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Original Investigation

Differences in diet and trophic interactions of Patagonian carnivores between areas with mostly native or exotic prey

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ABSTRACT

The prey base for Patagonian carnivores has been altered greatly over the past 150 years due to widespread overgrazing by livestock, invasions by exotic wildlife, and hunting. On ranches in northern Patagonia carnivores consume mostly exotic species, and native herbivores are ecologically extinct in their role as prey. In this study we compare diets of the culpeo (*Lycalopex culpaeus*), chilla (*L. griseus*), puma (*Puma concolor*), Geoffroy's cat (*Leopardus geoffroyi*), colocolo (*L. colocolo*), and hog-nosed skunks (*Conepatus chinga* and *C. humboldtii*) in a reserve with a mostly native prey base to their diets on the ranches, and evaluate how differences in prey bases affect trophic interactions among carnivores. Carnivores in the reserve consumed mostly native prey. Dietary overlap among carnivores was not significant on the reserve, but was highly significant on the ranches. This homogenization of diets where densities of native species are reduced could lead to stronger negative interactions among carnivores, altering the composition of the carnivore assemblage to the detriment of the more specialized species. Study of carnivore diets may be a relatively quick way to evaluate the conservation status and ecological functionality of prey assemblages in Patagonia and other areas where these have been altered.

Introduction

Human activities such as livestock husbandry, agriculture, hunting, introduction of exotic species, and predator control can alter the composition of carnivore and prey assemblages, and modify intraguild and predator–prey interactions (Michalski and Peres 2005; Shapira et al. 2008; Blaum et al. 2009). Over the last 150 years, populations of native herbivores of the Patagonian steppe of South America were reduced through hunting and active persecution to make way for sheep and other livestock. The top predator, the puma (*Puma concolor*), was extirpated from most of the region, but has rebounded in the last 30 years, and smaller carnivores were heavily hunted (Walker and Novaro 2010). These drastic changes in prey base resulted in a switch by carnivores and raptors from consumption of native prey to exotic species and livestock in many parts of Patagonia (Jimenez and Jaksic 1991; Johnson and Franklin 1991, 1994; Pavez et al. 1992; Hiraldo et al. 1995; Donazar et al. 1997; Novaro et al. 2000a, 2004; Monserrat et al. 2005; Lambertucci et al. 2009).

Nowadays, the introduced European hare is probably a more profitable prey item than most native prey, due to its numbers, size, and vulnerability (Novaro et al. 2004), and in areas of high density of livestock, carrion from livestock provides an ample and profitable source of food. Carnivores most capable of exploiting these plentiful introduced resources may increase their fitness and become more abundant than those less capable of doing so, changing the composition, relative abundances, and trophic interactions within the carnivore assemblage compared to areas with a less altered native prey base (Roemer et al. 2002; Berger 2008).

Most of the Patagonian steppe and scrub is in private hands, principally large ranches. On large ranches in northern Patagonia, livestock and introduced wildlife comprise 94% of the herbivore and omnivore biomass (Novaro et al. 2000a). Predator–prey interactions on those ranches were documented in a previous study (Novaro et al. 2000a), and large native herbivores were found to be "ecologically" extinct (Estes 1996), no longer fulfilling their ecological role as prey. Given the patterns of land use and tenure throughout Patagonia, this ecological extinction of native prey and altered predator–prey interactions is likely widespread.

In this study we describe diets of the carnivore assemblage in the Auca Mahuida Reserve in Patagonia where densities of livestock and exotic wildlife are low and density of guanacos, the previously dominant native herbivores of the Patagonian steppe, remains relatively high. We compare trophic interactions among carnivores in

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the reserve with those results published by Novaro et al. (2000a) on Patagonian ranches with high densities of exotic prey and low densities of large native prey. Conditions on the reserve likely represent more closely those prior to the arrival of Europeans than do the currently prevailing conditions throughout most of Patagonia, and may provide a benchmark for efforts to restore or conserve native carnivore assemblages and predator–prey interactions in protected areas and other places where the conservation of native ecosystems is a concern.

Material and methods

Study area

The Auca Mahuida Provincial Reserve encompasses 80,100 ha and lies in Neuquén Province, Argentina, between 37°30′–38°S and 68°30′–69°15′W. Although it is a reserve, it is used for grazing by livestock at low density, mainly sheep and goats. The landscape is a basaltic plate with numerous volcanic cones, with the reserve centered on the highest peak of 2253 m.a.s.l. The location of the reserve and its altitudinal gradient present a combination of biogeographical provinces, with dry scrub at the lowest elevations, Patagonian steppe over 1500 m.a.s.l., and high Andean elements at the peak of the volcano.

The carnivore assemblage in northern Patagonia includes two canid species—the culpeo (*Lycalopex culpaeus*) and chilla (*L. griseus*) (González del Solar and Rau 2004), five felid species—the puma (*Puma concolor*), Geoffroy's cat (*Leopardus geoffroyi*), colocolo (*L. colocolo*), the jaguarundi (*Puma yagouaroundi*), and the Andean cat (*Leopardus jacobita*), only recently discovered in the region, and four mustelids, including two hog-nosed skunks (*Conepatus chinga* and *C. humboldtii*), the grison (*Galictis cuja*) and the Patagonian weasel (*Lyncodon patagonicus*). The largest of these species by far is the puma (35–105 kg, Redford and Eisenberg 1992; Sunquist and Sunquist 2002), followed by the culpeo (6–12 kg, Fuentes and Jaksic 1979; Jiménez et al. 1997; Jiménez and Novaro 2004). The other cats and canids are intermediate (2–8 kg) in size, and the mustelids are the smallest of the carnivores (<1–3 kg).

The reserve is approximately 250 km northeast of the Patagonian ranches where large native wildlife was found to be ecologically extinct as prey (Novaro et al. 2000a). Habitats are similar, but with a greater proportion of steppe on the ranches and of scrub at the reserve. The carnivore assemblage is composed of the same species, and historically prey species were distributed throughout the whole area.

Diet

At the reserve carnivore scat samples were collected every 2 or 3 months between November 2002 and January 2004, through systematic searches of rocky outcrops, roads, and oil exploration trails, and along 23 transects, 500 m long and 4 m wide, placed randomly perpendicular to roads throughout the area. Scats were identified according to carnivore species by their size, morphology, associated tracks, and genetic analysis when possible. In this area culpeo foxes weigh 7.4–12.3 kg ($n = 26$) (Jiménez and Novaro 2004), and chilla foxes weigh 3.3–4 kg ($n = 44$) (González del Solar and Rau 2004). Scats of the two species are easily distinguished by diameter (Zapata et al. 2005, 2007). We considered canid scats <118 mm in diameter to be from chillas and >120 mm in diameter to be from culpeos (mean scat diameter and standard deviation were 99.3 mm ± 18.8 mm ($n = 56$) for chillas and 138.6 mm ± 18.6 mm ($n = 118$) for culpeos). Ten canid scats were discarded because we could not distinguish between the two species based on their intermediate size. As body sizes of small felids are similar among species and there are insufficient published data on sizes of scats produced by the different species, we distinguished small felid scats through DNA analysis. DNA was isolated from each scat with a QIAGEN Stool Kit (QIAGEN, CA, USA), amplifying the 16S rRNA mitochondrial gene (Johnson and O'Brien 1997), and comparing the resulting sequences to those of reference samples. This analysis was done at the Wildlife Genetics International (WGI) Laboratory, Nelson, BC, Canada. For all analyzed species, samples that were not clearly identified were discarded.

Diet at the ranches was obtained from previously published work (Novaro et al. 2000a), based on analysis of contents of stomachs of animals collected from hunters (320 culpeo, 42 chilla, 3 Geoffroy's cat, and 25 hog-nosed skunk), and scats (70 puma, 33 Geoffroy's cats, 1 colocolo) during 1989–1994. Because of low numbers of samples for colocolos at both sites and pumas on the reserve, we did not make comparisons between sites for those two species. Small and large prey have differential digestibility and the number of field-collectable scats can be inversely related to prey size (Ackerman et al. 1984; Weaver 1993). This problem is avoided in this report by using only percent occurrence and not biomass of different prey in the diet.

Scats were dried and washed, and their contents examined to determine food items. All prey items were identified to species when possible. Mammalian prey items were identified using teeth and hair patterns. Casts of hairs were made on stencil corrector fluid (Korschgen 1980), and their medulla and scale patterns were compared to those of mammals occurring in the study area using keys (Chehebar and Martin 1989; Pearson 1995; Fernández and Rossi 1998) or collection material at the Centro de Ecología Aplicada de Neuquén (CEAN; Center for Applied Ecology). Livestock were grouped as small (sheep, *Ovis aries* and goats, *Capra hircus*) or large (cattle, *Bos taurus* and horses, *Equus caballus*). Remains of large livestock found in the scats of carnivores other than pumas were considered scavenged and remains of small livestock and guanacos (*Lama guanicoe*) were considered scavenged by all but the puma and the culpeo. As our main interest was in evaluating the differences in diets related to differences in availability of native and exotic mammals, we grouped all arthropods, birds, and reptiles into independent single categories.

We present carnivore diets as percent occurrence of food items (number of times an item occurred as percentage of the total number of prey items in all scats), and the minimum number consumed of each prey item. To evaluate the adequacy of sample sizes obtained, we built accumulation curves of prey items, using the asymptote of the curve to identify the number of samples sufficient to describe the diet.

Prey density and biomass

Methods and sources for information on prey density and biomass on the ranches are presented in Novaro et al. (2000a). Data on density of potential prey species on the reserve were obtained from independent studies, identified in Table 1, except for the European hare.

Hare density was estimated using the pellet-count method and a calibration between pellet counts and line-transect data obtained in southern Neuquén (Lancia et al. 1994; Novaro et al. 1992, 2000a). We attempted to estimate hare densities using night counts along line transects (Buckland et al. 2001) in the reserve but densities were too low to record sufficient sightings. We estimated the yearly average of hare pellets recorded in January, April, August, and November 2003 along 46 transects of 500 × 4 m that were perpendicular to secondary roads and distributed randomly throughout the study area. Biomass of potential prey on the reserve was calculated as in Novaro et al. (2000a).

Table 1
Mean population densities (ind/km^2), body mass (kg) and overall percent biomass of dominant prey species and their carrion at two sites IN northern patagonia. AM is data obtained from the Auca Mahuida Provincial Reserve and Ranch is data extracted from Novaro et al. (2000a) for Patagonian ranches.

Prey	Body mass[a]	Density AM	Biomass AM	Density ranch[b]	Biomass ranch	Source
Introduced						
Large livestock	475–190–80	1.59 ± 2	22.3	4.78 ± 4.16	53.1	Rivas L. unpublished data
Small livestock	42–25–7	1.85 ± 3	2.5	26.31 ± 2.3	27.6	Rivas L. unpublished data
European hare	3.4–1.2	2.42 ± 3.17	0.3	47.48 ± 5	5.3	This study
Red deer (*Cervus elaphus*)	115–75–30	0	0	1.58 ± 0.3	4.7	
Subtotal			25.1		90.7	
Native						
Guanaco	120–80–30	9.53 ± 1.62	37.2	0.67 ± 0.13	2.1	Radovani (2004)
Lesser rhea	15–6–1	0.34 ± 0.19	0.1	0.62 ± 0.28	0.2	Rivas (2004)
Mara	8	1.15 ± 1.01	0.4	0	0	Rivas (2004); body mass: Campos et al. (2001)
Subtotal			37.7		2.3	
Carrion[b]						
Large ungulates[c]				0.55 ± 0.21	3.5	
Large livestock		1 ± 2	14.0			Heidel (2008)
Small livestock		4.38 ± 5.93	5.8	2.30 ± 0.54	2.4	Heidel (2008)
European hare			0	9.73 ± 2.36	1.1	
Guanaco		4.87 ± 4.53	17.4			Heidel (2008)
Total percent biomass			100.0		100.0	
TOTAL Kg/Km^2			2413.0		3048.2	

[a] Masses were obtained for adult, yearling and juvenile ungulates and rheas. For the reserve hare and mara body masses were considered to be that of an adult; at the ranches adult and young hares were considered and maras were not consumed.
[b] Data on carrion densities for ungulates and hares at the ranches was corrected from Novaro et al. (2000a), as densities were reversed.
[c] Includes cattle, horse, red deer and guanaco.

Data analysis

To evaluate and compare trophic interactions among carnivores, we analyzed the data from the reserve and the previously published data (Novaro et al. 2000a) on diets of carnivores from the Patagonian ranches. We used correspondence analyses to assess dietary separation (Ray and Sunquist 2001), and calculated niche overlap, niche breadth, and mean weight of vertebrate prey at each site. For the correspondence analyses we included only those food items that represented more than 5% of items for at least one of the carnivores. We calculated niche overlap using Pianka's index (1973) that ranges from 0 (no overlap) to 1 (complete overlap). To determine the probability that observed overlaps were greater or less than those that would be expected randomly, we did 1000 Monte Carlo randomizations to simulate possible overlaps among species with the program EcoSim 7.72 (Gotelli and Entsminger, 2001). If the observed overlap was significantly greater than the simulated mean overlap, it indicated that the food niche overlap among species was greater than the overlap expected by chance.

We determined niche breadth using Levin's formula (Levins 1968), standardized by Colwell and Futuyma (1971). The niche breadth index varies between 0 (restricted diet) and 1 (broad diet). Because of the wide range of body sizes of the carnivores in our sample, the maximum number of food items available (B_{max}) varies according to species, so we determined B_{max} for each species by counting the total number of food items the species would be capable of consuming out of all items that were consumed by at least one species.

We calculated mean weight of vertebrate prey (MWVP) following Jaksic and Braker (1983). We obtained mean weight values for each mammal prey species from the literature (Redford and Eisenberg 1992; Parera 2002; Bonino 2005). All prey items were considered to be adults, and for cricetine rodents we selected the most commonly consumed species (*Phyllotis darwinii*) and the two size extremes (*Eligmodontia typus* and *Reithrodon auritus*). For livestock the weights followed Novaro et al. (2004), assuming that the chilla could only prey on offspring of small livestock (5 kg). In the case of categories of grouped species (cricetine rodents, cavies, tuco-tucos, small marsupials and small livestock), we used the mean of all species as the mean for the category. For passerine birds and lizards we used a typical body mass.

Results

Prey base in the reserve and on the ranches

Percent biomass of introduced species for which we obtained data was nearly 4 times greater on the ranches than on the reserve, whereas biomass of native species was more than 16 times greater on the reserve than on the ranches (Table 1). In the reserve livestock were the dominant introduced species and guanaco the dominant native species. European hares were extremely rare on the reserve compared to on the ranches, with biomass per square kilometer less than that of the native mara.

Exotic red deer and wild boar were present on the ranches and not on the reserve, but those large species are available only to pumas except as carrion. Percent biomass of carrion was approximately 4 times greater on the reserve than on the ranches. This was in part due to the practice of collection and burying of livestock carcasses on the ranches, which herders do not carry out in the area of the reserve, and to higher livestock mortality on the reserve (A. Novaro, pers. obs.).

Diet and trophic interactions on the Auca Mahuida Reserve

We analyzed a total of 448 scat samples from the reserve, from six species (chilla $n = 84$, culpeo $n = 140$, hog-nosed skunk $n = 71$, Geoffroy's cat $n = 92$, colocolo $n = 16$, and puma $n = 6$; Table 2). Guanacos, maras (*Dolichotis patagonum*), and mountain vizcachas (*Lagidium viscacia*), the three largest-bodied native herbivorous mammals, were consumed on the reserve, but not on the ranches. Only six puma scats were analyzed, so we did no further analysis of puma diet. For all species except colocolo and puma, sample sizes were adequate for identifying principal prey items (Trites and Joy 2005). We did not calculate niche breadth or MWVP for colocolo due to the small sample size.

The five small and medium carnivores overwhelmingly consumed native food items, with introduced mammals representing

Table 2
Percentage of occurrence and minimum number of individuals (between brackets) of prey classes in a mesocarnivores assemblage for two sites in northern Patagonia. AM is data obtained from the Auca Mahuida Provincial Reserve and Ranch is data previously published by Novaro et al. (2000a) from Patagonian ranches.

Prey class	Chilla		Culpeo		Hognosed skunk		Geoffroyĭs cat		Puma		Colocolo	
	Ranch	AM	Ranch	AM	Ranch	AM	Ranch	AM	Ranch	AM	Ranch	AM
Introduced mammals (subtotal)		5.4		2.9		0.6		9.2		16.5		8.7
European hare	14.7	4.8 (10)	27.4	12.3 (37)		0.6 (1)	22.8	7.9 (14)	61.2		100	8.7 (2)
Small livestock			14.2	0.3 (1)						16.5 (1)		
Large livestock									0.4			
Carrion of livestock	26.2	0.6 (1)	9.4	0.3 (1)	4.8		3.8	1.3 (2)				
Native mammals (subtotal)		25.4		52.2		2.5		73.6		83.5		78.3
Cricetine rodents	26.2	5.7 (12)	31.1	18.9 (57)	0.6	0.6 (1)	58.2	23.6 (42)	26.0			
Tuco-tucos		13.8 (29)		14.2 (43)				17.3 (31)				65.3 (15)
Caviidae		2.9 (6)		6.3 (19)				23.6 (42)				8.7 (2)
Mara				2.0 (6)				0.6 (1)				
Mountain vizcacha		0.6 (1)		2.6 (8)				5.6 (10)				
Xenarthra	3.3		1.4	1.3 (4)				2.2 (4)	1.3			
Marsupialia		0.6 (1)		1.0 (3)								
Guanaco				3.0 (9)						83.5 (5)		
Carrion of guanaco		1.2 (2)		0.6 (2)				1.3 (2)				
Unidentified Carnivore				0.3 (1)								
Unidentified mammal	8.2	0.6 (1)	3.4	2.0 (6)	0.6	1.9 (3)		0.6 (1)				4.3 (1)
Other[a]	6.8		4.8				8.9				3.7	
Unidentified Carrion		0.6 (1)		1.3 (4)								
Birds	1.6	2.4 (5)	4.6	5.3 (16)			6.3	7.3 (13)	3.7			
Reptiles	4.9	5.2 (10)	1.8	5.3 (15)	1.8	5.6 (8)		3.4 (6)	1.9			
Unidentified vertebrate				0.6 (2)		3.1 (5)						
Arthropods	8.2	53.8		16.9	92.1	80.1		5.1				4.3
Plant component	1.6	7.1		5.4		8.1		0.6				8.7
Total food items	61	394	562	422	165	288	79	178	99	6		23
Total fecal samples		84		140		71	33	92	70	6	1	16
Total stomachs	42		320		25		3					

[a] Includes Mustelidae, Cavidae, *Ctenomys sp*, *Zaedyus pichyi*, *Thyllamys pusilla* (Novaro et al. 2000a).

less than 10% of the diet of each. Nevertheless, European hares were consumed at low frequencies by all species and carrion of livestock was occasionally consumed by culpeos, chillas, and Geoffroy's cats (Table 2). Small livestock was recorded only in one culpeo and one puma scat. The other five (83%) puma scats contained only guanaco.

Dietary separation among the carnivores of the reserve was evident in the correspondence analysis, as shown by the first two axes of variation that comprised 94% of total variation, 79% in the first axis and 14% in the second (Fig. 1). We identified two main dietary groups, with the culpeo and the two cats, on the left side of the graph, consuming mostly small and medium-sized rodents, and the chilla and hog-nosed skunk on the right side, consuming mostly arthropods and lizards. Among the smaller carnivores, the hog-nosed skunk was more strictly insectivorous than the chilla. The location of the two canid species close to the center of the graph suggests that they were the most generalist of the species analyzed, and the Geoffroy's cat's position close to the culpeo indicates similar diets regarding prey items, but the felid has a clear tendency to a more specialized diet on rodents. The culpeo consumed cricetines, arthropods, tuco-tucos (*Ctenomys* sp.), and hares most frequently (Table 2). Geoffroy's cats consumed few arthropods, and major prey items were cricetines, cavies (Caviidae), and tuco-tucos. The colocolo was the most differentiated of the "carnivorous" species, due to its heavy consumption of tuco-tucos.

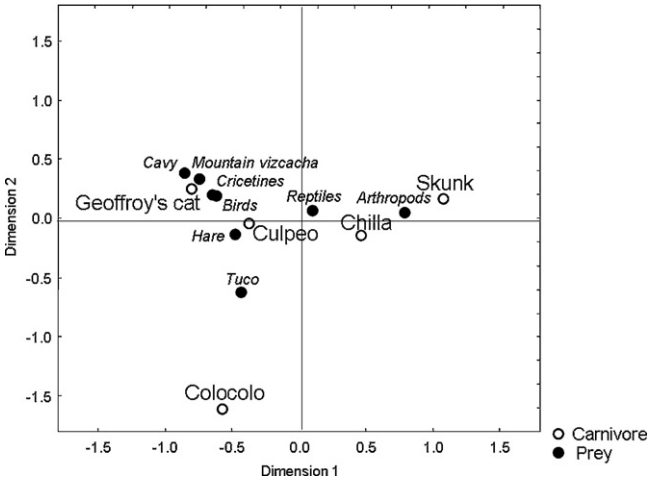

Fig. 1. Axes 1 and 2 in the correspondence analysis comparing frequencies of prey items (black circles) in scats for different carnivores (white circles) in the Auca Mahuida Reserve.

As indicated in the correspondence analysis, the species with the highest dietary overlap were the culpeo – Geoffroy's cat and hog-nosed skunk – chilla pairs (Fig. 1). The mean food niche overlap among all species (0.49; var. = 0.08) was marginally greater ($p = 0.054$) than the mean simulated overlap (0.37, var. = 0.07). Excluding the highly insectivorous hog-nosed skunk from the analysis resulted in a non-significant difference ($p = 0.10$) between the mean observed overlap among culpeos, chillas, Geoffroy's cats, and colocolos (0.54, var. = 0.04) and the mean simulated overlap (0.45, var. = 0.06), indicating that the food niche overlap among these four species was no greater than the overlap expected by chance given the prey base. Also as suggested in the correspondence analysis, the culpeo has the broadest niche breadth, followed by the chilla and the Geoffroy's cat (Table 3). MWVP was not calculated for the puma, given the small sample size, but as the only prey items in the sample were livestock and guanacos, the puma consumed the largest prey available. Among the other species, the Geoffroy's cat consumed the largest vertebrate prey (Tables 2 and 3).

In the reserve, we detected a distinctive pattern of defecation for the two small cats based on the genetic analyses of scats. The colocolo defecated in small hollows under shrubs, apparently dug out for that purpose, which we found along transects away from rock

Table 3
Food niche overlap[a], niche breadth[b] and mean weight of vertebrate prey for five carnivores of the (a) Auca Mahuida Reserve and (b) northern Patagonian ranches.

	Culpeo	Chilla	Hog-nosed skunk	Geoffroy's cat	Niche breadth	B_{max}[c]	MWVP (g)
(a)							
Culpeo					0.45	13	243
Chilla	0.72				0.06	12	166
Hog-nosed skunk	0.54	0.96			0.03	8	12
Geoffroy's cat	0.82	0.35	0.14		0.46	12	255
Colocolo	0.52	0.32	0.06	0.53			
(b)							
Culpeo					0.31	12	674
Chilla	0.89				0.19	10	215
Hog-nosed skunk	0.01	0.27			0.05	5	16
Geoffroy's cat	0.89	0.94	0.01		0.16	10	181
Puma	0.82	0.73	0.00	0.68	0.08	15	970

[a] calculated as Pianka (1973).
[b] calculated as Levins (1968) and standardized by Colwell and Futuyma (1971).
[c] B_{max} is the maximum number of food items available (niche breath), calculated as Levins (1968).

outcrops. Geoffroy's cats defecated in latrines in small caves and crevices on rocky outcrops. There was an almost complete altitudinal separation between the two species, with colocolo scats found below and Geoffroy's cat scats above 1000 m.a.s.l.

Comparison of diet and trophic interactions between the reserve and the Patagonian ranches

On the Patagonian ranches, sufficient puma samples ($n = 70$) were obtained to include that species in the analysis, but only one colocolo sample was obtained, containing only European hare. Introduced mammals were heavily consumed at the ranches, between 3 and 6 times more frequently than at the reserve (Table 1).

Dietary separation among the carnivores of Patagonian ranches was less pronounced than at the reserve, with only hog-nosed skunks on the right side of the graph in the correspondence analysis, due to its heavy consumption of arthropods (Fig. 2). The first two axes of variation in the correspondence analysis composed 92% of the total variation, 84% in the first axis and 8% in the second. In this analysis based on frequency of occurrence of food items, the hog-nosed skunk had virtually no food niche overlap with the culpeo, Geoffroy's cat, and puma, but overlap was high among these three species and the chilla (Table 3).

The observed mean dietary overlap among all species on the ranches (0.52, var. = 0.14) was significantly greater ($p = 0.03$) than the mean simulated overlap (0.32, var. = 0.01). Removing the highly insectivorous hog-nosed skunk from the analysis resulted in an observed food niche overlap for the canids and felids of 0.75 (var. = 0.01), which was much greater ($p = 0.002$) than the mean simulated overlap (0.38; var. = 0.01), indicating that the overlap among these species was greater than would be expected by chance.

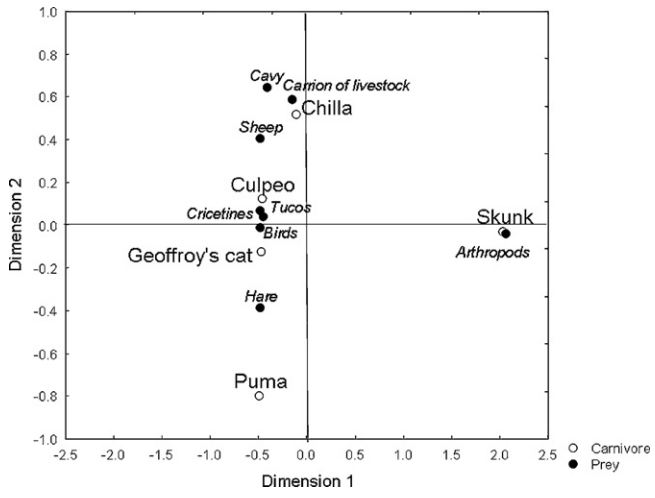

Fig. 2. Axes 1 and 2 in the correspondence analysis comparing frequencies of prey items (black circles) "in STOMACHS AND scats" for different carnivores (white circles) on the northern Patagonian ranches.

Dietary niche breadth on the ranches was less than at the reserve for culpeos and Geoffroy's cats, but was greater for chillas and the same for hog-nosed skunks (Table 3). The number of food items available to each species (B_{max}) was slightly lower on the ranches than at the reserve. MWVP was greater on the ranches than at the reserve for culpeos and chillas, but less for Geoffroy's cats and the same for hog-nosed skunks.

Discussion

Guanacos and maras were not ecologically extinct in their role as prey for carnivores on the Auca Mahuida reserve, in contrast to the Patagonian ranches. Of the six puma scats from the reserve five contained guanaco, compared to none of the 70 scats from the ranches. Guanacos were also found in 6% of culpeo scats, and livestock remains were found in only one puma and one culpeo scat, whereas livestock and exotic wildlife, mostly hares, were the main prey items at the Patagonian ranches, as in other areas of Patagonia (Crespo and De Carlo 1963; Bellati and Von Thungen 1990; Johnson and Franklin 1991, 1994; Novaro et al. 2000a, 2004). This is probably due to the large difference in proportions of native and introduced prey available in the reserve compared to other parts of Patagonia, such as these nearby ranches, where carnivore diets have been studied. However, densities and percent biomass represented by the lesser rhea (Rhea pennata), a flightless bird that is the second largest-bodied native herbivore of the region, were similar to those on the ranches and this species was not represented in the diet at the reserve. Thus, this native species appears to be ecologically extinct on the reserve as well as on the ranches.

Although European hares were not consumed at as great a frequency on the reserve as in other parts of Patagonia, they were consumed at low frequency by all of the carnivore species, highlighting the ubiquitousness of this exotic species throughout the region. Density of hares is extremely low in the reserve, almost 20 times less than on the ranches, probably related to habitat quality, but carnivores may be selectively preying on hares in spite of this low abundance, as has been found to occur in other areas (Novaro et al. 2004). Hares were consumed at greater frequencies by culpeos, chillas, and Geoffroy's cats than the two native prey species with most similar body size, the somewhat smaller mountain vizcacha and the larger mara, which may be less vulnerable than hares due to their anti-predator strategies. These two

native species were not consumed at all on the Patagonian ranches, although they are still present in the area.

No data are available on carnivore diets prior to the changes in the prey base brought about by the introduction of livestock and exotic wildlife, but our results suggest that partitioning of food resources among the carnivores is dramatically reduced in areas where the prey base is mostly exotic species. Although the five small and medium carnivores at the reserve used many of the same prey species, they were used in different proportions, and dietary overlap was no greater than expected randomly. On the other hand, except for the hog-nosed skunk, the carnivores of the Patagonian ranches exhibited much less dietary segregation. Diets of culpeos, chillas, Geoffroy's cats, and pumas overlapped significantly. This homogenization of carnivore diets due to the availability and consumption of the European hare and livestock carrion could increase interference competition among carnivores, particularly during periods of lower abundance of European hares, which fluctuates from year to year (Donadío and Buskirk 2006; Novaro et al. 2000a). Lagomorphs in boreal, desert and high-altitude ecosystems in other parts of the world play key ecological roles within trophic systems, with fluctuations in their abundances having major impacts on carnivore abundance and predation on alternative prey (Stoddart et al. 2001; Berger 2008). Even though lagomorphs are exotic in Patagonia, they may play a similar role in the region's altered ecosystems.

Carnivore species responded differently to the difference in prey base. In the reserve, the culpeo diet was more generalized and average weight of prey was lower than on the Patagonian ranches. The higher densities of large-bodied exotic prey on the ranches may allow the culpeo to specialize on these more profitable food items. Large lagomorphs are principal food items of the similarly sized canid, the coyote (*Canis latrans*) in North America (Stoddart et al. 2001). The chilla, on the other hand, was more specialized on arthropods and lizards in the reserve, compared to chillas on the Patagonian ranches and other areas of Patagonia, where small mammals, hares, and carrion of sheep were the principal food items (Johnson and Franklin 1994; Novaro et al. 2004). At the reserve, the chilla diet was very similar to that of the hog-nosed skunk, while on the ranches it was more similar to that of the culpeo and Geoffroy's cat.

The hog-nosed skunk in the reserve and on the ranches was mostly insectivorous, as in other studies in Patagonia (Travaini et al. 1998; Zapata et al. 2001; Donadío et al. 2004), and therefore niche breadth and size of vertebrate prey did not vary much between the two areas. Nevertheless, dietary overlap with other species was much greater in the reserve because the other carnivores ate more arthropods there than on the ranches. For both the chilla and the hog-nosed skunk, the importance of carrion in the diet may be underestimated in our study as our analysis is based on contents of scats rather than stomachs.

The Geoffroy's cat at the reserve consumed primarily native rodents. Cricetines and cavies were consumed with equal frequency, but cavies are up to ten times larger than most cricetines, so cavies are undoubtedly more important in the diet of the Geoffroy's cat in terms of biomass. The Geoffroy's cat consumed cavies at a similar rate as in the reserve at a nearby site in scrub habitat only in fall, with much lower consumption in the other seasons (Bisceglia et al. 2007). Hares and mountain vizcachas, although consumed at lower frequencies than the smaller species, also probably represented major components of the Geoffroy's cat diet at the reserve in terms of biomass. Dietary overlap between Geoffroy's cats and culpeos changed little between the reserve and the Patagonian ranches, but increased greatly with the chilla. The narrowed niche breadth and decreased average size of prey at the Patagonian ranches was probably due to the lower consumption of the larger rodents that were frequently consumed at the reserve.

A more complete analysis of the effects of an altered prey base on the carnivore assemblage would include an evaluation of relative abundances of different species, which was beyond the scope of this study. Numbers of scats and stomachs obtained for the different carnivore species cannot be assumed to represent their relative abundances at the ranches or the reserve. However, based on reports by local people and several years of fieldwork at the two sites, the puma and the culpeo appear to be much more abundant on the ranches than at the reserve. This may be due to the greater availability of larger-bodied exotic species which these largest carnivore species are more able to exploit. Nevertheless, pumas are the only native carnivores able to exploit adult guanacos, which are more abundant at the reserve. The puma had been largely extirpated from most of Patagonia, and only re-colonized the reserve area within the last 10 years, whereas it recolonized the Patagonian ranches more than 20 years ago (Novaro and Walker 2005). Culpeos may be less abundant at the reserve because of the greater proportion of scrub at that site, a habitat type which generally contains fewer culpeos (Novaro et al. 2000b).

In recent years, conservationists have recognized that beyond preventing demographic extinction of a species it may be desirable to conserve those species at densities high enough to maintain their roles, or ecological functions, in the ecosystem (Sanderson 2006). Most species have numerous ecological functions, which are often difficult to define, measure, and monitor. In areas where native herbivores are of conservation concern, analysis of carnivore diets may be a relatively quick and efficient way to determine their ecological functionality in terms of their role as prey. This role may be particularly threatened in areas where native carnivores are subsidized by livestock or introduced wildlife, as in Patagonia (Novaro and Walker 2005).

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References

Ackerman, B.B., Lindzey, F.G., Hempker, T.P., 1984. Cougar food habits in southern Utah. Journal of Wildlife Management 48, 147–155.

Bellati, J., Von Thungen, J., 1990. Lamb predation in Patagonian ranches. In: Davis, L.R., Marsh, R.E. (Eds.), Proceedings of the14th Vertebrate Pest Conference. University of California, Davis, CA, pp. 263–268.

Berger, J., 2008. Undetected species losses, food webs, and ecological baselines: a cautionary tale from the Greater Yellowstone Ecosystem, USA. Oryx 42, 139–142.

Bisceglia, S.B.C., Pereira, J.A., Teta, P., Quintana, R.D., 2007. Food habits of Geoffroy's cat (*Leopardus geoffroyi*) in the central Monte desert of Argentina. Journal of Arid Environments 72, 1120–1126.

Blaum, N., Tietjen, B., Rossmanith, E., 2009. Impact of livestock husbandry on small and medium sized carnivores in Kalahari savannah rangelands. Journal of Wildlife Management 73, 60–67.

Bonino, N., 2005. Guía de mamíferos de la Patagonia Argentina. Ediciones INTA, Buenos Aires, Argentina.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations, 1st ed. OXFORD University Press, 432 pp.

Campos, C.M., Tognelli, M.F., Ojeda, R.A., 2001. *Dolichotis patagonum*. Mammalian Species 652, 1–5.
Chehebar, C., Martin, S., 1989. Guía para el reconocimiento microscópico de los pelos de los mamíferos de la Patagonia, Doñana. Acta Vertebrata 16, 247–291.
Colwell, R.R., Futuyma, D.J., 1971. On the measurement of niche breadth and overlap. Ecology 52, 567–572.
Crespo, J.A., De Carlo, J.M., 1963. Estudio ecológico de una población de zorros colorados *Dusicyon culpaeus culpaeus* en el oeste de la provincia de Neuquén. Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia 1, 1–55.
Donadío, E., Buskirk, S.W., 2006. Diet, morphology, and interspecific killing in Carnivora. The American Naturalist 167, 524–536.
Donadío, E., Di Martino, S., Aubone, M., Novaro, A.J., 2004. Feeding ecology of the Andean hog-nosed skunk (*Conepatus chinga*) in areas under different land use in north-western Patagonia. Journal of Arid Environments 56, 709–718.
Donazar, J.A., Travaini, J., Ceballos, O., Delibes, M., Hiraldo, F., 1997. Food habits of the great horned owl in northwestern Argentine Patagonia: the role of introduced lagomorphs. Journal of Raptor Research 31, 364–369.
Estes, J.A., 1996. Predators and ecosystem management. Wildlife Society Bulletin 24, 390–396.
Fernández, G.J., Rossi, S.M., 1998. Medullar type and cuticular scale patterns of hairs of rodents and small marsupials from the Monte shrubland (San Luis province, Argentina). Mastozoología Neotropical 5, 109–116.
Fuentes, E.R., Jaksic, F.M., 1979. Latitudinal size variation of Chilean foxes: test of alternative hypotheses. Ecology 60, 43–47.
González del Solar, R., Rau, J., 2004. Chilla (*Pseudalopex griseus*). In: Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan. IUCN/SCC Canid Specialist Group, Gland and Cambridge, pp. 56–63.
Gotelli, N.J., Entsminger, G.L., 2001. EcoSim: Null Models Software for Ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://www.garyentsminger.com/ecosim.htm.
Heidel, L., 2008. Selección de áreas de forrajeo del cóndor andino (*Vultur gryphus*) y del jote de cabeza colorada (*Cathartes aura*) en la Reserva Provincial Auca Mahuida y su periferia. Undergraduate thesis, 21 pp.
Hiraldo, F., Donazar, J.A., Ceballos, O., Travaini, A., Bustamante, J., Funes, M.C., 1995. Breeding biology of the grey eagle-buzzard population in Patagonia. Wilson Bulletin 107, 675–685.
Jaksic, F.M., Braker, H.E., 1983. Food-niche relationships and guild structure of diurnal birds of prey: competition versus opportunism. Canadian Journal of Zoology 61, 2230–2241.
Jimenez, J.E., Jaksic, F.M., 1991. Behavioural ecology of red-backed hawks in central Chile. Wilson Bulletin 103, 132–137.
Jiménez, J.E., Novaro, A.J., 2004. Culpeo (*Pseudalopex culpaeus*). In: Sillero-Zubiri, C., Hoffmann, M., Macdonald, D.W. (Eds.), Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan. IUCN/SCC Canid Specialist Group, Gland and Cambridge, pp. 44–49.
Jiménez, J.E., Yañez, J.L., Tabilo, E.L., Jaksic, F.M., 1997. Body size of Chilean foxes: a new pattern in light of new data. Acta Theriologica 40, 321–326.
Johnson, W.E., Franklin, W.L., 1991. Feeding and spatial ecology of *Felis geoffroyi* in Southern Patagonia. Journal of Mammalogy 72, 815–820.
Johnson, W.E., Franklin, W.L., 1994. Role of body size in the diets of sympatric Gray and Culpeo foxes. Journal of Mammalogy 75, 163–174.
Johnson, W.E., O'Brien, S.J., 1997. Phylogenetic reconstruction of the Felidae using the 16S rRNA and NADH-5 mitochondrial genes. Journal of Molecular Evolution 44, 98–116.
Korschgen, L.J., 1980. Procedures for food habits analysis. In: Schemnitz, S.D. (Ed.), Wildlife Management Techniques Manual. The Wildlife Society Inc., Washington, pp. 113–128.
Lambertucci, S., Trejo, A., Di Martino, S., Sanchez-Zapata, J., Donazar, J., Hiraldo, F., 2009. Spatial and temporal patterns in the diet of the Andean Condor's diet in Patagonia: the strong dependence on the exotic mammals. Animal Conservation 12, 338–345.
Lancia, R.A., Nichols, J.D., Pollock, K.H., 1994. Estimating the number of animals in wildlife populations. In: Bookhout, T.A. (Ed.), Chapter 9 in Research and Management Techniques for Wildlife and Habitats. The Wildlife Society, Bethesda, MD, p. 704.
Levins, R., 1968. Evolution in Changing Environments. Princeton University Press, Princeton, NJ.
Michalski, F., Peres, C., 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biological Conservation 124, 383–396.
Monserrat, A.L., Funes, M.C., Novaro, A.J., 2005. Respuesta dietaria de tres rapaces frente a una presa introducida en Patagonia. Revista Chilena de Historia Natural 78, 425–439.
Novaro, A.J., Walker, R.S., 2005. Human-induced changes in the effect of top carnivores on biodiversity in Patagonia. In: Ray, J.C., Berger, J., Redford, K.H., Steneck, R. (Eds.), Large Carnivores and the Conservation of Biodiversity: Does Conserving One Save the Other? Island Press, Washington, pp. 268–288.
Novaro, A.J., Capurro, A.F., Travaini, A., Funes, M.C., Rabinovich, J.E., 1992. Pellet-count sampling based on spatial distribution: a case study of the European hare in Patagonia. Ecología Austral 2, 11–18.
Novaro, A.J., Funes, M.C., Walker, R.S., 2000a. Ecological extinction of native prey of a carnivore assemblage in Argentine Patagonia. Biological Conservation 92, 25–33.
Novaro, A.J., Funes, M.C., Rambeaud, C., Monsalvo, O., 2000b. Calibración del índice de estaciones odoríferas para estimar tendencias poblacionales del zorro colorado (*Pseudalopex culpaeus*) en Patagonia. Mastozoologia Neotropical 7, 81–88.
Novaro, A.J., Funes, M.C., Jiménez, J., 2004. Selection for introduced prey and conservation of culpeo and chilla zorros in Patagonia. In: MacDonald, D.W., Sillero-Zubiri, C. (Eds.), The Biology and Conservation Of Wild Canids. Oxford University Press, Oxford, pp. 243–254.
Parera, A., 2002. Los mamíferos de la Argentina y la región austral de Sudamérica, 1st ed. El Ateneo, Buenos Aires, Argentina, 453 pp.
Pavez, E.F., Gonzalez, C.A., Jimenez, J.E., 1992. Diet shifts of Black – chested Eagles (*Geranoaetus melanoleucus*) from native prey to European Rabbits in Chile. Journal of Raptor Research 26, 27–32.
Pearson, O.P., 1995. Annotated keys for identifying small mammals living in or near Nahuel Huapi Nacional Park or Lanin Nacional Park, Southern Argentina. Mastozoología Neotropical 2, 99–148.
Pianka, E.R., 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4, 53–74.
Radovani, N., 2004. Parámetros poblacionales del guanaco (*Lama guanicoe*) en el Área Protegida Auca Mahuida: efectos de las picadas petroleras y la topografía. Undergraduate thesis, 25 pp.
Ray, J.C., Sunquist, M.E., 2001. Trophic relations in a community of African rainforest carnivores. Oecologia 127, 395–408.
Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics: The Southern Cone, vol. 2. University of Chicago Press, Chicago.
Rivas, L., 2004. Choique (*Pterocnemia pennata pennata*) y Mara (*Dolichotis patagonum*) en la Reserva Provincial Auca Mahuida, Neuquén. Undergraduate thesis, 28 pp.
Roemer, G.W., Donlan, C.J., Courchamp, F., 2002. Golden eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. Proceedings of the National Academy of Science 99, 791–796.
Sanderson, E.W., 2006. How many animals do we want to save? The many ways of setting population target levels for conservation. BioScience 56, 911–922.
Shapira, I., Sultan, H., Shanas, U., 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. Animal Conservation 11, 1–8.
Stoddart, L.C., Griffiths, R.E., Knowlton, F.F., 2001. Coyote responses to changing jackrabbit abundances affect sheep predation. Journal of Range Management 54, 15–20.
Sunquist, M., Sunquist, F., 2002. Wild Cats of the World. University of Chicago Press, Chicago.
Travaini, A., Delibes, M., Ceballos, O., 1998. Summer foods of the Andean hog-nosed skunk (*Conepatus chinga*) in Patagonia. Journal of Zoology (London) 246, 45–460.
Trites, A.W., Joy, R., 2005. Dietary analysis from fecal samples: how many scats are enough? Journal of Mammalogy 86, 704–712.
Walker, R.S., Novaro, A.J., 2010. The world's southernmost cougars in Patagonia and the southern Andes. In: Hornocker, M., Negri, S. (Eds.), Cougar: Ecology and Conservation. University of Chicago Press, Chicago, pp. 91–99.
Weaver, J.L., 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57, 534–538.
Zapata, S., Travaini, A., Martinez-Peck, R., 2001. Seasonal feeding habits of the Patagonian hog nosed skunk (*Conepatus humboldtii*) in southern Patagonia. Acta Theriologica 46, 97–102.
Zapata, S., Travaini, A., Delibes, M., Martinez-Peck, R., 2005. Food habits and resource partitioning between grey and culpeo foxes in southeastern Argentine Patagonia. Studies in Neotropical Fauna and Environment 40, 97–103.
Zapata, S., Travaini, A., Ferreras, P., Delibes, M., 2007. Analysis of trophic structure of two carnivore assemblages by means of guild identification. European Journal of Wildlife Research 53, 276–286.