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Flexibility in the food selection by the European hare (*Lepus europaeus*) along the altitudinal gradient of the Southern Andean Precordillera (Argentina)

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Abstract Predictions derived from the optimal foraging theory are interesting to test on wild herbivores living in mountain environments, considering the expected vegetation changes across altitudinal gradients. A lower food richness and a more generalist diet are expected as altitude increases, with higher diet diversity and a shift to browsing as food availability decreases seasonally. With broad diets and ecological adaptability, *Lepus europaeus* is a non-native herbivore inhabiting Andean altitudinal gradients. Diet and vegetation were analyzed using microhistological analysis and point-quadrat transects at six sampling sites, representative of altitudinal phytogeographic belts. The diet included 67 of the 109 species present in the vegetation. *Lepus europaeus* proved to be an intermediate feeder with a generalist and selective diet. Following the prediction for altitudinal gradients, dietary generalism increased as plant cover and diversity decreased with altitude. Differences in plant phenology and toxins justified changes in food preferences, from shrubs at the summit to grasses at lower altitudes. Seasonal changes in diet diversity were consistent with different hypotheses depending on altitude. The tundra climate at the summit determined a strong phenological decline and food scarcity during winter, when the less diverse diet was more focused on a preferred shrub,

following the selective quality hypothesis. With a milder climate at lower altitudes, the winter increase in diet diversity, with inclusion of avoided shrubs, agrees with the food abundance hypothesis. Climate severity, food shortage, plant phenology, and secondary compounds are relevant for explaining the feeding strategy of European hares in these mountain environments.

Keywords Leporidae · Feeding ecology · Food availability · Dietary flexibility · Mountain environments

Introduction

The distribution, structure, and abundance of vegetation are expected to change across altitudinal gradients of mountain environments, conditioned by altitudinal differences in temperature, solar radiation, and rainfall (Körner 2000). As altitude increases, the vegetation presents a lower richness of species in the Andes (Gentry 1988), as well as in other mountain environments such as the Alps (Erschbamer et al. 2006) and the Himalayas above 1500 m a.s.l. (Grytnes and Vetaas 2002). In response to the decreased plant diversity at higher altitudes, a more generalist use of resources was observed in herbivores of the Alps (Pellissier et al. 2012). The guanaco (*Lama guanicoe*), a wild ungulate that shares the altitudinal gradient of the Southern Andean Precordillera with European hares, also showed an increased dietary generalism associated to a decreasing food availability with the altitude (Puig et al. 2014a).

Predictions derived from the optimal foraging theory are interesting to test on wild herbivores living in mountain environments, bearing in mind the expected changes in food availability and diversity along altitudinal gradients. The food abundance hypothesis proposes a dietary focus on the most

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nutritive items while food is abundant and a broader diet in situations of food scarcity (Stephens and Krebs 1986). On the other hand, the selective quality hypothesis (Weckerly and Kennedy 1992) proposes a higher selectivity for the few plant species with acceptable quality to meet nutritional requirements, when resources are strongly limited during extreme drought or in severely arid conditions. Branch et al. (1994) argued that high selectivity can occur at the upper end of the resource spectrum because of dietary preferences (food abundance hypothesis) and at the lower end of the spectrum because of constraints in food availability (selective quality hypothesis).

The presence of European hares in mountains of the Southern Andean Precordillera allows assessment of feeding strategies of this lagomorph and testing predictions for altitudinal gradients within the frame of the optimal foraging theory. The European hare is an interesting herbivore to study considering its adaptability, with broad diets that change in composition according to diverse environmental conditions, the current inclusion of this introduced species in South America's ecosystems, and its relevance as a prey for native aerial and terrestrial predators (Montserrat et al. 2005; Bonino et al. 2010).

Most hares (Order Lagomorpha, Family Leporidae) are characterized by great adaptability to ecologically diverse environments (Chapman and Flux 1990). Such adaptability in *Lepus europaeus* (Pallas), a native lagomorph from the Palearctic, favored its successful expansion after being introduced into Australasia, North America, and South America (Angermann et al. 1990). The broad diets of hares include mainly grasses, shrubs, and forbs, whose relative proportions vary with habitat characteristics such as food availability, severity of weather conditions, protection from predators, and interspecific competition. Regarding food availability, the structure of vegetation and the emergence of seasonal species influence the composition of the hare's diet (Flux and Angermann 1990). Some populations of *L. timidus* and *L. europaeus* showed shifts from grazing to browsing associated with declines in food availability (Hulbert et al. 2001; Rödel et al. 2004; Kufner et al. 2008). In fact, the senescence of grasses represents a food restriction for *Lepus timidus*, whose diet changes seasonally from grasses in summer to woody species in winter (Hulbert et al. 2001). The low palatability of grasses post-seeding is responsible for summer to autumn changes in the diet of *L. europaeus* (Green et al. 2013). About the severity of weather conditions, snowfall at high altitudes limit food accessibility in winter, forcing *L. europaeus* to use the vegetation protruding through the snow (Green et al. 2013) or growing in windswept areas without snow (Flux 1967). As accessibility to vegetation decreases with altitude in winter, twigs and barks of a greater number of woody species are included in the diet of hares (Rödel et al. 2004).

With respect to protection from predators, most hare species favor open habitats (tundra, steppe, agricultural land, savanna, desert), provided they have some kind of protective

cover (shrubs, bushes, rocks) (Flux and Angermann 1990). Snow cover and a low plant cover increase the requirements of protection during winter and can affect the diet of hares. Indeed, the foraging activity of *L. timidus* was restricted to the vegetation available in forest habitats (Rehnus et al. 2013), while *L. americanus* used poorer food items available on less risky sites (Hik 1995). About interspecific competition, competitive exclusion usually occurs between hare species in regions where they overlap geographically. The diet composition of each species can reflect differences in the vegetation of the habitat that it occupies as a consequence of this exclusion (Flux and Angermann 1990). Despite *L. europaeus* has been associated with the steppe and *L. timidus* with the tundra, these species can be mutually replaced if ecological conditions change (Flux and Angermann 1990). In environments where *L. timidus* is absent, the type of habitat originally associated with this species can be successfully occupied by *L. europaeus*, whose diet includes more shrub items as an adaptation to the vegetation of this habitat (Flux et al. 1990; Green et al. 2013).

The Southern Andean Precordillera and its Piedmont constitute an altitudinal gradient extending from 800 to 3200 m a.s.l. This gradient, comprising three phytogeographic provinces arranged in altitudinal belts (Dalmaso et al. 1999), presents important environmental changes in food availability for the European hare. Climate changes with altitude in the Southern Andean Precordillera are consistent with those expected for mountain environments (Körner 2000), with an increasing severity from a steppe climate at lower altitudes to a tundra climate at the summit (Videla and Suárez 1991). As altitude diminishes, the gradual increase in temperatures confirms the expected milder climate at the bottom of the altitudinal gradient (Puig et al. 2014a). Additionally, the snow cover decreases in extent and persistence from higher to middle altitudes and it is absent at lower altitudes. The growing severity of climate conditions and food scarcity as altitude increases also allows assessing the relevance of shifts from grazing to browsing in the European hare's diet.

The objective of this study is to analyze the seasonal composition of the European hare's diet, in relation to food availability and diversity in three phytogeographic provinces (Puna, Cardonal, and Monte) present across an altitudinal gradient within a protected area in the Southern Andean Precordillera. According to predictions for altitudinal gradients, we expect that plant species richness will be lower and that the European hare's diet will be more generalist as altitude increases. Considering the food abundance hypothesis, we expect a higher diet diversity and the seasonal inclusion of species used with avoidance when food availability decreases. Taking into account that shifts from grazing to browsing were observed in other hare populations when vegetation declines, we expect that the winter decline in the availability and diversity of vegetation and the increase of shrubs in the diet will be stronger on the summit than at the bottom of the altitudinal gradient.

Materials and methods

Study area and habitat characteristics

The study area, belonging to the “Reserva Villavicencio” protected area (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 3000 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 on the mountain summit, Cardonal in the Eastern valleys at intermediate altitudes, and Monte in the extensive East Piedmont corresponding to the lowest altitudes. Hunting, extraction of woody plants, fires, and livestock overgrazing have been historical negative impacts at lower altitudes. Since the protected area was created in 2000 and management actions were carried out, these impacts have markedly decreased. Consequently, there was a slow recovery in the historically impacted vegetation.

Field and laboratory design

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 (SD = 9) per landscape. A requisite for the selection of all these landscapes was the presence of European hares throughout the year. In order to achieve better representativeness of environmental heterogeneity, two landscapes were selected within each phytogeographic belt (Table 1).

Seasonal fecal sampling and vegetation recording were conducted in the six above-defined landscapes during 2010–2011, corresponding to winter (July), spring (October), summer (February), and autumn (April). A 5-ha sampling site was selected within each landscape, and the mean distance among sampling sites was 12 km. Throughout the year, 40 fecal samples were collected from each landscape and 40 vegetation

Table 1 Location and characteristics of sampling sites in the Villavicencio Reserve (extracted from Ambrosetti et al. 1986; Dalmasso 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: 2200 to 2800 m a.s.l.) Summit of Andean Precordillera. Open plains with soft hills and extended foothills. Lithosols of coarse sand and rocks fragmented due to criogenic 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, 3139 m a.s.l.) Canota (Pampa de Canota, 2931 m a.s.l.)
Phytogeographic province: Cardonal (surface in the study area: 150 km ² , altitudinal belt: 1500 to 1700 m a.s.l.) Andean Precordillera gorges. Shady slopes 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>Mitilinum 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, 2744 m a.s.l.) Mesitas (Quebrada Mesitas, 2661 m a.s.l.)
Phytogeographic province: Monte (surface in the study area: 220 km ² , altitudinal belt: 1700 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, 1381 m a.s.l.) Enjambre (Lomas del Enjambre, 1315 m a.s.l.)

records were carried out. Plant cover and relative frequencies of plant species were estimated for each season by the point-quadrat method (Daget and Poissonet 1971), applied to 10 fixed transects per sampling site. All 30-m transects, separated from one another by more than 100 m, were distributed within each sampling site in a stratified random design in order to better reflect the heterogeneity in topography and vegetation. 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 (i.e., bright brown feces), was collected from a different group of feces, which were more than 100 m apart.

Fecal samples were analyzed with the microhistological method of Baumgartner and Martin (1939), modified by Holechek (1982), and the relative frequency of food items was determined based on the count of fragments. Microhistological analyses, extensively used to evaluate the diet composition of wild herbivores, have been considered to have good precision despite that in some cases forbs can be underestimated and grasses overestimated due to differential digestion (Holechek et al. 1982). 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 prepared from the material trapped in the second sieve. This procedure allowed obtaining even-sized plant fragments, in order to avoid bias resulting from counting fragments that differ widely in size (Smith and Shandruk 1979; Kuijper et al. 2009). On each slide, fifty fields were systematically examined through a microscope at 400× and all identifiable fragments (those showing at least three diagnostic features) were counted. A microscopic field at the high resolution used 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 genus level and to species level when possible.

Statistical analyses

Plant cover (as complementary to bare soil) was determined for each point-quadrat transect by dividing the number of points at which vegetation was contacted (except dead plants) by the 100 points setup along the transect. Food availability analyses only considered potential food items for European hares, i.e., all plant species consumed by European hares in the study area on at least one occasion. Relative frequency of a given item in the available food was determined by dividing the absolute frequency of this species by the sum total of absolute frequencies for all food items identified on each point-quadrat transect. The relative frequency of a species in

the diet was determined for each fecal 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). Taking into account the expected altitudinal differences in diversity and richness of vegetation and its probable influence on diet diversity and richness, diet generalism was estimated using the proportion of plant species used by European hares on each site and season (i.e., the number of species included in the diet divided by the number of species present in the vegetation).

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 Simpson's diversity index (Krebs 1999). A linear model of plant cover (transformed by Box and Cox) was fitted as a function of distances among sampling units ($F = 34.06$ $P < 0.001$). The null hypothesis of spatial independence among sampling units was not rejected by the test of Diblasi and Bowman (2001), applied to residuals of the mentioned model ($P = 0.195$). Generalized linear models were fitted for vegetation and diet variables (plant cover, species richness, diversity, percentages of categories, and species), in order to detect the effects of altitude, seasons, and their interactions. A Poisson distribution of errors was used for integers, and a binomial distribution of errors with a logistic link function was used for proportions (Bolker 2007). Variables were not transformed for use in the models. Models with the lowest AIC values (Akaike information criterion) were selected through a stepwise function in both directions (MASS package). Normality and homoscedasticity of the model residuals were checked by means of a normal probability plot and a graph of residuals versus fitted values. GzLMs were performed with the R 3.1.0 software (The R Foundation for Statistical Computing Platform 2014). Food selectivity (i.e., a diet with food items represented disproportionately to their availability, Manly et al. 2002) was detected by significant differences between observed values (diet proportions) and expected values (food availability proportions) using the χ^2 test (Zar 1984). The Chesson's electivity index (Chesson 1983), with 95 % confidence interval estimated by bootstrapping (following Schai-Braun et al. 2015), identified selective use of each plant category and main species (species with mean frequency higher than 0.10 in the diet and/or availability). Plant use was qualified as indifference (use proportional to availability) if the lower and upper limits of the confidence interval had different algebraic signs; otherwise, the use was qualified as preference (positive selection) if the Chesson's index had a positive value or avoidance (negative selection) if the index value was negative. In 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. Similarity between the European hare's diet and food availability was estimated using the percent overlap index (Hurlbert 1978).

Results

Composition of the vegetation

The vegetation was characterized by grasses (65 %), supplemented with shrubs (19 %) or forbs (17 %) at higher altitudes (Puna sites), a codominance of shrubs (47 %) and grasses (34 %) or forbs (19 %) at middle altitudes (Cardonal sites), whereas shrubs (61 %), supplemented with grasses (34 %), prevailed at lower altitudes (Monte sites) (Fig. 1). The grass *Pappostipa* spp. was prevalent in the vegetation of Puna, together with the forb *A. caespitosa* in Canota (Table 2). The vegetation of Cardonal was dominated by the grass *Poa* spp. and the shrub *A. mendozana* in Hornillos, whereas the shrub *C. gilliesi* and the forb *C. arvense* were codominant in Mesitas. The shrub *L. divaricata* and the grass *Pappostipa* spp. predominated in the vegetation of Monte.

Plant cover and diversity decreased as altitude increased (Table 3). The decrease in plant cover with altitude became significantly more pronounced in winter than in spring and

summer. Plant cover showed a slight seasonal change at lower altitudes (6 %), but important winter decreases at higher and middle altitudes (27 % in both cases; Fig. 2). The altitude-related decrease in plant diversity did not differ among seasons. Vegetation species richness also decreased as altitude increased (Fig. 3), especially in the number of shrubs and forbs. The decrease in the number of forb species with increasing altitude became more pronounced in winter, when the forb richness was higher at lower altitudes.

Sixty five percent of all plant species recorded on the sampling sites (109 species) was food items for European hares: all grasses (9 species), 33 of 50 shrubs, 24 of 43 forbs, three of four succulents. The proportion of grasses in the food available increased with altitude (Fig. 1), whereas the proportion of shrubs and succulents decreased. The decrease in shrub proportion with altitude was less pronounced during winter (Fig. 4). Availability of the grass *Pappostipa* spp., the shrub *E. breana*, and the forb *A. caespitosa* increased with altitude, whereas the shrubs *L. divaricata* and *A. mendozana* decreased in availability (Table 3). The grass *Poa* spp. presented a higher proportion in winter, particularly in the vegetation of lower altitudes.

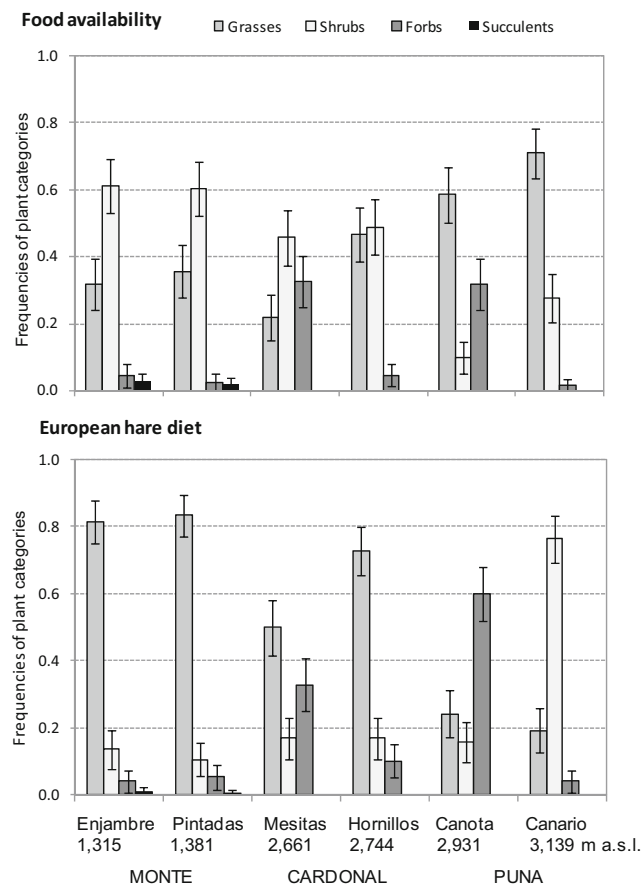


Fig. 1 Mean proportions of plant categories: grasses (*GR*), shrubs (*SH*), and forbs (*FO*) in available food and in the diet of the European hare at lower altitudes (the Monte sites Enjambre and Pintadas), middle altitudes (the Cardonal sites Hornillos and Mesitas), and higher altitudes (the Puna sites Canario and Canota) of Villavicencio Reserve. Vertical bars correspond to confidence intervals calculated using Neu et al. (1974)

Diet of the European hare

The diet included 67 plant species from the study area. Shrubs or forbs were the main food items at higher altitudes (Puna sites, Fig. 1), whereas grasses dominated the diet at middle and lower altitudes (Cardonal and Monte sites). The diet in Puna was dominated by the shrub *E. breana* in Canario and the forb *A. caespitosa* in Canota. The grass *Poa* spp. prevailed in the Cardonal diet followed by the grass *Pappostipa* spp. in Hornillos and by the forb *C. arvense* in Mesitas. The diet in Monte was dominated by the grasses *Pappostipa* spp. and *Poa* spp..

Diet diversity and species richness (particularly the number of grass species) decreased with increasing altitude, and these decreases were stronger in winter (Table 3). The number of shrub species was higher during winter at lower altitudes (Fig. 3), especially because the winter diet included the shrubs *L. divaricata* and *A. mendozana*. It is useful to mention that the microhistological structures of both shrubs helped to easily identify them during the fecal analysis.

The dietary proportion of shrubs (particularly *E. breana*) and forbs (with presence of *A. caespitosa* only in Puna) increased with altitude (Fig. 1, Table 3), whereas the proportion of grasses decreased (particularly *Poa* spp. and *Pappostipa* spp., with presence of *Eragrostis* spp. only in Monte). The decrease with altitude was stronger in winter for *Poa* spp., in spring for *Pappostipa* spp., and in summer for *Eragrostis* spp. The dietary proportion of shrubs (particularly *A. mendozana*) increased in winter, whereas grasses and forbs occupied lower proportions in the diet.

Table 2 Selective use of food items by *Lepus europaeus* at lower, middle, and higher altitudes of Villavieancio Reserve

	Lower altitudes: Monte			Middle altitudes: Cardonal			Higher altitudes: Puna		
	Enjambre	Pintadas	Mesitas	Hornillos	Canota	Canario			
Use of plant categories	$\chi^2 = 115.18, P < 0.001$	$\chi^2 = 110.39, P < 0.001$	$\chi^2 = 54.80, P < 0.001$	$\chi^2 = 42.40, P < 0.001$	$\chi^2 = 49.21, P < 0.001$	$\chi^2 = 128.78, P < 0.001$			
Use of main species	$\chi^2 = 269.54, P < 0.001$	$\chi^2 = 312.20, P < 0.001$	$\chi^2 = 294.31, P < 0.001$	$\chi^2 = 902.96, P < 0.001$	$\chi^2 = 158.41, P < 0.001$	$\chi^2 = 559.52, P < 0.001$			
<i>Eragrostis</i> spp. (grass)	0.17 (0.04), $\epsilon = 0.17$ BCI = -0.06, 0.37 I	0.19 (0.03), $\epsilon = -0.12$ BCI = -0.28, 0.07 I	0.25 (0.08), $\epsilon = -0.16$ BCI = -0.34, 0.07 I	0.36 (0.33), $\epsilon = -0.76$ BCI = -0.81, -0.66 A	0.17 (0.24), $\epsilon = -0.47$ BCI = -0.58, -0.32 A	0.11 (0.11), $\epsilon = -0.59$ BCI = -0.70, -0.45 A			
<i>Poa</i> spp. (grass)	0.28 (0.07), $\epsilon = 0.09$ BCI = -0.11, 0.28 I	0.30 (0.08), $\epsilon = -0.12$ BCI = -0.29, 0.04 I	0.31 (0.11), $\epsilon = -0.50$ BCI = -0.60, -0.38 A	0.31 (0.11), $\epsilon = -0.50$ BCI = -0.60, -0.38 A	0.06 (0.34), $\epsilon = -0.85$ BCI = -0.91, -0.71 A	0.06 (0.60), $\epsilon = -0.94$ BCI = -0.96, -0.91 A			
<i>Pappostipa</i> spp.	0.33 (0.20), $\epsilon = -0.36$ BCI = -0.48, -0.22 A	0.32 (0.23), $\epsilon = -0.49$ BCI = -0.59, -0.32 A	0.00 (0.23), $\epsilon = -1.00$ BCI = -1.00, -0.99 A	0.00 (0.23), $\epsilon = -1.00$ BCI = -1.00, -0.99 A	0.13 (0.03), $\epsilon = -0.15$ BCI = -0.41, 0.12 I	0.63 (0.07), $\epsilon = 0.51$ BCI = 0.36, 0.64 P			
<i>Artemisia mendozaana</i> (shrub)	0.00 (0.12), $\epsilon = -0.99$ BCI = -1.00, -0.98 A								
<i>Ephedra breana</i> (shrub)									
<i>Larrea divaricata</i> (shrub)	0.00 (0.17), $\epsilon = -0.99$ BCI = -1.00, -0.97 A	0.00 (0.26), $\epsilon = -1.00$ BCI = -1.00, -1.00 A							
<i>Acaena caespitosa</i> (forb)					0.56 (0.30), $\epsilon = -0.06$ BCI = -0.20, 0.10 I				

Annual dietary proportions (availability proportions between brackets) and Chesson electivity index (ϵ) for main plant species (proportions > 0.10) at sampling sites of the three altitudinal belts. Selective use of species (P for preference: $\epsilon > 0$, A for avoidance: $\epsilon < 0$) if the lower and upper 95 % confidence intervals by bootstrapping (BCI) feature the same algebraic sign or use with indifference (I, i.e., proportional use) if the lower and upper confidence intervals have different sign

A low similarity between diet and food availability occurred throughout the year at lower altitudes (Fig. 2). Similarity decreased in winter at middle and higher altitudes (Table 3), with very low values in Canario. As the altitude increased, the number of grass and forb species included in the diet corresponded to a higher proportion of the total number of species present in the vegetation. The winter diet included a higher proportion of the total species present than the summer diet, particularly at middle altitudes (Fig. 3, Table 3). A higher proportion of shrub species and a lower proportion of grass species were included in the winter diet, particularly at lower and middle altitudes.

Dietary preferences

An overall selective use of plant categories was detected throughout the year at the summit (Puna sites), middle altitudes (Cardonal sites), and lower altitudes (Monte sites) (Table 2, Fig. 4). Within the vegetation of higher altitudes, a preference was detected for using shrubs (almost all year round in Canario, during winter in Canota) and forbs (almost all year round in Canota, too scarce in Canario), whereas grasses were avoided throughout the year. Within the vegetation of middle and lower altitudes, shrubs were avoided all year round, grasses were mostly used with preference, and forbs were mostly used with indifference (even though they were used with preference in Hornillos during summer). Succulents were only consumed at lower altitudes and in very low proportions.

An overall selective use of plant species was detected throughout the year in all three altitudinal belts (Table 2). Among the main species present in the vegetation of higher altitudes, the shrub *E. breana* was used with preference in Canario, whereas the grasses *Pappostipa* spp. and *Poa* spp. were avoided at both summit sites. At middle altitudes, the shrub *A. mendozaana* and the grasses *Poa* spp. and *Pappostipa* spp. were avoided in Hornillos. Within the vegetation of lower altitudes, the grasses *Poa* spp. and *Eragrostis* spp. were used with indifference, *Pappostipa* spp. was used with avoidance, whereas the shrubs *L. divaricata* and *A. mendozaana* were avoided in winter and not eaten during the rest of the year.

Dietary proportions of plant categories increased as their relative availability in the vegetation increased, considering forbs ($R = 0.73 P < 0.001$, particularly *A. caespitosa* $R = 0.89 P < 0.001$), the main grasses *Pappostipa* spp. ($R = 0.70 P < 0.001$ in Canota, $R = 0.54 P = 0.019$ in Mesitas, $R = 0.59 P < 0.001$ in Enjambre) and *Poa* spp. ($R = 0.62 P < 0.001$ in Canario, $R = 0.60 P < 0.001$ in Hornillos). The dietary proportion of shrubs at middle and higher altitudes increased as their relative availability in the vegetation increased ($R = 0.66 P < 0.001$ in Canota, $R = 0.80 P < 0.001$ in Mesitas), particularly *E. breana* ($R = 0.52 P < 0.001$ in Canario, $R = 0.48 P = 0.002$ in Hornillos). At lower altitudes, where the shrub

Table 3 Effects of altitude and seasons on vegetation and diet variables, detected using generalized linear models

	Intercept	Altitude	Spring ^a	Summer	Autumn	Altitude:spring	Altitude:summer	Altitude:autumn	AIC
Composition of the vegetation									
Plant cover	8.09***	-5.39***				2.23*	2.04*		467.36
Diversity Simpson	16.58***	-7.65***							443.53
Number of plant species	43.02***	-5.49***							1213.00
Number of grass species	21.91***								719.06
Number of shrub species	26.79***	-6.60***							1003.80
Number of forb species	5.87***	-4.29***		-2.34*	-4.77***	2.15*	3.55***	6.04***	967.35
Food availability									
Proportion of grasses	-12.07***	11.78***			3.66***				362.52
Proportion of shrubs	4.09***	-4.83***				-2.28*		-3.15**	350.10
Proportion of forbs	-4.66***				-2.52*			2.64**	289.21
Proportion of succulents		-2.84**							326.22
<i>Poa</i> spp. (grass)	-4.85***			-2.44*		2.01*	2.49*		309.21
<i>Pappostipa</i> spp. (grass)	-9.68***	5.87***							308.66
<i>A. mendozana</i> (shrub)	-5.30***	-2.89**							224.22
<i>E. breana</i> (shrub)	-3.59***	2.24*							176.61
<i>L. divaricata</i> (shrub)	5.29***	-7.15***							272.85
<i>A. caespitosa</i> (forb)	-7.05***	5.18***							224.05
Diet of the European hare									
Diversity Simpson	3.58***	-2.42*					3.45***	3.48***	343.78
Number of species	17.65***	-3.09**					2.15*		1071.00
Number of grass species	11.18***	-5.64***		2.33*	2.16*				710.86
Number of shrub species	7.47***			-2.97**	-2.36*		2.65**		799.07
Number of forb species	2.16*				-2.03*			2.45*	783.61
Proportion of grasses	12.19***	-14.80***	2.67**	4.33***	4.07***				296.67
Proportion of shrubs	-8.58***	8.35***	-4.25***	-3.68***	-4.46***				280.41
Proportion of forbs	-9.31***	6.55***	2.29*						265.14
<i>Poa</i> spp. (grass)		-4.54***			-4.80***			4.91***	301.34
<i>Pappostipa</i> spp. (grass)		-2.71**	3.26**			-3.09**			256.32
<i>Eragrostis</i> spp. (grass)	3.34***	-4.55***		3.21**			-3.26**		274.27
<i>A. mendozana</i> (shrub)	-5.96***		-2.98**		-2.68**				127.94
<i>E. breana</i> (shrub)	-2.65**	2.34*							30.43
<i>L. divaricata</i> (shrub)	2.87**	-3.61***							218.52
<i>A. caespitosa</i> (forb)	-6.09***	4.95***							218.40
Number of species in the diet/number of species in the vegetation									
Plant species	-6.48***			-3.13**			3.51***	2.34*	559.75
Grasses		2.56*	3.56***	4.33***	4.56***				314.94
Shrubs	-3.93***		-2.31*	-4.68***	-3.58***		4.16***	2.66**	427.85
Forbs	-5.89***	4.29***							328.51
Similarity between diet and food availability									
Similarity	0.00**						3.42***	3.45***	428.98

^a Spring, summer, and autumn are referred to seasonal changes from winter to spring, from winter to summer, and from winter to autumn, respectively
* $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$ (significant levels of the z values)

L. divaricata prevailed, the proportion of shrubs in the diet decreased as their relative availability increased ($R = -0.35$ $P = 0.025$ in Pintadas, $R = -0.53$ $P < 0.001$ in Enjambre).

Discussion

The dietary generalism of European hares, observed in other environments including the High Andes mountains (Puig et al. 2015), was confirmed in the study area given that the number of species in the diet corresponded to a considerable percentage of the total number of species present in the vegetation. Generalism favors the survival of species in environments where food is a limiting resource, for it enhances their ability

to shift among food items (Schleuter and Eckmann 2007). *Lepus europaeus* behaves as an intermediate feeder in the Southern Andean Precordillera, since both grasses and shrubs were eaten at the different altitudes and seasons studied. The dietary relevance of grasses in summer and shrubs in winter also allowed considering *L. timidus* as an intermediate feeder on an annual basis (Hulbert et al. 2001). Differing from the case of hares that ate bark during winter (Rödel et al. 2004), woody stems of shrubs were never observed debarked by European hares in the study area. Diversity, richness of species, and proportion of several main items increased in the diet following the respective increases in food availability in the study area, which supports the expected dietary adaptability of European hares to diverse ecological conditions (Chapman

Fig. 2 Plant cover, species diversity in the diet of the European hare and in available food, and similarity between diet and food availability, during winter (*w*), spring (*sp*), summer (*su*), and autumn (*a*) at 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)

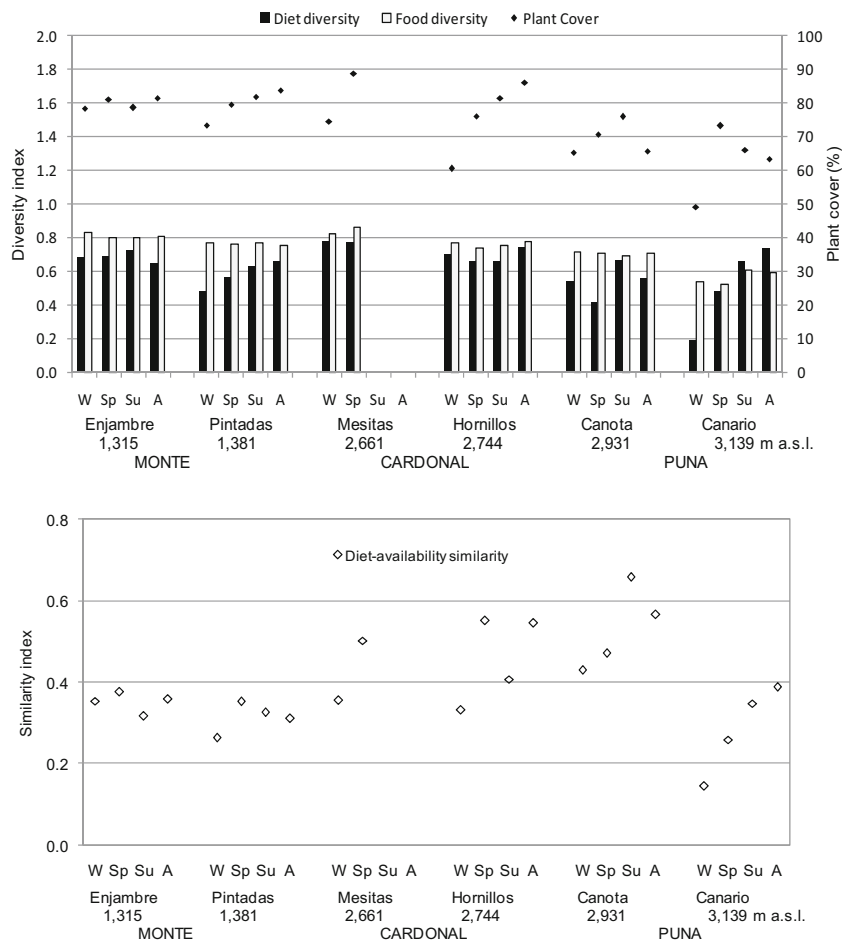
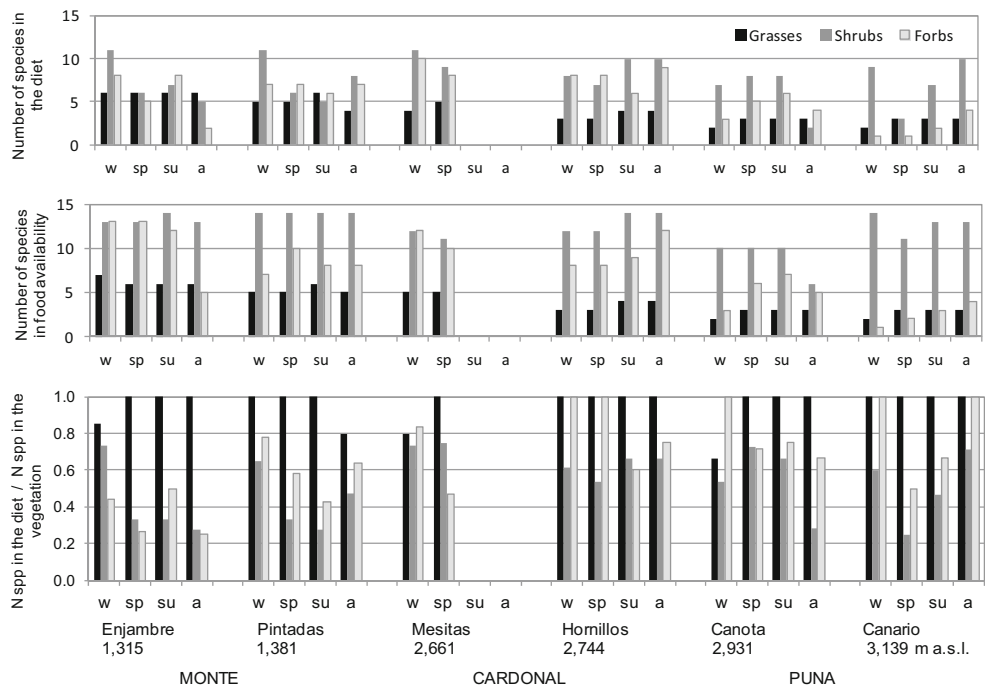


Fig. 3 Number of species corresponding to grasses, shrubs, and forbs in the diet and in available food. Proportions of the species in the diet (grasses, shrubs, and forbs), with respect to the total number of species present in the vegetation



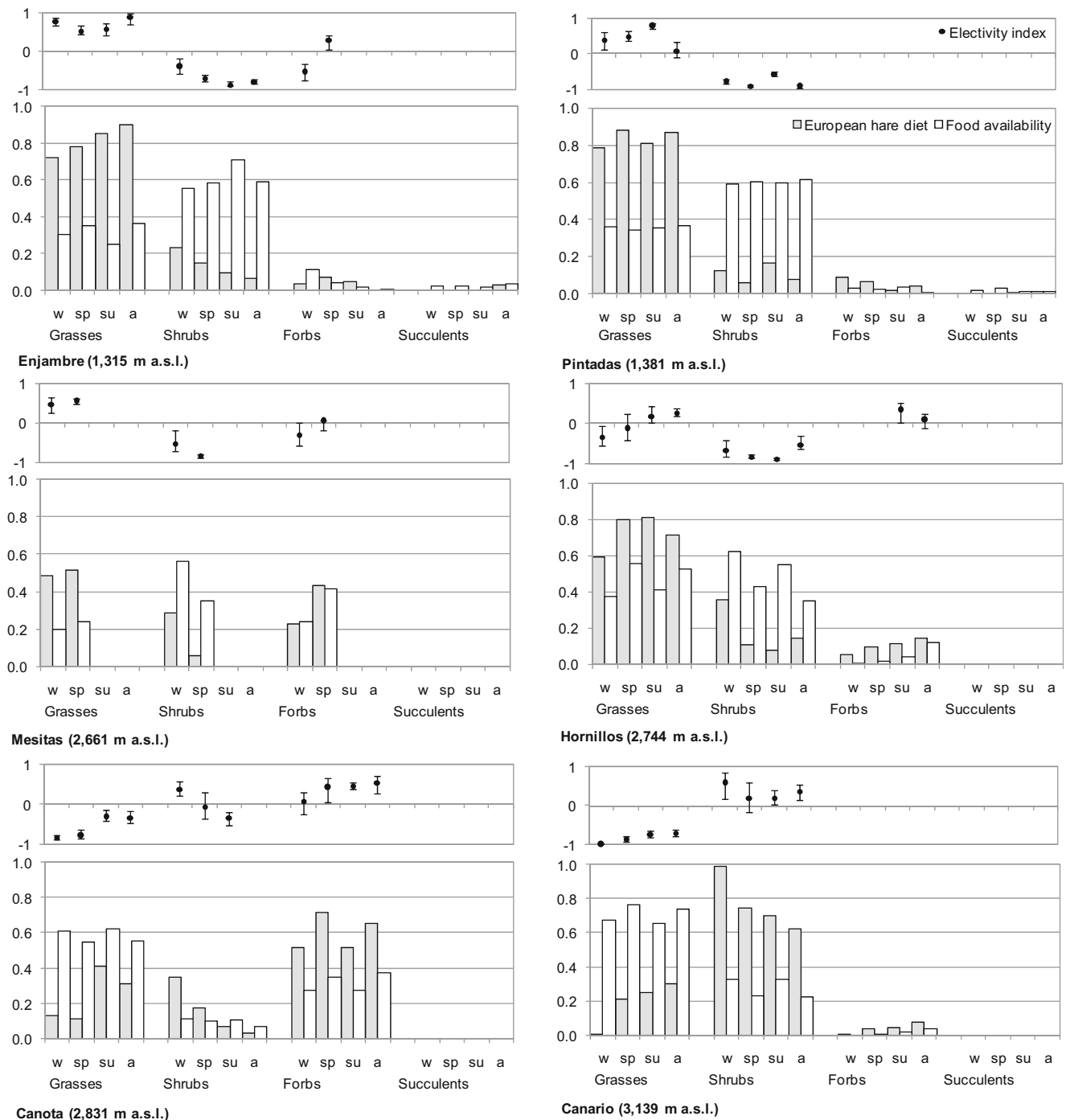


Fig. 4 Proportions of plant categories in the diet of the European hare and in available food during winter (*w*), spring (*sp*), summer (*su*), and autumn (*a*) at lower altitudes (the Monte sites Enjambre and Pintadas), middle altitudes (the Cardonal sites Homillos and Mesitas), and higher altitudes (the Puna sites Canario and Canota). Chesson's electivity index

($\pm 95\%$ confidence interval as *vertical lines*) indicates use with indifference (proportional use) if the confidence interval crosses the *horizontal line* at zero, otherwise a positive value of the index indicates use with preference (positive selection) and a negative value indicates use with avoidance (negative selection)

and Flux 1990). According to categories of herbivores defined by Hofmann and Stewart (1972), the European hare behaves during favorable seasons as a mixed herbivore at the summit and as a grazer at middle and lower altitudes, whereas during

unfavorable seasons it behaves as a browser at the summit and as a mixed herbivore at middle and lower altitudes.

On the other hand, the European hare presented a selective diet (i.e., a diet with significant differences from food

availability in terms of the relative frequencies of items) all year round, with low to moderate similarity with respect to the food available in the different altitudinal belts of the Southern Andean Precordillera. A selective use was also found in other populations of *L. europaeus* that differs in their food selection, with a preference for monocots in summer and dicots in winter in Chacoan forests (Kufner et al. 2008), a preference for shrubs all year round in open shrublands of Monte (Reus et al. 2013), a preference for shrubs and avoidance of the predominant grasses in steppes of Northern Patagonia (Puig et al. 2007), and a summer preference for shrubs and avoidance of grass-likes in the steppes with wetlands of the High Andes (Puig et al. 2015). Differences found in dietary preferences, not only among hare populations but also among altitudinal belts within the Andean Precordillera, can be answer to differences in several environmental variables. Besides food availability, the phenological status, nutritional content, and presence of secondary compounds in the potential food items also influence the selective feeding strategy of hares in different habitats, together with the severity of weather conditions, protection from predators, and interspecific competition (Flux 1967; Hik 1995; Hulbert et al. 2001; Rödel et al. 2004; Green et al. 2013; Rehnus et al. 2013).

Altitudinal changes

Changes in the vegetation with altitude across the studied gradient of the Southern Andean Precordillera agree with the prediction for altitudinal gradients and concur with observations made in other mountain environments (e.g., Gentry 1988; Grytnes and Vetaas 2002; Erschbamer et al. 2006). The European hare finds vegetation with less cover and diversity as temperature decreases from the bottom to the summit of the gradient, particularly a lower richness of grasses, shrubs, and forbs. According to the prediction for altitudinal gradients, the generalism of the European hare increased as plant species richness decreased with altitude, particularly considering the proportion of forb and grass species used. This tendency was also detected in herbivores of the Alps (Pellissier et al. 2012), as well as in the guanaco of the Southern Andean Precordillera (Puig et al. 2014a).

Influenced by altitudinal changes in the vegetation, European hares changed their selective use of food at different altitudes, from a preference for shrubs and forbs on the summit to a preference for grasses at middle and lower altitudes. Climate conditions at different altitudes affect phenological cycles, with a short period of sprouting and fast senescence of grasses at the summit, due to the rigorous tundra climate with strong winds, snow pressure, and freezing and solifluction processes (Roig and Martínez Carretero 1998). The specific composition of vegetation categories changes with altitude, with different nutritional content, and concentration of toxins in the dominant plant species. Indeed, the low

nutritional quality and high fiber content of *Pappostipa* spp. (Passera and Borsetto 1983), the dominant species in the extensive grasslands on the summit, justify the avoidance of grasses at higher altitudes. The fossorial rodent *C. mendocinus* also avoided *Pappostipa* spp. throughout the year on the summit of the Southern Andean Precordillera (Rosi et al. 2003). The dominance of *Pappostipa* spp. was particularly important in the vegetation of Canario, a landscape where the hare's diet had very low similarity to the available food, and the main dietary item was *Ephedra breana*, a shrub with considerable protein content and few secondary compounds (Borgnia et al. 2010). Contrasting with higher altitudes, shrubs dominated the vegetation of lower altitudes but were used with avoidance by *L. europaeus*. Despite that dicots are usually present, a better nutritional content than monocots (Borgnia et al. 2010; Wainstein and González 1971), the high concentration of secondary metabolites in the foliage of the dominant shrubs of Monte reduces their palatability and digestibility (Dearing et al. 2005). In fact, the main shrub species in the Monte, *Larrea* spp., was avoided not only by European hares but also by guanacos (Puig et al. 2014a) and other herbivores despite being evergreen spineless, due to the high resin content in the leaf cuticle (14 % of polyphenols, Rossi et al. 2008). The similarity between diet and food availability was particularly low, and the more specialized diet of *L. europaeus* was focused on grasses at lower altitudes in the Southern Andean Precordillera. Differing from higher altitudes, the milder climate at the bottom of the gradient favored the presence of grass species with high nutritional quality such as *Diplachne dubia* and *Eragrostis* spp. (Passera and Borsetto 1983), which were included in the diet of hares.

Protection from predators can also have influence over the feeding decisions of European hares, taking into account that Lagomorphs, with an intermediate size and great abundance, are considered the basis of many predator-prey systems (Chapman and Flux 1990). Although it is an introduced species in South America, the European hare has become an important prey for native aerial and terrestrial predators (Montserrat et al. 2005; Bonino et al. 2010). Like in the High Andes (Puig et al. 2015), both types of predators are present in the study area, with a lower richness at the summit than at middle and lower altitudes (Puig et al. 2008). Considering the absence of trees, the low plant cover and the seasonal snow cover, the sparse patches of shrubs in the open environments of higher altitudes become an important protective cover to minimize predation risk, may be influencing the feeding activity of hares as was observed in other populations (Flux and Angermann 1990; Hik 1995; Rehnus et al. 2013). Indeed, shrubs predominated in the diet of *L. europaeus* in the High Andes, where dry slopes constitute main feeding areas for hares, with shrub patches that provide useful food and cover against predation (Puig et al. 2015). Lower altitudes constitute more risky environments for hares, considering that

the dense vegetation conceals the approach of terrestrial predators, tall shrubs serve as a perch for prey detection by aerial predators, and the hare's strategy to avoid predation is based on distance of visibility and evasive fleeing (Bonino 2007; Flux and Angermann 1990).

Seasonal changes

Environmental conditions can be responsible for differences among populations of European hares in their seasonal dietary changes. Several populations of *L. europaeus* in arid environments of South America showed an increase in diet diversity during the season with better food availability (Puig et al. 2007; Kufner et al. 2008; Reus et al. 2013). On the other hand, the richness of species eaten by *L. europaeus* increased during winter in alpine habitats of Australia (Green et al. 2013) and so did the number of eaten woody species as climate severity increased with altitude in mountain environments of Germany (Rödel et al. 2004).

With regard to the study area, the stronger winter decline in plant cover with increasing altitude represents a stronger seasonal decrease in available food for the European hare. Food scarcity and severe climate conditions, which include large patches of snow cover, characterize winter on the summit and account for the lower dietary diversity and richness found during this season. These changes agree with the selective quality hypothesis (Weckerly and Kennedy 1992), in terms of a diet more focused on a few preferred food items during the unfavorable season, particularly severe at higher altitudes. Indeed, the similarity between diet and food availability decreased at higher altitudes during winter, when the diet was more focused on the preferred shrub *E. breana*. Stems of this species remain green during winter, unlike the dry woody stems of other shrubs and the senescent grasses burned by snow. The dietary relevance of shrubs during winter agrees with the expected higher increase in these food items at the summit than at the bottom of the altitudinal gradient. Additionally, shrubs represent useful shelter places against the severe climate conditions at higher altitudes and hares were several times observed underneath shrubs.

With a less important winter decline in plant cover at middle and lower altitudes, the seasonal change in generalism agrees with the food abundance hypothesis (Stephens and Krebs 1986). More shrub and forb species were included in the winter diet of European hares at the bottom of the gradient, especially the avoided shrubs *L. divaricata* and *A. mendozana*. Most shrubs of lower altitudes, being perennial and evergreen, still constitute available food during winter. Caecotrophy allows the hares to increase their efficiency to digest low-quality food items such as leaves and twigs of woody plants (Hirakawa 2001; Kuijper et al. 2004). Despite the prevalence of shrubs in the vegetation of lower altitudes, the high resin content explains the use with avoidance of *L. divaricata*, the

dominant shrub of Monte that was included in the diet only during the winter food decline. Reduced palatability and digestive efficiency due to the concentration of terpenoids (Meyer and Karasov 1991) are responsible for the avoidance of *Artemisia mendozana*, another shrub species included in the hare's diet only in winter. Dietary shifts, from grasses and forbs to woody plants, have been observed in situations of food scarcity in other hare populations (Flux and Angermann 1990). A higher predominance of shrubs in diets of *L. europaeus* also occurred during the winter grass senescence in other environments such as dry Chacoan forests (Kufner et al. 2008) and steppes of Northern Patagonia (Puig et al. 2007, 2014b).

The altitudinal differences found in the feeding strategy of European hares in the Southern Andean Precordillera highlight the relevant influence of climate severity. Seasonal dietary changes at lower altitudes agree with the food abundance hypothesis (Stephens and Krebs 1986), whereas at higher altitudes they agree with the selective quality hypothesis (Weckerly and Kennedy 1992). It has been proven that, when resource scarcity is extreme, a lack of palatable plant material restricts the dietary breadth of plain vizcachas (*Lagostomus maximus*, Branch et al. 1994), whereas the diet of white-tailed deer (*Odocoileus virginianus*) shifts to favor evergreen shrubs and drought-resistant plants, the only food available for consumption (Folks et al. 2014). The foraging strategy of deer, consistent with the food abundance hypothesis in mesic and stable environments, changed to a higher selectivity during drought conditions, and the dietary spectrum shrank to the few items of acceptable quality, in response to the decrease of crude protein in most plant species (Lashley and Harper 2012).

In conclusion, *L. europaeus* proved to be a generalist and selective herbivore, and an intermediate feeder in the altitudinal gradient of the Southern Andean Precordillera. Following the prediction for altitudinal gradients, generalism increases in the European hare's diet as plant cover and diversity decrease with altitude in this mountain environment. Altitudinal differences in the selective use of food, from a shrub preference on the summit to a grass preference at the bottom of the gradient, are ascribed to differences in climate conditions, plant phenology and concentration of secondary compounds. Seasonal changes in the diet diversity of European hares agree with different hypotheses depending on altitude and are consistent with the expected effects of extreme resource scarcity on the summit. Following the selective quality hypothesis, diet diversity decreases at the summit during the unfavorable season, affected by the severity of climate conditions, food scarcity, and an expected high risk of predation. A preferred shrub species becomes more prevalent in the diet of European hares during winter, when it remains accessible and green. With a less important seasonal decline in plant cover due to the milder climate of lower altitudes, diet diversity at the gradient bottom

increases during the unfavorable season, consistently with the food abundance hypothesis. Avoided shrubs are included in the diet only during winter, due to the high concentration of toxins in shrub species prevalent at lower altitudes and to the winter senescence of grasses. Climate severity, food shortage, plant phenology, and secondary compounds arise as relevant variables for explaining altitudinal and seasonal changes in the diet of European hares in mountain environments of the Southern Andean Precordillera.

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References

- 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
- Angermann R, Flux JEC, Chapman JA, Smith AT (1990) Lagomorph classification. In: Chapman JA, Flux JEC (eds) Rabbits, Hares and Pikas. Status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Cambridge, pp 7–13
- 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 Univ Press, NJ
- Bonino N (2007) Estrategia adaptativa de dos especies de lagomorfos introducidos en la Patagonia argentina, con especial referencia a sus hábitos alimentarios. Doctoral Thesis, Univ. Sevilla, Sevilla, España
- Bonino N, Cossios D, Menegheti J (2010) Dispersal of the European hare *Lepus europaeus* in South America. *Folia Zool* 59:9–15
- Borgnia M, Vilá BL, Cassini MH (2010) Foraging ecology of vicuña, *Vicugna vicugna*, in dry Puna of Argentina. *Small Rumin Res* 88: 44–53
- Branch LC, Villarreal D, Sbriller AP, Sosa RA (1994) Diet selection of the plains vizcacha (*Lagostomus maximus*, family Chinchillidae) in relation to resource abundance in semi-arid scrub. *Can J Zool* 72: 2210–2216
- Capitanelli R (1971) Climatología de Mendoza. Univ Nac Cuyo, Mendoza
- Chapman JA, Flux JEC (1990) Introduction and overview of the Lagomorphs. In: Chapman JA, Flux JEC (eds) Rabbits, Hares and Pikas. Status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Cambridge, pp 1–6
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304
- Daget P, Poissonet J (1971) Une méthode d'analyse physiologique des prairies. *Critères d'application. Ann Agron* 22:5–41
- Dalmasso 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
- Dearing MD, Foley WJ, McLean S (2005) The influence of plant secondary metabolites on the nutritional ecology of herbivorous terrestrial vertebrates. *Annu Rev Ecol Evol Syst* 36:169–189
- Dibiasi A, Bowman AW (2001) On the use of the variogram for checking independence in a Gaussian spatial process. *Biometrics* 57:211–218
- 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
- Flux JEC (1967) Hare numbers and diet in an alpine basin in New Zealand. *Proc N Z Ecol Soc* 14:27–33
- Flux JEC, Angermann R (1990) The hares and jackrabbits. In: Chapman JA, Flux JEC (eds) Rabbits, Hares and Pikas. Status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Cambridge, pp 61–95
- Flux JEC, Duthie AG, Robinson TJ, Chapman JA (1990) Exotic populations. In: Chapman JA, Flux JEC (eds) Rabbits, Hares and Pikas. Status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Cambridge, pp 147–153
- Folks DJ, Gann K, Filbright TE, Hewitt DG, DeYoung CA, Wester DB, Echols KN, Draeger DA (2014) Drought but not population density influences dietary niche breadth in white-tailed deer in a semi-arid environment. *Ecosphere* 5:162, doi: 10.1890/ES14-00196.1
- Gentry AH (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann Mo Bot Gard* 75:1–34
- Green K, Davis NE, Robinson WA, McAuliffe J, Good RB (2013) Diet selection by European hares (*Lepus europaeus*) in the alpine zone of the Snowy Mountains, Australia. *Eur J Wildl Res* 59:693–703
- 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, “Rablón”, provincias de Mendoza y San Juan. *Dir Nac Geología y Minería, Buenos Aires. Boletín* 114:1–87
- Hik DS (1995) Does risk of predation influence population dynamics? Evidence from cyclic decline of snowshoe hares. *Wildl Res* 22:115–129
- Hirakawa H (2001) Coprophagy in leporids and other mammalian herbivores. *Mammal Rev* 31:61–80
- Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. *Mammalia* 36:226–240
- Holeček JL (1982) Sample preparation techniques for microhistological analysis. *J Range Manage* 35:267–268
- Holeček JL, Gross BD (1982) Evaluation of different calculation procedures for microhistological analysis. *J Range Manage* 35:721–723
- Holeček JL, Vavra M, Pieper RD (1982) Botanical composition determination of range herbivore diets: a review. *J Range Manage* 35: 309–315
- Hulbert IAR, Iason GR, Mayes RW (2001) The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. *Oecologia* 129:197–205
- Hurlbert S (1978) The measurement of niche overlap and some relatives. *Ecology* 59:67–77
- Körner C (2000) Why are there global gradients in species richness? Mountains might hold the answer. *Trends Ecol Evol* 15:513–514
- Krebs CJ (1999) Ecological methodology. Addison-Wesley Educational Publishers, NY
- Kufner MB, Sepúlveda L, Gavier G, Madoery L, Giraud L (2008) Is the native deer *Mazama gouazoubira* threatened by competition for food with the exotic hare *Lepus europaeus* in the degraded Chaco in Córdoba, Argentina? *J Arid Environ* 72:2159–2167
- Kuijper DPJ, van Wieren SE, Bakker JP (2004) Digestive strategies in two sympatrically occurring lagomorphs. *J Zool (Lond)* 264:171–178
- 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

- Lashley MA, Harper CA (2012) The effects of extreme drought on native forage nutritional quality and white-tailed deer diet selection. *Southeast Nat* 11:699–710
- Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson W (2002) Resource selection by animals. Statistical design and analysis for field studies. Kluwer, Boston
- Meyer ME, Karasov WH (1991) Chemical aspects of herbivory in desert and semi-desert habitats. In: Palo RT, Robbins CT (eds) Plant chemical defenses against mammalian herbivory. CRC Press, London, pp 167–187
- Montserrat A, Funes M, Novaro A (2005) Respuesta dietaria de tres rapaces frente a una presa introducida en Patagonia. *Rev Chil Hist Nat* 78:425–439
- Neu CW, Byers CR, Peek JM (1974) A technique for analysis of utilisation-availability data. *J Wildl Manag* 38:541–545
- Passera CB, Borsetto O (1983) Determinación del “Índice de calidad específico”. *Actas Taller de Arbustos Forrajeros para Zonas Áridas y Semiáridas*, Mendoza, pp 80–89
- Pellissier L, Fiedler K, Ndiribe 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
- Polanski J (1954) Rasgos geomorfológicos del territorio de la provincia de Mendoza. Ministerio de Economía, Instituto de Investigaciones Económicas y Tecnológicas. *Cuad Invest Estud* 4:4–10
- Puig S, Videla F, Cona MI, Monge SA (2007) Diet of the brown hare (*Lepus europaeus*) and food availability in northern Patagonia (Mendoza, Argentina). *Mamm Biol* 72:240–250
- Puig S, Videla F, Martínez Carretero E, Dalmaso 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, Mendoza
- Puig S, Rosi MI, Videla F, Mendez E (2014a) Food selection by the guanaco (*Lama guanicoe*) along an altitudinal gradient in the Southern Andean Precordillera (Argentina). *Acta Theriol* 59:541–551
- Puig S, Cona MI, Videla F, Mendez E (2014b) Dietary overlap of coexisting exotic brown hare (*Lepus europaeus*) and endemic Mara (*Dolichotis patagonum*) in Northern Patagonia (Mendoza, Argentina). *Mammalia* 78:315–326
- Puig S, Rosi MI, Videla F, Mendez E (2015) Diet of brown hare (*Lepus europaeus*) and food availability in High Andean mountains (Mendoza, Argentina). *Mammalia* DOI 10.1515/mammalia-2014-0142
- Rehnus M, Marconi L, Hackländer K, Filli F (2013) Seasonal changes in habitat use and feeding strategy of the mountain hare (*Lepus timidus*) in the Central Alps. *Hystrix* 24:161–165
- Reus ML, Peco B, de los Ríos C, Giannoni SM, Campos CM (2013) Trophic interactions between two medium-sized mammals: the case of the native *Dolichotis patagonum* and the exotic *Lepus europaeus* in a hyper-arid ecosystem. *Acta Theriol* 58:205–214
- Rödel HG, Völkl W, Kilius H (2004) Winter browsing of brown hares: evidence for diet breadth expansion. *Mamm Biol* 69:410–419
- Roig FA (1994) La Provincia del Cardonal. In: Botánica y Fitosociología, IADIZA (ed) La vegetación de los Andes centrales de Argentina: Excursión botánica, Mendoza, pp 19–24
- Roig FA, Martínez Carretero E (1998) La vegetación puneña en la provincia de Mendoza, Argentina. *Phytocoenologia* 28:565–608
- Rosi MI, Cona MI, Videla F, Puig S, Monge MA, Roig VG (2003) Diet selection by the fossorial rodent *Ctenomys mendocinus* inhabiting an environment with low food availability (Mendoza, Argentina). *Stud Neotropical Fauna Environ* 38:159–166
- Rossi CA, De León M, González GL, Chagra Dib P, Pereyra AM (2008) Composición química, contenido de polifenoles totales y valor nutritivo en especies de ramoneo del sistema silvopastoril del Chaco árido argentino. *Zootec Trop* 26:105–115
- Schleuter D, Eckmann R (2007) Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. *Ecol Freshw Fish* 17:86–99
- Schai-Braun SC, Reichlin TS, Ruf T, Klansek E, Tataruch F, Arnold W, Hackländer K (2015) The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. *PLoS ONE* 10: e0134278. doi:10.1371/journal.pone.0134278
- 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
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton Univ. Press, New Jersey
- Videla MA, Suárez J (1991) Mendoza Andina: Precordillera y Alta Cordillera, Mendoza, Argentina. Adalid, Mendoza
- Wainstein P, González S (1971) Valor nutritivo de plantas forrajeras del este de la Provincia de Mendoza (Reserva Ecológica de Ñacuñán), II. *Deserta* 2:77–85
- Weckerly FW, Kennedy ML (1992) Examining hypotheses about feeding strategies of white-tailed deer. *Can J Zool* 70:432–439
- Zar JH (1984) Biostatistical Analysis, 2nd edn. Prentice-Hall Inc., New Jersey