Silvia Puig*, María I. Rosi, Fernando Videla and Eduardo Méndez

Diet of brown hare (*Lepus europaeus*) and food availability in High Andean mountains (Mendoza, Argentina)

Abstract: Diet selection by *Lepus europaeus* was studied in high-altitude mountain environments with severe weather, presence of wetlands, and no agricultural activities. Diet was assessed using fecal microhistological analysis, and food availability by point-quadrat transects in four habitats, two of them with wetlands. Significant differences were determined with Kruskal-Wallis ANOVA, similarities by Renkonen index, and feeding selection by χ^2-test and Bailey's confidence interval. The diet included 63% of all species present. Shrubs dominated the diet. Food use was opportunistic in habitats without wetlands, where grasses and shrubs were more available. Plant cover and availability of grass-like plants were higher in wetland habitats, where shrubs and forbs were preferred and grass-like plants were avoided. Similarity between diet and food availability was higher on dry soils, dominated by grasses and shrubs, than in wetland microhabitats with higher plant cover, diversity, and percentage of grass-like plants. Dietary generalism was confirmed, especially when excluding wetland vegetation. Hard Juncaceae cushions accounted for the pronounced selectivity in habitats with wetlands. Dry soils, where shrub patches provided good food and shelter, appear as major feeding microhabitats for *L. europaeus*. Spatial heterogeneity protection, at landscape and microhabitat scales, is relevant to the brown hare conservation in High Andean environments.

Keywords: arid environments; dietary selection; high altitudes; Leporidae.

Introduction

Lepus europaeus (Pallas 1837) is a native lagomorph from open woodlands, steppes, and subdeserts of the Palearctic that has been successfully introduced into Australasia, North America, and South America (Angermann et al. 1990). Such widespread expansion in range is believed to be related to the species' high rate of population turnover and its considerable adaptation to ecologically diverse environments (Chapman and Flux 1990). Expansion occurred from their native range into Siberia and the western Russian coast, naturally and through translocations, whereas the brown hare expanded naturally after being introduced into South America, and today occupies nearly the whole of Argentina, Chile, and Uruguay, as well as the southern regions of Peru, Bolivia, Paraguay, and Brazil (Bonino et al. 2010).

Brown hare occupies a wide variety of plant communities and habitats resulting in variable diets across its wide distribution range, particularly in environments where other species of *Lepus* are absent (Flux and Angermann 1990). A generalist diet characterizes diverse populations of brown hares, such as in the Australian Alps montane grasslands ecoregion, where dietary generalism increases when the snow cover restricts access to food (Green et al. 2013), or as in the Argentine High Monte and in the Northern Patagonia ecoregions, where the diet includes all plant categories (Puig et al. 2007, Reus et al. 2012).

Even though traditional agriculture in Europe benefited hares due to their preference for open habitats, a population decline occurred when chemical-intensive farming and extensive monoculture fields prevailed (Flux and Angermann 1990). The loss of landscape heterogeneity resulting from agricultural intensification meant less diversity of both food and shelter for the brown hare, as well as its increased vulnerability to predation and unfavorable weather (Smith et al. 2005).

*Corresponding author: Silvia Puig, Grupo Ecología y Manejo de Vertebrados Silvestres (GEMAVER), Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA, CONICET), CC. 507, 5500 Mendoza, Argentina, e-mail: spuig@mendoza-conicet.gov.ar
María I. Rosi and Fernando Videla: Grupo Ecología y Manejo de Vertebrados Silvestres (GEMAVER), Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA, CONICET), CC. 507, 5500 Mendoza, Argentina
Eduardo Méndez: Grupo Botánica y Fitosociología, Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA, CONICET), CC. 507, 5500 Mendoza, Argentina

Environments with steep topography, particularly those affected by heavy snowfall, tend to cause strong spatial differences in their food availability for herbivores (Zweifel-Schielly et al. 2009). The distribution range of *Lepus europaeus* includes environments of high altitude, such as the mountains of Australia and New Zealand (up to 2000–2200 m a.s.l.), and the High Andes of Chile and Argentina (up to 3500–4000 m a.s.l.) (Green et al. 2013). Andean environments are characterized by harsh climatic conditions and spatiotemporal heterogeneity in topography and vegetation (Cabrera and Willink 1980, Cavieres et al. 2000). These high-altitude environments offer valuable opportunities for evaluating the feeding strategies of brown hares under harsh climatic conditions and in the absence of environmental changes caused by agricultural, livestock, and forestry activities (López-Cortés et al. 2007). Several sites in the High Andes of Argentina and Chile are, however, affected by mining activities (Contreras et al. 2002, Brown et al. 2006).

High densities of brown hares were found in Patagonian "mallines" (wetlands covered with hydrophytic grasses and Juncaceae), where grasses prevailed in the diet of *Lepus europaeus* (Bonino 2007). "Vegas" are mountain wetlands of High Andean environments, where the dietary study of brown hares can help detect whether the feeding attractiveness of wetlands that was observed in Patagonian environments with mallines also holds for High Andean environments with vegas. High Andean wetlands have been differentiated into two types: wetlands with hydrophytic grasses and those with cushions of Juncaceae (Squeo et al. 2006a,b). In High Andean environments of northern Chile, where the wetlands are of the first type, the main dietary items for brown hares were hydrophytic grasses (López-Cortés et al. 2007).

The overall goal of this study is to analyze diet composition and food availability for a High Andean population of brown hares during summer. Specific objectives are to detect (a) whether the diet is broader and less selective at the sites where food availability is poorer (i.e., with less plant cover and food diversity), as is expected from the optimal foraging theory, and (b) whether plant species of dry soils are excluded from the diet in habitats with vegas, due to the expected feeding attractiveness of wetlands.

Materials and methods

Study area and habitat characteristics

The study area, belonging to the "Laguna del Diamante" protected area (34°10′S 69°41′W, 1700 km², Mendoza, Argentina), is representative of the High Andean biogeographic province (Cabrera and Willink 1980) and of the Southern Andean Steppe ecoregion (Dinerstein et al. 1995). With altitudes over 3300 m, this area corresponds to the Main Andes Cordillera (Mesozoic period). The Maipo volcanic complex (5323 m a.s.l.), the Diamante lagoon (18 km²), and the extensive Vegas del Yaucha mountain wetland (14 km²) stand out in the area. The environment is characterized by glacial deposits such as tills, moraines, thermokarst, rock glaciers, glacial valleys, avalanches, and landslides (Abraham 2000, Sruoga et al. 2005). Agricultural and mining activities are currently absent in the protected area (Mónaco et al. 2005).

A tundra climate dominates this high mountain environment, with an ice cap climate at the heights of the Maipo volcano (Norte 2000). The study area is only accessible during summer, because of the deep snow cover that persists for at least 8 months. Snowfall and frosts occur all the year round, mainly from April to September, and annual precipitation averages 600 mm (Mónaco et al. 2005). The numerous vegas in the study area are mountain wetlands of the first type described by Squeo et al. (2006a,b), dominated by hard cushions of grass-like plants (Juncaceae and Cyperaceae). These "islands" of green vegetation sharply contrast with the surrounding dry soils with arid vegetation characterized by nanophanerophytes (woody plants) and grasses (Roig et al. 2000). Four sampling sites were selected, representative of the main habitats used by brown hares during summer, with vegas being present in two habitats (Laguna and Yaucha) and absent from the other two (Durazno and Avestruces) (Table 1).

Field and laboratory design

Samplings were conducted during mid-summer (February 2007). Plant cover and relative percentages of plant species were estimated by the point-quadrat method (Daget and Poissonet 1971), applied on 10–20 transects per sampling site, depending on the habitat heterogeneity associated with the presence of wetlands. Vegetation sampling was stratified according to the contrasting microhabitats recognized at both sites with wetlands. All 30-m transects (100 points per transect) were distributed within each sampling site in a stratified random design, separated from one another by >100 m. Ten fecal samples were collected from each sampling site. Each fecal sample, composed of 10 fresh pellets, was collected from a different group of feces.

Fecal samples were analyzed with the microhistological method of Baumgartner and Martin (1939), modified by Duci (1949) and Holechek (1982). After

Table 1: Identification of the sampling sites, and characteristics of the corresponding habitats.

Sampling sites (altitude in m a.s.l.)	Topography and extension of the habitats (in km²)	Geomorphology and geology[a]	Vegetation
Durazno (3332)	Rolling piedmont near El Durazno stream (7.7)	Glacial deposits (Cenozoic)	Dry soils: codominance of nanophanerophytes and grasses
Laguna (3370)	Slopes of Laguna hill with several vegas (7.3)	Alluvial, colluvial, and mass-wasting deposits (Cenozoic)	Dry soils: dominance of nanophanerophytes, followed by grasses; edge of vegas: codominance of the four plant categories; vegas: dominance of grass-like plants, followed by grasses
Yaucha (3294)	Ravine with broad vegas from Yaucha stream (9.7)	Huincan Formation (Cenozoic)	Dry soils: dominance of nanophanerophytes; vegas: dominance of grass-like plants, followed by chamaephytes and grasses
Avestruces (3598)	High arid plain of Pampa Avestruces (8.3)	Andesites and dacites (Cenozoic)	Dry soils: dominance of grasses, followed by forbs and nanophanerophytes

Vegetation is described per microhabitat (dry soils, edge of vegas, and vegas) for the sites with vegas (moist zones associated to streams and ponds, with dense hydrophytic vegetation). [a]Extracted from Sruoga et al. 2005.

being oven-dried at 60°C, each fecal sample was milled, cleared with diluted lye (aqueous sodium hypochlorite, 25%, w/v), and passed through a 210-μm sieve. Two microscope slides were created from the material trapped in a second sieve (149 μm), placed under the first, in order to homogenize particle size (Smith and Shandruk 1979). Fifty fields on each slide were systematically examined under a microscope at 400×magnification, and all identifiable fragments (those showing at least three diagnostic features) were counted. A microscopic field at high resolution contained only one or two fragments, whose epidermal features were easily identified. Plant cuticle was identified to genus level, and to species level when possible, using reference plant material from the "Laguna del Diamante" Reserve, collected and identified during the present study and stored in the Ruiz Leal Herbarium (IADIZA, Argentina). Several authors have pointed out some limitations in the fecal microhistological analysis applied to studies of herbivore diets, related to differential digestibility and fragmentation among plant taxa and parts (Smith and Shandruk 1979, Holechek et al. 1982). Non-ruminant herbivores, like the brown hare, are less efficient in fiber digestion, and a bias due to differential digestibility is less expected (Holechek et al. 1982). Microhistology is a state-of-art tool for identifying diet composition and detecting general feeding selectivity patterns (Holechek and Gross 1982). In addition, it is a non-invasive technique as animals are not injured or killed.

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 transect points. The relative frequency of a given plant species in the environment was determined by dividing its absolute frequency by the sum of absolute frequencies for all species identified on each point-quadrat transect. Food availability included only those plant species observed in at least one fecal sample. The relative frequency of a given species in the diet was determined for each sample by dividing the number of microscopic fields where that species was observed by the number of fields for all observed species (Holechek and Gross 1982). Relative frequencies of species were determined without including undetermined fragments, because these represented negligible percentages of the fecal samples analyzed (0.3–2%). Plant species were grouped into four categories according to life form: grass-like plants, grasses, shrubs, and forbs. Diversity of food availability and diet was estimated using the Shannon-Wiener function (H′, Colwell and Futuyma 1971), along with Margalef's richness index and Pielou's equitability index (Moreno 2001). Percent overlap (O, Hurlbert 1978) was used to estimate similarities between diet and food availability, between diets at the different sites, between food availabilities at the different sites, and in the different microhabitats.

Significant spatial differences in plant cover, diversity, and percentage of plant species and categories were found using Kruskal-Wallis ANOVA and multiple comparisons of mean ranks for all groups (Siegel and Castellan 1988). The level of significance obtained was mostly $p \leq 0.001$; if otherwise, it is mentioned in the text. Feeding selection was detected from significant differences between observed and expected dietary percentages by using the χ^2-test (Zar 1984). Bailey's confidence interval (Cherry 1996) was used to identify selective use of the main plant species

(species with frequencies ≥5% in the diet and/or in the food availability). Plant use was classified as preference, use in proportion to availability or avoidance, depending on whether each species' availability fell, respectively, below, within, or above the confidence interval of dietary frequency.

Results

Food availability

Of the 60 plant species recorded on the four sampling sites, 63% were feed upon by brown hares. The percentage of species contained in the diet was high in habitats without vegas (87%), and considerable in habitats with vegas (72%). In habitats with vegas, the diet included almost all plant species of the adjacent dry soils (88%) and edges of vegas (84%), but only a moderate percentage of plant species present within the wetland itself (53%).

In terms of relative percentages of plant categories in food availability in the sampling sites, shrubs were dominant (37%), followed by grasses (31%) and grass-like plants (20%). Major available species were the shrubs *Adesmia aegiceras* (23%, Table 2) and *Discaria nana* (7%), the grasses *Poa durifolia* (15%) and *Poa holciformis* (7%), and the grass-like species *Oxychloe bisexualis* (9%).

Habitats without vegas (Durazno and Avestruces) differed from those with vegas (Table 2) by having higher

Table 2: Significant differences among habitats (and microhabitats) in food availability and in the diet of brown hares.

	Food availability in habitats	Food availability in microhabitats	Diet of brown hares
Plant cover	H=17.77	H=42.45	
Species diversity	H=9.20, p=0.027	H=25.80	
Species richness	H=10.13, p=0.018	H=19.50	
Equitability	H=10.88, p=0.012	H=25.83	
Similarity comparing habitats or microhabitats	H=30.59 (plant categories), H=45.48 (plant species)	H=57.96 (plant categories), H=63.17 (plant species)	H=30.86 (plant categories), H=36.27 (plant species)
GRASS-LIKE PLANTS	H=19.35	H=47.70	H=15.03, p=0.002
Oxychloe bisexualis Kuntze (Barros)	H=18.04	H=50.51	
Carex gayana E. Desv.	H=20.55	H=47.36	H=19.62
Patosia clandestina (Phil.) Buchenau		H=47.03	
Carex sp.		H=41.68	
GRASSES	H=32.55	H=9.22, p=0.010	H=19.83
Poa holciformis J. Presl.	H=36.46		H=26.03
Poa durifolia Giussani, Nicora and Roig	H=49.57		H=35.05
Hordeum pubiflorum Hook. f. (Griseb.) Baden and Bothmer	H=11.57, p=0.009	H=17.68	H=26.89
Festuca magellanica Lam.		H=47.85	
SHRUBS	H=15.42	H=15.13	H=17.15
Adesmia aegiceras Phil.	H=10.78, p=0.013 (in Durazno)	H=44.34	H=22.34
Azorella monantha Clos	H=43.50	H=13.60	
Ochetophila nana (Clos) J. Kellerm., Medan and Aegesen	H=19.32	H=43.48	
Senecio looseri Cabrera			H=19.20
FORBS	H=15.58	H=37.87	
Adesmia stenocaulon Hauman	H=39.93		H=18.25
Oxalis erythrorhiza Gillies *ex* Hook. and Arn.	H=24.33	H=15.46	H=20.54
Species in the diet (%)	H=16.61 (in Durazno)	H=24.84	
Similarity between diet and food availability	H=15.04, p=0.002 (plant categories), H=22.89 (plant species)	H=33.03 (plant categories), H=48.77 (plant species)	

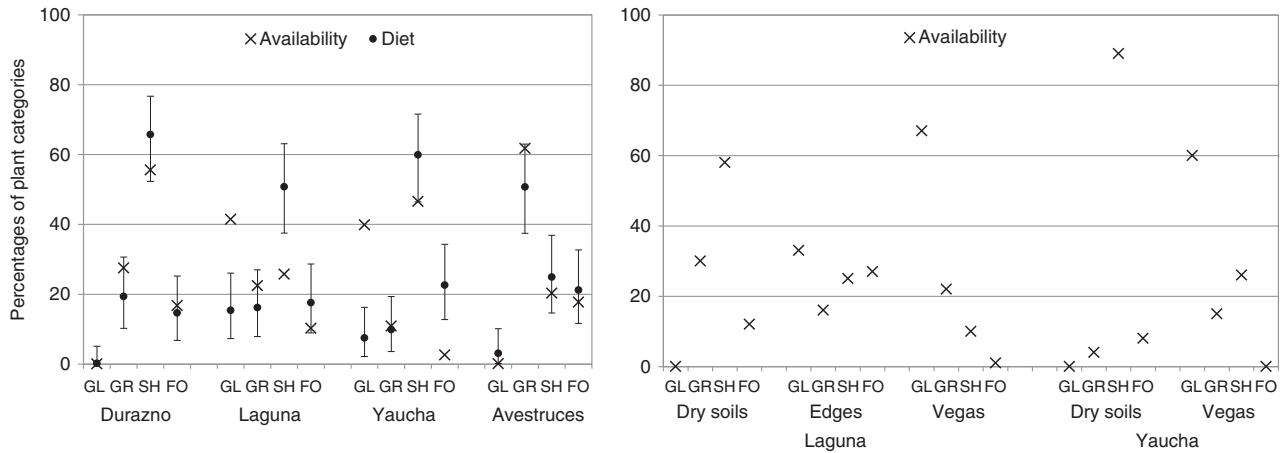H stands for the value of Kruskal-Wallis test.

Figure 1: Percentages of grass-like plants (GL), grasses (GR), shrubs (SH), and forbs (FO) in the diet of brown hares, and in food availability of habitats and microhabitats, whose description is in Table 1.

percentages of grasses (Figure 1, particularly *Poa holciformis* and *Poa durifolia*, Table 3) and forbs (particularly *Adesmia stenocaulon* and *Oxalis erythrorhiza*). The Durazno habitat showed a higher percentage of plant species included in the diet (Table 2), higher species richness in food availability (Figure 2), and a higher percentage of shrubs (Figure 1, particularly *Adesmia aegiceras* and *Azorella monantha*, Table 3).

On the other hand, habitats with vegas (Laguna and Yaucha) differed from those without vegas (Table 2) by having a higher plant cover (Figure 2), higher percentages of grass-like plants (Figure 1, especially *Carex gayana*, Table 3), and of the shrub *Discaria nana*. The Laguna habitat showed a higher percentage of the grass *Hordeum halophilum*, and Yaucha contained a higher percentage of the grass-like species *Oxychloe bisexualis*. Food diversity and equitability were higher at Laguna than at Avestruces (Figure 2).

Within the habitats with vegas, the adjacent dry soils differed from other microhabitats (Table 2) by having higher percentages of grasses and shrubs (Figure 1, particularly the shrubs *Adesmia aegiceras* and *Azorella monantha*, Table 3), lower plant cover and food diversity (Figure 2), and lower percentages of grass-like plants (Figure 1, particularly *Carex gayana*, Table 3) and of the shrub *Discaria nana*. The wetland itself differed from other microhabitats by having higher percentages of the grass-like species *Oxychloe bisexualis*, *Patosia clandestina*, and *Carex* sp., and of the grass *Festuca magellanica*, a lower percentage of forbs (particularly *Oxalis erythrorhiza*), lower species richness, higher equitability, and a lower percentage of plant species included in the diet (Table 2). Edges of vegas differed from other microhabitats

by having a higher percentage of the grass *Hordeum halophilum*.

There was higher similarity in food availability between sites with vegas than between these and dryland habitats, for both plant categories and plant species (Figure 3A, Table 2). As would be expected in microhabitats, similarity in food availability was higher between wetlands and between dry soils, than between wetlands and dry soils (Figure 3C).

Brown hare's diet

The diet included 38 plant species (4 grass-like plants, 8 grasses, 7 shrubs, and 19 forbs). Shrubs clearly dominated the diet (50% of relative percentage in the diet), followed by grasses (24%) and forbs (19%), with a minor percentage of grass-like plants (7%). The main dietary species were the shrubs *Adesmia aegiceras* (35% of relative percentage in the diet) and *Senecio looseri* (9%), and the grasses *Poa durifolia* (13%) and *Poa holciformis* (5%).

Hare diet in habitats without vegas (Durazno and Avestruces) differed from that in habitats with vegas (Table 2) by containing a higher percentage of grasses (Figure 1, particularly *Poa holciformis* at Durazno and *Poa durifolia* at Avestruces, Table 3), a lower percentage of shrubs (particularly *Adesmia aegiceras*), a higher percentage of the shrub *Senecio looseri*, and a lower percentage of the forb *Oxalis erythrorhiza* in Durazno.

Brown hare diet in habitats with vegas (Laguna and Yaucha) differed from that in habitats without vegas (Table 2) due to higher percentages of grass-like plants at Laguna (Figure 1, particularly *Carex gayana*, Table 3), and

Table 3: Percentage of plant species in food availability (Av) and in the diet of brown hares (Di).

	Durazno		Laguna		Yaucha		Avestruces	
	Av	Di	Av	Di	Av	Di	Av	Di
GRASS-LIKE PLANTS								
Carex gayana	0.08	0.23 (0.00–6.76)	13.17	10.60 (2.73–22.98)[U]	8.07	0.58 (0.00–7.55)[A]	0.06	2.37 (0.00–10.98)
Carex sp.	–		6.63	2.70 (0.00–11.56)[U]	2.52	2.04 (0.00–10.40)	0.07	0.76 (0.00–7.95)
Oxychloe bisexualis	–		13.58	0.16 (0.00–6.60)[A]	21.41	4.45 (0.23–14.37)[A]	–	
Patosia clandestina	–		8.00	1.93 (0.00–10.21)[U]	7.90	0.44 (0.00–7.24)[A]	–	
GRASSES								
Festuca magellanica	0.07	0.12 (0.00–6.49)	10.60	0.00 (0.00–6.20)[A]	6.82	0.84 (0.00–8.11)[U]	0.06	0.18 (0.00–6.65)
Hordeum halophyllum	1.86	1.02 (0.00–8.48)	7.44	11.25 (3.08–23.82)[U]	0.90	0.21 (0.00–6.71)	0.07	0.29 (0.00–6.91)
Poa durifolia	–		–		61.38	4.18 (0.17–13.95)	–	49.11 (32.18–64.37)[U]
Poa holciformis	25.21	15.51 (5.58–29.13)[U]	2.22	3.64 (0.07–13.10)	0.05	0.33 (0.00–6.98)		
SHRUBS								
Adesmia aegiceras	35.83	28.10 (14.45–43.39)[U]	14.28	40.28 (24.38–55.90)[P]	29.32	55.76 (38.37–70.45)[P]	11.54	17.15 (6.62–31.08)[U]
Azorella monantha	18.98	2.26 (0.00–10.79)[A]	0.03	3.14 (0.02–12.29)	0.04	0.41 (0.00–7.18)	0.04	0.64 (0.00–7.68)
Discaria nana	0.05	1.34 (0.00–9.09)	11.29	1.04 (0.00–8.51)[A]	17.02	2.10 (0.00–10.51)[A]	0.06	0.44 (0.00–7.24)
Senecio looseri	0.55	26.41 (13.16–41.56)[P]	0.02	2.97 (0.01–12.00)	0.07	1.16 (0.00–8.76)	0.07	3.80 (0.10–13.36)
FORBS								
Adesmia stenocaulon	7.35	1.22 (0.00–8.87)[U]	–		0.07	5.38 (0.48–15.78)	0.07	1.81 (0.00–9.99)
Cerastium arvense	0.06	1.96 (0.00–10.25)	0.02	1.70 (0.00–9.78)	0.05	1.04 (0.00–8.52)	2.91	5.25 (0.44–15.59)[U]
Gayophyton micranthum	3.00	0.55 (0.00–7.48)	4.74	0.00 (0.00–6.20)	0.05	0.11 (0.00–6.46)	3.84	0.00 (0.00–6.20)
Oxalis erythrorhiza	0.68	0.11 (0.00–6.47)	0.98	9.34 (2.09–21.32)[P]	0.29	6.49 (0.85–17.40)[P]	9.43	10.59 (2.72–22.96)[U]

Bailey's dietary intervals (between brackets) and type of use: preference (P), use in proportion to availability (U) and avoidance (A), for species with proportions >0.05; –, plant species absent from a sampling site.
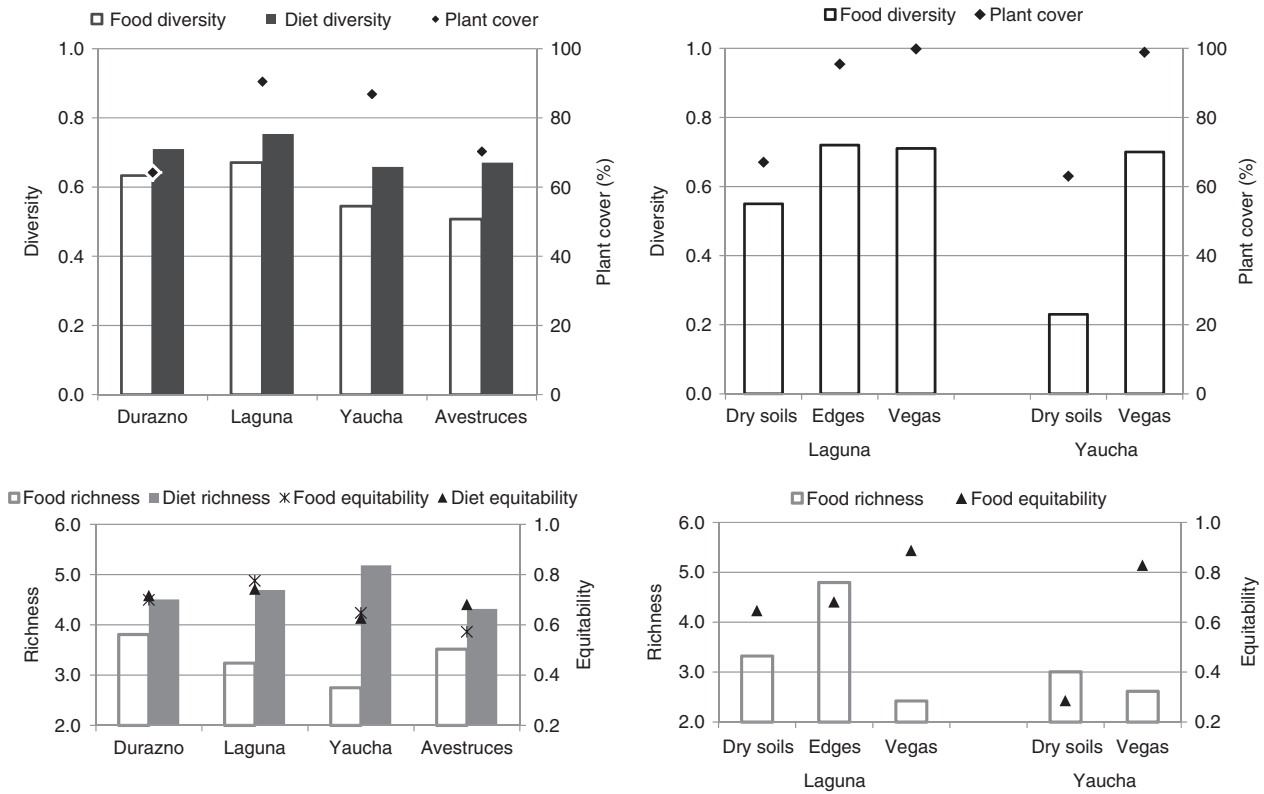
Figure 2: Dietary diversity of brown hares, food diversity, and percentage of plant cover in habitats and microhabitats, whose description is in Table 1; richness and equitability in the brown hare diet and in food availability.
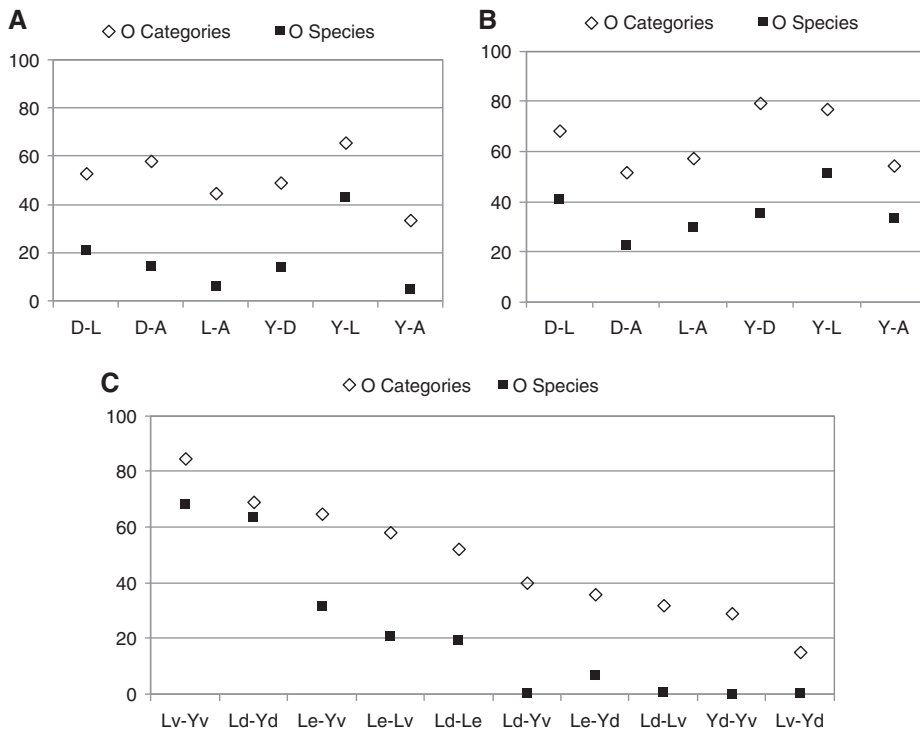

Figure 3: Similarity (O) between habitats (D: Durazno, L: Laguna, Y: Yaucha, A: Avestruces) in food availability (A) and in the brown hare diet (B). Similarity between microhabitats (d: dry soils, e: edges, v: vegas) in food availability (C).

higher percentages of the grass *Hordeum halophilum* and of the forb *Adesmia stenocaulon* at Yaucha.

Considering percentages of plant categories in the diet (Figure 3B), the similarity of Yaucha with Durazno and Laguna was higher than the similarity of Avestruces with the other sites (Table 2). Considering percentages of plant species in the diet (Figure 3C), the similarity between sites with vegas was higher than between sites with and without vegas.

Dietary preferences

Similarity between diet and food availability was higher (Table 2) in a habitat without vegas (Avestruces: O=89% for plant categories and 77% for species) than in either of the habitats with vegas (Laguna: O=68% and 43%; Yaucha: O=67% and 45%, respectively). Considering food availability in different microhabitats, the diet showed a higher similarity with food availability on dry soils (O=71% for plant categories and 60% for species) than in vegas (O=43% and 14%, respectively). A selective use of plant species was detected both in habitats without vegas (Durazno: χ^2=2050.68, Avestruces: χ^2=401.42) and in habitats with vegas (Laguna: χ^2=1530.38, Yaucha: χ^2=1324.40).

Regarding the habitats without vegas, there was an opportunistic use of plant categories at Durazno (χ^2=4.86 p=0.183), whereas at Avestruces the selective use was weak (χ^2=74.57) because grasses, shrubs, and forbs were used in proportion to availability (Figure 1). The main species were mostly used in proportion to availability (Table 3), such as the grasses *Poa holciformis* at Durazno and *Poa durifolia* at Avestruces, the shrub *Adesmia aegiceras* in both habitats, and the forbs *Oxalis erythrorhiza* at Durazno and *Cerastium arvense* at Avestruces. On the other hand, two shrubs were selectively used in Durazno: *Senecio looseri* was preferred and *Azorella monantha* was avoided.

A selective use of plant categories was found at Laguna (χ^2=112.24) and Yaucha (χ^2=229.08), the habitats with vegas, where grass-like plants were avoided (Figure 1, particularly *Oxychloe bisexualis* at both sites, as well as *Carex gayana* and *Patosia clandestina* at Yaucha, Table 3). Grasses were used in proportion to availability (particularly *Hordeum halophilum* at Laguna and *Festuca magellanica* at Yaucha); however, *Festuca magellanica*, a grass of vegas, was avoided at Laguna. Shrubs and forbs were preferred in Laguna and Yaucha, respectively. The shrub *Adesmia aegiceras* and the forb *Oxalis erythrorhiza* were preferred in both habitats, whereas the shrub *Discaria nana* was avoided.

Discussion and conclusion

The generalist diet of brown hares was confirmed in this High Andean mountain environment, as the diet included a considerable percentage of the plant species present in the vegetation, especially when excluding the vegetation of vegas. There were several evidences supporting the dietary opportunism of brown hares, such as the high similarity between diet and food availability, considering both plant categories and plant species. For example, the major species in the diet were also the main species in the available vegetation (the shrub *Adesmia aegiceras* and the grass *Poa durifolia*). The higher dietary similarity between habitats with vegas than between habitats with and without vegas also reflected the respective differences in food availability. In habitats without vegas, plant categories were used with weak selectivity, even with opportunism, and the most common grasses, shrubs, and forbs were used in proportion to availability. Most grasses were also used in proportion to availability in habitats with vegas. Dietary generalism and opportunism are part of the adaptive features of *Lepus europaeus* that facilitated the documented successful expansion of its distribution range, which occurred both naturally and by liberations (Flux and Angermann 1990).

Only two shrub species were used with selectivity by brown hares in habitats without vegas (one of these species was preferred and the other avoided). Conversely, a pronounced selectivity occurred in habitats with vegas, where shrubs and forbs were used with preference, particularly two dry-soil species: the shrub *Adesmia aegiceras* and the forb *Oxalis erythrorhiza*, whereas the most common species of vegas were avoided: all grass-like plants and the grass *Festuca magellanica*. Avoidance of wetland plant species appears to be in response to the type of vegas present in the study environments, consisting of dense hard cushions of *Oxychloe bisexualis* and *Patosia clandestina* (Juncaceae), taking into account the rigid leaves with sharp apexes of *O. bisexualis* and the low forage quality of *Oxychloe* species (Alzérreca et al. 2006, Novara 2009). Instead, in the other type of wetlands present in High Andean environments of Northern Chile, the dominant hydrophytic grasses (*Deschampsia cespitosa* and *Deyeuxia velutina*) were major food items for brown hares (López-Cortés et al. 2007). In the High Andean environments with one or another type of wetlands, the diet of *Lepus europaeus* contained plant species of dry soils. Also in Patagonian environments with mallines, the diet of brown hares included grasses and grass-like plants of wetlands, as well as dry-soil grasses and shrubs (Bonino 2007).

Seasonal and spatial changes have been observed in the diet of *Lepus europaeus* in response to available vegetation, with dietary shifts from grasses and forbs to woody plants in situations of food scarcity (Flux and Angermann 1990). Indeed, trees and shrubs constituted the prevalent items in the winter diets of brown hares in environments of its native (van der Wal et al. 2000, Rödel et al. 2004) and introduced ranges (Pelliza-Sbriller et al. 1997, Kufner et al. 2008, Green et al. 2013). Moreover, the dietary prevalence of woody plants was maintained throughout the year in scrublands of the Argentine High Monte ecoregion (Reus et al. 2012). In this study, the severe climate conditions, which included snowfall and daily frosts even in summer, and the high-altitude wetlands whose vegetation was restricted to hard cushions of Juncaceae species, provided poor quality of food for brown hares that accounted for the prevalence of shrubs in their summer diet studied here. This dietary prevalence of shrubs is expected to be even more important during winter, as occurred in other environments such as Northern Patagonia (Puig et al. 2007).

The mountain wetlands scattered across the dry Andean environments have been mentioned as confined but important sources of succulent food and water for wildlife (Roig and Roig 2004, Squeo et al. 2006a,b). The lower similarity in food availability between vegas and dry soils than between the same type of microhabitats (vegas on the one hand, dry soils on the other hand) proved that these wetlands are significantly different as feeding sites for brown hares. These vegas proved to have feeding attractiveness for the migratory population of guanacos in the "Laguna Diamante" protected area, as the highest similarity between the guanaco's diet and food availability was found in the wetland microhabitats (Puig et al. 2011). In contrast, the forage in these wetlands was unattractive to the brown hare, given the low similarity between the brown hare's diet and the available food in vegas and their edges, compared to the adjacent dry soils. Nearly half the plant species eaten by brown hares in habitats with vegas were used with avoidance; moreover, almost all species belonging to the wetland microhabitat were avoided. Dietary generalism was more pronounced in habitats without vegas, whereas in the other habitats the generalist feeding strategy was important once the wetland microhabitat was discarded in the analysis and only the vegetation of dry soils and edges of wetlands was considered.

More than one century after the introduction of brown hares into South America, this species has become fully integrated into the different ecosystems. Considering the top carnivores present in the study area (Mónaco et al. 2005): puma (*Puma concolor*), culpeo fox (*Pseudalopex culpaeus*), black-chested buzzard-eagle (*Geranoaetus melanoleucus*), and large hawks (*Buteo* spp.), *Lepus europaeus* constitutes a key prey for them (Montserrat et al. 2005, Bonino et al. 2010, Arriagada et al. 2011). Because other medium-sized, native preys such as the mountain vizcacha (*Lagidium viscacia*), plains vizcacha (*Lagostomus maximus*), and mara (*Dolichotis patagonum*) were not present in the studied high altitudes, the brown hare is not concerning as potential competitor as it is in other regions, for example, Northern Patagonia, where the brown hare and the mara showed a high dietary overlap (Puig et al. 2014). The conservation of these fragile High Andean environments is jeopardized due to increasing mining activities in the region (Brown et al. 2006), which in turn is a potential threat to top carnivores, as brown hares proved to be important prey for them in southern South America (Franklin et al. 1999).

The least selective diet found in habitats without vegas, which had lower food availability in terms of plant cover and diversity, particularly the equitability, is consistent with prediction (a), even though there were no significant differences among habitats in diet diversity, richness, or equitability. Results also agree with prediction (a) when comparing microhabitats, considering the few plant species selectively foraged in dry soils, where plant cover and food diversity, particularly richness, were lower than in wetlands and their edges.

The expected feeding attractiveness of wetlands for the brown hare, according to prediction (b), was not found in the study area. On the contrary, the diet of brown hares excluded a significantly higher percentage of plant species of wetlands than those of dry soils and edges. With the highest similarity between diet and food availability, dry soils were the main feeding areas for *Lepus europaeus* in this high-altitude environment. Not only the unattractive hard cushions of Juncaceae that prevail in wetlands, but also the shrub patches that provide useful food and shelter on dry soils, together with rocky outcrops, can explain the relevance of the dry-soil ecosystem for brown hares. Although it is an introduced species, the brown hare has become an important prey for a number of indigenous, top-carnivore species. As it has been found in native range environments for *L. europaeus*, protection of the spatial heterogeneity at landscape and microhabitat scales will be an important tool for the conservation of brown hare populations in High Andean environments.

References

Abraham, E. 2000. Geomorfología de la provincia de Mendoza. Caracterización ambiental y atlas básico. In: (E. Abraham and F. Rodríguez Martínez, eds.) Argentina, recursos y problemas ambientales de la zona árida. Junta de Andalucía, Gobierno y Universidades de la Región Andina Argentina, Buenos Aires. pp. 29–48.

Alzérreca, H., J. Laura, F. Loza, D. Luna and J. Ortega. 2006. Importance of carrying capacity in sustainable management of key High-Andean puna rangelands (Bofedales) in Ulla Ulla, Bolivia. In: (E.M. Spehn, M. Liberman and C. Korner, eds.) Land use change and mountain biodiversity. Taylor & Francis, Boca Raton, FL. pp. 153–166.

Angermann, R., J.E.C. Flux, J.A. Chapman and A.T. Smith. 1990. Lagomorph classification. In: (J.A. Chapman and J.E.C. Flux, eds.) Rabbits, hares and pikas: status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Oxford. pp. 7–13.

Arriagada, A.M., J.L. Arriagada, L.A. Baessolo and C.G. Suazo. 2011. Summer diet of black-chested buzzard-eagle (*Geranoaetus melanoleucus*) in Aysen District, Chilean Patagonia. Ecotrópicos 2: 164–171.

Baumgartner, L.L. and A.C. Martin. 1939. Plant histology as an aid in squirrel food-habit studies. J. Wildl. Manage. 3: 266–268.

Bonino, N.A. 2007. Estrategia adaptativa de dos especies de lagomorfos introducidos en la Patagonia argentina, con especial referencia a sus hábitos alimentarios. Tesis Doctoral, Univ. Sevilla. pp. 182.

Bonino, N., D. Cossíos and J. Menegheti. 2010. Dispersal of the European hare, *Lepus europaeus* in South America. Folia Zool. 59: 9–15.

Brown, A., U. Martinez Ortiz, M. Acerbi and J. Corcuera. 2006. La situación ambiental Argentina 2005. FVSA, Buenos Aires. pp. 587.

Cabrera, A.L. and A. Willink. 1980. Biogeografía de América Latina, 2nd ed. Biological Series of the Organization of American States, Washington. pp. 122.

Cavieres, L.A., A. Peñaloza and M.K. Arroyo. 2000. Altitudinal vegetation belts in the High-Andes of central Chile (33°S). Rev. Chil. Hist. Nat. 73: 331–344.

Chapman, J.A. and J.E.C. Flux. 1990. Introduction and overview of the lagomorphs. In: (J.A. Chapman and J.E.C. Flux, eds.) Rabbits, hares and pikas: status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Oxford. pp. 1–6.

Cherry, S. 1996. A comparison of confidence interval methods for habitat use availability. J. Wildl. Manage. 60: 653–658.

Colwell, R.K. and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567–576.

Contreras, J.P., E. Rodríguez, A. Santoro and H. Torres. 2002. Plan de acción para la conservación y uso sustentable de humedales altoandinos. CONAF and RAMSAR. pp. 22.

Daget, P. and J. Poissonet. 1971. Une méthode d'analyse phytologique des prairies. Critéres d'application. Ann. Agron. 22: 5–41.

Dinerstein, E., D.M. Olson, D.J. Graham, A.L. Webster, S.A. Primm, M.P. Bookbinder and G. Ledec. 1995. A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. World Bank, Washington DC. pp. 129.

Duci, J.L. 1949. Methods for the determination of food habits by plant microtechniques and histology and their application to cotton tail rabbit food habits. J. Wildl. Manage. 13: 295–298.

Flux, J.E.C. and R. Angermann. 1990. The hares and jackrabbits. In: (J.A. Chapman and J.E.C. Flux, eds.) Rabbits, hares and pikas: status survey and conservation action plan. IUCN/SSC Lagomorph Specialist Group, Oxford. pp. 61–95.

Franklin, W.L., W.E. Johnson, J.A. Iriarte and R.J. Sarno. 1999. Ecology of the Patagonia mountain lion, *Felis concolor patagonica*, in southern Chile. Biol. Conserv. 90: 33–40.

Green, K., N.E. Davis, W.A. Robinson, J. McAuliffe and R.B. Good. 2013. Diet selection by European hares (*Lepus europaeus*) in the alpine zone of the Snowy Mountains, Australia. Eur. J. Wildl. Res. 59: 693–703.

Holechek, J.L. 1982. Sample preparation techniques for microhistological analysis. J. Range Manage. 35: 267–268.

Holechek, J. and B. Gross. 1982. Evaluation of different calculation procedures for microhistological analysis. J. Range Manage. 35: 721–723.

Holechek, J.L., M. Vavra and R.D. Pieper. 1982. Botanical composition determination of range herbivore diets: a review. J. Range Manage. 35: 309–315.

Hurlbert, S. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67–77.

Kufner, M.B., L. Sepúlveda, G. Gavier, L. Madoery and L. Giraudo. 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.

López-Cortés, F., A. Cortés, E. Miranda and J.R. Rau. 2007. Dietas de *Abrothrix andinus, Phyllotis xanthopygus* (Rodentia) y *Lepus europaeus* (Lagomorpha) en un ambiente altoandino de Chile. Rev. Chil. Hist. Nat. 80: 3–12.

Mónaco, G., L. Arias, E.A. Orellano and A. Begaríe. 2005. Carta de situación de Reserva Laguna del Diamante: Aspectos Generales, Naturales y Culturales. Technical Report. Secretaría de Medio Ambiente, Gobierno de Mendoza, Argentina. pp. 97.

Montserrat, A., M. Funes and A. Novaro. 2005. Respuesta dietaria de tres rapaces frente a una presa introducida en Patagonia. Rev. Chil. Hist. Nat. 78: 425–439.

Moreno, C.E. 2001. Métodos para medir la biodiversidad. M&T Manuales y Tesis SEA, vol. 1. Zaragoza. pp. 84.

Norte, F. 2000. Mapa climático de Mendoza. In: (E. Abraham and F. Rodríguez Martínez, eds.) Argentina, recursos y problemas ambientales de la zona árida. Junta de Andalucía, Gobierno y Universidades de la Región Andina Argentina, Buenos Aires. pp. 25–27.

Novara, L.J. 2009. Juncaceae: Familia de los juncos o junquillos. In: (R. Kiesling, ed.) Flora de San Juan, Vol. IV, Fundación Universidad Nacional de San Juan, San Juan. pp. 377–391.

Pelliza-Sbriller, A., P. Willems, V. Nakamatsu, A. Manero and R. Solmo. 1997. Atlas dietario de herbívoros patagónicos. Prodesar, INTA, GTZ, Bariloche.

Puig, S., F. Videla, M.I. Cona and S.A. Monge. 2007. Diet of the brown hare (*Lepus europaeus*) and food availability in northern Patagonia (Mendoza, Argentina). Mamm. Biol. 72: 240–250.

Puig, S., M.I. Rosi, F. Videla and E. Mendez. 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., M.I. Cona, F. Videla and E. Mendez. 2014. Dietary overlap of coexisting exotic brown hare (*Lepus europaeus*) and endemic mara (*Dolichotis patagonum*) in Northern Patagonia (Mendoza, Argentina). Mammalia 78: 315–326.

Reus, M.L., B. Peco, C. de los Ríos, S.M. Giannoni and C.M. Campos. 2012. 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, H.G., W. Völkl and H. Kilias. 2004. Winter browsing of brown hares: evidence for diet breadth expansion. Mamm. Biol. 69: 410–419.

Roig, C. and F. Roig. 2004. Consideraciones generales. In: (D.E. Blanco and V.M. Balze, eds.) Los turbales de la Patagonia. Bases para su inventario y la conservación de su biodiversidad. Wetlands International. Bs. As., Argentina. pp. 5–21.

Roig, F.A., E. Martínez Carretero and E. Méndez. 2000. Vegetación de la provincia de Mendoza. Caracterización ambiental y atlas básico. Buenos Aires. In: (E. Abraham and F. Rodríguez Martínez, eds.) Argentina, recursos y problemas ambientales de la zona árida. Junta de Andalucía, Gobierno y Universidades de la Región Andina Argentina, Buenos Aires. pp. 63–64.

Siegel, S. and N.J. Castellan. 1988. Nonparametric statistics for the behavioral sciences, 2nd ed. McGraw-Hill, New York. pp. 399.

Smith, A.D. and L.J. Shandruk. 1979. Comparison of fecal, rumen and utilization methods for ascertaining pronghorn diets. J. Range Manage. 32: 275–279.

Smith, R.K., N.V. Jennings and S. Harris. 2005. A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. Mammal Rev. 35: 1–24.

Squeo, F.A., B.G. Warner, R. Aravena and D. Espinosa. 2006a. Bofedales: high altitude peatlands of the central Andes. Rev. Chil. Hist. Nat. 79: 245–255.

Squeo, F.A., E. Ibacache, B. Warner, D. Espinoza, R. Aravena and J.R. Gutiérrez. 2006b. Productividad y diversidad florística de la Vega Tambo, Cordillera de Doña Ana. In: (J. Cepeda-Pizarro, ed.) Geoecología de los Andes desérticos. La alta montaña del valle de Elqui. pp. 323–351.

Sruoga, P., E.J. Llambías, L. Fauqué, D. Schonwandt and D.G. Repol. 2005. Volcanological and geochemical evolution of the Diamante Caldera-Maipo volcano complex in the southern Andes of Argentina (34°10′S). J. S. Am. Earth Sci. 19: 399–414.

van der Wal, R., H. van Wijnen, S. van Wieren, O. Beucher and D. Bos. 2000. On facilitation between herbivores: how brent geese profit from brown hares. Ecology 81: 969–980.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall Inc., NJ. pp. 718.

Zweifel-Schielly, B., M. Kreuzer, K.C. Ewald and W. Suter. 2009. Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. Ecography 32: 103–113.