

# Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina

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## Keywords

puma; guanaco; vicuña; predation; South America.

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Editor: Andrew Kitchener

Received 14 July 2009; revised 25 July 2009; accepted 3 August 2009

doi:10.1111/j.1469-7998.2009.00638.x

## Abstract

Predatory interactions involving large carnivores and their ungulate prey are increasingly recognized as important in structuring terrestrial communities, but such interactions have seldom been studied in the temperate Neotropics. Here, the large carnivore guild is limited to a single species, the puma *Puma concolor*, native prey populations have been drastically reduced and lagomorphs and ungulates have been introduced. We examined puma dietary patterns under varying abundances of native camelid prey – guanacos and vicuñas – in protected areas of northwestern Argentina. We collected puma feces from seven protected areas, and sampled each area for the relative abundance of camelids using on-foot strip and vehicle transects. In one area, where longitudinal studies have been conducted, we examined the remains of vicuñas and guanacos for evidence of puma predation in 2004–2006. We compared our results with a study conducted in 1978–1983, and contrasted the frequency of carcasses showing signs of puma predation with estimates of camelid abundance. Across sites, we observed a positive and significant relationship between camelid consumption by pumas and camelid abundance, with pumas about nine times more likely to consume camelids where the latter were most abundant. The temporal variation in predation rates on camelids differed by species. Guanacos, which did not change in abundance between periods, showed a slight decrease (1.5 times) in the relative frequencies of individuals killed by pumas. Conversely, vicuñas increased in abundance by a factor of ~7 between periods, coinciding with an *c.* 3.4 times increase in individuals showing evidence of puma predation. Some protected areas of northwestern Argentina are conserving the trophic interaction between pumas and native camelid prey. This interaction may be the basis of the far-reaching community effects described for analogous systems on other continents. It also has implications for the possible recovery of or reintroduction of camelids to areas with high puma densities, where predation losses can be expected to be high, and possibly prohibitive.

## Introduction

Predator–prey interactions involving large mammalian carnivores and their ungulate prey can play a central role in structuring terrestrial communities (Ray *et al.*, 2005; Steenack, 2005). In North America, puma *Puma concolor*, brown bear *Ursus arctos* and wolf *Canis lupus* predation on a variety of ungulate species have been considered to perform various important community-level functions, including altering the densities and behaviors of prey, including habitat associations, with implications for a wide range of community members, including plants (Beyer *et al.*, 2007; Ripple & Beschta, 2008) and animals other than prey (Berger *et al.*, 2001; Ripple & Beschta, 2006). These strong interactions, the effects of which cascade to lower trophic levels, highlight the community-level significance of top

mammalian predators, and the importance of conserving ecological processes, such as predation.

Unlike in the northern Hemisphere, large mammalian predators and their prey in the Neotropics have been affected drastically by the elimination of the latter (Redford, 1992; Novaro & Walker, 2005). This is particularly evident in semiarid South America, where the abundance of the two wild camelids, guanacos *Lama guanicoe* and vicuñas *Vicugna vicugna*, declined by >90% during the last century (Jungius, 1971; Torres, 1985; Amaya, von Thüngen & De Lamo, 2001). Historically, these camelids were the dominant large herbivores in Patagonia and the Andes, and the main prey of the puma (Miller, 1980). With a few exceptions (Cajal & Lopez, 1987), this predatory interaction has been lost over most of the Pre-Columbian zone of sympatry of

pumas and their wild camelid prey (Novaro, Funes & Walker, 2000; Novaro & Walker, 2005).

Data on the diets of pumas from various semiarid habitats of southern South America reflect such losses. In the high Andes of Bolivia, pumas feed primarily on small- and medium-sized native rodents, while vicuñas, with domestic camelids, represent the second-most important prey category (Pacheco, Lucero & Villca, 2004). Over large areas of the Argentine Patagonian steppe, pumas eat mostly introduced species, and guanacos are virtually absent from their diet (Novaro *et al.*, 2000). In the Argentine Monte, pumas eat mainly plains vizcacha *Lagostomus maximus*, a large-bodied native colonial rodent. Where vizcachas are scarce, pumas switch to other prey, including introduced wild boar *Sus scrofa*, domestic sheep *Ovis aries* and native armadillos. Here, guanacos are rarely consumed (Branch, Pessino & Villarreal, 1996; Pessino *et al.*, 2001). Similarly, in the southern Chilean steppe and neighboring woodland areas, introduced lagomorphs were found more frequently than guanacos in puma scats, even after guanaco populations had recovered from low levels (Yáñez *et al.*, 1986; Iriarte, Johnson & Franklin, 1991; Franklin *et al.*, 1999). In this case, however, as guanaco abundance increased, they became most important in terms of biomass in the diet of pumas. Overall, we observe across studies the prevalence of non-camelid prey in the diet of pumas to be correlated with human reductions of guanacos or vicuñas and high availability of introduced species.

Consequently, predatory relationships (i.e. puma responses to changing abundances of prey) of southern South American pumas and their native ungulate prey are poorly understood. Inside one protected area in southern Chile, the occurrence of guanaco remains in puma scats increased by a factor of  $\sim 3$  as a result of increasing guanaco densities over 6 years (Yáñez *et al.*, 1986; Iriarte *et al.*, 1991). Similarly, recent research suggests that pumas can functionally respond to increasing abundances of guanacos (Novaro & Walker, 2005). No data are available on the puma–vicuña interaction.

Current information on puma diet in the southern Neotropics shows a widespread loss of the interaction between pumas and wild camelids. Data from Chile and Argentina, although scanty and obtained with differing methods, show that where wild camelids remain abundant, pumas seem to prey heavily on them. Because puma predation on camelids may be the basis of far-reaching community effects, we aimed to evaluate (1) to what extent protected areas of northwestern Argentina conserved this ecological interaction using diet data and (2) puma dietary responses to changing abundances of guanacos and vicuñas combining data on puma diet and camelid abundance across both spatial and temporal scales.

## Study area

We conducted field work at seven protected areas located in northwestern and central Argentina. San Guillermo National Park (SGNP), San Guillermo Provincial Reserve

(SGPR) and Laguna Brava Provincial Reserve (LBPR) are three contiguous protected areas that encompass a 1.4 million ha area within one of the most ecologically intact regions of South America (Sanderson *et al.*, 2002). SGNP and SGPR form the San Guillermo Biosphere Reserve. Low-elevation (2000–3000 m) valleys of shrub steppe, open plains or 'llanos' (3000–4300 m) of sparsely vegetated grass steppe and high-elevation deserts ( $\geq 4300$  m) with virtually no vegetation dominate the landscape (Cajal, Reza & Pujalte, 1981; Carrizo *et al.*, 1997). Vicuñas and guanacos inhabit all three protected areas. Particularly in SGNP, populations of locally sympatric guanacos and vicuñas showed different population trends during 1983–2005. As guanaco populations slightly decreased from 1.2 to 1.1 km<sup>-2</sup>, vicuñas increased from 1.5 to 10.1 km<sup>-2</sup> (Cajal & Bonaventura, 1998; Puig & Videla, 2007).

In Talampaya National Park (TNP) vegetation is characterized by a shrubby steppe. In El Leoncito National Park (ELNP) vegetation is characterized by shrubby steppes and high-altitude semi-arid grasslands. In Sierra de las Quijadas National Park (SQNP), vegetation is characterized by a shrubby steppe and small stands of thorny trees. In Los Cardones National Park (LCNP) shrubby steppes, saguaro forests, small stands of thorny trees and high-altitude grasslands characterize the vegetation. In TNP, ELNP, SQNP and LCNP guanacos are present while vicuñas are naturally absent. Pumas were present in all protected areas.

All the reserves surveyed are characterized by dry climates, with precipitations occurring mostly in summer. The main features of these areas, including the location, size, mean summer and winter temperatures, yearly precipitations, altitude range and livestock numbers, are summarized in Table 1.

## Methods

### Field sampling

At each protected area, we reconstructed diets of pumas by collecting and analyzing their fecal droppings. We collected feces in winter (June–August) 2004, summer (February), winter (June), and spring (October) 2006 and summer (February) 2007 at SGNP, and winter (June–August) 2004 at LBPR and SGPR. At TNP, ELNP, SQNP and LCNP puma scats were collected in winter (July–August) 2006. Additional fecal droppings were collected by park rangers in LCNP during September 2006 to February 2007. Feces were collected opportunistically and stored in labeled paper bags; in the laboratory, they were oven-dried at 60 °C and weighed. Then, they were covered with water and broken apart (Reynolds & Aebischer, 1991). Mammalian prey were identified to the lowest possible taxonomic level on the basis of bone fragments, teeth and hair (cuticular scale and medullae characteristics) (Chehebar & Martin, 1989; Pearson, 1995; Vázquez, Perovic & de Olsen, 2000). Diet data are presented as per cent frequency of occurrence, calculated as the number of times an item occurred as a percentage of the total number of prey items in all scats. The relative biomass of prey found in scats was not computed due to our inability

**Table 1** Main features of the seven protected areas surveyed during this study

Protected area	Province (coordinates)	Area (ha)	Mean summer and winter temperatures (°C)	Precipitations (mm year <sup>-1</sup> )	Elevation range (m)	Livestock and feral donkey numbers <sup>a</sup>
San Guillermo NP	San Juan (29°13'S–69°21'W)	166 000	15°; 1°	30–100	2200–5467	21 cows
Talampaya NP	La Rioja (29°46'S–67°54'W)	215 000	NA	170	1300–3200	50 cows and horses
Sierra de las Quijadas NP	San Luis (32°29'S–67°02'W)	73 533	23°; 12°	150	< 1000	1600 cows, 550 goats, 350 horses, 500 feral donkeys
Los Cardones NP	Salta (25°15'S–65°54'W)	64 117	18°; 11°	200	2700–5226	604 cows, 3375 goats, 2032 sheep, 1200 feral donkeys
El Leoncito NP	San Juan (31°46'S–69°10'W)	72 962	26°; 10°	200	1100–4300	10 cows and horses
Laguna Brava PR	La Rioja (38°39'S–69°02'W)	405 000	0.8 <sup>b</sup>	20	2000–6800	Unknown <sup>c</sup>
San Guillermo PR	San Juan (29°47'S–69°26'W)	815 460	7°; –7°	225	2000–6400	Unknown <sup>c</sup>

<sup>a</sup>Crude estimates reported by park rangers and reserve managers.

<sup>b</sup>Annual mean.

<sup>c</sup>Cows, horses and feral donkeys present but numbers are unknown. Cows *Bos taurus*, horses *Equus caballus*, donkeys *Equus asinus*, goats *Capra hircus* and sheep *Ovis aries*.

NP, national park; PR, provincial reserve.

to distinguish between vicuña and guanaco hair where sympatric (SGNP, LBPR and SGPR).

We estimated camelid relative densities at SGNP, TNP, ELNP, SQNP and LCNP in winter (June–August) 2006 using two different and independent methods. First, we established and surveyed during daylight hours (09:00–16:00 h) three to six transects of variable length (3.2–16 km) in each park based on the availability of roads and tracks. Transects were traveled by vehicle (speed 20–35 km h<sup>-1</sup>) with two observers standing in the back in all parks but SQNP, where the absence of roads forced us to conduct transects on foot. Each transect was surveyed one to four times depending on the road and track conditions. To minimize disturbance on animals, surveys of the same transect were never repeated on consecutive days. A total of 75, 86, 72, 44 and 156 km were covered in SGNP (3 transects; 9 surveys), TNP (6; 8) ELNP (5; 12), SQNP (5; 5) and LCNP (4; 14) respectively. For every group of animals encountered, we recorded the species and number of animals. The open habitats we surveyed made all reserves excellent sites to estimate abundance by direct observation. Relative density estimates are presented as the mean number of individuals counted per km of transect surveyed (individuals km<sup>-1</sup> transect).

Second, we established and surveyed 30, 500-m-long strip transects (total width = 7 m) in each park. All strip transects were perpendicular to roads or tracks, and randomly selected starting points were located on road or track edges. Generally, no more than six strip transects were established on each road or track. For each transect, we recorded the presence or absence of camelid latrines (i.e. dung piles) within the strip (Marques *et al.*, 2001). Relative density estimates are presented as the mean proportion of transects with  $\geq 1$  latrine. We evaluated whether spatial variation in both camelid relative density indexes resulted in changes in their frequency of occurrence in puma scats by comparing data on relative densities and puma diets across protected areas.

Problems related to using roads or tracks include the unfeasibility of random placement of line transects and potential avoidance of roads and tracks by animals. Surveyed roads and tracks as well as roadsides were similar across parks (i.e. mostly dirt roads, slightly used with pristine native vegetation on the sides). Avoidance of roads by camelids could result from camelids being harassed by poachers (Donadio & Buskirk, 2006) or by the existence of physical barriers such as fences that impede camelids to approach roadsides. However, poaching in the parks was almost nil (Donadio & Buskirk, 2006; Donadio *et al.*, 2007) and fences were absent. In fact, in all parks we observed animals on or nearby roads and tracks and they seldom fled when they detected us. These observations suggested that camelids were not actively avoiding roads and tracks. Therefore, we assumed this method was acceptable for the purpose of across-park comparisons.

At SGNP, we evaluated puma–camelid predatory interactions by examining vicuña and guanaco carcasses, which were necropsied to determine the cause of death. The presence of large tooth marks on the throat, skull or neck, and broken large bones were used as evidence of puma predation (Franklin *et al.*, 1999). We evaluated whether temporal variation in guanaco and vicuña densities was reflected in the relative frequency of puma predation on guanacos and vicuñas, comparing the period 2004–2006 with the period 1978–1983 (Cajal & Lopez, 1987). For the latter period, we did not include in our analysis data reported for 1984, when a large number of guanacos and vicuñas died due to an unusually harsh winter (Cajal & Lopez, 1987; Cajal & Ojeda, 1994).

## Data analysis

To test for variation in puma diets across reserves, the main prey items were grouped into four major categories: native rodents, native ungulates (wild camelids), introduced

ungulates (Equidae and Bovidae) and introduced European hares to produce a  $4 \times 7$  contingency table. These data were analyzed running a  $\chi^2$  test with program EcoSim (Gotelli & Entsminger, 2001), which uses a randomization test (1000 iterations) for the independence hypothesis in two-way contingency tables. Briefly, EcoSim estimates a  $\chi^2$  deviation statistic for the observed data and for each of the 1000 simulated data matrices. The larger the observed  $\chi^2$  deviation compared with the mean of the simulated  $\chi^2$  deviations, the less likely the observed data conform to the null model. Unlike conventional analyses, this randomization test is not sensitive to small expected frequencies.

We used bootstrapping to estimate camelid mean relative densities and associated 95% confidence intervals. From each dataset (30 transects per park), we drew 30 observations randomly with replacement and estimated the proportion of transects where a latrine was observed; we iterated this procedure 1000 times (Resampling Stats Inc., 2006). Similarly, we used bootstrapping to construct 95% confi-

dence intervals for the mean percentage of occurrence of camelid remains in puma scats for all parks. We used a similar procedure to estimate the mean number of individuals observed per km of transect. In this case, each dataset was composed of the number of surveys conducted in each park. Comparisons were made using the bootstrap 95% confidence intervals (Mukherjee *et al.*, 2004; Andheria, Karanth & Kumar, 2007).

We used the Pearson's product-moment statistic to explore the relationship between camelid relative density and their occurrence in puma scats collected in winter 2006 across protected areas. This analysis was conducted only for the national parks as we lacked information on camelid relative densities for SGPR and LBPR. At SGNP, we estimated the relative frequency of puma predation on camelids as the percentage of puma-killed camelids of both species in the total number of camelid carcasses found in each period. We generated 95% confidence intervals using bootstrapping as before. Comparisons between periods were based on these confidence intervals. Correlation

**Table 2** Frequency (Fo) and percentage of prey items found in puma *Puma concolor* scats at seven protected areas of northwestern Argentina

Prey item	SGNP		TNP		SQNP		LCNP		ELNP		LBPR		SGPR	
	Fo	% Fo	Fo	% Fo	Fo	% Fo	Fo	% Fo	Fo	% Fo	Fo	% Fo	Fo	% Fo
Rodents														
Cricetidae	22	5.1	0	0.0	0	0.0	1	12.5	2	5.3	0	0.0	0	0.0
Caviidae														
<i>Dolichotis patagonum</i>	0	0.0	4	40.0	4	44.4	0	0.0	0	0.0	0	0.0	0	0.0
Guinea pigs <sup>a</sup>	1	0	0	0.0	0	0.0	1	12.5	9	24	0	0.0	0	0.0
Ctenomidae														
<i>Ctenomys</i> sp.	15	3.5	0	0.0	0	0.0	1	12.5	2	5.3	1	5.3	2	8.3
Chinchillidae														
<i>Lagidium viscacia</i>	62	14.4	1	10.0	0	0.0	1	12.5	0	0.0	0	0.0	0	0.0
Unidentified rodents	0	0.5	0	0.0	0	0.0	0	0.0	3	7.9	0	0.0	0	0.0
Xenarthra														
Dasyopodidae	0	0.0	0	0.0	0	0.0	1	12.5	1	2.6	0	0.0	0	0.0
Ungulates														
Camelidae	276 <sup>b</sup>	64.2	1 <sup>c</sup>	10.0	1 <sup>c</sup>	11.1	1 <sup>c</sup>	12.5	13 <sup>c</sup>	34.2	11 <sup>b</sup>	57.9	11 <sup>b</sup>	45.8
Equidae <sup>d,e</sup>	0	0.0	2	20.0	2	22.2	0	0.0	0	0.0	0	0.0	0	0.0
Livestock <sup>e,f</sup>	2	0.5	0	0.0	0	0.0	0	0.0	0	0.0	1	5.3	0	0.0
Lagomorpha														
<i>Lepus europaeus</i> <sup>e</sup>	27	6.3	1	10.0	2	22.2	1	12.5	6	15.8	3	15.8	7	29.2
Carnivores	5	1.2	0	0.0	0	0.0	0	0.0	0	0.0	2	10.5	0	0.0
Unidentified mammals	4	0.9	1	10.0	0	0.0	1	12.5	1	2.6	0	0.0	0	0.0
Birds	12	2.8	0	0.0	0	0.0	0	0.0	1	2.6	1	5.3	4	16.7
Reptiles	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Unidentified vertebrates	1	0.2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Total prey items	430		10		9		8		38		19		24	
Total scats	366		10		8		7		31		18		20	

<sup>a</sup>*Galea*, *Cavia* or *Microcavia*.

<sup>b</sup>Vicuñas and guanacos.

<sup>c</sup>Only guanacos.

<sup>d</sup>Most likely feral donkeys *Equus asinus*.

<sup>e</sup>Introduced prey items.

<sup>f</sup>Cattle *Bos taurus*.

SGNP, San Guillermo National Park; TNP, Talampaya National Park; SQNP, Sierra de las Quijadas National Park; LCNP, Los Cardones National Park; ELNP, El Leoncito National Park; LBPR, Laguna Brava Provincial Reserve; SGPR, San Guillermo Provincial Reserve.

analyses were conducted using program R (Dalgaard, 2002; R Development Core Team, 2007).

## Results

The diet of pumas, as reflected by prey remains in feces, differed across protected areas [observed  $\chi^2 = 117$ , mean of simulated  $\chi^2 = 27$ , standardized effect size = 8.7,  $P$  (observed  $\geq$  simulated) = 0.0001]. Diets of pumas comprised mainly native prey ( $\geq 56\%$  of the prey items) at all protected areas; introduced species were relatively important in only three protected areas, TNP, SQNP and SGPR, where they composed 29.2–44.4% of prey occurrences (Table 2). Wild camelids were the most important prey item at SGNP, ELNP, LBPR and SGPR, where they represented  $\geq 34.2\%$  of prey occurrences in feces. Second in importance were mountain vizcachas *Lagidium viscacia* at SGNP, and European hares at ELNP, LBPR and SGPR. Pumas seldom consumed wild camelids at TNP, SQNP and LCNP, where small- [Cricetidae, *Ctenomys* and guinea-pigs (from 0.04 to 0.5 kg)] and medium-sized [mountain vizcachas and maras *Dolichotis patagonum* (from 2 to 12 kg)] native rodents represented most diet occurrences (Table 2). These findings should be interpreted cautiously for TNP, SQNP and LCNP due to the small number of feces analyzed.

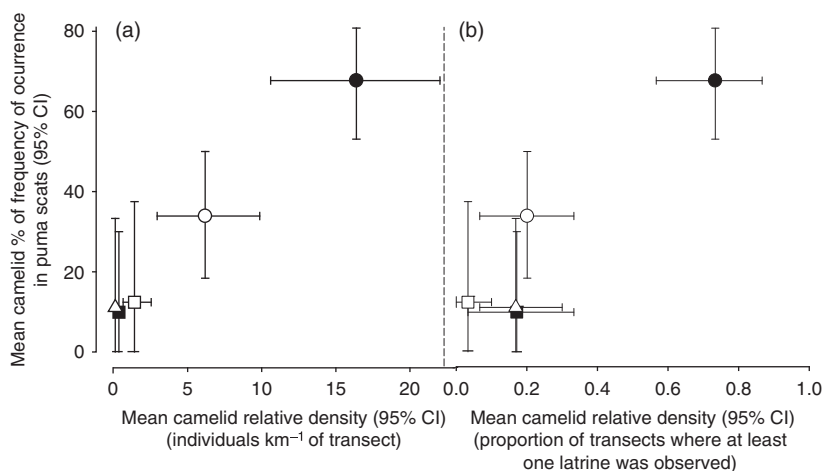
In the five national parks surveyed, the relative density indexes and occurrences of camelids in puma feces varied widely but consistently. The frequency of camelid occurrence in puma feces was positively and significantly correlated with the mean number of individuals per km of transect ( $r = 0.997$ , 95% CI = 0.962–0.999,  $t = 24.9$ , d.f. = 3,  $P < 0.001$ ; Fig. 1a), and the mean proportion of transects with presence of latrines ( $r = 0.922$ , 95% CI = 0.217–0.994,  $t = 4.1$ , d.f. = 3,  $P = 0.025$ ; Fig. 1b).

We examined 289 carcasses of camelids (106 guanacos, 183 vicuñas) at SGNP. Thirty-two per cent of vicuña carcasses and 23% of guanaco carcasses showed signs of puma predation. Changes in predation on both camelids tracked trends in their densities between 1978–1984 and 2004–2006. The relative frequency of puma predation differed between camelid species, with that on vicuñas increasing from 1978–1983 to 2004–2006 by a factor of  $\sim 3.4$ , and that on guanacos slightly decreasing by a factor of  $\sim 1.5$  (Fig. 2).

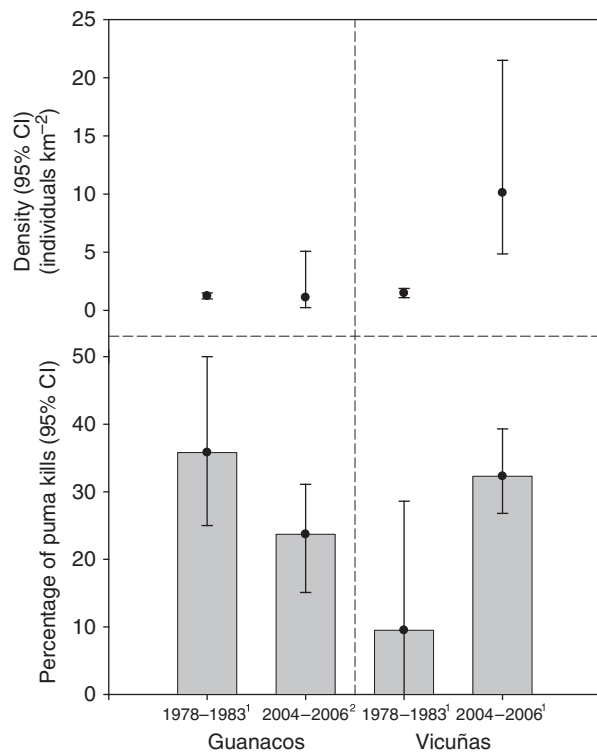
## Discussion

In all protected areas but one (SQNP), we found that pumas ate primarily native vertebrate prey, even in those areas that are small or influenced by introduced vertebrates (e.g. ELNP and LCNP). At four of the protected areas studied (SGNP, ELNP, LBPR and SGPR), camelids were the main prey of pumas. At the remaining protected areas (TNP and LCNP) other native prey, including rodents, armadillos and birds, composed the bulk of the diet. Therefore, native prey species, particularly wild camelids, still play a dominant ecological role as the main prey of pumas in most of our study areas. This finding contrasts with those of earlier studies elsewhere in the southern Neotropics, where pumas consumed primarily introduced prey species (e.g. Yáñez *et al.*, 1986; Iriarte *et al.*, 1991; Novaro *et al.*, 2000; Pessino *et al.*, 2001; Rau & Jimenez, 2002). Overall, these results highlight the importance of protected areas in conserving a predatory interaction that has been lost over vast regions of the southern Neotropics.

Our spatial and temporal analyses showed a positive relationship between camelid consumption by pumas and camelid abundance. A similar pattern was observed for



**Figure 1** Relative density of wild South American camelids and their per cent of frequency of occurrence in the diet of pumas *Puma concolor* at five national parks, northwestern Argentina, winter 2006. For San Guillermo National Park, the density estimators combine individuals or latrines of vicuñas and guanacos. (a) Relative densities based on animal counts. For Sierra de las Quijadas (95% CI: 0.03–0.19) and Talampaya (0.13–0.7) 95% CI were narrower than the width of the symbol. (b) Relative densities based on latrine counts. References: San Guillermo National Park (solid circle;  $n = 41$  scats), El Leoncito National Park (open circle;  $n = 31$ ), Talampaya National Park (solid square;  $n = 10$ ), Sierra de las Quijadas National Park (open triangle;  $n = 8$ ) and Los Cardones National Park (open square;  $n = 7$ ).



**Figure 2** Comparison of observed frequencies, as percentages, of guanaco and vicuña carcasses killed by pumas *Puma concolor*, during the periods 1978–1983 and 2004–2006, at San Guillermo National Park. Percentages were based on the number of carcasses of vicuñas or guanacos showing signs of puma predation divided by the total number of carcasses of each species found [1978–1983:  $n=77$  (guanacos = 56; vicuñas = 21); 2004–2006:  $n=289$  (guanacos = 106; vicuñas = 183)]. <sup>1</sup>Cajal & Lopez (1987); <sup>2</sup>this study. Density data taken from Cajal & Bonaventura (1998; mean density and 95% CI estimated from annual values reported for the period 1978–1983,  $n=6$ ) and Puig & Videla (2007; mean density and 95% CI represent average values reported for December 2004 and February 2005).

pumas preying on a recovering guanaco population in the Chilean Patagonia (Iriarte *et al.*, 1991). Such a pattern, which could result from increasing consumption rates of the main prey, increments on predator numbers or both, has been described for generalist predators (Bergerud & Elliot, 1986; Höner *et al.*, 2002), and its effect on the population dynamics of camelid populations remains unsolved. Novaro & Walker (2005) propose that pumas may be able to suppress the population growth of guanacos through a type III density-dependent response when guanaco population densities are  $< 8$  individuals  $\text{km}^{-2}$ . Data from two national parks (Torres del Paine, Chile and SGNP, Argentina), however, suggest otherwise. In these protected areas, guanacos (Torres del Paine) and vicuñas (SGNP) have dramatically increased in the last 20–25 years despite past low-density populations and increasing puma predation (Iriarte *et al.*, 1991; Cajal & Bonaventura, 1998; Puig & Videla, 2007; this study). This pattern could have resulted

from camelid reproduction outpacing mortality as reported for several puma–ungulate systems in North America (Hornocker, 1970; Lindzey *et al.*, 1994; Logan & Sweanor, 2001).

High levels of mortality due to factors other than predation could also explain the temporal pattern observed in SGNP. If such factors had accounted for most of the camelid mortality during 1978–1983, but seldom affected camelid populations during 2004–2006, the percentage of carcasses with evidence of puma predation would have been relatively lower in 1978–1983 despite potentially constant puma predation pressure across study periods. Although these confounding factors cannot be completely ruled out, data on carcasses suggest that winter-related events, starvation or disease were not important mortality factors during 1978–1983 (Cajal & Lopez, 1987). Moreover, in both periods, puma predation was likely underestimated. Pumas often kill camelids by delivering a bite to their throat (Wilson, 1984). Most camelid carcasses were found as incomplete skeletons with no hide vestiges. Consequently, finding teeth punctures in camelid throats or crushed tracheas was sometimes unfeasible and misclassification of cause of vicuña deaths could have occurred.

Overall, our data on puma diet and predation patterns suggest that, similar to North American pumas, South American pumas (1) heavily prey on large native ungulate species and (2) display predatory and dietary patterns largely dictated by availability of large mammal prey. We propose that the low representation of large native herbivores in the diet of pumas inhabiting the southern Neotropics (Iriarte *et al.*, 1990) is a result of a highly modified prey base resulting from widespread declines of native ungulates and extensive introductions of alternative prey species.

The intact puma–camelid interaction observed in some protected areas of northwestern Argentina is significant from ecological and management perspectives. Ecologically, it suggests that the pervasive influences of large mammalian predators on the dynamics of camelid populations and in the structuring and functioning of biological communities may still be expressed in some protected areas of northwestern Argentina. From a management perspective, knowledge gained on the puma–camelid interaction will prove essential for the successful recovery in areas where camelid numbers have been considerably reduced or reintroduction where they have been extirpated. Although the predatory relationships between pumas and camelids are not yet understood, available data suggest that reintroduction attempts should assess whether the investment of reintroducing camelids is worthwhile in areas with high densities of pumas; small founding populations of camelids may be limited or even eliminated by heavy puma predation.

## Acknowledgments

Fifteen volunteers and 16 park rangers and managers helped with data collection and logistical support. They deserve much credit for their invaluable assistance during this study. We also thank the Rufford Small Grants (first and second

grants), Denver Zoological Foundation, Lincoln Park Zoo, College of Art and Sciences and Program in Ecology (University of Wyoming), Wildlife Conservation Society (WCS) and Idea Wild for funding this project. We are grateful to Ron Sarno and an anonymous reviewer for providing an insightful review of this paper. Permission to conduct this research was granted by the governments of La Rioja Province (LB), and San Juan Province (SGBR), and the Dirección Nacional de Parques Nacionales Delegaciones Centro (SGNP, ELNP, TNP and SQNP) and Noroeste (LCNP). E.D. was partially supported by the University of Wyoming, WCS, and a Fulbright Fellowship awarded by the Department of State (USA).

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