensional method; both measurements were

Table 1
Forage availability (%), diet botanical composition (%) and diet selection by goats ($\hat{I}_i$) in summer and winter.

Species	Summer			Winter		
	Availability	Diet	$\hat{I}_i$	Availability	Diet	$\hat{I}_i$
Atriplex lampa	9.01	1.94 ± 0.4	−0.70	16.01	11.25 ± 1.8	−0.20
Bulnesia retama	2.33	0.06 ± 0.1	−1.00	4.11	0.67 ± 0.7	−0.90
Capparis atamisquea	1.76	7.20 ± 1.0	0.37	5.74	9.70 ± 2.5	0.16
Geoffroea decorticans	2.08	1.80 ± 0.5	−0.30	11.04	13.88 ± 2.0	0.09
Lycium spp.	1.75	0.24 ± 0.1	−0.80	–	–	–
Mimosa ephedroides	8.40	7.05 ± 1.4	−0.20	4.05	31.00 ± 2.2	0.76
Prosopis flexuosa	8.70	2.25 ± 0.5	−0.70	11.18	2.59 ± 0.8	−0.70
Tricomaria usillo	30.16	54.87 ± 2.5	0.46	32.19	28.62 ± 2.9	−0.20
Ximenia americana	0.24	1.43 ± 0.7	0.00	–	–	–
Total shrubs and trees	64.43	76.84 ± 2.1[a]		84.32	97.71 ± 1.84[b]	
Aristida mendocina	8.71	2.23 ± 0.4	−0.70	6.58	0.32 ± 0.2	−0.90
Panicun urvilleanum	20.01	13.64 ± 1.5	−0.50	1.00	0.25 ± 0.1	−0.80
Pappophorum caespitosum	2.50	1.15 ± 0.2	−0.20	1.89	0.25 ± 0.1	−0.80
Setaria leucophila	1.45	3.71 ± 0.5	0.36	2.88	0.73 ± 0.2	−0.70
Trichloris crinita	2.90	2.36 ± 0.4	−0.30	3.33	0.33 ± 0.1	−0.90
Total grasses	35.57	23.09 ± 2.0[a]		15.68	1.88 ± 0.5[b]	

Values are means ± SD ($n = 12$). Values in the same row with different letters differ significantly ($p < 0.05$). Empty cells indicate that plant species were not utilized by goats.
$\hat{I}_i$, Ivlev's electivity index.

made according to Cornelissen et al. (2003) on plant samples obtained in summer.

2.7. Statistical analysis

Data on forage species cover and percentage of plant species in the diet were arcsine-root transformed to normalize the distribution (Steel and Torrie, 1980). One-way ANOVA and Tukey's multiple comparison tests were used to detect differences between seasons. The sampling unit was the individual goat ($n = 12$) and seasons were considered factors. Spearman's rank correlation test was used to determine the relationship between seasonal forage availability and relative frequency of species occurrence in the diet. Principal component analysis (PCA) was performed to explain chemical variability in forage species and to describe the relationship between forage traits analyzed (Willems, 2002; Jayanegara et al., 2011). Only the first two principal components (PC1, PC2) were plotted, since they represented the majority of total variation. All variables were standardized with mean zero and variance one prior to PCA. In the experiment with grazing goats, for identifying which foliar traits best explained seasonal variation in $\hat{I}$, we employed generalized linear models (GLM) with Gaussian family distribution and logit link function (Crawley, 2007). Models were evaluated with information-theoretic procedures (Burnham and Anderson, 2002). As models including multiple individual foliar traits can be confounded if foliar traits are intercorrelated, before fitting the GLM we used PCA, variance inflation factors (VIF) and pairwise scatterplots to assess collinearity (Quinn and Keough, 2002). The explanatory variables tested in both seasons were: CP, OMD, NDF, ADF, lignin, cellulose; PT, TT, CT and BARD and, only in summer, SSD and SLA. We assumed a normal error distribution and homogeneity of variance for all models, which were confirmed by graphical methods (Quinn and Keough, 2002; Zuur et al., 2009). We considered models with all possible combinations of predictor variables and we used Akaike's information criterion corrected for small sample size (AIC$_c$) and Akaike's weight (w_i) to identify which models were best supported by the data (Burnham et al., 2011). The best model has the smallest AIC$_c$ and models within two ΔAIC$_c$ units of the best model are considered to have 'substantial support' (Burnham and Anderson, 2002). We evaluated the support for predictor variables summing w_i across all models that contained the parameter being considered and calculating 95% confidence interval limits (CL) of parameter estimates (Burnham and Anderson, 2002). In the feeding trial, differences in preference were tested on the basis of χ^2 critical value according to Jansen et al. (2007). Kappa index was classified as suggested by Monserud and Leemans (1992) and significant differences between index values were calculated following Jansen et al. (2007). Data were analyzed using InfoStat statistical software (InfoStat, 2012).

3. Results and discussion

3.1. Forage availability

Forage availability (expressed as percentage of forage cover) in the dry season was 42%, with over 80% represented by shrubs and trees. In summer, availability increased significantly to 59% ($p < 0.05$), the proportions of functional groups of plants were not maintained, with shrubs and trees contributing 58% and grass contributing 42%. Availability of each species was variable depending on the season (Table 1). In both seasons at least 10 species were available for consumption by the goats (species with availability less than 2% were considered negligible). *T. usillo* was the dominant species in both sampling periods and, among grasses, there was a high percentage of *P. urvilleanum* in summer.

3.2. Diet analysis

The botanical composition of the diet had a higher ($p < 0.001$) participation of woody species in relation to grass species in summer and winter (Table 1). Also, in summer, grass species constituted over 30% of the diet while in winter they only represented 2% of the diet (Table 1). The high participation of grasses according to their greater availability in the field would reflect the plasticity of the feeding behavior of goats in response to changes in foraging conditions (Dziba et al., 2003). This supports hypothesis 1 that goats display opportunistic feeding behavior, rather than being a typical browser or grazer. Moreover, a total of 14 and 12 species were recorded in goat diets in summer and winter, respectively. However, the proportion of some forage species was considered negligible (less than 2%) while other forage plants formed the bulk of the diet (more than 70%): *T. usillo* (55%), *P. urvilleanum* (13%) and *M. ephedroides* (7%) in summer and *M. ephedroides* (31%),

Table 2
Diet botanical composition (%) expressed as forage species preferred, indifferent and avoided.

Forage species	Diet	
	Summer	Winter
Preferred	$66.46 \pm 1.74^{a*}$	45.02 ± 2.82^{a}
Indifferent	$23.01 \pm 1.84^{b*}$	49.66 ± 3.56^{a}
Avoided	$10.45 \pm 0.76^{c*}$	3.55 ± 1.02^{b}

Values are means $\pm$ SD ($n = 12$). Values in the same row with different letters differ significantly ($p < 0.05$). Values in the same column with (*) differ significantly ($p < 0.05$).

T. usillo (29%) and *G. decorticans* (14%) in winter. The seasonal variation in diet composition was also put in evidence in studies conducted with Creole goats on our study site (Allegretti et al., 2012), with cattle in mid-west of Argentina (Guevara et al., 1996) and with other domestic ruminants, *Lama* spp., in Puna of Peru and Chile (Virgilio et al., 2003; Castellaro et al., 2004).

In both seasons, goats mainly consumed the terminal ends of stems (stems with leaves and/or leafless) in state of growth (growing shoots) of woody species and leaves and inflorescences of herbaceous species. These observations were consistent with results obtained in grazing goats by Allegretti et al. (2012) in the same study area. Similarly, Graham and Wilson (1980) consider that herbivores frequently eat growing shoots or young leaves rather than mature material, while stems that have undergone secondary growth are avoided. Furthermore, in the dry season, the animals consumed leaf litter from the deciduous trees *G. decorticans* and *P. flexuosa.* This behavior was also observed in goats grazing native forage in Brazil (Pfister and Malechek, 1986) and Argentina (Allegretti et al., 2012).

3.3. Specific selectivity

On the basis of the estimated values for $\hat{I}$, the botanical composition of the diet in each season was expressed in terms of: Preferred species, indifferent species and avoided species (Table 2). In summer, goats consumed diets with a higher proportion ($p < 0.001$) of preferred species (66%), whereas in winter the percentage of preferred species (45%) and indifferent species (50%) showed no significant differences ($p > 0.05$) (Table 2). Following this approach, but in relation to seasonal variation in diet selection, preferred species had more ($p < 0.001$) participation in the summer diet (66%) than in the winter diet (45%). Moreover, considering only the preferred species in each season, the highest proportions were represented by *T. usillo* (69%) in summer and by *M. ephedroides* (88%) in winter. Significant differences ($p < 0.001$) were also observed between the percentage of avoided species in summer and winter diets, 10% and 4% respectively. In summer, more than 60% of avoided species were represented by herbaceous species. This reinforces the concept of plasticity in the feeding behavior displayed by the goats, which increased the intake of herbaceous species according to their greater availability in the field.

From the above, it is noteworthy that nearly 50% of the winter diet was composed of forage species whose proportions reflect their availability in the field (indifferent species), while over 60% of the forage species in the summer diet were in proportions that exceeded their availability in the field (preferred species). In other words and, in accordance with the prediction of hypothesis 1, goats were more selective in the wet than the dry season. The observed relationship between diet and availability supported these observations, since in winter the botanical composition of the diet was positively and significantly correlated with availability ($r_s = 0.65$; $p < 0.05$), whereas in summer, the correlation between proportions of food items in the diet and their availability in the field was positive but not significant ($r_s = 0.45$; $p > 0.05$). These results support the observations of other authors (Dziba et al., 2003; Allegretti et al., 2012), who suggested that food availability may be a determinant of diet botanical composition when the resource is scarce.

3.4. Chemical and morphological variability of forage species

All chemical variables studied are showed in Table 3. These variables remained relatively constant between the two sampling periods. The effect of season on the chemical traits of plants was not consistent in all species and was only associated with some of the variables analyzed. This could be related to the fact that in both sampling periods, samples were composed by morphological parts of the plants consumed by goats; in general, terminal ends of stems, in a state of growth or what we agree to call growing shoots. Based on these observations, the description of the chemical variability of forage species presented below was performed considering a data set consisting of all values of chemical variables obtained for each species across both seasons. *T. usillo* and *M. ephedroides* were considered tanniniferous forage, not only because of the high content of phenolic compounds but also due to their elevated values of BARD (Table 3). The criterion used to classify these forage species as tanniniferous was based on the assertions of other authors (Mendes et al., 2006; Makkar, 2010).

As a result of the PCA, which only included the chemical traits of forage species; over 80% of the total variation in forage was explained by the first two principal components, 54% and 31% respectively (Fig. 1). PC1 was mainly related to fluctuations in the fibrous component, in particular cellulose, ADF and NDF, whereas the second component would be explained mainly by the PSMs (PT, CT and BARD). The position of each variable in the biplot (Fig. 1) allowed demonstrating the relationship with the other variables (Jayanegara et al., 2011). Consequently, OMD and CP were clustered and oriented in a direction opposite to the group of variables that described the fibrous component of the forage species (NDF, ADF and cellulose), while the variables characterizing the PSMs (PT, CT and BARD) were also clustered but their orientation in the biplot was not totally opposite to the other variables. The biplot clearly showed the negative effect of the fibrous component on OMD but less evident was the effect of tannins on OMD. However, the negative correlation coefficients that defined the relationship between both variables allowed visualizing more

Table 3

Chemical composition and morphological traits of morphological parts of forage species consumed by goats in summer and winter.

	Summer								Winter							
	AL	AM	CA	GD	ME	PF	PU	TU	AL	AM	CA	GD	ME	PF	PU	TU
OMD[a]	73.1	21.8	44.1	63.5	38.9	36.1	45.7	38.1	65.9	–	33.1	64.3	31.2	41.5	25.5	34.3
CP[a]	10.0	3.3	12.1	18.5	9.3	8.8	7.2	7.8	9.1	–	11.2	12.5	6.9	6.0	5.4	6.6
NDF[a]	25.1	66.7	53.1	44.6	50.5	61.3	60.0	54.7	25.6	–	59.5	25.9	55.5	46.3	72.3	52.9
ADF[a]	17.2	34.1	29.6	23.8	38.9	46.6	33.3	37.2	17.1	–	32.2	17.6	35.2	34.7	39.1	38.1
Lignin[a]	2.5	5.3	4.7	3.9	6.6	6.3	3.1	5.5	4.6	–	6.7	3.1	7.6	5.9	5.4	8.7
Cellulose[a]	14.2	28.5	24.3	18.8	32.0	40.8	29.5	33.3	13.7	–	26.8	14.7	28.4	25.1	34.5	30.3
ME Mcal kg^{-1}	2.6	0.8	1.6	2.3	1.4	1.3	1.6	1.3	2.4	–	1.2	2.3	1.1	1.5	0.9	1.2
TP[b]	0.2	0.1	0.7	4.4	7.1	1.5	0.3	8.4	0.5	0.1	0.6	4.7	8.4	1.8	0.3	5.7
TT[b]	0.1	0.1	0.3	2.1	3.4	0.9	0.3	2.7	0.2	0.1	0.1	2.1	6.2	0.8	0.0	3.7
CT[c]	0.1	0.0	2.4	9.1	25.9	2.6	0.0	47.7	0.3	0.5	1.1	2.4	26.8	0.8	0.6	54.2
BARD[d]	nd	nd	nd	nd	5.6	nd	nd	5.3	nd	nd	nd	nd	4.5	nd	nd	5.5
SLA m^2 kg^{-1}	5.4	–	6.5	4.9	23.5	8.8	–	9.1	–	–	–	–	–	–	–	–
SSD mg mm^{-3}	1.7	–	0.8	0.9	0.5	1.1	–	0.6	–	–	–	–	–	–	–	–

AL, *A. lampa*; AM, *A. mendocina*; CA, *C. atamisquea*; GD, *G. decorticans*; ME, *M. ephedroides*; PF, *P. flexuosa*; PU, *P. urvilleanum*; TU, *T. usillo*; OMD, organic matter digestibility; CP, crude protein; NDF, neutral detergent fiber; ADF, acid detergent fiber; ME, metabolic energy; TP, total phenols; TT, total tannins; CT, condensed tannins; BARD, biological activity measured as radial diffusion; SLA, specific leaf area; SSD, stem specific density; nd, not detected.

[a] Expressed as percentage on a dry matter basis.
[b] Expressed as tannic acid equivalent on a dry matter basis (%).
[c] Expressed as purified quebracho tannin equivalent on a dry matter basis (%).
[d] Measured as units of precipitation per g of plant relative to tannic acid.

clearly the antagonistic effect of tannins on OMD in summer ($r = -0.21$; $p < 0.05$) and winter ($r = -0.58$; $p < 0.001$).

When the morphological traits SLA and SSD were included in the PCA, the first two components allowed explaining 82% of summer variation in forage species (CP1: 63% and CP2: 19%). As shown in Fig. 1, the explanation of chemical variability of forage species was similar for both data sets, for which we focused only on the variability explained by SSD and SLA. Both variables contributed to a greater extent to the variation explained by PC1. Also, the opposite orientation of SSD and SLA in the biplot and the negative correlation between both variables indicated the inverse relationship between SSD and SLA. These results support the observations of other authors (Pickup et al., 2005; Ordoñez et al., 2010).

3.5. Which forage traits predict diet selection by goats?

3.5.1. Grazing goats: winter and summer

As noted above, the relationship between the botanical composition of goat's diets and forage availability in winter did not explain fully the selective behavior of the animals, since even in this season goats showed preference for certain forage plants (*M. ephedroides* was the most preferred species, followed by *C. atamisquea, G. decorticans, T. usillo, A. lampa* and *P. flexuosa*). When the data were sorted and pooled according to these browse species across the winter, the relationships between $\hat{I}$ and the chemical traits of forage species were obtained. In winter, the diet preference of goats was best explained by a model including CP, NDF and TP (Table 4). This model accounted for 36% of the observed variation in $\hat{I}$. The three variables were considered significant in predicting $\hat{I}$, because 0 was excluded from the estimated confidence intervals (Table 5). The coefficients for each variable in the model indicated that the preference of goats increased with these chemical traits (Table 5), but there were differences in the relative importance of the variables in the model, which

in decreasing order were: TP, CP and NDF. The positive relationship between $\hat{I}$ and CP in the dry season supports the hypothesis of nutrient intake maximization (Westoby, 1974) and agrees with some studies (Nyamangara and Ndlovu, 1995; Dziba et al., 2003), but not with others (Shipley et al., 1998; Jansen et al., 2007; Basha et al., 2012). Consistently with the prediction of hypothesis 2, the dietary choices of goats could not be explained in terms of minimization of PSMs ingestion, as tannins were positively related to $\hat{I}$ in the dry season. This was consistent with the results obtained by Allegretti et al. (2012) and Dziba et al. (2003), who considered the positive relationship between TP and diet selection as an inevitable consequence of

Table 4

Summary of model-selection results for models explaining variation in diet selection by goats in relation to chemical variables (CP, NDF and TP) of browse species in both seasons. Models are listed in decreasing order of importance. Models with $\Delta AIC_c \, i \leq 2$ have substantial support and are shown in bold.

Candidate models	k	AIC_c	ΔAIC_c	w_i
Winter				
CP NDF TP	**5**	**71.7**	**0.00**	**0.969**
CP NDF	4	78.6	6.92	0.031
TP	3	90.5	18.80	0.000
NDF TP	4	91.4	19.67	0.000
CP NDF	4	104.1	32.34	0.000
NDF	3	109.9	38.18	0.000
NDF	3	11.9	40.22	0.000
Summer				
NDF TP	**4**	**95.2**	**0.00**	**0.528**
CP NDF TP	**5**	**96.5**	**1.26**	**0.282**
NDF	3	99.5	4.34	0.060
TP	3	100.1	4.85	0.047
CP TP	4	100.3	5.08	0.042
CP NDF	4	100.3	5.12	0.041
CP	3	108.5	13.27	0.001

k = number of estimated parameters in the model. ΔAIC_c = difference in AIC_c between best model (models with smallest value of AIC_c) and model i. w_i = Akaike's weight, which indicates the weight of evidence in favor of model i.
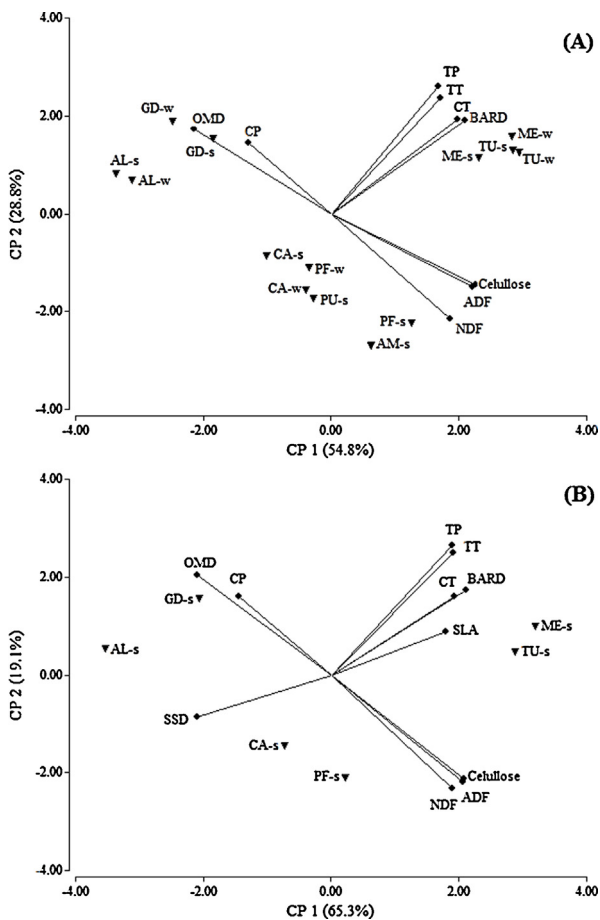
Fig. 1. Plot of the first two PC loading vectors, describing the relationship among chemical variables of plants in both seasons and the first two PC score vectors, describing the classification of forage species within the PC loading vectors (A). Plot of the first two PC loading vectors, describing the relationship among chemical and morphological variables of forage species in summer and the first two PC score vectors, describing the classification of forage species within the PC loading vectors (B). AL, *A. lampa*; AM, *A. mendocina*; CA, *C. atamisquea*; GD, *G. decorticans*; ME, *M. ephedroides*; PF, *P. flexuosa*; TU, *T. usillo*. -s and -w next to the forage species indicate season, summer and winter, respectively. OMD, organic matter digestibility; CP, crude protein; NDF, neutral detergent fiber; ADF, acid detergent fiber; TP, total phenols; TT, total tannins; CT, condensed tannins; BARD, biological activity measured as radial diffusion; SLA, specific leaf area; SSD, stem specific density. (●) Loading vectors; (▼) Score vectors.

Table 5
Parameter likelihoods, estimated parameter (±SE) and 95% confidence interval limits (CL) for chemical explanatory variables describing variation in diet selection in winter and summer. Explanatory variables with CL excluding zero are in bold.

Explanatory variable	Parameter likelihood	Estimated parameter	CL	
			Lower	Upper
Winter				
Intercept		−1.76 ± 0.29	−2.368	1.117
CP	**0.97**	**0.10 ± 0.02**	**0.059**	**0.142**
NDF	**1.00**	**0.01 ± 0.003**	**0.003**	**0.018**
TP	**1.00**	**0.11 ± 0.02**	**0.073**	**0.139**
Summer				
Intercept		−0.79 ± 0.31	−2.368	−1.117
CP	0.36	0.01 ± 0.01	−0.04	0.010
NDF	**0.90**	**0.01 ± 0.01**	**0.003**	**0.200**
TP	**0.91**	**0.04 ± 0.02**	**0.010**	**0.010**

Regarding the contents of the cell wall, specifically NDF, our results were consistent with Cerrillo et al. (2006), who reported higher NDF content in the diet of grazing goats in winter relative to goat's diet in spring. Furthermore, other studies also highlight the high content of other cell wall components (lignin, ADF) in the diet of grazing goats in winter (Ramirez et al., 1993). High fiber content in the winter diet could be due to higher consumption of woody species than other plants such as forbs or grasses. From the perspective of the functional behavioral response that underlies the selective behavior of herbivores, the positive relationship between fiber and diet selection emphasizes the need to produce large volumes of saliva buffer to achieve a greater ruminal pH in ruminants fed diets rich in tannins (Makkar, 2010). This favors ruminal fiber digestion and hence more energy available to the animal (Kumar and Vaithiyanathan, 1990; Weimer, 1996). Finally, herbivores may require an optimum density of fiber in their food to access cellular contents, as fiber provides a rigid material against which cells are pressed until its rupture during chewing (Vincent and Sibbing, 1992).

In summer, when the effect of availability on the botanical composition of goat's diets was positive but not significant, the relationship between $\hat{I}$ and chemical and morphological characteristics of the most preferred browse species (*T. usillo*, *C. atamisquea, M. ephedroides, G. decorticans, P. flexuosa* and *A. lampa)* were determined. Among the models in which only chemical variables were considered, two models had substantial support for explaining variation in the diet preferences of goats. The best model included NDF and TP as explanatory variables (Table 4) and accounted for 16% of the variation in $\hat{I}$. The second model included CP, NDF and TP and accounted for 14% of the variation in $\hat{I}$. The effect of the variables NDF and TP on diet selection by goats was significant in both models, while the effect of CP (second model) was not significant (Table 5). Among the significant variables, NDF had the highest relative importance in the model. In both seasons tannins and fiber had a positive effect on diet selection by goats. However, in summer, these variables only allowed accounting for 16% of the variation in $\hat{I}$. From the perspective of the small ecological scale at which the present study was framed, this could be attributed to the existence of other

nutrient intake optimization when food availability is low. Villalba et al. (2002) suggested that interactions between nutrients and PSMs may influence how herbivores mix their diets and use food resources, while PSMs ingestion may interfere with nutrient utilization, which could have effects on preference for energy and protein. Based on these statements, we interpret the positive relationship between CP and $\hat{I}$ as a behavioral strategy of goats to counteract the deleterious effects of tannins on OMD. In other studies conducted under controlled conditions, Villalba et al. (2002) observed that energy and protein supplementation increased the capacity of goats and sheep to consume tannins, and Papachristou et al. (2007) considered that high levels of protein in the diet of sheep probably neutralized the negative effects of tannins to bind proteins.

Table 6

Summary of model-selection results for models explaining variation in diet selection by goats in summer in relation to CP and SSD. Models are listed in decreasing order of importance. Models with $\Delta AIC_c \ i \leq 2$ have substantial support and are shown in bold.

Candidate models	k	AIC$_c$	ΔAIC_c	w_i
CP SSD	**4**	**74.3**	**0.00**	**0.557**
SSD	**3**	**74.8**	**0.46**	**0.443**
CP	3	108.5	34.17	0.000

k = number of estimated parameters in the model. ΔAIC_c = difference in AIC_c between best model (models with smallest value of AIC_c) and model i. w_i = Akaike's weight, which indicates the weight of evidence in favor of model i.

factors affecting food choices of grazing goats. Among these factors, other PSMs not measured in this paper could be considered (e.g. terpens, alkaloids, among others) (Pisani et al., 2001) and plant morphological traits that may affect the rate at which plant parts are removed by goats (Shipley et al., 1999).

When the morphological trait SSD was considered, the model containing CP and SSD had the most support for explaining the variation in $\hat{I}$ (Table 6). This model provided a better explanation for the diet selection behavior of goats than models containing only chemical traits since it accounted for 37% of the variation in $\hat{I}$. On the basis of the coefficients and estimated confidence intervals for both variables, the negative and significant effect of SSD on diet selection was put in evidence, as well as the positive but not significant relationship between CP and $\hat{I}$ (Table 7). This supported hypothesis 3 and was consistent with Spalinger et al. (1985), who suggest that food selection by ruminants could be better explained in terms of the mechanical features of food than in terms of its chemical features. Moreover, if we consider that high stem density is related to high toughness and high breaking strength (Lucas et al., 2000; Hacke et al., 2001), the negative relationship between $\hat{I}$ and SSD could be interpreted as a behavioral response of goats to optimize nutrient intake rate (Shipley et al., 1999; Illius et al., 1999). The negative relationship between SSD of *T. usillo, C. atamisquea* and *M. ephedroides* and their respective bite and intake rates sustained this hypothesis (unpublished data).

Considering that indices of diet selection are a simplification of a complex process (Hanley, 1987), we attempted to assess the robustness of results obtained in the field study in summer using a cafeteria-style trial.

Table 7

Parameter likelihoods, estimated parameter and 95% confidence interval limits (CL) for chemical and morphological explanatory variables describing variation in $\hat{I}$ in summer. Explanatory variables with CL excluding zero are in bold.

Explanatory variable	Parameter likelihood	Estimated parameter	CL Lower	CL Upper
Intercept		0.66 ± 0.17	0.210	0.920
CP	0.56	0.02 ± 0.01	−0.040	0.050
SSD	**1.00**	**−0.71 ± 0.10**	**−0.940**	**−0.510**

Table 8

Level of agreement between predictions and observations (K_{hat}) for the hypotheses based on CP maximization, TP minimization and SSD minimization.

Hypothesis	Level of agreement		
	K_{hat}	Varianza	Fit[a]
CP maximization	0.02	<0.001	Very poor
TP minimization	0.13	0.004	Poor
SSD minimization	0.51	0.008	Fair-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). p-Values of the pair wise multi comparison test between the K_{hat} values for the different hypotheses were all significant (<0.001).

3.5.2. Feeding trial: summer

The number of trials where there was no preference was significantly lower ($\chi^2 = 20.25$; d.f. = 3; $p < 0.001$) than expected under independence, indicating that goats selected among the offered species. Tanniniferous shrubs, *T. usillo* and *M. ephedroides* were preferred by goats ($\chi^2 = 30.37$; d.f. = 3; $p < 0.001$ and $\chi^2 = 24$; d.f. = 3; $p < 0.001$, respectively) while *C. atamisquea* was avoided ($\chi^2 = 24.0$; d.f. = 3; $p < 0.001$). In feeding trials where the combination ME + TU was offered there was no preference for either species ($\chi^2 = 2.27$; d.f. = 1; $p = 0.132$ and $\chi^2 = 1.45$; d.f. = 1; $p = 0.228$, respectively), which could be related to the chemical and morphological similarity between these forage plants. Considering the negligible content of tannins and the high levels of CP in *C. atamisquea* in relation to *T. usillo* and *M. ephedroides*, neither tannin minimization nor nutrient maximization explains the observed preferences. The high content of flavonoid aglycones in *C. atamisquea* (Pelotto and Del Pero Martinez, 1998) and the caustic smell and taste of this shrub (Ruiz Leal, 1975) could be alternative hypotheses to explain why this specie was consumed in free ranging conditions and avoided in feeding trials, where the deterrent effect of these compounds could be potentiated due to increased exposure. The preference for tanniniferous forage species, whose tannin concentration is above the limits deemed harmful to the animal, could be explained in terms of interactions between these PSMs and other plant metabolites. The possible effects of tannins on digestion and absorption of nutrients have been discussed in the previous section. Maximization of the nutrient intake rate by consuming forage higher SSD was the hypothesis that allowed finding the best agreement between observed and expected preferences in feeding trials (Table 8).

4. Conclusion

Our results provide clear evidence of the dynamism and adaptability of grazing behavior of goats, as these animals modified their feeding behavior in response to variable foraging conditions (food availability and physicochemical traits of forage), but maintained strong preferences for certain morphological parts of the tanniniferous forage species *M. ephedroides* and *T. usillo*. The ability to select a mixed diet was not considered a random process but, rather, we conclude that goats "actively selected" the plant parts

and species they consumed. Interpretation of the dietary decisions by goats in terms of intake rate optimization and supplementation with nutrients and secondary compounds, rather than the isolated effects of nutrient intake maximization or tannin intake minimization, would better explain the diet selection of goats grazing in rangelands.

Conflict of interest statement

Authors don't have any conflict of interest.

Acknowledgments

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