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Vicugna habitat use and interactions with domestic ungulates in Jujuy, Northwest Argentina

Abstract: Worldwide vicugna numbers are slowly recovering after the implementation of conservation measures in several areas of the Andean Puna. Amongst some communities, vicugnas are sustainably managed through captures, shearing, and release schemes. In this study, we explored habitat use and interactions between vicugnas and domestic livestock in Jujuy, Northwest Argentina. We measured the habitat selectivity of vicugna by evaluating the relationship between the availability and its use of vegetation. We estimated the extent and overlap of habitat niche, as well as the foraging effort of vicugnas on the basis of their individual behaviour. Vicugnas and domestic livestock were highly selective in their use of land. They also had similar foraging preferences, grazing rather on the mixed steppe grasses and grasslands that offered greater grass cover. The distribution of vicugna in relation to domestic animals differed according to species and density. With mean density of llamas, vicugnas showed mixed herds but with any other livestock and greater densities, they were segregated. In mixed grazing, when vicugnas engaged with llamas, no behavioural interaction or competition was observed. The presence of herders with dogs was the main stress factor for vicugnas. Here we discuss the importance of a multi-specific management approach.

Keywords: livestock; llamas; management; pastoralism; vicugna.

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Introduction

The vicugna (*Vicugna vicugna vicugna* Molina, 1782) is a wild South American camelid inhabiting the high Andean arid environment known as the Puna (Franklin 1974). The vicugna was almost extinct by the middle of the 20th century because of overhunting for its fine and high-quality fleece. After 30 years of proactive, effective protection and management of vicugnas, the number of this species has recovered and it is now considered as "least concern" by International Union for Conservation of Nature (Lichtenstein et al. 2008). In Argentina, the population currently totals more than 75,000 animals (Baigún et al. 2008). The species is listed in two appendices of CITES (1973) (Convention on International Trade in Endangered Species of Wild Fauna and Flora): some populations in Argentina and Chile are listed in Appendix 1 (international trade is prohibited), while the whole populations in Peru, Bolivia, and Ecuador, and some in Chile and Argentina (Catamarca and Jujuy provinces) are listed in Appendix II (controlled use of live shorn animals) (Laker et al. 2006, Sahley et al. 2007, Arzamendia and Vilá 2012).

There is strong pressure from local communities to start and develop the commercial exploitation of this species (Vilá and Lichteinstein 2006). However, sustainable management can only be achieved through a deep understanding of vicugna ecology. Hence, studies on key aspects, such as habitat use and potential competitors, are necessary to evaluate and subsequently plan the economic exploitation of certain target populations.

Koford's (1957) seminal paper demonstrated that vicugnas use only a small proportion of their potential habitat, a fact reiterated by later studies. These investigations revealed several factors that could be used to determine the distribution of desert animals. The most useful ones for explaining vicugna distribution are the availability of forage (Franklin 1983, Cajal 1989, Renaudeau d'Arc et al. 2000, Arzamendia and Vilá 2006, Arzamendia et al. 2006, Borgnia et al. 2008, Rojo et al. 2012), the nutritional quality of forage (Benítez et al. 2006, Borgnia et al. 2010, Mosca Torres and Puig 2010), and the availability of water sources (Franklin 1983, Arzamendia and Vilá 2006). Environmental conditions such as anthropogenic interventions (e.g.,

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roads, mines, or livestock herding strategies) and terrain characteristics (e.g., elevation or slope) also influence the distribution of vicugnas (Arzamendia and Vilá 2006, Borgnia et al. 2010). Understanding these factors and their relative importance to the ecological niche of vicugnas allows wildlife researchers to predict animal distribution and response to habitat alterations.

Across the world, a common practice in livestock production on rangelands is the eradication of large, wild indigenous herbivores. It is widely believed that these wild animals compete with livestock for food resources (du Toit 2011). Domestic ungulates in the Argentinean Puna include llamas (*Lama glama* Linnaeus, 1758) – domesticated in the Andes 5000 years ago – and cattle (*Bos taurus* Linnaeus, 1758), sheep (*Ovis aries* Linnaeus, 1758), goats (*Capra hircus* Linnaeus, 1758), and donkeys (*Equus asinus* Linnaeus, 1758), all of which arrived with the Spanish in the 16th century. By the 20th century, most Puna herders were dedicated to sheep husbandry. Some communities though have continued breeding llamas and alpacas (*Vicugna pacos* Linnaeus, 1758) as part of a mixed-herd strategy (Cajal 1989, Göbel 2001). In the case at hand, it is known that vicugnas are often illegally poached or chased away by dogs to exclude them from rich patches of pasture (Laker et al. 2006) used for the benefit of domestic ungulates.

Studies into the spatial relationship between vicugnas and domestic ungulates revealed that an overlapping diet resulted in competition for resources and the subsequent displacement of vicugnas to less productive and/or more degraded environments (Borgnia et al. 2008, 2010, Rojo et al. 2012).

The core objective of this study was to investigate (1) vicugna habitat use and selection using indicators of foraging effort and (2) the existence of habitat overlapping by vicugnas and livestock located in the Puna area of eastern Toquero, Jujuy, Northwest Argentina. The following hypotheses were tested: a) vicugna foraging activity shows selectivity towards grasses in all habitats; b) vicugnas and livestock prefer the same grazing habitats and overlap in their distribution; and, c) vicugnas and livestock are spatially segregated and, contrary to their foraging preferences, vicugnas use sub-optimal habitats as a direct consequence of the herding strategies.

Materials and methods

Study area

The eastern Toquero study area (320.5 ha) is located in central Andes in Argentina, within the Pozuelos Biosphere Reserve (66°15′W, 21°50′S), with an elevation of 3700–3900 m above sea level. This reservation, located in an endorheic basin within the dry Puna (Gomez Molina and Little 1981), has a central depression with a permanent lake flanked by two North-South ridges. The study area belongs to the piedmont and eastern sierras morphodynamic environments of the Reserve (Cendrero et al. 1993). Climate is extreme, with annual average temperatures below 9°C and frequent frosts. Diurnal fluctuations in temperature can be as high as 40°C. Rain (annual mean 350 mm) falls between November to March (Cendrero et al. 1993). Following the USDA Soil Classification (2010), the dominant soils in the study area are Entisols (Lithic Torripsamments and Typic Torriorthents) (Nadir and Chafatinos 1990). Phytogeographically, the area is a xerophytic steppe with a high degree of bare soil (Cabrera 1957). The distribution pattern of steppe-grass concentrations is not homogeneous. Additionally, antropogenic activities, mainly grazing, have influenced the vegetation distribution (Cendrero et al. 1993).

Vicugnas share this habitat with three human families and their livestock, namely, llamas, sheep, and cattle. The study area was divided into three distinct sectors, each occupied by one family: a northern fenced paddock (NF) of 27.7 ha; a northern pastureland without fences (N) of 61 ha; and, a southern pastureland without fences (S) of 228 ha. There were variations in the herding strategies of the three families. The family occupying sector NF used a transhumant pastoral strategy with livestock displacement during the wet (December to May) and dry (May to November) seasons. In the dry season, they grazed approximately 350 sheep, 30 llamas, and 10 cattle; during the wet season, they grazed 200 sheep, 122 llamas, and 10 cattle. We observed that vicugnas could easily jump over the fences. The two open pasturelands were grazed during the whole year by 300 sheep, 150 llamas, and 8 cattle in sector N; and 300 sheep, 250 llamas, and 30 cattle in sector S. During the second year of our survey, we observed one feral donkey in the dry season and six in the wet season in sectors N and S. Natural water sources were available to wild and domestic ungulates, although these were restricted in the dry season.

Data collection and analyses

Data were collected over the course of 2 years (2003 to 2004) from a high fixed point covering the whole area. The same sampling effort was applied during the different seasons.

We used binoculars (20×80) to record the individual behaviour of vicugnas. The whole study area was surveyed using the scan sampling method (Martin and Bateson 1986) for a total of 160 scans (in 21 days: 9 days in the dry season and 12 days in the wet season). Each workday was subdivided into four time slots (07.00–10.00, 10.00–13.00, 13.00–16.00, 16.00–19.00 h.), and two scans were performed in each slot.

The following variables were recorded for each vicugna and livestock group sampled: location (habitat type determined by plant community; sector NF, N, or S); type and size of group (i.e., family: 1 male with several females and calves; bachelor group: male troops, solitary, or unidentified), behaviour of most members of the group (focusing on grazing in this study); and, for the vicugnas group, the presence and distance (measured in vicugna unit) of humans, dogs, and livestock.

The foraging activity of vicugnas and the interactions between vicugnas and livestock were collected using animal focal methods (Martin and Bateson 1986). We obtained 135 animal focal samplings of 15 min each evenly distributed among the four time slots. Each behavioural input referred to the number of minutes in which a particular behaviour occurred in a 15 min sampling. Each day, focal animals were randomly chosen. We discriminated vicugnas by sex (given the proximity to the animals, it was possible to observe sexual organs with binoculars), age (calves and adults), and social group (family male, females, calves, bachelors, and solitary). We carefully avoided sampling the same individual twice each day.

Analysis and interpretation of aerial pictures (scale: 1:45,000) permitted the classification of the study area into habitat types. Following the methodology of Matteucci and Colma (1982), the study area was classified according to plant community characterised by their physiognomy and dominant plant species present, and their location in sectors with different land use as paddocks. The study area was demarcated in the field through spot-points taken with a handheld geographical positioning system. Following the methodology of Matteucci and Colma (1982), 2 × 2 m sampling plots were studied within each habitat type in each season, documenting vegetation composition, height, cover (measured by visual estimation), and dominance. A total of 52 plots were sampled, covering all habitat types proportional to their ubiquity. We collected specimens of all the plants found in the study area for taxonomic identification (Zuloaga et al. 2008). We tested differences in vegetation cover over the seasons and the 2 years using the Friedman test, and post-test for multiple comparisons between ranks to study significant differences at $p<0.05$ (Siegel 1991, Balzarini et al. 2008).

We measured habitat use and selection using foraging effort, which was estimated using two scales: (a) proportion of time in each focal sampling in which the vicugna was foraging each plant species or functional group within a vegetation community, thereby yielding the individual foraging time; and (b) proportion of foraging individuals in each habitat type. Habitat selectivity was also measured in two ways: (1) by evaluating the relationship between the use of a resource and its availability in the study area (Manly et al. 1993) and (2) by estimating the habitat niche extent (Krebs 1998).

Vicugna foraging activity was measured by direct observation in each focal animal and analysed in relation to foraging time following characteristics used by Borgnia et al. (2010): distribution of plants by vegetation community; stratum: low (up to 10 cm high) and high (above 10 cm high); functional groups: shrubs (or sub-shrubs), grasses, grass-like plants (which include juncaceous and cyperaceous plants), and forbs (or herbaceous dicotyledonous); and, taxonomy: plant species or genus. We compared the mean number of minutes/focal sample in which vicugnas foraged each plant species by vegetation community surveyed using Friedman test and post-test for multiple comparisons between ranks to study significant differences at $p<0.05$ (Balzarini et al. 2008).

Forage availability was estimated as a mean percentage of vegetation cover for each vegetation category (vegetation community, stratum, functional groups, and individual species). Forage selection was analysed using vegetation cover as estimator of availability according to Jacob's modification of Ivlev's selectivity index:

$$S=(r_i-p_i)/(r_i+p_i-2r_ip_i)$$

where r_i and p_i are the proportion (between 0 and 1) 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).

Habitat use was determined by the frequency in which groups of vicugna were observed in each habitat type. Habitat availability was the proportion of the area occupied by each vegetation community within each sector (NF, N, and S).

Habitat selection was analysed by the relationship between the use of a resource and its availability (Manly et al. 1993) combined in a selection index tested with a log-likelihood x^2. The selection index was calculated as

$$a=r_i/n_i(1/(S_{rj}/_{nj}))$$

where r_i and r_j are proportions of prey type i or j in diet, and n_i and n_j are proportions of prey types i or j in the environment. The a values are normalized so that the sum of all values equals 1. When selective feeding does not occur, *a* is equal to the inverse of the total number of food types. Bonferroni confidence intervals were estimated to evaluate the significance of each index (Manly et al. 1993).

Niche overlap at habitat scale was estimated using the Pianka overlap index (Krebs 1998):

$$\sum p_{ik} \star p_{ij} / (\sum^{2}_{p_{ik}} / \sum^{2}_{p_{ij}})$$

where p_{ij} is the proportion of resource *i* to total resources used by species *j*, and p_{ik} is the proportion of resource *i* to total resources used by species *k*, which is measured from the number of individuals using each habitat type. The habitat niche extent was estimated using the standardised Levins' index:

$$((1/P_{p_i} \star 2)\text{-}1)/(S\text{-}1)$$

where p_i is the proportion of resource *i*, and *S* is the amount of resources.

For each season and species of ungulate, abundance was estimated as the mean number of animals counted per scan (n=160) in the surveyed area and density was the abundance per square kilometre. A Kruskal-Wallis nonparametric test and a post-test for multiple comparisons among ranks (Balzarini et al. 2008) were performed to look for statistical differences in abundance and density. We applied a Spearman correlation analysis (Balzarini et al. 2008) among vicugna density and llamas, sheep, and cattle densities.

Results

Vicugna foraging activity

Vicugnas foraged on 17 of the 33 (51%) plant species available in the study area, of which 50% were grasses, 28% shrubs, 11% forbs, and 11% grass-like plants (Table 1). Independently of the presence of domestic livestock, vicugnas grazed both low- (15 plant species) and high- (14 plant species) stratum plants with no noticeable difference in the number of plant species consumed (Table 1). However, they spent more time foraging low-stratum grasses (Figure 1). The mean time vicugnas foraged each plant species by vegetation community did not vary between seasons (T^2=0.16, p=0.69, n=44), except for *Adesmia* sp., which vicugnas foraged more during the wet season (T^2=2.5, p=0.01).

Low-stratum grasses, such as *Bouteloua simplex* and *Aristida Antoniana*, were consumed in greater proportion to their availability with a strong selection (mean of Ivlev index=0.84, min=0.66, max=1) in particular vegetation communities, such as: tolar, Pa: bunchgrass; E B.b.: *Baccharis boliviensis* steppe; Pe: Peladar; E P.p.- De.: *Parastrephia lucida*; and *Deyeuxia* sp. steppe. Comparisons by stratum showed that low-stratum grasses were always used in higher proportions, except in the case of *P. lucida*, *Deyeuxia* sp. steppe, and *Deyeuxia* sp. grassland. In these vegetation communities, where *Deyeuxia* sp. belonged both to high and low strata, we quantified grass consumption in both strata and observed that grasses were consumed in greater proportion to their availability, with a strong selection in the *P. lucida* and *Deyeuxia* sp. mixed steppe (Figure 1). In *Deyeuxia* sp. grassland, with a cover of 85% and 100%, grasses were foraged in proportion to their availability across all seasons. Only the shrub *Adesmia* sp. was highly selected for (0.75) in *Parastrephia quadrangularis* shrub steppe and *Fabiana densa* mixed steppe, whereas *Jarava* sp. and *P. quadrangularis* were used in proportion to their availability. Inversely, other high-stratum plants, such as *Festuca* sp. and *Tetraglochin cristatum*, were avoided across the vegetation communities (Figure 1).

Habitat use

Vicugnas used all habitats in the study area (Tables 2 and 3, Figure 2). A comparison between habitat availability and use indicated that foraging vicugnas were selective throughout the sampling period (χ^2_{20} >40, p<0.005).

The mean cover of vegetation communities varied according to the seasons and the year (T^2=26.19; p<0.0001), with higher abundance in the wet season (WS) and lower abundance in the dry season (DS), although there was a significant decline in vegetation cover over the duration of this study (WS year 1:71.3%>WS year 2:62.8%>DS year 1:64.1%>DS year 2: 55.66%; Figure 3). The average percentage of vegetation cover in the first year (65%) was significantly higher than that during the second year (59%) (T^2=16, p=0.003). Statistical analysis of the selectivity indices for each habitat using Bonferroni confidence intervals (Table 3) indicated that vicugnas did not change their selective strategy during these 2 years.

Vicugnas tended to concentrate in the southern pastureland (sector S) sharing it with the native domestic livestock (llamas), whereas the sheep, cattle, and their attendant herders and dogs tended towards both northern pasturelands (sectors NF and N) of the study area (Figure 2). The donkeys grazed mainly in the southern pastureland (sector S), but we only registered between one and six animals in 10 separate scans.

Table 1 Plant species at the study area in eastern Toquero, Jujuy, Argentina, and species consumed (1) by vicugnas in the sampling period by functional group (FG) and stratum.

Families	Plant species or genera	Stratum	FG	Consumed
Asteraceae	Asteraceae undetermined	Low	Forb	
	Baccharis boliviensis (Wed.) Cabrera	High	Shrub	
	B. incarum Wedd.	High	Shrub	
	Parastrephia quadrangularis (Meyen) Cabrera	High	Shrub	1
	Parastrephia lucida (Meyen) Cabrera	High	Shrub	1
Ballanophoraceae	*Ombrophytum subterraneum* (Asplund) B. Hansen	Low	Forb	
Boraginaceae	*Heliotropium microstachyum* Ruiz and Pav.	Low	Forb	
Cactaceae	Cactaceae	Low	Shrub	
	Maihueniopsis sp. Speg.	Low	Shrub	
Cyperaceae	Ciperaceae	Low	Grass-like	1
Ephedraceae	*Ephedra* sp.	High	Srhub	
Euphorbiaceae	*Euphorbia serpens* Kunth	Low	Forb	
Fabaceae	*Adesmia* cf. *erinacea* Phill.	Low	Shrub	1
	Adesmia sp.	High	Shrub	1
	Unidentified	Low	Forb	1
Juncaceae	*Juncus* sp.	High	Grass-like	
Oleraceae	*Menodora pulchella* Markgraf	Low	Forb	
Oxalidaceae	*Hypseocharis pimpinellifolius* J. Remy	Low	Forb	
Poaceae	*Aristida antoniana* Steud ex Döll	Low	Grasses	1
	Bouteloua simplex Lag.	Low	Grasses	1
	Cortaderia sp.	High	Grasses	
	Cynodon sp.	Low	Grasses	1
	Deyeuxia sp.	High	Grasses	1
	Distichlis sp.	Low	Grasses	1
	Festuca sp.	High	Grasses	1
	Festuca cf. *orthophylla*	High	Grasses	1
	Muhlembergia sp.	Low	Grasses	1
	cf. *Jarava ichu*	High	Grasses	1
Portulacaceae	Portulacaceae	Low	Forb	
Rhammnaceae	*Colletia spinossisima* Gmel.	High	Shrub	
Rosaceae	*Lachemilla* sp.	Low	Forb	1
	Tetraglochin cristatum (Britton) Rothm.	High	Shrub	1
Solanaceae	*Fabiana densa* J. Rémy	High	Shrub	

Both vicugnas and livestock (llamas, sheep, and cattle) showed a marked preference for *Parastrephia lucida* and *Deyeuxia* sp. steppe, as well as for *Deyeuxia* sp. grasslands (Figure 2). Thus, a higher proportion of wild and domestic animals (51% of vicugnas, 62% of llamas, 75% of sheep, and 88.4% of cattle) regularly used these vegetation communities. Vicugnas and domesticated animals avoided *Baccharis boliviensis* and *Fabiana densa* steppes. The only exception was to the vicugnas in the northern pastureland (sector N) (Figure 2), where there was a high density of both sheep (619 sheep/km^2) and llamas (78 llamas/km^2), occupying the former preferred habitat types. Moreover, we observed vicugnas in only one scan of the northern pastureland (sector N), and in five scans in the northern fenced pastureland (sector NF) in *P. lucida* and *Deyeuxia* sp. steppe, and *Deyeuxia* sp. grassland.

Spatial segregation and density

Although vicugnas and non-native livestock shared similar foraging preferences, they were spatially segregated in the study area (Figure 2). Inter-specific associations in niche extent and overlap also showed that vicugnas and non-native livestock displayed a significant level of segregation across most samples, whereas vicugnas and llamas presented a significant association across all samples. Niche breadth yielded higher values for wild (0.46) and domestic (0.29–0.54) camelids than for sheep (0.14–0.28) and cattle (0.05–0.2), which were distributed almost exclusively within two habitats. Pianka's index of habitat resources between vicugnas and llamas (79%) was significantly higher than that between vicugnas and sheep (30%) and that between vicugnas and cattle (10%).

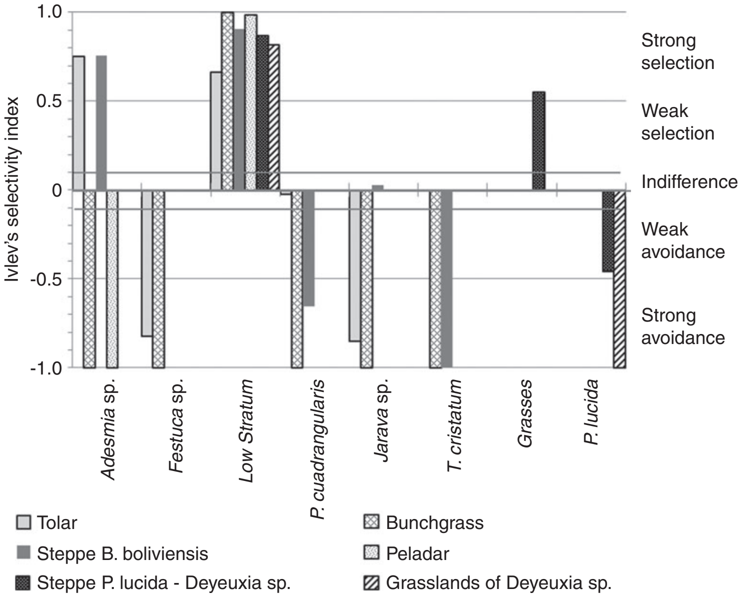

Figure 1 Vicugna forage selection in eastern Toquero, Jujuy, Argentina: Ivlev's selectivity index by species or functional group estimated from time proportion in each focal sampling in which the vicugna is foraging each plant species or functional group within the sampled vegetation community, and food availability measured as a mean percentage of vegetation cover for each vegetation category.
*Time consumption was not quoted in Ca: Riparian; E F.d.: *Fabiana densa* steppe; E C.e.: *Colletia spinossisima* steppe; and Ju: Juncal vegetation communities.

Vicugnas were less abundant (mean 47.8±1.7, Figure 4) than sheep (mean 266.05±11.37) and llamas (mean 121.64±5.66, with different densities between years, Figure 4), although they were more abundant than cattle (mean 11.73±0.66) and donkeys (H=387.13, p=<0,001). Indeed, there was a negative correlation among the density of vicugnas and that of domestic ungulates (llamas ρ=-0.26, sheep ρ=-0.49, cattle ρ=-0.29, p<0.0001).

When vicugnas and domestic ungulates were seen foraging in the same areas at the same time at a distance of up to 3 m between the distinct groups, we did not record any forcible displacements or agonistic interactions between the species. However, vicugnas never came within 100 m of people and dogs, which tended to chase and bark at vicugnas, inducing them to runaway.

Discussion

The foraging activity of vicugna demonstrated a strong tendency towards selection of low-stratum grasses such as *Bouteloua simplex* and *Aristida antoniana*, which are present both in areas with high and low cover (grasslands and mix steppe, or shrub steppes). Vicugna also selected tall grasses such as *Jarava* sp. and *Deyeuxia* sp. This trend has been observed in others areas (Koford 1957, Franklin 1983, Cajal 1989, Aguilar et al. 1999, Villalba 2003, Arzamendia et al. 2006, Benítez et al. 2006, Borgnia et al. 2008, 2010, Mosca Torres and Puig 2010, Rojo et al. 2012).

In accordance with our second hypothesis, we found that both vicugnas and livestock preferred the same type of grazing habitat. Both wild and domestic animals selected habitats dominated by grasses with high cover in both high and low strata, which were present throughout the year, such as *Deyeuxia* sp., *Jarava* sp., *Bouteloua simplex*, and *Aristida antoniana*.

We did not detect temporal changes in habitat selectivity between the 2 years of this study, although the availability of vegetation decreased during the second year of fieldwork. Conversely in Cieneguillas, vicugnas were more selective during the wet year with higher vegetation availability than in the subsequent dry year. This observation was probably related to a higher density of vicugnas and lower vegetation cover. In the dry season, there was a tendency towards the use of vegetation communities with high grass and shrub cover from both strata (Arzamendia et al. 2006). This phenomenon is known as the "buffer effect", and its intensity depends on the nature of intra-specific competition (Sutherland 1996, Gill et al. 2001).

Vicugnas and domestic livestock avoided habitats with low cover dominated by bushes, such as *Baccharis boliviensis* and *Fabiana densa*, where forage was limited during the dry season, of low quality, and of poor

Table 2 Habitat types in eastern Toquero, Jujuy, Argentina, identified by the vegetal community and their location in sectors with different land use (NF: northern fenced; N: northern pastureland; and S: southern pastureland), with the area, associated species, and total mean cover of vegetation (% minimum and maximum recorded).

ID	Habitat types (HT)	Associated species	Cover (%)	Pasture field area (ha.)			Total area
				NF	N	S	HT
To	Tolar[a], *Parastrephia quadrangularis* shrub steppe and	Tall (*Festuca* sp. or *Deyeuxia* sp.) and short grasses (*Muhlembergia* sp. and *Lachemilla* sp.)	50–80	0.4	5.2	64.7	70.3
Ca	Riparian	Groves of *Cortaderia speciosa*, small swamp areas with dense low vegetation and *Deyeuxia* sp. and *Muhlembergia* sp. grassland	60–85			3.8	3.8
Pa	Bunchgrass, dominated by tall grasses (*Festuca* spp.)	*P. quadrangularis*, with a low stratum of *Adesmia* sp., *Aristida antoniana* and *Bouteloua simplex*	50–80	2.9	1.8	1	5.7
E B.b.	*Baccharis boliviensis*, shrub steppe	Grass (*Jarava* sp.) and/or shrubs (*Adesmia* sp. and *Tetraglochin cristatum*) on mountain slopes	15–30	10.6	47.3	117.8	175.7
E F.d.	*Fabiana densa* shrub steppe	*Baccharis incarum* and *Adesmia* sp.	50–70			18.9	18.9
Pe	Peladar[a]	Open rocky areas at the edges of two roads with *B. simplex* and *A. antoniana*	10–60		0.1	2.3	2.4
E C.e.	*Colletia spinossisima* shrub steppe on the steepest slopes	Low stratum of *B. simplex* and *A. antoniana*.	50		2.7	1.8	4.5
Ju	Juncal: Wetlands with *Juncus* sp.		100			0.4	0.4
E P.l.- De.	*Parastrephia lucida* and *Deyeuxia* sp. steppe	Tall (*Festuca* sp.) and short grasses (*Muhlembergia* sp. and *Lachemilla* sp.)	85–90	4.8		12.1	16.9
Pa De.	*Deyeuxia* sp. grassland	short grasses (*Muhlembergia* sp. and *Lachemilla* sp.)	85–100	9	3.9	9	21.9
Surface of study area and each sectors				27.7	61	231.8	320.5

[a] Local names for these habitat types.

digestibility (San Martin and Bryant 1989, Benítez et al. 2006, Borgnia et al. 2010).

Our results concurred partially with our third hypothesis because although vicugnas were spatially segregated from non-native livestock, they were still able to graze in their preferred habitats when mixed with low to medium llama densities, which had the highest degree of habitat overlap. In all the other cases where there were high densities of sheep and cattle and increased presence of people, vicugnas tended towards segregation and grazed on less preferred habitats. Similar results were observed by Borgnia et al. (2008, 2010) at Laguna Blanca, Catamarca, Argentina, and by Villalba (2003) at Ulla-Ulla, Bolivia. Other studies have shown that interactions between wild and domestic ungulates can be both competitive and facilitative, with the net effect determined by the relative densities of each herbivore type and how their populations vary across time and space (De Gabriel et al. 2011; Odadi et al. 2011). In Bolivian vicugna populations, Muñoz and Faz (2012) found that the zones that exhibited lowest vicugna density had the highest number of alpacas, and identified an inverse relationship between total organic carbon contents in soil profiles and alpaca concentrations. Disturbed vegetation and soil exhaustion were identified in areas with the highest densities of domestic camelids, but not in zones with high vicugna density associated with medium density of livestock (Muñoz and Faz 2012).

Spatial segregation is a frequent mechanism supposed to reduce inter-specific competition and, in some cases, permits coexistence (Holt 2001). Our results agree with those of Gordon (2000), who described that the variables that explain the patterns of a species' use and occupancy of habitats depends on the densities of the interacting

Table 3 Habitat use and selection: proportion of foraging vicugnas observed and expected in different habitat types of eastern Toquero, Jujuy, Argentina, selection index and Bonferroni confidence limits for habitat types availability. Sectors: NF: northern fenced; N: northern pastureland; S: southern pastureland. Vegetation communities: To: Tolar (*Parastrephia quadrangularis*); Ca: Riparian; Pa: bunchgrass; E B.b: *Baccharis boliviensis* steppe; E F.d.: *Fabiana densa* steppe; Pe: Peladar; E C.e.: *Colletia spinossisima* steppe; E P.l.- De.: *P. lucida* and *Deyeuxia* sp. steppe; Pa De.; *Deyeuxia* sp. grassland.

Habitat types	Expected proportion	Observed proportion		Selection index		Confidence limits[a]			
		Year 1	Year 2	Year 1	Year 2	Year 1		Year 2	
						Lower	Upper	Lower	Upper
NF- To+Ca	0.00	0.01	0.01	8.39	10.4	6.68	10.10	9.12	7.88
NF- Pa	0.01	0.01	0.01	0.61	1.35	0.00	1.39	0.66	0.00
NF- E B.b.	0.03	0.00	0.00	0.04	0.99	0.00	1.00	0.06	0.00
NF- E Pl.-De.	0.02	0.00	0.00	0.23	1.01	0.00	0.98	0.28	0.00
NF- Pa De.	0.03	0.05	0.05	1.88	2.07	1.50	2.26	1.76	1.46
N- To+Ca	0.02	0.00	0.00	0.06	1.26	0.00	1.28	0.08	0.00
N- Pa	0.01	0.00	0.00	0.09	1.74	0.00	1.79	0.14	0.00
N- E B.b.	0.15	0.04	0.05	0.28	0.55	0.07	0.50	0.34	0.13
N- Pe	0.00	0.00	0.00	2.07	0.00	0.00	5.69	0.00	
N- E C.e.	0.01	0.00	0.00	0.00	0.00	0.00		0.00	
N- E Pl.-De.	0.01	0.00	0.00	0.00	0.00	0.00		0.00	
S- To+Ca	0.20	0.25	0.252	1.24	1.23	1.11	1.38	1.12	1.34
S- Pa	0.00	0.00	0.00	0.99	0.86	0.00	2.22	0.00	1.95
S- E B.b.	0.37	0.14	0.14	0.38	0.38	0.26	0.49	0.27	0.50
S- E F.d.	0.06	0.01	0.01	0.21	0.18	0.00	0.60	0.00	0.61
S- Pe	0.01	0.01	0.01	1.19	1.45	0.40	1.98	0.81	2.09
S- E C.e.	0.01	0.00	0.00	0.35	0.21	0.00	1.45	0.00	1.55
S- Juncal	0.00	0.00	0.00	1.35	3.45	0.00	3.22	2.01	0.57
S- E Pl.-De.	0.04	0.17	0.16	4.51	4.49	4.20	4.82	4.27	4.03
S- Pa De.	0.03	0.29	0.29	10.04	10.3	9.69	10.40	10.07	9.81

[a] The proportions were estimated using a sample of 2521 vicugna observations from 2003 scans, and 5124 vicugna observations from 2004 scans, in relation to the habitat type available area. $p<0.05$ for Bonferroni confidence intervals $\alpha/2K$ of the selectivity index. A negative lower limit for the confidence interval of 0% has been replaced by 0.00 because negative values for the selection indices are impossible. Confidence limits: Lower>1 is selection, Upper<1 is avoidance.

species, the competitive hierarchy among them, the presence of detectable intra-type variation in patch quality, and on their fundamental habitat preferences. We proved that vicugnas can maintain their foraging preferences and coexist with livestock when they are llamas in low and medium densities. In all other situations, they were both spatially segregated and vicugnas tended towards the use of sub-optimal habitats. Vicugna could be described as a generalist herbivore with the ability to modify its diet in response to trophic availability and to competitive interactions with domestic livestock. This fact has been previously described for wild camelids in other areas in South America (Borgnia et al. 2008, Acebes et al. 2010, Rojo et al. 2012).

In the case of guanacos (*Lama guanicoe* Müller, 1776), the other wild South American camelid, some studies noted competitive interactions with spatial segregation between them and domestic livestock (Baldi et al. 2001, 2004). Other studies observed the absence of spatial segregation between guanacos and non-native animals at meso-scale, with habitat partitioning between guanacos and feral livestock (donkey and cattle) or vicugnas at micro-scale (Ovejero et al. 2011, Acebes et al. 2012, Wurstten et al. 2014).

We did not observe negative interactions, such as displacements or agonistic interactions, between vicugnas and domestic ungulates foraging close by. Vicugnas and llamas can graze together at <2 m away from each other. Llamas are domesticated guanacos, and vicugnas have a close phylogenetic relationship with them (Marín et al. 2006). Their differences in behaviour, physiology, adaptations, and vocalizations are obviously lesser than those between them and any other ungulates. It is also probable that vicugnas are more used to the presence of llamas than to that of any other animal. Many llamas graze freely during the day and return unaided to their corrals at night

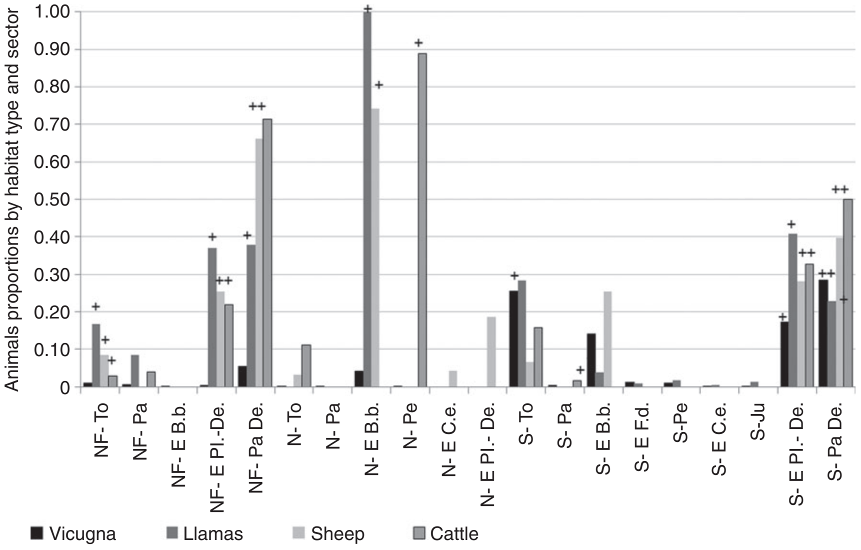

Figure 2 Use and selection of habitats by vicugnas and livestock (llamas, sheep, and cattle) in each sector of eastern Toquero, Jujuy, Argentina.
Sectors: NF: northern fenced; N: northern pastureland; S: southern pastureland. Vegetation communities: To: Tolar (*Parastrephia quadrangularis*) and riparian; Pa: Bunchgrass; E B.b *Baccharis boliviensis* steppe; E F.d.: *Fabiana densa* steppe; Pe: Peladar; E C.e.: *Colletia spinossisima* steppe; E P.l.- De.: *P. lucida* and *Deyeuxia* sp. steppe; Pa De.: *Deyeuxia* sp. grassland; Ju: Juncal. (+) preferred habitat ($p<0.05$ for Bonferroni confidence intervals $\alpha/2K$ of the selectivity index; n=7645 vicugnas, 13,016 llamas, 30,330 sheep, and 1314 cattle observations).

(Wawrzyk and Vilá 2013), so the presence of llamas is not necessarily associated with the adverse stimuli of humans and dogs, as is the case with sheep grazing. Dogs are one of the biggest stressors of vicugnas, which tend to avoid them as a matter of course. Incidents of vicugnas being attacked by dogs are common (Villalba 2003).

Indeed, the mixed grazing partners of vicugna-llama could be related to a forage resource partitioning by both species. In Bolivia, Villca and Genin (1995) observed a certain complementarity in the food strategies of llamas and sheep that made better use of available forage resources. They found a greater selection of tough grasses, such as *Festuca orthophylla* and *Jarava ichu*, by llamas, whereas sheep preferred soft herbaceous and annual low grasses, such as *Bouteloua simplex* and *Aristida* sp. Thus, in the present study, food complementarity could be a possibility between vicugna and llama, whereas there could be a greater possibility of competition between vicugnas and sheep given that vicugnas also select these annual low grasses.

Thus, the density and type of domestic livestock in an area could induce vicugnas to either segregate or occupy sub-optimal habitats. The predominant use of sub-optimal areas strongly limits the possibility of increase in vicugna population. Fewer animals generate lower overall densities of vicugnas in these areas, making it more difficult, if not impossible, to plan captures geared towards gathering their valuable fleece.

Therefore, a clear trade-off between population density and habitat availability emerges for areas grazed by vicugnas and domestic livestock. Consequently, the final decision lies with the local people, who have to decide whether to maintain their traditional production system in which vicugnas are seen as a competitor for pasture, or to develop a new paradigm that would include vicugnas as part of a multi-specific productive system. In a multi-specific scheme, vicugnas can bring in revenue through periodic captures and shearing. We have shown that vicugnas can quickly become used to grazing as part of a mixed-grazing strategy with llamas.

Currently, the human tolerance of vicugnas is one of the most accurate indicators of the presence and distribution of this species. Competitive interaction between livestock and wildlife, whether perceived or real, constitutes the main source of human-wildlife conflict with wildlife invariably being on the losing side (du Toit 2011). Nevertheless, mixed-grazing strategies involving livestock and wildlife can be beneficial for biodiversity (De Gabriel et al. 2011). A strategy integrating different types of herbivores would provide herders with additional opportunities that would capitalize on facilitative interactions, and thereby help nullify perceived or

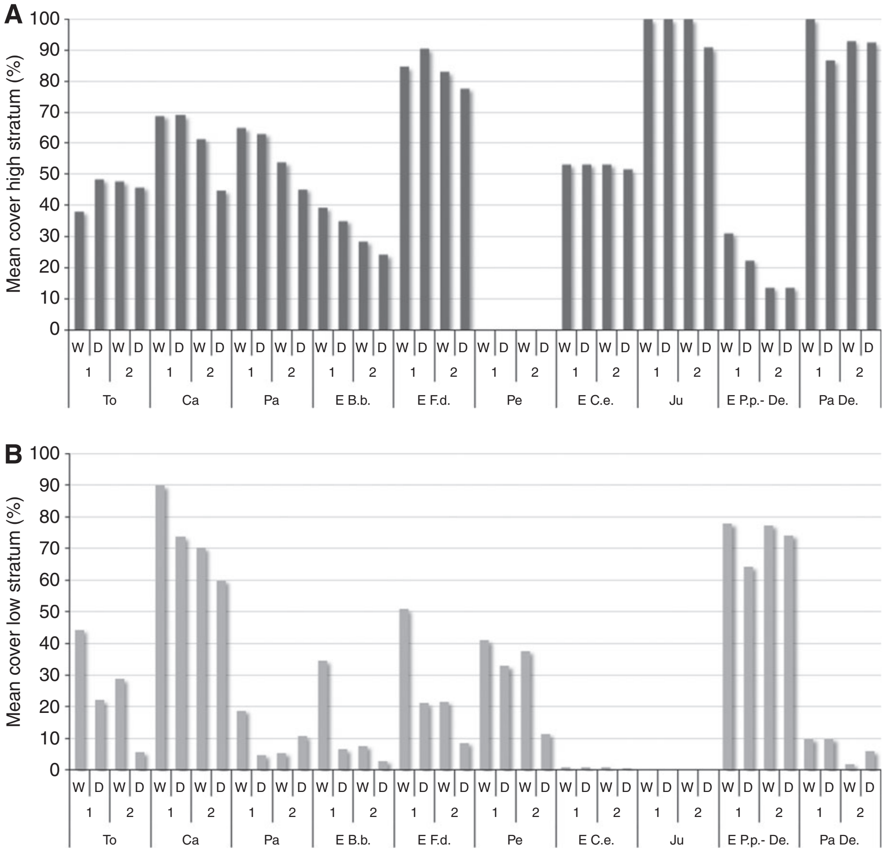

Figure 3 Mean cover of high (A) and low (B) strata of each vegetal community in eastern Toquero, Jujuy, Argentina by season (D: Dry and W: wet) and year (1: first and 2: second).
Vegetation communities: To: Tolar (*Parastrephia quadrangularis*); Ca: Riparian; Pa: grasslands; E B.b.: *B. boliviensis* steppe; E F.d.: *Fabiana densa* steppe; Pe: Peladar; E C.e.: *Colletia spinossisima* steppe; Ju: Juncal; E P.l.- De.: *P. lucida* and *Deyeuxia* sp. steppe; Pa De.; *Deyeuxia* sp. grasslands.

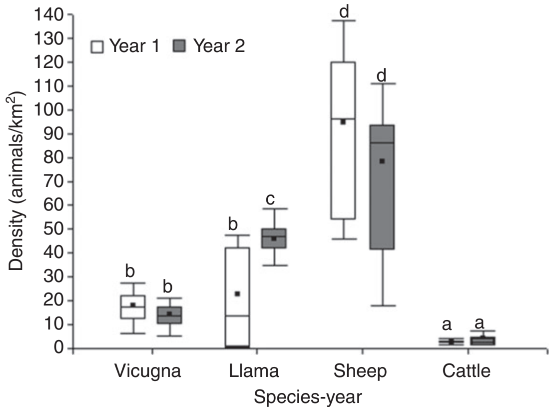

Figure 4 Mean density by species (vicugna, llama, sheep, and cattle) and year (white: year 1; grey: year 2) in eastern Toquero, Jujuy, Argentina. (Letters indicate significant differences at $p<0.05$ for the post-hoc test for multiple comparisons among ranks.)

actual competition between these animals (du Toit 2011). Indeed, the possibility of sustainable management of vicugna through the live shearing of their fleece provides an opportunity to increase and extend local economic opportunities, alleviate poverty, as well as conserve and preserve biodiversity.

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