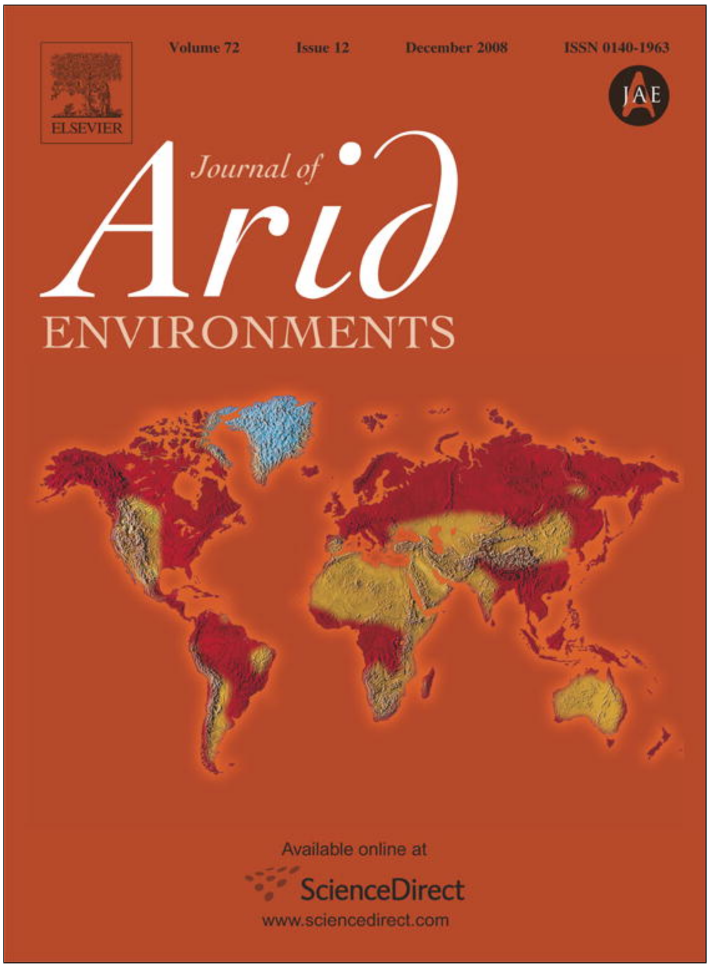
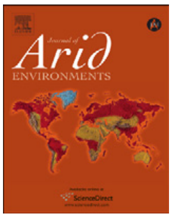

Volume 72
Issue 12
December 2008
ISSN 0140-1963
JAE
ELSEVIER
Journal of Arid Environments
Available online at
ScienceDirect
www.sciencedirect.com

Journal of Arid Environments 72 (2008) 2150–2158

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv



Interaction between wild camelids and livestock in an Andean semi-desert

M. Borgnia [a], B.L. Vilá [b], M.H. Cassini [c,*]

[a] Group of Studies in Ecology of Mammals (GEMA), National University of Luján (UNLu), Cc221, B6700ZBA Luján, Buenos Aires, Argentina
[b] VICAM Group (Vicuñas, Camélidos, Ambiente), CONICET, National University of Luján (UNLu), Cc221, B6700ZBA Luján, Buenos Aires, Argentina
[c] GEMA, CONICET, PROFAUNA Organisation, National University of Luján (UNLu), Cc221, B6700ZBA Luján, Buenos Aires, Argentina

ARTICLE INFO

Article history:
Received 18 February 2008
Received in revised form
18 July 2008
Accepted 22 July 2008
Available online 23 August 2008

Keywords:
Altiplano
Biosphere reserve
Diet
Habitat segregation
Inter-specific competition
Ungulates
Vicugna vicugna

ABSTRACT

Isoleg theory predicts that coexistence between two competing species can occur when the subordinate, generalist species uses alternative patches of resources as the density of the dominant specialist species increases. These models provide a framework to determine if a native species is subordinate to an introduced one, thus requires conservation considerations. We investigated habitat interactions between a wild neotropical camelid and domestic exotic ungulates in the Andean Puna semi-desert of South America. The Puna or Altiplano is an arid environment located in high altitudes, with cold and dry weather, and two main types of habitats, steppes and swamp areas. There was a high overlap of diets between species. Vicuñas were generalists in the use of habitat, but invested foraging effort in swamp habitats, while livestock were taken to swamp habitats by local people. Vicuñas and livestock were spatially segregated. Vicuñas used the preferred habitat less than expected from their foraging preference. We concluded that vicuñas and livestock coexist because vicuñas occupy sub-optimal habitats whilst livestock concentrate in the richest ones. Vicuñas can deal with poor habitats because they have several adaptations to live in deserts.

1. Introduction

Competition between exotic livestock and native ungulates is a frequent conservation problem around the world, especially in arid environments where food is scarce (e.g., Baldi et al., 2004; Coe et al., 2005; Fritz et al., 1996; Mishra et al., 2004; Schwartz and Ellis, 1981; Voeten and Prins, 1999). Coexistence can occur, however, native species can suffer a displacement to sub-optimal habitats. Because native species are normally better adapted to their environment than exotic livestock, the use of secondary habitats can be wrongly interpreted as habitat preference.

Isoleg theory (Rosenzweig, 1981) is a refined version of classical niche theory (MacArthur and Levins, 1967), which provides a theoretical framework for interpreting this type of inter-specific interaction. It proposes that the possibility of coexistence between two species that share niche components depends on two main factors: degree of specialisation in the use of these components of each competing species, and spatial heterogeneity of the environment. Two conditions increase the probability of coexistence between competing species: (1) when at least one of the species is generalist, i.e., it can use different types of resources and (2) when the shared resource shows a heterogeneous distribution. Rosenzweig (1981) models are based on the principle that each competitor (normally foragers competing for food) of both populations used the resource patch that maximises its fitness (indirectly measured as food intake rate).

---

* Corresponding author. Tel.: +54 02320470939.
E-mail addresses: mborgnia@mail.unlu.edu.ar (M. Borgnia), bibianavila@gmail.com (B.L. Vilá), mcassini@mail.unlu.edu.ar (M.H. Cassini).

0140-1963/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2008.07.012

Pimm et al. (1985) developed an isoleg model that is specifically applied to the interaction between a dominant, specialist species and a subordinate, generalist species, both preferring the same type of resources, in an environment where this resource is distributed in patches. Coexistence can occur because the subordinate, generalist species uses alternative patches of resources while the density of the dominant specialist species increases. These models provide a framework to determine if a native species is subordinate to an introduced one, thus requiring conservation considerations.

The Puna or Altiplano is an arid environment located in high altitudes of the Andes, with cold and dry weather. Most Puna desert is covered by steppe characterised by xerophytic vegetation and high proportion of bare soil. However, in water body margins and swamp soils, there is a type of habitat known as 'vegas' or 'bofedales', where pastoral activity is concentrated almost exclusively. These are the 'oases' of the Puna desert, with high biomass and vegetation cover during the whole year and with plant species usually of relatively high nutritional content (Massy and Weeda, 2003; Sixto, 2003).

Vicuña (*Vicugna vicugna*) is one of the few large native herbivores of the South American arid environment (Franklin, 1983). By 1960s, this species was almost extinct due to excessive hunting (Laker et al., 2006). Conservation laws, protection measurements and the creation of protected areas allowed the recovery of vicuñas. The total wild population is about 280,000 individuals, and there are about 40,000 individuals in Argentina (Laker et al., 2006). Vicuñas are camelids well adapted to live in high deserts (Baied and Wheeler, 1993; Franklin, 1982; Koford, 1957). They can use most resources provided by the Puna environment and can be considered generalists in their capacities to use habitats and food resources (Arzamendia and Vilá, 2006; Arzamendia et al., 2006; Borgnia et al., unpublished data; Cajal, 1989). Being generalists, they still prefer to forage in vegas, which are considered the optimal foraging habitat for vicuñas, while steppe are seen as sub-optimal habitats (Aguilar et al., 1999; Alzérreca et al., 2003; Renaudeau d'Arc et al., 2000).

Domestic ungulates (cattle, sheep, goats, horses and donkeys) have occupied the Puna region since the Spanish conquest in the sixteen century. Although local people used to have their own native domestic herds of llamas (*Lama glama*) and alpacas (*Lama pacos*), the use of exotic ungulates was gradually adopted as the process of colonisation progressed and mix herds are preferred (Cajal, 1998; Göbel, 2001). Habitat use by domestic ungulates in the Puna is determined by the shepherds (Göbel, 1994; González, 2001), not the animals.

The objectives of this work were to describe diet and habitat use of sympatric vicuñas, feral donkeys and livestock of Laguna Blanca Reserve (Catamarca) Argentinean Puna, and to test the qualitative predictions of the model of habitat coexistence of Pimm et al. (1985). We tested two assumptions and one qualitative prediction of this isoleg model: (1) both vicuñas and domestics prefer the same type of foraging habitat, (2) vicuñas are generalists while domestics are specialists and (3) vicuñas and domestics are spatially segregated and vicuñas use sub-optimal habitats more than expected from their foraging preferences. We measured habitat preferences using foraging effort. This effort was estimated in two ways: (a) proportion of foraging individuals in each habitat and (b) proportion of plants of a type of habitat in the total diet. Habitat selectivity was measured also in two ways: (1) evaluating the evenness in distribution in the whole study area and (2) estimating the habitat niche extent.

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, 66°40′O) (Fig. 1). Laguna Blanca is the main water body in the low area region (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 (Morlans, 1995).

Borgnia et al. (2006) published a detailed description of vegetation, habitat types and landscapes of the study area. Vegetation is mainly a xerophilous steppe with a large proportion of bare soil. There are two main types of habitat: (1) 'steppe', which can be divided in grass, shrub, mixed steppes (shrubs and bunch grasses) and peladares (open rocky areas with less than 10% of vegetation cover, occupying less than 2% of whole study area) and (2) 'swamps' habitats, including 'vegas' (wetlands with high vegetation cover), and 'salinas' (swamp areas with surface salt and short grasses and high vegetation cover). There are three main grass steppe, dominated by *Panicum chloroleucum*, *Stipa* spp. (*Stipa frigida* and *Stipa vaginata*) and by *Festuca* spp. (*Festuca orthophylla* and *Festuca chrysophylla*). Mixed steppe are a combination of these species of grass with some shrubs like *Adesmia horrida*, *Junellia seriphioides*, *Baccharis incarum*, *Atriplex* spp., *Fabiana* spp., *Acantholippia salsoloides*, between others. There are three kinds of shrubs steppes: one type dominated by *A. salsoloides* (called "rica rica"), other steppe dominated by *Fabiana densa* (called high "tolilla") and a third type dominated by other species of genera *Fabiana* (called low "tolilla"). Vegetation of vegas includes short grasses and grasslikes like *Distichlis* spp., *Deyeuxia brevofolia*, *Amphiscirpus nevadensis*, *Scirpus desertícola*, *Juncus* spp., between others, and tall grasses like *Cortaderia rudiuscula*, *Festuca argentinensis*, *Deyeuxia polygama*. Also includes the shrub *Parastrephia* spp. (called as "Tola"). The Salinas share some vegetation of vegas mentioned before and also includes the shrub *Frankenia triandra* and the forb *Sarcocornia pulvinata*. As in most parts of the Puna, in Laguna Blanca the area occupied by steppe (95%) is substantially larger than swamps areas (5%), although vegetation cover and biomass within steppes (25%) are significantly lower than in swamps areas (75%).

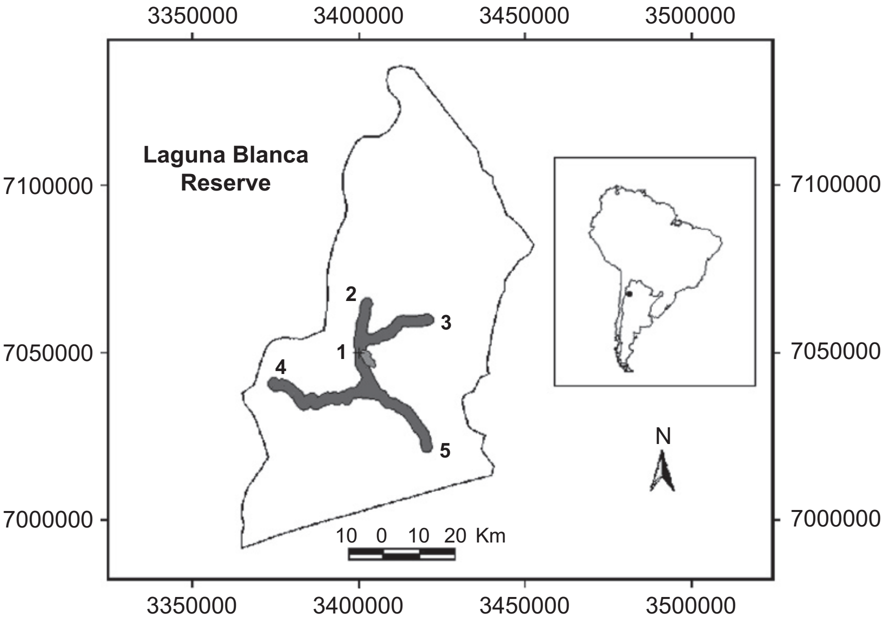


Fig. 1. Study area inside Laguna Blanca Reserve: (1) 'Laguna Blanca' village; (2) 'Corral Blanco' village; (3) 'Rio Rio' Ranch; (4) 'Guzman' ranch and (5) Randolfo's Hill.

In Laguna Blanca Reserve, there are nearly 600 inhabitants and 100 dwellings distributed in three villages: Laguna Blanca, Corral Blanco and Aguas Calientes (Forni, 1981). This last locality was not included in study area. Vicuñas shared the habitat with local people and their pastoral activities. People breed mainly mix herds of sheep (*Ovis aries*) and goats (*Capra hircus*), and also have llamas (*L. glama*), cows (*Bos taurus*) and horses (*Equus caballus*) (Rabinovich et al., 1991; Vilá and Roig, 1992). It is also important the presence of feral donkeys (*Equus asinus*). The use of donkeys as loading animals was important in some parts of Argentinean Puna and they became gradually in feral animals (Cajal, 1998).

Vicuñas are protected inside Reserve although there are few records of poaching in the area (Barbarán, 2002).

2.2. Field and laboratory work

To quantify abundance of animals and to describe their distribution in study area, census counts were performed during May–June 2002, October 2002, March 2003, and September 2003 (Borgnia et al., 2006), covering 57 census hours and 102 km of trails. Counts of animals were made in the morning (08.00–13.00) using binoculars from a vehicle, recording approximately 1.2 km to each side of trails. This maximal distance was calibrated in the field by two observers with Global Position System (GPS). 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 Randolfo's Hill (37 km) and (4) from Laguna Blanca village to Guzmán settlement (47 km). A GPS Garmin 12 was used to record the location and size of groups of vicuñas, donkeys and livestock, the activity of the group ('foraging', 'walking', 'standing up' and 'others'), and habitat type (described above). During censuses the location of villages and human settlements was also recorded.

Faeces of vicuñas, donkeys and livestock were collected in 29 steppe and 25 swamp areas. In each site, vicuñas faeces were taken from three dung piles with fresh pellets. Dung piles were selected randomly from trails used for animal census. Botanical composition of the diet was determined by micro-histological technique (Arriaga, 1986; Holechek, 1982). The sampled unit for vicuñas diet analysis was a mix of 100 fresh faeces from three dung piles and 15–30 fresh faeces for donkeys and livestock, collected from each site (Hansen and Lucich, 1978). Five slides per sample were prepared and 20 fields per slide were analysed at 100 × level of magnification. Identification of plant epidermis fragments were compared with a reference plant collection of study area and relative frequencies of food items in each sample were quantified (Holechek and Gross, 1982).

2.3. Data analysis

Location of groups, herds or individual animals, and anthropogenic centres at study area were mapped from censuses data using Arc View 3.2 and Geographic Marble calculation software. Digital shapes were performed in flat coordinate system (Gauss Krugger, band 3). Nearest Features v3.8 extension of Arc View software was used for calculating the distance from each animal record to settlements. Diet composition was analysed in relation to three vegetation characteristics: (1) taxonomy: plant species or genera; (2) functional groups: shrubs (or sub-shrubs), grasses, grasslikes (that included juncaceous and cyperaceous plants), and forbs (herbaceous dicots and algae); and (3) location: plants from steppe or swamp areas.

For each season and type of ungulate, abundance was estimated as the number of animals counted in the surveyed area, and density was the abundance per square kilometre of that area. Animals associations were investigate by two grids of 1 and 4 km^2 quadrats, which were generated over the distribution map area. Presence–absence data of animals in each quadrat were recorded, and two types of analysis were conducted (Ludwig and Reynolds, 1988): 2×2 contingency tables and Ochiai indices. Evenness (estimated as the number of 1 km^2 quadrats with presence/total quadrats) of vicuñas, donkeys and livestock was also calculated.

Another method used to evaluate impact of inter-specific interactions was to compare niche extent and overlapping. Under Rosenzweig's hypothesis, species should overlap in diet preferences, but should segregate in habitat preferences, and the subordinate species should show a wider habitat niche than the dominant one. The extent of habitat and diet use was calculated with standardised Levins' index: $(1/\sum p_i^2)-1)/(S-1)$, where p_i is the proportion of resource i, and S is the amount of resources. Significant differences between animals were tested with Kruskall–Wallis analysis ($N = 4$ for each animal). Overlapping between pairs of ungulates was calculated with Pianka's index: $(\sum p_{ik} \times p_{ij})/(\sum p_{ik}^2 \times \sum p_{ij}^2)^{1/2}$, where p_{ik} and p_{ij} are the proportions of resources used by animal k and animal j. Values of proportions used in these analyses were obtained for habitat and diet use. Proportions of habitat use were estimated as the number of individuals using a habitat type (from six habitats described in Borgnia et al. (2006): grass steppe, shrub steppe, mix steppe, vega, salina and peladar) divided by the total number of observations. Diet proportions were estimated as the number of fragments of a plant type over the total number of fragments observed.

In this study area llamas were observed very rarely in comparison to other Puna regions. Similarly, horses were rarely observed. Both llamas and horses were only included in the analysis of overall distribution. Goats and sheep are considered "small ruminants" and were referred both as 'shoats' (Namgail, 2004). Data from these animals were account together in this study because they were in mix herds in several sites and it was not easy to discriminate their faeces.

A Kruskal–Wallis non-parametric test and Q test for multiple comparisons (Zar, 1984) was performed to look for statistical differences in diet composition, abundance, density and evenness, and between types of ungulates.

3. Results

3.1. Diet, activity and habitat use

P. chloroleucum, a steppe plant, was the most important plant in the diet of all animals, representing 15–60% of the diet, depending on the ungulate species (Table 1). The second most consumed plant corresponded to genera *Distichlis* (mainly *Distichlis humilis*), a swamp plant species, with percentage between 6% and 20%. Other plants were consumed in relatively large proportions: *F. argentinensis* (reaching 8% in donkey diet) and *A. nevadensis* (reaching 8% in vicuña diet). Some plant species were consumed by donkeys or livestock but they were poor represented in vicuñas diet (*C. rudiuscula*, *Scirpus deserticola*, *Juncus* sp.).

Vicuñas, shoats and cows ate similar percentages of steppe and swamp plants, but donkeys foraged on higher proportions of swamp plants (Table 2). Grasses were the most important group in the diet of all animals. Vicuñas, cows and shoats consumed similar proportions of shrubs and grasslikes, and donkeys consumed more grasslikes than shrubs; forbs were consumed in low proportions by all animals.

Foraging was the most frequent behaviour in vicuñas, donkeys and livestock, followed by walking or standing up (Fig. 2). When we compared the foraging activity of animals between steppe and swamp areas, we found that vicuñas ($\chi^2 = 9.75$, $P<0.05$, df $= 1$) foraged proportionally more in swamp areas (mean $= 72.9$, sd $= 6.9$) than in steppe (mean $= 68.0$, sd $= 8.0$). Donkeys ($\chi^2 = 84.04$, $P<0.01$, df $= 1$) also foraged more in swamp areas (mean $= 82.9$, sd $= 4.0$) than in steppe (mean $= 58.5$, sd $= 13.2$). Livestock invested similar foraging activity ($\chi^2 = 2.01$, $P>0.05$, df $= 1$) in swamp areas (mean $= 54.0$, sd $= 20.0$) than in steppe (mean $= 58.4$, sd $= 17.4$).

If vicuñas had used habitats in accordance to their foraging preferences, they should have used swamps more than steppes. However, the observed habitat utilisation of vicuñas significantly differed from the expectation based on diet composition ($\chi^2 = 2418.5$, df $= 1$, $P<0.0001$). They used less swamp habitat (mean $= 25.3$, sd $= 4.8$) than steppes (mean $= 73.5$, sd $= 4.8$). Cows and shoats were more in swamp habitat (mean $= 65.0$, sd $= 29.1$; and mean $= 68.0$, sd $= 32.8$; respectively) than steppes (mean $= 35.0$, sd $= 29.1$; and mean $= 32.0$, sd $= 32.8$; respectively) from the expectation based in diet composition of each ungulate ($\chi^2 = 68.5$, df $= 1$, $P<0.0001$ for cows, and $\chi^2 = 796.161$, df $= 1$, $P<0.0001$ for shoats). Habitat utilization by donkeys did not differ from the expectation based on diet composition ($\chi^2 = 0.6$, df $= 1$, $P = 0.42$): they used more swamp areas and consumed mostly this type of plants.

In summary, vicuñas can eat a wide range of plant species. However, they invested their foraging effort in consuming plants that grow in swamp habitats, which were less accessible. In contrast, livestock consumed similar proportions of plants from swamp areas than from the surrounding steppe even when local people moved them to forage in swamps.

3.2. Distribution of animals

Vicuñas had similar abundances (total number) or density (animals/km^2) than total livestock ($Q = 1.39$; $P>0.05$) but they were more abundant than donkeys ($Q = 2.63$; $P>0.05$; Table 3). Vicuñas were most widely distributed, with higher

Table 1
Diet composition of animals (relative frequency percentage of plant species)

	FG	H	Vicuñas	Donkeys	Cows	Shoats
Panicum chloroleucum	G	St	25.00	27.61	61.05	35.15
Distichlis spp.	G	Sw	19.48	8.36	6.03	8.33
Eleocharis spp.	GL	Sw	1.57	8.42	2.93	5.60
Festuca argentinensis	G	Sw	5.66	8.16	3.05	2.18
Cortaderia rudiuscula	G	Sw	0.33	5.13	4.46	7.10
Scirpus deserticola	GL	Sw	0.02	4.49	1.46	2.25
Amphiscirpus nevadensis	GL	Sw	8.65	4.36	0.00	2.74
Deyeuxia brevifolia	G	Sw	0.76	4.00	2.13	0.52
Deyeuxia larga	G	Sw	3.95	3.20	3.23	0.00
Acantholippia salsoloides	S	St	3.54	2.34	0.26	5.31
Festuca spp.	G	St	2.10	0.00	0.00	0.00
Sporobolus rigens	G	St	0.21	1.68	0.14	0.21
Ciperaceae unidentify	GL	Sw	1.64	1.45	0.78	0.38
Deyeuxia polygama	G	Sw	0.46	1.28	0.67	0.00
Atriplex sp.	S	St	1.15	0.31	0.16	3.16
Hordeum hallophyllum	G	Sw	0.21	1.00	1.08	0.57
Muhlembergia peruvi	G	Sw	0.39	0.90	2.00	1.37
Fabiana spp.	S	St	0.90	0.76	0.71	1.73
Triglochin palustris	GL	Sw	1.09	0.88	0.00	0.05
Juncus spp.	GL	Sw	0.69	5.57	3.23	7.19
Stipa sp.	G	Sw	0.69	0.90	0.30	0.06
Aristida sp.	G	St	0.64	0.67	0.63	5.71
Maihueniopsis spp.	S	St	0.96	0.53	0.05	1.17
Adesmia horrida	S	St	2.51	0.46	0.05	2.74
Eragrostis nigricans	G	St	0.00	0.21	2.75	0.67
Stipa frigida y S. vaginata	G	St	5.80	0.17	1.48	1.82
Junellia seriphioides	S	St	4.64	0.16	0.42	0.61
Sarcocornia pulvinata	F	Sw	2.08	0.13	0.00	0.00
Frankenia triandra	S	Sw	2.50	0.09	0.00	0.19
Arenaria	F	Sw	0.05	1.53	0.00	0.07
Algae	F[a]	Sw	0.00	2.88	0.00	0.65

FG, functional group (S: shrubs, G: grasses, GL: grasslikes, F, forbs: no ligneous dicots); H, Habitat type (St: steppe, Sw: swamp). Plants with lower proportions than 1% are not shown. Shoats = sheep and goats.

[a] Algae consumption was considered as forbs for analyses.

Table 2
Mean ($\pm$sd) dietary composition (%) in relation to habitat type and functional group ($n = 4$)

	Vicuñas	Donkeys	Cows	Shoats
Habitat type				
Steppe	45.2 (10.9) a	32.6 (8.9) a	63.4 (28.8) a	54.5 (25.0) a
Swamp	54.8 (10.9) a	67.4 (8.9) b	36.6 (28.8) a	45.5 (25.0) a
Z	0.764	−2.310	0.248	0.289
Functional group				
Shrubs	16.3 (1.8) a	6.9 (3.7) a	2.2 (2.0) a	14.5 (15.7) a
Grasses	66.1 (5.5) b	62.1 (6.7) b	88.1 (12.4) b	63.1 (7.9) b
Grasslikes	14.8 (3.4) a	26.2 (11.9) c	9.7 (12.3) a	21.4 (9.7) a
Forbs	2.8 (2.7) c	2.2 (4.3) a	0.0 a	1.1 (1.6) c
H	12.79	12.24	7.38	13.08

Different letters show significant differences in comparisons for each animal type.

evenness values than donkeys ($Q = 2.98$; $P < 0.05$) and livestock ($Q = 3.67$; $P < 0.05$). Vicuñas were well represented in four of the five trials, while livestock and donkeys were concentrated in the north and centre (Fig. 3).

The percentage of vicuñas observed at less than 1 km from human settlements was only 11.7%, while 81.4% of livestock was observed at less than 1 km. Donkeys showed an intermediate value (44.6%). A Kruskal–Wallis test (3 types of ungulates × 4 censuses) to analyse distances from human settlements showed significant differences ($H = 8.00$, $N = 12$, $P = 0.0183$), with vicuñas staying at significant larger distances from settlement than donkeys ($Q = 2.77$) and livestock ($Q = 3.88$), and no differences between the latter two ($Q = 1.11$).

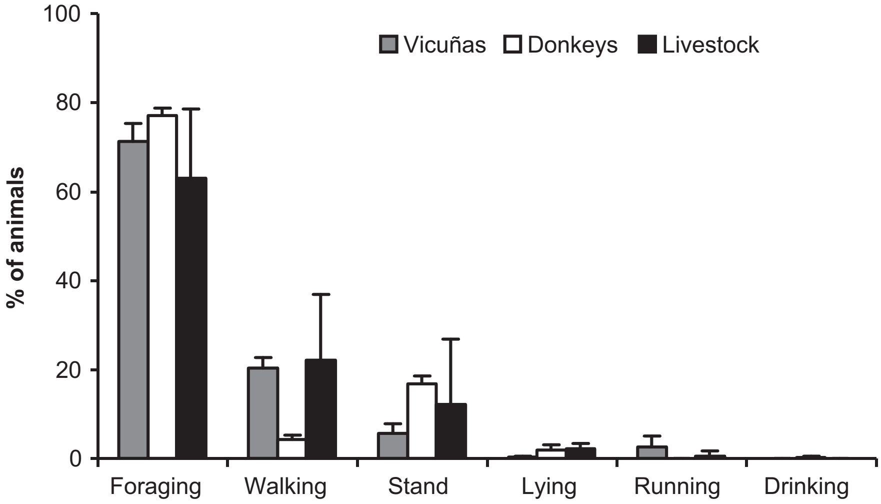


Fig. 2. Activity frequency of animals during all sample periods.

Table 3
Abundance (total number of animals), density (animals/km^2) and evenness for each category of ungulate

	Abundance	Density	Evenness
H	8.35	8.37	7.71
Vicuñas	1449 (215) a	5.7 (0.9) a	0.53 a (0.04) a
Livestock	1102 (364) a	4.4 (1.3) a	0.20 b (0.04) b
Donkeys	241 (88) b	1.0 b (0.3) b	0.20 b (0.01) b

Eveness is estimated as the number of quadrants of 1 km^2 (see Methods) occupied by the species. Different letters shows significant differences between ungulates.

3.3. *Inter-specific association, niche extent and overlapping*

Vicuñas and livestock showed a significant level of segregation in most samples while donkeys and domestic herds presented a significant association in all samples (Table 4).

Overlapping (using Pianka's index) in diet resources was higher than 70% for all pair of ungulates and higher than values for habitat overlapping ($U = -2.61$, $P = 0.0090$, $N = 10$) (Table 5). Habitat niche extent was significant different between vicuñas, donkeys and livestock ($H = 11.54$, $P = 0.0091$, $N = 16$). This index was higher for vicuñas in comparison with cows ($Q = 2.78$) and shoats ($Q = 4.78$) (Table 5).

4. Discussion

There was high overlap of diets between vicuñas, feral donkeys and livestock (cows, shoats). Vicuñas were generalists in the use of habitat but invested foraging effort in swamp habitats, while livestock were specialised in swamp habitats, where shepherds took them for grazing. Vicuñas and livestock were spatially segregated. Previous studies have also shown that vicuñas preferred for swamp habitats (Franklin, 1982; Koford, 1957; Lucherini et al., 2000; Renaudeau d'Arc et al., 2000; Vilá and Roig, 1992). However, vicuñas used these habitats less than expected from their foraging preference. Based on an isoleg model developed by Pimm et al. (1985) for this type of competitive context, we concluded that vicuñas and livestock coexist because vicuñas occupy sub-optimal habitats whilst livestock concentrate their foraging in the richest parts. Vicuñas can deal with poor habitats because they have several morphological and physiological adaptations to live in deserts (Hofmann et al., 1983) and to forage on the poor, ligneous and fibrous vegetation of the Puna region (Sponheimer et al., 2003; Vallenas, 1991). One possible explanation for the large amount of vegetation from vegas in vicuñas diet is that there is a temporal segregation with domestic ungulates, in a way that vicuñas used vegas when cattle were moved to other location. Considering that census were conducted in the morning, the use of vegas could have increase in the afternoon, when livestock is moved to other areas or yards, a common practice in the region (Castro Lucic, 2000; Forni et al., 1993). This type of temporal segregation has been previously report in other contexts of interaction between livestock and vicuñas (Koford, 1957).

In South America, there are few studies about interactions between livestock and wild camelids, mainly guanacos (*Lama guanicoe*, camelids) in Patagonia (Baldi et al., 2001, 2004; Bonacic et al., 1996; Bonino and Pelliza Sbriller, 1991; Puig et al.,

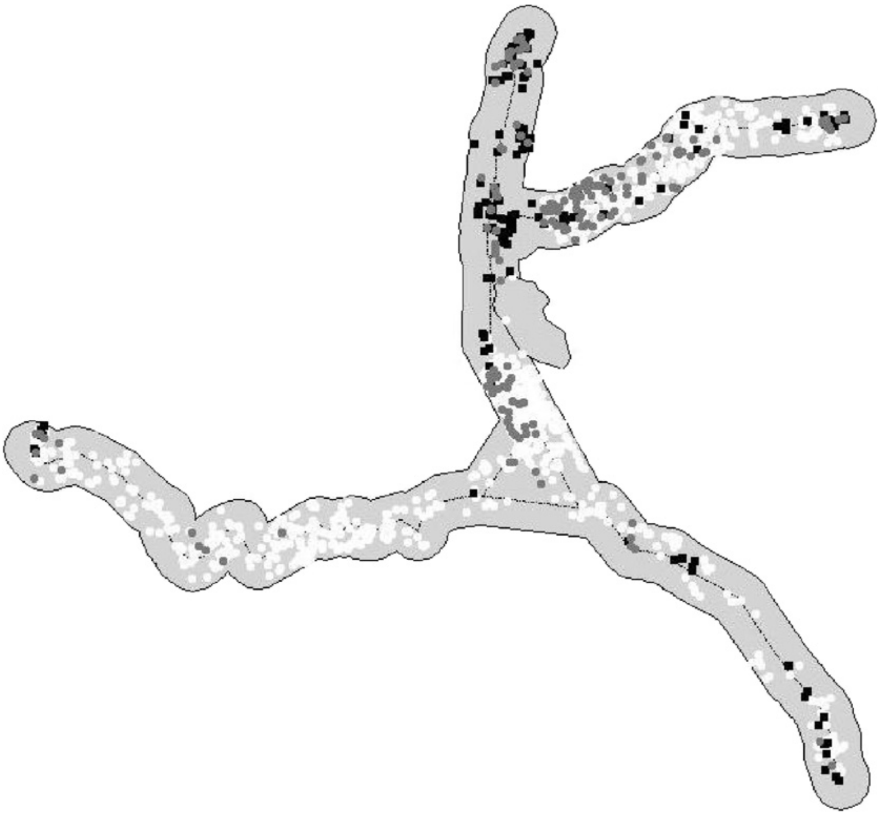


Fig. 3. Spatial distribution of vicuñas (white points), donkeys (grey points) and livestock (black points) in study area for all censuses. Each point refers to an animal group, herd or solitary individual record.

Table 4
Interspecific associations

Species associations	1 km^2			4 km^2		
		χ^2	Ochiai		χ^2	Ochiai
2 May						
Vicuñas–donkey	+	7.35*	0.49	+	4.28*	0.60
Vicuñas–livestock	–	1.81	0.22	–	0.78	0.38
Donkeys–livestock	+	8.03*	0.42	+	6.92*	0.58
2 October						
Vicuñas–donkeys	+	8.24*	0.52	+	2.27	0.56
Vicuñas–livestock	–	6.53*	0.20	–	6.30*	0.30
Donkeys–livestock	+	4.02*	0.38	+	5.76*	0.56
3 March						
Vicuñas–donkey	–	0.08	0.33	–	11.46*	0.37
Vicuñas–livestock	–	4.92*	0.25	–	4.68*	0.50
Donkeys–livestock	+	22.58*	0.59	+	11.93*	0.71
3 September						
Vicuñas–donkeys	+	0.16	0.33	–	1.10	0.40
Vicuñas–livestock	–	6.57*	0.15	–	9.62*	0.27
Donkeys–livestock	+	11.82*	0.45	+	2.21	0.47

Asterisks shows significant associations with $P<0.05$. (+), positive association; (–), negative association or segregation. Ochiai index vary from 0 (no association) to 1 (high association).

2001, 2006). These authors found a negative correlation between guanacos and livestock densities and positive correlation with preferred forage abundance. Guanacos also appear to be subordinate to livestock and coexist by adapting to sub-optimal habitats. Although no systematic studies have been conducted on vicuñas–livestock interactions, previous authors

Table 5
Overlapping (Pianka's index values) and niche extent (Levins' index values)

	Habitat	Diet
Overlapping		
Vicuñas–donkey	0.67	0.83
Vicuñas–cow	0.60	0.78
Vicuñas–shoat	0.45	0.84
Donkey–cow	0.46	0.90
Donkey–shoat	0.55	0.94
Niche extent		
Vicuñas	0.60 a	0.19 a
Donkeys	0.26 ab	0.25 a
Cows	0.24 bc	0.05 a
Shoats	0.19 bc	0.16 a

Different letters indicate significant differences between animals for each niche extent index ($P < 0.05$).

have mentioned the possibility of vicuñas being affected by livestock and their shepherds (Boswall, 1972; Jungius, 1971; Villalba, 2003). In Bolivia, vicuñas were displaced from most good grazing sites, and small populations survived in areas less attractive to livestock and difficult of access (Jungius, 1972).

Feral donkeys appeared to have an intermediate distribution in comparison to vicuñas and livestock. They were positively associated with vicuñas and livestock, they had similar pattern of habitat use as livestock, overlap with vicuñas and domestic animals in diet and are tolerant of arid environments. Their inability to ruminate or recycle urea makes protein content in their diet an important limiting factor and required them to consume large quantities of food (Saltz et al., 2000). Even though donkeys did not appear to displace vicuñas from optimal patches to the same degree as domestic livestock, they can have substantial negative impacts on Puna environment through overgrazing, trampling of the soil, and contamination of water sources.

Laguna Blanca is a The Man and the Biosphere (MAB) reserve. This type of reserve aims to improve the relationship of people with their environment globally. Economic activities within the reserve are promoted both by local government and the MAB program philosophy. This study provides a first scientific suggestion of a negative impact on the native wildlife by the introduction of exotic livestock on the reserve. Swamps are important as grazing areas and water sources. Vicuñas must drink daily, so access to at least small swamp areas is critical. In the absence of livestock, we could expect that vicuñas would have used 'vegas' more frequently, allowing a significant increase in their population density.

Acknowledgements

We thank to V. Benitez, G. Cassini and M. Morales for help in field work; to Villagra family and to E. Frá (Catamarca Environment Secretary) for logistic support; to L. Difranco for help in Arc View Software. This work was financed by European Union through the Grant INCO-DEV for MACS Programme (Sustainable use of South American Camelids), by Scientific and Technologic Agency of Argentina through Grant PICT99 01-06639 and by National University of Luján, Argentina.

References

Aguilar, M.G., Chagra Dib, E.P., Neumann, R., 1999. Rangeland in the diet of vicugnas. In: Gerken, M., Renieri, C. (Eds.), Progress in South American Camelids Research, vol. 105. EAAP, Götitingen, Germany, pp. 329–333.

Alzérreca, H., Prieto, G., Laura, J., 2003. Utilización de forraje de los bofedales y gramadales en el altiplano y altoandino de Bolivia. pp. 415–421.

Arriaga, M., 1986. Metodología adaptada al estudio de hábitos alimentarios en insectos herbívoros. Comunicaciones del MACN Tomo II, no. 15, SIN 0374-6801.

Arzamendia, Y., Vilá, B.L., 2006. Estudios etoecológicos de vicuñas en el marco de un plan de manejo sustentable: Cieneguilla, Jujuy. In: Vilá–Proyecto Macs, B. (Ed.), Investigación, Conservación y manejo de vicuñas.

Arzamendia, Y., Cassini, M.H., Vilá, B.L., 2006. Habitat use by vicuñas, *Vicugna vicugna*, in Laguna Pozuelos Reserve (Jujuy, Argentina). Oryx 40, 1–6.

Baied, C., Wheeler, J., 1993. Evolution of high Andean Puna ecosystems: environment, climate, and culture change over the last 12,000 years in the central andes. Mountain Res. Dev. 13, 145–156.

Baldi, R., Albon, S.A., Elston, D., 2001. Guanacos and sheep: evidence for continuing competition in arid Patagonia. Oecologia 129, 561–570.

Baldi, R., Pelliza-Sbriller, A., Elston, D., Albon, S., 2004. High potential for competition between guanacos and sheep in Patagonia. J. Wildlife Manage. 68, 924–938.

Barbarán, F.R., 2002. CITES and the Convention on Biological Diversity, in Search of Sustainable Use of the Vicuña (*Vicugna vicugna*) in Northwestern Argentina. Forum M (Ed.).

Bonacic, C., Iriarte, J.A., Bas, F.J., 1996. Endangered guanaco (*Lama guanicoe*) population habitat use in the Andean mountains of Chile. J. Wildlife Res. 1, 85–88.

Bonino, N., Pelliza Sbriller, A., 1991. Comparación de las dietas del guanaco, ovino y bovino en Tierra del Fuego, Argentina. Turrialba 41, 452–457.

Borgnia, M., Maggi, A., Arriaga, M., Aued, B., Vilá, B.L., Cassini, M.H., 2006. Caracterización de la vegetación en la Reserva Provincial Laguna Blanca (Catamarca, Argentina). Eco. Austral. 16, 29–45.

Boswall, J., 1972. Vicuña in Argentina. Orix 11, 449–453.

Cajal, J.L., 1989. Uso de hábitat por vicuñas y guanacos en la Reserva de Biósfera San Guillermo. Vida Silvestre Neotropical 2, 21–31.

Cajal, J.L., 1998. La conservación de los camélidos silvestre en la puna central y cordillera frontal. In: Cajal, J.L., García Fernández y R. Tecchi (Eds.), Bases Para la Conservación y Manejo de la Puna y Cordillera Frontal. FUCEMA-UNESCO, Uruguay, pp. 267–285.

Castro Lucic, M., 2000. Llameros de puna salada en los Andes del Norte de Chile. In: Pastoreo Altoandino, Ochoa, J. y., Kobashaski, Y. (Eds.), Editorial Plural.

Coe, P.K., Johnson, B.K., Stewart, K.M., Kie, J.G., 2005. Spatial and temporal interactions of elk, mule deer, and cattle. In: Wisdom, M.J., technical, editor. The Starkey Project: A Synthesis of Long Term Studies of Elk And Mule Deer. Reprinted from the 2004. Transactions of the North American Wildlife and Natural Resources Conferences, Alliance Communications Group, KS, USA, pp. 150–158.

Forni, F., 1981. Laguna Blanca, una comunidad de pastores de llamas en la puna catamarqueña. Boletín CEIL 7, Buenos Aires, pp. 23–27.

Forni, F., Tort, M.I., Jiménez, D. y. Pessina, L., 1993. Estudios socioantropológicos de la puna catamarqueña. Informe de Investigación. Consejo Latinoamericano de Ciencias Sociales (CLACSO).

Franklin, W., 1982. Biology, ecology and relationship to man of the South American Camelids. In: Mares, M., Genoways, H. (Eds.), Mammalian Biology in South America.

Franklin, W., 1983. Contrasting sociecologies of South America's wild camelids: the vicuña and the guanaco. In: Eisemberg, J.F., Kleiman, D.G. (Eds), Advances in the Study of Mammalian Behaviour.

Fritz, H., De Garine-Wichatitsky, M., Letessier, G., 1996. Habitat use by sympatric wild and domestic herbivores in an African savanna woodland: the influence of cattle spatial behaviour. J. Appl. Ecol. 33, 589–598.

Göbel, B., 1994. El manejo del riesgo en la economía pastoril de Susques. Zooarqueol. Camélidos 1, 43–56.

Göbel, B., 2001. El ciclo anual de la producción pastoril en Huancar (Jujuy, Argentina). In: El uso de los camélidos a través del tiempo. Ed Del Tridente.

González, J., 2001. Manejo de camélidos domésticos en Aiquina (norte de Chile, II región). In: El uso de los camélidos a través del tiempo. Ed Del Tridente.

Hansen, R.M., Lucich, G.C., 1978. A Field Procedure and Study Design for Fecal Collections to be used to Determine Wildlife and Livestock Food Habits. Colorado State University, Fort Collins, CO.

Hofmann R.K., Otte, K., Ponce, C.F., Ríos, M.A., 1983. El Manejo de la Vicuña Silvestre. Eschborn: GTZ 2 vols., 705pp.

Holechek, J., 1982. Sample preparation techniques for microhistological analysis. J. Range Manage. 35, 267–268.

Holechek, J., Gross, B., 1982. Evaluation of different calculation procedures for microhistological analysis. J. Range Manage. 35, 721–726.

Jungius, H., 1971. The vicuña in Bolivia: the status of an endangered species, and recommendations for its conservation. Z. Saugetierkunde 36, 129–192.

Jungius, H., 1972. Bolivia and the vicuña. Oryx 11 (5), 335–346.

Koford, C.B., 1957. The vicuña and the puna. Ecol. Monogr. 27, 153–219.

Laker, J., Baldo, J., Arzamendia, Y., Yacobaccio, H., 2006. La vicuñas en los andes, In: Vilá–Proyecto Macs, B. (Ed.), Investigación, Conservación y Manejo de Vicuñas.

Lucherini, M., Birochio, D.E., Marinelli, C., Legato, A.M., 2000. Spatial niche overlap between vicuñas and guanacos. Acta Theriol. 45, 57–70.

Ludwig, J.A., Reynolds, J.F., 1988. Statistical Ecology. A Primer on Methods and Computing. Wiley, New York.

MacArthur, R.H., Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101, 377–385.

Massy, N., Weeda, A., 2003. Zonificación de la aptitud ganadera del departamento de Potosí. In: Procedings III Congreso Mundial sobre Camélidos y I Taller Internacional de DECAM,. Potosí, Bolivia.

Mishra, C.H., Van Wieren, S.E., Ketner, P., Heitkonig, I.M., Prins, H., 2004. Competition between domestic livestock and wild bharal *Pseudois nayaur* in the Indian trans-Himalaya. Ecology 41, 344–354.

Morlans, C., 1995. Regiones Naturales de Catamarca. Provincias Geológicas y Provincias Fitogeográficas. Revista de Ciencia y técnica. Volumen II. N°2, año 1. Universidad Nacional de Catamarca. Secretaría de Ciencia y Tecnología. Consejo de Investigacioes. San Fernando del Valle de Catamarca. Catamarca, Argentina.

Namgail, T., 2004. Interactions between argali and livestock, Gya-Miru Wildlife Sanctuary, Ladakh, India. Final Project Report submitted to International Snow Leopard Trust.

Pimm, S.L., Rosenzweig, M.L., Mitchell, W., 1985. Competition and food selection: field test of a theory. Ecology 66, 798–807.

Puig, S., Videla, F., Cona, M.I., Monge, S.A., 2001. Use of food availability by guanacos (*Lama guanicoe*) and livestock in Northern Patatonia (Mendoza, Argentina). J. Arid Environ. 47, 291–308.

Puig, S., Videla, F., Cona, M., Rossi, M., Roig, V., 2006. Relaciones entre el guanaco, ganado y vegetación en la Reserva LaPayunia (Mendoza, Argentina). In: IV Congreso Mundial sobre Camélidos. Santa María, Catamarca, Argentina.

Rabinovich, J.E., Capurro, A.F., Pessina, L., 1991. Vicuña use and the bioeconomics of an Andean Peasant Community in Catamarca, Argentina. In: Robinson, J.G., Redford, K.H. (Eds.), Neotropical Wildlife use and Conservation. Chicago Press University.

Renaudeau d'Arc, N., Cassini, M.H., Vilá, B.L., 2000. Habitat use of vicuñas in Laguna Blanca Reserve (Catamarca, Argentina). J. Arid Environ. 46, 107–115.

Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology 62, 327–335.

Saltz, D., Rowen, M., Rubenstein, D.I., 2000. The impact of space use patterns of reintroduced Asiatic wild ass on effective population size. Conserv. Biol. 14, 1852–1862.

Schwartz, Ch. C., Ellis, J.E., 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18, 343–353.

Sixto, M., 2003. Determinación de la capacidad de carga y carga animal en bofedales de la comunidad de Cosapa, provincia Sajama, Oruro, Bolivia. In: Procedings III Congreso Mundial sobre Camélidos y I Taller Internacional de DECAMA, Potosí, Bolivia.

Sponheimer, M., Robinson, T., Roeder, B., Hammer, J., Ayliffe, L., Passey, B., Cerling, T., Dearing, D., Ehleringer, J., 2003. Digestion and passage rates of grass hays by llamas, alpacas, goats, rabbits, and horses. Small Ruminant Res. 48, 149–154.

Vallenas, A., 1991. Características anatomofisiológicas. In: Fernández Baca, S. (Ed.), Avances y perspectivas del conocimiento de camélidos sudamericanos, Santiago, Chile.

Vilá, B.L., Roig, V.G., 1992. Diurnal movements, family groups and alertness of vicuña (*Vicugna vicugna*) during the late dry season in the Laguna Blanca Reserve (Catamarca, Argentina). Small Ruminant Res. 7, 289–297.

Villalba, L., 2003. Uso de hábitat e interacciones entre la vicuña y la alpaca en la reserva nacional de fauna Ulla Ulla, Bolivia, in Memorias del III Congreso Mundial sobre Camélidos, 1er. Taller internacioal de DECAMA (Eds CIF,FCAy P- UMSS), vol I, Potosí, Bolivia, pp. 205–210.

Voeten, M.M., Prins, H.H.T., 1999. Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. Oecologia 120, 287–294.

Zar, J.H., 1984. Biostatistical Analysis, second ed. Prentice-Hall International, Englewood Cliffs, NJ.