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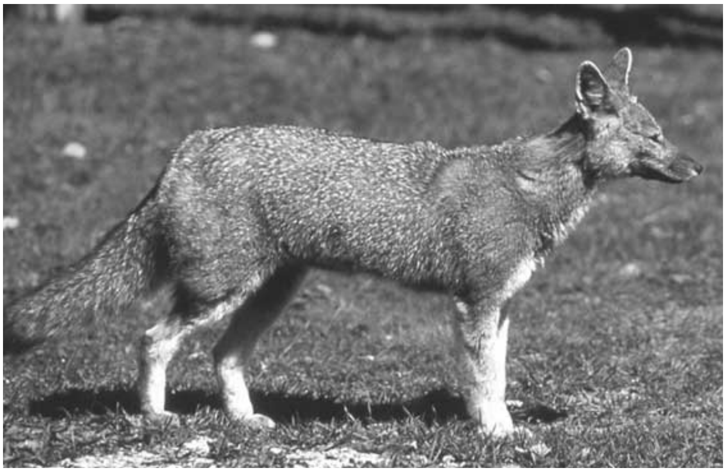
CHAPTER 15

Patagonian foxes

Selection for introduced prey and conservation of culpeo and chilla zorros in Patagonia

Andrés J. Novaro, Martín C. Funes, and Jaime E. Jiménez



Pseudalopex culpaeus (Culpeo fox) © Enrique Couve Montané.

Introduction

AQ: Pls. specify if 'a' or 'b' for Wayne *et al* 1989

The culpeo (*Pseudalopex culpaeus*) and the South American grey zorro or chilla (*Pseudalopex griseus*) are closely related canids (Wayne *et al*. 1989) that live in western and southern South America. The distributions of the culpeo and chilla overlap through most of the chilla range in Chile and western Argentina (Johnson *et al*. 1996; Fig. 15.1). Adult culpeos usually weigh 6–12 kg, adult chillas weigh 2–5 kg, and their sizes and size differences increase towards the south (Johnson and Franklin 1994a; Jiménez *et al*. 1995). Culpeo and chilla are opportunistic predators. Both canids feed primarily on small mammals but frequently consume introduced lagomorphs and livestock or its carrion wherever these have become abundant (i.e. Simonetti 1988; Johnson and Franklin 1994a; Jiménez *et al*. 1996; Novaro *et al*. 2000). Additional foods are birds, lizards, insects, and fruits (Medel and Jaksic 1988).

The mechanisms that allow coexistence between culpeos and chillas have been the subject of debate (Fuentes and Jaksic 1979; Jiménez *et al*. 1995, 1996; Johnson *et al*. 1996). Fuentes and Jaksic (1979) argued that complementarity (Schoener 1974) in the use of trophic and spatial resources allows coexistence because they compensate high overlap in one niche dimension with low overlap in the other. Evidence from radio-tracking studies in two areas of sympatry in Chile, however, suggests that culpeos select habitats with higher prey densities and exclude chillas, which are thus confined to less productive habitats (Johnson and Franklin 1994b; Jiménez *et al*. 1996).

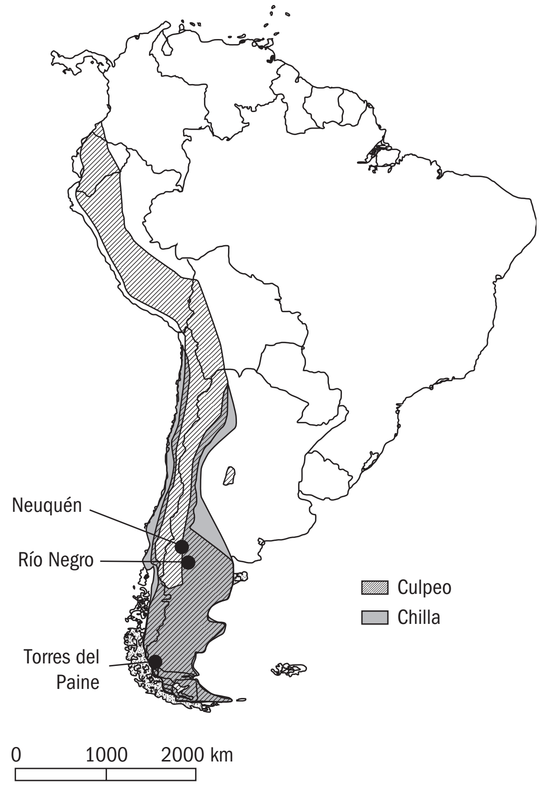


Figure 15.1 Distribution of culpeo (shaded) and chilla (lines) zorros in South America and location of study areas in Neuquén and Río Negro rangelands, Argentina, and Torres del Paine National Park, Chile.

Jiménez *et al*. (1996) expanded Fuentes and Jaksic's hypothesis by proposing that the presence of high-quality (large) prey such as lagomorphs may allow coexistence of culpeos and chillas in sympatry if the habitat is sufficiently complex to provide shelter for the smaller chilla from culpeos. Increasing body size differences between culpeos and chillas towards the southern portion of their range may also favour coexistence by permitting specialization in different food resources (Fuentes and Jaksic 1979; but see Jiménez *et al*. 1995). Unfortunately, the patterns of prey selection by culpeos and chillas are little known because most studies of their diets (reviewed by Medel and Jaksic 1988; Jiménez *et al*. 1996) did not include evaluations of prey availability or did not test for prey selection.

The culpeo and chilla are intensively hunted throughout Argentina and Chile because they are perceived as major predators of sheep, goats, and poultry (Bellati and von Thüngen 1990). In the Argentine provinces of Río Negro and Chubut, for example, control agencies paid US$10–25 between 1996 and 2001 for culpeo bounties, killing *c*.19,400 and 30,000 culpeos, respectively (Direcciones de Fauna of Río Negro and Chubut provinces unpublished data). In spite of their small size, chillas are perceived as lamb predators by many rural people in Argentina and Chile (Jiménez *et al*. 1996; Travaini *et al*. 2000b). Pressure to offer bounties for chillas in Argentine Patagonia has been mounting since the decline in fur demand in the 1990s led to increased chilla densities and anecdotal reports of chilla predation on sheep. The studies of the feeding ecology of both culpeos and chillas appear to contribute little to reducing this perceived conflict with people and, in particular, shed little light on what factors determine the incidence of predation on domestic species (Novaro *et al*. 2000).

Here, our aims were to assess patterns of prey selection by culpeos and chillas in areas where the two species were sympatric and: (1) where sheep were abundant and the main wild prey, lagomorphs, had different densities; (2) where both canids were protected and sheep density was low. We use these comparisons to evaluate the competitive relationships between the culpeo and chilla and the factors that determine predation on livestock.

Our comparisons were based on two studies that reported data on culpeo and chilla food habits and a broad array of prey availability, and on unpublished information from one of these studies. In sheep rangelands of Neuquén, Argentina (Fig. 15.1), culpeo and chilla diets were studied from stomach contents provided by hunters (Novaro *et al*. 2000). Culpeos and chillas selected strongly for European hares and culpeos also selected for sheep according to prey densities, whereas culpeos selected for hares and chillas for sheep carrion according to the biomasses of available foods. In this study, however, culpeos were sympatric with chillas only in the east of the study area, where hare densities were low (29.5 + 11.6 hares/km^2). Only culpeos were present to the west, where hare densities were 54.3 + 27.2 hares/km^2. Here, we compare culpeo and chilla prey selection in sympatry and culpeo prey selection between areas of allopatry and sympatry with chillas. Additionally, we compare data on diets from sympatric culpeo and chilla in a third area to the southeast (Río Negro; Fig. 15. 1) where sheep were in similar numbers and hare were more abundant than in the allopatric Neuquén area (R. Cardon personal communication). We expected that different hare numbers would affect the trophic interactions between culpeos and chillas and their consumption of sheep, because population changes of principal prey can have significant effects on predator populations and their behaviour (Knick 1990; Poole 1994). In particular, considering the importance of hares in the diet of culpeos and chillas, we predicted that low hare numbers might be associated with increased overlap in their diets, presumably increasing competition for food, and increased predation on domestic livestock, and consequently increased animosity of farmers towards these canids. In addition to its focus on the highly practical question of depredations by these canids on domestic stock, this study brings together two highly topical areas of ecological theory, namely intra-guild competition and the ecosystem effects of introduced predators and prey (as reviewed, for example by Macdonald *et al*. 2001).

Johnson and Franklin (1994a) presented a comprehensive analysis of culpeo and chilla diets and prey abundances in Torres del Paine National Park in Chile (Fig. 15.1). Using data from faeces, these authors reported that culpeo and chilla diets differed in three main components: culpeos preyed more on hares, chillas consumed more carrion, and chillas were more omnivorous than culpeos, feeding more on arthropods and plants. Johnson and Franklin also reported that the differences in culpeo and chilla diets were associated with different prey availabilities in the habitats that both species used. Culpeo home ranges included habitats that had higher densities of hares, and chilla ranges included habitats where carrion was more abundant (Johnson and Franklin 1994b). A comparison of prey selection patterns between Torres del Paine and Neuquén sheds further light on prey selection by culpeos and chillas, and provides a contrast between circumstances where sheep were present in low numbers as opposed to densities typical of Patagonian ranches. A prerequisite for this comparison is a reconciliation of statistical methods used for the two studies.

Study areas

The Neuquén study area was located in northwestern Argentine Patagonia (40°S, 71°W), Province of Neuquén, on six sheep and cattle ranches encompassing a total area of 1420 km^2 (Fig. 15. 1). Culpeo and chilla were sympatric on the two ranches to the east and only culpeos occurred on the other four ranches. The vegetation was characterized by a mixed steppe of grass and shrubs. Weather was dry and cold, with frosts throughout the year. Mean annual temperature was 11°C, and mean annual precipitation ranged from 28 to 75 cm on an east–west gradient and was concentrated during the winter. The Río Negro study area was located 150 km southeast of the Neuquén area, on small sheep ranches in the vicinity of the town of Comallo (41°S, 70°W); Vegetation and mean temperature were similar to Neuquén, but mean annual precipitation was 200 cm.

Torres del Paine National Park is located in the western foothills of the Andes Mountains in southern Chilean Patagonia (51°S, 73°W; Johnson and Franklin 1994a; Fig. 15.1). Seventy per cent of Torres del Paine was a dry steppe similar to the study area in Neuquén, but deciduous forest (*Nothofagus* spp.) patches were common in Torres del Paine. Mean annual precipitation (55 cm) was similar to that in Neuquén, but summers were wetter and mean annual temperature was lower in Torres del Paine (approximately 6°C). The mammal assemblage in Torres del Paine (Johnson *et al*. 1990) was similar to that in the Neuquén steppe, but guanacos (*Lama guanicoe*) were more abundant and sheep were rare in the park.

Methods

Neuquén and Río Negro rangelands

Food habits were determined through the analysis of stomach contents of 320 culpeo and 42 chilla killed by hunters in Neuquén between 1989 and 1994 and 18 culpeo and 19 chilla killed in Río Negro in 1989. The methodology is detailed in Novaro *et al*. (2000). Prey items were identified as carrion if they were too large to have been killed by the zorros (e.g. cattle or horse) or when they contained larvae of Diptera. Sheep were considered as prey (Bellati and von Thüngen 1990), although they were likely scavenged in many cases. This avoided underestimating potential predation on sheep.

We present results as per cent occurrence (number of times an item occurred as percentage of the total number of prey items in all stomachs) and as per cent mass of each item for stomach contents. We compared culpeo and chilla diets and dietary overlap between areas with different hare densities. Diets were compared between areas using log-linear analysis for frequencies (Zar 1996) and the von Mises test for continuous proportions (Stephens 1982; Maher and Brady 1986) for biomass consumed. We calculated food-niche overlap or diet similarity using Pianka's (1973) index: $O = p_{xi}\, p_{yi}/(p_{xi}^{2} \cdot p_{yi}^{2})^{1/2}$, which ranges from 0 (complete dissimilarity) to 1 (similarity).

We estimated prey biomass in Neuquén as the product of prey density and mean body mass and assumed that prey biomass and density were acceptable combined estimators of prey availability (Jaksic *et al*. 1992). Prey activity patterns and habitat use also may be important components of prey availability but were not estimated. Density estimation methods for different prey and for carrion are described in Novaro *et al*. (2000). Sheep availability was based on densities and body masses of sheep up to 1 year old for culpeos and up to 2 months old for chillas. Results are presented as mean density ±1 SE. Diet and prey availability data were averaged throughout seasons.

To evaluate the role of prey body-size and density in selection by culpeo we analysed selectivity according to relative biomass and frequency of prey consumed and available. Both selectivity measures are necessary to assess selection of available prey. Prey selection was studied by comparing proportions of biomass of prey in stomachs to proportions of biomass available using overall MANOVA procedures based on an *F*-test (Girden 1992; PROC GLM, SAS Institute Inc. 1996). Prey selection also was studied by comparing frequencies of occurrence in diets to relative densities of each prey using a goodness-of-fit *G*-test (Zar 1996). When differences were significant ($p < 0.05$), we tested for selection or rejection of individual prey with individual MANOVA tests for each prey biomass (PROC GLM, SAS Institute Inc. 1996) and 95% Bonferroni confidence intervals for each prey frequency (Byers *et al*. 1984). Expected proportions were the proportions of biomass or density of each prey available to culpeos in allopatry and sympatry with chilla. Prey selection by sympatric chillas is reported in Novaro *et al*. (2000).

Torres del Paine National Park

Johnson and Franklin (1994a) reported the per cent occurrence of prey in culpeo and chilla faeces. Per cent occurrences, however, do not represent the relative numbers of prey consumed, due to differential digestibility of prey of different sizes and types (Ackerman *et al*. 1984; Weaver 1993). Furthermore, the per cent biomass of prey consumed, needed to compare to the proportions of available prey to estimate selectivity (Novaro *et al*. 2000), cannot be obtained directly from faecal samples as it can be from stomach contents. Therefore, we estimated the per cent biomass and number of prey consumed by culpeos and chillas using correction factors calculated by Lockie (1959) for *Vulpes vulpes*, a canid that is intermediate in size between Patagonian culpeos and chillas (and comparable to values measured for jackals by Atkinson *et al*. 2002). We assumed that per cent occurrence of prey in faeces was an acceptable approximation to per cent mass of undigested matter for each prey. Carrion consumption could not be estimated because correction factors were not available, so the per cent consumption of other items was overestimated in relation to percentages reported for culpeos and chillas from Neuquén and Río Negro. We did not calculate diet overlaps for corrected data from Torres del Paine because our diet correction for only some of the food items would have yielded overestimated overlap indices.

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We calculated relative densities and biomass of the main prey in Torres del Paine from information on hare densities from Johnson and Franklin (1994a) and on sheep and upland goose (*Chloephaga picta*) densities from Iriarte *et al*. (1991). Some sheep occurred in Torres del Paine, mostly within chilla home ranges (Johnson and Franklin 1994a). We assumed a similar age structure and differential availability of sheep as for culpeos and chillas on Neuquén ranches. We calculated mean densities of cricetine rodents from Johnson and Franklin

(1994a)'s cricetine abundance data and mean body masses from Johnson *et al*. (1990). We divided cricetine abundances by the size of the trapping grids plus an extrapolated border strip of width equal to the mean distance moved by individuals (Seber 1982; Pearson *et al*. 1984) of a similar species assemblage in Neuquén (Novaro 1991; Corley *et al*. 1995).

Results

Culpeo and chilla diets

European hare and sheep comprised the majority of the biomass in the diet of culpeo and chilla in Neuquén, and hare comprised the majority of their diets in Río Negro and Torres del Paine (Tables 15.1 and 15.2). Culpeo diets differed significantly between areas of sympatry with chilla in Neuquén and Río Negro according to biomass ($Z = 5.01$, $\mathrm{df}_1 = 9$, $\mathrm{df}_2 = 729$, $P < 0.001$) and numbers of prey consumed ($\chi^2 = 10.7$, $\mathrm{df} = 4$, $P < 0.05$). Chilla diets also differed significantly between areas of sympatry with culpeos in Neuquén and Río Negro according to biomass ($Z = 4.24$, $\mathrm{df}_1 = 4$, $\mathrm{df}_2 = 116$, $P < 0.001$) and numbers of prey consumed ($\chi^2 = 11.6$, $\mathrm{df} = 4$, $P = 0.041$). The biomass and number of hares consumed by culpeos and chillas were less than half in Neuquén than in Río Negro, whereas sheep and carrion were consumed more frequently in Neuquén.

In spite of the similarity of sheep densities between areas of sympatry in Neuquén and Río Negro, culpeo and chilla diets in Río Negro were most similar to diets in Torres del Paine, where sheep were almost absent. The dominance of hare in the culpeo and chilla diets in Torres del Paine is more pronounced when the diets are presented as per cent biomass consumed as opposed to per cent occurrence in faeces. Conversely, the dominance of cricetines is emphasized when the numbers of prey consumed are reported (Table 15.2).

Contrary to our prediction, overlap between the diets of culpeos and chillas appeared higher where hares were more abundant. Overlap in Neuquén was 0.899 according to biomass and 0.950 according to numbers of prey consumed, and in Río Negro was 0.986 and 0.965, respectively (Fig. 15.2)

Culpeo and chilla prey selection

In Neuquén, both culpeos and chillas were selective in their food habits, but selectivity for certain prey differed according to whether biomass or densities of prey were considered. Prey selection by culpeos changed between areas of allopatry and sympatry with chillas (Tables 15.3 and 15.4). In spite of the lower hare density in the area of sympatry, in both areas culpeos consumed hares more than expected according to their biomass available, carrion less than expected, and cricetines in similar proportion

Figure 15.2 *Pseudalopex griseus* (Chilla). © Rafael González del Solar.

Table 15.1 Culpeo and chilla diets in an area of sympatry (and low European-hare density) and culpeo diet in an adjacent area of allopatry (and intermediate hare density) in Neuquén rangelands, and culpeo and chilla diets in an area of sympatry (and high hare density) in Río Negro rangelands, Argentina

	Neuquén						Río Negro			
	Allopatric culpeo		Sympatric culpeo		Sympatric chilla		Sympatric culpeo		Sympatric chilla	
Prey type	%N	%B	%N[a]	%B[b]	%N[a]	%B[b]	%N[c]	%B[d]	%N[c]	%B[d]
Mammals										
Order Rodentia										
Cricetine	30.9	9.2	29.2	9.5	25.5	11.4	23.1	2.2	27.6	5.9
Ctenomys spp.	5.8	3.9	5.6	2.0			3.8	3.1	3.4	1.5
Caviidae	2.2	1.5	0.6	tr	3.6	6.5	3.8	7.8	3.4	5.4
Order Marsupialia										
Thylamys pusilla					3.6	0.1				
Order Edentata										
Chaetophractus and Zaedyus	2.4	1.1			5.5	0.8			6.9	10.8
Order Lagomorpha										
Lepus europaeus	29.0	56.6	20.5	35.1	16.4	14.6	57.7	85.2	41.4	71.6
Oryctolagus cuniculus	0.5	0.8								
Order Artiodactyla										
Sheep	12.7	14.8	17.4	34.4	20.0	40.3	3.8	0.4	3.4	3.9
Carrion[e]	8.3	10.5	11.2	15.7	9.1	21.0				
Unidentified mammals	2.9	0.2	4.3	1.3	9.1	0.5				
Total mammals	94.7	98.6	88.8	98.0	92.8	95.2	92.2	98.7	86.1	99.1
Birds										
Pterocnemia pennata			0.7	0.2						
Unidentified birds	3.6	1.3	6.8	1.8	1.8	2.5	7.7	1.4	10.3	1.0
Lizards	1.7	tr	3.7	tr	5.5	0.5			3.4	tr
Number of vertebrate food items	411		161		55		26		29	
Number of stomachs	239		81		42		18		19	
Percentage of stomachs with										
Invertebrates					17.6				47.4	
Schinus spp. seeds					2.9		16.7		21.1	

Note: %N = per cent occurrence, and %B = per cent biomass in stomachs.

Pianka indices of trophic overlap: [a] 0.950; [b] 0.899; [c] 0.965; [d] 0.986. [e] *Equus, Bos, Cervus, and Lama*, tr = trace, <0.05%.

Table 15.2 Per cent occurrence of prey in culpeo and chilla faeces (%O, from Johnson and Franklin 1994a) and per cent biomass (%B) and number of prey consumed (%N) in an area of high European-hare density in Torres del Paine National Park, Chile

	Culpeo			Chilla		
Prey type	%O	%B	%N	%O	%B	%N
Mammals						
Order Rodentia						
Cricetine	20.3	10.6	81.6	23.9	16.0	72.9
Order Lagomorpha						
Lepus europaeus	68.5	81.4	11.7	45.0	68.7	7.6
Order Carnivora						
Conepatus humboldti	0.8	1.1	1.1	0.5	0.9	0.5
Order Artiodactyla						
Sheep	0.8	0.8	0.4	6.4	8.7	2.5
Carrion (*Lama and Bos*)	2.2	–	–	13.8	–	–
Total mammals	92.6			89.6		
Birds						
Chloephaga picta	5.1	5.7	2.9	1.8	2.6	0.7
Unidentified birds	1.8	–	–	4.6	–	–
Frogs	0.0			0.2		
Lizards	0.5	0.3	2.2	3.8	3.1	15.6
Number of vertebrate food items	784			851		
Number of faeces	645			890		
Percentage of faeces with						
Beetles	2.0			41.8		
Scorpions	0.0			1.2		
Seeds	0.0			0.6		
Vegetation	2.8			7.0		
Berberis buxifolia	1.0			7.5		
Egg shells	0.7			3.4		

Note: %B and %N were calculated with correction factors from Lockie (1959). Missing percentages (–) are those that could not be calculated with correction factors.

to their availability. In the area of sympatry culpeos consumed sheep more than expected and in the area of allopatry they consumed sheep in similar proportion to its availability (Table 15.3). The frequencies of prey in the diets of culpeos also differed significantly from the relative densities of prey available in sympatry ($G = 403.9$, df = 2, $P < 0.001$) and allopatry ($G = 956.6$, df = 3, $P < 0.001$; Table 15.4). In both areas culpeos consumed hares and sheep significantly more than expected according to their densities and cricetines less than expected.

In Torres del Paine, culpeos and chillas were selective in their food habits according to numbers of prey consumed (Table 15.5) but their patterns of prey selection were different when we considered the biomass of prey (Table 15.6). The numbers of prey consumed by culpeos differed significantly from the relative densities of prey available ($G = 195.8$, df = 3, $P < 0.001$; Table 15.5). Culpeos consumed hares and geese significantly more than expected according to their densities and cricetines less than expected. According to biomass of prey,

Table 15.3 Prey selection by culpeos based on biomass consumed and available in areas of allopatry and sympatry with chillas in Neuquén, Argentina

	Prey	%EB	%B	Wilks' Lambda	df_1	df_2	*P* level
Sympatry (95)	Overall			0.133	3	31	0.0001
	Hare	18.0	37.0	0.221	1	54	0.0001
	Lamb	24.0	36.3	0.736	1	54	0.0323
	Carrion	41.2	16.6	0.362	1	54	0.0001
	Cricetines	9.8	10.1	0.995	1	54	0.9634
	Edentates	7.0	0.0	–	–	–	–
Allopatry (92)	Overall			0.015	4	188	0.0001
	Hare	28.7	61.4	0.141	1	192	0.0001
	Lamb	20.8	16.1	0.861	1	192	0.5472
	Carrion	35.8	11.4	0.382	1	192	0.0001
	Cricetines	8.6	10.0	0.958	1	192	0.7934
	Edentates	6.0	1.1	0.904	1	192	0.0182

Notes: Percentages of biomass available and in the diet are only for prey for which availability data were obtained. Percentages of prey in the diet (%B) were compared to percentages expected according to availability (%EB) using a MANOVA test. Per cent biomass of diet considered out of overall diet is indicated between parentheses.

Table 15.4 Prey selection by culpeos based on per cent prey occurrence in stomachs (%N) and density of prey in areas of sympatry and allopatry with chilla in Neuquén, Argentina

	Sympatry			Allopatry		
Prey type	Density (ind./km^2)	%EN[a]	%N ± BCI	Density (ind./km^2)	%EN[a]	%N ± BCI
Hare	29.5 ± 11.6	1.2 *M*	30.6 ± 11.1	54.3 ± 27.2	2.2 *M*	38.6 ± 7.1
Sheep	5.4 ± 0.5	0.2 *M*	25.9 ± 10.5	5.4 ± 0.5	0.2 *M*	16.9 ± 5.5
Cricetine rodents	2422.9 ± 1597	98.6 *L*	43.5 ± 11.9	2422.9 ± 1597	97.1 *L*	41.2 ± 7.2
Edentates	13.1 ± 6.9	0.5	0.0	13.1 ± 6.9	0.5 *M*	3.2 ± 2.6
Total prey items			108			308

Notes: Numbers added or subtracted from %N are 95% Bonferroni confidence intervals (BCI) for %N; expected percentages of prey consumed (%EN) were calculated from prey densities.

[a] Prey items are consumed significantly more (*M*) or less (*L*) than expected according to their availability if %EN are smaller than the lower limit or larger than the upper limit of each BCI, respectively ($P < 0.05$).

however, culpeos consumed most prey (except cricetines) in similar proportions to their availabilities (Table 15.6).

The numbers of prey consumed by chillas also differed significantly from the relative densities of prey available in Torres del Paine ($G = 394.6$, df = 3, $P < 0.001$; Table 15.5). Chillas consumed hares and sheep significantly more than expected according to their densities and cricetines less than expected. The chilla diet also differed from the biomass of available prey: chilla consumption of cricetines was *c.* 1/3 of that expected and hares and sheep were consumed in larger proportions than their availabilities (Table 15.6).

Table 15.5 Prey selection by culpeos and chillas based on per cent prey occurrence in faeces (%O, from Johnson and Franklin 1994a), numbers of prey consumed (%N), and density of prey in Torres del Paine

	Culpeo				Chilla			
Prey type	%O	Density (ind./km^2)	%EN[a]	%N ± BCI	%O	Density (ind./km^2)	%EN[a]	%N ± BCI
Hare	72.3	86.6 ± 30.3	3.64 *M*	12.1 ± 3.0	58.4	24.8 ± 7.7	1.07 *M*	9.1 ± 2.8
Sheep	0.8	0.2	0.01	0.5 ± 0.6	8.3	0.08	0.003 *M*	3.0 ± 1.7
Cricetines	21.4	2290 ± 1759	96.13 *L*	84.5 ± 3.3	31.0	2290 ± 1759	98.7 *L*	87.1 ± 3.3
C. picta	5.4	5.3	0.22 *M*	3.0 ± 1.6	2.3	5.3	0.23	0.8 ± 0.9
Total prey	742				656			

Notes: %N were calculated applying correction factors from Lockie (1959); numbers added or subtracted from %N are 95% Bonferroni confidence intervals (BCI) for %N; expected percentages of prey consumed (%EN) were calculated from prey densities (from Johnson and Franklin 1994a, and Iriarte *et al*. 1991).

[a] Prey items are consumed significantly more (*M*) or less (*L*) than expected according to their availability if %EN are smaller than the lower limit or larger than the upper limit of each BCI, respectively ($P < 0.05$).

Table 15.6 Prey selection by culpeos and chillas based on biomass of prey consumed and biomass of prey available in Torres del Paine

		Culpeo		Chilla	
Prey type	Weight (kg)	%B	%EB	%B	%EB
Hare	3.35	82.6	71.9	71.6	43.5
Sheep	25 and 5[a]	0.9	1.4	9.1	0.2
Cricetines	0.04	10.7	22.7	16.7	48.0
C. picta	3.0	5.8	3.9	2.7	8.3

Notes: Average body weight for cricetines are from Johnson *et al*. (1990), for hare from Johnson *et al*. (unpublished manuscript), and for sheep (lambs and 1-year-olds) from Novaro (unpublished data). Biomasses of prey consumed (% B in diet) were calculated applying correction factors from Lockie (1959) to data from Johnson and Franklin (1994a); expected percentages of biomass of prey available (%EB) were calculated from density data from Johnson and Franklin (1994a) and Iriarte *et al*. (1991).

[a] Body mass of sheep available to culpeos and chillas, respectively.

Discussion

Culpeo and chilla diets and prey selection

Diets and prey selection by culpeos and chillas in Patagonia were strongly affected by the local abundance of European hare and domestic sheep. In the Neuquén area where hare were scarce, which was also an area of sympatry with chillas, culpeos consumed more sheep than in the area of allopatry. In the Río Negro area of sympatry, where sheep were also present, culpeo and chilla consumed more hares than in either of the Neuquén areas. The changes in prey selection associated with hare abundance were different, however, depending on whether biomass or frequencies were used as the measure. Using biomasses as the yardstick, culpeos selected hares positively in both areas and selected sheep where hares were in low numbers (Table 15.3). When frequencies were the measure, hares and sheep were selected regardless of the abundance of hares. Conversely, in Torres del Paine, where hares were most abundant, consumption of hare by culpeos was not different from hare availability according to biomass. Thus, culpeos appear to select intensively for hares at intermediate and low hare densities, even in the presence of abundant sheep. Perhaps hare is a more profitable (Pyke *et al*. 1977) prey than sheep, due to greater vulnerability (Corbett and Newsome 1987). In the case of the chilla, strong selectivity for hares even at low hare densities (and when sheep and its carrion are abundant; Novaro *et al*. 2000) suggests that hares are also a highly profitable prey. These results also agree with food preferences of other canids, which only take sheep when their preferred prey are scarce (i.e. *Vulpes vulpes*, Macdonald 1977a; *Canis latrans*, Sacks and Neale 2002).

The low consumption of sheep in Río Negro in comparison with Neuquén may be related to differences in sheep management practices. In the study area in Río Negro sheep are raised in more labour-intensive, smaller ranches where humans proximity may deter predation. In the large ranches of the Neuquén study area, on the other hand, ranch hands check less frequently on the sheep. These differences may lead to lower predation on sheep or to lower carrion availability in Río Negro.

Our results suggest that spatial or temporal changes in hare densities could lead to increased predation on sheep and also on native prey in some areas in Patagonia. The increase in sheep predation is more likely in culpeos which, due to their larger size, are better able to kill lambs and even adult sheep than are chillas (Bellati and von Thüngen 1990). Our inability to distinguish between sheep that were scavenged or preyed upon prevents us from drawing conclusions about chilla predation on sheep. However, lower hare densities are likely to be associated with increased chilla consumption of sheep carrion and probable predation on lambs. In summary, areas and periods with low hare density may have increased conflicts between canids and humans in Patagonia.

The low selection for small cricetine rodents (according to both biomass and numbers) in relation to other prey suggests that these prey also may be less profitable than hares. This appears to be the case both in the presence of high (Neuquén) and low (Torres del Paine) numbers and biomass of sheep and its carrion as alternative foods. Low profitability of cricetines supports the conclusions of Jiménez *et al*. (1996) and Johnson and Franklin (1994a) that culpeos select habitats with higher densities of larger rodents or lagomorphs, but is at odds with their conclusion that cricetines would be selected by chillas. Chillas appear to be selecting strongly for hares, and may consume more cricetines than culpeos but not necessarily select for them in comparison with other prey.

Lower hare densities may not lead to increased competition for food between culpeo and chilla in Patagonia. The slightly lower indices of trophic overlap in Neuquén than in Río Negro were mainly due to higher consumption of sheep by culpeos and of carrion by chillas, as well as reduced consumption of hare by both. The ultimate explanation for the small change in trophic overlap, however, may be the overall high density of hare, livestock, and its carrion in Patagonian rangelands and the relatively low canid densities after several decades of intense hunting for fur (Novaro 1997b). These results support the overall conclusion by Johnson and Franklin (1994a) about the similarity of optimal diets by culpeo and chilla. The diet similarity index in Torres del Paine may be in fact much higher (0.94) than reported by these authors (0.14), apparently due to miscalculation of Pianka's index. In particular, our results indicate that selection for or against specific prey such as hares and cricetines is almost identical between these canids, even in the presence of larger prey such as sheep. As a consequence, the use of different habitat types reported by Johnson and Franklin is probably the result of exclusion of chillas by culpeos from more productive habitats and not a consequence of different selection patterns for habitat or food.

Coexistence and conservation of culpeos and chillas in Patagonia

Our findings suggest that in areas of sympatry in southern Chile and Argentina, diets and prey selection patterns of culpeo and chilla may be more similar than expected, especially when the numbers and biomass of prey consumed are considered. Overall, culpeo and chilla diets and prey selection differed mostly among areas with different prey densities and were strikingly similar between species in each area. Furthermore, this similarity in prey selection occurs in two areas where culpeo and chilla body sizes are most dissimilar (Novaro 1991; Johnson and Franklin 1994a). Thus, segregation of food resources through selection for different prey or for habitats with different prey availabilities are unlikely mechanisms to allow coexistence between these canids throughout their range. In summary, if the food component of the niche-complementary hypothesis does not allow segregation even under the most extreme body-size differences, habitat segregation may be the only mechanism promoting coexistence throughout their range.

Most of the habitats occupied today by culpeos and chillas, including the Patagonian steppe, have been highly modified by humans. Some of these modifications may promote local conditions that would alter the result of chilla displacement from productive habitats by culpeos. In the area of sympatry of the

Neuquén steppe, for example, culpeo and chilla home ranges overlap and they are frequently found in the same habitats, particularly where habitat structure is more homogeneous (Novaro and Funes unpublished data). Based on the similarity of prey selection patterns presented in this study, we conclude that the presence of introduced hares in Patagonia may be insufficient to explain the coexistence between culpeo and chilla. Conversely, three other human-related factors may contribute to promote or reduce coexistence in this region. First, the availability of large numbers of sheep (both as live prey and carrion) may help reduce interference between the two foxes, because food availability may be so high that aggressive interactions from culpeos towards chillas may occur only rarely. Additionally, hunting of culpeos to reduce sheep predation is much more intense than of chillas in Patagonian sheep ranges (Novaro 1997). This source of mortality for culpeos may be sufficient to maintain culpeo numbers low at specific sites and thus allow the persistence of chillas even in homogeneous habitats. Finally, the introduction of sheep to Patagonia in the early 1900s was followed by the eradication of a larger carnivore, the puma (*Puma concolor*) from most of the steppe. The removal of pumas, which may have kept culpeo numbers low in many areas, might have affected chilla numbers negatively, as it has occurred with other carnivore guilds (Johnson *et al*. 1996, Linnell and Strand 2000). The current recolonization of much of Patagonia by pumas, probably due to a decline in sheep production, may lead to reduced culpeo densities and may allow higher densities or range expansions of chillas.

We therefore suggest that human disturbance through food supplementation or differential mortality may promote local (even within habitat) coexistence between culpeos and chillas in Patagonia, and likely in other areas of Chile and Argentina. However, the complexity of the interactions involving food availability, hunting by humans, and predation by larger carnivores determines that conditions for coexistence may depend on the local balance of these processes as well as on habitat complexity. As Johnson *et al*. (1996) point out, manipulation experiments (of food or mortality, even by closely monitoring removal or population reductions in removal conducted on sheep ranches) could provide additional understanding of the coexistence mechanisms between culpeos and chillas.

One implication of our results for managing canid–livestock conflicts in Patagonia is that predation on sheep and other domestic species may be more likely in areas where European hare densities are lower. Also, because hare numbers may fluctuate in Patagonia (Novaro *et al*. 2000), predation on sheep may increase during hare declines. These predictions apply mostly to culpeo predation, but also may apply to predation by chillas on lambs and other small domestic animals. Preliminary data from Neuquén may confirm these predictions (Novaro and Funes, unpublished data). First, sheep and goat losses to culpeos in 1999 averaged 24% and 21%, respectively, for 12 families in the Chiquilihuin Mapuche-Indian land, where ranges are degraded and densities of wild prey (including hares) are low, whereas losses usually average 5–10% on large private ranches. Second, estimated predation on sheep in one of our study ranches increased from an annual average of 10–40% in 1995–96 after a hare decline. The implications of these conclusions are that predation control efforts (either by canid control and/or livestock protection) should be restricted temporally and spatially to areas and times that are more likely to experience high predation, and should not be applied indiscriminately, as is commonly done in Patagonia.

AQ: Pls specify if Novaro 2000 'a' or 'b'

Another implication of our results is that strong selection for hares by culpeos and chillas may result in regulation of hare populations at low densities, reducing competition for pastures between hares, sheep, and native herbivores. An ongoing study of the effect of culpeo removal on hare population dynamics suggests that culpeo predation may help regulate hare numbers at low densities (Novaro *et al*. unpublished data). If these results are confirmed, Patagonian sheep ranchers may be better off by tolerating a certain level of canid predation on sheep, because their benefits from canid predation on hares may outweigh their losses due to occasional attacks on sheep (this parallels calculations by Macdonald *et al*. 2003 for the benefits to cereal farmers in the United Kingdom of tolerating red foxes which eat rabbits). Modelling and economic studies are needed to evaluate further the interactions between canids, hares, sheep, and pastures in the Patagonian steppe.

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