Habitat use and selection by the vicuña (*Vicugna vicugna*, Camelidae) during summer and winter in the High Andean Puna of Argentina

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ABSTRACT

Habitat use and selection by vicuñas and particularly by individuals of different categories were evaluated during the summer and winter of two years (2006 and 2007) that differed in their precipitation pattern. Both, use and selection, were analyzed within the framework of the optimal foraging theory (OFT) that predicts a high proportion of individuals using habitats where the most nutritional food items are present, and if other things are equal, habitats should be chosen if they yield the highest average rate of energy intake, which fits with this theory. Indeed, a prediction of the habitat selection theory (HST) was evaluated during winter (dry season). Over the study period high proportions of vicuñas occupied habitats with availability of high quality food, which supports the OFT. However, habitat selection differed between seasons and years due to the decrease in plant resource availability in the winter of both years and in the summer of 2007 (with drought conditions). In the dry season of the good year (2006), vicuñas (familial individuals, particularly) were more homogeneously distributed among habitats than in summer, which is consistent with the HST. High proportions of individuals at the wetland (called *vega*) were more evident during the bad year (2007) than in the good one. Therefore, habitat use (and selection) by vicuñas in this sector of the Puna region is influenced by the availability of high quality food resources and by the presence of water, and the relevance of the latter increased with drought conditions. An assessment of the interactions between individuals of different social categories will contribute to better understanding the distribution of animals among different habitats.

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1. Introduction

Habitat use and selection studies are essential for understanding the animals' biological requirements and the strategies they use to fulfill their needs (Manly et al., 1993). Habitat selection occurs when an animal chooses which habitat resources (physical and biological) to use for growing, surviving, and reproducing (Green and Stamps, 1991; Johnson, 1980; Manly et al., 1993), whereas habitat use is the way an individual uses different resources present in a particular habitat (Hall et al., 1997). In animals who live in groups, social interactions may influence habitat use affecting the efficiency with which the individuals satisfy their appetite drive, through competitive or agonistic interactions (Duncan and Gordon, 1999). In that sense, Mosley (1999) suggested that social competition may force subordinate individuals away from preferred areas.

Availability of water sources and seasonal differences in food availability are other factors that can strongly influence habitat use and selection by ungulates (Duncan and Gordon, 1999; Fryxell and Sinclair, 1988; Redfern et al., 2003; Sinclair and Fryxell, 1985; Traill, 2004), particularly in arid or semi-arid environments where quality and

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availability of food resources decrease dramatically during the dry season (Owen-Smith and Novellie, 1982). Interannual variations in precipitation patterns are common in these environments. In the High Andes these variations are generally a consequence of El Niño-Southern Oscillation (Trenberth and Caron, 2000), causing droughts during the wet season and exacerbating the scarcity of food resources in the environment (Holmgren et al., 2001).

The optimal foraging theory (Pyke et al., 1977; Stephens and Krebs, 1986) proposes a model to explain habitat use by animals. One of the predictions of this theory is that individuals should concentrate in habitat types where the availability of the most nutritional food items are high (Quintana et al., 2002). In the case of habitat selection, models predict that habitats should be chosen if they yield the highest average rate of energy intake, which fits with the optimal foraging theory (Krebs et al., 1981; Schoener, 1971). Therefore, it is predicted that the proportions of individuals observed in high quality habitats will be higher than the proportions expected from a random distribution, due to animals preference for those habitats. When resource availability decreases in the best habitats (particularly in winter), the habitat selection theory predicts that the distribution of animals among habitats should become more homogeneous (Sutherland, 1996).

The vicuña (*Vicugna vicugna* Molina 1872) is the smallest South American camelid and has been hunted to near extinction until 1960 (Torres, 1992). The establishment of conservation programs since 1969 have been effective for several populations of vicuñas, and this species has been changed to the current "least concern" IUCN status (IUCN, 2001). The distribution range of this species in Argentina comprises high altitude environments of the High Andean and Puna biogeographic provinces (Torres, 1992). Vicuñas are considered an important economical resource because they have the finest animal fiber in the world (FAO, 1987). Therefore, the demand for their products is considerable, and the ability to generate employment is high (Lichtenstein, 2006).

This camelid has a stable social structure, composed of family groups (territorial animals), bachelor groups (non-territorial animals), and solitary individuals (with or without an established territory; Cassini et al., 2009; Franklin, 1983; Koford, 1957). The territorial behavior of familial males would determine vicuña distribution in the environment because they defend sites with high quality resources to provide sufficient food to females, particularly during pregnancy and lactation periods (Mosca Torres and Puig, 2010; Vilá and Cassini, 1993). Bachelor males display greater movement due to lack of territory (Arzamendia and Vilá, 2006; Mosca Torres et al., 2006) and generally occupy environments with variable or marginal quality vegetation away from territorial areas with higher quality resources (Cajal, 1989; Franklin, 1983; Koford, 1957). The vicuña is considered an obligate-drinker due to its strong dependence on water (Franklin, 1983; Vilá and Roig, 1992).

Habitat use by vicuñas in the Puna of Peru (Franklin, 1983; Koford, 1957) and some areas of Argentina (Cajal, 1989; Renaudeau d'Arc et al., 2000; Vilá and Cassini, 1993; Vilá and Roig, 1992) is determined mainly by the terrain, availability of resources (water, food and shelter), climatic factors, time of day and social structure. However, there is scant information available about habitat use and selection by this species within the framework of the optimal foraging theory. Moreover, no information is available on the ecology of this species in Salta, Argentina. Therefore, results of this research provide more knowledge of the selective behavior of this small ruminant.

This study analyzes the different habitat types occupied by the vicuña in Unquillal (High Andes, Salta, Argentina), the habitat use and selection by this species particularly by different social categories, during the summer and winter (corresponding to maximal and minimal resource availability, respectively) of 2006 and 2007. The specific objectives are to detect: (a) whether there are changes in the habitat occupancy by social categories of vicuñas among years, seasons and times of the day, and (b) whether vicuñas actively select different habitats within the study site, particularly when food resource availability is maximal.

We predict that the proportion of vicuñas using habitats with high availability and high quality of food resources will be greater than in habitats with lower food quality and availability. Additionally, since this species has a strong dependence on water, especially during the dry season (Renaudeau d'Arc et al., 2000), we expect to find a higher proportion of animals in wetlands (called *vegas*) during the winter than in summer, and during a dry year than in a good year. Finally, we predict that vicuñas will show differences in the daily pattern of habitat use between seasons and years, due to the changes in food quality and availability.

In relation to habitat selection, we expect that the proportion of vicuñas will be higher in habitats with high food availability than the proportion expected from a random distribution, particularly during the summer of a good year when food availability is maximal. On the other hand, distribution of individuals among different habitats should be more homogeneous in winter when food availability decreases. At intraspecific level we predict that familial individuals will prefer habitats with high quality food resources because of the high energy demands of female vicuñas during lactation and gestation periods.

2. Materials and methods

2.1. Study Area

The study area, *Unquillal* (24°27′S and 67°12′W, 8.6 km^2) is located within the Los Andes Reserve in the NW region of Salta province (Argentina). The Reserve is a 14,400 km^2 protected area representative of the Puna biogeographic province (Cabrera and Willink, 1980), whose objective is to conserve natural resources (especially the vicuña). The climate is cool and dry, with broad daily and seasonal temperature range (between 2 °C and 18 °C in summer, and 12 °C and 16 °C in winter), scarce rainfall (130 mm/yr) occurring only in summer (e.g. wet season; December–March) and intense frosts.

Seasonal growth and quality of vegetation are determined by the precipitation pattern. During the wet season (summer) plants grow quickly and have high nutritional quality, but this period is only 3–4 months in duration

(Van Saun, 2006). However, food availability is extremely limited during the dry season (autumn and winter) when plants are too mature and low in quality (San Martín and Bryant, 1989). In the study area, the El Niño-Southern Oscillation event caused a rainfall decline in summer of 2007, prevailing drought conditions.

Vegetation on the study site is dominated by shrubs (particularly the genera Adesmia, Baccharis, Parastrephia, Acantholippia, Fabiana and Junellia) associated with annual forbs (Hoffmansegia, Tarasa and Eragrostis) and grasses (Poa, Festuca and Stipa). Vegas (wetlands with high plant cover) show short vegetation, where graminoids (Cyperaceae and Juncaceae) are usually present in association with species of the genera Juncus, Plantago and Deyeuxia (Mosca Torres and Puig, 2010).

The study site was selected far away from roads and with access difficulties in order to avoid existing human disturbances (poaching and mining). The site presented a stable abundance of vicuñas, with a much higher density (12.8 individuals/km^2) than the mean density estimated in whole Reserve (0.75 individuals/km^2, Baigún et al., 2008).

2.2. Fieldwork

2.2.1. Characterization of habitats at the study site

Five types of habitats were defined according to characteristics of topography, vegetation and to the presence of water (Table 1). Plant cover was estimated using the point-quadrat method (Daget and Poissonet, 1971) along ten 30-m transects per habitat during the summer and winter of 2006 and 2007. There were some difficulties during the sampling of the grassy slope due to its steepness and height over 4000 m elevation and only three of the ten sample transects were completed to determine plant cover and species composition. Given that the values of both variables were similar to the results obtained for the grassy foothill; these estimations were extrapolated to the grassy slope.

Seasonal and annual variations in plant cover on the entire study site were analyzed with the Wilcoxon Rank Sum test (Sokal and Rohlf, 1995). Additionally, comparisons of plant cover among habitats were analyzed with the Kruskal Wallis test, and multiple comparisons were performed with the Q test (Zar, 1999).

2.2.2. Habitat use and selection

The scan sampling method (Altmann, 1973) was used to analyze habitat use by vicuñas. Individuals observed on each sampling occasion were classified according to their social category, in order to estimate the proportion of individuals belonging to different social groups: family groups, bachelor groups and solitary individuals. Vicuñas that could not be identified within some social group were classified as non-determined individuals.

Each scan sampling was conducted in a clockwise direction, covering an area of 180°, and at regular intervals of 1 h, with an average of six samples per day. Samplings were made using a telescope 12–36 × 60, spreadsheets and a tape recorder. Type of individual (familial male, female, offspring, bachelor, solitary and non-determined individuals), social group (familial and bachelor group), and habitat where vicuñas have been observed were registered in order

to estimate the proportions of individuals and groups occupying different habitat types.

Summer samplings were taken from 8 am to 6 pm, for 14 days in 2006, and eight days in 2007, whereas winter samplings were done from 8 am to 5 pm, during 12 days in 2006 and 8 days in 2007. Differences in sampling length between years were due to the bad weather conditions prevailing at the study site during 2007.

Significant differences in the proportions of social groups between years and seasons in each habitat were detected using the Kruskal Wallis test (Sokal and Rohlf, 1995), and multiple comparisons were made with the Q test (Zar, 1999). Significant associations between number of vicuñas at different times of the day and habitat type during both seasons of both years were detected using simple correspondence analyses. The χ^2 goodness-of-fit test was used to evaluate habitat selectivity, i.e. whether observed proportions of social groups differed significantly from those expected from the relative habitat area. Bailey's index (Cherry, 1996) was applied to detect whether habitats were used in higher, lower or equal proportions than their relative land area (preference, avoidance or indifference, respectively). This index computes confidence intervals for multinomial proportions using Bonferroni's inequality, and provides the best combination of low error and interval length (Cherry, 1996). All computations were performed with R 2.12.1 (R Development Core Team, 2010).

3. Results

3.1. Characterization of habitats at the study site

Plant cover in each habitat was significantly higher in summer than in winter during both years [2006: $W = 1$, $p < 0.001$ in the shrubby slopes (SS); $W = 33.5$, $p < 0.001$ in the shrubby foothill (SF); $W = 0$, $p < 0.001$ in the grassy foothill (GF) and $W = 14$, $p = 0.005$ in the *vega* (VE); 2007: $W = 75$, $p < 0.001$ in SS; $W = 125$, $p = 0.042$ in SF; $W = 4$, $p < 0.001$ in GF and $W = 1$, $p < 0.001$ in VE, Table 1].

Plant cover on SS and SF was higher in the summer of 2006 than in the same season of 2007 ($W = 399$, $p < 0.001$, $W = 300$, $p = 0.007$ for SS and SF respectively, Table 2), similar results were detected on the SS during winter, with coverage being higher in 2006 than in 2007 ($W = 275$, $p = 0.043$).

Significant differences in plant cover among habitat types were evident during the summer and winter of 2006 ($H = 29$, $p < 0.001$ and $H = 35$, $p < 0.001$ for summer and winter respectively) and 2007 ($H = 40$, $p < 0.001$ and $H = 37$, $p < 0.001$ respectively; Table 3). The VE showed the highest percentage of plant cover in all study periods, followed by the shrubby and grassy foothills.

3.2. Habitat use

Significant differences between proportions of individuals using different habitats were detected in both seasons of 2006 (Table 4). Proportions of vicuñas on SS and SF were significantly higher than on the grassy slope, GF and VE during the summer and winter of 2006. Also in winter vicuñas were proportionally more abundant in the GF than at the

Table 1
Description of the five habitats types defined in the study area. Habitat types were ground-surveyed to determine plant cover.

Acronym	Habitat type (percentage of the study area)	Relief	Vegetation structure	Main plant species	Water bodies
SF	Shrubby foothill (35%)	Smooth slope (<15°)	Low shrub layer (30–90 cm), associated with annual forbs in summer	Shrubs: *Fabiana denudata*, *Junellia seriphioides* and *Adesmia horridiuscula*. Grass: *Poa* sp. Annual forb: *Tarasa tenella*, particularly in summer 2006	Absent
SS	Shrubby slopes (45%)	Steep slope (>30°)	Low shrub layer (30–90 cm), associated with annual forbs in summer	Shrubs: *Adesmia horridiuscula*, *Artemisia copa* and *Lycium chañar*. Grass: *Poa* sp. Annual forbs: *Tarasa tenella* and *Schkuhria pinnata*, particularly in summer 2006	Absent
GF	Grassy foothill (10%)	Smooth slope (<15°)	Grassy layer, with the presence of some shrubs of medium height (90–150 cm)	Grasses: *Festuca* sp. and *Stipa* spp. Graminoids in the *vega*: *Eleocharis* aff. *albibracteata*, *Carex* sp. (Cyperaceae) and *Juncus* aff. *articus* (Juncaceae). Grasses in the *vega*: *Deyeuxia* sp. and *D. chrysostachya*	A small wetland (called *vega*) of 0.02 km^2 at one end of GF
GS	Grassy slope (5%)	Steep slope (>30°)	Grassy layer, with the presence of some shrubs of medium height (90–150 cm)	Grasses: *Festuca* sp. and *Stipa* spp.	Absent
VE	*Vega* (5%)	Steep slope (>30°)	Dense layer of species of the Cyperaceae and Juncaceae families, accompanied by some grasses	Graminoids: *Eleocharis* aff. *albibracteata*, two species of the genera *Carex*, and *Juncus* aff. *articus*. Grasses: *Deyeuxia* sp., *D. chrysostachya*, *Festuca* sp. *Stipa* spp.	The presence of water in this habitat was constant during the two years of sampling

Table 2
Plant cover percentage in each habitat during 2006 and 2007.

Year	Season	SS	SF	GS and GF	VE
2006	Summer	45[*S,Y]	36[*S,Y]	53[*S]	88[*S]
	Winter	20[*Y]	26	17	63
2007	Summer	24[*S]	30[*S]	46[*S]	87[*S]
	Winter	16	24	18	61

SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill; VE: *vega*.
  [*] Significant differences ($p \leq 0.05$) between seasons (S) and years (Y).

Table 3
Significant differences in plant cover among habitat types during 2006 and 2007 showing the observed Q value compared with the expected value ($Q_{0.05,5} = 2.81$) where 0.05 is the significant level, and 5 is the number of habitats compared.

Year	Season	Habitats	Plant cover (%)	$Q_{0.05,5}$	Conclusion
2006	Summer	VE vs. SF	88 vs. 53	5.33[(2.81)]	VE > SF
		VE vs. SS	88 vs. 45	3.65[(2.81)]	VE > SS
	Winter	VE vs. SF	63 vs. 26	2.99[(2.81)]	VE > SF
		VE vs. SS	63 vs. 20	5.09[(2.81)]	VE > SS
		VE vs. GF	63 vs. 17	5.18[(2.81)]	VE > GF
		SF vs. GF	26 vs. 17	2.96[(2.81)]	SF > GF
2007	Summer	VE vs. SF	87 vs. 30	4.10[(2.81)]	VE > SF
		VE vs. SS	87 vs. 24	5.91[(2.81)]	VE > SS
		GF vs. SS	46 vs. 24	3.93[(2.81)]	GF > SS
	Winter	VE vs. SF	61 vs. 24	2.95[(2.81)]	VE > SF
		VE vs. SS	61 vs. 16	5.75[(2.81)]	VE > SS
		VE vs. GF	61 vs. 18	4.13[(2.81)]	VE > GF
		SF vs. SS	24 vs. 16	3.43[(2.81)]	SF > SS

SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill; VE: *vega*.

Table 4
Proportion of vicuñas in different types of habitats during summer and winter of 2006 and 2007.

Year	Season	Shrubby slopes	Grassy slope	Shrubby foothill	Grassy foothill	*Vega*	H	*p*-value
2006	Summer	0.44[GS,GF,VE]	0.10	0.46[GS,GF,VE]	0.05	0.04[S '07]	100	<0.001
	Winter	0.55[GS,GF,VE]	0.05	0.30[GS,GF,VE]	0.11[VE]	0.03[W '07]	89	<0.001
2007	Summer	0.37[GS,GF,VE]	0.08	0.30[GS]	0.13	0.14	32	<0.001
	Winter	0.33[GS]	0.05	0.25[GS]	0.20[GS]	0.17	41	<0.001

H: value of the Kruskal–Wallis statistic. (GS,GF,Ve) significant differences ($Q \geq 2.8$, $p = 0.05$) between the proportion of vicuñas in the habitat and the proportions registered in grassy slope, grassy foothill and *vega*; (GS) significant differences ($Q \geq 2.8$, $p = 0.05$) between the proportion of vicuñas in the habitat and the proportion registered in grassy slope; (VE) significant differences ($Q \geq 2.8$, $p = 0.05$) between the proportion of vicuñas in the habitat and the proportion registered in the *vega*. S '07: significant differences ($W = 123$, $p = 0.001$) between the proportion of vicuñas in the *vega* during summer of 2006 and 2007. W '07: significant differences ($W = 58$, $p = 0.001$) between the proportion of vicuñas in the *vega* during winter of 2006 and 2007.

VE. Similar results to those of 2006 were found in the summer of 2007 for the SS, whereas the proportion of vicuñas was only significantly higher for the SF than for the GS. Finally, during winter, vicuñas on the SS and in the SF and GF were proportionally more abundant than on the GS.

The proportion of individuals of each social category differed significantly among habitats. All social categories showed higher proportions on the SS and SF than in the other habitats during the summer and winter of 2006 (Table 4). Besides, bachelors were more abundant on the SS than in the SF during the winter of this year, whereas the proportion of solitary vicuñas was higher in the GF than at the VE.

The proportion of familial individuals was higher on the shrubby slopes and foothill than on the grassy slope and *vega* during the summer of 2007 (Table 4), whereas bachelor, solitary and non-determined vicuñas were proportionally more abundant on shrubby slopes and foothill than in the other habitats. Individuals of all social categories were better represented in the shrubby foothill than on the grassy slope in the winter of 2007. Familial and bachelor vicuñas were proportionally more abundant in the grassy foothill than on the grassy slope, whereas the proportions of familial, solitary and non-determined individuals were higher on the shrubby slopes than on the grassy slope. Finally, solitary animals were more abundant in the shrubby than the grassy foothill, whereas non-determined vicuñas were more represented in the shrubby habitats than at the *vega*.

The proportion of individuals at the *vega* was higher in 2007 than in 2006 ($W = 341$, $p < 0.001$) and such difference was evident during both the summer and winter (Table 4). No significant differences were found between seasons of the same year when comparing the proportions of individuals in this habitat. Only the proportion of solitary vicuñas at the *vega* was higher in the summer than the winter of 2006 ($W = 228$, $p = 0.003$; Fig. 1), whereas familial and non-determined individuals were proportionally more abundant during the summer than the winter of 2007 ($W = 14$, $p < 0.045$).

Significant associations ($p < 0.001$) were detected between the number of vicuñas using different habitats and the times of the day in both seasons and years of study. The first two dimensions of the simple correspondence analyses used contributed to a high percentage of the total inertia, both in summer (93.8% for 2006 and 96.1% for 2007) and winter (96.4% for 2006 and 96.3% for 2007).

Therefore the observed dependencies are adequately captured by the first two dimensions (Figs. 2 and 3).

During the summer of 2006, vicuñas were associated to the shrubby slope early in the morning (9 am) and late in the afternoon (5 pm), whereas at noon they were associated to the grassy foothill (Fig. 2a). In winter, vicuñas used primarily the grassy and shrubby slopes in the morning, they moved to the grassy foothill at 11 am and 1 pm, and also to the *vega* at noon, whereas at 3 pm most individuals were in the shrubby foothill (Fig. 2b).

During the summer of 2007, vicuñas were associated to the shrubby foothill between 9 and 11 am. At 1 pm they occupied mainly the grassy foothill and to a lesser extent the *vega*, while in the afternoon there was an association of individuals with the shrubby slopes (Fig. 3a). During winter, there was a tendency of the vicuña to mostly use the shrubby slopes and foothill at 9 am. At 11 am and 1 pm they were more related to the grassy foothill and to a lesser extent to the grassy slope, while in the afternoon there was an association of the individuals with the *vega* (Fig. 3b).
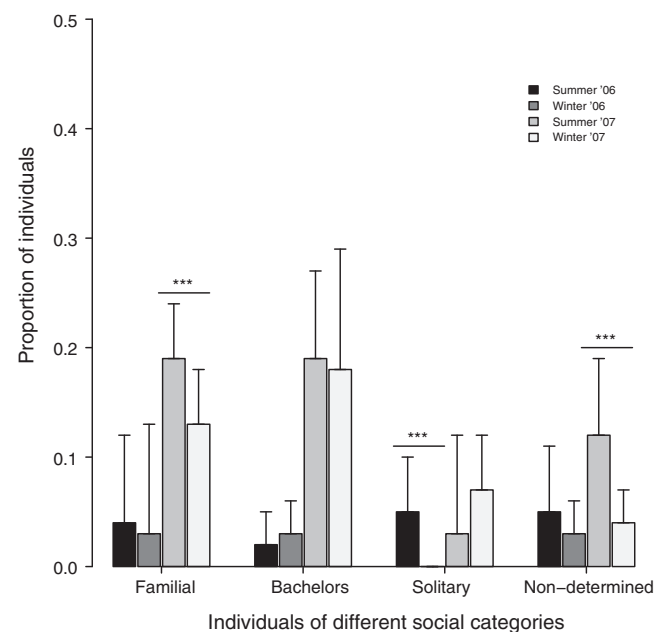

Fig. 1. Proportions of vicuñas of different social categories at the *vega* during the summer and winter of 2006 and 2007. (*) Significant differences ($p \leq 0.05$) between seasons of the same year. Bars indicate the SD.
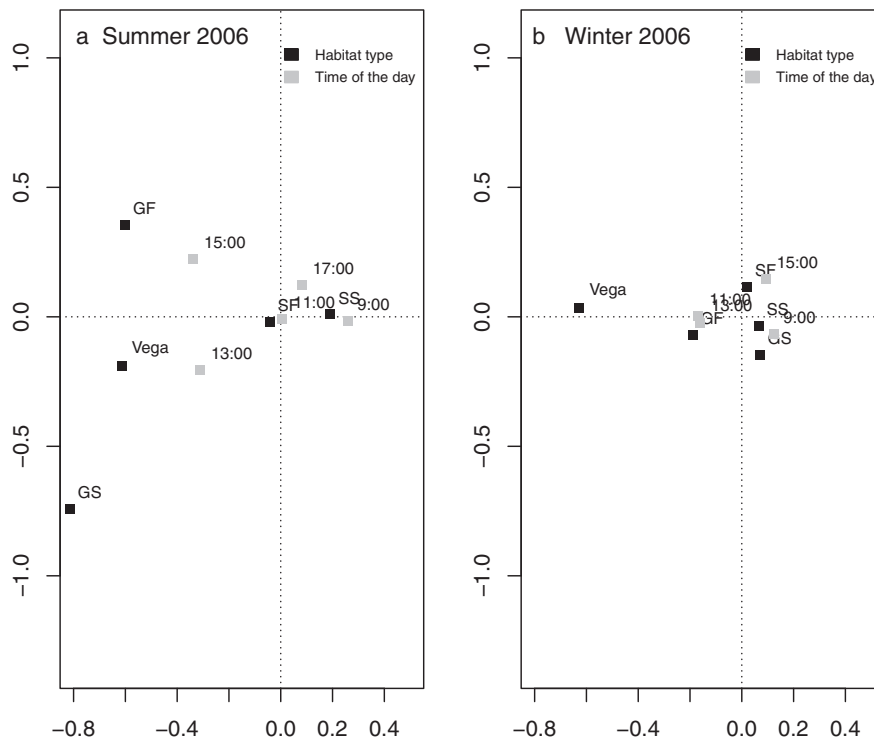
Fig. 2. Results of simple correspondence analyses showing the association between the variables "habitat types" and "time of the day" during the summer (a) and winter (b) of 2006. SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill.

3.3. Habitat selection

Vicuñas preferred the shrubby foothill in the summer of 2006 ($\chi^2 = 14.9$, $p = 0.005$; Table 5), whereas the other habitats were used proportionally to their summer and winter availability ($\chi^2 = 1.8$, $p = 0.771$). Vicuñas avoided eating on the shrubby slopes and preferred the *vega* during both seasons of 2007, whereas the grassy foothill was preferred only during the winter of that year ($\chi^2 = 82.2$, $p < 0.001$; Table 5).
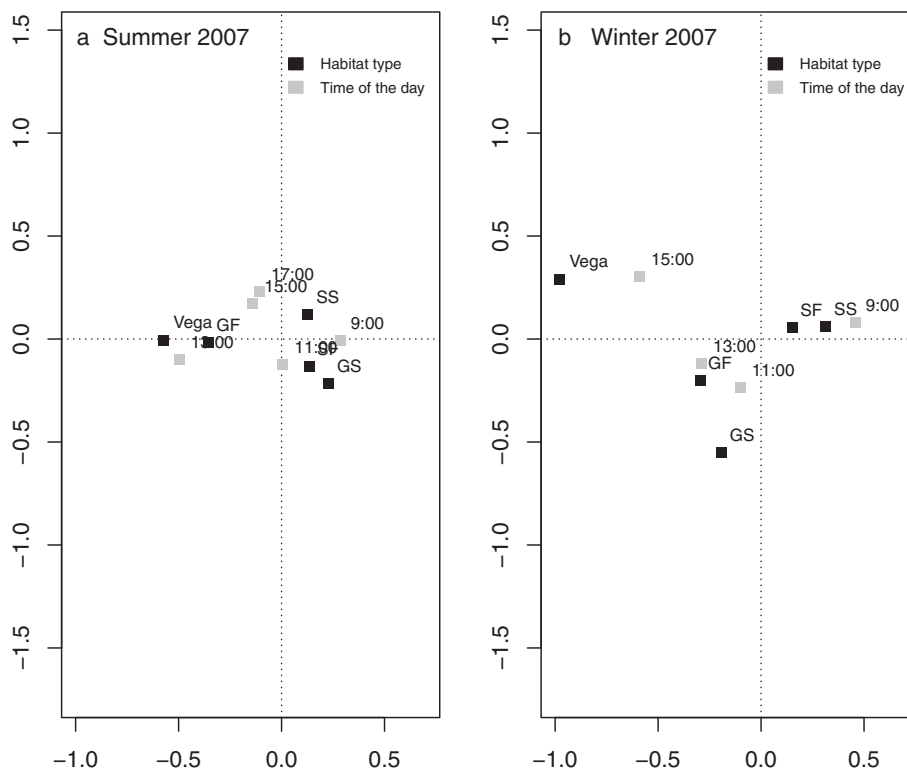

Fig. 3. Results of simple correspondence analyses showing the association between the variables "habitat types" and "time of the day" during the summer (a) and winter (b) of 2007. SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill.

Table 5
Habitat types preferred (P), avoided (A) or used with indifference (I) by vicuñas during the summer and winter of 2006 and 2007.

Habitat	Availability	2006		2007	
		Summer	Winter	Summer	Winter
		Use	Use	Use	Use
SS	0.51	0.46 (0.36–0.58) I	0.57 (0.46–0.68) I	0.40 (0.30–0.39) E	0.25 (0.16–0.25) E
GS	0.05	0.01 (0.00–0.07) I	0.06 (0.02–0.13) I	0.08 (0.03–0.08) I	0.06 (0.02–0.06) I
SF	0.30	0.45 (0.34–0.56) P	0.24 (0.16–0.35) I	0.31 (0.22–0.31) I	0.33 (0.23–0.33) I
GF	0.11	0.04 (0.01–0.11) I	0.11 (0.05–0.20) I	0.11 (0.05–0.11) I	0.23 (0.15–0.23) P
VE	0.03	0.04 (0.01–0.10) I	0.03 (0.00–0.09) I	0.11 (0.05–0.12) P	0.14 (0.08–0.15) P

Proportions observed (Use), proportions expected from each habitat's area (Availability) and Bailey's confidence intervals of use (between parentheses). SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill; VE: *vega*.

Familial, bachelor, solitary and non-determined vicuñas used selectively all habitats in the study area during the summer of 2006 (familial individuals: $\chi^2 = 11.3$, $p = 0.023$; bachelors: $\chi^2 = 18.4$, $p = 0.001$; solitary individuals: $\chi^2 = 35.0$, $p < 0.001$ and non-determined individuals: $\chi^2 = 27.0$, $p < 0.001$). All social categories preferred the shrubby foothill (Table 6), bachelor, solitary and non-determined animals avoided the grassy foothill, solitary vicuñas also avoided the shrubby slopes, and non-determined individuals avoided the grassy slope. Familial and non-determined vicuñas used with indifference all habitat types in the winter of 2006, whereas bachelor and solitary animals preferred the shrubby slopes.

Familial individuals and bachelors preferred the *vega* in the summer of 2007 ($\chi^2 = 73.6$, $p < 0.001$ and $\chi^2 = 189.4$, $p < 0.001$, respectively), bachelors also avoided the shrubby slope (Table 6). Solitary and non-determined vicuñas used all habitats in the same proportion as their availability ($\chi^2 = 5.4$, $p = 0.148$ and $\chi^2 = 3.3$, $p = 0.508$, respectively). In the winter of 2007, familial and bachelor animals still preferred the *vega* ($\chi^2 = 31.1$, $p < 0.001$ and $\chi^2 = 174.0$, $p < 0.001$, respectively), as well as the grassy foothill and avoided the shrubby slopes. Solitary individuals preferred the shrubby slopes and avoided the other habitats, whereas non-determined vicuñas showed the same foraging behavior as in summer (Table 6).

4. Discussion

Differences in plant cover between seasons and years would be attributable to the dry conditions of the winter of both years and to lack of enough rainfall during the summer of 2007, the latter due to the "El Niño" event that caused droughts in the High Andes of South America that year (Argentina National Weather Service, 2007).

Consistently with the optimal foraging theory (Krebs et al., 1981; Schoener, 1971), vicuñas used those habitats with the most profitable plant species although not high in food availability. In relation with habitat selection, vicuñas (mainly familial individuals) preferred habitat types with the most quality food, particularly in the wet season of 2006 when availability of resources was maximal. Therefore, differences in habitat use (and selection) by vicuñas and particularly by individuals of different social categories would be explained by the availability of food resources in the environment, conditioned by the social structure of this species.

4.1. Habitat use

The high proportions of individuals on the shrubby slopes and foothill during the two years of sampling would support the prediction of the OFT that states that individuals will prefer to forage in habitats that offer the highest energy gain (Krebs et al., 1981), because in both habitats are present two high quality food resources, the grass *Poa* sp. and the annual forb *Tarasa tenella*, particularly during the summer of 2006 (Mosca Torres and Puig, 2010). These species were the primary food resources consumed by the vicuña in this study area, despite their low availability (Mosca Torres and Puig, 2010). The presence of high proportions of vicuñas in the shrubby habitats seems to be more related to the presence of high quality food resources than to the abundance of vegetation, given that plant cover was below 50%, on both shrubby slopes and foothill. The high proportion of individuals detected in those habitats does not agree with that reported by Arzamendia and Vilá (2006) in Laguna de los Pozuelos Biosphere Reserve (Jujuy, Argentina) where vicuñas used intensively those vegetation units (e.g. habitats) with more than 50% plant cover.

The relatively flat and wet ground represents an advantage of the shrubby foothill as a feeding site, and accounts for the high proportion of vicuñas using this type of habitat, as occurred in Pampa Galeras, Peru (Koford, 1957). On the other hand, although Cajal (1989) and Rosati et al. (1998) observed that slopes were occupied secondarily by vicuñas in the San Guillermo Reserve (San Juan, Argentina) and in the Laguna Brava Reserve (La Rioja, Argentina), the results at our study site show that this type of habitat was used by a high proportion of vicuñas, particularly in 2006. Again, a possible explanation for the high proportions of individuals could be the presence of *Poa* sp. and the large area of this habitat.

The moderate use of the grassy foothill during the winter of both years could be attributed to the presence of *Stipa* spp., the second grass species consumed by the vicuña (Mosca Torres, 2010; Mosca Torres and Puig, 2010). Genin et al. (1995) reported the considerable use of the grassland by domestic camelids (llamas and alpacas) when resource availability decreases in the dry season due to the great ability of these animals to digest plant species with high silica content.

The drought conditions mentioned could have produced a decrease in the moisture content of food, which may explain the increased use of the *vega* in 2007.

Table 6
Habitat types (Hab) preferred (P), avoided (A) or used with indifference (I) by different social categories of vicuñas during the summer and winter of 2006 and 2007.

Hab	Avail	Summer 2006 Use	Signif	Winter 2006 Use	Signif	Summer 2007 Use	Signif	Winter 2007 Use	Signif
Familial individuals									
SS	0.51	0.46 (0.36–0.58) I	GS, GF, VE	0.52 (0.42–0.64) I	GS, GF, VE	0.48 (0.38–0.59) I	GS, VE	0.35 (0.25–0.46) A	GS
GS	0.05	0.02 (0.00–0.07) I		0.07 (0.02–0.15) I		0.04 (0.04–0.18) I		0.04 (0.01–0.11) I	
SF	0.30	0.42 (0.32–0.54) P	GS, GF, VE	0.23 (0.15–0.34) I	GS, GF, VE	0.27 (0.18–0.38) I	GS, VE	0.19 (0.12–0.30) I	GS
GF	0.11	0.05 (0.02–0.13) I		0.13 (0.07–0.22) I		0.13 (0.07–0.22) I		0.27 (0.18–0.38) P	GS
VE	0.03	0.05 (0.01–0.12) I		0.04 (0.10–0.12) I		0.03 (0.00–0.10) P		0.15 (0.08–0.24) P	GS
Bachelors									
SS	0.51	0.47 (0.39–0.59) I	GS, GF, VE	0.70 (060–0.80) P	GS, SF, GF, VE	0.38 (0.29–0.50) A	GS, GF, VE	0.18 (0.11–0.29) A	
GS	0.05	0.01 (0.00–0.06) I		0.02 (0.00–0.08) I		0.11 (0.05–0.20) I		0.03 (0.00–0.10) I	
SF	0.30	0.46 (0.36–0.58) P	GS, GF, VE	0.22 (0.14–0.33) I	GS, GF, VE	0.30 (0.21–0.42) I	GS, GF, VE	0.24 (0.16–0.35) I	GS
GF	0.11	0.04 (0.01–0.10) A		0.05 (0.01–0.12) I		0.07 (0.02–0.14) I		0.30 (0.21–0.41) P	GS
VE	0.03	0.02 (0.00–0.08) I		0.01 (0.00–0.05) I		0.14 (0.08–0.24) P		0.24 (0.16–0.35) P P	
Solitary individuals									
SS	0.51	0.38 (0.28–0.49) A	GS, GF, VE	0.63 (0.53–0.73) P	GS, GF, VE	0.46 (0.36–0.57) I	GS, GF, VE	0.68 (0.58–0.59) P	GS, GF, VE
GS	0.05	0.01 (0.00–0.06) I		0.09 (0.04–0.17) I		0.10 (0.05–0.19) I		0.06 (0.02–0.03) A	
SF	0.30	0.55 (0.45–0.66) P	GS, GF, VE	0.19 (0.12–0.30) I	GS, GF, VE	0.28 (0.19–0.39) I	GS, GF, VE	0.21 (0.13–0.14) A	GS, GF
GF	0.11	0.03 (0.00–0.09) A	Ve	0.09 (0.03–0.17) I		0.10 (0.05–0.19) I		0.04 (0.01–0.01) A	
VE	0.03	0.04 (0.01–0.11) I		0.00 (0.00–0.05) I		0.06 (0.02–0.13) I		0.00 (0.00–0.00) A	
Non-determined individuals									
SS	0.51	0.44 (0.34–0.56) I	GS, GF, VE	0.50 (0.40–0.61) I	GS, GF, VE	0.45 (0.35–0.56) I	GS, GF, VE	0.59 (0.49–0.70) I	GS, VE
GS	0.05	0.00 (0.00–0.05) A		0.03 (0.00–0.09) I		0.10 (0.05–0.19) I		0.02 (0.00–0.09) I	
SF	0.30	0.49 (0.39–0.61) P	GS, GF, VE	0.34 (0.25–0.46) I	GS, GF, VE	0.28 (0.19–0.39) I	GS, GF, VE	0.02 (0.13–0.31) I	GS, VE
GF	0.11	0.02 (0.00–0.08) I		0.12 (0.06–0.21) I		0.14 (0.07–0.24) I		0.16 (0.09–0.16) I	
VE	0.03	0.04 (0.01–0.11) I		0.02 (0.00–0.07) I		0.04 (0.01–0.10) I		0.02 (0.00–0.09) I	

Proportions observed (Use), proportions expected from available surface of each habitat (Avail) and Bailey's confidence intervals of use (between brackets). SS: shrubby slopes; GS: grassy slope; SF: shrubby foothill; GF: grassy foothill; VE: *vega*. Significant differences (Signif, $Q \geq 2.8$, $p = 0.05$) of observed proportions among habitats in each sampling date.

This intensive use of water resources in drier conditions was also observed in other populations of this camelid in Argentina (Renaudeau d'Arc et al., 2000; Vilá and Roig, 1992), Bolivia (Villalba, 1998) and Peru (Franklin, 1983). The small area of the *vega* in our study site has limited the use of this habitat characterized by high plant cover, since areas with large *vegas* like the Pozuelos Biosphere Reserve and the Laguna Blanca Reserve are occupied by high proportions of vicuñas (Arzamendia and Vilá, 2006; Borgnia et al., 2008; Renaudeau d'Arc et al., 2000).

4.2. Habitat use by individuals of different social categories

Despite the low plant cover (33%) on the shrubby slopes, a high proportion of familial individuals was observed in that habitat, particularly in 2006. This result differs from that observed in Pozuelos (Arzamendia, 2008), where familial vicuñas were more related to areas with gentle slopes and high food availability. The food advantages offered by shrubby slopes and foothill in the study area, as the presence of *Poa* sp. (Mosca Torres, 2010), could justify the important use of these habitats by familial individuals. Indeed, this type of individuals must incorporate high proportions of high quality resources, particularly during the reproduction season (summer), to meet the energy costs of pregnancy and lactation (Vilá and Cassini, 1993) and of territorial defense (Franklin, 1983; Vilá and Roig, 1992). Moreover, the high plant cover in the shrubby foothill during the winter of 2006, compared to that of 2007, would explain the presence of higher proportions of familial, bachelor and solitary individuals in this environment.

Habitats with high food availability and/or presence of water, such as the *vega* and the grassy habitats (particularly in summer), were generally occupied by familial and also by bachelor individuals, contrary to what was expected from the strong territoriality of the families. This coexistence occurred due to a spatial segregation between different types of social groups in each habitat. Wilson (1980) argues that the spatial separation between groups is an important selective advantage in terms of minimizing disturbance during foraging, reducing interference while fleeing from danger and avoiding the spread of disease. Spatial segregation between familial and bachelor individuals would not be as evident in the *vega* as in the other habitats, because the *vega* was the habitat with smallest area on our study site. Water is an essential resource in this arid environment and the *vega* might be considered a neutral zone, and therefore untenable, which justifies the simultaneous presence of both types of individuals in this habitat as occurred in Pampa Galeras (Franklin, 1983).

The higher proportion of familial vicuñas in the *vega* in the summer than the winter of 2007 reinforces the suggestion that the severe environmental drought during the second year of sampling increased needs for water, particularly by females in advanced pregnancy.

The high number of vicuñas observed in different habitat types at different times of the day, suggest that the individuals display a pattern of daily movements among habitats. They performed a morning journey from the slopes (rest and/or grazing areas) to the *vega* and a reverse movement in the afternoon, this pattern was also observed in the Puna of Catamarca (Vilá and Roig, 1992) and Jujuy (Vilá and Cassini, 1993). The decreased food availability during 2007 would be responsible for the changes in that pattern in our study site, detected particularly in winter, when a high number of vicuñas remained in the grassy habitats until noon and only in the afternoon they moved to the *vega*. This ability to shift the habitat use behavior in response to changes in environmental conditions has also been observed in vicuñas of Pampa Galeras, Peru (Franklin, 1983).

4.3. Habitat selection

The preference for the shrubby foothill in the summer of 2006, when availability of high quality food resources was maximal, is consistent with the optimal foraging theory. This selective behavior would be accounted for by the presence of *Poa* sp., a high quality species and the main plant consumed by the vicuña in this study area (Mosca Torres, 2010; Mosca Torres and Puig, 2010). The selection of habitats with similar characteristics to those mentioned for the shrubby foothill has also been observed in other environments with vicuñas (Arzamendia and Vilá, 2006; Cajal, 1989; Franklin, 1983; Renaudeau d'Arc et al., 2000).

The lack of habitat selection observed during the winter of 2006, particularly by familial vicuñas, would reveal their more homogeneous distribution among habitats than in summer, consistently with the habitat selection theory (Sutherland, 1996). Indeed, this theory predicts that the distribution of individuals among different types of habitats becomes more homogeneous when resource availability decreases in the best habitats. On the other hand, it is possible that families tend to expand their territories and occupy parts of different habitats during the period of limited resources, as was documented in Pampa Galeras, Peru (Koford, 1957).

The presence of high quality species in the shrubby foothill could downplay the importance of intake of other plant species during the summer of 2006 (Mosca Torres, 2010), and would be responsible for the detected avoidance of the grassy foothill by bachelor, solitary and non-determined individuals, who also avoided the grassy slope. Otherwise, the preference for the shrubby slope by bachelor and solitary vicuñas during the winter of 2006 would be more related to their displacement from this habitat by familial vicuñas when pasture quality declines. An association of bachelors with mountain areas was also observed in Pozuelos (Arzamendia, 2008).

Use of the *vega* with indifference by all social categories during the winter of 2006 did not reflect the higher water dependence in this dry season than in summer (Franklin, 1983; Koford, 1957; Renaudeau d'Arc et al., 2000). The integration of all scan samplings conducted throughout the day seems to have masked the use of the *vega*, given that this use was concentrated in the hours around noon, while occupation of this habitat was generally low during the rest of the day.

The preference by vicuñas for habitats with high cover of grasses and graminoids in 2007, especially by familial and bachelor animals, is consistent with the composition of the

diet recorded in the study area (Mosca Torres, 2010; Mosca Torres and Puig, 2010). Indeed, the grass species present in those habitats, as well the graminoids at the *vega* were eaten in high proportions during that year. These results are consistent with the vicuña's classification as grazer mentioned in other studies (Aguilar et al., 1995; Benítez et al., 2006; Cajal, 1989; Franklin, 1983; Koford, 1957). On the other hand, the avoidance of the shrubby slope would be explained by the low plant cover detected there in both seasons of 2007.

5. Conclusions

The results of this study allow the conclusion that vicuñas behave according to the optimal foraging theory in this sector of the Puna region, given that they prefer high quality habitats in summer of a good year. Moreover, individuals are randomly distributed among different habitats when food availability decreases, which also agree with this theory. Habitat use (and selection) by the vicuña is influenced by the availability of high quality food resources and the presence of water, and that the relevance of the latter increases with drought conditions.

Consideration of the relationships between habitat and diet selection is important to understand ecological interactions of this wild South American camelid with its environment. In addition, an assessment of the agonistic and/or territorial interactions between individuals of different social categories will contribute to better understanding the ecological behavior of this camelid, and especially how this type of interactions constrain the distribution of animals among different habitats.

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