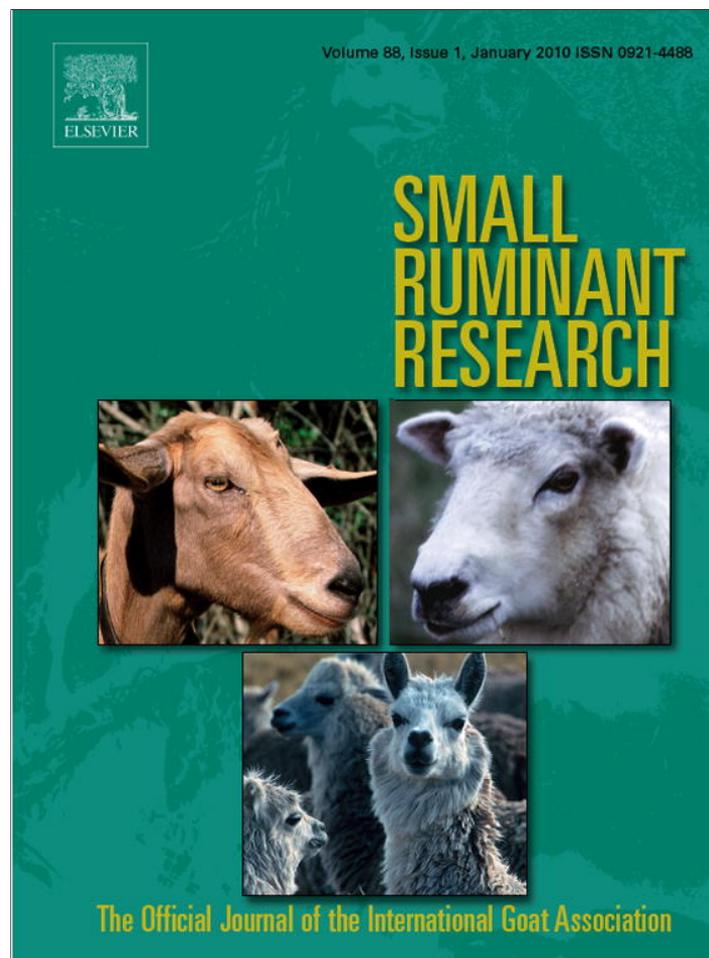


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journal homepage: www.elsevier.com/locate/smallrumresForaging ecology of Vicuña, *Vicugna vicugna*, in dry Puna of ArgentinaMariela Borgnia^{a,*}, Bibiana L. Vilá^b, Marcelo H. Cassini^c^a GEMA Group, Basic Sciences Department, National University of Luján (UNLu). Cc221, (B6700ZBA) Luján, Buenos Aires, Argentina^b VICAM Group, CONICET, Social Sciences Department, UNLu. Cc221, (B6700ZBA) Luján, Buenos Aires, Argentina^c GEMA Group, PROFAUNA Organization, CONICET, Basic Sciences Department, UNLu. Cc221, (B6700ZBA) Luján, Buenos Aires, Argentina

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ABSTRACT

Vicuña, *Vicugna vicugna*, is one of the few large native herbivores of South American and it is considered a keystone resource for the Andean Region. We studied foraging ecology of free ranging vicuñas at Laguna Blanca MAB-UNESCO Biosphere Reserve (Catamarca, Argentina), within dry Puna environment. Vicuñas showed a stable diet throughout the year, with marked differences at spatial scale. Diet of vicuñas included vegetation from all habitats, all vegetation strata and all functional groups of plants, suggesting that vicuñas can use a large range of plant species that are distributed in almost all portions of their range (they used 39 of 75 available plant species), behaving as a generalist ungulate. Vicuñas consumed large proportion of grasses (59–72%) and shrubs represented 16–19% of vicuña overall diet, reaching 45% at local sites, so we proposed that in this puna ecosystem vicuñas do not behave as strict grazers. Although vicuñas showed high diet plasticity, only two grasses, *Panicum chloroleucum* and *Distichlis* spp. represented nearly 50% of the diet. In relation to photosynthesis pathways of the plants, C₄ grasses contributed higher to proportions in diet than C₃ grasses. Vicuñas showed a selectivity foraging behaviour by consuming swamp forages, low and medium vegetation strata, and a few plant species in more proportion to their availability. Vicuñas did not eat plant species with more overall nutritional quality in higher proportion than species with less nutritional contents. However, the consumption of steppe grasses was in direct proportion to its crude protein content. This work brings a broad description of the foraging ecology of southern subspecies of vicuña, *V. v. vicugna*, by researching botanical composition and nutritional quality of the diet. These features of diet of vicuñas can be considered as part of its wide range of feeding responses to live in the poor environment of altiplano.

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1. Introduction

Vicuñas are one of the few large native herbivores of the South American arid environment (Franklin, 1983) and it is a 'Near Threatened' species (IUCN, 2001). Their fleece is one of the finest fibres in the world and it is considered a keystone resource for inhabitants of the Andean

region of Latin America (Laker and Gordon, 2006). Vicuñas live in the high Andean deserts called the 'altiplano' of four countries: Argentina, Chile, Bolivia and Perú. The altiplano is a fragile environment with rigorous and fluctuated climatic conditions and low and variable abundance and quality of food. It's divided in two ecosystems: 'altoandino' (over 4300 m.a.s.l.) and 'puna' (from 3000 to 4300 m.a.s.l.) (Cabrera, 1957).

Studies on foraging ecology ranging vicuñas are scarce, mainly conducted in small areas or short periods of time and most of diet information arises from the altoandino ecosystem of Peru (Koford, 1957; Franklin, 1982; Ménard, 1984), more humid than the Argentinean systems.

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The objective of this study was to investigate the foraging ecology of free ranging vicuñas in a Puna ecosystem of Argentina in terms of intensity and distribution of foraging activity, taxonomic composition of the diet, availability and chemical composition of vegetation, food selection, and diet diversity in relation to seasonal variations. We tested the following hypotheses:

- (1) Vicuñas (like the other members of the Camelidae family) have physiologic adaptations to consume the poor, ligneous and fibrous vegetation of the desert (Vallenas, 1991; Sponheimer et al., 2003): (i) a long time in which food is retained in the rumen (San Martín and Bryant, 1989), (ii) high concentration of microorganism in rumen (Jouany, 2000), (iii) high nitrogen recycling efficiency, and (iv) high concentration of volatile fat acids (López et al., 1998). If vicuñas show all these adaptations for eating desert vegetation, it is expected they will be able to consume a large range of Puna plant species than exotic ungulates; therefore they will be generalists, rather than specialists' herbivores.
- (2) Herbivore ungulates have been classically divided according to the functional group of plants they consumed, such as grazers and browsers (Hofmann and Stewart, 1972; Langer, 1988; Bodmer, 1990; Gagnon and Chew, 2000). Vicuñas have been classified as 'strict grass feeder' (Koford, 1957; Franklin, 1982; Feranec, 2003) in wet puna. We analysed if vicuñas are also strict grazers in dry puna.
- (3) Herbivores can eat plants in proportion to its availability in the environment or show food selectivity (Manly et al., 1991), by selecting some plants (consuming them in greater proportion to its availability) and avoiding other plants (consuming them in lower proportion to its availability). We expect vicuñas show some level of food selectivity.
- (4) Vicuñas have a prehensile split upper lip, and open-rooted, continuously growing incisors that allow them to feed from the lowest vegetation stratum. Franklin (1982) and Cajal (1989) confirmed that vicuñas graze mainly on forbs and perennial grasses close to the ground. So we expected that vicuñas eat from the low stratum.
- (5) Plants have different CO₂ fixation pathways (C₃, C₄, CAM), showing different anatomical, biochemical, physiological and ecological characteristics (Cavagnaro, 1988). About 85% of the world's plants are C₃ and there are a 10% of C₄ plants. The third photosynthesis way, CAM or crassulacean acid metabolism, is used by a small fraction of terrestrial plants, as succulents; C₄ and CAM pathways are both adaptations to arid conditions because they result in better water use efficiency. Many herbivores have a diet based on C₃ plants (Caswell et al., 1973; Erhleringer et al., 1997; Squeo and Erhleringer, 2004) because C₄ grasses tend to have lower nitrogen and higher cell wall concentrations than their C₃ counterparts, and they concentrate protein in highly vascularised bundle sheath cells, which are difficult to digest (review by Sponheimer et al., 2003). Under these considerations, vicuñas were expected to eat most C₃ plants.

- (6) Like other arid regions of the world, the Puna region showed marked seasonality in rainfall that affects plant community composition and also nutritional values (San Martín, 1996). Ungulates living in this type of environment frequently respond to these climatic changes, showing seasonal variations in their diets (Marshall et al., 2004; Ezcurra et al., 2006; Jacques et al., 2006). We expected that vicuñas also express different diet composition between seasons.
- (7) Food quality can be tested using indicators like crude protein of plants that correlates positively with digestible protein (Robbins, 1983; Lesage et al., 2000) or cellular wall carbohydrates as fibre and lignin that are generally negative correlated with digestibility and nutritional value of food (Robbins, 1983). Several ungulates show preference for vegetation with high nutritional crude protein and low cellular wall carbohydrates (Field, 1975; Robbins, 1983; Murray and Brown, 1993; Henley and Ward, 2006). This phenomenon has not been studied in free ranging vicuñas, so we tested if vicuñas select plants with high nutritional quality.

In recent years, several management projects in Peru, Chile and Argentina were initiated (Lichtenstein and Vilá, 2003). The information provided in this paper can serve as a baseline to be included in a successful planning of sustainable practices in the wild population management.

2. Materials and methods

2.1. Study area

The study was conducted in an area of 25 500 ha within the transition zone of Laguna Blanca Biosphere Reserve (from 3200 to 5500 m.a.s.l.), located in the NW region of Catamarca province, Argentina (26°30'S y 66°40'W) (Fig. 1). Low areas have lagoons (the largest one is Laguna Blanca with an area of 3450 ha). The climate is dry and cool with great daily fluctuations in temperature and with scarce rainfall (100–250 mm annually) that occurs between December and March. Soils are stony, sandy or salty (SAR, 1991). Laguna Blanca is part of the dry puna, limiting with salt puna (Troll, 1958; Baied and Wheeler, 1993; Delfino, 2001).

Borgnia et al. (2006a) have described in detail vegetation, habitat types and landscapes of the study area, with seventy-five plants species being listed.

Vegetation is mainly a xerophile steppe with a large proportion of bare ground. There are two main types of habitat: 'steppes', which can be divided in grass, shrub and mixed steppes, and 'swamp' habitats, which include 'vegas' (swamp areas with high vegetation cover also called 'bofedales'), and 'salinas' (small areas with surface salt, crawling or bunch grasses and high vegetation cover).

Borgnia et al. (2006b) estimated total number of vicuñas in the study area as 1500 individuals. Vicuñas shared the habitat with local people and their pastoral activities (Rabinovich et al., 1991). In Laguna Blanca Reserve, vicuñas are legally protected although there are records of poaching in the area (Barbarán, 2002).

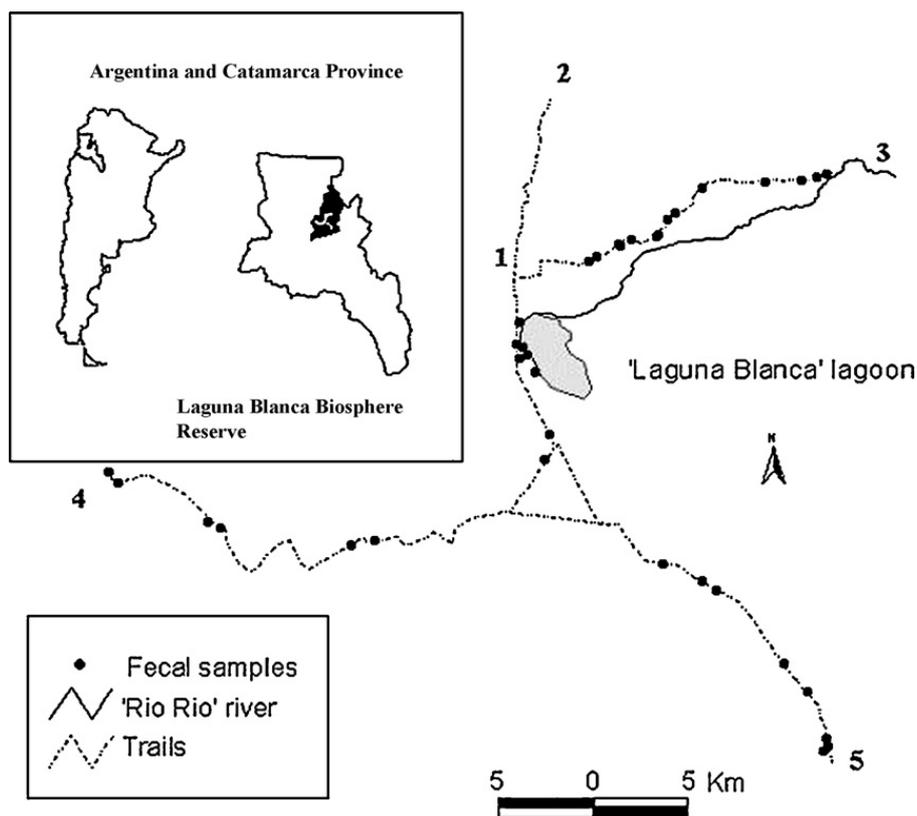


Fig. 1. Study area details. 1. 'Laguna Blanca' village. 2. 'Corral Blanco' village. 3. 'Rio Rio' Ranch of. 4. 'Guzman' ranch. 5. Randolph's Hill.

2.2. Fieldwork

Four trails were surveyed (Fig. 1): (1) from Laguna Blanca village to Rio Rio settlement (23 km), (2) from Laguna Blanca village to Corral Blanco village (11 km), (3) from Laguna Blanca village to Randolph Hill (37 km) and (4) from Laguna Blanca village to Guzmán settlement (47 km). At 51 sites randomly distributed along these trails, the vegetation was sampled and faeces were collected. At perpendicular distances it was also sampled within a range of 1 km. In each site, faeces were collected from three dung piles recently used (with fresh pellets). Three to five samples of all plant species present in the surroundings (for chemical analysis and for building an epidermis reference collection) were also collected. Faeces samples were stored at -5°C until analysis. Plants were cleaned, dried at 60°C and stored in paper bags until analysis. In the same sites (in October 2002 and March 2003), a line-intercept method (Kent and Coker, 1992) was applied (for estimations of vegetation availability), as follows: two 25 m length transects were randomly located in each site and the length and height of plant species touching the line were recorded. Twelve sites were sampled in May 2002, 17 sites in October 2002, 16 sites in March 2003 and 6 sites in September 2003. March 2003 was the wettest studied period (finishing wet season) and the other months corresponded to dry season, with September 2003 being the driest (CIEDECAT).

2.3. Laboratory analyses

Botanical composition of diet was determined by micro-histological techniques (Holechek, 1982). The sampled unit

for diet analysis was a mixed group of 100 fresh faeces of three dung piles from each site (Hansen and Lucich, 1978). Faeces were cleaned, ground, sieved and treated with hot NaOH 5% (Holechek, 1982; Arriaga, 1986). Five slides per sample were prepared and 20 fields per slide were analysed at $100\times$ level of magnification. Relative frequencies of food items in each sample were quantified (Holechek and Gross, 1982). The identification of plant fragments required the comparison with an epidermis reference collection (D'ambrogio de Argueso, 1986).

Nutritional quality of vegetation was analysed by determinations of four chemical components (Goering and Van Soest, 1970; AOAC, 1980): total nitrogen, fibre, lignin, and ash content. Quality of vegetation was analysed from those aerial parts of plants that are usually consumed by animals (leaves and sheath in the case of grasses or grasslikes, leaves and small thin branches with leaves in the case of some xerophilous shrubs). Samples were cleaned, grinded and screened prior to analysis. Total nitrogen content was determined with semi-micro Kjeldahl analyser (TEKATOR). Neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and acid-detergent lignin (ADL) was determined with the detergent method using an ANKOM fibre analyser. Ash content was determined by incinerating 1–2 g of plant tissue for 4 h at 500°C .

2.4. Data analysis

Diet composition was analyzed in relation to five vegetation characteristics: (1) distribution of plants at a landscape scale, i.e., plants of steppe areas or plants of swamp areas; (2) stratum: low (plants until 10 cm high),

medium (plants between 10 and 50 cm high) and high (plants with more than 50 cm); (3) functional groups: shrubs (or sub-shrubs), grasses, grasslikes (which include juncaceous and cyperaceous plants), and forbs (or herbaceous dicots); (4) taxonomy: plant species or genera, and (5) by the photosynthesis pathway: C₃, C₄ and CAM plants. An ANOVA with a previous arcsine transformation data using mean percentages of consumption for each category ($n=4$, for the four sample periods) were performed to investigate the occurrence of significant differences between habitat types, strata and functional groups.

Habitat availability was estimated like a mean percentage of vegetation cover from all sampled sites, for each vegetation categories (habitat plant, stratum, functional groups, and individual species). Diet selection was analysed considering vegetation cover as an estimation of food availability, according to Jacob's modification of Ivlev's selectivity index, $S = (r_i - p_i) / (r_i + p_i - 2r_i p_i)$, where r_i and p_i are the proportion of use and availability, respectively. S ranges from 0.5 to 1 for strong selection, from 0.1 to 0.49 for weak selection, from -0.09 to 0.09 for indifference, from -0.1 to -0.49 for weak avoidance, and from -0.5 to -1.0 for strong avoidance (Fraser and Gordon, 1997).

Diet similarity between pair of seasons was evaluated using Spearman Correlations (R_s) for plant species proportion in diets, and Sorensen's index, $S = 2c/a + b$, where c is the number of species used in common, a is the number of species used only in one season and b is the number of species used only in the other season. Similarity indexes (S) and correlation analyses were applied to the comparison between all six possible pairs of seasons. Diet diversity for each sample period was also calculated using the Shannon's index, $H' = -\sum (\ln p_i * p_i)$. Diet evenness (E) was calculated like H/H' , where H' is the maximal value of H for each sample period: $H' = \ln(s)$, where s is the number of food items ate by vicuñas (Krebs, 1989).

Data on nitrogen, fibre, lignin and ash contents are presented as total dry matter percentages. Crude protein was calculated by multiplying nitrogen content by 6.25 (Robbins, 1983). Nutritional contents were averaged among plant species and among sample periods, and they were analysed using ANOVA with previous arcsine transformation data, and Tukey HSD test for unequal sample size, for multiple comparisons. The relationship between consumption and quality (crude protein content) was evaluated by regression analyses for each plant groups: steppe grasses, steppe shrubs, and swamp grasses.

3. Results

3.1. Diversity, stability and composition of diet

Ninety-five percent of plant fragments found in faeces were identifiable at the genus level. Vicuñas faeces samples contained 39 of the 75 plant species available in the study area (Table 1). The composition of diet was similar along the study period: Sorensen indices were high ($S \geq 0.78$), and Spearman correlations were significant ($R_s \geq 0.5$, $P < 0.05$) in all comparisons. Diversity and evenness of overall diet composition were similar along the research period ($H = 1.7 \pm 0.2$ and $E = 0.7 \pm 0.1$), with the

lowest values in March 2003. Diet varied substantially in diversity at local scale ($0.8 < H < 2.4$, and $0.5 < E < 0.9$, $n = 53$).

Only two plant species, both grasses (*Panicum chloroleucum* and *Distichlis* spp.), were found higher than 10% of the diet, and they represented together 37–55% of the diet. Only one (*Amphiscirpus nevadensis*) from five grasslike species was consumed more than 10% in March 2003. There were more plants that contributed largely at local scale (Table 1): four grasses (*Stipa* spp., *Festuca argentinensis*, *Festuca* spp., and *Deyeuxia* sp.), five shrubs (*Acantholippia salsoloides*, *Adesmia horrida*, *Junellia seriphioides*, *Frankenia triandra*, and *Atriplex* sp.), two grasslikes (*Triglochin palustris* and one unidentified ciperaceae), and one forb (*Sarcocornia pulvinata*).

Table 2 summarises diet of vicuña in terms of habitat, stratum and functional group of plants. Consumptions of plants species from steppe and swamp habitats were similar. Vicuñas ate mainly plants from low and medium strata and less on plants from high vegetation stratum. There were also significant differences in the use of different functional groups. Grasses were the most important functional group in the diet, followed by shrubs and grasslikes, which were eaten in similar proportions (with local variations); forbs were consumed in very low proportions.

Considering the metabolic photosynthesis pathway of plants (Table 1), C₄ grasses contributed higher to diet ($46.0 \pm 7.5\%$) than C₃ grasses ($20.5 \pm 6.8\%$) all year round. There was only one C₄ shrub in vicuña's diet (*Atriplex* sp.), six species of C₃ shrubs and one genera of CAM (*Maihueniopsis*).

3.2. Diet quality

Nitrogen, fibre, lignin, and ash contents in vegetation are summarised in Table 1 and Table 2. Steppe plant species showed non-significant differences in chemical composition with species from swamp areas. Plants species of low stratum had higher concentrations of ash than plants from high stratum. Crude protein content was higher for shrubs than for grasses. Neutral fibre content was less for shrubs than for grasses and grasslikes. Acid fibre content was higher for grasses than for shrubs. There was no significant difference in lignin and ash content among functional groups.

It was expected that vicuñas preferred plants with high concentration of crude protein and low concentrations of fibre and lignin. However, vicuñas did not eat in higher proportion from plant species with (1) more overall crude protein content than species with less crude protein content, neither with (2) low fibre or lignin content. The most consumed scrubs had moderate (*A. salsoloides*, *A. horrida*) or low (*J. seriphioides* and *F. triandra*) crude protein content. Other shrubs had higher crude protein content but vicuñas ate them in low proportion (*Fabiana* sp. and *Parastrephia* spp.) or ate none of them (*B. boliviensis* and *Senecio* spp.). The grasslikes with the highest crude protein content (e.a. *Eleocharis* sp.) were consumed in low amounts. The most important grasses in the diet, *P. chloroleucum* and *Distichlis* spp., had similar or less crude protein contents than other grasses that were consumed in low proportion.

Table 1
Percentages of consumption for each sample period and nutritional contents (means % dry matter between sample periods) of plant species in Laguna Blanca.

Plant Species	PP	FG ¹	HT ²	S ³	May 02	October 02	March 03	September 03	Crude protein	Neutral fibre ^a	Acid fibre	Lignin	Ash
<i>Acantholippia salsoloides</i>	–	S	St	H	6.7 (5.8)	2.2 (1.8)	2.5 (2.8)	2.7 (5.7)	9.3 (2.4)	55.7	42.4 (18.8)	15.9 (1.4)	8.58 (3.95)
<i>Adesmia horrida</i>	C3	S	St	M	1.7 (2.8)	0.5 (0.9)	7.9 (9.7)	0.0	7.0 (1.2)	47.5	37.5 (9.7)	19.6 (1.3)	6.18 (3.99)
<i>Adesmia</i> sp.	C3	S	St	M	t	0.00	t	0.0	–	–	–	–	–
<i>Amphiscirpus nevadensis</i>	–	GL	Sw	L	9.3 (6.9)	6.3 (7.1)	10.4 (11.9)	8.6 (14.1)	2.5 (–)	61.6	35.9	12.8	19.25
<i>Arenaria</i> spp.	–	F	Sw	L	t	0.00	t	0.0	12.6	–	28.4	15.8	–
<i>Aristida</i> sp.	C4	G	St	L	0.7 (1.8)	0.9 (1.4)	0.9 (2.1)	t	4.3	73.0	39.5	8.3	–
<i>Atriplex</i> spp.	C4	S	St	H	0.7 (1.4)	0.4 (1.7)	0.0	3.4 (6.1)	8.6 (3.0)	35.3	18.5 (0.4)	10.1 (0.6)	14.19 (11.55)
<i>Baccharis acaulis</i>	C3	F	Sw	L	0.6 (1.5)	0.1 (0.3)	0.1 (0.6)	0.2 (0.7)	3.8	41.5	30.1	15.4	–
<i>Baccharis boliviensis</i>	C3	S	St	H	0.00	t	0.0	t	9.0 (1.4)	–	23.6 (9.7)	15.2 (9.4)	17.57 (7.27)
<i>Baccharis incarum</i>	C3	S	St	M	0.2 (0.6)	0.00	0.2 (0.9)	0.0	6.0 (1.3)	–	32.8 (4.8)	26.7 (4.5)	26.77 (6.71)
<i>Chondrosium simplex</i>	C4	G	St	L	0.9 (1.4)	t	0.3 (0.6)	0.2 (0.5)	–	–	–	–	–
<i>Ciperaceae</i> unidentifly	–	GL	Sw	L	0.3 (0.6)	1.4 (5.0)	1.5 (4.2)	3.5 (9.2)	5.6	–	41.1	18.2	16.14
<i>Cortaderia rudiocula</i>	C3	G	Sw	H	0.3 (0.6)	0.4 (0.8)	0.4 (1.0)	t	2.4 (0.6)	82.3	46.6 (1.3)	12.3 (2.0)	6.31 (1.19)
<i>Deyouxia brevifolia</i>	C3	G	Sw	L	1.2 (1.5)	1.1 (2.3)	0.2 (0.5)	1.0 (1.5)	4.5 (1.7)	72.6	42.7 (2.9)	15.4 (0.8)	18.81 (1.61)
<i>Deyouxia cabreranae</i>	C3	G	St	H	0.6 (1.6)	1.0 (2.9)	0.2 (0.6)	0.00	3.4 (0.1)	–	49.4 (0.6)	15.5 (0.6)	12.54 (0.98)
<i>Deyouxia polygama</i>	C3	G	Sw	H	0.00	0.6 (2.5)	0.0	1.3 (3.3)	2.8 (0.7)	–	46.3 (1.6)	16.0 (6.6)	14.69
<i>Deyouxia</i> sp.	C3	G	Sw	H	6.9 (13.1)	3.4 (9.9)	1.0 (2.8)	4.5 (8.2)	–	–	–	–	–
<i>Distichlis</i> spp. (a)	C4	G	Sw	L	22.9 (20.3)	16.3 (15.9)	18.3 (17.7)	20.4 (11.1)	6.5 (2.2)	58.9	37.8 (2.9)	13.8 (4.6)	15.15 (6.58)
<i>Eleocharis</i> spp. (b)	C3	GL	Sw	L	1.2 (2.1)	0.8 (1.1)	3.3 (7.3)	1.0 (1.2)	9.9	68.7	39.9	16.9	–
<i>Ephedra breana</i>	C3	S	St	M	t	0.00	0.0	t	8.1 (3.7)	53.6	45.4 (6.3)	19.8 (3.8)	9.92 (2.28)
<i>Fabiana</i> spp. (c)	–	S	St	H	t	0.7 (1.19)	0.2 (0.5)	2.6 (4.4)	7.6 (1.2)	39.0	27.5 (2.8)	12.1 (1.3)	3.68 (0.15)
<i>Festuca argentinensis</i>	C3	G	Sw	H	3.7 (6.5)	8.9 (11.7)	0.7 (1.3)	9.4 (12.0)	2.7 (1.7)	67.6	51.0 (5.5)	10.3 (2.6)	11.57 (8.73)
<i>Festuca</i> spp. (d)	C3	G	St	H	2.2 (5.1)	3.3 (13.6)	2.8 (9.2)	0.0	3.3 (0.8)	–	52.3 (0.5)	19.1 (8.5)	20.10 (0.51)
<i>Frankenia triandra</i>	–	S	Sw	L	2.6 (5.3)	2.7 (5.6)	1.7 (3.5)	3.0 (2.6)	3.5 (1.7)	–	52.6 (16.0)	26.0 (5.3)	42.01 (24.09)
<i>Hordeum hallophyllum</i>	C3	G	Sw	L	0.3 (0.7)	0.3 (1.0)	0.2 (0.5)	0.0	–	–	–	–	–
<i>Juncus</i> spp. (e)	C3	GL	Sw	M	0.9 (2.2)	1.2 (2.3)	0.1 (0.2)	0.5 (0.6)	6.9 (3.0)	76.4	32.8 (3.6)	4.5 (1.7)	5.96 (2.03)
<i>Junellia seriphoides</i>	C3	S	St	M	3.5 (7.1)	8.0 (8.3)	1.1 (3.1)	6.0 (8.5)	5.4 (1.0)	47.1	37.7 (8.2)	17.6 (5.2)	12.82 (2.32)
<i>Lycium chañar</i>	–	S	St	H	0.2 (0.4)	0.1 (0.5)	0.1 (0.3)	0.0	18.2	–	–	–	–
<i>Maihueiopsis</i> spp. (f)	CAM	S	St	M	0.5 (1.0)	0.6 (0.9)	0.6 (1.2)	2.1 (3.4)	6.0	–	27.3	9.7	21.81
<i>Muhlenbergia peruviana</i>	C4	G	Sw	L	0.3 (0.6)	0.2 (0.4)	0.3 (0.9)	0.7 (1.2)	4.3 (1.8)	–	–	–	–
<i>Panicum chloroleucum</i>	C4	G	St	M	18.2 (20.2)	28.4 (27.0)	36.4 (25.0)	17.0 (16.0)	2.5 (0.9)	76.5	45.7 (12.3)	13.2 (9.7)	9.09 (6.01)
<i>Parastrephia</i> spp. (g)	–	S	Sw	H	0.5 (0.8)	1.3 (2.0)	0.1 (0.4)	0.7 (1.3)	8.0 (0.4)	32.9	23.8 (7.1)	14.0 (4.2)	6.16 (0.51)
<i>Sarcocornia pulvinata</i>	C3	F	Sw	L	0.9 (1.9)	1.2 (2.4)	0.9 (3.3)	5.3 (9.8)	–	–	–	–	–
<i>Senecio filaginoides</i>	–	S	St	M	0.0	0.0	0.0	0.0	12.8 (0.9)	19.9	21.4 (12.6)	11.8 (8.6)	13.68 (3.39)
<i>Senecio subulatus</i>	–	S	St	M	0.0	0.0	0.0	0.0	9.1 (1.0)	–	13.7	5.0	–
<i>Scirpus deserticola</i>	–	GL	Sw	L	0.0	0.1 (0.3)	0.0	0.0	–	–	–	–	–
<i>Sporobolus rigens</i>	C4	G	St	H	0.6 (2.2)	0.1 (0.5)	0.0	T	4.4 (1.3)	71.7	42.1 (0.9)	15.7 (0.2)	7.89 (0.55)
<i>Stipa</i> spp. (h)	C3	G	St	M	9.4 (14.2)	6.1 (15.3)	5.4 (15.4)	2.3 (4.5)	4.5 (0.6)	75.3 (0.3)	46.7 (3.0)	16.7 (3.0)	16.36 (5.65)
<i>Stipa</i> sp.	C3	G	Sw	M	0.2 (0.9)	0.7 (2.7)	0.0	1.8 (4.9)	2.9	–	–	–	6.38
<i>Triglochin palustris</i>	–	GL	Sw	L	0.8 (2.1)	0.5 (1.0)	2.0 (2.7)	1.0 (1.9)	4.7	–	–	–	–

Photosynthesis pathway (PP), Functional Group (FG), Habitat type (HT), Stratum (S); S: shrubs, G: grasses, GL: grasslikes, F: forbs; St: steppe, Sw: swamp; H: high, M: medium, L: low; (–): data no found; t, trace, consumed in proportion less 1% in all samples for that date. Standard deviations are shown between brackets.

^a NDF: data only from autumn 2002; (a) *D. humilis* and *D. spicata*, (b) principally *E. Albibracteata*, (c) principally *F. densa*, (d) *F. chrysophylla* and *F. orthophylla* (e) *J. articus* and *J. imbricatus*, (f) *M. glomerata*, (g) principally *P. Lucida*, (h) *S. frigida* and *S. vaginata*.

Table 2

Consumption (% in diet), cover (% in field), and nutritional contents (% of dry matter) of plant species that were grouped according to habitat types strata and functional groups.

	Consumed	Cover	Crude protein	Neutral fibre	Acid fibre	Lignin	Ash
Habitat type							
Steppe	48.8 (11.2)	84.9 (0.9)	6.9 (3.4)	55.8 (18.8)	35.6 (11.5)	14.8 (5.0)	13.4 (6.3)
Swamp	51.2 (8.9)	15.0 (0.9)	5.3 (2.8)	62.5 (16.1)	38.9 (9.6)	15.0 (4.5)	14.8 (10.4)
<i>t</i>	0.15	–	1.61	0.74	0.83	0.04	0.08
<i>P</i>	0.70	–	0.19	0.39	0.30	0.84	0.77
<i>n</i>	8	–	39	20	34	34	25
Height stratum							
High	18.7 (7.1) ^a	47.5 (11.3)	6.8 (4.3)	50.5 (22.0)	35.5 (14.3)	13.8 (3.5)	11.4 (5.0) ^a
Medium	40.7 (9.6) ^b	40.5 (9.3)	5.8 (2.0)	64.5 (14.3)	38.2 (7.5)	15.7 (6.1)	12.8 (7.4) ^{ab}
Low	40.6 (6.6) ^b	11.9 (2.0)	5.7 (3.0)	62.7 (11.9)	38.6 (6.8)	15.6 (4.8)	22.3 (11.2) ^b
<i>F</i>	10.12	–	0.26	1.42	0.41	0.50	4.12
<i>P</i>	0.0050	–	0.77	0.27	0.66	0.61	0.029
<i>n</i>	12	–	39	20	34	34	25
Functional group							
Shrubs	17.3 (2.7) ^b	55.4 (8.0)	8.4 (3.2) ^a	41.4 (11.9) ^a	30.4 (11.0) ^a	15.3 (6.0)	15.3 (10.8)
Grasses	66.7 (5.5) ^a	37.3 (8.1)	3.9 (1.4) ^b	72.5 (6.5) ^b	45.5 (5.1) ^b	14.9 (3.0)	12.6 (4.8)
Grasslikes	13.7 (2.9) ^b	7.0 (0.4)	5.9 (2.7) ^{ab}	68.9 (7.4) ^b	37.4 (3.8) ^{ab}	13.1 (6.1)	13.8 (6.9)
Forbs	2.4 (2.1) ^c	*	8.2 (6.2) ^{ab}	41.5	29.3 (1.2) ^{ab}	15.6 (0.3)	–
<i>F</i>	181.8	–	10.04	17.66	8.69	0.29	0.15
<i>P</i>	<0.000001	–	0.000060	0.00018	0.00025	0.83	0.86
<i>n</i>	16	–	39	20	34	34	25

All values are means between sample periods. Different letters mean significant differences ($P < 0.05$). Standard deviations are shown between brackets. *: no data.

Vicuñas consumed a higher proportion of steppe grasses when they showed more crude protein content than in seasons with less crude protein content ($r = 0.82$, $P < 0.01$, $n = 9$) (Fig. 2). This pattern was not observed in swamp grasses ($r = 0.18$; $n = 6$) and steppe shrubs ($r = 0.20$, $n = 9$).

3.3. Diet selection

Table 2 presents plant cover percentages according to functional group, habitat type and stratum. Plants of swamp areas were positively selected and plants of steppes were negative selected with the exception of steppe grasses (Fig. 3a). Swamp grasses and grasslikes were consumed in greater proportion to their availability, with a strong selection for the first group (Fig. 3a).

Comparisons by stratum (Fig. 3b) showed that plants of low stratum were always used in greater proportions

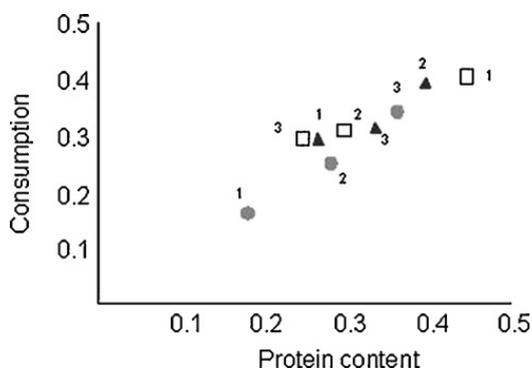


Fig. 2. The relationship between the proportion of grasses in the diet of vicuñas (plants with percentage of consumption higher than 1%) and the crude protein content of the grasses. Each point refers to proportion of protein content and consumption in one season refers to total values for each plant species. (1) May 2002; (2) October 2002; (3) March 2003. (●) *Panicum*, (□) *Stipa*, (▲) *Festuca*.

to their availability and, inversely, for plants of high stratum. Plants of medium stratum were positively selected in March and they were used proportionally to their availability in October.

Comparisons at the level of plant species and genera were conducted including those plant species that were consumed in higher proportion than 1%. *Panicum* sp., *Distichlis* spp. and *A. nevadensis* were selected in both samples periods (Ivlev index for October/March: 0.26/0.47, 0.73/0.76 and 0.58/0.72, respectively). *A. salsoides* was always used in lower proportion to its availability. Other plants had contrasting indices between periods: *A. horrida*

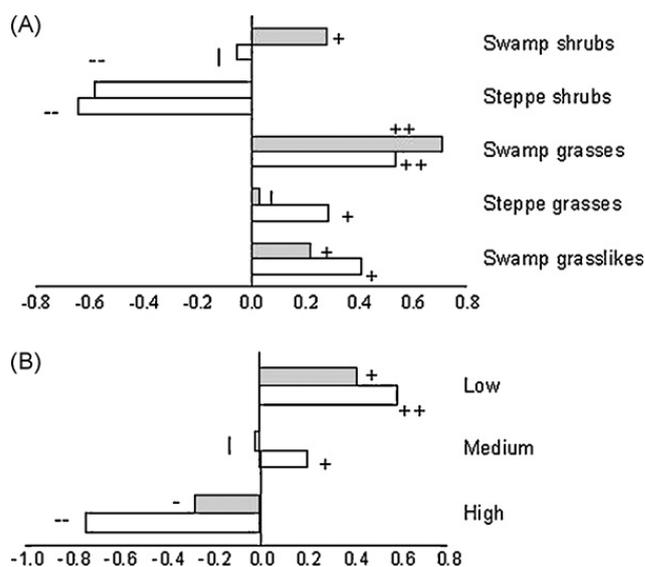


Fig. 3. (A) Ivlev's selectivity index for plant functional group and plant habitat type, and (B) for plant stratum. +++=Strong selection; +=Weak selection; --=Strong avoidance; -=Weak avoidance; I=Indifference. (●) October, (□) March.

had an Ivlev index of 0.41 in March but of -0.76 in October, and conversely occur with *J. seriphioides*, *Juncus* spp. and *F. argentinensis* that had positive values (0.57, 0.84 and 0.29, respectively) in October and high negative values (-0.65 , -0.94 and -0.30 , respectively) in March.

4. Discussion

4.1. Generalist or specialist herbivores

We found support to hypothesis 1. Considering the overall diet, vicuñas behaved as generalist ungulates. They consumed from more than a half of plant species present in the reserve. Diet of vicuñas included vegetation from all habitats, all vegetation strata and all functional groups of plants, suggesting that vicuñas can use a large range of plant species that are distributed in almost all portions of their range. Generalist habits seems to be common in other ungulates of arid environments, like the Oryx (*Oryx leucoryx*) of Serengeti desert, the gazelle (*Gazella dorcas*) of Sahara desert (Ezcurra et al., 2006), the Californian desert deer (*Odocoileus hemionus eremicus*) (Marshall et al., 2004) and several Himalayan ungulates (Awasthi et al., 2003). Having a broad diet can be an answer to a poor environment like deserts or semi deserts (Stephens and Krebs, 1986).

4.2. Forager strategy

Vicuñas have been classified 'strict grass feeders' (Franklin, 1983; Ménard, 1984; Aguilar et al., 1999). In Laguna Blanca, they consumed a large proportion of grasses (59–72%) but substantially lower than it was previously described (85–90%, Aguilar et al., 1999). The use of shrubs was relatively high, between 16% and 19% of overall diet and reached 45% at local sites. Vicuñas appear to adapt their diet from one based strictly on grasses in the altoandino system and wet puna to more shrubs feeders at dry puna ecosystem. Cajal (1989) in San Juan, Argentina, and Arzamendia (2008) in Jujuy, Argentina, also reported the use of shrubs by vicuñas. In Laguna Blanca, there were three species of shrubs that were consumed in larger proportion than availability in one season, suggesting that vicuñas actively searched for species other than grasses. So, in relation to hypothesis 2, vicuñas did not behave as strict grazer, so they should be reclassified to the category of 'facultative grazers' (Fernández et al., 1991) or "variable grazers" (Gagnon and Chew, 2000), i.e. herbivores that eat large proportions of grasses, but in local places they are able to include considerable amounts of shrubs.

4.3. Food selectivity

Although vicuña can consume a wide variety of plant species, they do not consume all the forage in proportion to their availability, showing clear patterns of selectivity in the diet. This result supports hypothesis 3. In our study, two grasses (*Distichlis* spp. and *Panicum* spp.) represented together almost half of the total bulk of diet. These species were the most consumed and selected grasses in Laguna Blanca. Although our faecal analysis indicated that these

animals foraged similar quantities of steppe and swamp plants, the latter were used in much more proportion to their availability.

As expected in hypothesis 4, vicuñas selected plants from the low and medium strata, and they tended to consume crawling grasses, rush grasslikes and short bunch grasses. These results confirm the ability of vicuñas to take advantage of the relative small patches of short, green vegetation of the puna. This feature could be useful for vicuñas in a competition context with other ungulates. There are many exotic livestock in Laguna Blanca Reserve and it was found a high overlap in diet between animals (Borgnia et al., 2008). The access to low stratum can be an advantage for vicuñas in relation to cows or donkeys they cannot feed on it.

4.4. Photosynthesis pathway of consumed plants

Contrary to expectation for the behaviour of most ungulates (hypothesis 5), vicuñas consumed a large proportion of C4 plants. Similarly, MacFadden and Shockey (1997) found that Pleistocene camelids of genera *Vicugna* and *Lama* were C4 grazers in Tarija (Bolivia) and Fernández et al. (1991) found that in the Pleistocene these camelids had a 30% of C4 diet in Argentinean altiplano. Recently, Sponheimer et al. (2003) found that South American camelids have higher digestive efficiencies than goats (*Capra hircus*) when fed on C4 grass hay, but not on C3 grass hay. This differential digestive capacity probability explained the ability of camelids to eat C4 plants.

4.5. Seasonal, spatial, and regional variations in diet

Contrary to expectation generated by the behaviour of other arid ungulates (hypothesis 6), vicuñas showed a stable diet throughout the year, without a significant variation in diet composition, in terms of similarity and diversity index between sample periods. However, there was a slight difference between the selectivity of specific plants in March compared to October. Other South American camelids showed significant changes in diet taxonomical composition between dry and wet seasons but these studies were conducted for domestic alpacas *Lama pacos* in puna of Perú and Chile (Virgilio et al., 2003; Castellaro et al., 2004), and for domestic llamas *Lama glama* and the wild guanaco *Lama guanicoe* in Patagonia, Argentina (Posse and Livraghi, 1997; Baldi et al., 2004; Puig et al., 1996). However, Ménard (1984) found no differences in diet between seasons in Pampa Galeras (Peru). This contrasting behaviour between vicuñas and the other arid ungulates is probably related to a unique social peculiarity among mammalian species: vicuñas defend territories all year round. This behaviour probably constrains the foraging areas that they can use. Besides this, during the study period there was not great nutritional differences in nutritional values (Borgnia, unpublished data) due probably to unusual drier conditions in March comparing with other years (CIEDECAT).

Although diet of vicuña remained stable in the timescale, it showed differences in spatial scale. Diet was substantially different in diversity at local scale and this

can be also related to territorial and sedentary features on vicuñas. It was also found a regional variation in most consumed species of grasses, even when all species were represented along the Altiplano. *Panicum* sp. had not been previously described as part of vicuñas diet, while here it was very common. In contrast, grasses of genera *Stipa* and *Festuca* were poorly represented in Laguna Blanca but were highly consumed in Pampa Galeras and other areas of Peru (Koford, 1957; Franklin, 1983) and La Rioja, Argentina (Rosati, 2001).

4.6. Diet quality

Contrary to expectations in hypothesis 7, Vicuñas did not show preference for plant groups like shrubs, containing high crude protein or low wall cell compounds values. A large generalist herbivore must select a diet within the constraints of minimal level of specific plant nutrients as well as maximal level of specific secondary plant compounds (Westoby, 1974; Freeland and Janzen, 1974). It is probable that other nutritional factors of diet (mainly secondary metabolites, and palatability) could be affecting the consumption of specific plants in free ranging vicuñas. Although vicuña eat shrubs to compensate the diet, the quantities of this group in the diet may be limited by these factors. Most shrubs of this region have tannins or resins, and some genera of shrubs like *Fabiana*, *Lycium*, *Senecio*, *Baccharis* and *Parastrephia* have also alkaloids (Florez et al., 2004) or high proportions of NFE (nitrogen-free extracts) that diminish the palatability of plants (Villca and Genin, 1995).

Some studies with domestic camelids compared to other ruminants such as sheep, have shown that camelids have more effective digestion when they eat low quality food (San Martín, 1991) and can digest fibrous plants due to its higher retention time. Protein requirements in camelids are lower than in sheep, because they can recycle and reuse body urea for microbial protein synthesis, especially when consuming low-quality pasture. It's probably that vicuñas have similar nutrition features that allow them to survive in the poor steppes of the puna.

Although vicuña did not consumed greater proportions of plants with high quality (in terms of crude protein and fibre), there was a correlation between crude protein content and consumption of steppe grasses, suggesting that the vicuña can select foods high quality under specific conditions. This could be other strategy of foraging front of the low quality of the highland pastures.

Other important consideration is that several low stratum plants consumed by vicuñas (*Distichlis*, *Sarcocornia*, *Frankenia*, *Amphiscirpus*) are associated with saline soils and have a high osmotic potential that allow them to obtain water from environment (García and Beck, 2006). It's likely to be an important salt supply to balance minerals contents in the diet (Alzérreca et al., 2003). Low stratum plants had high values in ash content, and this parameter in an indicator of mineral component of diet (Lesage et al., 2000). Again, the high consumption for plants of low stratum can be a way to intake mineral supply.

Future studies related to digestibility, secondary metabolites and water content of plants should be consid-

ered to achieve a better understanding of nutrition of this wild camelid.

Foraging decisions of wild herbivores such as the vicuña are likely limited by many factors: energy requirements, plant palatability, availability of high quality vegetation, water availability, and behaviours such as territoriality, the sedentary and training groups; also the competitive interactions and risk of predation (Wiens, 1976; Lima and Dill, 1990; Hanley, 1997); all these factors can influence their overall feeding strategy.

5. Conclusions

This is one of the first researches about the diet of the southern species of vicuña, *V. v. vicugna*, inhabiting dry puna of Argentina, which includes a description of botanical composition of the diet, foraging behaviour, and nutritional quality of vegetation. We can summarize some features about foraging ecology of vicuñas: (1) they behave as a generalist ungulate; (2) they are not strict grazers in dry puna; (3) they show selectivity; (4) they are sensible to changes in nutritional content of poor grasses. These characteristics can be considered as part of a wide range of feeding responses of vicuñas to live in the poor environment of altiplano.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.smallrumres.2009.11.009.

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