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European Journal of Wildlife Research

ISSN 1612-4642

Eur J Wildl Res

DOI 10.1007/s10344-013-0748-1



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Habitat use and preference by guanacos, vicuñas, and livestock in an altitudinal gradient in northwest Argentina

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Received: 8 March 2013 / Revised: 12 June 2013 / Accepted: 16 June 2013
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Abstract Distribution of ungulates is regulated by natural factors, such as presence of other species, climate, and habitat variability, as well as human activities, including livestock grazing and mining. Understanding the spatial dynamics of landscape use can help solve problems of access to key resources by native herbivores. Laguna Brava Reserve is a protected area of Argentina where the two wild South American camelids, guanacos and vicuñas, coexist with cattle, mules, horses, and goats. Information about the effects of livestock and mining activities, which are widespread throughout the region, on wild camelids is scarce. We used variable-width transects to determine the distribution of guanacos, vicuñas, equids, and cattle in relation to five habitat types defined according to vegetation and topography in the reserve. We carried out a correspondence analysis between the proportion of groups observed in and the proportion of area occupied by each habitat, and a χ^2 goodness of fit test to establish if camelids and livestock selected a particular habitat type. Vicuñas were associated with grasslands at high altitudes while guanacos and livestock were associated with shrublands at lower elevations. This coevolutionary segregation between guanacos and vicuñas possibly reduced competition between the two species. Competition between camelids and livestock is probably low because of the low density of livestock. Vegas were preferred by all species year round but used more intensively in summer. In order to conserve the wild camelids of the region, governments must

implement measures to conserve the critical habitat provided by the vegas.

Keyword Habitat utilization · Guanacos · Vicuñas · Livestock · Competition · Mining

Introduction

Understanding the spatial dynamics of landscape use can help solve problems of access to key resources by native herbivores (Williamson et al. 1988; Coughenour and Singer 1991; Yeo et al. 1993). Ungulates commonly experience considerable seasonal, climatic, and spatial variation in resource availability, especially in arid and semiarid tropical environments, where such variation is extreme (Illius and O'Connor 2000). Forage availability and productivity is primarily affected by climatic variation in annual precipitation that typically has a coefficient of variation greater than 25 % and strong seasonality (Ellis and Swift 1988; Owen-Smith 1990), while spatial variation arises from differences in soil characteristics and topography, causing changes in nutrient content and hydrology (Illius and O'Connor 2000). Human activities can also limit the access of native ungulates to key resources. Information on the relationships among species of an herbivore assemblage, its environment, and the possible negative effect of human activities can help in the design and implementation of effective management measures.

The two most representative ungulates of western South America are the camelids, guanaco (*Lama guanicoe guanicoe*, Müller 1776; Marin et al. 2008) and vicuña (*Vicugna vicugna*, Molina 1782; Marín et al. 2007). Both species inhabit arid regions of Argentina, Peru, Bolivia, and Chile. Although their populations were abundant before the arrival of the Europeans, over the past century their numbers have declined and their ranges have been reduced, mainly due to overhunting, habitat destruction, and the introduction of livestock (Mares

Communicated by C. Gortázar

A. Wurstten (✉) · A. J. Novaro
Instituto de Investigaciones en Biodiversidad y Medio Ambiente,
CONICET, Epulafquen 30, Junín de los Andes, Neuquén,
Argentina
e-mail: alvarowurstten@gmail.com

A. J. Novaro · R. S. Walker
Patagonian and Andean Steppe Program, Wildlife Conservation
Society, Curruhue 395, Junín de los Andes, Argentina

and Ojeda 1984; González et al. 2006; Baigún et al. 2008; Baldi et al. 2010). The overlap in the distribution of guanacos and vicuñas is limited to the foothills of the Andes of Chile, Peru, and the northwestern Argentinian provinces of San Juan, La Rioja, and Catamarca.

The two species have different strategies of habitat use. Guanacos can occupy habitats with different vegetation structure, topography, and climate, from sea level up to 4,500 masl, and can move seasonally where the winters are rigorous (Puig 1995; De Lamo et al. 1998), whereas vicuñas only occupy areas above 3,300 masl and are found mainly on grasslands throughout the year (Arzamendia et al. 2006; Borgnia et al. 2008, 2010), although they can use shrubby habitats when grass cover is high (Mosca Torres and Puig 2012).

The probability that two sympatric native species compete is low because coevolution favors resource partitioning (Voeten and Prins 1999). There is little information about how resources are partitioned between the two camelids in areas of sympatry. Cajal et al. (2010) defined three levels of interactions between guanacos and vicuñas: (a) in the northern portion of their distribution, they are altitudinally segregated; (b) in the central portion of their distribution except the Puna, they are found at the same altitude but with a small degree of spatial segregation; and (c) in the altipampas of the Cordillera Frontal between 27°56' S and 29° 35' S, they are not spatially segregated at all. This pattern is supported by findings in the Puna of Catamarca, where the two camelids segregated spatially along an altitudinal gradient (Lucherini 1996; Lucherini and Birochio 1997), and in the foothills of the Andes of San Juan and La Rioja, where both camelids shared available habitats (Cajal 1998).

Since European colonization, livestock (mainly cows, mules, horses, donkeys, and goats) coexist with wild camelids in the Andean foothills. One of the most important problems associated with the introduction of species is competition, defined as the shortage of a forage resource being used by two or more species (Birch 1957; Putnam 1996). The recent, in evolutionary terms, introduction of exotic species to native assemblages such as the introduction of livestock to guanacos and vicuñas populations of Laguna Brava can generate interspecific competition because not enough time has passed for partitioning of resources to occur (Putnam 1996; Voeten and Prins 1999).

Although some studies have found evidence that livestock can compete with camelids (Baldi et al. 2001, 2004; Bonacic et al. 2002; Puig et al. 2003; Borgnia et al. 2008; Rojo et al. 2012), others have found no evidence of negative effects of livestock on native camelid populations (Ovejero et al. 2011; Acebes et al. 2012). The studies which found no evidence of competition took place in areas of very low livestock density (Ovejero et al. 2011) or where the spatial pattern of livestock distribution was distinct from that of guanacos (Acebes et al. 2012).

The ungulate species of the Andean foothills have different behaviors or are subject to different management. Part of the guanaco population moves seasonally to gain access to resources and escape harsh weather conditions, while vicuñas remain in the same areas throughout the year (Cajal 1998; Wurstten, unpublished data). Goats and cows are moved by shepherds to highlands in summer and to the lowlands in the dry season, and horses and donkeys are mainly feral and move freely. A more complete understanding of the potential for competition between camelids and livestock in their arid environment could be obtained by studying their habitat use throughout the year and along an altitudinal gradient.

Since 1990, national and provincial governments of Argentina have promoted mineral extraction along the Andes Mountains through tax benefits. Intensive mining exploration has taken place in recent years in areas of sympatry of guanacos and vicuñas along the northern Andes of Argentina, where at least four large new mines were built and many more are in the planning stage (see <http://mineria.gov.ar> for more information). Mining can have negative effects on ungulate populations by causing habitat destruction through direct removal of vegetation and soil or through accidental waste discharge into streams and water courses (Singh and Chowdhury 1999; Reglero et al. 2008; Ito et al. 2013). In the arid habitats of the Andes where guanacos and vicuñas coexist, water and plant resources are extremely scarce and concentrated mainly in vegas, wet areas located mostly along water courses, where vegetation cover is close to 100 %. Vegas have been reported to be important for wild camelids (Lawrence 1986; Vilá and Roig 1992; Renaudeau d'Arc et al. 2000; Mosca Torres and Puig 2012), so the impacts of mining may be more severe than in other habitats.

The objectives of this study were as follows: (a) to determine if there is preferential use of particular habitat types by guanacos, vicuñas, and domestic livestock; (b) to analyze the overlap among camelids and livestock to evaluate the potential for competition for resource use; and (c) to evaluate the potential negative effects of human activities, particularly mining, on camelid populations. Studies of the relationships between native and domestic ungulates in arid and semiarid biomes are relatively numerous for African savannas and Asian steppes, but there are few studies from similar biomes of South America (Acebes et al. 2012), and this is the first that compares variation in habitat selection during winter and summer seasons by sympatric guanacos, vicuñas, and livestock in an area of low livestock density in the Andean foothills. Studies about the effects of mining on ungulate populations have also been carried out in other regions (Grimalt et al. 1999; Weir et al. 2007; Bleich et al. 2009), but this work is the first attempt to assess the potential effects of mining on wild South American camelid populations. A better understanding of the habitat use patterns of the ungulate assemblage, the potential for competition between livestock

and camelids, and the ways extractive industries can affect wild South American camelids can provide information for managing the human activities in and around reserves to reduce the impact of humans on guanaco and vicuña populations.

Materials and methods

Study area

The study area covers approximately 6,700 km² and included part of the Laguna Brava Reserve and adjacent areas in the province of La Rioja in Argentina (between 28° 18' S and 28° 53' S and 68° 30' W and 68° 57' O) with an altitudinal gradient between 2,000 and 4,000 masl (Fig. 1). The landscape includes plains, mountain chains, and salt flats and ponds produced by closed basins. The average annual temperature is 12 °C, with a maximum annual average of 28 °C and minimum annual average of -2 °C. The annual rainfall is less than 100 mm per year and occurs mainly during summer. The scarce precipitation in autumn and winter is in the form of snow (Combina and Pasarello 1980).

The dominant vegetation up to 3,100 masl corresponds to the Monte Phytogeographic Province. Between 3,100 and 3,800 masl, the vegetation is characteristic of the Prepuna,

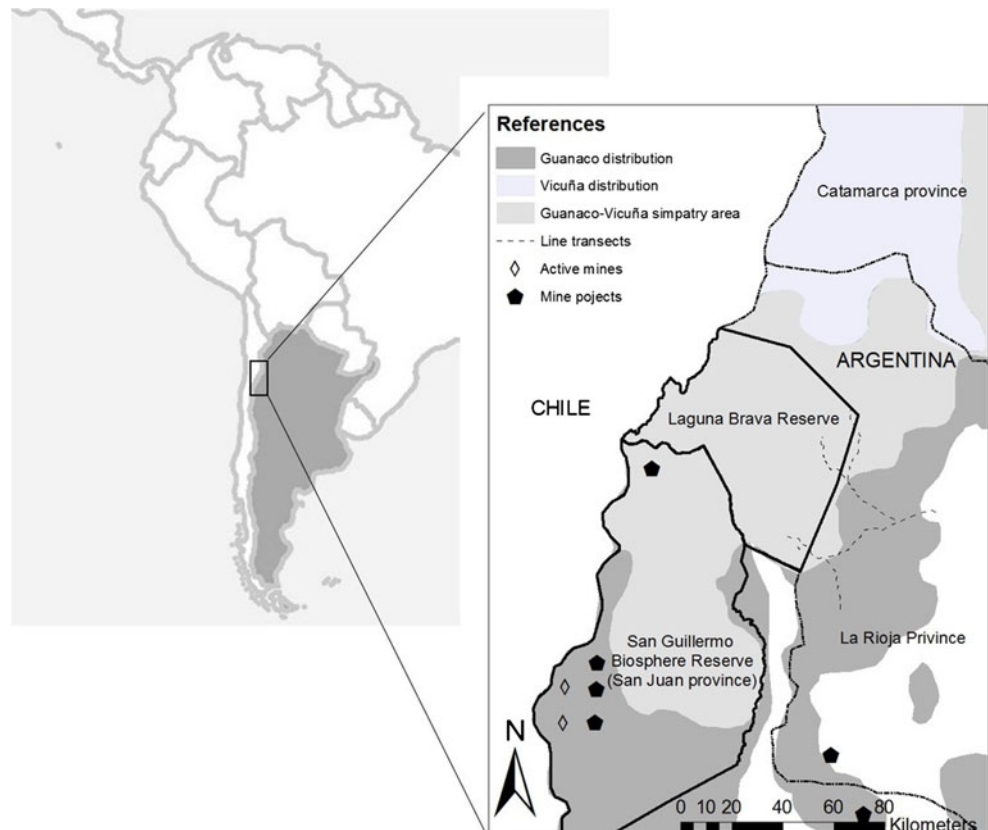
represented mainly by a xerophytic steppe of shrubs where the genera *Larrea*, typical of the Monte Province, is absent. About 3,800 masl, the vegetation belongs exclusively to the Puna and is limited to scattered grasses of the genus *Stipa* and cushion plants of the genus *Adesmia* (Hunzicker 1952; Cabrera 1976).

A single village of 400 inhabitants dedicated mainly to livestock breeding at a minor scale lies 20 km south of the study area. The southern entrance to the Laguna Brava Reserve (Fig. 1) is used for access to an area of active mining exploration in the northwestern part of the San Guillermo Biosphere Reserve.

Data collection and habitat classification

Variable-width transects were used to determine the distribution of guanacos, vicuñas, and livestock (Buckland et al. 2001). Six surveys were carried out between January 2008 and February 2011: one during each summer (770 km in all the surveys combined), one during winter of 2008, and one during winter of 2010 (585 km in the two surveys combined) in Laguna Brava Reserve and adjacent areas. The same routes were surveyed in each season, at least two times in summer and three times in winter between 1000 and 1800 hours. Transects were traveled by vehicle with two observers standing in the back. For each ungulate observation, location, group size, and habitat type were recorded.

Fig. 1 Location of the study area in La Rioja Province. Guanaco and vicuña distributions are adapted from Baigún et al. (2008). Information about mining activities is from the webpage of the Secretary of Mining of Argentina (<http://www.mineria.gov.ar>)



The study area was divided into five habitat types according to vegetation physiognomy and topography: (a) shrubland on plains (SHRPL), located between 2,000 and 3,500 masl on flat areas with slopes less than 15°, with larger, more scattered shrubs of *Larrea* spp., *Bulnesia retamo*, and *Flourenzia polyclada* in the lowlands, and shorter, more densely grouped shrubs of *Adesmia* spp., *Lycium* spp., and *Artemisia mendozana* in the uplands; (b) shrubland on steep terrain (SHRST), located between 2,900 and 3,500 masl, with a slope greater than 15°, and vegetation represented mainly by shrubs of genera *Ephedra*, *Gognatchia*, and *Atriplex*; (c) grassland on steep terrain (GRAST) represented by areas with slopes steeper than 15° with cushion plants of genus *Adesmia* and variable grass cover of *Stipa* spp. located about 3,700 masl; (d) grassland on plains (GRAPL) at the same altitude and with the same vegetation type as GRAST but with slopes lesser than 15°; and (e) vegas (VEGA) habitats found in the wet areas close to streams with high vegetation cover (greater than 70 %) of species such as *Festuca scirpifolia* and *Juncus balticus*.

ArcGIS was used to delimit the habitat types and quantify the area occupied by each. A strip of 800 m at each side of the transect was considered to be the study area, as this was the maximum distance at which it was possible to detect the animals.

Statistical analyses

Proportions of groups were used for all statistical analyses instead of proportions of individuals because we assume that due to the social nature of these herbivores, the selection of an area by an animal is not independent of the selections of the rest of the animals in the group. However, the average group size may differ among habitat types. As count data fail to meet the parametric statistical assumptions due to their nature, and our sample sizes varied greatly between ungulates species, we used nonparametric statistical tests.

To evaluate associations of each species with different habitat types, we carried out a correspondence analysis between the proportion of groups recorded in each habitat type and the proportion of area occupied by each habitat. This method consists of representation of objects (sites, species, and sampling stations) as points through one or more axis maximizing the correspondence between the variables and the units. To avoid the arch effect produced by the use of the χ^2 distance, we used a detrended correspondence analysis (Legendre and Legendre 1998). Due to the differences in body size and efficiency of resource use among species, we converted all ungulate groups into equivalent guanaco groups. We used a relationship between group size of guanacos, vicuñas, cows, and equids of 1:1.43:0.6:0.48 (Vallentine 2001; Bonacic et al. 2002; Tadey 2008). To evaluate the effect of group size on the correspondence analysis, we tested differences between group size of guanacos and vicuñas in

different habitat types using Mann–Whitney U tests when only two habitat types were used and Kruskal–Wallis tests for more than two habitat types (Zar 1996).

We used a sequential Bonferroni procedure (Holm 1979) as post hoc analyses when Kruskal–Wallis tests detected significant differences. The sequential Bonferroni is an improvement over the Bonferroni procedure, where p values are ranked from largest to smallest and the smallest p value is tested at α/c , the next at $\alpha/c-1$, and the next at $\alpha/c-2$, etc., where α is the probability of making a type I error and c is the number of paired tests. Testing stops when a nonsignificant result occurs (Quinn and Keough 2002). The proportion of expected guanaco, vicuña, and livestock groups in all habitats type was estimated as the proportion of the area occupied by each habitat type. We performed a χ^2 goodness of fit test to establish if there were statistically significant differences between the expected and observed frequencies of guanaco, vicuña, and livestock groups in different habitat types (Zar 1996).

Results

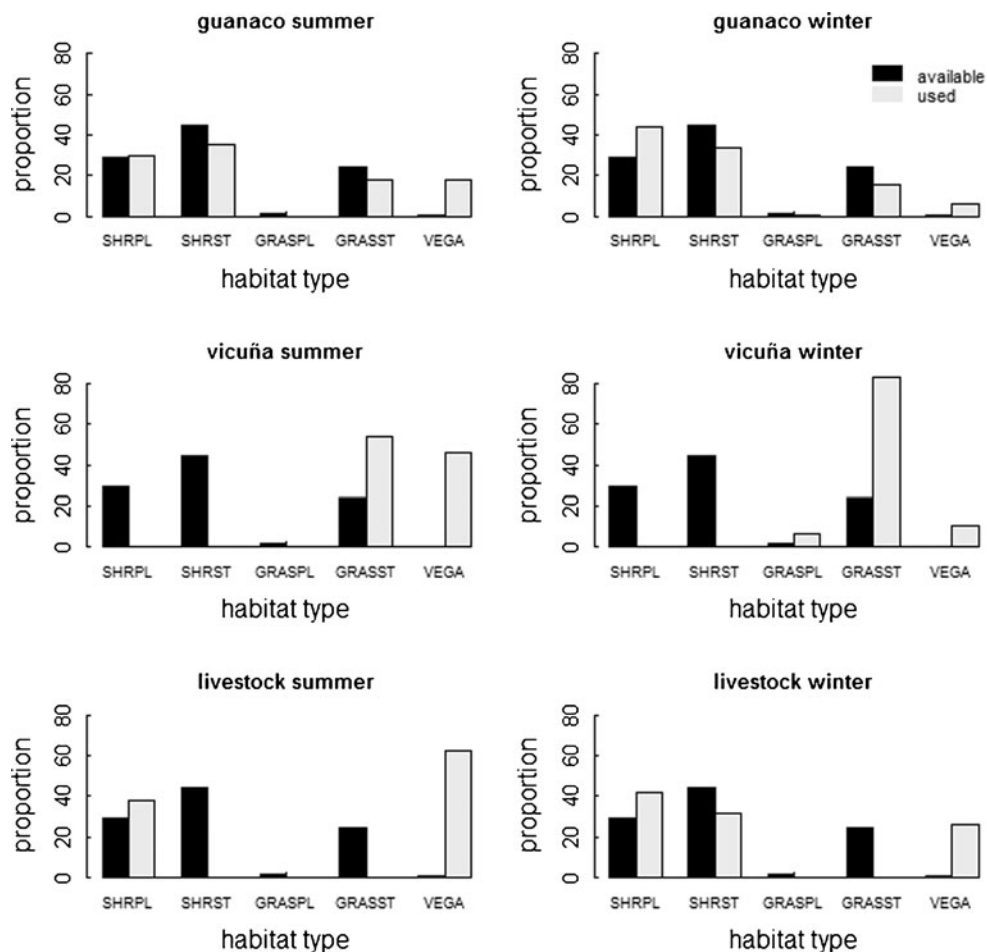
Habitat use

We observed 391 groups of guanacos, 101 groups of vicuñas, 13 groups of horses and donkeys, and 12 groups of cattle during the 2008–2011 surveys. Besides the species mentioned, we observed two groups of approximately 150 goats, one in a shrubby habitat and one in a vega. Due to the distortion that these data can generate, we eliminated it from both correspondence analysis and the goodness of fit test.

Observations of guanacos were more abundant in summer than winter, but observations of the other species did not vary markedly between seasons. Seventy percent of the groups of guanacos were found in shrublands (SHRPL and SHRST) with equal proportions of groups on plains and steep terrains, while 70.3 % of the groups of vicuñas were observed in grasslands, mostly in areas with steep terrain (GRAST). The shrublands and the grassland on steep terrain were the habitat types used most by both camelids when summer and winter data are combined (25.8 and 28.3 %, respectively), while 17 % of the groups of both species were observed on vegas and less than 1 % in grassland on plains. From winter to summer, the use of shrubland on plains by guanacos decreased from 34.72 to 23.67 % and the use of vegas increased from 7.76 to 25 % (Fig. 2).

The correspondence analysis for winter surveys generated three axes that explained 55 % of the observed variability in the data: the first explained 53.4 %, the second 1.6 %, and the third 0.02 %. For summer, the correspondence analysis generated two axes, the first explained 25.02 % of the variability and the second one 1.26 % (Fig. 3a, b). Vicuñas were almost

Fig. 2 Proportion of area occupied by each habitat type and proportion of groups of guanacos, vicuñas, and livestock recorded in each habitat type. *SHRST* shrubland on steep terrain, *SHRPL* shrubland on plains, *GRASST* grassland on steep terrain, *GRAPL* grassland on plains, *VEGA* meadow on plains



exclusively associated with grasslands while guanacos and livestock were associated mostly with shrublands. Vegas were not important as winter habitat for any of the species considered. In summer, the pattern of habitat use changed; guanacos, vicuñas, and livestock were all strongly associated with vegas, where 18–60 % of sightings were recorded

despite the very small proportion of the study area (less than 1 %) represented by vegas (Fig. 3).

Guanaco and vicuña group sizes were uneven between habitat types, species, and seasons (Fig. 4). Average guanaco group size was significantly greater in summer than in winter (Mann–Whitney U test=20,631.5, $p=0.021$). Guanaco group

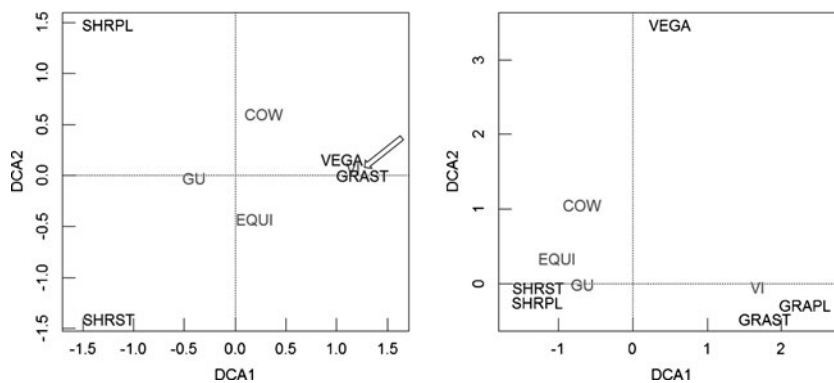
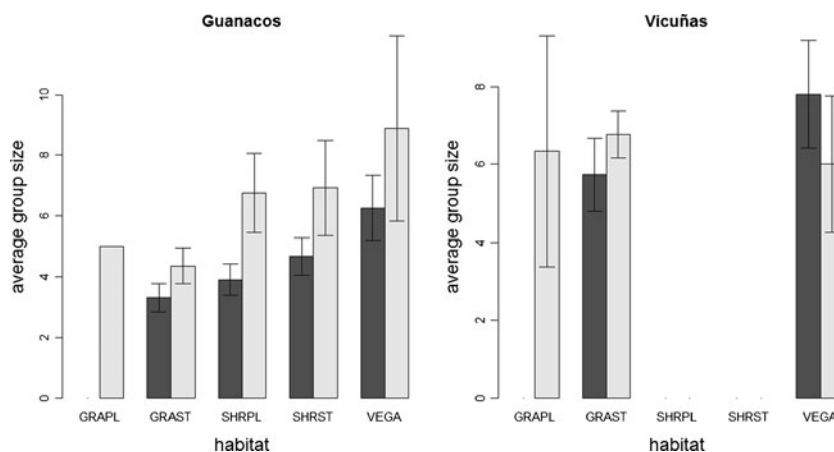


Fig. 3 Correspondence analysis between groups of ungulates and habitats in summer (left) and winter (right). Equivalent guanaco groups were used instead of actual ungulate groups, relationship between guanacos, vicuñas, cows, and equids groups were 1:1.48:0.6:0.48.

SHRST shrubland on steep terrain, *SHRPL* shrubland on plains, *GRASST* grassland on steep terrain, *GRAPL* grassland on plains, *VEGA* meadow, *GU* guanacos, *VI* vicuñas, *COW* cattle, *EQUI* equines (horses, mules, and donkeys)

Fig. 4 Average group size and standard error of guanacos and vicuñas in the different habitat type in each season. Summer data are shown in *black* and winter data in *gray*. *SHRST* shrubland on steep terrain, *SHRPL* shrubland on plains, *GRAST* grassland on steep terrain, *GRAPL* grassland on plains, *VEGA* meadow



size did not differ significantly among habitat types in winter (Kruskal–Wallis $\chi^2=2.60$, $df=3$, $p=0.457$), but differed significantly during summer (Kruskal–Wallis $\chi^2=8.22$, $df=3$, $p=0.041$). Guanaco group size in summer was significantly greater in vegas than in shrubland on plains (Mann–Whitney U test=1,001.5, $p=0.0128$) and grassland on steep terrain (Mann–Whitney U test=560, $p=0.0085$), but not shrubland on steep terrain (Mann–Whitney U test=1,273.5, $p=0.0417$). Guanaco group size did not vary significantly among non-vega habitats (Kruskal–Wallis $\chi^2=11.1741$, $df=14$, $p=0.6723$). Vicuña group size did not vary significantly between habitats in winter (Kruskal–Wallis $\chi^2=0.1466$, $df=2$, $p=0.9293$), but group size was significantly greater in vegas than in grassland on steep slopes in summer (Mann–Whitney U test=243.5, $p=0.0384$).

Habitat selection

All habitat types were used disproportionately in relation to availability in winter ($\chi^2=199.04$, $df=4$, $p<0.001$) and summer ($\chi^2=2,395.50$, $df=4$, $p<0.001$). The greatest departure from the expected frequencies was observed in the shrubland on steep slope (used less than expected) and vegas (used more than expected) by all the species considered.

Differences between expected and observed proportions of groups of guanacos and vicuñas were statistically significant for both summer and winter (Table 1). During winter, guanacos used vegas and shrublands on plains located in the low areas more than expected according to their availability, avoiding the grasslands of the high altitudes. During summer, the only habitat type used by guanacos more than its availability was vega while shrubland on steppe slope and shrubland on plains were used according to their availability. Vicuñas were absent on shrublands in winter and in shrublands and grasslands on plains in summer, and used vegas and grasslands on steep slopes more than expected during both seasons. Horses, donkeys, and cattle used vegas more than expected in all seasons. Vegas were strongly selected by both camelids and livestock

during both seasons. More than 95 % of the total values of the χ^2 statistics for all species and seasons were due to the values obtained for the vega habitat type.

Discussion

Guanacos and vicuñas were spatially segregated for the most part in this study, although guanacos were habitat generalists that used all types of habitat to some extent and vicuñas were restricted to the grasslands and vegas above 3,500 masl. The shrubland habitats where guanacos were often found were at lower altitudes (2,000 to 3,500 masl) than the grasslands and vegas used by vicuñas, so this segregation was largely altitudinal, as reported for guanacos and vicuñas in northern Argentina (Lucherini 1996; Lucherini and Birochio 1997). Our results differ from those which found no spatial segregation between the two camelids in the provinces of La Rioja and San Juan (Cajal et al. 2010), and no spatial segregation in the San Guillermo Reserve adjacent to the Laguna Brava Reserve (Cajal 1998). These differences in results probably are due to the fact that the other studies were carried out only at higher altitudes (between 3,300 and 3,800 masl) where Guanacos are scarce. Sympatric species of similar foraging strategies can compete if there is high overlap in their use of space and the resources are scarce (Prins and Olf 1998; Hulbert and Andersen 2001; Owen-Smith 2002). However, segregation in habitat use can facilitate the coexistence of similar species by reducing interspecific competition (Pianka 1978). It is probable that the spatial segregation between guanacos and vicuñas reported in our study, which occurred over a wide (ca. 2,000 m) altitudinal range, facilitated their coexistence. This segregation pattern was observed in other assemblages of ungulates with similar foraging strategies (Nangail et al. 2004; Focardi et al. 2006).

The large degree of overlap in habitat use between livestock and guanacos during winter and between livestock, guanacos, and vicuñas during summer is in contrast to minimal overlap

Table 1 χ^2 goodness of fit test. χ^2 of expected vs. observed number of groups in each habitat type for each ungulate species and season

Species	Season	Habitat type	Partial χ^2	Total χ^2	<i>df</i>	<i>p</i> value
Guanaco	Winter	SHRPL	92.41	1,302	4	<0.001
		SHRST	17.06			
		GRAPL	7.49			
		GRAST	81.16			
	Summer	VEGA	1,103.88			
		SHRPL	5.59			
		SHRST	18.32			
		GRAST	54.79			
Vicuña	Winter	VEGA	12,382.53	12,461.23	3	<0.001
		GRAPL	0.03			
		GRAST	2.15			
		VEGA	100.24			
	Summer	VEGA	102.42			
		GRAST	99.73			
		VEGA	4,943.73			
		VEGA	5,043.46			
Cattle	Winter	SHRPL	9.89	3,067.6	2	<0.001
		SHRST	10.44			
		VEGA	3,047.27			
		VEGA	3,047.27			
	Summer	SHRPL	18.42			
		VEGA	1,105.51			
		VEGA	1,123.93			
		VEGA	1,123.93			
Equids	Winter	SHRPL	0.07	81.04	2	<0.001
		SHRST	1.34			
		VEGA	79.63			
	Summer	SHRPL	27			
		VEGA	1,620.4			
		VEGA	1,647.4			

Values of χ^2 statistic (χ^2), degree of freedom (*df*), and *p* values are shown

SHRPL shrubland on plains, *SHRST* shrubland on steep terrain, *GRAPL* grassland on plains, *GRAST* grassland on steep terrain, *VEGA* vegas

between guanacos and livestock found in the Talampaya National Park in the Argentine Monte (Acebes et al. 2012). This difference could be due to differences in methodology between the two studies, as Acebes et al. did not evaluate overlap in habitat use but rather the main habitat attributes selected by each species. However, this does not mean that the native and introduced herbivores in Laguna Brava Reserve compete for resources. It is probable that competition between camelids and livestock was minimal in the study area because of the low density of cattle and equids (fewer than 30 guanaco units in all the study area compared to 500 guanaco units of camelids, personal observation). In studies of vicuñas and guanacos where evidence of competition with livestock has been observed, the density of livestock was similar to or higher than that of the camelids (Baldi et al. 2001, 2004; Bonacic et al. 2002; Puig et al. 2003; Rojo et al. 2012). Nevertheless, it is necessary to evaluate dietary overlap between livestock and camelids in our study area to assess thoroughly their potential for competition.

Vegas were selected by all ungulates in this study, probably due to the greater productivity, grass cover, and vegetation quality of this habitat (Massy and Weeda 2003; Sixto 2003). The use of vegas by all species (native and exotic) increased significantly in summer, as reflected both by the number of

groups and group size relative to other habitat types. This increase in use was likely the result of the increase in plant biomass during summer, when productivity of vegas doubles or triples that of winter months, while productivity of other habitat types did not increase in a significant manner during that season (Wurstten, unpublished data). Vegas are critical habitats for guanacos and vicuñas during the breeding season allowing increased reproductive success compared to other habitats by providing succulent nutritional forage for females when they are coping with energetic demands of gestation and lactation, as well as high visibility that facilitates escape from predation (Bank et al. 2003; Donadio 2012). Therefore, any anthropogenic activity that reduces the extent of vegas or affects their forage quality will impact guanaco and vicuña populations.

Large-scale mining exploration and exploitation expanded greatly after 1990 in the high-altitude areas of the Andes where vegas are present, including the Laguna Brava Reserve. Because vegas represent a small proportion of the land cover, this habitat type is often underestimated in the environmental impact assessments that mining companies present to government agencies (e.g., Knight Piésold Consulting 2006) but may suffer the greatest relative impacts of all habitats. For example, much of the road networks, camps, and all tailing dams of open

pit mines built in the area have been constructed in valleys, often involving the destruction of vegas (personal observation by authors). Also, most mining projects in mountain areas are accessible only by roads built to follow mountain streams often modifying or disrupting the flow of water and drying up vegas downstream.

According to local governments and mining companies, many more large-scale mines for precious metals will be built in the region in the coming years. This expansion of mining will directly affect wild South American camelids and other mountain biodiversity. To minimize these impacts, governments must plan and implement measures to conserve vegas, true oases in an arid environment with high solar radiation and a short vegetation growing season.

Acknowledgments We thank the Secretary of Environment of La Rioja Province and the Secretary of Environment and the Subsecretary of Conservation and Protected Areas of San Juan Province. We also thank the custodial staff of Laguna Brava and San Guillermo provincial reserves and the volunteers who provided invaluable help in the field. We also thank the two anonymous reviewers for the helpful comments that resulted in improvements to the manuscript. This study was funded by the National Council of Scientific and Technical Research (€ 35,800) and Wildlife Conservation Society (vehicle use and fuel, € 6,000). We declare that all the experiments comply with the current laws of Argentina.

References

- Acebes P, Traba J, Malo JE (2012) Co-occurrence and potential for competition between wild and domestic large herbivores in a South American desert. *J Arid Environ* 77:39–44
- Arzamendia Y, Cassini MH, Vilá BL (2006) Habitat use by vicuña *Vicugna vicugna* in Laguna Pozuelos Reserve, Jujuy, Argentina. *Oryx* 40:198–203
- Baigún RJ, Bolkovic ML, Aued MB, Li Puma MC, Scandalo RC (2008) Manejo de fauna silvestre en la Argentina: Primer censo nacional de camélidos silvestres al norte del Río Colorado. Secretaría de Ambiente y Desarrollo Sustentable de la Nación, Buenos Aires
- Baldi R, Albon SD, 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 SD (2004) High potential for competition between guanacos and sheep in Patagonia. *J Wildlife Manage* 68:924–938
- Baldi R, Novaro AJ, Walker S, Funes M, Ferrando P, Failla M, Carmanchahi P (2010) Guanaco management in Patagonian rangelands: a conservation opportunity on the brink of collapse. In: du Toit J, Kock R, Deutsch J (eds) *Wild rangelands: conserving wildlife while maintaining livestock in semi-arid ecosystem*. Blackwell, London, pp 266–290
- Bank MS, Sarno RJ, Franklin WL (2003) Spatial distribution of guanaco mating sites in southern Chile: conservation implications. *Biol Conserv* 112:427–434
- Birch LC (1957) The meaning of competition. *Am Nat* 91:5–18
- Bleich VC, Davis JH, Marshal JP, Torres SG, Gonzales BG (2009) Mining activity and habitat use by mountain sheep (*Ovis canadensis*). *Eur J Wildlife Res* 55:183–191
- Bonacic C, McDonald DW, Galaz J, Sibly RM (2002) Density dependence in the camelid *Vicugna vicugna*: the recovery of a protected population in Chile. *Oryx* 36:118–125
- Borgnia M, Vilá BL, Cassini MH (2008) Interaction between wild camelids and livestock in an Andean semi-desert. *J Arid Environ* 72:2150–2158
- Borgnia M, Vilá BL, Cassini MH (2010) Foraging ecology of vicuña, *Vicugna vicugna*, in dry Puna of Argentina. *Small Ruminant Res* 88:44–53
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford, New York
- Cabrera A (1976) *Regiones fitogeográficas argentinas*. Enciclopedia Argentina de Agricultura y Ganadería 2, ACME, Buenos Aires
- Cajal JL (1998) La conservación de los camélidos silvestres en la puna y cordillera frontal. Situación de la vicuña en la región, pautas para su manejo. In: Cajal JL, García J (eds) *Bases para la conservación y manejo de la puna y cordillera frontal de Argentina: el rol de las reservas de biosfera*. FUCEMA, Montevideo, pp 273–297
- Cajal J, Tonni EP, Tartarini V (2010) The extinction of some South American camelids: the case of *Lama (Vicugna) gracilis*. *Mastozoología Neotropical* 17:129–134
- Combina M, Pasarello JC (1980) *Evaluación geológica y estimación sulfurata: Laguna Brava*. Dirección Provincial de Minería, La Rioja
- Coughenour MB, Singer FJ (1991) The concept of overgrazing and its application to Yellowstone's northern range. In: Keiter R, Boyce M (eds) *The greater Yellowstone ecosystem: redefining America's wilderness heritage*. Yale University, New Haven, pp 209–230
- De Lamo DA, Sanborn AF, Carrasco CD, Scott DJ (1998) Daily activity and behavioral thermoregulation of the guanaco (*Lama guanicoe*) in winter. *Can J Zool* 76:1388–1393
- Donadio E (2012) *The interaction among pumas, wild camelids and grasses in the high plateaus of the Andes, Argentina*. PhD Thesis, University of Wyoming
- Ellis JE, Swift DM (1988) Stability of African pastoral ecosystems: alternate paradigms and implications for development. *J Range Manage* 41:450–459
- Focardi S, Aragno P, Montanaro P, Riga F (2006) Inter-specific competition from fallow deer *Dama dama* reduces habitat quality for the Italian roe deer *Capreolus capreolus italicus*. *Ecography* 29:407–417
- González BA, Palma RE, Zapata B, Marín JC (2006) Taxonomic and biogeographic status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). *Mammal Rev* 36:157–178
- Grimalt JO, Ferrer M, Macpherson E (1999) The mine tailing accident in Aznalcollar. *Total Sci Environ* 242:3–11
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scan J Stat* 6:65–70
- Hulbert IA, Andersen R (2001) Food competition between a large ruminant and a small hindgut fermentor: the case of the roe deer and mountain hare. *Oecologia* 128:499–508
- Hunzicker JH (1952) Las comunidades vegetales de la Cordillera de La Rioja. *Revista de Investigaciones Científicas Agrícolas* 6:167–196
- Illius AW, O'Connor TG (2000) Resource heterogeneity and ungulate population dynamics. *Oikos* 89:283–294
- Ito TY, Lhagvasuren B, Tsunekawa A, Shinoda M, Takatsuki S, Buuveibaatar B, Chimeddorj B (2013) Fragmentation of the habitat of wild ungulates by anthropogenic barriers in Mongolia. *PLoS One*. doi:10.1371/journal.pone.0056995
- Knight Piésold Consulting (2006) Informe de impacto ambiental. Proyecto Pascua Lama. <http://mineria.sanjuan.gov.ar>. Accessed 22 Feb 2013
- Lawrence RK (1986) *Factors influencing guanaco habitat use and group size in Torres del Paine National Park*. MSc Thesis, Iowa State University
- Legendre P, Legendre L (1998) *Numerical ecology*. Elsevier, Amsterdam
- Lucherini M (1996) Group size, spatial segregation and activity of wild sympatric vicuñas *Vicugna vicugna* and guanacos *Lama guanicoe*. *Small Ruminant Res* 20:193–198

- Lucherini M, Birochio DE (1997) Lack of aggression and avoidance between vicuña and guanaco herds grazing in the same Andean habitat. *Studies on Neotropical Fauna and Environment* 32:72–75
- Mares MA, Ojeda RA (1984) Faunal commercialization and conservation in South America. *BioScience* 34:580–584
- Marin JC, Casey CS, Kadwell M, Yaya K, Hoces D, Olazabal J, Rosadio R, Rodriguez J, Sportono A, Bruford MW, Wheeler JC (2007) Mitochondrial phylogeography and demographic history of the vicuña: implications for conservation. *Heredity* 99:70–80
- Marin JC, Spotorno A, Gonzalez B, Bonacic C, Wheeler JC, Casey CS, Bruford MW, Palma RE, Poulin E (2008) Mitochondrial DNA variation, phylogeography and systematics of guanaco (*Lama guanicoe*, Artiodactyla: Camelidae). *J Mammal* 89:269–281
- Massy N, Weeda A (2003) Zonificación de la aptitud ganadera del departamento de Potosí. In: *Proceedings III Congreso Mundial sobre Camélidos y I Taller Internacional*, DECAMA, Potosí
- Molina JI (1782) *Saggio Sulle Storia Naturale del Chile*. Bologna, Italy
- Mosca Torres ME, Puig S (2012) Habitat use and selection by the vicuña (*Vicugna vicugna*, Camelidae) during summer and winter in the High Andean Puna of Argentina. *Small Ruminant Res* 104:17–27
- Müller PLS (1776). Erste Classe, Säugende Thiere. In: von Linné (ed) *Des Ritters Carl von Linné vollständiges Naturalsystem nach der zwölften Lateinischen Ausgabe, 1773–1776* Nurnberg
- Namgail T, Fox JL, Bhatnagar YV (2004) Habitat segregation between sympatric Tibetan argali *Ovis ammon hodgsoni* and blue sheep *Pseudoisna yaur* in the Indian Trans-Himalaya. *J Zool* 262:57–63
- Ovejero RJ, Aacebes P, Malo JE, Traba J, Mosca-Torres ME, Borghi CE (2011) Lack of feral livestock interference with native guanaco during the dry season in a South American desert. *Eur J Wildlife Res* 57:1007–1015
- Owen-Smith N (1990) Demography of a large herbivore, the greater kudu, *Tragelaphus strepsiceros*, in relation to rainfall. *J Anim Ecol* 59:893–913
- Owen-Smith N (2002) Adaptive herbivore ecology: from resources to populations in variable environments. Wits University, Johannesburg
- Pianka ER (1978) *Evolutionary ecology*. Harper & Row, New York
- Prins HH, Olff H (1998) Species richness of African grazer assemblages: towards a functional explanation. In: Newbery D, Prins HHT, Brown N (eds) *Dynamics of Tropical Communities*. Blackwell, Oxford, pp 448–490
- Puig S (1995) Abundancia y distribución de las poblaciones de guanacos. In: Puig S (ed) *Técnicas para el Manejo del Guanaco*. IUCN, Gland, pp 57–70
- Puig S, Ferraris G, Superina M, Videla F (2003) Distribución de densidades de guanacos (*Lama guanicoe*) en el norte de la Reserva La Payunia. *Multequina* 12:37–48
- Putnam RJ (1996) *Competition and resource partitioning in temperate ungulate assemblages*. Chapman and Hall, London
- Quinn G, Keough M (2002) *Experimental design and data analysis for biologists*. Cambridge University, New York
- Reglero MM, Monsalve-González L, Taggart MA, Mateo R (2008) Transfer of metals to plants and red deer in an old lead mining area in Spain. *Sci Total Environ* 406:287–297
- Renaudeau d'Arc N, Cassini MH, Vilá BL (2000) Habitat use of vicuñas in Laguna Blanca Reserve (Catamarca, Argentina). *J Arid Environ* 46:107–115
- Rojo V, Arzamendia Y, Vilá BL (2012) Uso del hábitad por vicuñas (*Vicugna vicugna*) en un sistema agropastoril en Suripujio, Jujuy. *Mastozoología Neotropical* 19:127–138
- Sixto M (2003) Determinación de la capacidad de carga y carga animal en bofedales de la comunidad de Cosapa, provincia Sajama, Oruro, Bolivia. In: *Proceedings III Congreso Mundial sobre Camélidos y I Taller Internacional*. DECAMA, Potosí
- Singh RK, Chowdhury S (1999) Effect of mine discharge on the pattern of riverine habitat use of elephants *Elephas maximus* and other mammals in Singhbhum forests, Bihar, India. *J Environ Manage* 57:177–192
- Tadey M (2008) Efecto del ganado sobre los niveles de polinización en especies vegetales del monte patagónico. *Ecología Austral* 18:89–100
- Vallentine JF (2001) *Grazing management*. Academic, San Diego
- Vilá BL, Roig VG (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
- Voeten MM, Prins HH (1999) Resource partitioning between sympatric wild and domestic herbivores in the Tarangire region of Tanzania. *Oecologia* 120:287–294
- Weir JN, Mahoney SP, McLaren B, Ferguson SH (2007) Effects of mine development on woodland caribou *Rangifer tarandus* distribution. *Wildlife Biol* 13:66–74
- Williamson D, Williamson J, Ngwamotsoko KT (1988) Wildebeest migration in the Kalahari (South Africa). *Afr J Ecol* 26:269–280
- Yeo JJ, Peek JM, Wittinger WT, Kvale CT (1993) Influence of rest-rotation cattle grazing on mule deer and elk habitat use in east-central Idaho. *J Range Manage* 46:245–250
- Zar JH (1996) *Biostatistical analysis*, 3rd edn. Prentice Hall, New Jersey