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Does the presence of livestock alter the trophic behaviour of sympatric populations of wild camelids *Vicugna vicugna* Molina 1782 and *Lama guanicoe* Müller 1976 (Artiodactyla: Camelidae)? Evidence from Central Andes

¿La presencia de ganado domesticado altera la conducta trófica de poblaciones simpátricas de los camélidos silvestres *Vicugna vicugna* Molina 1782 y *Lama guanicoe* Müller 1976 (Artiodactyla: Camelidae)? Evidencia de los Andes Centrales

Carlos Tirado[1]*, A. Cortés[2], M. A. Carretero[3] & Francisco Bozinovic[4]

[1]Departamento de Química y Biología, Facultad de Ciencias Naturales, Universidad de Atacama, Casilla 576, Copiapó, Chile
[2]Departamento de Biología, Facultad de Ciencias, Universidad La Serena, Casilla 599, La Serena, Chile
[3]CIBIO Research Centre in Biodiversity and Genetic Resources, InBIO, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, Nº 7. 4485-661 Vairão, Vila do Conde, Portugal[d]
[4]Departamento de Ecología and Center of Applied Ecology & Sustainability (CAPES), Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile
*E-mail: carlos.tirado@uda.cl (C. Tirado).

ABSTRACT

We described and compared the diets of two sympatric Andean camelids, during the humid season (austral summer) in a site of Northern Chile, in presence of domestic livestock. Results indicate that: 1) grasses and shrubs are the main component in the diet of both camelids, 2) shrubs were more consumed by *V. vicugna*; 3) *V. vicugna* and *L. guanicoe* used the same trophic resources but in different proportions; 4) in mountain environments, wetlands exploitation by wild camelids seems restricted by domestic cattle, which would cause the displacement of Vicuñas and Guanacos to suboptimal habitat for feeding.

Keywords: Guanaco, Vicuña, livestock, diet, herbivory.

RESUMEN

Describimos y comparamos la dieta de dos poblaciones simpátricas de camélidos silvestres, durante la estación húmeda (verano) en un sector del norte de Chile en presencia de ganado domesticado. Nuestros resultados indican que: 1) gramíneas y arbustos son el principal componente de la dieta de ambos camélidos; 2) arbustos fueron consumidos principalmente por *V. vicugna*; 3) *V. vicugna* and *L. guanicoe* utilizan los mismos recursos tróficos pero en diferentes proporciones; 4) en ambientes de montaña, el uso de vegas altoandinas por parte de camélidos silvestres estaría siendo restringido por la presencia de ganado domesticado, el cual provocaría el desplazamiento de ambos camélidos a zonas subóptimas de alimentación.

Palabras claves: Guanaco, Vicuña, ganado, dieta, herbivoría.

INTRODUCTION

In places where vegetation has developed adaptations to cope with herbivores (Granados–Sánchez *et al*. 2008), herbivorous mammals must have strategies for obtaining, processing, and using food. A clear example of this is the high Andean environment, where food is not only scarce, but highly variable in time and space (Baied & Wheeler 1993). Under these conditions, resources are distributed in two main areas: steppe, where vegetation is mostly grasses and resinous shrubs; and wetlands, where grasses and pseudograsses, with a relatively constant water supply, prevail (Villagrán *et al*. 1983). Wetlands play an important role because they harbor an important biodiversity (Squeo *et al*. 2006a), constituting in some cases critical habitat for wild vertebrates, such as the case of South American camelids (Wurstten *et al*. 2014).

The presence of herbivorous mammalian species, which are able to take advantage of this type of greatly restrictive environment, sets up the perfect scenario to evaluate their mechanisms involved in using and processing food resources. In these environments, interspecific competition may be reduced through niche segregation (Jaksic & Marone 2007), hence, closely related species can coexist in sympatry. Alternatively, it may lead to suboptimal use of resources by one of the competitors, condition that has been documented for wild camels that coexist in sympatry with exotic species (Borgnia *et al*. 2008).

Wild South American camelids represent one of the main groups of vertebrates which have been able to take advantage of this type of environment (Franklin 1982). *Vicugna vicugna* and *Lama guanicoe* are two wild camelids currently inhabiting arid and semiarid environments of South America. Although both species differ in their distribution patterns (altitudinal and latitudinal), they may live sympatrically in highlands (Franklin 1982). Such is the case with the camelids populations of the high Andean area of the north of Chile, specifically “El Morro” (28º37’46’’S – 69º56’13’’W, Alto del Carmen, Región de Atacama), which is also used as summer meadows (summer cattle) to feed livestock.

The aim of this work is to describe and compare the diets of two sympatric Andean camelids, during the humid season in a site of Northern Chile, in presence of domestic livestock. It is worth mentioning that studies about the ecology of sympatric populations of wild camelids are not only scarce (Lucherini 1996, Lucherini & Birochio, 1997, Wurstten *et al*. 2014) but also essential for their conservation and management.

Consequently, the hypotheses we tested were: 1) if both camelids live in sympatry with livestock, taking advantage of areas where resources vary on their quantity and quality (reduced palatability), we would expect a significant segregation of both camelids’ trophic niche; 2) due to the presence of domesticated cattle, wild camels would reduce the use of wetlands as feeding areas, favoring the use of steppe areas.

In order to test these hypotheses, trophic ecology was evaluated based on the availability of food, chemical composition of food items, trophic resources, trophic selection, and trophic overlap of the sympatric populations of *V. vicugna* and *L. guanicoe*, in presence of cattle.

MATERIALS AND METHOD

Study area

This study was carried out during summer (February 2010) in “El Morro” (28º37’46’’S – 69º56’13’’W, altitudinal range: from 3500 to 4300 m.a.s.l., Alto del Carmen, Región de Atacama), in an area of 8235 ha. The climate is arid, with a mean temperature of 3ºC (maximum temperature = 14°C, and minimum = -6.4ºC), and an average annual precipitation of 214 mm, which is mainly concentrated as snow between June and November (Knight Piésold S. A. 2008). The two prevailing types of vegetation are evergreen herbs, mainly located in azonal vegetation areas (wetlands or Andean meadows), and shrubby vegetation distributed in areas of zonal vegetation (slopes). El Morro is used as summer pastures to feed domestic livestock, which principally includes horses and goats. During the study period, 299 animals belonging to the species *Capra hircus* (Goat, n= 267), *Equus caballus* (Horse, n= 27) and *E. asinus* (Donkey, n= 3) were detected.

Study species

V. vicugna has an average body mass of 35 kg. This species is distributed just in Andean and high plateau areas (3000 - 4600 m.a.s.l.) (Franklin 2011). In Chile, it is considered an endangered species (SAG 2012). Studies of the trophic ecology of *V. vicugna* are scarce in Chile (Tirado *et al*. 2012), although there is comparative information on this topic for populations from other countries (Cajal 1989, Aguilar *et al*. 1995, Borgnia *et al*. 2008, Cassini *et al*. 2009). *V. vicugna* has been considered a strict grazer (Ménard 1984, Aguilar *et al*. 1999), whereas other studies also report their consumption of shrubs (Aguilar *et al*. 1995, Cajal 1989, Borgnia *et al*. 2008, Borgnia *et al*. 2010, Tirado *et al*. 2012). On the other hand, *L. guanicoe* has a larger body mass (90 - 140 kg). Populations of this species occupy a wide altitudinal distribution (0 - 4350 m.a.s.l.), being either sedentary or migratory (Franklin 1982, Contreras *et al*. 2006). In the North of Chile, *L. guanicoe* is considered locally as Endangered Species (SAG 2012). As for this species diet, in high Andean areas with wetlands *L. guanicoe* has been reported to eat mainly grasses and pseudograsses, whereas in wetlands absence its diet consists mainly on grasses, and secondarily shrubs (Cortés *et al*. 2003, Puig *et al*. 2011).

Food resource availability

Vegetation cover (%) was obtained by the point quadrat method (Mueller-Dombois & Ellerberg 1974). A total of 40 transects of 50 meters long were performed in areas where camelids frequently foraged, and/or where the presence of fresh feces were detected (community dung piles). Each transect was divided into 50 points, and separated each 100 cm. The foliage cover of plant species was determined by the sum of all transects, with a total of 2000 points sampled.

Reference sampling

Leaves, flowers, and stalks of plant species detected in the study area (Table 1) were collected during summer time, which were identified in the herbarium of Universidad de La Serena. The epidermal tissues were used to prepare the microhistological reference sampling (Williams 1962).

Feces sampling and histological preparations

10 samples of *V. vicugna* and 10 samples of *L. guanicoe* fresh feces were collected in areas where individuals were foraging. Each sample was made up of 10 feces samples from adult individuals, which were randomly picked from community dung piles. To obtain fecal samples from each species, we observed both camelids with binoculars, and collected the pellets just after vicuñas and guanacos defecated in the dung piles.

Samples were dried out and kept at 60°C. From a feces pool made from each sample, a microhistological preparation was composed through Williams's technique (Williams 1962, Dizeo de Strittmatter 1984). This method was repeated for each of the samples collected, obtaining a total of 10 preparations per species (Cortés *et al*. 2003, Cortés *et al*. 2006, Tirado *et al*. 2012).

Diet assessment

A total of 20 microscopic fields randomly picked from each of the histological preparations were analyzed. In total, 200 microscopic fields were observed (20 fields x 10 preparations) for each species. To avoid analyzing a field more than once, the coordinates of each field were recorded. Observations were carried out with a Nikon® (Eclipse E-200) with a reticulate lens of 20 x 20 quadrants with a magnification of 40X. Fields with less than 50% of the area used were excluded (Cortés *et al*. 2003, Cortés *et al*. 2006). Epidermic material was identified at species level using the reference collection. Diet composition was estimated as the relative area occupied by each plant species, which allowed calculating the frequency of the consumed items. Fiber content and non-identified material was displayed in percentage.

Chemical analysis of vegetal samples

During the measuring of vegetal cover, samples of identified species were collected; 50 grams (dry weight) of each of the species included in the diet were chemically analyzed according to A.O.A.C (1970). The determined parameters were raw protein (g/100g) and raw fiber (g/100g).

Statistical analysis

Trophic diversity was calculated through the Shannon-Wiener's diversity index (Shannon 1948): $H' = -\Sigma\, p_i \times \ln p_i$ where $p_i = n_i/N$, is the proportion of a certain plant species being n_i = number of items of the species i in the diet and N = total number of items in the diet. To assess trophic overlap, Schoener's Index (1968) was used: $PS = 1 - 1/2 \sum | pi - qi |$, where: PS = Schoener overlap index for species p and q, p_i = proportion of item i in species p diet, q_i = proportion of i in species q diet. A higher value than 0.6 or 60% of this index is considered of biological importance (Mathur 1977). To obtain parametric estimators of the means and to estimate confidence intervals of the diversity indexes and overlap, the jackknife technique was used (Jaksic & Medel 1987). The interspecific comparison of Shannon-Wiener's diversity index and fiber content were compared with the Student t test, using a value of $p < 0.05$.

The proportions of resources used and available were compared applying log-likelihood ratio test (X_L^2), proposed by Manly et al. (2002). As this test does not provide statistical differences among proportions, Manly's selection coefficient (w_i) was calculated (Manly *et al*. 2002). To validate statistically that index, a confidence interval on w_i was estimated, using the Bonferroni inequality modified by Manly *et al*. (2002). It was considered a positive selection or "preferred" if the inferior limit of the interval is superior to 1, whereas if the superior limit of the interval is less than 1, it was considered a negative selection or "avoided". Intervals including 1 were considered as random consumption. For calculating resources selection, the adehabitat package (Calenge 2006) for R (R Development Core Team 2008) was used.

RESULTS

Absolute plant cover

A total of 30 plant species from 16 different families were identified from the study area. The vegetation cover was equivalent to 47.01%, whereas the bare soil represented 52.99% (Table 1). Of the 30 species mentioned, 13 were found in zonal vegetation areas and 17 in azonal vegetation areas.

Relative plant cover (potential availability of food resource)

The most abundant ones were pseudograsses *Carex gayana*, grasses *Deyeuxia velutina*, and shrub *Adesmia hystrix* which covered 20.62, 19.94 and 6.26 % respectively (Table 1).

Diet composition

Both camelids consumed 37% of the available resources, including each of them, 10 items (Table 2). Botanical composition of *V. vicugna*'s diet consisted mainly of grasses (40.10%) and shrubs (33.86%), and, to a lesser extent, of pseudograsses (7.17%) and herbs (0.06%). The most representative species in the grasses group were *Jarava frigida* and *D. velutina*, which were consumed at

16.90%, and 16.00%. The shrubs in the diet consisted of just two species, *A. subterranea* (30.34%) being the most abundant. The group of pseudograsses was represented by four species; the most consumed was *C. gayana* (5.46%). In contrast to *V. vicugna, L. guanicoe* presented a higher intake of grasses up to 64.44%, whereas bushy plants and pseudograsses intake were just 7.27% and 6.70%, respectively. From the group of grasses, *L. guanicoe* mainly consumed *J. frigida* (40.81%) and *Deschampsia caespitosa* (22.80%). On the other hand, *L. guanicoe*'s diet included less proportion of shrubs such as *A. subterranea* (4.64%). The most consumed pseudograsses were *C. gayana* (3.48%) (Table 2). By clustering the relative consumption of vegetal species according to the type of vegetation (zonal – azonal), it was found out that the main item in both species diet was zonal vegetation (*V. vicugna*: 50.82% and *L. guanicoe*: 48.08%). Species richness was similar (Table 2). Regarding fiber content of feces, it was 17.60% for *V. vicugna* and 20.31% for *L. guanicoe*, but both values were statistically different (t: 15, df: 18; $p < 0.0001$).

Trophic diversity and diet overlap

Trophic diversity, estimated through the Shannon Wiener's index (H'), was 1.66 for *V. vicugna* and 1.54 for *L. guanicoe*, values which differed statistically (t: 8.34; df: 10986; $p < 0.0001$) (Table 2). Trophic overlap, determined by Schoener's index (PS), was 38% (Table 2).

Trophic selection

Comparing the proportion of items in the diet (excluding unknown material and fiber) with the expected values of consumption estimated from plant cover, significant differences were found in both camelids (*V. vicugna*: X_L^2: 46024; df: 9; $p < 0.0001$ *L. guanicoe*: X_L^2: 48965; df: 9; $p < 0.0001$), indicating that certain plant species were either preferred or avoided (Table 3). Of the 10 species consumed by *V. vicugna*, just four were preferred. Among them, the bushy plants *A. subterranea* and *J. uniflora* were highly selected, while *Festuca wernermannii* and *J. frigida* were preferred to a lesser extent. The other species consumed were avoided (Table 3). Similar to *V. vicugna*, *L. guanicoe* preferred four of the 10 items included in its diet, showing strong preference towards *J. frigida*, *D. caespitosa*, *Junellia uniflora* and *A. subterranea*, while the other species were avoided (Table 3). When assessing the selection considering functional groups only, both camelids showed preference towards shrubs and grasses (Table 4).

Chemical properties of preferred items

Chemical analyses (g / 100g) indicated that plant species selected by vicuñas and guanacos showed average nitrogen content of 5.4 ± 2.1 g / 100g. Shrub species *A. subterranea* had the highest value (7.7 g / 100g). As for fiber, selected species had an average value of 24.8 ± 8.8 g / 100g, and shrub species *A. subterranea* had the lowest value (14.6 g / 100g).

Table 1. Vegetal species in the study area. For each of them, tables indicate functional group, family, distribution (zonal = Z or azonal = A), absolute and relative cover.

Tabla 1. Especies vegetales en el área de estudio. Para cada una de ellas se indica grupo funcional, familia y distribución (zonal= Z o azonal= A), cobertura absoluta y relativa.

FUNCTIONAL GROUP FAMILY Species	**Distribution**	Cover **(%)**	
		Absolute	**Relative**
SHURBS			
FABACEAE			
Adesmia echinus	Z	0.18	0.39
Adesmia hystrix	Z	2.94	6.26
Adesmia subterranea	Z	0.63	1.35
SOLANACEAE			
Fabiana imbricata	Z	0.72	1.54
VERBENACEAE			
Junellia uniflora	Z	0.18	0.39
UMBELLIFERAE			
Azorella compacta	Z	0.18	0.39
Azorella madreporica	Z	0.54	1.16
Subtotal (%)		**5.39**	**11.46**
HERBACEOUS			

FUNCTIONAL GROUP FAMILY Species	**Distribution**	Cover **(%)**	
		Absolute	**Relative**
CAMPANULACEAE			
Lobelia oligophylla	A	0.18	0.39
CRUCIFERAE			
Descurainia pimpinellifolia	Z	0.23	0.48
FABACEAE			
Astragalus bustillosii	A	0.18	0.39
HALORAGACEAE			
Myriophyllum quitense	A	0.09	0.19
MALVACEAE			
Cristaria andicola	Z	1.81	3.85
PLANTAGINACEAE			
Plantago barbata	A	0.68	1.45
PORTULACEAE			
Lenzia chamaepitys	Z	0.54	1.16
RANUNCULACEAE			
Ranunculus cymbalaria	A	0.91	1.93
URTICACEAE			
Urtica mollis	Z	0.18	0.39
Subtotal (%)		**4.80**	**10.21**
GRASSES			
POACEAE			
Deschampsia caespitosa	A	1.63	3.47
Deyeuxia velutina	A	9.38	19.94
Festuca rubra	A	0.50	1.06
Festuca werdermannii	A	0.50	1.06
Hordeum comosum	Z	0.09	0.19
Jarava frigida	Z	2.13	4.53
Poa pratensi	A	0.27	0.58
Puccinellia frigida	A	0.50	1.06
Sub total (%)		**14.99**	**31.89**
PSEUDOGRASSES			
CYPERACEAE			
Carex gayana	A	9.69	20.62
Eleocharis albibracteata	A	1.18	2.50
Phylloscirpus deserticota	A	4.30	9.15
JUNCACEAE			
Juncus arcticus	A	2.13	4.53
Juncus bufonius	A	0.59	1.25
Oxychloe andina	A	3.94	8.38
Subtotal (%)		**21.83**	**46.44**
Vegetal cover		47.01	100.00
Bare soil		52.99	-
Total		100.00	100.00
Species Richness		30	

Table 2. Availability and use of trophic resources, diet items, trophic diversity (Shannon Wiener index ± IC 95%) and trophic overlap (Schoener's index ± IC 95%) of camelids *Vicugna vicugna* and *Lama guanicoe*, in El Morro area (Atacama Region). The chemical composition of food resources is shown (g/100g). P: Row protein; F: Row fiber.

Tabla 2. Disponibilidad y uso de los recursos tróficos, ítems dietarios, diversidad dietaria (Índice de Shannon Wiener ± IC 95%) y sobreposición trófica (Índice de Schoener ± IC 95%) de los camélidos *Vicugna vicugna* y *Lama guanicoe* en el sector El Morro (Región de Atacama). Se señala la composición química de los ítems alimenticios (g/100g). P: Proteína cruda; F: Fibra cruda.

FUNCTIONAL GROUP		**Chemical composition**		***Vicugna vicugna***			***Lama guanicoe***	
FAMILY Species	**Distribution**	**P**	**F**	***Available resources (%)***	***Used resources (%)***		***Available resources (%)***	*Used resources (%)*
SHRUBS								
FABACEAE								
Adesmia subterranea	Zonal	7.7	14.6	1.88	30.34		1.93	4.4
VERBENACEAE								
Junellia uniflora	Zonal	5.7	24.0	0.54	3.52		0.55	2.63
Subtotal (%)				**2.42**	**33.86**		**2.48**	**7.27**
Average ± DE		6.7 ± 1.4	19.3 ± 6.7					
HERBACEOUS								
MALVACEAEA								
Cristaria andicola	Zonal	5.6	17.7	5.37	0.06		-	-
Subtotal (%)				**5.37**	**0.06**			
GRASSES								
POACEAE								
Deschamsia caespitosa	Azonal	5.6	24.6	-	-		4.96	22.80
Deyeuxia velutina	Azonal	4.3	22.9	27.79	16.00		28.51	0.66
Festuca werdermanii	Azonal	2.5	36.1	1.48	7.20		1.52	0.17
Jarava frigida	Zonal	3.6	23.4	6.31	16.90		4.41	40.81
Subtotal (%)				**35,58**	**40,10**		**39,40**	**64,44**
Average ± DE		4.0 ± 1.3	26.8 ± 6.3					
PSEUDOGRASSES								
CYPERACEAE								
Carex gayana	Azonal	13.6	22.8	28.72	5.46		29.48	3.48
Eleocharis albibracteata	Azonal	5.4	34.6	3.49	0.76		3.58	2.14
Phylloscirpus deserticola	Azonal	5.2	21.4	12.75	0.49		13.09	0.53
JUNCACEAE								
Oxychloe andina	Azonal	5.5	21.6	11.68	0.46		11.98	0.55
Subtotal (%)				**56,64**	**7,17**		**58,13**	**6,70**
Average ± DE		7.4 ± 4.1	25.1 ± 6.4					
Fibers					17.60			20.31
Unknown material					1.20			1.28
Total (%)				100,0	100.0		100.0	100.0
Shannon Wiener Index (H' ± IC 95%)					1.66 (1.64 – 1.66)			1.54 (1.51 – 1.56)
Schoener Índex (PS ± IC 95%)						0.38 (0.26 – 0.55)		

TABLE 3. Vegetal species selected by camelids *V. vicugna* and *L. guanicoe* determined through Bonferroni inequality made for Manly's selection coefficient (w_i). *pu* proportion used by the resource; p_d, available proportion of the resource; w_i: Manly's selection coefficient; (+ ó -), show if w_i index is different from 1 a $p \leq 0.001$; **(+)** Positive selection or higher consumption than available, **(-)** Negative selection or less consumption than available.

TABLA 3. Selección de especies vegetales por parte de los camélidos *V. vicugna* y *L. guanicoe* determinada a través de la inequidad de Bonferroni construida para el coeficiente selección de Manly (w_i). *pu* proporción utilizada del recurso; p_d, proporción disponible del recurso; w_i: Coeficiente de selección de Manly; (+ ó -), indica si el índice w_i difiere de 1 a $p \leq 0.001$; **(+)** Selección positiva o consumo mayor a lo disponible, **(-)** Selección negativa o consumo menor al disponible.

FUNCTIONAL GROUP	*Vicugna vicugna*					*Lama guanicoe*				
FAMILY / Species	*pu*	*pd*	Wi	wi ± CI (95%)	Selection p < 0,025	*pu*	*pd*	wi	wi ± CI (95%)	Selection p < 0,025
SHRUBS										
FABACEAE										
Adesmia subterranea	0.374	0.019	19.686	(19.155 - 20.178)	(+)	0.059	0.019	3.114	(2.840 - 3.382)	(+)
VERBENACEAE										
Junellia uniflora	0.043	0.005	8.682	(7.856 - 9.491)	(+)	0.034	0.006	5.595	(4.935 - 6.245)	(+)
HERBACEOUS										
MALVACEAEA										
Cristaria andicola	0.001	0.054	0.015	(0.004 - 0.025)	(-)	-	-	-	- -	
GRASSES										
POACEAE										
Deschamsia caespitosa	-	-	-			0.291	0.050	5.820	(5.616 - 6.013)	(+)
Deyeuxia velutina	0.197	0.278	0.709	(0.680 - 0.737)	(-)	0.008	0.285	0.030	(0.022 - 0.036)	(-)
Festuca werdermanii	0.089	0.015	5.922	(5.535 - 6.297)	(+)	0.002	0.015	0.144	(0.076 - 0.211)	(-)
Jarava frigida	0.208	0.063	3.307	(3.175 - 3.433)	(+)	0.521	0.044	11.842	(11.583 - 12.078)	(+)
PSEUDOGRASSES										
CYPERACEAE										
Carex gayana	0.067	0.287	0.234	(0.217 - 0.252)	(-)	0.044	0.295	0.151	(0.133 - 0.166)	(-)
Eleocharis albibracteata	0.009	0.035	0.269	(0.214 - 0.324)	(-)	0.027	0.036	0.761	(0.661 - 0.859)	(-)
Phylloscirpus deserticola	0.006	0.128	0.047	(0.035 - 0.059)	(-)	0.007	0.131	0.052	(0.038 - 0.065)	(-)
JUNCACEAE										
Oxychloe andina	0.006	0.117	0.048	(0.035 - 0.061)	(-)	0.007	0.120	0.059	(0.002 - 0.074)	(-)

TABLE 4. Functional groups selected by camelids *V. vicugna* and *L. guanicoe* determined by Bonferroni inequality made for Manly's selection coefficient (w_i).

TABLA 4. Selección de grupos funcionales por parte de los camélidos *V. vicugna* y *L. guanicoe* determinada a través de la inequidad de Bonferroni construida para el coeficiente de selección de Manly (w_i).

	Vicugna vicugna						*Lama guanicoe*					
	pu	*pd*	w_i	w_i ± CI (95%)		Selection	*Pu*	*pd*	w_i	w_i ± CI (95%)		Selection
FUNCTIONAL GROUP						(p < 0,0125)						(p < 0,0167)
SHRUBS	0.417	0.024	17.233	(16.877	17.589	(+)	0.093	0.025	3.737	(3.526	3.948)	(+)
HERBACEOUS	0.001	0.054	0.015	(0.006	0.024)	(-)	-	-	-	-	-	
GRASSES	0.494	0.356	1.389	(1.364	1.413)	(+)	0.822	0.394	2.086	(2.069	2.104)	(+)
PSEUDOGRASSES	0.088	0.566	0.156	(0.147	0.165)	(-)	0.086	0.581	0.147	(0.138	0.156)	(-)

DISCUSSION

Availability and quality of food resources

The potential resource availability consisted of 30 plant species distributed among zonal (43%) and azonal (57%) vegetation areas. Of those identified during summer in the study zone, both camelids consumed only 10, distributed among groups of typical plants from Andean grasslands (grasses, pseudograsses, shrubs, and herbs). These groups also contained different proportions of protein and fiber. These last variables may not be the best parameter, but which allows characterizing, in a general way, the nutritional quality of forage. Shrubs and herbaceous species showed fiber content ranging between 14% and 24%, whereas grasses and pseudograsses were characterized by fiber content values ranging between 21% and 36%. As for the protein content, functional groups with higher percentage were shrubs (6.7%) and pseudograsses (7.4%). Among the highest values, *Adesmia subterranea*, species belonging to the family Fabaceae, is characterized by its nitrogen fixing ability (Squeo *et al*. 2006b).

Botanical composition of the diet

As reported for other areas (Cortés *et al*. 2006, Cassini *et al*. 2009, Puig *et al*. 2011, Tirado *et al*. 2012), grasses were the main component of *V. vicugna* and *L. guanicoe* diet, which were also preferred. The fact that both species consumed high amount of grasses is clearly associated with the different adaptations for digesting fiber of camelids such as: 1) stomach compartments, which allow them to increase fermentation, water and salts absorption (San Martín 1987), 2) their long times of retention compared to other artiodactyls (Sponheimer *et al*. 2003), 3) their ability to reduce urea excretion at a renal level (Engelhardt & Holler 1982). Even though both camelids shared this pattern, grasses intake was 1.6 times higher in *L. guanicoe* than in *V. vicugna*. In fact, being bigger *L. guanicoe* also had larger stomach compartments, which likely had a significant effect on retention times that tend to be 1.2 times higher for this species compared to *V. vicugna* (San Martín 1987). Although shrubs have been characterized by their high protein content and low cell walls components content (Borgnia *et al*. 2010), they were represented by only two species in the diet of both camelids. Nevertheless, they constituted the second most representative group in *V. vicugna* and *L. guanicoe* diet. Even though this functional group was preferred by both species, *V. vicugna* showed a 4.6 times higher value of consumption and selection. This has to be interpreted in the light of the high intake of the nitrogen- fixing *A. subterranea*, which was characterized by its higher content of raw protein. It is here suggested that the high percentage of *A. subterranea* in the diet of vicuña is due to a higher nitrogen requirement necessary to meet the metabolic needs, which could be a result of the lower efficiency of nitrogen retention, similar to the reported by Davies *et al*. (2007).

As for the pseudograsses intake, both camelids consumed them in similar proportions (*V. vicugna*: 7.2%; *L. guanicoe*: 6.7%). These low numbers were expected in *V. vicugna,* according to what was reported by Aguilar *et al*. (1995) and Borgnia *et al*. (2008). However, the results for *L. guanicoe* differ from what was reported by Puig *et al*. (2011) working in wetland environments, who describe a high intake of pseudograsses. Nevertheless, it is important to bear in mind that this same resource in wetlands was avoided by both camelids. This seems to be a consequence of the presence of domesticated cattle, which would cause the displacement of populations of wild camelids to feeding suboptimal habitats, similar to the reported by Borgnia *et al*. (2008). Since wetlands are critical habitats for wilds camelids during the stages of pregnancy and lactation, the presence of domesticated cattle can have a significant negative effect on their populations (Wurstten *et al*. 2014). In this sense, digestive flexibility seems to be one of the most important and widely used adjustments to changes in food quality. Thus, the hypertrophy caused by the increased food intake seems to be a response of the digestive tract, which may result in the maintenance of a constant coefficient of digestibility at increased levels of food consumption (Torres-Contreras & Bozinovic 1997).

Use of zonal and azonal vegetation

As for the use of feeding areas, the higher contribution to both camelids diet were steppe areas species, which is explained mainly by *A. subterranea* (vicuñas) and *J. frigida* (vicuñas and guanacos) high intakes. This foraging behavior could be explained by: 1) *J. frigida* dominance in slopes (Osorio *et al*. 2011); 2) large areas covered by zonal vegetation (Osorio *et al*. 2011), which can be used by camelids due to its wide home range (Vicuña: 22,1 to 43,5 km^2, González *et al*. 2013; Guanaco: 65 to 163 km^2, Contreras *et al*. 2006); and 3), the presence of domesticated animals, which have a negative effect on resource used by wild camelids (Borgnia *et al*. 2008; Muñoz & Simonetti 2013). It is worth mentioning that 299 domesticated animals were registered in the study area (wetlands) (Goats: 267; horses: 32, unpublished data). In this scenario, *V. vicugna* and *L. guanicoe* may have shifted their plant consumption to steppe areas, which would imply processing low quality vegetation.

Despite wetland species represent less than 31% of their diet composition, they are qualitatively more important since they provide 60 and 70% of the total of consumed plant species. Therefore, the consumption and selection of wetland vegetal species seems determined by micronutrients and mineral salts content but limited by the presence of domestic fauna. This latter aspect is an important factor affecting the feeding of wild camelids, because they would cause the displacement of both populations of wild ungulates to feeding suboptimal habitats, reducing the use of wetlands, critical habitats, during gestation and lactation periods of wild camels (Wurstten *et al*. 2014). Both aspects must be evaluated to understand in detail vicuñas and guanacos foraging behavior in high Andean environments.

Trophic interaction

Although both camelids consumed the same kind of plant species, the ecological similarity of the diets of both species was 38%. This is due to the differentiating use of these resources. *V. vicugna* uses mainly shrubs and grasses species, *L. guanicoe* includes in its diet less proportion of shrubs, focusing mainly in grasses. The mentioned differences are also observed in trophic selection. *V. vicugna* preferred mainly shrub species *A. subterranea* and *J. uniflora*, whereas *L. guanicoe* preferred grasses *J. frigida* and *D. caespitosa*. The differential use of resources is also reflected in diet diversity (trophic niche breadth), which contrasts with the findings of Cajal (1989), who reported higher dietary diversity in *V. vicugna* than in *L. guanicoe*. The latter may result from the presence of domesticated cattle in the study area, which would have a negative effect on the trophic behavior of wild camels. This scenario should be assessed, in the future, among seasons or contrasting periods with availability of food resources.

Conclusions

In summary, we can conclude that: 1) the diet of both camelids was made up mainly by grass, and secondly by shrubs being more abundant in Vicuña than Guanaco diets; 2) *A. subterranea* may provide significant source of nitrogen to *V. vicugna* in zonal vegetation areas; 3) in a mountain environments, wetlands exploitation by wild camelids seems restricted by domestic cattle, which would cause the displacement of Vicuñas and Guanacos to suboptimal habitat for food; 4) the differential use of food resources by both camelids (trophic niche segregation) in High Andean areas may allow them to coexist in sympatry and 5) finally, these results are relevant to the management of wetlands in highlands, which are used as feeding grounds for wild and domesticated species.

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