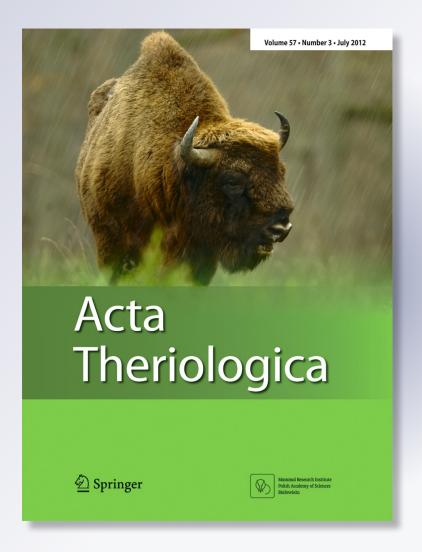
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Gladys I. Galende & Estela Raffaele

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ORIGINAL PAPER

Diet selection of the southern vizcacha (*Lagidium viscacia*): a rock specialist in north western Patagonian steppe, Argentina

Gladys I. Galende · Estela Raffaele

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Abstract The southern vizcacha (*Lagidium viscacia*) is a rock specialist that inhabits small colonies in isolated rocky outcrops of northwestern Patagonia. This study analyzes its diet selection in relation to food availability, establishes the degree of dietary specialization, and discusses the potential competition with exotic herbivores. Diet composition and food availability were determined in summer and winter in eight rocky outcrops by microhistological analysis of fecal pellets, and food availability was estimated by the Braun Blanquet cover abundance scale. Vegetation cover differences were detected by using a random analysis of variance (ANOVA) factorial block design, and dietary preferences were determined by the confidence interval of Bonferroni. The southern vizcacha showed a specialized feeding behavior despite the consumption of a wide variety of items. Their diet was concentrated on a few types of food, mainly grasses, and the trophic niche was narrow and without seasonal variations. In winter, when food was scarce and of lower quality than summer, diet was dominated by Stipa speciosa, suggesting a selection according to the selective quality hypothesis. Our results (narrow trophic niche, restricted activity near rocky outcrops, and a diet with high

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G. I. Galende (⋈)
Department of Zoology, Bariloche Regional University Center,
National University of Comahue,
Quintral 1250,
(8400), Bariloche, Río Negro, Argentina
e-mail: gladysgalende1@gmail.com

E. Raffaele

Laboratory Ecotono, Research Institute for Biodiversity and Environment, (INIBIOMA) National University of Comahue-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bariloche, Río Negro, Argentina proportions of low-quality grasses) showed that the vizcacha is an obligatory dietary specialist, and these characteristics made it highly vulnerable to changes in food availability. In this scenario, overgrazing caused by alien species with similar diets, as the European hare and livestock, could negatively affect their colonies.

Keywords Trophic niche · Food quality hypothesis · Rocky outcrops · Selectivity

Introduction

The diet selection of herbivores is a complex process that depends on the interaction of various factors such as the abundance and quality of food, the presence of toxins in plants, predation risk, and competition (Crawley 1983; Belovsky 1986; Stephens and Krebs 1986; Senft et al. 1987; Brown 1988; Stuth 1991; Sih 1993; Dearing et al. 2000). Moreover, the use of refuges, water availability, and topography can also influence dietary selection (Covich 1976; Ellis et al. 1976; Senft et al. 1987; Stuth 1991; Kotler and Brown 1999). Rocky habitats are unique environments in the world, with a wide variety of flora and fauna, and have many endemic species of high conservation value. They serve as refuges from climatic fluctuations, fire, human activities, and predation (Matheson and Larson 1998; Nutt 2007). The feeding behavior of specialized animals in this type of habitat is limited to the vicinity of the rocky refuge, because travel costs and risk of predation increase with distance to rocks (Covich 1976; Huntly 1987; Holmes 1991; Kotler et al. 1999; Galende 2010). For these consumers, feeding distances depend mainly on the abundance of food in the proximities and the risk of predation; therefore, the selection of diet will be influenced

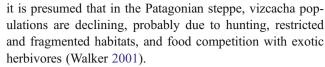


by these costs. This feeding behavior produced a high intensity of grazing in the vicinity of the rocky shelter and in some cases, modifies the surrounding plant communities (e.g., Huntly 1987; Branch and Sosa 1994; Branch et al. 1996). In addition, the coexistence with herbivores of similar diets could reduce food availability and lead to changes in the diets (Sih 1993).

The selection and use of a particular type of food also depends on the physiological limitations (Hanley 1982; Penry 1993), the smaller herbivores have a nonspecialized digestive system to extract nutrients from low-quality food, and they must eat low fiber and high in protein items (Milton 1979; Crawley 1983; Dement and Van Soest 1985; Bergeron and Jodoin 1987; Caughley and Sinclair 1994). Despite of these restrictions, some rodents obtain energy and nutrients from low-quality grasses by increasing the digestive tract capacity, post-gastric fermentation, or coprophagy (Bozinovic et al. 1988; Veloso and Bozinovic 1993; Bozinovic 1995; Sassi et al. 2007; Naya et al. 2008). The degree of dietary specialization of an herbivore could be determined by parameters such as the trophic niche breadth, responses to seasonal changes in food availability, spatial scales, and the processing of "difficult foods." For example, specialist herbivores possess unique physiological, behavioral, and anatomical characteristics that allow them to consume large amounts of one type of food, which could be unpalatable to other herbivores (Shipley et al. 2009). However, these characteristics could limit a population's capacity to respond to environmental changes (Crawley 1983) and enhance its vulnerability, particularly for specialized herbivores in restricted habitats.

The southern vizcacha (Lagidium viscacia, Molina 1872) is an ideal species for studying the feeding behavior of a rock specialist, because its activity is associated to the rocky substrate and decreases at greater distances from rocky outcrops (Walker et al. 2000a; Walker 2001; Reus Ruiz 2006; Galende and Raffaele 2008; Galende 2010). In northwestern Patagonia, the vizcachas are distributed throughout the Andes Mountains at altitudes over 2000 m; and toward the east, in rocky outcrops located at ca. 700 m in the steppe (Crespo 1963; Pearson 1995; Galende et al. 1998). In this region, this medium-sized rodent (2000 g) lives in colonies (<20 individuals) constituted by small family groups and produces one offspring per year (Weir 1971; Walker et al. 2000b; Walker 2001). Diet composition is based on grasses (Galende et al. 1998; Galende and Grigera 1998; Puig et al. 1998), and have high similarity with diets of exotic herbivores as European hare (Lepus europaeus) and livestock (Galende and Grigera 1998). Their predators are eagles (Geranoatus melanoleucus) and owls (Bubo magellanicum), but the rate of predation is low (Galende and Trejo 2003).

In Argentina, the conservation status of this species is of low risk and least concern (Díaz and Ojeda 2000). However,



The objectives of this study were to determine the diet composition and food selection in relation to availability and to establish the dietary specialization degree of this rock specialist herbivore. We also discuss the possible competition with the exotic European hare and livestock.

We propose the hypothesis that due to specialized behaviors, these rock specialist rodents are selective consumers and have a narrow trophic niche. We expect a high consumption of grasses available near the rocky outcrops.

Material and methods

Study area

This study was carried out in eight rocky outcrops of NW Patagonian steppe (41°05 S; 70°03 W) in the western district of the Patagonian phytogeographic province. The steppe is dominated by grasses: Stipa speciosa, Festuca pallescens; and shrubs: Mulinum spinosum and Senecio spp. (León et al. 1998; Galende 2010). In this area, the rocky outcrops (vizcacha's typical habitats) are distinct entities, with a mean altitude of 750 m, and separated between them by more than 5 km in a homogeneous landscape. In Patagonia, as in some other sites of the world, the rocky outcrops are complex habitats surrounded by arid environment, which explains in part the limited information about them (Nutt 2007; Galende 2010). Mean annual precipitation is ca. 600 mm with high fluctuations among years (Farji-Brener and Ghermandi 2004). The mean temperature of the coldest month is 2.1 °C (July) and the warmest month is 15.3 °C (January; Muñoz and Garay 1985; Bustos 1996). There are significant seasonal changes in vegetation cover and winter is a critical period for the survival of animals (Somlo et al. 1985, 1994). The overgrazing by introduced livestock since the early 1900s, resulted in high degree of desertification in large areas of steppe and the rocky outcrops (Bertiller and Bisigato 1998; Adler et al. 2001). In addition to livestock in the last middle century, wild species such as the red deer (Cervus elaphus) and European hare (L. europaeus), which invaded different environments including the study area (Grigera and Rapoport 1983; Vázquez 2002), were introduced.

Field sampling

During the last days of August 2005 (winter season), at eight rocky outcrops (sampling areas) selected at random, we carried out vegetation sampling at three distances from the



rocks: close (0-20 m), medium (20-50 m), and far (50-90 m). We established four 100 m transects at each outcrop, and 2×2 m plots every 10 m along each transect, with a total of ten plots per transect. At each plot, we estimate the cover percentage per species and functional groups (shrubs, grasses, and herbs), using the cover abundance scale of Braun-Blanquet. The average cover values were obtained from the scale values of conversion of this method (Mateucci and Colma 1982). To estimate seasonal variation in food availability, summer vegetation data were reanalyzed from Galende and Raffaele (2008). These data were collected with the same sampling methods and in the same rocky outcrops, during January 2005. Simultaneously during summer and winter, in 40 sampling units of 1 m diameter per outcrop, we collected 30 fresh fecal pellets in the vegetation transects. Fecal samples were formed by ten pellets randomly extracted from ten groups of feces, obtaining three samples from each sampling area, being in total 48 fecal samples. Freshness was evaluated on the basis of appearance and degree of aggregation of pellets.

Laboratory analysis

The diet of the southern vizcacha was studied by microhistological analysis of fecal pellets (Baumgartner and Martin 1939; Sparks and Malechek 1968). Unknown species of plants were collected to be included in the reference collection of our laboratory microhistological, which has a total of 96 plant species of the region. The fecal pellets and plants were processed with a similar treatment which consisted in drying them at 60 °C and milled to a size of 1 mm to reduce variation. The material was depigmented with 90 % alcohol, cleared with sodium hypochlorite and colored with safranin. Finally, the sample was mounted with glycerin jelly for microscopic observation (Sparks and Malechek 1968; Latour and Pelliza de Sbriller 1981).

A number of five slides per fecal sample were made to recognize plant fragments, and 20 microscopic fields in 100× magnification were observed for each slide. The presence of food items was recorded for each microscope field, and its percentage of occurrence was determined for all microscope fields (Holechek and Gross 1982). Plants consumed were grouped by epidermal characteristics into three functional groups: shrubs, herbs, and grasses (Gramineae and Cyperaceae and Juncaceae). The plant material found in fecal pellets was identified to species level whenever possible, using the reference collection of epidermal tissues of leaves, fruits, and flowers from our laboratory. Identification was based on the characteristics of the epidermis: the cell wall, the size of the fragments, stomata, and trichomes.

Statistical analysis

In summer and winter (2005), we analyzed the effect of distance from the outcrops on the vegetation by using a random block design with a factorial 3×3 analysis of variance (ANOVA; Zar 1999), where D=distances from the rocky outcrops (with three levels: close, medium, and far) and functional groups (FG=shrubs, herbs, grasses) were applied as factors. We used part of the summer vegetation data provided from our previous study (Galende and Raffaele 2008) and the winter sampling vegetation from this study to compare food availability between these seasons. Differences in plant cover between summer and winter were evaluated in eight rocky outcrops by a 2×3 factorial randomized block arrangement design with these factors: season (S; wintersummer) and functional groups (FG; herbs, grasses, and shrubs). Variability between outcrops was controlled considering each outcrop as a block, and the mean total cover of functional groups was used as a dependent variable. Data on the percentage of plant cover were transformed by square root, and normality assumptions were verified. We tested the significant differences in the ANOVA by applying posteriori Tukey test.

To assess seasonal differences in diet and cover of dominant species, we applied the Wilcoxon rank sum test for dependent samples (Zar 1999). In summer and winter, proportions of functional groups in diet were compared by Kruskal–Wallis ANOVA for multiple comparisons and significant differences between functional groups were detected by posteriori test.

The selection by functional groups and plant species (>5 %) in relation to their availability was detected by using simultaneous confidence intervals of Bonferroni (Neu et al. 1974; Byers et al. 1984). These intervals determine the actual proportion of use (pu) for each vegetation group and compare them to the expected proportion (pe=relative plant cover×diet frequency). Plant use was qualified as: selected, proportional, or avoided, depending on whether the expected proportion was located below, within, or above the confidence interval of the dietary frequency.

As an estimator of trophic specialization, in summer and winter, we estimated trophic niche breadth (B) with Levins' standardized index (Bst): Bst=(B-1)/(n-1), where B is the Levins niche breadth and n is the number of resources available (Feinsinger et al. 1981; Krebs 1989). Values of this index near 0 indicate narrow trophic niche or more specialized diet, and values near 1 indicate a broader niche or more generalized diet.

Seasonal differences (winter-summer) in trophic niche breadth were evaluated using mean index values, and we applied the Wilcoxon test for dependent samples (Zar 1999).



Results

Vegetation composition

The vegetation was constituted by 77 plant species, and there were no differences in cover abundance (%) among sites (outcrops, Table 1). In summer, cover abundance (%) showed significant differences among functional vegetation groups (Table 1), and the herbs were less abundant (Tukey test, p=0.01). Functional groups no showed significant changes in relation to distance from rocky outcrops (Table 1).

Winter was similar to summer showing significant differences in cover abundance (%) between functional groups (Table 1), with low abundance of herbs (Tukey test, p=0.01). As in summer, functional groups no showed significant changes in relation to distance (Table 1). The cover of different functional groups depended on the season (Table 2). In winter, the shrubs (F(1,56)=3794, p=0.01) and grasses (F(1,56)=763.7, p=0.02) decreased significantly compare to summer.

The dominant grasses F. pallescens (Wilcoxon test W=1.54, p=0.12) and S. speciosa (W=0.40, p=0.84) showed no significant seasonal differences in cover. However, Poa lanuginosa (W=1.96, p=0.04) and the shrubs M. spinosum (W=2.38, p=0.01) and Senecio spp. (W=2.38, p=0.01) decreased significantly in winter (Table 3).

Diet selection

Southern vizcacha consumed 47 species from the total 77 available species (61 %) growing in the vicinity of the rocky

Table 1 Distance effects from the outcrop on the structure of the vegetation by using a random block design with a factorial 3×3 analysis of variance (ANOVA), where distances from rocky outcrops (D), with three levels—close, medium, and far—and functional groups (FG) with three levels—shrubs, herbs, and grasses—are applied as factors

	DF	MS	F	P
Winter				
Distances (D)	2	151.07	1.82	0.170
Functional groups (FG)	2	1085.71	13.11	0.001
$D \times FG$	4	44.50	0.53	0.708
Rocky outcrops (R)	7	176.12	2.12	0.050
Error	56	82.80		
Summer				
Distances (D)	2	261.59	1.23	0.299
Functional groups (FG)	2	2795.35	13.17	0.001
$D \times FG$	4	422.89	1.99	0.108
Rocky outcrops (R)	7	217.84	1.02	0.423
Error	56	212.21		

Table 2 Results of 2×3 factorial ANOVAs for the effects of seasonal variation (S), on the abundance of the functional plant groups (FG)

	DF	MS	F	P
Season (S)	1	9.276665	21.93	0.004
Groups (FG)	2	7.51281	17.76	0.001
$S \times FG$	2	1.575279	3.72	0.034
Rocky outcrops (R)	7	0.678110	1.60	0.166
Error	35	0.422868		

The dependent variable is cover abundance (%) of functional plant groups: shrubs, herbs and grasses. n=8 are random blocks, seasons=winter-summer

R Rocky outcrops

outcrops, although the annual trophic niche breadth was narrow (Bst=0.25±0.01) and without significant variation between summer and winter (Wilcoxon test, W=1.18, p=0.23). The grasses were the main component and S. speciosa, P. lanuginosa, Bromus spp., and F. pallescens constituted 50 % of the diet (Table 3). The proportions of plants groups in diet showed no significant changes between summer and winter: grasses (W=1.26, p=0.20), shrubs (W=0.56, p=0.57), and herbs (W=1.82, p=0.06).

Table 3 Food availability and diet composition of *Lagidium viscacia* in eight rocky outcrops in summer and winter

	Summer	Winter	Summer	Winter	
Grasses					
Poa lanuginosa	2.49 ± 1.01	0.89 ± 0.38	7.62 ± 0.97	6.41 ± 0.95	
Festuca pallescens	$6.43\!\pm\!1.32$	$4.40.\pm 1.32$	9.74 ± 1.64	5.59 ± 1.12	
Stipa speciosa	9.66 ± 2.11	8.15 ± 2.59	23.0 ± 2.13	38.3 ± 1.97	
Bromus spp.	2.29 ± 1.21	1.25 ± 0.79	5.09 ± 1.39	5.16 ± 1.46	
Hordeum spp.	1.23 ± 0.65	0.61 ± 0.60	2.38 ± 0.96	2.41 ± 0.89	
Juncus balticus	0.11±0.11 0.01±0.01 1.97±0.80		1.97 ± 0.86	0.53 ± 0.46	
Shrubs					
Mulinum spinosum	7.51 ± 1.76	1.18 ± 0.51	16.2 ± 2.27	2.77 ± 0.84	
Senecio spp.	4.52 ± 1.00	2.20 ± 0.88	2.81 ± 0.72	1.33 ± 0.58	
Berberis heterophyla	3.73 ± 1.20	2.17 ± 0.84	1.45 ± 0.38	5.37±0.94	
Adesmia spp.	1.26 ± 1.07	_	0.56 ± 0.18	2.53 ± 1.35	
Fabiana imbricata	1.60 ± 0.79	$0.34 {\pm} 0.28$	1.42 ± 0.57	8.89 ± 1.82	
Nasauvia glomerulosa	1.92 ± 1.23	1.65 ± 1.12	0.47 ± 0.13	3.68 ± 1.62	
Herbs					
Eryngium paniculatum	0.47 ± 0.30	0.62±0.38 2.60±1.19		4.34±1.56	
Cerastium arvense (E)	1.36 ± 0.27	0.38±0.27 1.46±0.29		1.51 ± 0.26	
Rumex acetosella (E)	3.30 ± 0.30	0.46 ± 0.30 3.63 ± 0.84		0.27 ± 0.12	
Verbascum thapsus (E)	0.09 ± 0.06	_	2.16 ± 0.58	0.78 ± 0.26	
Plantago lanceolata (E)	0.95 ± 0.95	_	1.22 ± 0.36	0.21 ± 0.11	
Hypochoeris spp.	0.03 ± 0.03	_	2.52 ± 0.59	0.63 ± 0.26	
No identity			1.37 ± 0.61	0.53 ± 0.23	

Availability is expressed as cover abundance (%) and food items (proportions>1%) as percentage of frequency (\pm ES), n=48 fecal samples E Exotic species



In summer, food resources were more abundant, and the southern vizcacha consumed 47 plant species (Bst=0.28±0.06). There were significant differences in the contributions of plant groups (Kruskal–Wallis, H(2,24)=16.4, p=0.03), and the grasses were consumed in greater proportion than shrubs (p=0.012, Posteriori test p values) and herbs (p=0.001; Fig. 1). The main dietary components were S. speciosa, F. pallescens and P. lanuginosa; in addition, the consumption of flowers and fruits of the shrub M. spinosum was important (Table 3).

During winter, the diet was composed of 40 items, and there were significant differences in the proportions of functional plant groups (H(2,24)=19.8, p=0.001), these results being similar to summer. The grasses were consumed in highest proportions in comparison to herbs (p=0.001, Posteriori test p values). The trophic breadth was narrow (Bst=0.24±0.01), with the highest values of S. speciosa, and its consumption increased significantly in this season (Wilcoxon test, W=2.24, p=0.02). A similar pattern showed the shrubs Fabiana imbricata (W=2.36, p=0.01) and Berberis heterophyla (W=2.24, p=0.02). In contrast, the shrub M. spinosum decreased in the diet (W=2.52, p=0.01; Fig. 2).

The southern vizcacha showed a selective feeding behavior by grasses that were consumed in a highest proportion to their availability in summer and winter (Table 4). Among the main species of diet, *S. speciosa*, *P. lanuginosa*, and the herb *Eryngium paniculatum* were the only selected species in the two seasons; also selected were the shrubs *M. spinosum* and *F. imbricata* in summer and winter, respectively (Table 4).

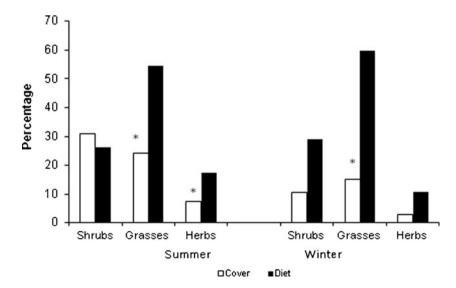
Discussion

The southern vizcacha in northwestern of Patagonia showed a specialized feeding behavior despite of the consumption of

Fig. 1 Selection of functional groups by the southern vizcacha (*Lagidium viscacia*), in summer and winter, in the northwestern Patagonian steppe. Values are given in percentage, and asterisks (*) indicate selected item and significant differences (p<0.05)

a wide variety of plant species. The diet was concentrated on high proportions of a few types of food, and trophic niche was narrow and without significant variations between summer and winter.

This feeding behavior was reflected in a high consumption and selectivity for grasses in both seasons, despite the strong seasonal changes in food availability. In other regions of the country, the southern vizcacha's diet presented a similar pattern, showing a selective feeding behavior for grasses, and S. speciosa was the main dietary component (Galende and Grigera 1998; Puig et al. 1998; Galende et al. 1998; Reus Ruiz 2006). Our results showed that the vizcachas modified the proportions of some species in the diet according to the season (summer and winter), but they did not expand nor changed their trophic niche, thus showing a high dietary specialization. In contrast, in the Chilean altiplane, the vizcachas presented a more general dietary trend, and grasses were only selected in summer, probably because food resources were very limited, highly fluctuating, and unpredictable (Cortés et al. 2002). In Patagonia, the main forage species (P. lanuginosa, S. speciosa, and M. spinosum) contain the highest nutritional values in summer (Somlo et al. 1985) and constituted the most consumed items in the southern vizcacha diet. In winter, when the food availability declined and forage species had lower quality (Somlo et al. 1985), the diet of the southern vizcacha was characterized by high proportions of S. speciosa. Despite of its low quality, the grasses and this plant species generally have higher values of digestibility and protein and lower levels of secondary compounds (tannins and terpenes) than most of the shrubs growing near the rocky outcrops (Somlo et al. 1985; Cavagnaro et al. 2003). Our results suggested that the southern vizcacha was more selective when food abundance declined, because high-quality items were scarce or not palatable, as predicted in selective quality hypothesis (Weckerly and Kenedy 1992; Branch et al. 1994). This





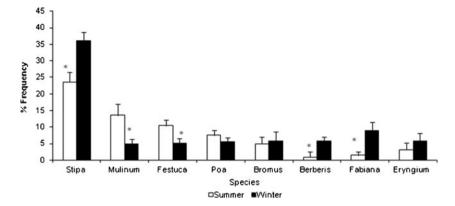


Fig. 2 Seasonal variation (summer–winter) of food items (>5 %) in the diet of the southern vizcacha (*Lagidium viscacia*). Values are expressed as the percentage of frequency (\pm SE), and asterisks (*) indicate significant differences (p<0.05). Dietary items: *Stipa: Stipa speciosa*, *Mulinum*:

Mulinum spinosum, Bromus: Bromus spp. Poa: Poa lanuginosa, Festuca: Festuca pallescens, Eryngium: Eryngium paniculatum, Fabiana: Fabiana imbricata, and Beberis: Berberis heterophyla

feeding behavior was also observed in herbivores of semiarid environments, such as guanacos (*Lama guanicoe*, Puig et al. 1997), the plains vizcacha (*Lagostomus maximus*, Branch et al. 1994), and tuco tuco (*Ctenomys haigi*, Rosi et al. 2003), which increased the dietary selectivity in periods of food scarcity.

The selective feeding behavior of the southern vizcacha for grasses can be explained in several ways. In the Patagonian steppe, they are perennial species, while main palatable shrubs are deciduous (Somlo et al. 1985). Moreover, the biomass of high-quality herbs is low, so their consumption could be limited by the higher cost of searching time (Dement and Van Soest 1985), especially for this herbivore

Table 4 Plant species and functional groups selected (S), avoided (A), or used proportionally (P) by the southern vizcacha during summer and winter in the northwestern Patagonia

	Summer			Winter			
Functional groups	Pe	Pu		Pe	Pu		
Shrubs	0.495	(0.305-0.335)	Α	0.376	(0.257-0.295)	A	
Grasses	0.388	(0.507-0.540)	S	0.524	(0.596-0.638)	S	
Herbs	0.117	(0.143-0.167)	S	0.100	(0.092-0.115)	P	
Species							
Stipa speciosa	0.250	(0.305-0.349)	S	0.384	(0.449-0.505)	S	
Mulinum spinosum	0.194	(0.212-0.252)	S	0.056	(0.023-0.043)	Α	
Bromus spp.	0.059	(0.057-0.081)	P	0.059	(0.053-0.081)	P	
Poa lanuginosa	0.064	(0.094-0.123)	S	0.042	(0.066-0.097)	S	
Festuca pallescens	0.166	(0.124-0.157)	Α	0.207	(0.054-0.083)	A	
Eryngium paniculatum	0.012	(0.027-0.044)	S	0.029	(0.044-0.076)	S	
Fabiana imbricata	0.042	(0.013-0.023)	A	0.016	(0.107-0.145)	S	
Berberis heterophyla	0.097	(0.013-0.026)	A	0.102	(0.056-0.085)	A	
Senecio spp.	0.117	(0.034-0.054)	A	0.104	(0.008-0.021)	A	

Data in parentheses are Bonferroni confidence intervals

Pe Proportion expected (relative cover×frequency in diet), Pu observed proportion of use in diet



restricted to rocky outcrops. Other native Hystricomorphs of medium size, such as the mara (*Dolichotis patagonum*), a typical running herbivore of Patagonia, and the plains vizcacha (*L. maximus*), which lives in burrow systems, also preferred grasses despite differences in habitat use (Jackson 1985; Branch and Sosa 1994; Rodriguez and Dacar 2008). These herbivores have high digestive efficiency and through coprophagy make better use of consumed forage, especially in poor areas (Jackson 1985). At the present, there are no studies of the digestive morphophysiology of the southern vizcacha, although it was observed that this species is coprophagic (Walker et al. 2000b; Galende 2010), which may allow it to overcome the difficulties presented by a diet with high proportions of grasses of low quality.

On the other hand, the choice of foraging areas of rock specialists, such as the pikas (Ochotona spp.) and hyraxes (Procavia johnstoni and Heterohyrax brunei), depends on the rocky protection and food availability in the surroundings, because the greater the feeding distances, the greater is the risk of predation (Hoeck 1975; Huntly et al. 1986; Holmes 1991; Kotler et al. 1999). However, the rock cavy (Kerodon rupestris) exhibited distinct food selection patterns in response to changes in food availability, and the nutrient content could play an important role in diet selection (Willig and Mares 1991). The spatial activity of the southern vizcacha was concentrated in 30 m from the rocky outcrops vicinity, and there were no significant seasonal variations despite the decline in food resources (Walker 2001; Reus Ruiz 2006; Galende and Raffaele 2008; Galende 2010). In contrast, the degus (Octodon degu) changed their range areas in response to seasonal changes in food supply (Quirici et al. 2010). The restricted spatial activity of the southern vizcacha was reflected in a high consumption and preference for S. speciosa, a dominant low-quality grass (Somlo et al. 1985) in the rocky outcrops proximity and without seasonal changes in its abundance. This is a key

species in Patagonia, because it is an available food throughout the year and constitutes a basic component in the winter diet of exotic and native herbivores such as *L. europaeus*, *L. guanicoe*, *D. patagonum*, and sheep *Ovies aries* (Pelliza et al. 1997; Baldi et al. 2004; Puig et al. 2007, 2009). Moreover, the vizcachas also selected a high quality grass as *P. lanuginosa* (Somlo et al. 1985) although their abundance is currently low due to the overgrazing by exotic herbivores (Paruelo et al. 1993; Bonino 1995; Pelliza et al. 1997; Puig et al. 2007).

Selectivity for grasses could also be explained by restrictions in the detoxification of secondary metabolites and the elimination of plant toxins. For example, the vizcachas avoided feeding on *Senecio* spp., an abundant shrub near rocky outcrops, probably due to its high content of secondary components (Cavagnaro et al. 2003). Similarly, the mara (*D. patagonum*) consumed high values of grasses and seemed to avoid shrubs high in secondary metabolites (Sombra and Mangione 2005).

The southern vizcacha's activity resulted in a narrow trophic niche and without significant seasonal variations despite strong changes in food availability. Moreover, their diet contained a high proportion of grasses that are difficult to process (Dement and Van Soest 1985); due to these characteristics, we classified the southern vizcacha as an obligatory dietary specialist sensu Shipley et al. (2009).

In summary, diet selection of the southern vizcacha was influenced by the food abundance and reflected specialized behaviors to life on the rocks. The high consumption of a low-quality grass, such as S. speciosa, could favor their survival, since it is an abundant resource in the vicinity of rocky outcrops. However, this species is also very important in the diet of several exotic herbivores, especially in winter (Pelliza et al. 1997). For example a case of particular attention is the exotic European hare because of its similar size, great capacity of dispersal (Grigera and Rapoport 1983; Cossíos 2004; Merino et al. 2009), and high population densities that fluctuate in time (Novaro et al. 1992). In situations of food restrictions, the hare expands its foraging area and uses different plant communities (Somlo et al. 1994), and it has a significant impact on the vegetation (Bonino 1995; Kitzberger et al. 2005). These characteristics, in addition to the dietary overlap and the similar use of space in the middle distances to the rocky outcrops with the southern vizcacha (Galende and Grigera 1998; Galende and Raffaele 2008), could lead to an interspecific competition for food.

In this scenario, the specialized behaviors of the southern vizcacha limited to the proximity of rocky outcrops make it very vulnerable to changes in food availability, so that grazing by exotic species probably affect their small colonies.

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References

- Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–469
- Baldi R, Pelliza Sbriller A, Albon SD (2004) Hight potencial for competition between guanacos and sheep in Patagonia. J Wildl Manage 68:924–938
- Baumgartner LA, Martin A (1939) Plant histology as an aid in squirrel food habit studies. J Wildl Manage 3:266–268
- Belovsky GE (1986) Optimal foraging and community structure: implications for a guild generalist grassland herbivores. Oecologia 70:35– 52
- Bergeron JM, Jodoin L (1987) Defining "high quality" food resources of herbivores: the case for meadow voles (**Microtus pennsylvanicus**). Oecologia 71:510–517
- Bertiller M, Bisigato A (1998) Vegetation dynamics under grazing disturbance. The state and transition model for the Patagonian steppes. Ecol Austr 8:191–201
- Bonino NA (1995) Introduced mammals into Patagonia, Southern Argentina: consequences, problems and management strategies. Paper presented at the integrating people and wildlife for a sustainable future, First international wildlife management congress
- Bozinovic F (1995) Nutritional energetics and digestive responses of an herbivorous rodent (**Octodon degus**) to different levels of dietary fiber. J Mamm 76:627–637
- Bozinovic F, Veloso C, Rosenmann M (1988) Cambios del tracto digestivo de **Abroitrix andinus** (Cricetidae) efecto de la calidad de dieta y requerimientos de energia. Rev Chil Hist Nat 61:245–251
- Branch L, Sosa R (1994) Foraging behavior of the plains vizcacha **Lagostomus maximus** (Rodentia: Chinchillidae), in semi-arid srub of central Argentina. V Sil Neo 3:96–99
- Branch L, Villareal D, Pelliza Sbriller A, Sosa R (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
- Branch L, Villareal D, Fierro JL, Portier KM (1996) Effects of local extinction of the plains vizcacha (**Lagostomus maximus**) on vegetation patterns in semi-arid scrub. Oecologia 106:389–399
- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol 22:37–47
- Bustos C (1996) Climodiagramas de localidades seleccionadas de la Provincia de Río Negro. Comunicación técnica, vol 16. Área Recursos Naturales Agrometeorología INTA, Bariloche
- Byers CR, Steinhorst R, Krausman PR (1984) Clarification of a technique for analysis of utilizacion-availability data. J Wildl Manage 48:1050–1053
- Caughley G, Sinclair A (1994) Wildlife ecology and management. Blackwell Scientific, Boston
- Cavagnaro F, Golluscio R, Wassner D, Ravetta D (2003) Caracterización química de los arbustos patagónicos con diferente preferencia por parte de los herbívoros. Ecol Aust 13:215–222
- Cortés A, Rau JR, Miranda E, Jimémez JE (2002) Hábitos alimentarios de Lagidium viscacia y Abrocoma cinerea: dos roedores sintópicos en ambientes altoandino del norte de Chile. Rev Chil Hist Nat 75:583–593



340 Acta Theriol (2012) 57:333–341

- Cossíos D (2004) La liebre europea, Lepus europaeus (Mammalia, Leporidae), especie invasora en el sur del Perú. Rev Per Biol 11:209–212
- Covich A (1976) Analysing shapes of foraging areas: some ecological and economics theories. Ann Rev Ecol 7:235–257
- Crawley M (1983) Herbivory. The dynamics of animal plants interactions. Blackwell Scientific, Oxford
- Crespo J (1963) Dispersión del Chinchillón *Lagidium viscacia* (Molina) en el Noroeste de la Patagonia y descripción de una nueva especie (Mammalia; Rodentia). Neotropica 9:61–63
- Dearing DM, Mangione AM, Karasov WH (2000) Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. Oecologia 123:397–405
- Dement MW, Van Soest P (1985) A nutritional explanation for bodysize patterns of ruminant and nonruminant herbivores. Am Nat 125:641–672
- Díaz GB, Ojeda RA (2000) Libro Rojo de Mamíferos Amenazados de la Argentina. Sociedad Argentina para el estudio de los Mamíferos SAREM, Mendoza
- Ellis JE, Wiens JA, Rodell CF, Anway JC (1976) A conceptual model of diet selection as an ecosystem process. J Theor Biol 60:93–108
- Farji-Brener A, Ghermandi L (2004) Seedling recruitment in a semiarid Patagonian steppe: facilitative effects of refuse dumps of leafcutting ants. J Veg Sci 15:823–830
- Feinsinger P, Spears E, Poole R (1981) A simple mesure of niche breadth. Ecol Lett 62:27–33
- Galende GI (2010) Patrones de uso de recursos alimentarios y espaciales del chinchillón (*Lagidium viscacia*) y la liebre europea (*Lepus europaeus*) en roquedales del NO Patagónico. Universidad Nacional de La Plata, [PhD dissertation] La Plata
- Galende GI, Grigera D (1998) Relaciones alimentarias de Lagidium viscacia (Rodentia, Chinchillidae) con herbívoros introducidos en el Parque Nacional Nahuel Huapi, Argentina. Iheringia, Sér Zool 84:3–10
- Galende GI, Raffaele E (2008) Space use of a non-native species, the european hare (*Lepus europaeus*), in habitats of the southern vizcacha (*Lagidium viscacia*) in Nothwestern Patagonia, Argentina. Eur J Wildl Res 54:299–304
- Galende GI, Trejo A (2003) Depredación del águila mora (Geranoaetus melanoleucus) y el búho (Bubo magellanicus) sobre el chinchillón (Lagidium viscacia) en el noroeste de la Patagonia. Mastozool Neotrop 10:143–147
- Galende GI, Grigera D, von Thüngen J (1998) Composición de la dieta del chinchillón (*Lagidium viscacia*, Chinchillidae) en el noroeste de la Patagonia. Mastozool Neotrop 5:123–128
- Grigera D, Rapoport E (1983) Status and distribution of the European hare in South America. J Mamm 64:163–166
- Hanley TA (1982) The nutritional basis for food selection by ungulates. J Range Manage 35:148-150
- Hoeck HN (1975) Differential feeding behaviour of the sympatric hyrax *Procavia johnstoni* and *Heterohyrax brucei*. Oecologia 22:15–47
- Holechek JL, Gross B (1982) Evaluation of different calculation procedures for microhistological analysis. J Range Manage 35:721– 730
- Holmes WG (1991) Predator risk affects foraging behavior of pikas: observational and experimental evidence. Anim Behav 42:111–119
- Huntly N (1987) Influence of refuging consumers (Pikas: Ochotona princeps) on subalpine meadow vegetation. Ecology 68:274–283
- Huntly N, Smith A, Ivins B (1986) Foraging behaviour of the pika (*Ochotona princeps*), with comparations of grazing versus having. J Mamm 67:139–148
- Jackson JE (1985) Ingestión voluntaria y digestibilidad en la vizcacha (*Lagostomus maximus*). Rev Arg Prod Anim 5:113–119
- Kitzberger T, Raffaele E, Heinemann K, Mazzarino MJ (2005) Multiple effects of fire severity on tree regeneration in northern

- Patagonian subalpine forests: an experimental approach. J Veg Sci 16:5-12
- Kotler BP, Brown JS (1999) Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of deserts granivores. J Mamm 80:361–374
- Kotler BP, Brown JS, Knight MH (1999) Habitat and patch use by hyraxes: there's no place like home? Ecol Lett 2:82–88
- Krebs C (1989) Ecological methodology. Harper & Row, New York
- Latour M, Pelliza de Sbriller A (1981) Clave para la determinación de la dieta de herbívoros en el NO de Patagonia. Rev Inv Agr INTA XV:109–157
- León RJ, Bran D, Collantes M, Paruelo JM, Soriano A (1998) Grandes unidades de vegetación de la Patagonia extra andina. Ecol Aust 8:125–144
- Mateucci S, Colma A (1982) Metodología para el estudio de la vegetación. Monografía N 22. OEA, Washington DC
- Matheson JD, Larson DW (1998) Influence of cliffs on bird community Diversity. Can J Zool 76:278–287
- Merino ML, Carpinetti BN, Abba AM (2009) Invasive mammals in the national parks system of Argentina. Nat Areas J 29:42–49
- Milton K (1979) Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. Am Nat 114:362–378
- Muñoz E, Garay A (1985) Régimen de precipitaciones de la Provincia de Río Negro. Comunicacion técnica. Instituto de Tecnología Agropecuaria, Bariloche
- Naya D, Bozinovic F, Karasov W (2008) Latitudinal trends in digestive flexibility: testing the climatic variability hypothesis with data on the intestinal length of Rodents. Am Nat 172:122–134
- Neu C, Byers CR, Peek J (1974) A technique for analysis of utilization availability data. J Wildl Manage 38:541–545
- Novaro AJ, Capurro AF, Travaini A, Funes MC, Ravinovich JE (1992) Pellet-count sampling based on spatial distribution: a case study of European hare in Patagonia. Ecol Aust 2:11–18
- Nutt KJ (2007) Socioecology of rock-dwelling rodents. In: Wolf JO, Sherman PW (eds) Rodent societies: an ecological and evolutionary perspective. Chicago University Press, Chicago, pp 35–48
- Paruelo J, Bertiller MB, Schlichter TM, Coronato F (1993) Secuencias de deterioro en distintos ambientes Patagónicos. Su caracterización mediante el modelo de Estados y Transiciones. Informe Técnico INTA-GTZ. Intituto de Tecnología Agropecuaria INTA, Bariloche
- Pearson O (1995) Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, Southern Argentina. Museum of Vertebrate Zoology. University of California, Berkeley, CA, USA
- Pelliza A, Willems P, Nakamatsu V, Manero A (eds) (1997) Atlas dietario de Herbívoros patagónicos. PRODESAR-INTA-GTZ. Bariloche, Argentina
- Penry DL (1993) Digestive constrains on diet selection. In: Hughes RN (ed) Diet selection. An interdisciplinary approach to foraging behaviour. Blackwell Scientific, Oxford, UK, pp 32–55
- Puig S, Videla F, Cona MI (1997) Diet and abundance of the guanaco (*Lama guanicoe Müller 1776*) in four habitats of northern Patagonia, Argentina. J Arid Environ 47:291–308
- Puig S, Videla E, Cona M, Monge S, Roig V (1998) Diet of the mountain vizcacha (*Lagidium viscacia* Molina, 1782) and food availability in the northern Patagonia, Argentina. Mamm Biol 63:228–238
- 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, M C, Videla F, Mendez E (2009) Diet of the mara (*Dolichotis patagonum*), food availability and effects of an extended drought in Northern Patagonia (Mendoza, Argentina). doi:101016/jmambio200912003



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- Quirici V, Castro R, Ortiz-Tolhuysen L, Chesh A, Burger J, Miranda E, Cortés S, Hayes L, Ebensperger L (2010) Seasonal variation in the range areas of the diurnal rodent *Octodon degus*. J Mamm 91:458–466
- Reus Ruiz ML (2006) Caracterización del habitat y composición de la dieta de Lagidium viscacia (Chinchillidae), en la Puna-San Juan-Argentina. Lic. thesis, Universidad Nacional de San Juan, San Juan, Argentina
- Rodriguez MD, Dacar M (2008) Composisción de la dieta de la mara (*Dolichotis patagonum*) en el sudeste del monte pampeano (La Pampa, Argentina). Mast Neotr 15:215–220
- Rosi M, Cona M, Videla F, Puig S, Monge S, Roig V (2003) Diet selection by the fossorial Rodent *Ctenomys mendocinus* inhabiting an environment with low food availability. Stud Neotropical Fauna Environ 38:159–166
- Sassi P, Borghi C, Bozinovic F (2007) Spatial and seasonal plasticity in digestive morphology of cavies (*Microcavia australis*) inhabiting habitats with different plant qualities. J Mamm 88:165–172
- Senft RL, Coughenour MB, Bailey DW, Ritttenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. BioScience 37:789–799
- Shipley L, Forbey J, Moore B (2009) Revising the dietary niche: when is a mammalian herbivore a specialist? Integr Comp Biol 49:274–290
- Sih A (1993) Effects of ecological interactions on forager diets: competition, predation risk, parasitism and prey behaviour. In: Hughes RN (ed) Diet selection. An interdisciplinary approach to foraging behaviour. Blackwell Scientific, Oxford (UK), pp 182–211
- Sombra M, Mangione A (2005) Obsessed with grasses? The case of mara *Dolichotis patagonun* (Caviidae: Rodentia). Rev Chil Hist Nat 78:401–408
- Somlo R, Durañona C, Ortiz R (1985) Valor nutritivo de las principales especies forrajeras patagónicas. Rev Arg Prod Anim 5:589-605
- Somlo R, Bonvissuto G, Sbriller A, Bonino N, Motriz E (1994) La influencia de la condición del pastizal sobre la dieta estacional de

- los herbívoros y el pastoreo múltiple, en sierras y mesetas occidentales de Patagonia. Rev Erg Prod Anim 14:187–207
- Sparks DR, Malechek JC (1968) Estimating percentage of dry weits in diets using a microscopic technique. J Range Manage 21:264–265
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press. Princeton. NJ. USA
- Stuth JW (1991) Foraging behaviour. An ecological perspective. In: Stuth JM (ed) Grazing management. Timber Press, Portland, OR, USA, pp 65–83
- Vázquez DP (2002) Multiple effects of introduced mammalian herbivores in a temperate forest. Biol Invasions 4:175–191
- Veloso C, Bozinovic F (1993) Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecol Lett 74:2003–2010
- Walker SR (2001) Effects of landscape structure on the distribution of mountain vizcachas (*Lagidium viscacia*) in the Patagonian Steppe. PhD dissertation, University of Florida, Gainesville, FL, USA
- Walker SR, Ackerman G, Schachter-Broide J, Pancotto V, Novaro AJ (2000a) Habitat use by mountain vizcachas (*Lagidium viscacia* Molina, 1782) in the Patagonia steppe. Mamm Biol 65:293–300
- Walker SR, Pancotto V, Schachter-Broide J, Ackerman G, Novaro AJ (2000b) Evaluation of a fecal-pellet index of abundance for mountain vizcachas (*Lagidium viscacia*). Mastozool Neotr 7:89– 94
- Weckerly FW, Kenedy ML (1992) Examining hypotheses about feeding strategies of white-tailed deer. Can J Zool 70:432–439
- Weir BJ (1971) Some notes on reproduction in the Patagonia Mountain viscachas *Lagidium boxi* (Mammalia; Rodentia). J Zool Lond 164:463–467
- Willig M, Mares T (1991) Food selection of a tropical Mammalian folivore in relation to leaf-nutrient content. J Mamm 72:314–321
- Zar JH (1999) Biostatistical analysis, 6th edn. Prentice-Hall, Upper Saddle River, NJ, USA

