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Niche-complementarity of South American foxes: reanalysis and test of a hypothesis

Complementariedad de nicho en zorros sudamericanos: reanálisis y puesta a prueba de una hipótesis

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ABSTRACT

The niche-complementarity hypothesis states that for coexistence to occur, high overlap in one dimension of the niche must be compensated by low overlap in another. Fuentes & Jaksic (1979) noted that two fox species (*Pseudalopex culpaeus* and *P. griseus*) along the western coast of South America displayed this phenomenon, compensating low habitat overlap (allopatry) with high dietary overlap, and high habitat overlap (sympatry) with low dietary overlap and character displacement in body size. Fuentes & Jaksic offered scant quantitative evidence for their proposed hypothesis of fox coexistence patterns, and the habitat scale used was rather coarse: lowlands versus highlands (Andean Ranges). With the benefit of hindsight and a much better database that included one site (Aucó) where the two foxes are sympatric when they should not be according to the Fuentes & Jaksic hypothesis, we reanalyze the sources used by these authors as well as reports accumulated over the subsequent years. We also report an in-depth study of resource partitioning (food, habitat, and activity time) and coexistence of sympatric foxes at Aucó. At this site, the two foxes coexist by partitioning habitat at a fine-scale, maintaining interspersed non-overlapping species-specific home ranges in the patchy environment. Through interference, the larger *P. culpaeus* excludes the smaller *P. griseus* from high-quality (abundant prey) habitat patches. Though sympatric they are not syntopic: the two foxes overlap little at the habitat-type scale, have intermediate food overlap and complete overlap in activity time, thus supporting the niche-complementarity hypothesis but at a finer scale. In conclusion, the Fuentes & Jaksic hypothesis is still valid, but requires consideration of two factors previously ignored: the spatial scale at which coexistence occurs, and the availability of high-quality (large) prey.

Key words: Niche-complementarity hypothesis, *Pseudalopex* spp., spatial scale, resource partitioning, Chile.

RESUMEN

La hipótesis de complementariedad de nicho establece que para que ocurra coexistencia, alta sobreposición en una dimensión debe ser compensada por baja sobreposición en otra. Fuentes & Jaksic (1979) notaron que dos especies de zorros (*Pseudalopex culpaeus* y *P. griseus*) distribuidas a lo largo de la costa occidental de Sudamérica exhibían este fenómeno, compensando baja sobreposición de hábitat (alopatría) con alta sobreposición en dieta y alta sobreposición espacial (simpatría) con baja sobreposición dietaria y desplazamiento del carácter en tamaño corporal. Fuentes & Jaksic ofrecieron escasa evidencia cuantitativa para su modelo de coexistencia de zorros y la escala de hábitat con que trabajaron era bastante gruesa: llanuras costeras y del Valle Central versus montañas (Cordillera de los Andes). Con beneficio de la retrospectiva y de una mejor base de datos que incluye un sitio (Aucó) en que los dos zorros son simpátridos cuando ello no debiera ocurrir de acuerdo a la hipótesis de Fuentes & Jaksic, nosotros reanalizamos las fuentes usadas por dichos autores así como datos que se han acumulado en años recientes. También documentamos un estudio en profundidad de la partición de recursos (alimento, hábitat y tiempo de actividad) y de la coexistencia de zorros simpátridos en Aucó. En este sitio, las dos especies coexisten a través de repartirse el hábitat a una escala fina, manteniendo ámbitos de hogar inter-dispersos, no sobrepuestos, y especie-específicos en un ambiente naturalmente heterogéneo. Mediante interferencia, el zorro más grande (*P. culpaeus*) excluye al más pequeño (*P. griseus*) de los parches de hábitat de mayor calidad (con abundantes presas). Aunque son simpátridos, estos zorros no son sintópicos: las dos especies se sobreponen poco en la escala del tipo de hábitat, tienen sobreposición dietaria intermedia, y sobreposición completa en tiempo de actividad, corroborando así la hipótesis de complementariedad de nicho a una escala más fina. En conclusión, la hipótesis de Fuentes & Jaksic aún es válida, pero requiere consideración de dos factores previamente ignorados: la escala espacial en que ocurre la coexistencia y la disponibilidad de presas de alta calidad (grandes).

Palabras clave: Hipótesis de complementariedad de nicho, *Pseudalopex* spp., escala espacial, partición de recursos, Chile.

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INTRODUCTION

Culpeos (*Pseudalopex culpaeus*) and chillas (*P. griseus*) are among the most widespread South American foxes (Ginsberg & MacDonald 1990, Sheldon 1992). However, their distributions do not completely overlap, thus creating different biogeographical contexts of sympatry and allopatry of their populations. In the northern part of the culpeo's range (Ecuador and Peru), chillas are absent. The opposite happens in southeastern Argentina, where chillas are abundant and culpeos are not found. Across Chile and western Argentina, the two species are allopatric in the north (Mares et al. 1989) and sympatric in the south (Osgood 1943, Medel & Jaksic 1988). Throughout their ranges, these foxes face varying landscapes and environmental conditions (habitat types, temperature and precipitation regimes, etc.), as well as varying biotic networks (different arrays of prey types, sizes, and abundances).

Based on the distribution patterns of chillas and culpeos between 33° and 53° S in Chile, Fuentes & Jaksic (1979) hypothesized that niche-complementarity of diet and habitat accounted for their distributions and body sizes. The niche-complementarity hypothesis states that in order for two species with high habitat overlap to coexist, they must differ in diet, and vice-versa (Schoener 1974). Fuentes & Jaksic (1979) examined body-length data of chillas and culpeos, and body length of prey over 20 degrees of latitude in Chile. They found that chillas and culpeos were similar in size in central Chile, where they were reported to be allopatric. In southernmost Chile, these foxes were sympatric and differed in body size (the culpeo always being larger). According to Fuentes & Jaksic (1979), where the foxes did not overlap in space, body sizes were similar supposedly because of relaxed competition for prey of similar sizes.

Further, Fuentes & Jaksic (1979) suggested that because of the profile of the Andean Ranges (which in Chile decrease in altitude toward the south), habitat partitioning by altitudinal segregation would only be possible in the central part of the country. Here, chillas would use lowlands and culpeos use the mountains. In the south, both foxes would use the lowlands. These authors interpreted the foxes' size differences in terms of character divergence related to use of differently-sized prey when in sympatry (e.g., Rosenzweig 1966, Gittleman 1985, Vézina 1985).

Several subsequent studies conducted throughout Chile support Fuentes & Jaksic's hypothesis. In a north-south sequence in Chile, where the culpeo is present the chilla is absent: in parts of Tarapacá, I Region (Marquet et al. 1992); at Parque Nacional Fray Jorge, IV Region (Meserve et al. 1987, Jaksic et al. 1993); at Fundo San Carlos de Apoquindo, Metropolitan Region (Jaksic et al. 1980, Simonetti 1986, Iriarte et al. 1989); and at Fundo El Pangue, V Region (Ebensperger et al. 1991, Bustamante et al. 1992). The reverse is true for the culpeo where the chilla is present: in parts of Tarapacá, I Region (Marquet et al. 1992); at Chañaral, III Region (Simonetti et al. 1984); at Fundo Santa Laura, V Region (Jaksic et al. 1980); at Parque Nacional Nahuelbuta, IX Region (Medel et al. 1990); at Parque Nacional Puyehue, X Region (Rau et al. 1995); and at Bosque Experimental San Martín, X Region (Martínez et al. 1993). In southernmost Chile, Johnson (1992) found chillas and culpeos in sympatry at Parque Nacional Torres del Paine (XII Region), as predicted by the hypothesis.

Dietary analyses of chillas and culpeos support the niche-complementarity hypothesis. Although with a small sample size, Fuentes & Jaksic (1979) found that allopatric central Chilean foxes showed high diet similarity and that southern Chilean chillas ate prey of smaller sizes than northern ones (they did not have data on southern culpeo diets). Later, Jaksic et al. (1980, 1983) provided a much larger sample size that corroborated the initial findings.

However, contrary to expectations of the Fuentes & Jaksic hypothesis, De La Maza (1981) reported chillas and culpeos in sympatry in a north-central Chilean site: in the Reserva Nacional Las Chinchillas, at Aucó, IV Region. The sympatry of chillas and culpeos at Aucó was subsequently confirmed by Durán et al. (1987) and Jaksic et al. (1992). How do these two foxes coexist at Aucó? This site, which lies roughly 1.5

degrees to the north of the northernmost populations analyzed by Fuentes & Jaksic (1979), seems ideal for examining their proposed hypothesis in greater detail.

We will show that although niche-complementarity and resource partitioning indeed occur between foxes at Aucó, they are substantiated at a much smaller spatial scale than the one originally proposed. We will not focus on the character displacement expressed as change in body size of chillas and culpeos along their ranges, because we have already reported on that elsewhere (Jiménez et al. 1995). The new data here reported enable us to revise the original hypothesis of Fuentes & Jaksic (1979), and thus explain "anomalous" situations of fox sympatry.

MATERIAL AND METHODS

Literature review

We reviewed and analyzed the published information on chillas and culpeos under the light of Fuentes & Jaksic's (1979) approach. This time, we paid special attention to exactly where the information was collected and its implications for the spatial distribution of foxes.

Field study

The Reserva Nacional Las Chinchillas at Aucó (31°30' S, 71°06' W), IV Region, is a 4,570-ha (corrected by slope) fenced area about 300 km north of Santiago. It has a mediterranean-arid climate with rain concentrated during the cold winter. Interannual rain variability is high with a mean of about 175 mm. The rugged topography (400 - 1,700 m elevation) determines a landscape dominated by ridges, interspersed ravines and slopes, with scarce flatlands in the lower areas. The vegetation is dominated by thorn scrub, with species composition varying with slope exposure. On the drier, north-facing slopes, cacti and bromeliads constitute the dominant vegetation. South-facing slopes are more mesic, with more evergreen shrubs and the ground covered by abundant grasses. The remainder of the area is physiognomically intermediate between north- and south-facing slopes. A more detailed description of the site is found in Jiménez (1993).

In order to test the niche-complementarity hypothesis, we evaluated the evidence for resource-partitioning by foxes at Aucó during the entire year of 1992. We evaluated the resources used by chillas and culpeos along what have been considered the three most important niche dimensions for vertebrates: food, habitat, and activity time (Schoener 1974).

Food

We studied fox diets by examining the contents of feces. Because the bile acid technique failed to distinguished between feces of the two foxes (Jiménez et al., ms. accepted), we used two other criteria combined: (1) The diameter of the scat had to be within the 95% confidence interval of the feces of known foxes (Jiménez 1993); (2) the feces had to be collected within a known fox territory (see below). About one third (31.4%) of the scats did not meet both criteria simultaneously and were therefore discarded from the analyses. Feces were collected every other week throughout the area, especially along established transects (see below). For comparative purposes, we computed three food-niche metrics: (a) Geometric mean weight of prey; (b) Levins' food-niche breadth or diet diversity index; (c) Pianka's symmetrical food-niche overlap or diet similarity index (see Jaksic et al. 1983 for computations of these indices).

Habitat

We studied the spatial dimension of the niche using three different methods:

(1) Scent stations (Linhart & Knowlton 1975), lured with fox N° 1 urine (Cronk's Outdoor Supplies, Wiscasset, Maine), were run once a month during a 24-h period. Six scent stations, set 400 m apart, were distributed along a 2,000-m transect. Transects were established in: (a) flatlands, (b) ravines, (c) north-facing, and (d) south-facing slopes, which were the most extensive habitat types recognized. We replicated each habitat type

four times in each of four sectors within the Reserve. We checked transects during mornings and measured tracks with a 1-mm precision calipers. Tracks were assigned to either chilla or culpeo by comparing them to those from radio-tracked foxes (see Jiménez 1993 for details). We computed an index of visitation rate for each transect and species.

(2) Foxes were captured along transects in flatlands and ravines after checking the scent stations (Andelt et al. 1983). We used 13 Victor 1.5 padded leg-hold traps baited with canned fish, set apart every 300 m. Traps were checked every 12 h and trapped every month for 2-10 days in a row. We tranquilized captured foxes with ketamine (Ramsden et al. 1976), and they were sexed, aged, measured, weighed, and released within two hours.

(3) Four chillas and five culpeos were fitted with radiocollars. Two individuals of each species were fit with motion-sensitive transmitters. We estimated fox locations by triangulation from several places scattered within the Reserve, as well as by direct sightings. Fixes were obtained for varying periods at random times. We drew locations on maps and assigned them to one of the four habitat types already described, but in addition we considered east- and west-facing slopes. The 50-m contour lines for the Reserve as well as for the fox radio-locations were digitized in a PC geographical information system (GIS) in ARC/INFO format. We computed habitat availability as the proportion of the total area covered by each habitat type (see Jiménez 1993 for details).

Activity time

We estimated the activity status of foxes as the percent of the radio fixes that indicated movement within 3-hour periods. We also estimated activity by comparing the number of foxes caught in traps at night versus those caught during daylight.

RESULTS

Literature review

Qualitative reports typically describe culpeos as inhabitants of rugged, arid or semiarid mountain ranges, either open or forested, usually associated with the Andean Ranges up to 4,500 m elevation (Allen 1905, Osgood 1943, Mann 1945, Housse 1953, Crespo & De Carlo 1963, Greer 1965). Chillas are described as occurring in lowland and coastal habitats, grasslands with rolling topography, and other relatively flat habitats with short, open vegetation (Housse 1953, Greer 1965). However, some authors indicate that both foxes sometimes occupy open habitats in plains and low mountains (Osgood 1943, Housse 1953, Novaro 1991, Redford & Eisenberg 1992). Although culpeos in highlands and chillas in lowlands appears to be the most recurrent pattern, there are several geographical areas where their sympatry or allopatry is not clear, and these warrant further analysis. These cases have been overlooked, ignored, or not given sufficient importance. Here, we will focus mainly on those places where Fuentes & Jaksic (1979) as well as Jaksic et al. (1980, 1983) studied the foxes' diet quantitatively (i.e., central and southernmost Chile).

Fuentes & Jaksic's hypothesis predicts that in central Chile, chilla and culpeo should be allopatric. This prediction was corroborated by Jaksic et al. (1980) when studying foxes in Fundo Santa Laura (a coastal hilly area in the V Region) and in four neighboring sites in the Andean foothills near Santiago (Metropolitan Region). The first site, where only chillas were seen, is only 68 km across the Central Valley from the closest of the four pre-Andean sites, where only culpeos were observed. More recently, Ebensperger et al. (1991) studied the diet of culpeos at Fundo El Pangue (V Region), which lies approximately 18 km west of Fundo Santa Laura. Apparently, these two fox populations are parapatric (i.e., have adjoining geographic distributions) rather than allopatric (i.e., separated by a broad hiatus). Indeed, there are historical records of parapatric distribution of these two foxes in central Chile. Osgood (1943: 64) observed "... it [culpeo] appears to be fairly common in the coast hills near Valparaiso ..." and "... chilla is very abundant in central Chile ... even persists within the city of Santiago as I discovered by seeing several ... in the parklike surroundings of the Cerro San

Cristobal ..." (1943: 69-70). Osgood (1943: 64, 70) stated that he also examined chillas and culpeos from Papudo and Limache (V Region). Thus, both recent and past information on fox distribution in central Chile indicates that chillas and culpeos are sympatric (see below).

On the other hand, Fuentes & Jaksic (1979: 45) predicted that in southernmost Chile foxes should be sympatric. However, they studied chillas from Onaisín (on Tierra del Fuego Island, XII Region), where they were introduced in 1951 (Jaksic & Yáñez 1983: 370). Further, these chillas introduced in the flat northern part of Tierra del Fuego were considered as sympatric with native culpeos that occur only in the forested and more rugged southern part of the island (Jaksic et al. 1983). The closest record of a culpeo was at least 70 km away (see Fuentes & Jaksic 1979). Atalah et al. (1980) studied insular chillas (only 3/69 came from potential culpeo ranges) without reporting the presence of culpeos at any of their study sites. In fact, in three different trips to Tierra del Fuego JEJ saw chillas but no culpeos on the northern half of the island.

Across from Tierra del Fuego, on mainland Magallanes, Jaksic et al. (1983) did not mention the presence of chillas at Parque Nacional Torres del Paine. Further, Jaksic et al. (1983: 693) reported only chillas from Monte Aymond, 253 km northeast of Parque Nacional Torres del Paine. Durán et al. (1985) surveyed foxes on six different areas on flatlands and rolling hills along a 767-km transect between Torres del Paine and Punta Arenas (XII Region) and saw nothing but chillas. They stated that culpeo "... inhabits the forest area and more closed vegetation sites throughout the region ... these species are allopatric ..." (1985: 142) and that "... grey fox habitat was characterized by the 'coirón' steppe chaparral ..." (1985: 146). Allen (1905: 161) had already implied that most fox populations in Patagonia were allopatric or parapatric, stating that "... In my experience the range of the grey fox [his *Cerdocyon griseus*] seems to cease at the foothills of the Cordillera, where the Magellan wolf (*Canis magellanicus*) [culpeo] is to be found ..." However, Johnson (1992) conducted an intensive study of foxes at Parque Nacional Torres del Paine and found that chillas and culpeos were in sympatry, as predicted by Fuentes & Jaksic (1979). It is unlikely that the presence of chillas at this site was due solely to the expansion of their ranges during the last decade (Abello 1979 in Johnson 1992) and perhaps their presence was overlooked during the earlier studies.

Therefore, the biogeography of foxes in the XII Region is more complex than originally thought. It appears that chillas and culpeos are not sympatric, but rather allopatric in southernmost Chile. Thus far, the only truly sympatric chillas and culpeos have been found in Parque Nacional Torres del Paine. All the other records indicate that chillas use flatlands (even in areas where they were introduced) and culpeos use rugged and forested landscape.

In summary, chillas and culpeos in central Chile are not strictly allopatric, but rather parapatric or even sympatric (see below), whereas in southernmost Chile they are mostly allopatric except for Parque Nacional Torres del Paine.

Food

The feces of chilla and culpeo that we analyzed contained vertebrates, invertebrates, and fruits throughout the year. Although the ordinal ranking of prey classes is similar between fox species, their proportional occurrences are different. By number, culpeos consume about twice as many mammals, birds, and reptiles than do chillas (Table 1). Chillas eat more insects and fruits than culpeos.

On a biomass basis, the differences between chillas and culpeos become less obvious and proportions of vertebrates more even (indeed, there were no significant differences between the two fox species, Table 1). The only significant difference is for insects, which contributed seven times more biomass to chilla than to culpeo diets (Table 1). By far, most of the biomass in the two foxes' diets was made up of mammals (> 80%, Jiménez 1993). On average, chillas consume more than twice the small mammal (rodents and marsupials) biomass taken by culpeos (38.9 vs. 16.9%). Conversely, chillas

TABLE 1

Percent representation of prey by numbers and by biomass in the diet of chillas (131 feces) and culpeos (285) at Aucó, north-central Chile. Values are means of four calendar seasons. Kruskal-Wallis tests with Chi-square approximation were used to compare biomass figures between foxes

Representación porcentual por número y biomasa de presas en las dietas de chillas (131 fecas) y culpeos (285) en Aucó, centro-norte de Chile. Los valores son medias de cuatro estaciones calendario. Pruebas de Kruskal-Wallis con aproximación de Chi-cuadrado se usaron para comparar los valores de biomasa entre los zorros

Prey	% Number		% Biomass[1]		χ^2	P
	Chilla	Culpeo	Chilla	Culpeo		
Mammals	14.4	37.6	80.7	92.2	3.00	0.083
Birds	2.2	5.4	5.8	3.2	3.00	0.083
Reptiles	2.1	4.9	6.8	3.6	0.76	0.384
Insects[2]	81.4	52.1	4.1	0.6	5.33	0.021
Fruits	21.9[3]	5.9[3]	2.6	0.4	2.19	0.139

[1] See Jiménez (1993) for computations

[2] Includes a few arachnids

[3] These values correspond to percentage of occurrence among feces.

consume lower biomass of lagomorphs than do culpeos (41.8 vs. 68.0%, Jiménez 1993).

The yearly average of the geometric mean weight of culpeo prey was almost four times that of chillas (Table 2). This certainly resulted from the higher consumption of insects by chillas, given that there was no significant difference in the geometric mean weight of vertebrate prey taken by the two foxes (Table 2). Food-niche breadth was almost twice as high in culpeos than in chillas, but when standardized by the number of taxa taken (B_{sta}), the two foxes did not differ significantly in this regard (Table 2). Diet similarity ranged from 0.431 to 0.865 throughout the year (Jiménez 1993).

Habitat

Both fox species combined had four times more visits to scent stations on flatlands (20.6% stations visited) and ravines (20.1%) than on north- or south-facing slopes (both with 4.7% stations visited; F = 7.68; d.f. = 3, 105; P = 0.0001). Visitation rates showed strong interaction between species and habitat (F = 4.00; d.f. = 3, 105; P = 0.0094), which indicates differential use of habitat types by chillas and culpeos. On average, over the four calendar seasons, the rank order of culpeo visitation rates to habitat types was: ravines > flatlands > north-facing slopes = south-facing slopes. For chillas the sequence was: flatlands > ravines > north-facing slopes = south-facing slopes.

Fox trapping results were similar. More chillas than culpeos were captured in flatlands (G = 12.20, d.f. = 1, P < 0.001). The opposite was true for ravines (G = 4.86, d.f. = 1, P < 0.05).

Radiotelemetry also indicates that chillas and culpeos differed in their habitat use (G = 117.65, d.f. = 5, P < 0.0001). Based on the use and availability of different habitat types (using Z Bonferroni confidence intervals and $\alpha = 0.05$), the four radio-tracked culpeos appeared to prefer ravines and to avoid both south- and west-facing slopes. The remaining three habitat types (north- and east-facing slopes and flat areas) were used according to their respective availability. The five radio-tracked chillas also showed clear differences in habitat use. Overall, they appeared to prefer flat areas and to avoid north- and south-facing slopes. The remaining three habitat types were used by chillas in proportion to their respective availability.

The three methods used to estimate habitat use lead to the conclusion that chillas use flat areas more than culpeos and that the latter use ravines more than the former.

TABLE 2

Comparison of food-niche metrics between chillas and culpeos at Aucó, north central Chile. Values are means of four calendar seasons. Kruskal-Wallis tests with Chi-square approximation were used to compare metrics between foxes

Comparación de estadígrafos de nicho alimentario entre chillas y culpeos en Aucó, centro-norte de Chile. Los valores son medias de cuatro estaciones calendario. Pruebas de Kruskal-Wallis con aproximación de Chi-cuadrado se usaron para comparar los estadígrafos entre los zorros

Food-niche metrics	Chilla	Culpeo	X^2	P
Geometric mean weight of total prey (g)	2.2	8.4	5.33	0.021
Geometric mean weight of vertebrate prey (g)	71.2	71.9	0.00	0.999
Food-niche breadth (44 prey categories)	4.8	8.4	5.33	0.021
Standardized food-niche breadth	0.2	0.3	3.00	0.083

Activity time

Sufficient radio-tracking data were obtained from two individuals of each species. One culpeo ($G = 9.6$, d.f. = 1, $P < 0.005$) and one chilla ($G = 13.6$, d.f. = 1, $P < 0.001$) were more active during the afternoon and nightly periods. The other chilla ($G = 0.061$, d.f. = 1, $P > 0.50$) and the other culpeo ($G = 0.067$, d.f. = 1, $P > 0.50$) were active throughout day and night. The frequency distribution of active radio locations for the two chillas was not different from those of three culpeos (Smirnov large sample two-tailed test, $\chi^2 = 0.6697$, four time periods, $m = 59$, $n = 78$, $P > 0.10$), thus indicating that chillas and culpeos overall do not differ in their activity time. Activity as assessed by fox trappings shows that chillas were more active during the night than during daylight ($G = 11.25$, d.f. = 1, $P < 0.001$). Although more culpeos were captured at night, the difference with daylight captures was not significant ($G = 2.61$, d.f. = 1, $P > 0.10$).

DISCUSSION

The niche complementarity hypothesis of coexistence

Fuentes & Jaksic (1979) hypothesized that the biogeographical pattern of chillas and culpeos south of 33° in Chile is the consequence of partitioning prey resources to lessen interspecific competition. This in turn results in body size differences, i.e., character displacement of sympatric foxes. When habitat can be partitioned, the hypothesis predicts that foxes become allopatric by habitat segregation and converge to similar body sizes. In this allopatric situation, competition for food relaxes and diet similarity between the species increases. When habitat cannot be partitioned, the foxes diverge in body size and hence in prey size consumed, thus resulting in decreased diet similarity. This hypothesis is supported by most studies of chillas and culpeos (e.g., Jaksic et al. 1980, 1983, Johnson 1992) and has been considered as a neat example of character displacement (Wayne et al. 1989).

Unfortunately there are not too many instances wherein diet similarity has been calculated for allopatric versus sympatric foxes. Jaksic et al. (1983) calculated that food-niche overlap between allopatric chillas and culpeos was 90% in central Chile (Metropolitan Region) and 63% in southernmost Chile (XII Region). Jiménez (1993) reported that yearly diet overlap between sympatric chillas and culpeos was 64% in Aucó (IV Region), and Johnson (1992, and Johnson & Franklin 1994) that it was only 14% in Parque Nacional Torres del Paine (XII Region). Therefore, the prediction that foxes should have higher diet similarity in allopatry than in sympatry is sustained (90 vs. 64% in central Chile, 63 vs. 14% in southernmost Chile, respectively).

In Fuentes & Jaksic's hypothesis, the expected partitioning of habitat between chillas and culpeos was by altitude, the former in the lowlands, the latter in the highlands. However, elevation per se seems not be the adequate spatial dimension to be partitioned by foxes. In fact, Fuentes & Jaksic (1979) reported on culpeo feces collected at a site in central Chile at an elevation similar to a collection site for chilla feces (784 m at Los Dominicos = Fundo San Carlos de Apoquindo, and 600 m at Tiltil = Fundo Santa Laura). Parenthetically, Jaksic et al. (1980: 255) report that the same samples were collected at 950 and 1,000 m elevation, respectively. Culpeos from Fundo El Pangue (Ebensperger et al. 1991) may even be at lower elevation than chillas from Fundo Santa Laura. Something similar has been documented in southern Chile, wherein culpeos from Collipulli and Angol and chillas from Nahuelbuta are found at roughly the same elevation (Greer 1965: 136, Medel et al. 1990). There, at the IX Region, the actual distribution of foxes seems the opposite of that predicted: culpeos are frequently found in the Central Valley lowlands and chillas in both the Andes and Nahuelbuta ranges (JE Jiménez saw only chillas in the Andes at Conguillío, 1,600 m elevation, and WE Johnson, pers. comm., captured chillas in Conguillío at 1,100 m elevation and in Nahuelbuta at about 1,000 m elevation). It does appear that the two foxes have interspersed altitudinal ranges in the IX Region (culpeos have been collected in Curacautín, Cunco, Collipulli, Angol, and Nacimiento, and chillas in Curacautín, Los Sauces, Angol, Mulchén, and Cabrero; see Osgood 1943, Greer 1965, B Guiñez, pers. comm.). Further, L Pincheira (pers. comm.) observed an event of predation of culpeo upon chilla on the outskirts of Nahuelbuta Range. Therefore, elevation is too coarse and indirect a measure of habitat segregation for foxes. Below we discuss what may be a more widespread mode of habitat partitioning between chillas and culpeos.

Resource partitioning

The Fuentes & Jaksic hypothesis predicts that at the latitude of Aucó, chillas should be found in lowlands and culpeos in the mountains (i.e., they should be allopatric), be of similar size and have high diet similarities. We found (Jiménez et al. 1995) that foxes at Aucó are sympatric, differ somewhat in total body length (culpeo: chilla = 1.22, the same ratio as at Parque Nacional Torres del Paine), differ markedly in body mass (culpeo: chilla = 1.73), and have intermediate diet overlap (mean = 0.643, range = 0.431 - 0.865).

Foxes at Aucó are sympatric but not syntopic. Although chillas and culpeos do not partition habitat altitudinally, despite the rugged topography and different elevations available at the site, they do segregate spatially by selecting different habitat types. Chillas were consistently found in flat areas whereas culpeos primarily occupied ravines. Therefore their fine-scale habitat overlap was low. This pattern is unlikely to be a methodological artifact, because three different methods gave the same result. Habitat use appears to be a dynamic process as revealed by radio-telemetry. At Aucó, as well as in Parque Nacional Torres del Paine, chillas and culpeos maintain interspersed and almost non-overlapping species-specific home ranges throughout the year (Johnson 1992, Jiménez 1993). In Aucó, we detected twice as many agonistic incidents at interspecific home-range boundaries than at intraspecific ones. When a culpeo moved into a chilla home range, the chilla retreated to the farthest extreme of its home range. When the culpeo left the area, the chilla moved back again.

These observations concur with Johnson's (1992) findings in Parque Nacional Torres del Paine, and support his hypothesis that interference between chillas and culpeos may be the mechanism by which they partition habitat. Predation, an extreme form of interference, may also be involved. Durán et al. (1987) reported 5.6% of fox vertebrate prey at Aucó was made up of unidentified carnivores (see also L Pincheira's pers. comm. above). The ultimate factor for this pattern of habitat partitioning may be related to energy requirements (Johnson et al., ms. submitted). The larger culpeo seems to exclude chilla from better-quality habitats (i.e., ravines), which on average had almost seven times more small mammals than flat areas in Aucó (Jiménez 1993). As a result of the culpeo's dominance, chillas occupy the less-productive and more risk-exposed flat areas where most human activities are concentrated. Following Johnson et al.'s arguments (ms. submitted), unlike chillas, culpeos would be unable to meet their energy demands in low-quality habitats such as flat areas in Aucó. Nonetheless, the partitioning of habitat found at Aucó, reveals that foxes do not select their activity ranges based solely on food abundance, because south- and north-facing slopes have more small mammals than ravines or flat areas (Jiménez 1993). But prey abundance is not the same as prey availability. Perhaps foxes hunt less efficiently in the steep slopes of Aucó and thus avoid those habitats and prefer more level terrain.

The pattern of habitat partitioning at a finer-scale and the interspersion of home ranges displayed by foxes at Aucó, also found by Johnson (1992) in Parque Nacional Torres del Paine, may be more common than previously thought. Apart from the Chilean studies cited above, there is a report of sympatric chillas and culpeos in Neuquén, Argentina (Novaro 1991).

Foxes at Aucó also partition prey resources. Mean diet overlap for chillas and culpeos was relatively low (64.3%), although not as low to that reported for sympatric foxes at Parque Nacional Torres del Paine (14.0%, Johnson 1992, Johnson & Franklin

1994). Culpeos at Aucó have a broader diet than chillas, although the reverse was found in Parque Nacional Torres del Paine, at least for vertebrate prey. These differences are difficult to explain in light of the information available. The fact that southern foxes have a three-fold higher mean weight of vertebrate prey (2,170 - 2,590 g) than northern foxes (71 - 72 g) may be a reflection of the different availability of prey sizes in the environment. In particular, European hares are abundant, large, and preyed upon by both foxes in Parque Nacional Torres del Paine.

Aucó foxes do not segregate their activities throughout the 24 h daily cycle. Chillas and culpeos were active at any time. Similarly, Johnson (1992) did not find different patterns of activity between chillas and culpeos in Parque Nacional Torres del Paine, although they both were more active at night.

In summary, sympatric chillas and culpeos at Aucó present low spatial overlap, intermediate diet overlap, and complete temporal overlap. It is remarkable that sympatric foxes at Parque Nacional Torres del Paine, under quite different environmental conditions, partition resources in the same way as foxes in Aucó.

A revised hypothesis

Habitat selection is scale dependent. Without definition of scale, this concept is too broad and vague. Fuentes & Jaksic's (1979) use of habitat partitioning was applied to a large geographical scale, or first-order selection (sensu Johnson 1980). This may be the first step for understanding coexistence of wide ranging, mobile, and opportunistic mammals such as foxes. However, the information analyzed here shows that chillas and culpeos also respond to second- and third-order selection (individual home ranges and habitat components, respectively). These smaller spatial scales, were not considered in Fuentes & Jaksic's hypothesis.

Therefore, the hypothesis needs to be modified to render it more realistic in light of the new evidence and detailed reanalysis of previous evidence. Current information indicates that fox distributions are much more complicated than previously believed. Throughout Chile chillas and culpeos are found in both allopatric (or parapatric) and sympatric contexts, independent of their body sizes (Jiménez et al. 1995). Although not all combinations of species occurrences and habitat types are found, culpeos appear more frequently associated with higher elevations and more rugged landscapes than chillas. The latter occur more often in lowlands and level landscapes. These foxes are sympatric at intermediate elevations and in areas where the landscape appears more complex at an intermediate spatial scale, and habitat patches are interspersed. Patchy prey productivity compounded with habitat heterogeneity may be important features of intermediate-elevation sites. Therein, foxes may partition space at a fine scale, so that they coexist in sympatry but not in syntopy (Johnson 1992, Jiménez 1993). The proximate mechanism appears to be interference, a process driven by the dominant culpeo, which monopolizes high-quality patches and excludes chilla to low-quality ones (Johnson et al., ms. submitted).

Mountains where culpeos occur allopatrically may not be heterogeneous enough to enable the presence of chillas. Conversely, lowland and coastal habitats may not have the larger prey species needed by the more energetically demanding culpeo. Evidence of food-limitation for culpeo, as well as intolerance of chillas and other culpeos, is provided by Crespo & De Carlo (1963) and Abello (1979, as cited in Johnson 1992). In the first case, culpeos expanded their range and became more abundant owing to an increase of food supply (sheep ranching) in Neuquén, Argentina. In the second case, the removal of livestock (potential food for culpeos, Crespo & De Carlo 1963, Novaro 1991), resulting from the establishment of a National Park at Torres del Paine, correlated with the invasion of chillas, presumably as a result of culpeo decrease in abundance.

However, under the scenario described, it is still not clear why Parque Nacional Fray Jorge, at a latitude, altitude, and with an environmental heterogeneity similar to Aucó, supports culpeos but not chillas. There, culpeos are also larger than those at Aucó (Jiménez et al. 1995). Competitive release (i.e., absence of chillas) does not fully explain the pattern at Fray Jorge. Prey size distribution (Meserve et al. 1987) does not account for the larger body size of Fray Jorge culpeos. Indeed, Chinchillas (*Chinchilla lanigera*) and hares (*Lepus capensis*) which are the largest mammalian prey at Aucó, are absent from the otherwise similar prey base at Fray Jorge (where the largest prey is approximately 200 g, Meserve et al. 1987). The fact that nowadays chinchilla abundance at Aucó is very low (Jiménez 1993) goes counter the prey-size availability hypothesis to explain fox coexistence. However, the increase in rabbit populations may have compensated for the loss of chinchillas (e.g., Simonetti 1986), thus supporting the coexistence of chillas and culpeos.

In conclusion, Fuentes & Jaksic's hypothesis is partially valid (see Jiménez et al. 1995), but requires consideration of two factors previously ignored: the spatial scale at which coexistence occurs, and the availability of high-quality (large) prey. Where large prey such as rabbits or hares (*Lepus capensis*) are present, the two fox species may co-occur in sympatry provided that the habitat is sufficiently complex to offer shelter for the smaller fox from the aggressively dominant culpeo. Where only small prey is present, only one fox species will survive, most often (but not necessarily) the smaller chilla.

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