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Trophic interactions between puma and endemic culpeo fox after livestock removal in the high mountains of central Argentina

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Abstract: This study presents the first data on the diet of the puma (*Puma concolor*) and an endemic culpeo fox (*Pseudalopex culpaues smithersi*) in the high mountains of central Argentina, based on scat analysis. Trophic interactions of both carnivores were examined from 2003 to 2008 inside a protected area after livestock removal. A total of 604 scats were analyzed. Native species (small cavids and cricetine rodents) were most frequently consumed (58%–100%) by both carnivores. Exotic prey were consumed more in 2003 than in other years by both carnivores. Culpeo foxes consumed a higher number of prey items and a lower mean weight of mammalian prey than pumas. Niche breadth was high for pumas in 2003 and for culpeo foxes in 2004, decreasing in subsequent years with the same tendency in both carnivores. Diet overlap was high in all years. Pumas seemed to prey on available prey items, suggesting a trend toward diet specialization in small prey in both carnivores. Native prey are the most important food items for both carnivores inside the park; these results are encouraging in terms of the resilience of at least some components of the predator-prey assemblage in the high mountains of central Argentina.

Keywords: dietary breadth; livestock; national park; overlap; small mammals.

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Introduction

Livestock rearing occupies 25% of the global land surface and produces profound environmental changes, mainly in mountain areas (Cabido et al. 1999, Cingolani et al. 2008). Livestock grazing affects vegetation by reducing biomass and the density of grasses and litter cover and by producing soil disturbance, which leads to soil erosion and changes in fire regimes and plant species composition (Fleischner 1994, Belsky and Blumenthal 1997, Cingolani et al. 2008, Renison et al. 2010). In turn, these livestock-induced changes can alter the density, habitat use and vulnerability of potential prey of carnivores – wild herbivores and omnivores – by reducing food and cover availability (Jones 1981, Hayward et al. 1997, Eccard et al. 2000, Stanley and Knopf 2002, Pia et al. 2003). Hence, livestock affect the feeding ecology of carnivores directly, by becoming potential prey, and indirectly, by modifying prey selection by carnivores (Pia et al. 2003, Pereira et al. 2012). However, when livestock are not accessible, if other large prey are not available, large carnivores may feed on smaller prey, which are also a food source for other smaller carnivores, with potential effects on interspecific competition for prey (Gause 1934, Sunquist et al. 1989).

In central Argentina, livestock rearing has been practiced since the 17th century (Díaz et al. 1994). This activity, coupled with intensive hunting, caused the decline and, in some cases, the local extinction of populations of medium and large native herbivores that were the main prey of native carnivores (Novaro et al. 2000, Baldi et al. 2001, Novaro and Walker 2005, Pia and Novaro 2005, Donadio et al. 2010). The displacement of native herbivores (guanaco *Lama guanicoe*) by livestock (cattle, sheep, goats and horses) in central Argentina provided large and medium carnivores with food subsidies. This partly explains why native herbivore populations have declined, but carnivore populations, which have had a stable food source, have not (Novaro and Walker 2005). In environments with low diversity of native herbivores, small native herbivores are generally less affected by competition with livestock than large ones (Fedriani et al. 2000, Pia et al. 2003).

Top predators inhabiting the high mountains of central Argentina include the puma (*Puma concolor*) and an endemic culpeo fox subspecies (*Pseudalopex culpaeus smithersi*). The puma occurs in almost the entire American continent and is the largest cat in central Argentina (40–80 kg). It persists in much of its historical range; however, it has disappeared from areas with intensive human development (Currier 1983). Dietary responses to

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changes in prey abundance have been better documented in North America (Ackerman et al. 1984, Iriarte et al. 1990, Logan and Sweanor 2001) than in South America (Branch at al. 1996, Novaro et al. 2000, Rau and Jiménez 2002, Donadio et al. 2010, Zanón Martínez et al. 2012). Pumas consume smaller prey and have broader diets in South America than in North America (Iriarte et al. 1990). The culpeo fox is restricted to South America and is the second largest canine within its range (4–10 kg) and the largest within the genus (Jiménez and Novaro 2004). It is distributed from northern Ecuador to southern Chile and Argentina, along the foothills of the Andes, including Tierra del Fuego, and the Argentine Patagonian steppe. It includes six subspecies, two of which have isolated populations, such as the target species *P. c. smithersi*, a subspecies endemic to a 500-km^2 portion of the high mountains of central Argentina (Novaro 1997). Both carnivores prey on domestic livestock and are therefore in conflict with humans (Pia 2004); however, ecological studies focusing on these species in the area are scarce (Pia et al. 2003, Pia 2011). Pumas and culpeo foxes coexist in a large portion of their South American distribution. However, the culpeo fox population from the high mountains of central Argentina is 400 km away from other populations present in the Andes mountains, to the west of Córdoba, with the plains of La Rioja and San Juan provinces in between (Cabrera 1931). Hence, the high mountains of Córdoba are the only site of central Argentina where both carnivores are sympatric. Throughout their sympatric range, the diets of pumas and culpeo foxes vary in prey size; when they consume the same prey, their diets vary in prey frequency (Iriarte et al. 1991, Jaksic et al. 1992, Johnson and Franklin 1994, Meserve et al. 1996, Franklin et al. 1999, Novaro et al. 2000, Rau and Jiménez 2002, Pia et al. 2003, Zapata et al. 2005, Walker et al. 2007). Several studies have concluded that both species are opportunistic and display trophic plasticity (Crespo and De Carlo 1963, Jaksic et al. 1980, Iriarte et al. 1990, Sunquist and Sunquist 2002, Novaro et al. 2004). A number of studies in Argentina and Chile have focused on the ecology of each species separately (Jaksic et al. 1980, Iriarte et al. 1991, Johnson and Franklin 1994, Branch et al. 1996, Jiménez et al. 1996, Pessino et al. 2001, Donadio et al. 2010). The only comparative studies analyzing the diet and trophic interactions of both carnivores were conducted in southern (Pia and Novaro 2005) and northwestern Patagonia (Novaro et al. 2000). A 6-year study of the diet of pumas and culpeo foxes was conducted in Quebrada del Condorito National Park, in the mountains of Córdoba, where livestock were almost entirely removed (see study area), and the small herbivore biomass is higher than in the surrounding areas (Pia et al. 2003). Also, the dietary breadth and overlap and mean body weight of prey taken by pumas and culpeo foxes were compared among years in an effort to understand the effect of the livestock removal after the creation of the park and the interactions between these carnivores and their prey in the high mountains of central Argentina. The information obtained will help to understand factors affecting top predator prey intake and the mechanisms that facilitate coexistence of both carnivores and will therefore contribute to conservation planning for these predators and their prey in the face of traditional and emerging threats.

Materials and methods

Study area

The high mountains of Córdoba are located in central Argentina (north-south direction, 2884 meters above sea level (m asl), 31°34′S, 64°50′W) (Figure 1). Mean monthly temperatures at 2100 m asl range between 5°C in winter and 11.4°C in summer (Cabido and Acosta 1985). The mean annual precipitation is 850 mm and is mainly concentrated between October and April (Cabrera 1976). The landscape is heterogeneous, dominated by granite outcrops (56% of the surface area) with mosaic of grasses, lawns at higher altitude, areas with exposed rock surfaces due to erosion and *Polylepis* forests or shrublands restricted to steep slopes in mid to low topographic positions (Cingolani et al. 2004). The area represents a biogeographical island with more than 40 endemic plant and animal taxa, including the culpeo fox subspecies (Thomas 1914, Luti et al. 1979). The main economic activity in the high mountains of Córdoba is livestock rearing (cattle, sheep, horses and goats), which was introduced in the 17th century and represents the main driver affecting vegetation composition at the local scale (Cabido et al. 1999). Quebrada del Condorito National Park (26,000 ha) was created in 1996. Since then, poaching has been largely reduced. Livestock began to be removed from the park in 1998, until densities were lower than in the surroundings (0–0.4 vs. 1.1–4.8 cattle equivalent per ha) (Cingolani et al. 2008). Livestock reduction resulted in an increase in vegetation cover and height, which in turn contributed to an increased presence of rodents (Pia et al. 2003). The lands surrounding the park were declared Provincial Water Reserves (117,000 ha); however, they continue to be privately owned and traditional livestock management is still practiced at high livestock densities, which keeps

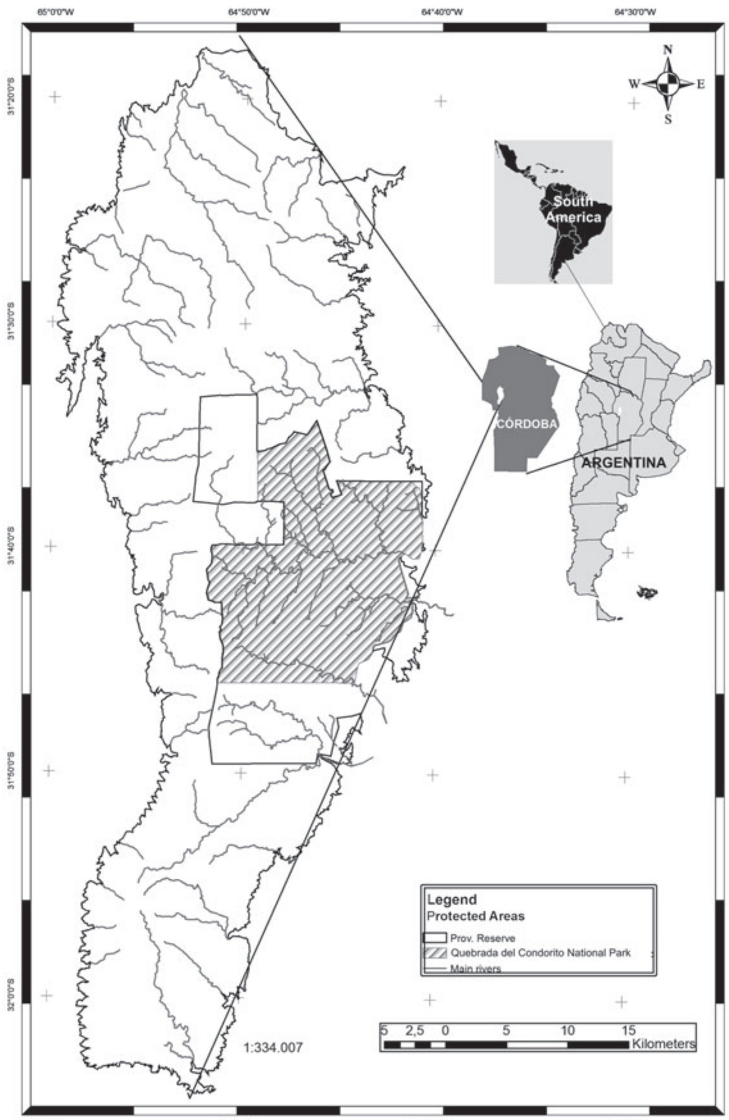

Figure 1 Location of Quebrada del Condorito National Park at high mountains of Córdoba Province in Central Argentina.

vegetation short (Cingolani et al. 2008) and reduces small mammal abundance (Pia et al. 2003).

Large native herbivores, such as the guanaco (*Lama guanicoe*), became locally extinct due to competition with domestic livestock and hunting pressure at the beginning of the 20th century (Díaz et al., 1994). At present, small rodents (40 to 500 g) are the most abundant native herbivores occurring in the study area. In 2007 a group of 100 guanacos was reintroduced to the park, of which <10% have survived (Schneider and Aprile 2009), and pumas, therefore, have limited access to them. The European hare (*Lepus europaeus*), an exotic species introduced to Argentina in the late 19th century (Bonino et al. 2010), is the largest wild herbivore present. Hares and domestic livestock represent the highest biomass of herbivores available for medium and large native carnivores across the high mountains of Córdoba (Pia et al. 2003).

Diet

The diet of the puma and the culpeo fox was determined by identification of prey remains in 604 scats (puma=234, culpeo=370), which were collected from the study area through systematic searches along transects established for another study (Pia 2011) and opportunistically on rock outcrops and internal roads during 2003–2008. Scats of pumas and culpeo foxes were identified based on shape and diameter. The pampa fox (*Pseudalopex gymnocercus*) occurs at lower elevations than the culpeo fox in the

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mountains of central Argentina but does not reach the area covered in this study; hence, there were no possibilities of confusing culpeo fox scats with those of the pampa fox (M.V. Pia, unpublished data). Non-identifiable scats were discarded. Scats were stored in labelled paper bags and washed in the laboratory. Scat contents were analyzed to determine food items, following the methods of Reynolds and Aebischer (1991). Microscopic and macroscopic fractions were examined and mammalian prey remains were identified by comparing hair and teeth with voucher specimens from the region and with the aid of keys (Chehébar and Martín 1989, Pearson 1995). Birds and reptiles were identified to class level based on feathers, scales and bones. Livestock were divided into two groups: large prey (*Bos Taurus*, cattle; *Equus caballus*, horses) and small prey (*Ovis aries*, sheep; *Capra hircus*, goats).

Data analysis

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Carnivore diet composition was expressed as the percentage of occurrence of prey items (number of times each item was found in the scats in relation to the total number of items in all scats) and percentage of biomass of prey consumed. The correction factors used were those calculated by Ackerman et al. (1984) for pumas and by Lockie (1959) for *Vulpes vulpes*, a canid of similar size to that of the culpeo fox [mean body masses of *Pseudalopex culpaeus* and *V. vulpes* range between 4–10 and 3–11 kg, respectively (Lariviere and Pasitschniak-Arts 1996, Novaro 1997)]. Dietary niche breadth (B_{sta}) was calculated using the formula provided by Levins (1968) and standardized by Colwell and Futuyma (1971) as $B_{sta}=(B_{obs}-B_{min})/(B_{max}-B_{min})$, where $B_{obs}=1/\sum p_i^2$, p_i is the proportion of taxon i in the diet, B_{min} is the minimum diversity possible (=1) and B_{max} is the maximum diversity possible (=n, total number of different taxa consumed by the two species). This index ranges from 0 (specialist species) to 1 (generalist species). Dietary niche overlap was calculated with Pianka's (1973) index, $\alpha=\sum p_i q_i/(\sum p_i^2 \sum q_i^2)^{1/2}$, where p_i is the proportion of taxon i in the diet of the first species, and q_i is the proportion of taxon i in the diet of the second species. This index ranges from 0 (no overlap) to 1 (complete overlap). Prey size may influence a predator's choice for a particular species. As an additional method to compare diet partitioning between the puma and culpeo fox, we used the mean weight of mammalian prey (MWMP; Walker et al. 2007). Weight for avian and reptilian prey was not estimated because it was not possible to identify those items to species level; hence, only the weights of mammalian prey were compared. Cattle and guanaco remains were included in this analysis only for pumas and were excluded for culpeo foxes as we assume that they are only scavenged by the latter. Mean weigh was calculated as the arithmetic mean of the weights of all individual prey found in scats (Walker et al. 2007). Weights of mammalian prey (Tables 1 and 2) were obtained from the literature (Redford and Eisenberg 1992, Novaro et al. 2000) and from a previous work in the study area (Pia et al. 2003). Diets were compared between years and species with the Exact Chi-square test, when appropriate, using the program InfoStat 1.1 (Zar 1996, Novaro et al. 2000, InfoStat 2002). To reduce the number of categories for this analysis, all cricetine rodents were grouped.

Results

Mammals were present in 98% of the scats of both carnivores. We identified 15 and seven types of prey and 371 and 533 prey items in scats of pumas and culpeo foxes, respectively (Tables 1 and 2). Small cavids (guinea pigs *Microcavia* sp., *Galea* sp. <0.5 kg) made up the bulk of the diet of both carnivores in all years according to frequency (puma: 39%–75%; culpeo: 45%–75%) and biomass (puma: 30%–67%; culpeo: 64%–86%), except in 2003, when exotic prey (livestock and hares) were more frequently consumed by pumas (39%) (Tables 1 and 2). The second most frequently consumed item was hares in 2003 and cricetine rodents the following years for pumas, and cricetine rodents for culpeo foxes. According to biomass, the second most frequently item consumed by pumas was cricetine rodents in 2003 and exotic prey in subsequent years; for culpeo foxes, cricetine rodent and hares were the most frequently consumed items in the first year and only cricetine rodents in succeeding years (Tables 1 and 2). Consumption of fossorial rodents (Ctenomidae) was low; however, a slight increase was observed over the years. No insect remains were found in the scats. Culpeo foxes consumed a higher number of prey items than pumas; however, the number of items consumed by pumas increased over the study years (Tables 1 and 2, Figure 2). Diet composition differed significantly between carnivores (χ^2=343.22, *d.f.*=187, $p<0.05$). Interannual variation in diet composition was observed in both carnivores (pumas: χ^2=99.72, *d.f.*=75, $p<0.05$; culpeo foxes: χ^2=92.46, *d.f.*=40, $p<0.05$).

Overall, standardized niche breadth was high for pumas in 2003 (B_{sta}=0.60) and for culpeos in 2004 (B_{sta}=0.63), but decreased in subsequent years in both carnivores (Table 3). The MWMP was greater for pumas than for culpeo foxes in all years (Tables 1 and 2, Figure 3). The

Table 1 Diet of puma *Puma concolor* in Quebrada del Condorito National Park between 2003 and 2008 presented as percentage occurrence of prey item (%O), biomass consumed (%B) and mean weight of mammalian prey (MWMP).

Prey types	Body mass[a] (kg)	2003		2004		2005		2006		2007		2008		Mean values	
		%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	% O	% B	% O	% B
Native		**57.6**	**44.2**	**87.50**	**72.3**	**91.4**	**86.1**	**86.5**	**82.3**	**84.3**	**75.3**	**89.7**	**81.1**	**82.84**	**73.56**
Mammals															
Rodents (subtotal)		**57.6**	**44.2**	**87.5**	**72.3**	**89.7**	**83.2**	**79.8**	**75.9**	**75.9**	**65.3**	**89.7**	**81.1**	**80.02**	**70.32**
Cricetidae[1]	0.04	18.2	13.9	10.0	8.2	15.5	14.3	33.7	31.9	25.3	21.7	33.8	30.5	22.76	20.07
Caviidae															
Guinea pigs[4]	0.46	39.4	30.3	75.0	62.0	72.4	67.3	42.7	40.8	45.8	39.5	51.5	46.7	54.46	47.75
Chinchillidae															
Lagostomus maximus[6]	4.40	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	0.0	0.0	0.19	0.19
Ctenomidae															
Ctenomis sp[4]	0.15	0.0	0.0	2.5	2.1	1.7	1.6	2.2	2.1	4.8	4.1	4.4	4.0	2.62	2.32
Carnivores (subtotal)		**0.0**	**0.0**	**0.0**	**0.0**	**1.7**	**3.0**	**1.1**	**1.1**	**2.4**	**2.1**	**0.0**	**0.0**	**0.88**	**1.04**
Puma concolor[2]	50.00	0.0	0.0	0.0	0.0	1.7	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.29	0.50
Mustelidae[2]	1.85	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.1	2.4	2.1	0.0	0.0	0.59	0.54
Marsupials															
Didelphidae[3]	0.03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	1.0	0.0	0.0	0.20	0.17
Ungulates															
Camelidae															
Lama guanicoe[5]	77.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.4	4.9	0.0	0.0	0.40	0.81
Birds[5]	0.06	0.0	0.0	0.0	0.0	0.0	0.0	5.6	5.3	2.4	2.1	0.0	0.0	1.34	1.23
Reptiles	ND	3.0	ND	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.50	ND
Exotic		**39.4**	**55.8**	**12.5**	**27.8**	**8.6**	**13.9**	**13.5**	**17.6**	**15.7**	**24.7**	**10.3**	**18.9**	**16.66**	**26.43**
Mammals															
Lagomorpha															
Lepus europaeus[5]	3.40	21.2	17.2	2.5	2.2	5.2	5.1	11.2	11.3	6.0	5.5	4.4	4.2	8.43	7.57
Ungulates (subtotal)		**18.2**	**38.6**	**10.0**	**25.6**	**3.4**	**8.8**	**2.2**	**6.3**	**9.6**	**19.2**	**5.9**	**14.7**	**8.23**	**18.86**
Large livestock[1]	178.00	9.1	28.8	5.0	17.0	1.7	6.6	0.0	0.0	2.4	8.6	2.9	11.0	3.53	11.98
Small livestock[1]	23.00	9.1	9.8	2.5	2.9	1.7	2.2	1.1	1.5	6.0	7.3	2.9	3.7	3.90	4.56
Lama glama[2]	130.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	3.4	0.0	0.0	0.20	0.57
Antilope cervicapra[3]	100.00	0.0	0.0	2.5	5.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.42	0.95
Sus scrofa[3]	200.00	0.0	0.0	0.0	0.0	0.0	0.0	1.1	4.8	0.0	0.0	0.0	0.0	0.19	0.80
Total prey ítems			**33**		**40**		**58**		**89**		**83**		**68**		

(**Table 1** Continued)

Prey types	Body mass[a] (kg)	2003		2004		2005		2006		2007		2008		Mean values	
		%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	% O	% B	% O	% B
Total scats			**23**		**35**		**44**		**46**		**48**		**38**		
MWMP (kg)			**19.78**		**12.41**		**4.85**		**3.36**		**9.81**		**6.32**		

Subtotal in bold.
[a]Body mass used for calculation of mean weight of mammalian prey. Sources: [1]Pia et al. 2003; [2]This study; [3]Redford and Eisenberg1992; [4]Taraborelli and Moreno 2009; [5]Novaro et al. 2000; [6]H. Ferreyra, personal communication.
ND, no data: biomass consumed could not be calculated because of a lack of correction factors and weight of prey.

consumption of large prey (livestock, guanacos and other ungulates) by pumas contributed to a higher MWMP in 2003, 2004 and 2007 than in the remaining years (Table 1); in culpeo foxes, the increase of MWMP occurred with the consumption of small livestock in 2003 and 2008 (Table 2, Figure 3). Dietary overlap between carnivore species was high in all years (Table 3).

Discussion

After livestock removal, both carnivores consumed small native prey species instead of moving to sites where larger prey was available. Although pumas are 10 times larger than culpeo foxes, both consumed primarily small native prey (cavids and cricetines). However, livestock was present in the diet of the puma throughout the study period, but biomass contribution decreased over the years. Small livestock were less frequently consumed by culpeo foxes; hence, biomass contribution to the diet was also low.

The removal of livestock had a direct effect on the diet of both carnivores because they were no longer available to these top predators and an indirect effect through plant recovery, which increased densities of cavids, cricetines and fossorial rodents (Pia et al. 2003). However, before removal, livestock grazing maintained short grasses and reduced shrub cover, which promoted the presence of the European hare (Meyers et al. 1994), a prey item consumed by both carnivores. So, with the removal of livestock and the consequent recovery of grasses, a reduced consumption of European hares inside the park was expected because they became less available or profitable to top carnivores, as observed over the years. In other parts of the country, such as Patagonia, where shrub cover is low and livestock has not been removed, European hare density is more than four times higher (Novaro et al. 2000) than in the study area (Pia et al. 2003), and they are an important prey consumed by medium and large carnivores in those areas.

Q8: Please confirm the following sentence "So with the..... over years" if they are correct

Pumas seemed to adapt their feeding behavior to preying on more likely available prey items than searching for larger prey inside or outside the park. Because of the small size of Quebrada del Condorito National Park, both carnivores, especially pumas, could be expected to move out of the park to feed on larger prey; however, this does not seem to occur frequently in the park, perhaps because of the strong hunting pressure prevailing in the surrounding areas. The switch from exotic prey (livestock and hares) to smaller native prey (cavids and cricetines) shows a generalist behavior by pumas.

Table 2 Diet of culpeo fox *Pseudalopex culpaeus smithersi* in Quebrada del Condorito National Park between 2003 to 2008 presented as percentage occurrence of prey items (%O), biomass consumed (%B) and mean weight of mammalian prey (MWMP).

Prey ítems	Body mass[a] (kg)	2003		2004		2005		2006		2007		2008		Mean values	
		%O	%B	%O	%B	%O	%B	%O	%B	%O	%B	% O	% B	% O	% B
Native		**86.8**	**86.3**	**98.3**	**100.0**	**100.0**	**100.0**	**97.3**	**96.7**	**98.0**	**98.6**	**94.8**	**93.7**	**95.86**	**95.88**
Mammals															
Rodents (subtotal)		**82.4**	**82.9**	**98.3**	**100.0**	**100.0**	**100.0**	**93.2**	**91.5**	**92.9**	**94.3**	**92.2**	**90.2**	**93.17**	**93.15**
Cricetidae[1]	0.0	19.1	11.3	23.7	14.3	30.9	19.4	36.5	23.9	41.4	30.4	33.8	22.9	30.91	20.36
Caviidae															
Guinea pigs[4]	0.46	63.2	71.6	74.6	85.7	67.0	80.6	54.1	67.6	45.5	63.9	51.9	67.4	59.38	72.79
Ctenomidae															
Ctenomis sp.[4]		0.0	0.0	0.0	0.0	2.1	SD	2.7	ND	6.1	ND	6.5	ND	2.89	ND
Carnivores															
Mustelidae[2]	1.85	1.5	ND	0.0	0.0	0.0	0.0	0.0	0.0	2.0	ND	0.0	0.0	0.58	ND
Birds[5]	0.06	2.9	3.4	0.0	0.0	0.0	0.0	4.1	5.2	3.0	4.4	2.6	3.4	2.10	2.73
Exotic		**11.8**	**13.7**	**0.0**	**0.0**	**0.0**	**0.0**	**2.7**	**3.3**	**2.0**	**1.4**	**5.2**	**6.3**	**3.61**	**4.12**
Mammals															
Lagomorpha															
Lepus europaeus[5]	3.4	10.3	11.4	0.0	0.0	0.0	0.0	2.7	3.3	1.0	1.4	1.3	1.7	2.55	2.96
Ungulates (subtotal)		**1.5**	**2.3**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**0.0**	**1.0**	**0.0**	**3.9**	**4.7**	**1.06**	**1.16**
Large livestock[1]	178.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	ND	1.3	ND	0.38	ND
Small livestock[1]	23.0	1.5	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.6	4.7	0.68	1.16
Plant matter		1.4	ND	1.7	ND	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.52	ND
Total prey ítems			**68**		**118**		**97**		**74**		**99**		**77**		
Total scats			**49**		**90**		**74**		**48**		**58**		**51**		
MWMP (kg)			**1.03**		**0.35**		**0.32**		**0.37**		**0.32**		**0.94**		

Subtotal in bold.
[a]Body mass used for calculation of mean weight of mammalian prey. Sources: [1]Pia et al. 2003; [2]This study; [3]Redford and Eisenberg1992; [4]Taraborelli and Moreno 2009; [5]Novaro et al. 2000; [6]H. Ferreyra, personal communication.
ND, no data: biomass consumed was not calculated because of a lack of correction factors.

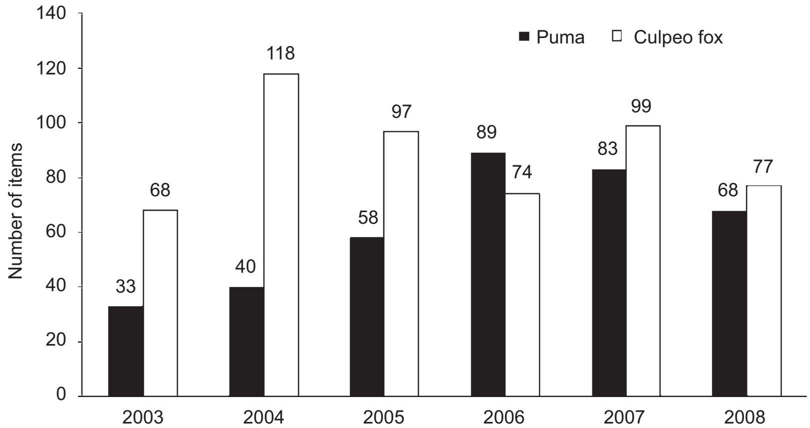

Figure 2 Number of prey items consumed by puma *Puma concolor* and culpeo fox *Pseudalopex culpaeus smithersi* during 6 years of study inside Quebrada del Condorito National Park.

Despite the tendency to choose small prey, pumas consumed a higher number of medium and large prey than culpeo foxes did, as reflected by the smaller number of prey items and the higher MWMP taken by pumas. Pumas consumed guanacos only occasionally due to the low availability of this prey, although high levels of predation (34%; Schneider and Aprile 2009) were recorded soon after reintroduction in 2007. This was also observed in other protected areas of central Argentina, where pumas prey more commonly on large prey and not on small rodents, even though the latter are more abundant (Donadio et al. 2010) and in southern Patagonia, where guanacos are important prey for pumas (Pia and Novaro 2005, Zanón Martínez et al. 2012). By contrast, in southwestern Patagonia, pumas and culpeo foxes primarily consumed introduced prey species, such as the European hare, even within protected areas with a high abundance of camelids (e.g., Yánez et al. 1986, Iriarte et al. 1991, Johnson and Franklin 1994, Novaro et al. 2000). However, in many regions of South America, the interaction between the puma and its large prey was lost due to the drastic decline in populations of wild camelids (>90%; Donadio et al. 2010). This was observed in southern Chile, where pumas increased hare consumption when densities of guanacos declined (Iriarte et al. 1990) and in northwestern Patagonia, where guanacos are an ecologically extinct prey (Novaro et al. 2000). The switch of this predator from its main to an alternative prey was also observed in La Pampa, Argentina, where, after a decline in vizcacha (*Lagostomus maximus*) populations, pumas switched to prey that had not been consumed in the area before, such as livestock and small mammals, thus diversifying their diet (Branch et al. 1996, Pessino et al. 2001). Our results are consistent with those findings, because pumas consumed small prey or shifted to alternative resources due to the decline of large prey.

Q9: Reference "Yáñez et al. (1986)" has been changed to "Yánez et al. (1986)" to match the reference list. Please check and confirm

The culpeo fox has increased the use of small mammals since the removal of livestock from the park,

Table 3 Trophic niche breadth (Levins' index, B_{sta}) and trophic niche overlap (Pianka's index, α) between puma *Puma concolor* and culpeo fox *Pseudalopex culpaeus smithersi* in Quebrada del Condorito National Park, central Argentina.

Year	B_{sta}		α
	Puma	Culpeo fox	Overlap
2003	0.60	0.25	0.92
2004	0.12	0.63	0.98
2005	0.14	0.42	0.97
2006	0.27	0.33	0.98
2007	0.25	0.27	0.96
2008	0.32	0.26	0.99
Mean	**0.28**	**0.36**	**0.97**

Mean values are in bold.

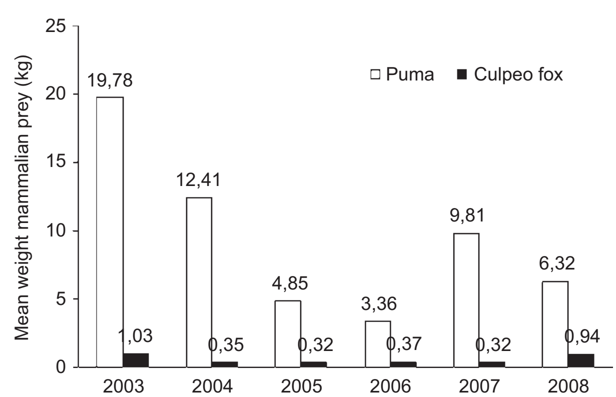

Figure 3 Mean weight of vertebrate prey consumed by puma *Puma concolor* and culpeo fox *Pseudalopex culpaeus smithersi* inside Quebrada del Condorito National Park over 6 years of study.

Q10: Are the , correct in the values in the figures or should these the .

compared with findings reported by Pia et al. (2003), and its diet now resembles that described for individuals occurring in the Argentine Puna (Walker et al. 2007) and central Chile (Jaksic et al. 1980, Johnson and Franklin 1994, Correa and Roa 2005). In those regions, culpeo foxes consume mainly small native mammals, unlike in southern Argentina and Chile, where they feed mainly on exotic European hares (Johnson and Franklin 1994, Novaro et al. 2000, Pia and Novaro 2005). A role of culpeo fox as seed disperser, as frequently reported for other subspecies (Castro et al. 1994, Cornejo Farfán and Jimenez Milón 2001), was not observed.

Over the years, both carnivores exhibited a trend toward diet specialization in small prey, as evidenced by the low niche breadth, high diet overlap and decrease of the MWMP with gradual livestock removal. This might represent a phenomenon due to the creation of the park because, outside the park, an increased consumption of exotic prey by culpeo foxes was recorded (Pia et al. 2003, Pia 2011). However, since livestock removal, pumas have shown more feeding plasticity than culpeo foxes. Small native prey proved to be an important resource when the availability of medium or large prey decreased because a growing trend towards predation mainly on small mammals was observed in both carnivores. Both carnivores had a relatively narrow dietary breadth, as has been recorded for pumas in a national park in central Argentina (Branch et al. 1996, Pessino et al. 2001) and for culpeo foxes in northern Chile (Jiménez et al. 1996).

Also, both carnivores exhibited high dietary overlap in response to low diversity and changes in the prey base. The lowest overlap value was recorded in 2003, when livestock was available to both carnivores within the park (α=92%). When guanacos were reintroduced, overlap was high (α=96%), probably due to the low number of individuals reintroduced. High overlap in the diet indicates that the two predators consume almost the same food types inside the park. In contrast, in southern Patagonia under very different conditions of prey abundance, pumas and culpeo foxes preyed on animals of different body size (Pia and Novaro 2005). Therefore, diet breadth was wider and diet overlap was lower than values found in the present study; no other studies comparing trophic overlap between these species have been published.

The high overlap found in the diet of these carnivores might be causing interspecific competition, as they have shown a trend toward use of the same resource since livestock removal; further studies are necessary to explore whether other (spatial or temporal) mechanisms of resource partitioning are involved in avoidance of competition.

The creation of the protected area had a positive influence on both carnivores directly, through hunting control, and indirectly, through the increase of small native prey and the reduction of livestock predation and the consequent conflict with humans. This was clearly reflected in the diet composition of both carnivores, which showed a reduction of 30% and 7%, respectively, in livestock consumption. Hence, livestock remains found in scats after livestock removal indicate that resident carnivores may sometimes prey upon livestock inside or outside the park or that carnivores inhabiting the areas surrounding the park enter the park. The behavioral response of carnivores switching from exotic to native prey could also be positive for offspring. Indeed, if carnivore offspring inside the park are trained to hunt native species, the probability that they hunt livestock outside the park as adults is reduced, thus reducing the possibilities of conflict with people living around the park.

The fact that native prey are the most important food items for both carnivores inside a protected area of central Argentina is encouraging in terms of the resilience of at least some components of the mammalian predator-prey assemblage in the high mountains (Holling 1986, Pia et al. 2003). Livestock removal from the park began 5 years before our study, and livestock abundance in the park before removal was as high as it was in areas surrounding the park during our study. Thus, it appears that the effect of livestock on small mammal abundance and puma and culpeo diet composition can be reversed relatively rapidly (Pia et al. 2003, Pereira et al. 2012). Therefore, the creation of a protected area that provides refuge and feeding and breeding sites for predators is very important to counteract the effects of anthropogenic activities on native carnivores. Restoration of native prey populations as well as guanaco reintroduction have been found to induce a shift to native species in the diet of carnivores, reducing livestock predation; hence, those conservation actions should be encouraged.

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