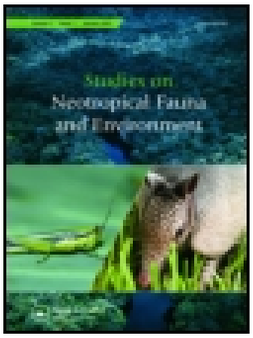

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ORIGINAL ARTICLE

Predator feeding ecology on Patagonian rocky outcrops: implications for colonies of mountain vizcacha (*Lagidium viscacia*)

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ABSTRACT
On 10 rocky outcrops with mountain vizcacha colonies, diets and trophic relations of five predator species were analyzed to evaluate their impact in vizcacha populations. Diets included 17 prey items of which mammals represented 97% of biomass. Lagomorphs were the most important prey, followed by sigmodontines, tuco-tucos, and mountain vizcachas. The Barn Owl was a specialized predator, while the culpeo and lesser grison were generalized consumers. Predation of mountain vizcacha by Magellanic Horned Owls and culpeo foxes could increase vizcacha vulnerability because vizcacha populations are small and fragmented, and females produce only one offspring per year.

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Lagidium viscacia; Magellanic Horned Owl; Barn Owl; mink; culpeo; lesser grison

Introduction

Rocky outcrops in varied forms are globally common ecosystems (Larson et al. 2000). These formations are little-disturbed habitats that include a wide variety of flora and fauna; in many cases species of high conservation value (Freeland et al. 1988; Ward & Anderson 1988; Matheson & Larson 1998). In Patagonia, as in other regions of the world, the ecology of rocky ecosystems is little studied, because they are usually in areas with extreme environmental conditions and are difficult to access (Larson et al. 2000; Nutt 2007). Several terrestrial predators are associated with these habitats in Patagonian steppe, among them the culpeo fox (*Lycalopex culpaeus*), gray fox (*Lycalopex griseus*), lesser grison (*Galictis cuja*), puma (*Puma concolor*), and in recent years, the exotic American mink (*Neovison vison*) has been recorded in rivers of the Patagonian steppe (Novaro et al. 2000; Delibes et al. 2003; Monserrat et al. 2005; Galende 2010). Rocky outcrops are used as refuge, for resting, nesting, and feeding by raptors such as the Barn Owl (*Tyto alba*), Black-chested Buzzard-eagle (*Geranoaetus melanoleucus*), and Magellanic Horned Owl (*Bubo magellanicus*) (Massoia & Pardiñas 1988; Trejo & Grigera 1998; Galende & Trejo 2003; Monserrat et al. 2005; Galende 2010).

The mountain vizcacha (*Lagidium viscacia*) is a native herbivore and strict habitat specialist (Walker et al. 2003) with spatial and feeding activities restricted to the areas surrounding rocky outcrops (Galende & Raffaele 2008, 2013). In recent years, a reduction in the number of individuals and colonies of *L. viscacia* has been observed in the study area. It is thought that this is a consequence of the specialization in a fragmented habitat, overgrazing by exotic herbivores, and hunting (Walker et al. 2000a). There is evidence that in the high Andes, mountain vizcachas are the main prey of Andean cats (*Oreailurus jacobita*) (Walker et al. 2007), and they are also prey of *Oncifelis* spp. in La Payunia Reserve (Berg 2007). In Patagonian rocky habitats, predation on populations of mountain vizcacha has not been assessed because in most studies they have not been recorded in predator diets (Hiraldo et al. 1995; Donázar et al. 1997; Travaini et al. 1997; Trejo & Grigera 1998; Novaro et al. 2000; Pillado & Trejo 2000; Monserrat et al. 2005; Zapata et al. 2007). Only two studies in steppe rocky outcrops have recorded the mountain vizcacha as prey (Massoia & Pardiñas 1988; Galende & Trejo 2003), but sampling design issues could have prevented its detection in predator diets. Our goal in this study was to describe the feeding ecology of five predators within rocky outcrops with mountain vizcacha colonies, and to evaluate the possible importance of predation on the mountain vizcacha populations.

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Materials and methods

Study area

Our study took place during summer (January 2004 and January 2005), in 14 rocky outcrops with mountain vizcacha colonies in the northwestern Patagonian steppe. Four rocky outcrops (Ne 1–4) were in Neuquén Province (39°35′ S, 70°80′ W) and 10 rocky outcrops (RN 1–10) in Río Negro Province (41°05′ S, 70°03′ W) in a range of altitude between 900 and 2700 m asl. In the Andes at from 41°S eastward, the rainfall gradient (> 3500 mm to 300 mm annually) is accompanied by changes in plant communities (Veblen & Lorenz 1988). The rocky outcrops are discrete entities that form "patches" within a homogeneous landscape of dwarf shrubs and grasses, among which the dominant species are the grasses *Stipa speciosa* and *Festuca pallescens* (both Poaceae), and the shrub *Mulinum spinosum* (Apiaceae) (León et al. 1998; Galende 2010). The climate is arid to semi-arid with cold winters and rain or snowfall, and dry and mild summers. The average temperature is from 2.1°C (July) to 15.3°C (January) (Muñoz & Garay 1985; Bustos 1996).

Sample collection

In 10 outcrops we collected and analyzed a total of 485 samples (raptor pellets and feces) from five potential predators of mountain vizcacha identified by direct sightings and indirect evidence (feces, feathers, hairs). The presence of predators was not recorded in three rocky outcrops of Neuquén Province and one near Bariloche city.

We established four parallel 100 m transects from the rocky outcrops, spaced at intervals of 10 m. Along each transect we collected fecal samples of terrestrial carnivores (n = 190). The total samples included: culpeo fox (10 rocky outcrops, N = 66), lesser grison (two rocky outcrops, N = 115), and American mink (one rocky outcrop, N = 9). Raptor pellets were collected in caves, crevices, and perches of the rocks. In seven rocky outcrops, we collected Barn Owl pellets (N = 245), and in one, we collected Magellanic Horned Owl pellets (N = 50). Some of the latter were not fresh when collected and probably dated from previous seasons of the year.

Laboratory analysis and identification

The raptor pellets were air dried, and fecal samples of terrestrial carnivores were dried at 50°C (Marti 1987). Prey was identified by skull fragments, teeth, feathers, and hairs, using reference collection (UNCo). The scale patterns from cuticle and hair medulla were identified microscopically and compared to specimens from the reference collection of Comahue University (UNCo). For the scale patterns, we cleaned and soaked three subsamples of hairs per sample in hot water for three minutes and then immersed them in sulfuric ether. Once dried, we mounted the hairs in a thin layer of nail enamel. For microscopic observation of the medulla, we immersed hairs in 70% alcohol. Rodents and exotic ungulates were identified by skulls and taxonomic keys of hair (Chehébar & Martin 1989; Pearson 1995; De Marinis & Asprea 2006).

Birds and reptiles were identified on the basis of feathers, scales, and bones. Reptile scales and bird feathers found in one sample were considered as one individual. The arthropods were identified to the lowest taxonomic level possible. In the lesser grison feces, we were unable to distinguish between hare and rabbit hairs and so they were grouped as lagomorphs.

Plant fragments present in fecal samples were analyzed by microhistological methodology (Baumgartner & Martin 1939) and identified based on reference specimens from the Comahue University Laboratory. Two species of sympatric canids (culpeo and gray fox) coexist in the area; we determined by fecal size, altitude, and habitat type that our samples were all from culpeo foxes.

Data analysis

The frequency of prey items (F) was expressed as a proportion of the total number of prey items per species, and the frequency of occurrence (FO) as a percentage of the total fecal samples with that item. For fruits, only the frequency of occurrence in the feces was calculated since the fragmented tissues did not allow us to estimate the number of fruits consumed.

The dietary niche breadth for each carnivore was described by Levins' measure (1968), and standardized by Colwell and Futuyma (Feinsinger et al. 1981) $Bst = (B-1)/(n-1)$, where $B = 1/\Sigma(p_i)^2$, pi is the proportion of item i in the diet and n is the total number of taxa consumed by each species. These values vary between 0–1 and values nearest to 1 indicate the most generalized diet.

The geometric mean weight of vertebrate prey (MWVP) in a diet sample was calculated for each predator by multiplying the log-transformed mean weight of each vertebrate prey type by the number of that prey in the sample, adding these products, dividing them by the total number of vertebrate prey, and backtransforming this sum (Iriarte et al. 1991). This calculation partially

compensates for the skewed distribution of prey sizes and the potential over- or under-estimating of the mean weight of prey from using mean weights for each prey type (Marti et al. 1993). Frequency of occurrence (percentage of total feces in which an item was found) by the mass was used to calculate relative biomass consumed (Iriarte et al. 1991).

The weight of each prey species was taken from bibliography and previous studies (Redford & Eisenberg 1992; Pearson 1995; Trejo et al. 2005). The weight of sigmodontines was calculated as the mean of most commonly consumed species in the study area (Galende & Trejo 2003). For juveniles and adults of *L. viscacia*, we used 500 and 1000 g respectively, and the weight of lagomorph juveniles was estimated from comparisons with skeletons of our reference collection. We could not estimate mass for bird eggs because we did not know the species, thus they were excluded in the analysis.

For *Capra aegagrus* and *Ovis aries* we assumed prey weights of small livestock at 5 kg. In the diet of lesser grison livestock remains were assumed to be carrion, and they were excluded from calculations of mean weight of vertebrate prey.

Associations between carnivore species and food items were described by correspondence factorial analysis (CFA) (Lebart et al. 1995). Frequencies of dietary items were grouped into nine categories: (1) sigmodontines; (2) tucos (*Ctenomys haigi*); (3) mountain vizcacha (*Lagidium viscacia*); (4) lagomorphs (European hare (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*)); (5) ungulates (sheep (*Ovies aries*) and goats (*Capra aegagrus*); (6) birds; (7) reptiles; (8) arthropods; and (9) plants. Hares and rabbits coexisted on a rocky outcrop with lesser grisons, and were treated as lagomorphs in their diet.

The five species of predators were treated individually in the data matrix. Plants were treated as an illustrative variable and the American mink as an illustrative individual because they were underrepresented in the feces. Edentates and marsupials were prey of minor value that were excluded in this analysis.

Results

Five species of predators were identified in 10 rocky outcrops studied in northwestern Patagonia: the lesser grison, the culpeo fox, the American mink, the Barn Owl, and the Magellanic Horned Owl. The diets included 16 prey types (Table 1) and sigmodontine rodents were the main prey category of all rocky outcrop predators, with a mean frequency of 51%. The European hare was found in the diet of two carnivores and one raptor (17.2%) and was important especially for culpeo fox, accounting for about half of the prey items. *Ctenomys haigi* was consumed by four predators, averaging 6.3%, and the mountain vizcacha was preyed upon by the Magellanic Horned Owl and culpeo fox (1.6%). Arthropods were frequently consumed by all predators while birds and reptiles occurred in very low frequencies. The plant material found in 66% of the feces from lesser grison consisted mainly of *Berberis* sp. fruits, and grasses.

The culpeo fox had the highest mean weight of vertebrate prey (MWVP), due to the high consumption of hares (Table 1). In terms of consumed biomass, mammals represented 98%, with lagomorphs and sigmodontines the most important prey (Table 2). Tuco-tucos were important for raptors, and mountain vizcachas for Magellanic Horned Owls. In total biomass, the contribution of reptiles, birds, and arthropods was low. However, reptiles and birds represented 2.16% of the biomass consumed by the lesser grison; while arthropods constituted the second most important prey of mink (Table 2).

Lesser grisons showed the widest dietary niche (B_{st} = 0.228) followed by the culpeo (B_{st} = 0.172), Magellanic Horned Owl (B_{st} = 0.171), American mink (B_{st} = 0.085), and Barn Owl (B_{st} = 0.084, Table 1).

The relationships between carnivores and prey described by CFA explained 89% of the data variation in the first two axes and reflected the prey category breadth calculated for the predators. The first axis differentiated specialized diets from more generalized diets (Figure 1). Barn Owls showed the most specialized niche, with a diet based mainly on sigmodontines, followed by American mink, while Magellanic Horned Owls showed an intermediate feeding behavior. In contrast, lesser grisons were the most generalized predators, with the consumption of sigmodontines, tuco-tucos, lagomorphs, ungulates (probably as carrion), birds, and plants. The prey spectrum of culpeos was also wide but mainly dominated by European hares (Table 1).

Discussion

Sigmodontine rodents were the most frequent prey in the diets of predators in the rocky outcrops, and constituted over half the diet of minks and owls. In Chile the most important prey for mink was the exotic muskrat (*Ondatra zibethicus*), and together

Table 1. Diet composition in feces of lesser grison, culpeo fox, American mink, Barn Owl, and Magellanic Horned Owl, in 10 rocky outcrops on northwestern Patagonia.

		Lesser grison			Culpeo fox			American mink			Barn Owl			Magellanic Horned Owl		
Prey species	Body mass (g)	N	F	FO	N	F	FO	N	F	FO	N	F	FO	N	F	FO
Rodentia																
Sigmodontinae	47.4	58	31.9	50.4	26	26.3	39.4	9	60	100	372	87.9	100	48	49	96
Ctenomys haigi	146.2	10	5.5	8.7	9	9.1	13.6	—	—	—	29	6.9	12	10	10.2	20
Lagidium viscacia	(500–1000*)	—	—	—	2*	2	3	—	—	—	—	—	—	5–1*	6.1	12
Lagomorpha																
L. europaeus- O. cuniculus	(500)	50	27.5	43.5	—	—	—	—	—	—	—	—	—	—	—	—
Lepus europaeus	(500–3100*)	—	—	—	48*	48.5	72.7	—	—	—	—	—	—	10	10.2	20
Edentata	300	1	0.5	0.9	—	—	—	—	—	—	—	—	—	—	—	—
Marsupialia	20	—	—	—	—	—	—	—	—	—	1	0.2	0.4	—	—	—
Ungulates (*Capra aegagrus/Ovis aries*)	5000	36[a]	19.8	31.3	5	5.1	7.6	—	—	—	—	—	—	—	—	—
Birds	70	8	4.4	7	2	2	3	—	—	—	—	—	—	—	—	—
Eggs	—	1	0.5	0.9	—	—	—	—	—	—	11	2.6	4.48	—	—	—
Reptiles	19	5	2.7	4.3	—	—	—	—	—	—	—	—	—	—	—	—
Arthropods																
Orthoptera	2	10	5.5	8.7	7	7.1	10.6	—	—	—	—	—	—	—	—	—
Coleoptera	2	3	1.6	2.6	—	—	—	3	20	33.3	8	1.9	3.26	19	19.4	38
Crustaceans	7	—	—	—	—	—	—	3	20	33.3	—	—	—	—	—	—
Scorpions	4	—	—	—	—	—	—	—	—	—	2	0.5	0.81	4	4.1	8
Phasmatodea	2	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2
Plants/fruits	—	76	—	66.1	7		10.6	1	—	11.1	—	—	—	—	—	—
Total animal items		182	—	—	99	100	—	15	—	—	423	—	—	98	—	—
Total vertebrates items		132			92			9			402			74		
Total samples		115	—	—	66	—	—	9	—	—	245	—	—	50	—	—
MWVP (g)		126.3			650.6			49.8			51.6			92.7		
Bst			0.228			0.172			0.085			0.084			0.171	

[a]Includes carrion of *Capra aegagrus* and *Ovis aries*.

Abbreviations: *N*, the total number of individuals of each item found in feces; F, their proportion (in %) of total number of food items; FO, the proportion (%) of fecal samples that contained that food item. *indicates the maximum weight value of the prey.

Table 2. Percent biomass of main prey taxa at 10 rocky outcrops in northwestern Patagonia.

	Lesser grison %	Culpeo fox %	Magellanic Horned Owl %	Barn Owl %	American mink %	Biomass %
Lagomorphs	82.80	83.30	40.70	0.00	0.00	41.36
Sigmodontines	9.10	0.70	18.50	80.41	94.05	40.54
Ctenomys haigi	4.84	0.70	11.80	19.33	0.00	7.33
Lagidium viscacia	0.00	1.12	28.40	0.00	0.00	5.90
Edentata	0.99	0.00	0.00	0.00	0.00	0.20
Marsupialia	0.00	0.00	0.00	0.09	0.00	0.02
Ungulates*	0.00	14.00	0.00	0.00	0.00	2.80
Arthropods	0.09	0.01	0.40	0.10	5.95	1.31
Reptiles	0.31	0.00	0.00	0.00	0.00	0.06
Birds	1.85	0.08	0.00	0.00	0.00	0.39

*Ungulates includes *Capra aegagrus/Ovis aries*

with the native rodent *Abrothrix xanthorhinus* it accounted for 78% of the biomass intake (Schüttler et al. 2008). In our study, Barn Owls consumed rodents almost exclusively, and they showed specialized feeding behavior. These results are similar to those found by other studies in the region, where sigmodontines accounted for from 93.2–96.6% of Barn Owl prey numbers (Travaini et al. 1997; Trejo et al. 2005) and 96.6% of the consumed biomass, while the most important species in terms of total biomass was *Ctenomys haigi* (Trejo et al. 2005).

In the diet of Magellan Horned Owls, arthropods were a frequent prey, but hares, mountain vizcachas, sigmodontines, and *Ctenomys haigi* totaled 95% of the biomass consumed. The detection of vizcachas in the diet of this raptor shows that they might be an important predator. These results confirm the generalist feeding behavior of Magellanic Horned Owls (Donázar et al. 1997; Monserrat et al. 2005; Trejo et al. 2005).

Lagomorphs comprised the main prey in biomass for both the culpeo fox and lesser grison, although these predators consumed varied diets that were

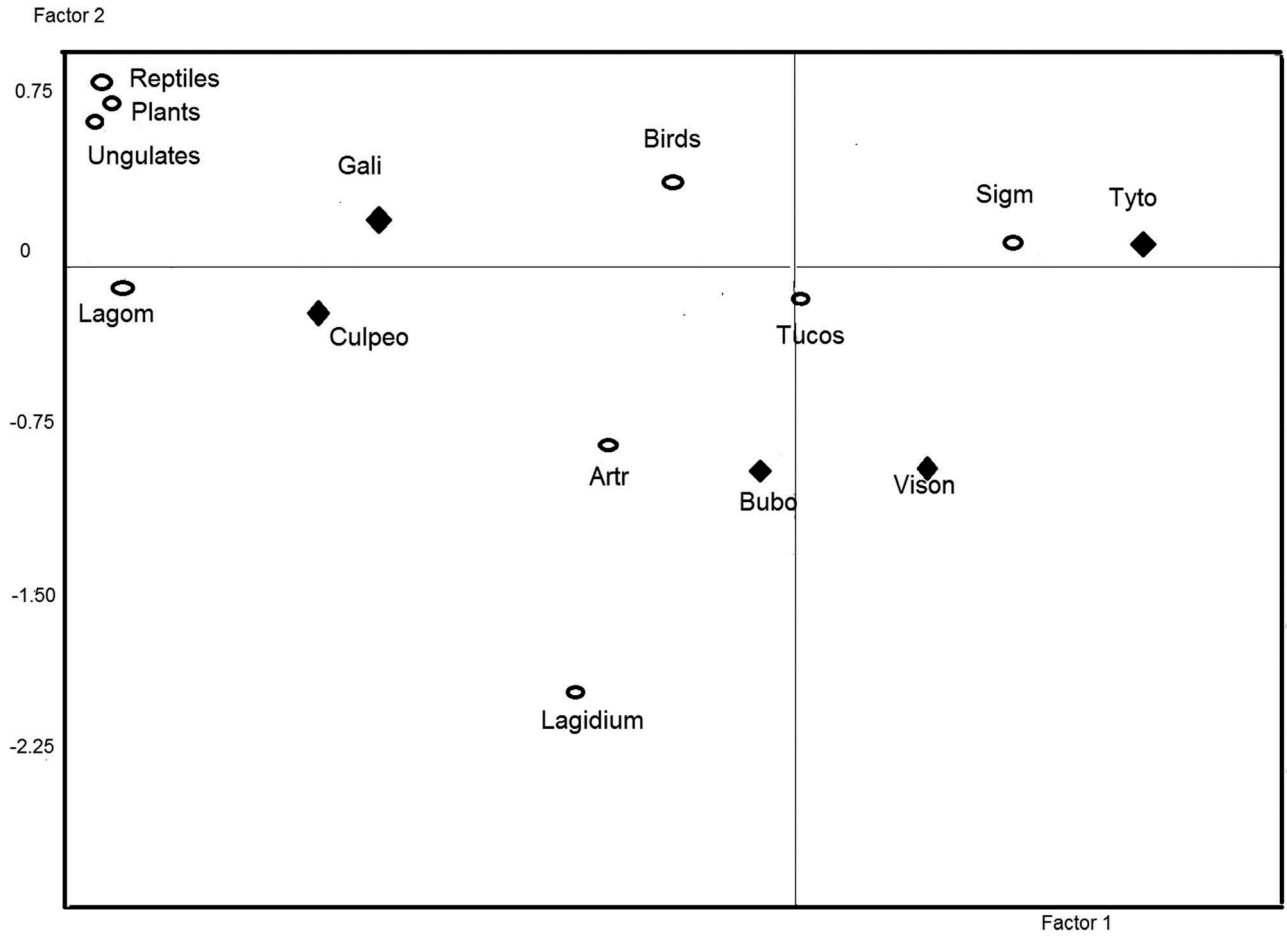

Figure 1. Diet associations comparing frequency of occurrence of food items by carnivore. Factorial correspondence analysis in dimensions 1 and 2. Carnivores: Gali: *Galictis cuja*, Tyto: *Tyto alba*, Culpeo: *Lycalopex culpaeus*, Bubo: *Bubo magellanicus*, Vison: *Neovison vison*. Prey: Artr: Arthropods, Sigm: Sigmodontines, Lagom: Lagomorphs, Tucos: Ctenomyidae.

reflected in the widest dietary niche breadth. Similar diets have been reported in several studies from the Patagonia region (Novaro et al. 2000; Delibes et al. 2003; Zapata et al. 2007).

Diet of aerial predators

Magellanic Horned Owls were intermediate in prey diversity among rocky outcrop predators, and due to prey of vizcacha juveniles, the mean weight of vertebrate prey in our sample was almost double that determined in previous studies (36.5–47 g) (Donázar et al. 1997; Trejo et al. 2005). Juveniles of exotic hares comprise the main prey biomass. The range in prey size of this raptor is as broad as reported in other studies (17.4–1000 g) (Donázar et al. 1997; Trejo et al. 2005). The consumption of young lagomorphs (<1000 g) shows that juvenile vizcachas are within the size range of prey, but the larger size of adult vizcachas (>2000 g) could restrict capture, as has been suggested for adults of hares (Donázar et al. 1997). The capture of vizcachas is probably influenced by the antipredator behaviors, such as the use of vigilance sites and alarm vocalizations, which decrease predation risk (Galende 2010). At sunset, when the vizcachas are feeding, temporal overlap with Magellanic Horned Owls makes them vulnerable to predation (Walker et al. 2007; Galende 2010). Our finding of vizcachas in the diet of Magellanic Horned Owls differs from the results of other studies performed in the region (Donázar et al. 1997; Trejo et al. 1998; Monserrat et al. 2005; Trejo et al. 2005). A previous study in the same rocky outcrop reported that only six vizcachas inhabited the colony (Galende & Trejo 2003). Predation, even at low levels, contributes to the vulnerability of small (3–20) isolated colonies (Walker et al. 2000b).

Mountain vizcachas were not recorded as prey of the nocturnal Barn Owls, which agrees with other studies from the region (Travaini et al. 1997; Pillado & Trejo 2000; Trejo et al. 2005). This owl captured small prey (47–146 g) and hares were not found in its

diet. The mean prey weight reported for Barn Owls ranges from 15.5–300 g (Trejo et al. 2005); vizcachas are therefore outside the capture size range of this raptor.

Diet of terrestrial carnivores

The diet of culpeo foxes included a wide range of prey, which confirms the generalist behavior reported previously (Silva et al. 2005; Walker et al. 2007; Zapata et al. 2007, Palacios et al. 2012). Regarding mountain vizcachas, a similar feeding behavior was found in Andean habitats of northern Argentina, where these accounted only 3.2% of their diet (Walker et al. 2007).

Low predation levels on a native species like the vizcacha could be due to its patchy distribution and low relative abundance compared to the European hare, a more profitable prey item by its numbers and size (Novaro et al. 2000; Walker et al. 2000a, 2007; Palacios et al. 2012). Other reasons for low predation on vizcachas might be the limited prey-capture ability of culpeos and the morphological and behavioral characteristics of vizcachas. It was observed in Peru that culpeos lurk to hunt vizcachas (*Lagidium peruanum*), but that their capture on the rocks had low success rates (Pearson 1948). The plantar pads and short claws of vizcachas enable rapid escape on the rocks near which they forage.

A generalist diet of lesser grisons has been described in several studies (Ebensperger et al. 1991; Diuk-Wasser & Cassini 1998; Delibes et al. 2003; Zapata et al. 2007), with results similar to ours, although we found greater consumption of carrion. This was probably due to local livestock management in the region (G. Galende pers. obs.). An unusual finding was the consistently high presence of plants and fruits in the analyzed feces, indicating that plants are an important component of the diet of lesser grison. In Italy, the mustelids *Mustela nivalis* and *M. erminea* eat mainly small rodents, but wild fruits are also eaten throughout the year, suggesting an opportunistic behavior (Remonti et al. 2007). In Chile, fruits of *Cryptocarya alba* (Ebensperger et al. 1991) were identified once in a grison diet, and thus far not at all in Argentinean Patagonia (Delibes et al. 2003; Zapata et al. 2007). Our microhistological technique allowed us to identify small plant fragments that might have been previously overlooked.

These first data on mink diets in steppe habitats showed that mammals were the most important items of consumed biomass. In contrast, in Patagonian Andean lakes, diets included a high frequency of crustaceans and low frequencies of mammals, although data on biomass was lacking (Previtali et al. 1998). This generalist predator hunts prey from both aquatic and terrestrial sources in variable proportions depending on local and seasonal availability of prey (Schüttler et al. 2008). The opportunistic behavior of this highly adaptable predator can be detrimental to native species (Previtali et al. 1998; Schüttler et al. 2008; Peris et al. 2009). Delibes et al. (2003) mentioned that hunting-habitat preference segregates lesser grisons from American minks (*Mustela vison*) because the latter has a diet based on aquatic species. However, the progressive expansion of this exotic carnivore into the steppe, and its high consumption of sigmodontines, require re-evaluating the spatial and dietary overlap with grisons and other Patagonian carnivores.

The mustelids are known for their skill in entering the galleries of rodents (Delibes et al. 2003) and they have been noted to capture chinchillas (*Chinchilla lanigera*) from their caves (Redford & Eisenberg 1992). This ability of minks is a new threat to the conservation of native species such as mountain vizcachas. Populations merit monitoring because minks are currently expanding into the area of rocky outcrops.

In summary, our results on carnivore feeding ecology show that rocky outcrops concentrate a high diversity of predators and prey. Understanding predation on vizcachas is important for their conservation, because with only one offspring per year (Weir 1971), and small and fragmented populations even low predation levels could cause the decline of local populations (Walker et al. 2000b, 2003).

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