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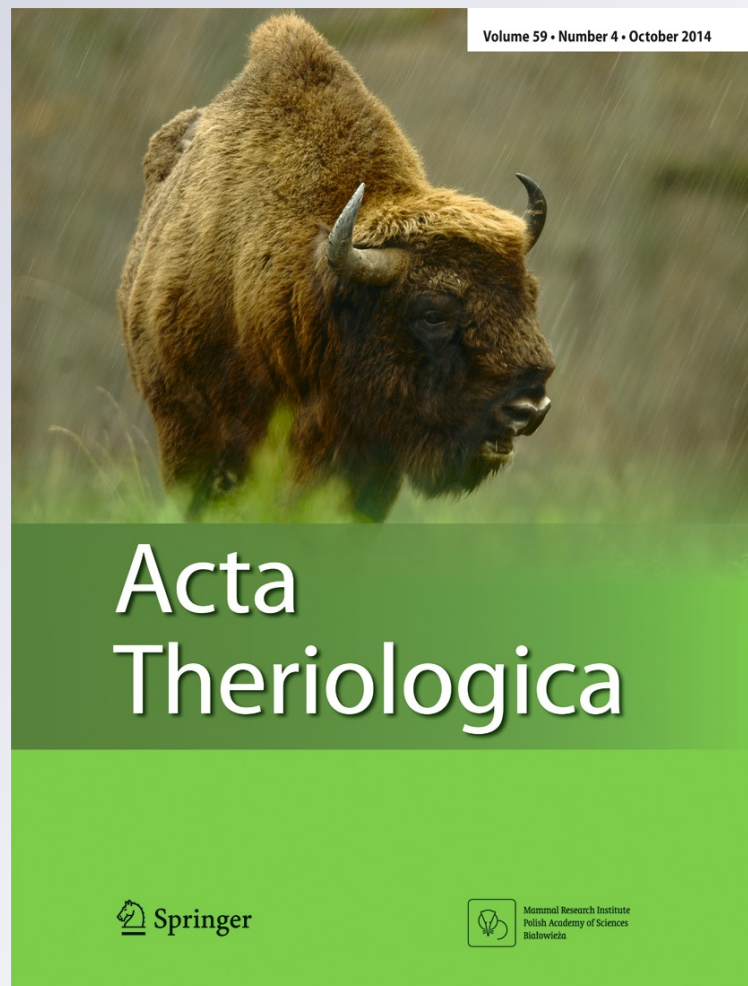
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Food selection by the guanaco (*Lama guanicoe*) along an altitudinal gradient in the Southern Andean Precordillera (Argentina)

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Abstract Wild ungulates like the guanaco are exposed to important changes in climate and plant diversity along altitudinal gradients in the Andes Mountains, such as in the Southern Andean Precordillera where three phytogeographic provinces are present in altitudinal belts. The guanaco's diet and food availability were seasonally analyzed using microhistological analysis and point-quadrat transects at six sampling sites, representative of the phytogeographic belts along the altitudinal gradient. Plant cover and diversity decreased with growing altitude. Richness of plant species was poorer at the summit than in the lower altitudes, whereas the proportion of species eaten by guanacos increased with altitude. The diet included 77 species. Grasses were preferred and shrubs were avoided all year round. The grass *Poa* spp. occupied more than 50 % of the diet at all altitudes. Grasses were the main dietary item even at low altitudes, where shrubs constituted the main food available. Decreasing generalism with descending phytogeographic belts agrees with the prediction for altitudinal gradients. The increase of diversity in the diet during the winter decline of plant cover at high and middle altitudes follows that expected from the optimal foraging theory. The winter decline of vegetation and the dietary shift from grazing to browsing proved to be stronger as altitude increases and the climate become more rigorous. Plant species richness, food scarcity, and climate severity are relevant variables to explain altitudinal and seasonal changes

in the diet of adaptive ungulates in mountain environments, such as the guanaco in the Southern Andean Precordillera.

Keywords Wild camelids · Feeding ecology · Food availability · Phytogeographic provinces · Mountain environments

Introduction

Climate gradients are associated with altitudinal gradients in mountain environments showing sharp or gradual changes in temperature, relative humidity, sun radiation, and rainfall. These changes affect animals directly and indirectly, given that they constrain the distribution, structure, and abundance of vegetation (Körner 2000). Strong spatial and seasonal differences in food availability are expected in mountains with steep topography (Zweifel-Schielly et al. 2009). Physiological requirements and food availability usually influence the animals' distribution and selection of resources along altitudinal gradients (Terborgh 1977; Carothers et al. 1996; Martínez and Rechberger 2007). Indeed, a decreasing species richness as altitude increases was detected in the vegetation of the Andes (Gentry 1988) and other mountain environments such as the Alps (Erschbamer et al. 2006) and the Himalayas above 1,500 m above sea level (a.s.l.) (Grytnes and Vetaas 2002). In response to the decrease in plant diversity at the higher altitudes, increasing generalization in the use of resources was observed in herbivores of the Alps (Pellissier et al. 2012).

Wild ungulates such as the guanaco (*Lama guanicoe*) face important environmental changes in food availability along the altitudinal gradients of Andean mountains, e.g., the three phytogeographic provinces present in altitudinal belts of the Southern Andean Precordillera and its piedmont, which lie from 800 to 3,200 m a.s.l. (Dalmasso et al. 1999). Extremely severe weather and extensive deep snow cover in High

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Andean environments force the guanaco to migrate seasonally across the altitudinal gradient and consequently to make changes in food selection according to the available vegetation in their winter and summer ranges (Puig et al. 2011). With a less severe weather in the Southern Andean Precordillera, guanacos can stay all year in any of the three phytogeographic provinces (Puig et al. 2008).

Spatial-temporal changes in the food available for herbivores usually occur in arid mountain environments such as the Andean Precordillera, where it is interesting to test predictions derived from the optimal foraging theory, in terms of a dietary concentration on the more nutritive items while food is abundant and a broader diet in situations of food scarcity (Stephens and Krebs 1986). The foraging flexibility of ungulates is one of the typical responses to the strong climate variation in arid environments, where drought periods occur frequently (Stafford Smith 1996). The ability to use alternative food sources is an advantage for ungulates to survive drought periods with increasing intensity, according to the climate change predictions (Lehmann et al. 2013; Duncan et al. 2012). The guanaco, one of the most adaptive wild camelids, shows a dietary flexibility that allows it to live in a diversity of habitats with contrasting vegetation structure and composition (Franklin 1982), such as coastal deserts where guanacos consume lichens (Raedeke and Simonetti 1988) or cold forests where they browse (Muñoz and Simonetti 2013). Alternation between grazing and browsing was found in several guanaco populations, in response to seasonal declines in the vegetation (Franklin and Puig 2014). The altitudinal gradient of the Andean Precordillera allows analyzing whether a growing severity in the decline of vegetation during winter, according the altitude increases, is relevant for seasonal shifts from grazing to browsing in the guanaco's diet.

The objective of this study is to analyze diet selection by the guanaco as related to seasonal food availability in three phytogeographic provinces (Puna, Cardonal, and Monte) present across an altitudinal gradient within a protected area from the Southern Andean Precordillera. According to predictions for altitudinal gradients, we expect that plant species richness will be lower and that the guanaco's diet will be more generalized as altitude increases. In the framework of the optimal foraging theory, we expect a seasonal increase in diet diversity and a lower proportion of preferred species when food availability decreases. On account of the seasonal shifts from grazing and browsing when vegetation declines, as observed in other guanaco populations, we expect that the winter decline in vegetation and the increase of shrubs in the diet will be stronger in the summit than in the bottom of the altitudinal gradient.

Materials and methods

Study area and habitat characteristics

The study area, belonging to the protected area “Reserva Villavicencio” (32° 35' S 69° 02' W, 620 km², Mendoza, Argentina), is representative of the southernmost part of the Andean Precordillera (Polanski 1954), as well as of Puna and Cardonal phytogeographic provinces (Roig and Martínez Carretero 1998; Roig 1994). The scarce rainfall, elevated evapotranspiration, and immature surface soils allow characterizing the Southern Puna as an Andean desert (Roig and Martínez Carretero 1998). A tundra climate occurs above 3,000 m a.s.l., with permafrost soils from May to September, whereas a steppe climate occurs below this altitude, characterized by scarce rains (Videla and Suárez 1991). Temperatures in this area show high variability, according to altitude, exposure of slopes to sun, and relative humidity (De Fina 1992). Annual precipitation ranges from 120 to 300 mm and occurs mainly from October to March (Capitanelli 1971).

The area is composed of a central elevated plateau surrounded by slopes with a strong altitudinal gradient, with the steepest slopes facing eastward and crossed by narrow valleys following the line of tension joints (Harrington 1971). Three phytogeographic provinces are represented in the study area (Ambrosetti et al. 1986; Dalmasso et al. 1999): Puna in the large plateau of the mountain summit, Cardonal in the eastern valleys at intermediate altitudes, and Monte in the extensive east piedmont corresponding to the lowest altitudes. Negative impacts such as hunting, extraction of woody plants, fires, and livestock overgrazing, important at low altitudes, markedly decreased since the protected area was created in 2000 and management actions were carried out. Consequently, there was a slow recovery in the vegetation historically impacted, whereas the guanaco population showed higher densities and a less evasive behavior (Puig et al. 2008). Current guanaco distribution is heterogeneous, with densities between 0.3 and 14 guanacos/km² depending on the different places of the protected area (Puig et al. 2014). A minor number of cattle and horses from neighboring livestock-raising places occasionally get into the protected area.

Considering the steep altitudinal gradient, the phytogeographic belts, and geomorphologic heterogeneity, six landscapes were selected in the study area, with a mean area of 16 km² per landscape. A requisite for the selection of all these landscapes was the presence of guanacos throughout the year. In order to have a better representativeness of environmental heterogeneity, two landscapes were selected within each phytogeographic belt (Table 1).

Table 1 Location and characteristics of sampling sites in the Villavicencio Reserve (extracted from Ambrosetti et al. 1986; Dalmaso et al. 1999; De Fina 1992)

Topography and soil	Climate	Vegetation structure	Sampling sites (location and altitude)
Phytogeographic province: Puna (surface in the study area 250 km ² , altitudinal belt 3,200 to 2,800 m a.s.l.)			
Summit of the Andean Precordillera, open plains with soft hills and extended foothills, lithosols of coarse sand and rocks fragmented due to cryogenic processes	Mean temperatures 13 °C in summer, 0.8 °C in winter; scarce rainfall (175 mm) with irregular distribution; large deep patches of snow cover during winter, persistent until mid spring in eastern slopes; strong west winds, especially foehn	Coarse grasslands of <i>Pappostipa</i> spp., with low subfrutices; high proportion of nude soil; open shrubby patches in sites protected from the wind	Canario (Pampa de Paramillos, 3,139 m a.s.l.) Canota (Pampa de Canota, 2,931 m a.s.l.)
Phytogeographic province: Cardonal (surface in the study area 150 km ² , altitudinal belt 2,800 to 1,700 m a.s.l.)			
Andean Precordillera gorges, shady slopes with very pronounced with rocky soils	Mean temperatures 17 °C in summer, 5 °C in winter; rainfall (325 mm) concentrated in autumn; snow cover during more than a month in shady slopes during winter	Low shrublands of <i>Adesmia uspallatensis</i> and <i>Mulinum spinosum</i> in shady slopes, with high herbaceous cover; sunny slopes with cacti (<i>Lobivia formosa</i> and <i>Denmoza rhodacantha</i>)	Hornillos (Quebrada Hornillos, 2,744 m a.s.l.) Mesitas (Quebrada Mesitas, 2,661 m a.s.l.)
Phytogeographic province: Monte (surface in the study area 220 km ² , altitudinal belt 1,700 to 800 m a.s.l.)			
Upper part of the East piedmont, deep lithosols with gravel and coarse sand	Mean temperatures 21 °C in summer, 7 °C in winter; rainfall sporadic and localized (196 mm), concentrated in summer; frequent hot dry winds, foehn type; great heliophany	High dense scrublands of <i>Larrea divaricata</i> , with tall shrubs, low shrubs, and grasses; commercial extractions of woody species, mainly <i>Prosopis flexuosa</i> , historically impacted the vegetation.	Pintadas (Piedras Pintadas, 1,381 m a.s.l.) Enjambre (Lomas del Enjambre, 1,315 m a.s.l.)

Field and laboratory design

Seasonal fecal sampling and vegetation recording were made in the six above-defined landscapes during 2010–2011, corresponding to winter (July), spring (October), summer (February), and autumn (April). Throughout the year, 40 fecal samples were collected from each landscape, and 40 vegetation records were carried out. The mean distance among sampling sites was 12 km. Plant cover and relative frequencies of plant species were estimated in each season by the point-quadrat method (Daget and Poissonet 1971), applied on 10 fixed transects per sampling site. All 30-m transects were distributed within each sampling site in a stratified random design, separated from one another by more than 100 m. Each transect had 100 sampling points, separated from one another by 30 cm. Ten fecal samples were collected in each season from each sampling site. Each fecal sample, composed of 10 fresh pellets, was collected from a different dung pile.

Fecal samples were analyzed with the microhistological method from Baumgartner and Martin (1939), modified by Holeček (1982), and the relative frequency of food items was determined based on the count of fragments. After being oven-dried at 60 °C, each fecal sample was ground, cleared with diluted lye (aqueous sodium hypochlorite, 25 % w/v), and passed through two sieves, one over the other, with aperture sizes of 0.249 and 0.149 mm, respectively. Two microscope

slides were created from the material trapped in the second sieve. This procedure allowed to obtain even-sized plant fragments, in order to avoid bias resulting from the count of fragments that differ widely in size (Smith and Shandruk 1979; Kuijper et al. 2009). Fifty fields on each slide were systematically examined through a microscope at $\times 400$, and all identifiable fragments (those showing at least three diagnostic features) were counted. A microscopic field at high resolution had only one or two fragments, whose epidermal features were easily identified.

Plant reference material from the Villavicencio Reserve was collected and stored in the Ruiz Leal Herbarium (IADIZA, Argentina). Plant cuticle was identified to the genus level and to the species level when possible. The absence of specific epidermal traits in woody parts of shrubs has been mentioned as a possible cause for overestimation of grasses using microhistological analysis of feces (Holeček and Valdez 1985). This problem can be ruled out in the study area, given that most shrubs are evergreen, with leaves throughout the year. Indeed, Alipayo et al. (1992) found that shrubs with leaves and young stems were accurately estimated using microhistology of feces. Besides, the microhistological analysis showed good correspondence with a DNA method of fecal analysis in terms of species proportions, beyond that the DNA method had a better resolution for species identification (Kowalczyk et al. 2011).

Statistical analyses

Plant cover was determined for each point-quadrat transect by dividing the number of points at which any plant species was contacted (except dead individuals) by the 100 points set up on the transect. Food availability analyses only considered the potential food items for guanacos, i.e., all plant species consumed by guanacos on at least one occasion in the study area. Relative frequency of a given plant species in the environment was determined by dividing the absolute frequency of this species by the total sum of absolute frequencies for all species identified on each point-quadrat transect. The relative frequency of a species in the diet was determined for each sample by dividing the number of microscopic fields in which a given species occurred by the sum total of frequencies for all species identified (Holechek and Gross 1982).

Plant species were grouped into four categories according to life form: grasses, shrubs, forbs, and succulents. Diversity in food availability and diet was estimated using the Shannon-Wiener function (H' , Colwell and Futuyma 1971). A linear model of plant cover (transformed by Box and Cox) as a function of distances among sampling units ($F=34.06$, $P<0.001$) was fitted. The null hypothesis of spatial independence among sampling units was not rejected by the test of Dijkstra and Bowman (2001), applied to residuals of the mentioned model ($P=0.195$). Generalized linear models were fitted for vegetation and diet variables, in order to detect the effects of altitude, seasons, and their interactions. A Poisson distribution was used for integers, and a binomial distribution with a logistic link function was used for proportions (Bolker 2007). The GLMs were performed with the R 3.1.0 software (The R Foundation for Statistical Computing Platform 2014). Models were selected with the MASS package, through a stepwise function that searches the lowest Akaike information criterion (AIC) values. Feeding selection was detected by significant differences between observed values (diet proportions) and expected values (food availability proportions) using the χ^2 test (Zar 1984). The Jacobs index D identified selective use of plant categories and of main species (species with mean frequencies higher than 0.10 in the diet and/or availability) (Jacobs 1974). Plant use was qualified as preference, indifference (use proportional to availability), or avoidance depending on whether availability fell respectively below, within, or above the 95 % confidence interval of dietary frequency (Neu et al. 1974). The Spearman's rank correlation coefficient R (Siegel and Castellan 1988) determined the association between diet and food availability, in terms of relative frequencies of species.

Results

Composition of the vegetation

The vegetation was characterized by grasses, supplemented with shrubs or forbs in the higher altitudes (the Puna sites), a codominance of shrubs and grasses or forbs in the middle altitudes (the Cardonal sites), whereas prevailed shrubs, supplemented with grasses in the lower altitudes (the Monte sites) (Fig. 1).

Plant cover and diversity decreased as the altitude is increased (Table 2). The decrease of plant cover with growing altitude became significantly more steep in winter, when plant cover showed a slight change in the lower altitudes but important decreases in the higher and middle altitudes (Fig. 2). The decrease of plant diversity according to the altitude did not differ among seasons. Species richness also decreased in the vegetation as the altitude increased, especially in the number of grasses, shrubs, and forbs. The decrease of species richness with growing altitude became more steep in winter, particularly in the number of grasses and forbs. There was a less steep decrease in the number of shrubs during winter.

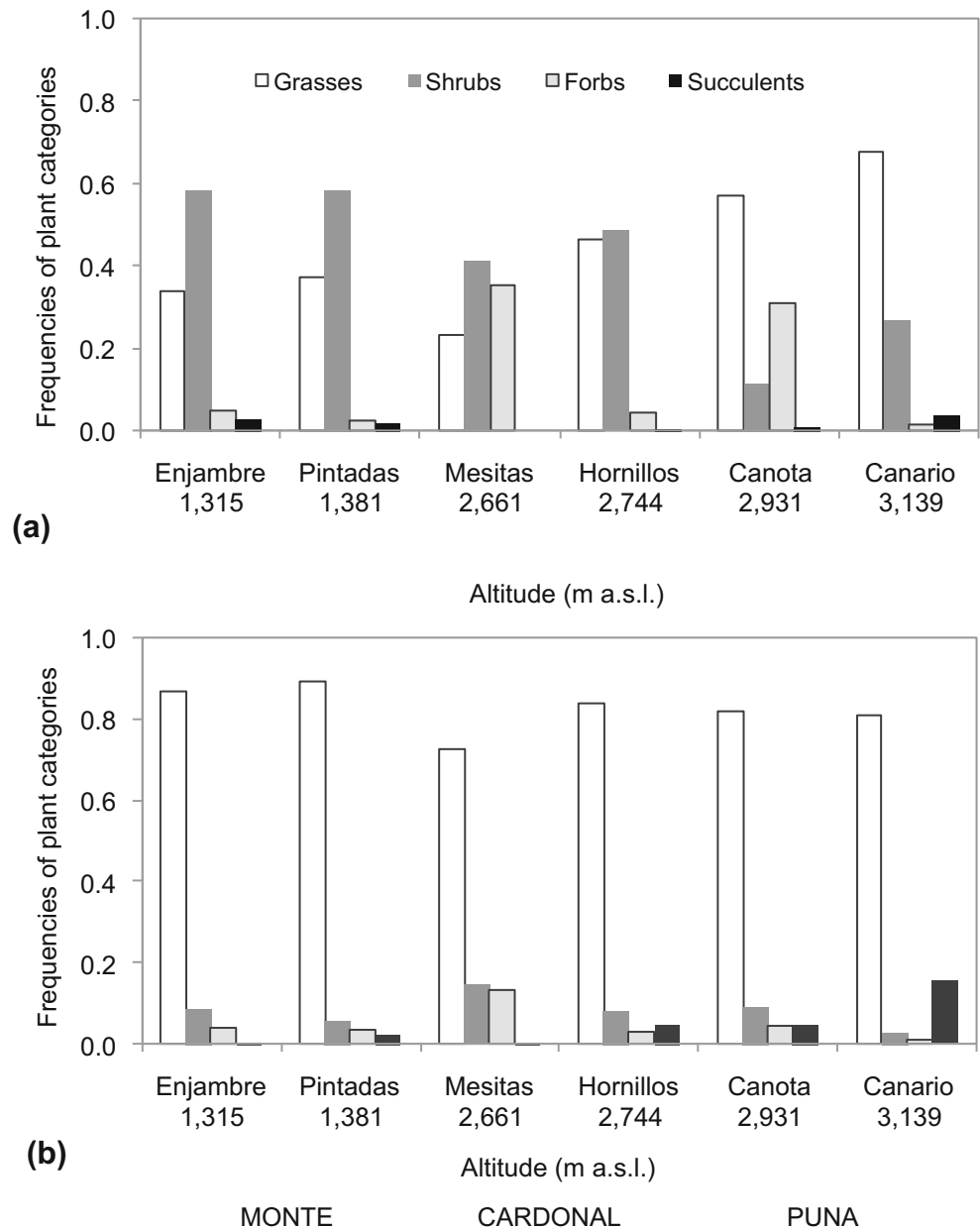
The proportion of grasses in the vegetation increased together with the altitude (Fig. 1), whereas the proportion of shrubs decreased. The altitudinal difference in the proportion of grasses did not show significant seasonal changes. The decrease of shrub proportion with growing altitude was less steep during winter (Fig. 3). The proportion of the succulent *Maihueniopsis* sp. increased with the altitude, without significant seasonal changes. The grass *Poa* spp. increased its relative proportion during winter, particularly in the lower altitudes.

Diet of the guanaco

Grasses constituted the main food items at all altitudes (Fig. 1), supplemented with succulents and shrubs in the higher altitudes (the Puna sites) and only with shrubs in the middle and lower altitudes (the Cardonal and Monte sites). The diet included 77 plant species in the study area. The grass *Poa* spp. occupied more than 50 % of the diet at all sites (Table 3), followed by the grass *Pappostipa* spp. and the succulent *Maihueniopsis* sp. in the higher altitudes, *Pappostipa* spp. and the shrub *Artemisia* spp. in the middle altitudes, and other grasses in the lower altitudes. Seventy-one percent of all plant species recorded in the sampling sites (109 species) were potential food items for guanacos: all grasses and succulents (11 and 6 species, respectively), 38 of 51 shrubs, and 26 of 43 forbs.

The guanaco diet increased in diversity with growing altitude. This altitudinal increase was significantly more steep during winter, when diet diversity decreased in the lower altitudes whereas it increased in the higher and middle

Fig. 1 Mean proportions of plant categories in available food (a) and in the diet of guanaco (b) in the lower altitudes (the Monte sites Enjambre and Pintadas), middle altitudes (the Cardonal sites Hornillos and Mesitas), and higher altitudes (the Puna sites Canario and Canota) of the Villavicencio Reserve



altitudes (Fig. 2, Table 2). The richness of species in the diet decreased during winter with exception of shrub species, whose number increased in winter. There was a lower richness of grasses and forbs as altitude increased. The decrease in the number of forb species with growing altitude became more steep during winter.

The dietary proportion of grasses (particularly *Poa* spp.) decreased with growing altitude, whereas the proportion of shrubs increased (Fig. 1, Table 3). These altitudinal changes were all more steep during winter. The dietary proportion of grasses showed slight seasonal changes in the lower altitudes but important winter decreases in the higher and middle altitudes (Fig. 3). During winter, the proportion of *Poa* spp. increased in the lower altitudes whereas it decreased in the

higher and middle altitudes. The opposite pattern was detected in the proportion of shrubs, given that during winter a decrease in the lower altitudes and an increase in the higher and middle altitudes occurred. The dietary proportions of the grass *Pappostipa* spp., the shrub *Artemisia* spp., and the succulent *Maihueniopsis* sp. increased with growing altitude, and the three food items showed higher proportions during winter. The increase in the proportion of *Maihueniopsis* sp. with growing altitude was more steep during winter.

A higher proportion of the species present in the vegetation was included in the guanaco diet as the altitude increased, particularly grasses and forbs (Fig. 2). This altitudinal increase was significantly more steep during winter, when the proportion of species eaten decreased in the lower altitudes whereas

Table 2 Effects of altitude and seasons on vegetation and diet variables, detected using generalized linear models

	Intercept	Altitude	Spring	Summer	Autumn	Altitude: Spring	Altitude: Summer	Altitude: Autumn	AIC
Composition of the vegetation									
Plant cover	8.09***	-5.39***	-0.47	-0.28	1.14	2.24*	2.04*	0.62	467.36
Diversity	11.57***	-6.74***							402.44
Richness of species	54.67***	-10.52***	-3.72***	-3.20**	0.30	4.51***	6.05***	0.46	1,420.50
Richness of grasses	15.77***	-5.77***	-1.10	-2.27*	-1.34	0.88	2.68**	0.68	883.88
Richness of shrubs	28.02***	-3.57***	-1.55	-0.32	2.67**	1.70	1.33	-2.82**	1,157.60
Richness of forbs	24.19***	-10.14***	-4.42***	-4.12***	-2.40*	6.03***	7.59***	4.67***	1,174.60
Grasses	-9.44***	8.33***							370.20
Shrubs	3.64***	-4.54***	1.38	1.97*	1.87	-2.39*	-2.18*	-3.09**	393.06
<i>Poa</i> spp.	-4.54***	0.85	-1.85	-2.42*	-1.35	2.00*	2.30*	1.49	329.64
<i>Maihueniopsis</i> sp.	-7.72***	6.72***	-1.34	0.47	-1.89	1.35	-0.62	1.85	336.96
Guanaco diet									
Diversity	-6.26***	6.91***	1.37	7.17***	6.04***	-2.00*	-7.76***	-7.18***	424.87
Richness of species	45.00***		2.16*	2.79**	0.74				1,117.60
Richness of grasses	13.67***	-3.96***							776.86
Richness of shrubs	15.20***		0.10	-0.32	-2.73**				884.26
Richness of forbs	4.39***	-3.06**	-0.46	-0.38	-3.51***	1.51	1.89	4.54***	805.98
Grasses	8.68***	-5.49***	-1.84	-0.91	-1.51	2.65**	2.20*	3.00**	383.94
Shrubs	-7.60***	2.66**	2.03*	0.85	0.98	-3.10**	-2.31*	-2.47*	352.01
<i>Poa</i> spp.	9.41***	-9.57***	-1.65	-8.42***	-7.76***	2.93**	9.65***	9.69***	378.10
<i>Pappostipa</i> spp.	-18.57***	15.11***	-4.38***	-7.09***	-9.83***				432.72
<i>Artemisia</i> spp.	-8.26***	3.35***	-3.19**	-4.66***	-4.53***				210.51
<i>Maihueniopsis</i> sp.	-9.19***	7.77***	-2.69**	-4.15***	-1.62	2.47*	3.99***	1.18	343.85
Number of species in the diet/number of species in the vegetation									
Plant species	-9.91***	5.93***	2.85**	3.86***	-1.00	-2.73**	-4.92***	0.85	610.45
Grasses	-4.35***	5.60***	0.95	5.20***	2.65**	0.20	-5.45***	-0.69	356.05
Shrubs	-6.57***	1.79	1.13	-0.17	-2.81**	-1.20	-0.42	2.15*	460.58
Forbs	-4.77***	2.27*	1.60	1.96	-2.24*	-1.61	-2.50*	2.19*	359.77

Seasonal changes from winter to spring, summer, or autumn are mentioned as Spring, Summer, or Autumn

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (significant levels of z values)

it increased in the higher and middle altitudes (Fig. 2, Table 2). Similar altitudinal and seasonal changes were detected in the proportion of grass species included in the diet. The proportion of shrub species eaten was higher during winter. Also, the proportion of forb species included in the diet increased in winter, when the increase of this proportion with growing altitude was more steep.

Dietary preferences

A selective use of plant categories was detected throughout the year in the study area (winter: $\chi^2 = 72.64$, spring: $\chi^2 = 56.12$, summer: $\chi^2 = 100.62$, and autumn: $\chi^2 = 65.57$, in all cases $P < 0.001$), particularly in the summit (Puna sites, Table 3), middle altitudes (Cardonal sites), and lower altitudes (Monte sites). Grasses were preferred and shrubs were avoided on all sites almost all year, with the exception of an

indifferent use found for grasses and shrubs in the summit during winter (Fig. 3). In cases where the mean proportion of other plant categories reached 0.10, forbs were avoided in all altitudes and succulents were preferred in the higher and middle altitudes.

A selective use of plant species was detected throughout the year in the study area (winter: $\chi^2 = 160.69$, spring: $\chi^2 = 222.40$, summer: $\chi^2 = 2866.90$, and autumn: $\chi^2 = 532.47$, in all cases $P < 0.001$) and particularly in the three altitudinal belts (Table 3). Among the main species (with mean frequencies higher than 0.10 in diet and/or availability), the grass *Poa* spp. was preferred on all sites (Table 3), whereas the grass *Pappostipa* spp. was mostly avoided although it was preferred or used with indifference in the middle altitudes. The succulent *Maihueniopsis* sp. was preferred in the summit. The only shrub preferred was *Artemisia* spp. in the higher and middle altitudes, whereas it was avoided in the lower altitudes.

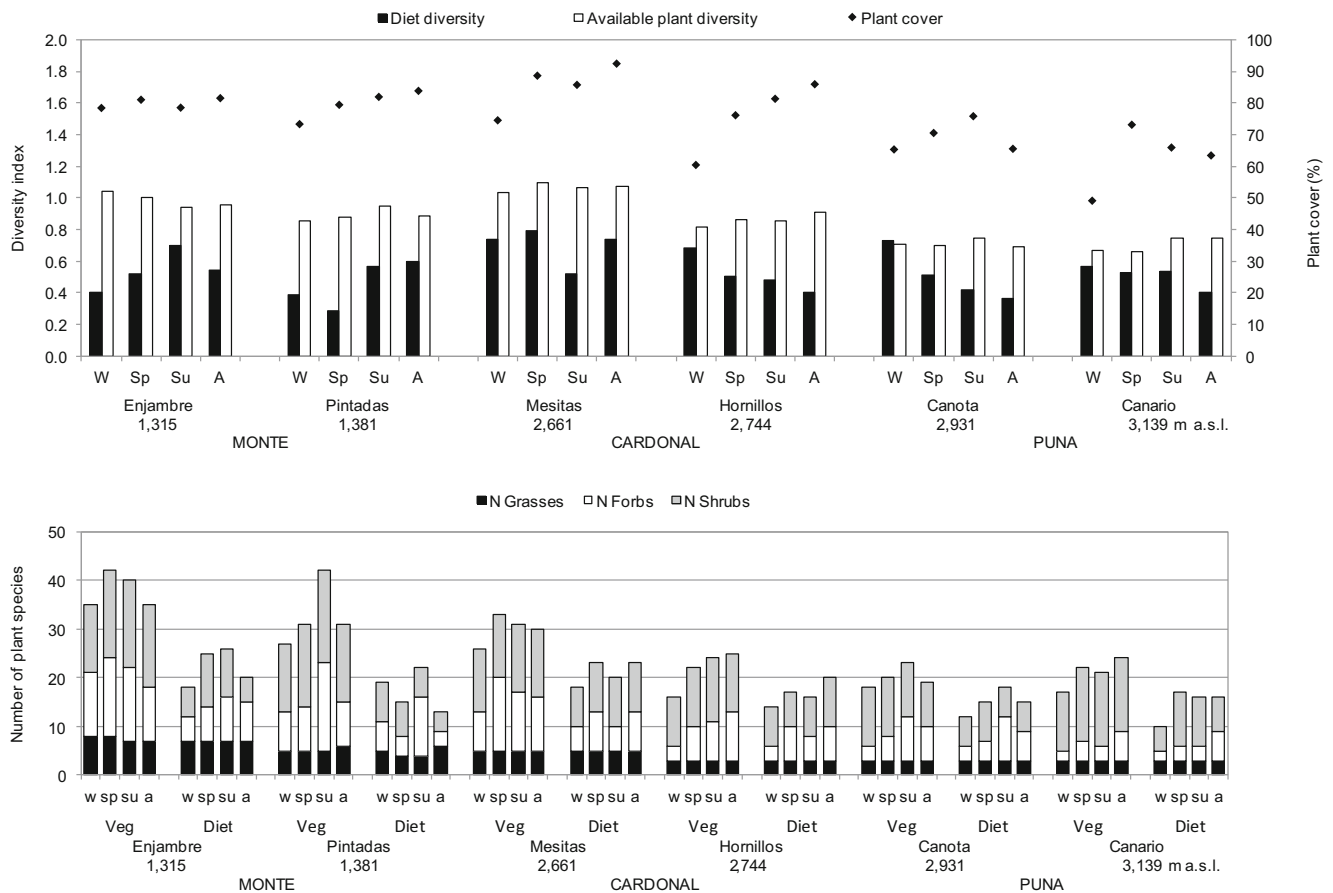


Fig. 2 Plant cover and species diversity in the diet of guanaco and in available food during winter (W), spring (Sp), summer (Su), and autumn (A) in the lower altitudes (the Monte sites Enjambre and Pintadas), middle

altitudes (the Cardonal sites Hornillos and Mesitas), and higher altitudes (the Puna sites Canario and Canota). Number of grass, forb, and shrub species in the vegetation (Veg) and in the diet (Diet)

Dietary proportions of plant categories increased as the relative availability of these categories increased in the vegetation, considering forbs ($R=0.565, P<0.001$) and succulents ($R=0.223, P<0.001$, especially in spring $R=0.330, P=0.010$ and summer $R=0.262, P=0.043$). Besides, the dietary proportion of the main grass *Poa* spp. increased as its relative availability increased in the vegetation ($R=0.230, P<0.001$, especially in summer $R=0.563, P<0.001$ and autumn $R=0.664, P<0.001$).

Discussion

The guanaco’s diet showed a considerable diversity, including all available plant categories and a high proportion of the species present in the vegetation of the Southern Andean Precordillera. This generalism was also observed in guanaco populations of other ecoregions (Linares et al. 2010; Baldi et al. 2004; Puig et al. 1996, 2011). The dietary generalism of the guanaco appears as an adaptive mixture of diverse foraging strategies of its ancestors and constitutes an important

advantage to survive in the diverse arid habitats that are part of its extensive range of distribution (Franklin and Puig 2014). Ungulates with generalized diets have nutritional advantages to cope with natural and human-caused changes, such as drought periods, habitat fragmentation, and habitat conversion (Abbas et al. 2011).

Altitudinal changes

Changes in climate with altitude in the Southern Andean Precordillera are consistent with those expected for mountain environments (Körner 2000), with increasing adversity from the steppe climate at the lower altitudes to the tundra climate in the summit (Videla and Suárez 1991). The gradual increase in temperatures as altitude diminishes, together with decreasing extent and persistence of snow cover descending the gradient from Puna to Cardonal and its absence in the Monte, confirmed the expected milder climate at the bottom of the altitudinal gradient.

Plant species richness, together with plant cover and diversity, proved to be lower as temperature decreases from the lower altitudes to the summit, as was predicted for altitudinal

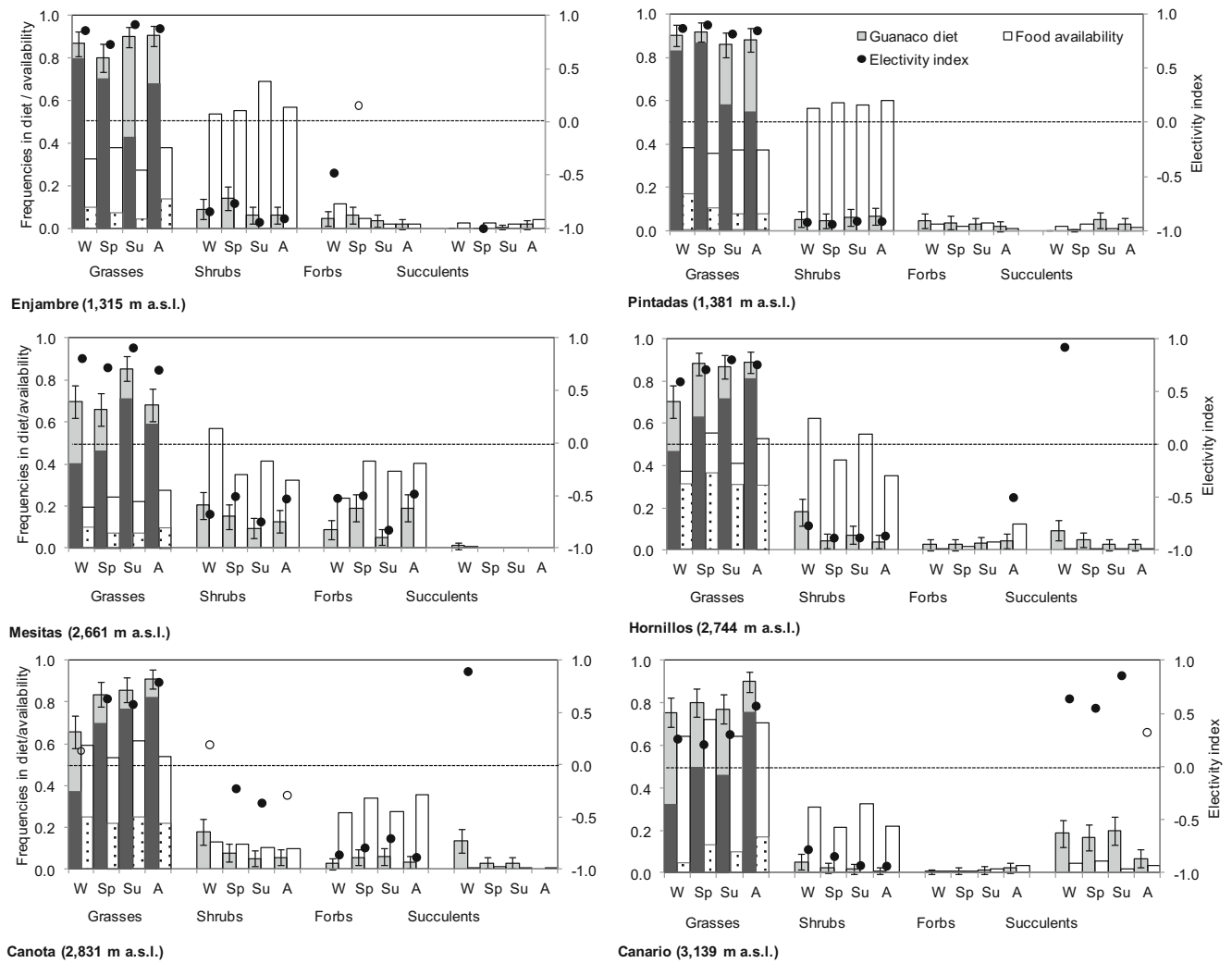


Fig. 3 Proportions of plant categories in the diet of guanaco ($\pm 95\%$ confidence interval as vertical lines) and in available food during winter (W), spring (Sp), summer (Su), and autumn (A) in the lower altitudes (the Monte sites Enjambre and Pintadas), middle altitudes (the Cardonal sites Hornillos and Mesitas), and higher altitudes (the Puna sites Canario and

Canota). Proportions of the grass *Poa* spp. in diet (dark gray) and in availability (dotted frame). Jacobs electivity index indicated significant preference ($D > 0$) and avoidance ($D < 0$) if mean availability was outside the diet confidence interval (black dots) or indifference (proportional use) if availability was inside the diet confidence interval (white dots)

gradients, and concurred with observations made in other mountain environments (e.g., Gentry 1988; Erschbamer et al. 2006; Grytnes and Vetaas 2002). This prediction was confirmed within grasses, shrubs, and forbs, whose respective richness was higher in the lower altitudes compared with that in the summit of the gradient. The increase in species richness at the lower altitudes would be more pronounced if the tree layer, originally dominated by *Prosopis flexuosa* (Roig 1993), had not virtually disappeared from the Monte belt due to historical removal of woody species, fires, and livestock raising and discontinued when the protected area was created. Declining native plant species diversity is frequently related to fragmentation and degradation due to human-caused disturbances, which achieve greater strength in lowlands than at higher elevations in mountain environments (Rojas et al. 2011).

The dietary generalism of the guanaco, which is very clear at the summit, showed a decreasing gradient as altitudinal belts descend and plant species richness increases, which agrees with the prediction for altitudinal gradients in terms of a more specialized diet as altitude decreases. There was a reduction in the proportion of plant species used by guanacos following the increase in the richness of vegetation, a tendency also detected in herbivores of the Alps (Pellissier et al. 2012). The more specialized diet found at the bottom of the Southern Andean Precordillera occurred with a strong avoidance of shrubs, the dominant plant category in the Monte. On the three altitudinal belts, grasses were the main dietary component, always used with preference regardless of their availability. Maintaining the prevalence of grasses in the diet undoubtedly represented an increasing searching effort for guanacos descending the altitudinal gradient, from the

Table 3 Selective use of food items, detected with chi-square test (χ^2)

	Higher altitudes: Puna		Middle altitudes: Cardonal		Lower altitudes: Monte	
	Canario	Canota	Hormillos	Mesitas	Pintadas	Enjambre
Use of plant categories	$\chi^2=58.71, P<0.001$	$\chi^2=56.19, P<0.001$	$\chi^2=201.36, P<0.001$	$\chi^2=140.57, P<0.001$	$\chi^2=119.98, P<0.001$	$\chi^2=126.76, P<0.001$
Use of main species	$\chi^2=236.31, P<0.001$	$\chi^2=253.72, P<0.001$	$\chi^2=230.39, P<0.001$	$\chi^2=410.68, P<0.001$	$\chi^2=1,636.12, P<0.001$	$\chi^2=1,438.73, P<0.001$
<i>Poa</i> spp. (grass)	0.51 (0.11), $D=0.80$ P	0.67 (0.23), $D=0.74$ P	0.66 (0.33), $D=0.60$ P	0.54 (0.08), $D=0.86$ P	0.70 (0.09), $D=0.92$ P	0.65 (0.07), $D=0.92$ P
<i>Pappostipa</i> spp. (grass)	0.29 (0.57), $D=-0.53$ A	0.14 (0.34), $D=-0.52$ A	0.17 (0.11), $D=0.24$ I	0.15 (0.04), $D=0.65$ P	0.03 (0.24), $D=-0.83$ A	0.03 (0.22), $D=-0.83$ A
<i>Artemisia</i> spp. (shrub)		Winter: 0.11 (0.00), $D=0.99$ P	0.02 (0.23), $D=-0.85$ A	0.10 (0.04), $D=0.46$ P	0.01 (0.09), $D=-0.86$ A	0.01 (0.13), $D=-0.92$ A
<i>Maihuenuiopsis</i> sp. (succulent)	0.15 (0.04), $D=0.64$ P	Winter: 0.14 (0.01), $D=0.90$ P				

Annual dietary proportions (availability proportions between brackets) and Jacobs index (D) for main plant species (proportions >0.10) on sampling sites of the three altitudinal belts. Selective use of species (P for preference: $D>0$, A for avoidance: $D<0$) if mean availability was outside the diet confidence interval or use with indifference (I, i.e., proportional use) if availability was inside the diet confidence interval

grasslands at the summit to the dense high shrublands at the bottom. More than half of the guanaco's diet on all sites was occupied by a grass (*Poa* spp.), whose clear dietary prevalence can be ascribed to its nutritional quality, with a high digestibility and low loss of protein content as the phenological cycle progresses (Hidalgo et al. 1998).

Besides responding to plant cover and diversity, diet composition responds to food quality, and ungulates usually select plant species for their nutritional value and low concentration of toxins (Launchbaugh et al. 1999; Pfister 1999). Humidity content is also relevant to herbivores in arid environments, and succulent species are significantly used by ungulates in arid and drought conditions (Lehmann et al. 2013). The succulent *Maihuenuiopsis* sp. represents a valuable food for guanacos on the summit, as was preferred, and its dietary proportion was positively associated with abundance in the vegetation. The high water content of succulents explains why guanacos preferred them despite their long spines, especially in extremely arid environments such as those of the southernmost part of Puna (Roig and Martínez Carretero 1998). The roughness of the extensive grasslands of *Pappostipa* spp. on the summit justifies that this grass was avoided, given that its high cellulose content affects protein digestibility when it reaches reproductive status (Hidalgo et al. 1998). Contrasting with this, *Pappostipa* spp. were used with indifference, even with preference on intermediate altitudes where environmental humidity in shady slopes of gorges could favor new sprouts with acceptable forage value (Wainstein and González 1962).

Seasonal changes

The winter decline of plant cover in the higher and middle altitudes of the gradient represents an important decrease in available food for the guanaco. The increase of species diversity in the guanaco diet during this winter food scarcity follows that expected from the optimal foraging theory (Stephens and Krebs 1986). The winter dietary diversity did not increase in richness but in equitability, i.e., the diet was less centered on the more nutritive items such as the grass *Poa* spp. (Hidalgo et al. 1998), without inclusion of new food items. The winter food scarcity, together with severe climate conditions that include large patches of snow cover, justified the increase of the dietary proportions of non-preferred items, in order to supply the feeding requirements of the guanaco.

Differing from the other altitudinal steps, the milder climate at the bottom of the gradient accounts for the fact that seasonal changes in plant cover were less evident. However, a decline in nutritional quality is expected in the vegetation during winter, as most species mature and increase in lignin and hemicellulose (Van Soest 1996). The winter reduction of diet diversity with a higher proportion of *Poa* spp. agrees with the selective quality hypothesis (Weckerly and Kennedy 1992) that predicts a diet to be more concentrated in the few food

items that maintain an acceptable quality during the unfavorable season. The winter diet showed a higher proportion of *Poa* spp., the main food item, which would be ascribed to the climate conditions in the lower altitudes that favor high availability and tenderness of *Poa* spp. during winter, the growing season of this grass (Cabral 2009).

Results were consistent with the prediction of stronger winter changes in the summit than in the bottom of the altitudinal gradient, concerning decline of vegetation and shift from grazing to browsing. The consumption of shrubs increased during winter in the higher and middle altitudes of the Precordillera, where a shortage of food occurred, whereas food availability was more stable throughout the year at the lower altitudes and a grazing behavior was maintained. With most shrubs being perennial and evergreen in the Southern Andean Precordillera, they constituted winter-available food in the higher altitudes where plant cover strongly decreased and large patches of snow cover reduced the accessibility to the herbaceous layer. At the lower altitudes, where food availability was more stable, shrubs were always used with strong avoidance although shrublands constituted the dominant vegetation in the Monte belt. This reinforces the categorization of the guanaco as an adaptive herbivore, able to alternate between grazing and browsing (Franklin 1982). Herbivores with such ability are stronger to cope with prolonged drought periods, whereas specialist grazers will be under severe nutritional stress, such as zebra and buffalo (Landman and Kerley 2001).

In conclusion, the guanaco's diet became more specialized from the higher to lower altitudes, in response to increases in temperature and plant species richness. Whether the past human impacts have not partially affected the bottom of the gradient, a vegetation with greater spatial heterogeneity, higher plant species richness, and a diet even more specialized would be expected. Associated to the winter food scarcity and severe climate conditions at the higher and middle altitudes, the guanaco increased its dietary generalism with a higher use of non-preferred items. On the contrary, the guanaco diet was more specialized during the milder winter at the lower altitudes, with higher prevalence of the few preferred items that maintained acceptable availability and tenderness. Although shrubs were used with avoidance across the gradient, a shift from grazing to browsing was confirmed during the rigorous winter at the higher and middle altitudes, whereas the guanaco maintained its grazing behavior throughout the year at the lower altitudes, where food availability was more stable. Plant species richness, food shortage, and climate severity are relevant variables to explain the altitudinal and seasonal changes in the diet of adaptive ungulates in mountain environments, such as the guanaco in the Southern Andean Precordillera.

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References

- Abbas F, Morellet N, Hewison AJ, Merlet J, Cargnelutti B, Lourtet B, Angibault JM, Daufresne T, Aulagnier S, Verheyden H (2011) Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia* 167:401–411
- Alipayo D, Valdez R, Holechek JL, Cardenas M (1992) Evaluation of microhistological analysis for determining ruminant diet botanical composition. *J Range Manage* 45:148–152
- Ambrosetti JA, Del Vitto LA, Roig FA (1986) The vegetation of the "Paso de Uspallata", Province Mendoza, Argentina. *Veröff Geobot Inst ETH* 91:141–180
- Baldi R, Pelliza Sbriller A, Elston D, Albon SD (2004) High potential for competition between guanacos and sheep in Patagonia. *J Wildl Manage* 68:924–938
- Baumgartner LL, Martin AC (1939) Plant histology as an aid in squirrel food-habit studies. *J Wildl Manage* 3:266–268
- Bolker B (2007) Ecological models and data in R. Princeton University Press, Princeton
- Cabral D (2009) Plantas nativas de Mendoza. www.floramendocina.com.ar/fichas. Accessed 10 May 2013
- Capitanelli R (1971) Climatología de Mendoza. Univ Nac Cuyo, Mendoza
- Carothers JH, Jaksic FM, Marquet PA (1996) A model for species distributions along a gradient: lizards as study systems. *Rev Chil Hist Nat* 69:301–307
- Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. *Ecology* 52:567–576
- Daget P, Poissonet J (1971) Une méthode d'analyse phytologique des prairies. Critères d'application. *Ann Agron* 22:5–41
- Dalmaso AD, Martínez Carretero E, Videla F, Puig S, Candia R (1999) Reserva natural Villavicencio, Mendoza, Argentina: Plan de Manejo. *Multequina* 8:11–50
- De Fina A (1992) Aptitud Agroclimática de la Argentina. Acad Nac Agron Vet, Buenos Aires
- Diblasi A, Bowman AW (2001) On the use of the variogram for checking independence in a Gaussian spatial process. *Biometrics* 57:211–218
- Duncan C, Chauvenet ALM, McRae LM, Pettorelli N (2012) Predicting the future impact of droughts on ungulates populations in arid and semi-arid environments. *PlosOne* 7:1–9. doi:10.1371/journal.pone.0051490
- Erschbamer B, Mallaun M, Unterluggauer P (2006) Plant diversity along altitudinal gradients in the southern and central Alps of south Tyrol and Trentino (Italy). *Gredleriana* 6:47–68
- Franklin WL (1982) Biology, ecology, and relationship of man to the South American camelids. In: Mares MA, Genoways HH (eds) *Mammalian biology in South America*. Pymatuning Laboratory of Ecology, University of Pittsburgh, Pittsburgh, pp 457–487
- Franklin WL, Puig S (2014) Guanaco feeding strategies: an analysis by ecoregions and forage types of an extraordinary adaptive and digestively efficient herbivore. In Franklin W.L. (ed.) *Guanaco ecology and conservation*, (in press)

- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann Missouri Bot Gard* 75:1–34
- Grytnes JA, Vetaas OR (2002) Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient. *Nepal Am Nat* 159:294–304
- Harrington JH (1971) Descripción geológica de la Hoja 22c, “Ramblón”, provincias de Mendoza y San Juan. *Dir Nac Geología y Minería, Buenos Aires. Boletín* 114:1–87
- Hidalgo LG, Cauhepe MA, Ermi AN (1998) Digestibilidad de materia seca y contenido de proteína bruta en especies de pastizal de la Pampa deprimida, Argentina. *Investigaciones Agrarias: Producción y Sanidad Animal* 13:165–177
- Holeček JL (1982) Sample preparation techniques for microhistological analysis. *J Range Manage* 35:267–268
- Holeček J, Gross B (1982) Evaluation of different calculation procedures for microhistological analysis. *J Range Manage* 35:721–723
- Holeček JL, Valdez R (1985) Magnification and shrub stemmy material influence on fecal analysis accuracy. *J Range Manage* 38:350–352
- Jacobs J (1974) Quantitative measurement of food selection. *Oecologia* 14:413–417
- Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol Evol* 15:513–514
- Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel C, Kamiński T, Wójcik JM (2011) Influence of management practices on large herbivore diet: case of European bison in Białowieża Primeval Forest (Poland). *Forest Ecol Manage* 261:821–828
- Kuijper DPJ, Ubels R, Loonen MJJE (2009) Density dependent switches in diet; a likely mechanism for negative feedbacks on goose population increase? *Polar Biol* 32:1789–1803
- Landman M, Kerley GIH (2001) Dietary shifts: do grazers become browsers in the Thicket Biome? *Koedoe* 44:31–36
- Launchbaugh KL, Walker JW, Taylor CA (1999) Foraging behavior: experience or inheritance? In: Launchbaugh KL, Mosley JC, Sanders KD (eds) *Grazing behavior in livestock and wildlife*. University of Idaho, Moscow, pp 28–35
- Lehmann D, Mfune JKE, Gewers E, Cloete J, Brain C, Voigt CC (2013) Dietary plasticity of generalist and specialist ungulates in the Namibian Desert: a stable isotopes approach. *PlosOne* 8:1–10. doi:10.1371/journal.pone.0072190
- Linares L, Linares V, Mendoz G, Peláez F, Rodríguez E, Phum C (2010) Food preferences of guanaco (*Lama guanicoe cacsilensis*) and its competence with cattle in the Calipuy National Reserve, Peru. *Scientia Agropecuaria* 1:225–234
- Martínez O, Rechberger J (2007) Características de la avifauna en un gradiente altitudinal de un bosque nublado andino en La Paz, Bolivia. *Rev Peru Biol* 14:225–236
- Muñoz AE, Simonetti JA (2013) Diet of guanaco in sheep-free rangeland in Tierra del Fuego, Chile. *Cien Inv Agr* 40:185–191
- Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilisation-availability data. *J Wildl Mgmt* 38:541–545
- Pellissier L, Fiedler K, Ndríbe C, Dibuis A, Pradervand JN, Guisan A, Rasmann S (2012) Shifts in species richness, herbivore specialization, and plant resistance along elevation gradients. *Ecol Evol* 2:1818–1825
- Pfister JA (1999) Behavioral strategies for coping with poisonous plants. In: Launchbaugh KL, Mosley JC, Sanders KD (eds) *Grazing behavior in livestock and wildlife*. University of Idaho, Moscow, pp 45–59
- Polanski J (1954) Rasgos geomorfológicos del territorio de la provincia de Mendoza. Ministerio de Economía, Instituto de Investigaciones Económicas y Tecnológicas. Cuaderno de Investigaciones y Estudios 4:4–10
- Puig S, Videla F, Monge S, Roig V (1996) Seasonal variations in guanaco diet (*Lama guanicoe* Müller 1776) and in food availability in Northern Patagonia, Argentina. *J Arid Environ* 34:215–224
- Puig S, Videla F, Martínez Carretero E, Dalmasso A, Durán V, Cortegoso V, Lucero G, Carminati A, Moreno D (2008) Plan de Manejo para la Reserva Villavicencio, período 2009–2013. IADIZA-FVSA-UNCuyo. Technical Report, p 263
- Puig S, Rosi MI, Videla F, Mendez E (2011) Summer and winter diet of the guanaco and food availability for a High Andean migratory population (Mendoza, Argentina). *Mamm Biol* 76:727–734
- Puig S, Videla F, Rosi MI (2014) Seasonal distribution and habitat selection by the guanaco (*Lama guanicoe*) along an altitudinal gradient in the Southern Andean Precordillera (Argentina), (in press)
- Raedeke KJ, Simonetti JA (1988) Food habits of *Lama guanicoe* in the Atacama desert in northern Chile. *J Mammal* 69:198–201
- Roig FA (1993) Aportes a la etnobotánica del género *Prosopis*. In: IADIZA (ed), *Contribuciones Mendocinas a la Quinta Reunión de Regional para América Latina y el Caribe de la Red de Forestación del CIID*. IADIZA-CRICYT-CIID, Mendoza, Argentina, pp 99–119
- Roig FA (1994) La Provincia del Cardonal. In: *Botánica y Fitosociología, IADIZA (ed) La vegetación de los Andes centrales de Argentina: Excursión botánica*, pp 19–24
- Roig FA, Martínez Carretero E (1998) La vegetación puneña en la provincia de Mendoza, Argentina. *Phytocoenologia* 28:565–608
- Rojas I, Becerra P, Gálvez N, Laker J, Bonacic C, Hester A (2011) Relationship between fragmentation, degradation and native and exotic species richness in an Andean temperate forest of Chile. *Gayana Bot* 68:163–175
- Siegel S, Castellan NJ (1988) *Nonparametric statistics for the behavioral sciences*, 2nd edn. McGraw-Hill, New York
- Smith AD, Shandruk LJ (1979) Comparison of fecal, rumen and utilization. Methods for ascertaining pronghorn diets. *J Range Manage* 32:275–279
- Stafford Smith M (1996) Management of rangelands: paradigms at their limits. In: Hodgson J, Illius A (eds) *The ecology and management of grazing systems*. CAB International, Wallingford, pp 325–358
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Terborgh J (1977) Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007–1019
- Van Soest PJ (1996) Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology* 15:455–479
- Videla MA, Suárez J (1991) *Mendoza Andina: Precordillera y Alta Cordillera*, Mendoza, Argentina. Adalid, Mendoza
- Wainstein P, González S (1962) Valor forrajero de trece especies de Stipa de Mendoza. *Rev Fac Cs Agrarias Univ Nac Cuyo* 9:3–18
- Weckerly FW, Kennedy ML (1992) Examining hypotheses about feeding strategies of white-tailed deer. *Canadian J Zool* 70:432–439
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall Inc., Upper Saddle River
- Zweifel-Schielly B, Kreuzer M, Ewald KC, Suter W (2009) Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. *Ecography* 32:103–113