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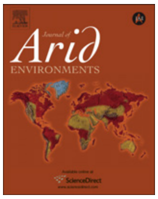

Seasonal diet of vicuñas in the Los Andes protected area (Salta, Argentina): Are they optimal foragers?

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A B S T R A C T

Optimal foraging theory states that individuals focus on the most profitable items when resources are abundant, and expand their diet when food availability decreases. In polygynous ungulates, territoriality and reproduction can strongly affect this foraging strategy. Vicuñas (*Vicugna vicugna*) are an interesting model system to test these hypotheses, because they present a stable social structure with territorial and non-territorial animals, and survive in arid environments where plant cover and quality are low. We assessed food availability (point-quadrat method) and diet composition (faecal analysis) of vicuñas to analyze whether they are optimal foragers and whether territoriality and reproduction affect their foraging strategy during summer and winter in the Argentinean Puna. Differences in food availability and diet composition between seasons and groups were addressed by Wilcoxon Rank Sum test. The χ^2 goodness-of-fit test and Bailey's index allowed detection of food selectivity. Vicuñas focused their summer diet on high-quality species and increased the number of species eaten in winter, as predicted by the optimal foraging theory. Seasonal patterns were more evident in the territory, where females compensate for high energy costs of reproduction, whereas the lower energy requirements of non-territorial vicuñas would explain the lower dietary proportions of nutritive species in their diet.

1. Introduction

Herbivores usually face low forage quality, and must therefore obtain as much food as possible to satisfy their energy requirements (Senft et al., 1987). This situation is more evident in arid and semiarid environments, where animals experience nutritional stress (Illius and O'Connor, 2000) because the nutritional value of most plant species is high only during the short rainy season (Bautista et al., 2003; Cajal, 1989). During the dry season, when food resources become even fewer and with lower nutritional value (Owen-Smith and Novellie, 1982; Redfern et al., 2003), many mammalian herbivores are forced to change their diet composition (Alm et al., 2002) and/or migrate to habitats with better food and water availability (Hughes, 1993; Illius and Gordon, 1993; Owen-Smith, 1994).

The optimal foraging theory proposes a solution to the problem of spatial and temporal changes in food availability (Pyke, 1984; Schoener, 1971; Stephens and Krebs, 1986): individuals should focus on the most profitable items when resources are abundant (MacArthur and Pianka, 1966), and broaden their diet when resource availability is low (Owen-Smith and Novellie, 1982; Stephens and Krebs, 1986). Additionally, their foraging behavior can be selective or opportunistic, depending on relative resource availability (Jaksic, 1989). Therefore, the proportions of food items will show significant differences between diet and availability in selective animals, whereas non-significant differences will occur in opportunistic animals.

Other factors such as territoriality and current energy requirements of the forager can strongly affect this foraging strategy, particularly in animals living in groups (Hanley, 1997; Prache et al., 1998; Wiens, 1976). In many species that interact socially, dominant individuals may use their social status to occupy good feeding sites and territories, forcing subordinates to use habitats with lower food quality (Masteller and Bailey, 1988; Prins, 1989; Rutberg, 1986). Territorial males defend an area with high quality food to provide sufficient resources for females, especially during periods of gestation and lactation, in polygynous ungulates such us the impala (*Aepyceros melampus*, Van Rooyen and Skinner, 1989) and the vicuña (*Vicugna vicugna*, Franklin, 1983; Vilá and Cassini, 1993).

Populations of wild vicuñas (*V. vicugna*, Molina 1782, Camelidae) are an interesting model system to test the hypotheses described above. This species is the smallest and the most threatened South American camelid (SAC), and it is included in the Appendix II of

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CITES with several exceptions in Appendix I, such as the wild vicuñas of Salta (Argentina) where this study was conducted. Both vicuñas and guanacos (*Lama guanicoe*) are the only wild SAC species, whereas llamas (*Lama glama*) and alpacas (*Lama pacos*) are domestic. The distribution range of the vicuña in Argentina comprises high altitude environments of the High Andean and Puna biogeographic provinces (Torres, 1992), and vicuñas were also observed on sites of the Prepuna province (Mosca Torres and Puig, per. comm.). Vegetation in these areas is scarce and food quality changes with spatial and temporal scales (Cabrera, 1957; Cajal, 1989). This camelid displays sedentary habits and 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 (Franklin, 1983; Koford, 1957). Family groups can distinguish habitats with the most nutritional food and defend them for exclusive use (Franklin, 1983). This species has a strong dependence on water (Franklin, 1983; Vilá and Roig, 1992), and was considered as a strict feeder on grasses and forbs by Pujalte and Reca (1985). However, Benítez et al. (2006) and Arzamendia (2008) observed vicuñas foraging on shrubs in other areas of the Argentinean Puna.

According to the optimal foraging theory, vicuñas are expected to consume the most nutritional species when food availability is maximal (summer), and to broaden their diet when food availability is minimal (winter). Although there are no studies on the nutritional requirements of vicuñas, data from the literature for the alpaca, the domestic species derived from the vicuña (Wheeler, 1995), are useful to predict whether vicuñas are optimal feeders. Because vicuñas, like alpacas, are primarily grazers (Benítez et al., 2006; Cassini et al., 2009; Franklin, 1983; Koford, 1957) one prediction of this study is that they should consume high proportions of those grass, graminoid and forb species with the highest protein level. Besides, low proportions of shrubs should be eaten because of their low forage values, due to the presence of secondary compounds (Cajal, 1989). In addition, the proportion of high-quality species should be higher in family groups than in bachelor groups, because of the nutritional requirements of females during the last three months of pregnancy (late dry season), and during lactation (wet season), such as was observed in alpacas (Castellaro et al., 1999; San Martín, 1991).

The objectives of this study are to analyze the botanical composition of the vicuña's diet and food availability in summer and winter, in order to detect: 1) whether use of food resources by vicuñas is selective, 2) whether this camelid is an optimal forager, and 3) whether territoriality and nutritional requirements of social groups affect the dietary composition and foraging strategy of this species.

2. Materials and methods

2.1. Study area

This study was conducted within the Los Andes Reserve (Salta, Argentina), a 14,400-km^2 protected area located within the Puna biogeographic province, according to the identification by Cabrera and Willink (1980). 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), low rainfall (130 mm/yr) occurring only in summer (December–March) and intense frosts. Seasonal growth and forage quality are determined by this precipitation pattern. The brushland vegetation 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 other small graminoids and grasses (*Juncus depauperatus*, *Plantago tubulosa* and *Deyeuxia* spp.; Cabrera, 1957). Vegetation seasonal growth and quality are determined by the precipitation pattern. Plant growth is rapid and of high quality during the wet season, but this period is only 3–4 months in duration (Van Saun, 2008). Forage availability is extremely limited during the dry season and forage is too mature and of low-quality (San Martín and Bryant, 1989).

The study area (24° 27′ S and 67° 12′ W, 8.6 km^2) is representative of the Los Andes Reserve. The relief presents extended slopes and foothills, both with *vegas*. Because of the human disturbances observed (poaching and mining), and the low density of vicuñas recorded in the reserve (0.75 indiv./km^2, Baigún et al., 2008), we selected our study area far away from roads and difficult to access. The latter presented a stable abundance of vicuñas, with a density of 12.8 indiv./km^2, that was much higher compared to the surrounding areas, and occasional presence of livestock (goats and donkeys) in very low densities (0.1 and 0.05 indiv./km^2, respectively). Two sampling sites were selected according to their use by different vicuña social groups: a territorial site (hereafter called territory 0.92 km^2), permanently used by one family group in summer and two families in winter, and a non-territorial site (hereafter non-territory, 1.41 km^2), used by bachelor groups and occasionally by one or two solitary individuals in both seasons. Families were composed of one male, two females and one offspring. Densities at the territorial site were 4.3 indiv./km^2 in summer, and 15.6 indiv./km^2 in winter. This site was occasionally traversed by bachelor groups and solitary individuals, although both were immediately expelled by the territorial male. Bachelors groups were made up of an average of six or seven individuals in summer and winter, respectively, at the non-territorial site. Mean densities at this site were 12.1 indiv./km^2 in summer and 16.5 indiv./km^2 in winter. Despite the high mobility of bachelors, they spent considerable time foraging at the non-territorial sampling site (Mosca et al., 2006).

Both sites were dominated by shrubby slopes and foothills. There was a small *vega* (0.02 km^2) at the territory, monopolized by families, and a bigger *vega* (0.1 km^2) at the non-territory. A grassy foothill was present only at the territorial site. Although both sites were close (100 m approximately), a small hillock separated one from the other.

2.2. Field and laboratory design

Plant cover and species composition were estimated using the point-quadrat method (Daget and Poissonet, 1971) along 30-m transects per site and sampling season, located on each site following a stratified randomized design according to types of vegetation. Plant species were grouped into five categories according to their life forms: grasses, graminoids, shrubs, forbs and succulents, although the succulent category was not considered in the analyses because it was very rare in both the environment and the diet.

Plant reference material from the study site was collected, taxonomically identified and stored in the Ruiz Leal Herbarium (IADIZA, Argentina). Reference microhistological slides, a catalogue of drawings, and microphotographs were prepared for these plant species, and later used for plant identification from slides of fecal material (Holechek and Gross, 1982).

Direct observation of what plants vicuñas are consuming is difficult due to the impossibility to get close to them without interfering with their normal grazing behavior. For this reason, ten fresh feces were collected from each of ten dung piles in the territory and ten in the non-territory during summer and winter.

Fecal samples were collected immediately after the animals defecated, in order to be sure that samples belonged to each type of social group. Each fecal sample was milled and processed for identification of plant fragments using the microhistological technique described by Baumgartner and Martin (1939) modified by Duci (1949). Four microscope slides were made for each dung pile, and 80 fields per slide were systematically examined through a 400-× microscope. Plant identification was made to the genus level, and to the species level when possible.

Several authors have pointed out some limitations in the use of the microhistological technique for identifying plant fragments (for accuracies and biases of this technique, see Holechek et al., 1982; McInnis et al., 1983). However, microhistology is a very useful tool to identify diet composition and detect general selectivity patterns (Holechek and Gross, 1982). Besides, this technique is a non-invasive tool, as animals are not injured or sacrificed, and it is an important requirement because of the threatened situation of the vicuña in the protected area.

Finally, data on the quality of different plant species (protein, fiber and lignin) registered at the study site, and in other Puna regions of Argentina, Bolivia and Peru, were obtained from the literature (Table 1).

2.3. *Statistical analysis*

The Shannon–Wiener function (H', Colwell and Futuyma, 1971) was used to estimate diversity of forage availability and use during summer and winter. The mean proportion of species eaten per season and site was calculated as the ratio between number of species in the diet and number of available species. Plant availability and diet composition were compared between sites and seasons using the Wilcoxon Rank Sum test (Sokal and Rohlf, 1995). The χ^2 goodness-of-fit test was used to evaluate food selectivity, that is, whether observed proportions of dietary items differed significantly from those expected from the relative plant availability. Only differences in plant species with relative frequencies of use or availability above 5% were considered for comparisons between sites and seasons. Bailey's index (Cherry, 1996) was applied to detect whether food items were used in higher, lower or equal proportions than their availability in the field (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 2.7.0 (R Development Core Team, 2008).

3. Results

3.1. *Availability of food resources*

During summer, there was 50% of plant cover, and species diversity was 1.14 in the study area. Vicuñas ate 31 species (Table 1) out of the 36 observed in the field. Shrubs and grasses were the predominant categories, supplemented with graminoids and annual forbs. The main species were the grasses *Festuca* sp. and *Poa* sp., the graminoids *Eleocharis* aff. *albibracteata* and *Juncus articus*, the shrubs *Adesmia horridiuscula*, *Artemisia copa*, *Junellia seriphioides* and *Fabiana denudata*, and the annual forb *Tarasa tenella*. Several significant differences between seasons were found in the relative availability of plant categories and species (Table 1).

Summer plant cover in the territory (41%) was lower than in the non-territory (57%; $W = 626$, $p = 0.009$), whereas plant diversity was similar at both sites ($H' = 1.13$ and $H' = 1.05$, respectively), with no significant differences in the number of available species (29 in the territory and 24 in the non-territory; $W = 424$, $p = 0.706$). Shrubs and grasses were the predominant categories, supplemented with graminoids at both sites, whereas annual forbs were more available in the territory than in the non-territory ($W = 307$,

Table 1
Percent plant availability and consumption by the vicuña in the study area during summer (Su) and winter (Wi), significant differences between seasons ($p \leq 0.05$) in species availability ^{*A} or dietary proportions ^{*D}, and content of protein, fiber and lignin per species and season documented in $^{(1)}$Genin et al. (1995), $^{(2)}$Benítez et al. (2006), $^{(3)}$Cajal (1989), $^{(4)}$Florez Martínez (1993).

	Availability (%)		Diet (%)		Protein (%)		Fiber (%)		Lignin (%)	
	Su	Wi	Su	Wi	Su	Wi	Su	Wi	Su	Wi
Poa sp.^{*D}	5.6	5.5	42.9	23.8	11.9+$^{(4)}$	–	27.9+$^{(4)}$	–	–	–
Stipa sp.^{*D}	2.2	1.2	17.9	24.7	7.6+$^{(1)}$	2.7+$^{(1)}$	37.2+$^{(1)}$	38.6+$^{(1)}$	–	–
Festuca sp.^{*D}	15.0	28.2	3.3	12.9	6.0+$^{(1)}$	2.8$^{(1)}$	39.2+$^{(1)}$	42.7+$^{(1)}$	–	–
Deyeuxia sp.^{*D}	4.0	1.6	3.2	9.7	5.7+$^{(2)}$	–	72.6+$^{(2)}$	–	16.0+$^{(2)}$	–
Hordeum halophylum	0.0	0.1	1.1	0.1	1.6$^{(3)}$	–	–	–	–	–
Deschampsia aff. *caespitosa*	0.0	0.1	0.4	0.1	3+$^{(3)}$	–	–	–	–	–
TOTAL GRASSES	27.0	36.7	69.6	73.0	–	–	–	–	–	–
Carex sp.	0.6	0.1	4.0	0.3	6.7+$^{(5)}$	–	–	–	–	–
Juncus articus	5.5	4.8	0.2	0.0	4.5+$^{(2)}$	–	76.4+$^{(2)}$	–	4.1+$^{(2)}$	–
Eleocharis aff. *albibracteata*^{*D}	16.1	10.1	5.5	7.6	9.9$^{(2)}$	–	68.7$^{(2)}$	–	16.9$^{(2)}$	–
TOTAL GRAMINOIDS	22.2	14.9	9.7	7.9	–	–	–	–	–	–
Adesmia horridiuscula	11.2	13.8	1.2	0.2	6.2$^{(2)}$	–	47.5$^{(2)}$	–	20.5$^{(2)}$	–
Junellia seriphioides^{*D}	5.1	7.1	4.5	10.3	4.3$^{(2)}$	–	47.1$^{(2)}$	–	–	–
Artemisia copa	8.0	13.8	2.5	5.6	–	–	–	–	–	–
Lycium chanar^{*A}	3.3	0.5	1.0	0.3	5.22+$^{(3)}$	–	–	–	–	–
Acantholippia punensis	0.3	2.2	0.0	0.4	7.4+$^{(2)}$	–	55.7+$^{(2)}$	–	16.8+$^{(2)}$	–
Parastrephia quadrangularis	0.2	1.0	0.0	0.2	6.3$^{(1)}$	4.4$^{(1)}$	–	–	17+$^{(2)}$	–
Fabiana denudata	5.0	8.2	0.0	0.0	8.4+$^{(2)}$	–	39.0+$^{(2)}$	–	13.9+$^{(2)}$	–
Baccharis incarum	0.1	0.0	0.0	0.0	10.8$^{(1)}$	6.1$^{(1)}$	15.3$^{(1)}$	15.5$^{(1)}$	–	–
TOTAL SHRUBS$^{*A\ *D}$	36.2	48.2	10.5	18.9	–	–	–	–	–	–
Tarasa tenella $^{*A\ *D}$	9.9	0.0	8.6	0.2	–	–	–	–	–	–
Euphorbia aff. *amandii* ^{*A}	1.0	0.0	0.8	0.0	–	–	–	–	–	–
Schkuhria pinnata ^{*A}	0.8	0.0	0.7	0.0	–	–	–	–	–	–
Nicotiana ondulata	0.9	0.1	0.0	0.0	2.13+$^{(3)}$	–	–	–	–	–
TOTAL ANNUAL FORBS $^{*A\ *D}$	13.3	0.1	10.3	0.3	–	–	–	–	–	–

+ Values given for another species or as an average among species of the same genus; – Without documented value. Other species eaten by vicuñas below the threshold of 5% were: *Deyeuxia chrisostachya*, *Adesmia* sp., *Senecio dryophylus*, *Senecio viridis*, *Frankenia triandra*, *Lepidium bonariense*, *Cristaria andicola*, *Gilia crassifolia*, *Nitrophila australis*.

$p = 0.023$; Fig. 1a). Plant species availability showed some significant differences between sites in summer. The shrub *A. horridiuscula* was proportionately more abundant in the territory than in the non-territory ($W = 253$, $p = 0.002$; Fig. 1a), whereas proportions of *J. seriphioides* and *E.* aff. *albibracteata* were higher in the non-territory than in the territory ($W = 610$, $p = 0.001$ and $W = 566$, $p = 0.014$, respectively).

Winter plant cover at the study site declined to 29% ($W = 758$, $p < 0.001$), and plant diversity also decreased ($H' = 0.96$; $W = 1147$, $p = 0.001$). The number of available species at the study area dropped to 23 ($W = 1787$, $p < 0.001$), mainly because six annual forbs disappeared (Table 1).

Annual forbs were practically absent in winter ($W = 946$, $p < 0.001$) and shrubs were proportionally more abundant in winter than in summer ($W = 1405$, $p = 0.038$), whereas grasses and graminoids showed no seasonal changes in availability (Table 1). Dominant species were the same ones detected during summer and no significant differences were found between their availabilities, except for the annual forb *T. tenella* that disappeared during the dry season (Table 1).

Winter plant cover declined in both, the territory (22%; $W = 144$, $p < 0.001$) and the non-territory (36%; $W = 10$, $p < 0.001$), but was significantly lower in the former ($W = 681$, $p < 0.001$). Plant diversity decreased only in the non-territory ($H' = 0.86$; $W = 165$, $p < 0.001$), being lower than winter diversity in the territory ($H' = 0.95$; $W = 165$, $p < 0.001$). The number of available species declined significantly only in the territory (22 species; $W = 310$, $p = 0.016$), although it did not differ from the winter number in the non-territory (20 species).

Winter proportions of shrubs increased in both, the territory ($W = 608$, $p = 0.020$) and the non-territory ($W = 629$, $p = 0.001$), whereas grass and graminoid availabilities remained similar between seasons. The shrub *J. seriphioides* ($W = 640$, $p = 0.001$) and the grass *Deyeuxia* sp. ($W = 567$, $p = 0.008$) were higher in the non-territory than in the territory (Fig. 1b).

3.2. Diet of the vicuña

In summer, diet diversity across the whole area was $H' = 0.86$ and vicuñas ate 25 of the 31 species available, because five shrubs were not consumed in this season (Table 1). Mean proportion of species eaten was 45%, with grasses being the main resource used, followed by shrubs, annual forbs and graminoids (Table 1). The most important species were the grasses *Poa* sp. and *Stipa* sp., the graminoid *E.* aff. *albibracteata*, the shrub *J. seriphioides*, and the annual forb *T. tenella* (Table 1).

In summer, diet diversity did not differ between territory ($H' = 0.81$) and non-territory ($H' = 0.87$), and the number of consumed species was similar at both sites (24 and 23, respectively). However, the mean proportion of available species consumed in the territory (46%) was lower than in the non-territory (60%; $W = 81$, $p = 0.002$).

Grasses were the main category eaten by both groups in summer, supplemented with shrubs (Fig. 2a). The territory differed from the non-territory in the dietary proportions of the grasses *Poa* sp. ($W = 14$, $p = 0.007$) and *Stipa* sp. ($W = 97$, $p < 0.001$) and annual forbs ($W = 9$, $p = 0.002$), particularly *T. tenella* ($W = 4$, $p = 0.001$; Fig. 2a).

During winter in the study area, vicuñas ate a lower number of species (23) than in summer ($W = 1075$, $p = 0.039$), although dietary diversity ($H' = 0.89$) did not differ between seasons. The mean proportion of available species consumed increased in winter (49%, $W = 74$, $p = 0.001$).

Grasses still were the main dietary category in the dry season, supplemented with graminoids, with no seasonal changes in their dietary proportions (Table 1). Shrubs were eaten in higher

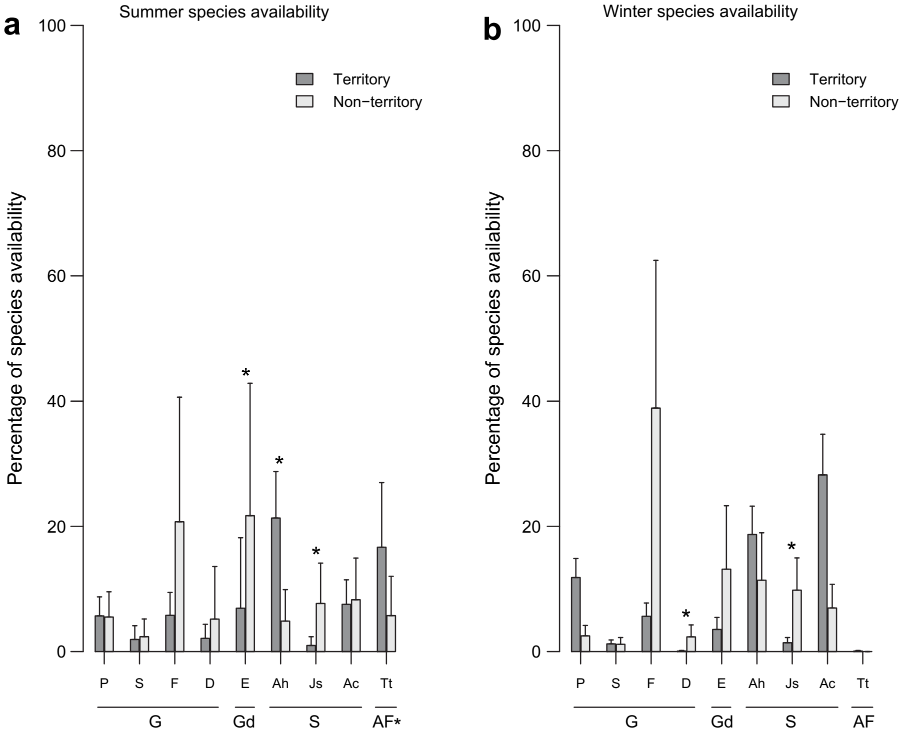

Fig. 1. Percentages of plant species availability in territory and non-territory during (a) summer, and (b) winter. G: Grasses; Gd: Graminoids; S: Shrubs; AF: annual forbs. P: *Poa* sp., S: *Stipa* sp., F: *Festuca* sp., D: *Deyeuxia* sp., Graminoids: E: *Eleocharis* aff. *albibracteata*, Shrubs: Ah: *Adesmia horridiuscula*, Js: *Junellia seriphioides*, Ac: *Artemisia copa*, Lch: *Lycium chañar*, Annual forbs: Tt: *Tarasa tenella*. *: Significant differences ($p \leq 0.05$) between sites. Only those species available (or consumed) in more than 5% were included in the graph.

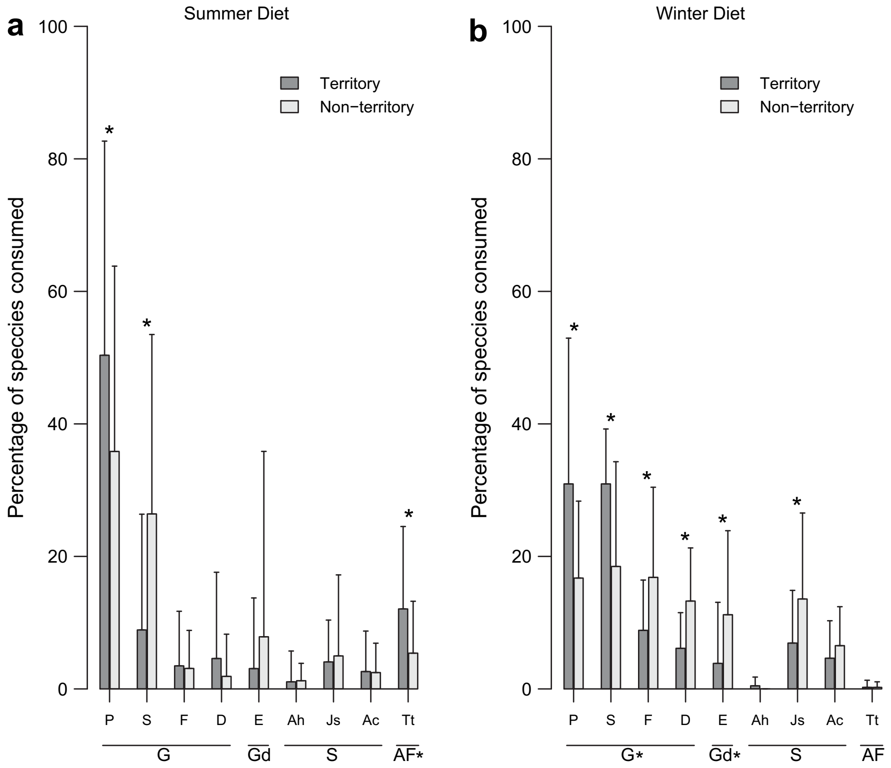

Fig. 2. Dietary percentages of plant species in territory and non-territory during (a) summer, and (b) winter. G: Grasses; Gd: Graminoids; S: Shrubs; AF: annual forbs. P: *Poa* sp., S: *Stipa* sp., F: *Festuca* sp., D: *Deyeuxia* sp., Graminoids: E: *Eleocharis* aff. *albibracteata*, Shrubs: Ah: *Adesmia horridiuscula*, Js: *Junellia seriphioides*, Ac: *Artemisia copa*, Lch: Lycium chañar, Annual forbs: Tt: *Tarasa tenella*. *: Significant differences ($p \leq 0.05$) between sites. Only those species consumed (or available) in more than 5% were included in the graph.

proportions in winter than in summer ($W = 336$, $p < 0.001$), whereas annual forbs were practically absent from the diet ($W = 0$, $p < 0.001$; Table 1).

The main species used in winter were the same as in summer, although *Poa* sp. was less eaten ($W = 45$, $p < 0.001$), whereas *Stipa* sp., *Festuca* sp., *Deyeuxia* sp., *E.* aff. *albibracteata*, *A. copa* and *J. seriphioides* were proportionally more consumed during the dry season ($W = 283$, $p = 0.025$; $W = 381$, $p < 0.001$; $W = 348$, $p < 0.001$; $W = 279$, $p = 0.033$; $W = 340$, $p < 0.001$ and $W = 333$, $p < 0.001$, respectively; Table 1).

Dietary diversity at each site did not differ between seasons. However, winter diversity was lower in the territory ($H' = 0.83$) than in the non-territory ($H' = 0.89$; $W = 83$, $p = 0.012$). Families consumed a higher proportion of available species in winter (54%) than in summer ($W = 8$, $p = 0.021$), whereas non-territorial animals ate similar proportions in both seasons (55%). Nevertheless, no significant differences between sites were found in the proportion of available species eaten.

In winter, the grass proportion in the diet of family groups was higher than in summer ($W = 84$, $p = 0.010$). Besides, it was higher than in the winter diet of non-territorial groups ($W = 12$, $p = 0.004$; Fig. 2b), which ate similar proportions of grasses in both seasons. The dietary proportion of graminoids at each site did not differ between seasons, although families used a lower proportion than non-territorial individuals ($W = 91$, $p = 0.002$; Fig. 2b). Shrubs were more consumed in winter only by non-territorial groups ($W = 89$, $p = 0.003$), and annual forbs were practically absent from the winter diet of both groups ($W = 0$, $p < 0.001$).

Among the main species, the winter proportion of *Poa* sp. decreased in the diets of families ($W = 7$, $p = 0.001$) and non-territorial groups ($W = 0$, $p < 0.001$), whereas the proportion of *Festuca* sp. was higher than in summer at both sites (territory: $W = 91$, $p = 0.002$; non-territory: $W = 100$, $p < 0.001$). Only in the territory did vicuñas consume more *Stipa* sp. in winter than in summer ($W = 100$, $p < 0.001$). The shrubs more consumed in winter than in summer at both sites were *A. copa* ($W = 96$, $p < 0.001$ for both, territory and non-territory), and *J. seriphioides* (territory: $W = 77$, $p = 0.040$; non-territory: $W = 89$, $p = 0.003$).

Significant differences between sites were found in winter dietary proportions of several species (Fig. 2b). In the territory, *Poa* sp. and *Stipa* sp. were proportionally more consumed by families than by bachelors groups ($W = 7$, $p = 0.001$ and $W = 6$, $p < 0.001$, respectively; Fig. 2b). On the other hand, dietary proportions of *Festuca* sp., *Deyeuxia* sp., *E.* aff. *albibracteata* and *J. seriphioides* (Fig. 2b) were higher in the non-territory than in the territory ($W = 93$, $p = 0.001$; $W = 94$, $p < 0.001$; $W = 92$, $p = 0.002$, and $W = 86$, $p = 0.007$).

3.3. Comparisons between use and availability

During summer, significant differences were detected between use and availability of plant categories ($\chi^2 = 77$, $p < 0.001$) and species ($\chi^2 = 446$, $p < 0.001$). According to Bailey's index, vicuñas preferred grasses (particularly *Poa* sp. and *Stipa* sp.), avoided shrubs (particularly *A. horridiuscula*) and used graminoids and annual forbs with indifference. The same preferences were observed at territorial and non-territorial sites (Table 2).

Among the main species, the grass *Festuca* sp. and the graminoid *E.* aff. *albibracteata* were avoided by non-territorial groups, whereas family groups were indifferent to both species. The forb *T. tenella* was used with indifference at both sites (Table 2).

Significant differences between use and availability were also detected during winter for both, plant categories ($\chi^2 = 38$, $p < 0.001$) and species ($\chi^2 = 632$, $p < 0.001$). Among plant categories, grasses were preferred (particularly *Poa* sp., *Stipa* sp. and *Deyeuxia* sp.), whereas graminoids and shrubs were mostly used

Table 2
Plant species preferred (P), avoided (A) or used with indifference (I) by vicuñas during summer and winter in the whole study area (W), and in territory (T) and non-territory (NT), based on whether the expected proportion (Av, environmental availability) is located below, within or above the confidence interval of the observed proportion (Di, vicuña diet). Figures outside the parentheses are observed proportions (Di), and figures in parentheses are Bailey confidence intervals of Di. – Species eaten or available below the threshold of 5%.

	Av(W)	Di(W)	Av(T)	Di(T)	Av(NT)	Di(NT)
Summer						
Grasses	0.27	0.68 (0.55–0.79) P	0.16	0.67 (0.54–.078) P	0.34	0.70 (0.56–0.79) P
Graminoids	0.17	0.10 (0.03–0.19) I	0.07	0.06 (0.02–0.15) I	0.22	0.12 (0.05–0.22) I
Shrubs	0.25	0.09 (0.03–0.19) A	0.35	0.10 (0.04–0.20) A	0.21	0.09 (0.03–0.18) A
Forbs	0.10	0.09 (0.03–0.18) I	0.19	0.14 (0.06–0.24) I	0.06	0.07 (0.02–0.15) I
Poa sp.	0.06	0.43 (0.28–0.57) P	0.06	0.50 (0.35–0.64) P	0.06	0.36 (0.22–0.50) P
Stipa sp.	0.02	0.18 (0.08–0.31) P	0.02	0.09 (0.02–0.20) P	0.02	0.26 (0.14–0.40) P
Festuca sp.	0.15	0.03 (0.00–0.11) A	0.06	0.03 (0.00–0.12) I	0.21	0.03 (0.00–0.11) A
Deyeuxia sp.	0.04	0.03 (0.00–0.11) I	0.02	0.05 (0.00–014) I	0.05	0.02 (0.00–0.09) I
Carex sp.	0.01	0.04 (0.00–0.13) I	0.00	0.03 (0.00–0.12) I	0.01	0.05 (0.00–0.13) I
Eleocharis aff. *albibracteata*	0.16	0.06 (0.01–0.15) A	0.07	0.03 (0.00–0.11) I	0.22	0.08 (0.02–0.18) A
Adesmia horridiuscula	0.11	0.01 (0.00–0.08) A	0.21	0.01(0.00–0.08) A	0.05	0.01 (0.00–0.08) I
Junelia seriphioides	0.05	0.05 (0.00–0.13) I	0.01	0.04 (0.00–0.13) I	0.08	0.05 (0.01–0.14) I
Artemisia copa	0.08	0.03 (0.00–0.10) I	0.08	0.03 (0.00–0.10) I	0.08	0.02 (0.00–0.10) I
Tarasa tenella	0.10	0.09 (0.02–0.19) I	0.17	0.12 (0.04–0.24) I	0.06	0.05 (0.01–0.15) I
Winter						
Grasses	0.37	0.73 (0.60–0.82) P	0.19	0.78 (0.66–0.87) P	0.45	0.67 (0.55–0.78) P
Graminoids	0.10	0.08 (0.02–0.16) I	0.04	0.04 (0.00–0.11) I	0.13	0.11 (0.05–0.21) I
Shrubs	0.22	0.17 (0.09–0.28) I	0.33	0.14 (0.06–0.25) A	0.17	0.20 (0.11–0.31) I
Forbs	0.00	0.00 (0.00–0.05) I	–	–	–	–
Poa sp.	0.06	0.24 (0.13–0.37) P	0.12	0.31 (0.18–0.44) P	0.03	0.17 (0.08–0.29) P
Stipa sp.	0.01	0.25 (0.13–0.38) P	0.01	0.31 (0.18–0.44) P	0.01	0.18 (0.09–0.31) P
Festuca sp.	0.28	0.13 (0.05–0.24) A	0.06	0.09 (0.03––0.19) I	0.39	0.17 (0.08–0.29) A
Deyeuxia sp.	0.02	0.10 (0.03–0.20) P	0.00	0.06 (0.01–0.15) P	0.02	0.13 (0.05–0.24) P
Carex sp.	–	–	–	–	–	–
Eleocharis aff. *albibracteata*	0.10	0.08 (0.02–0.17) I	0.04	0.04 (0.00–0.12) I	0.13	0.11 (0.04–0.22) I
Adesmia horridiuscula	–	–	–	–	–	–
Junelia seriphioides	0.07	0.10 (0.03–0.21) I	0.01	0.07 (0.02–0.16) P	0.10	0.14 (0.50–0.25) I
Artemisia copa	0.14	0.06 (0.01–0.15) I	0.28	0.05 (0.01–0.13) A	0.07	0.07 (0.01–0.16) I
Tarasa tenella	–	–	–	–	–	–

with indifference, the latter particularly by non-territorial vicuñas, although the territorial groups use shrubs with avoidance (Table 2).

Among species, *Deyeuxia* sp. became a preferred species in the dry season at both sites. Non-territorial vicuñas avoided *Festuca* sp., whereas territorial individuals consumed it with indifference. The graminoid *E.* aff. *albibracteata* became an item used by bachelors and solitary animals with indifference. On the other hand, the shrubs *A. horridiuscula* and *A. copa* was avoided and *J. seriphioides* was preferred by families, whereas non-territorial vicuñas consumed these species with indifference (Table 2).

4. Discussion

Vicuñas in our study area seemed to maximize nutrient intake as predicted by the optimal foraging theory (Stephens and Krebs, 1986), given that they focused their summer diet on the grasses *Poa* sp. and *Stipa* sp., and the graminoid, *E.* aff. *albibracteata*, which are the species of highest forage value (Table 1; Benítez et al., 2006; Genin et al., 1995). The expansion of their trophic niche over the dry season, shown by the increased number of species eaten in winter, also agrees with this theory (Owen-Smith and Novellie, 1982; Stephens and Krebs, 1986). The mentioned summer pattern was more evident in the territory, where females must compensate for the high energy costs of lactation, such as was observed in alpacas by Castellaro et al. (1999) in the Chilean High Andes, and territorial males have to defend the territory more strongly. In contrast, the lower energy requirements of non-territorial vicuñas (Franklin, 1983; Vilá, 2000) would explain the lower dietary proportions of *Poa* sp. found in their summer diet. During the dry season, only families behaved like optimal foragers, increasing the mean proportion of available items eaten, whereas non-territorial individuals did not broaden their diet. These differences could be because during the dry season females were in the last months of gestation, when nutritional requirements are high, such as was observed in the alpaca (Castellaro et al., 1999; San Martín, 1996), so they have to increase consumption of available species to compensate for the scarce nutritive value of the vegetation and meet the appropriate nutrient requirements.

A greater availability of species of high nutritional value, such as forbs (Benítez et al., 2006), may constitute summer advantages for the territory, where diet composition of families was of higher quality compared to the diet of non-territorial individuals. This observation would agree with the assertion of Franklin (1983) about the ability of family vicuñas to distinguish and defend those habitats with the most nutritious resources. Conversely, the lower dietary proportions of *Poa* sp. in non-territorial vicuñas could be associated with their low energy requirements, as they need food resources only to maintain constant their body, an do not defend a territory (Franklin, 1983; Renaudeau d' Arc et al., 2000; Vilá, 1998). Similar results were found for alpaca males by Castellaro et al. (1999), who observed that their energy requirements were relatively invariable throughout the year.

The year-round defense of a territory by family groups presents some disadvantages such as the decline of food resource availability due to their intensive use, which can explain the lower plant cover in the territory than in the non-territory during both seasons. The density of animals can be ruled out as responsible for the lower plant cover, given that the territory did not show a higher density than the non-territory. Nevertheless, the higher food diversity appeared to be a winter foraging advantage for territorial animals.

The detected importance of grasses in the diet of vicuñas, in spite of the dominance of shrubs in the study area, agrees with the grazing tendency mentioned for this camelid in other Puna environments from Argentina (Aguilar et al., 1995; Benítez et al., 2006;

Renaudeau d' Arc et al., 2000) and Peru (Franklin, 1974, 1983). In addition, the inclusion of shrubs, especially *J. seriphioides* and *A. copa* during winter, support the dietary flexibility recognized by several authors (Arzamendia, 2008; Benítez et al., 2006; Borgnia et al., 2008; Franklin, 1983), stressing the relevance of this plant category for the winter survival of the vicuña in other areas of its distribution range.

Territorial and non-territorial vicuñas preferred grasses even during their vegetative rest in winter, when a higher use of *Stipa* sp., *Festuca* sp. and *Deyeuxia* sp. would compensate for the scarcity of food resources. The winter preference for *Deyeuxia* sp., a grass only observed at *vegas* of both sites, could be associated with the usual movements of vicuñas to this microhabitat particularly during the dry season (Cajal, 1989; Franklin, 1983; Renaudeau d' Arc et al., 2000), when the nutritional value of foothill vegetation is low (Benítez et al., 2006). *Stipa* sp., *Festuca* sp. and *Deyeuxia* sp. were also observed in Peru as main dietary items for vicuñas (Koford, 1957); whereas Cajal (1989) pointed out that *Stipa* sp. was the most important grass in the diet of vicuñas and guanacos in the Puna of San Juan (Argentina).

The high protein levels of *Poa* spp. throughout their phenological cycle (Hidalgo et al., 1998) would explain why this grass was the main dietary item in both seasons, despite its low availability. The intense use of *Stipa* sp. could be attributed to the high forage value of this grass, despite the variable protein concentrations present in the species of this genus (Genin and Alzérreca, 2006; Hidalgo et al., 1998).

Preference by camelids for grasses with high fiber levels is expected due to both a greater efficiency to ferment dietary fiber (Van Saun, 2006), and a longer retention time that allows these animals a greater degradation of ingested feed material compared to other ruminants (Genin and Tichit, 1997; Lopez et al., 1998; San Martín et al., 1986; San Martín, 1991). Moreover, the digestive advantage of camelids over other ruminants (cattle and sheep) is most obvious when comparing the digestion of poor quality or low protein forages (Genin and Tichit, 1997; Lopez et al., 1998; San Martín and Bryant, 1989; San Martín, 1991).

The winter decline of vegetation and the reduction of *Carex* sp. availability may be also responsible for the increased proportion of *E.* aff. *albibracteata* in the diet of vicuñas, and for the switch from summer avoidance to winter indifference in the use of this graminoid. The moderate consumption of graminoids disagrees with the high nutritional value of *E.* aff. *albibracteata* and *Carex* sp. (Benítez et al., 2006). Borgnia (unpubl. data, in Benítez, 2005) also observed that vicuñas consumed low proportions of *E. albibracteata* in Catamarca (Argentina).

Avoidance of shrubs during summer could be explained by the low forage value of these species, and by the presence of spines and secondary compounds such as tannins (Alzérreca et al., 2003; Benítez et al., 2006; Cajal, 1989). Nevertheless, *J. seriphioides* and *A. copa*, appeared to be valuable species for the vicuña in winter. Jansen et al. (2007) suggested that ruminants include tannin in their diets, even though other plants (with less or even no tannin) are available, because this compound seems to increase the intake of certain nutrients, as was observed in sheep and goats (Ebong, 1995). Thus, the increased proportion of shrubs in the diet of vicuñas during the dry season, and the switch from summer avoidance to indifferent use in winter, may be the result of seasonal reduction in plant cover and diversity, phenological decline of grasses and absence of forbs in the study area.

Annual forbs, particularly *T. tenella*, constituted a summer dietary supplement for the vicuña, as they practically disappeared during winter in the study area. Although they were consumed in high proportions, the indifferent use of forbs disagrees with that expectable from their higher nutritional value than grasses (Benítez et al., 2006), and their higher forage value than shrubs (Cajal, 1989). These findings could be partially attributed to differential digestibility of forbs (Vavra et al., 1978), where certain species are entirely digested or plant fragments are so transparent that cellular structure is not easily discernible (McInnis et al., 1983). However, Puig et al. (1996, 2001) observed that guanacos in La Payunia (Mendoza, Argentina) consumed forbs with preference, which could compensate for the low availability of water and profitable food items in the environment. Because vicuñas do not obtain water, either from the oxidative metabolism or from the food they eat (Bosch and Svendsen, 1987; Franklin, 1983; Vilá and Roig, 1992), they would be eating forbs because of their profitable value rather than their water content.

The vicuña in the study area could be described as a generalist herbivore with a strong selectivity towards grasses, mainly *Poa* sp., *Stipa* sp. and *Deyeuxia* sp. The forb *T. tenella* and the graminoid *E.* aff. a*lbibracteata* appear as supplementary nutritional food during summer. Additionally, the inclusion of a higher proportion of shrubs in winter, especially *J. seriphioides* and *A. copa*, could be a foraging strategy of this species to balance the intake of food in spite of the low forage value and tannin concentrations.

Finally, the differences found between proportions of species eaten by territorial and non-territorial vicuñas would be partially accounted for the territorial behavior of this camelid (Franklin, 1983) and the energy requirements of the different social groups, as was also observed in domestic alpacas (Genin and Tichit, 1997; Lopez et al., 1998; San Martín et al., 1986; San Martín, 1991) and other herbivores (Prache et al., 1998). Scan and focal animal sampling carried out in the same area of this study will allow us to analyze whether territorial and non-territorial groups differ in the effort allocated to searching for food during both seasons, particularly when resource availability is minimal.

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