Body size of Chilean foxes:
a new pattern in light of new data

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By using body measurements and weight data of culpeo fox *Dusicyon culpaeus* Molina, 1782 and chilla fox *D. griseus* Gray, 1837 from the Chinchilla National Reserve (north-central Chile) and Torres del Paine National Park (southern Chile), the body size distribution of Chilean foxes was analyzed and compared to data previously published by Fuentes and Jaksić (1979). Contrary to those authors, our data show that not only the larger but both species increase in size in southern Chile. Thus, latitudinal size distribution of *D. culpaeus* and *D. griseus* may not be the result of character displacement through exploitation competition, as previously interpreted, but of bioenergetic adaptations.

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Introduction

Culpeos *Dusicyon culpaeus* Molina, 1782 and chillas *D. griseus* Gray, 1837 are widely distributed throughout western South America (Ginsberg and MacDonald 1990). *D. culpaeus* is larger, and found along the Andes from southern Colombia (Nariño Province, E. Barriga, pers. comm.) to Magallanes in southern Chile, including the island of Tierra del Fuego. *D. griseus* has a more restricted distribution and inhabits the lowlands of Chile and Argentina from 25 degrees south (Sheldon 1992, but see Marquet *et al.* 1993). *D. griseus* was introduced into Tierra del Fuego in 1951 to control European rabbit infestations (Jaksić and Yáñez 1983). Generally, *D. culpaeus* inhabits mountains, rugged terrain, or forested habitats, whereas *D. griseus* is associated with lowlands and open areas (Osgood 1943, Greer

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1965). Despite their extensive and broadly overlapping ranges, *D. culpaeus* and *D. griseus* are usually allopatric. Johnson (1992) and Jiménez (1993), however, working in southern and north-central Chile, respectively, found sympatric populations of *D. griseus* and *D. culpaeus* to partition habitat at a microhabitat scale.

Based on the distributional pattern of *D. culpaeus* and *D. griseus* from 33°S to 53°S along Chile, Fuentes and Jaksić (1979) tested the hypothesis of niche--complementarity (Schoener 1974) between diet and habitat to explain the distributions and body sizes of these foxes. Fuentes and Jaksić (1979) examined body length data of *D. culpaeus* and *D. griseus* and found that foxes in northern Chile, where they were supposedly allopatric, had more similar body sizes. Toward their southern ranges, however, *D. culpaeus* and *D. griseus* became sympatric and were found to diverge in body size. Fuentes and Jaksić (1979) implied that the high elevation of the Andes in the north allowed the foxes to partition habitat altitudinally. As the Andes decreased in altitude toward the south, no such segregation was possible, and competition by sympatric foxes for food thus led to displacement in body size. This model of niche complementarity has never been tested again.

Here, the body size pattern of *D. culpaeus* and *D. griseus* at both extremes of Fuentes and Jaksić's (1979) gradient was examined. The robustness of Fuentes and Jaksić's model for body size of *D. culpaeus* and *D. griseus* was tested by comparing new data from north-central Chilean foxes with those from southern Chile. Specifically, the null hypothesis that both foxes have equal body sizes in northern and southern Chile was tested, against the alternative hypothesis that *D. culpaeus* and *D. griseus* diverge in body size in comparison to their northern counterparts.

Methods

Data for sympatric *D. culpaeus* and *D. griseus* from both the Chinchilla National Reserve at Aucó (31°30' S, 71°06' W, north-central Chile) and from Torres del Paine National Park (51°03' S, 72°55' W, southern Chile) was obtained. Detailed descriptions of these sites are found, respectively, in Jiménez (1993) and Johnson and Franklin (1994).

Foxes were trapped at Aucó with 1.5 padded leg-hold traps from January to August 1992. Captured *D. culpaeus* and *D. griseus* were measured and weighed. As measures of body size body mass, body length (head + trunk), and total body length (body length + tail) were used. For the southern locality Johnson's data (1992, and unpublished data) were used. He used the same field techniques and metrics as in the Aucó study.

Data analyses

Data from adult foxes only were analyzed and tested for differences in body size by species between the two localities. Bootstrap analyses (Efron and Gong 1983, Noreen 1989) were performed, because they are more powerful than other standard methods for this small and unbalanced data set (Potvin and Roff 1993). Essentially, what bootstrapping does is to take random samples from the original sample considering that the null hypothesis is true. The samples are taken independently,

with replacement, and each value has the same probability of being sampled. This procedure is repeated many times and every time a test statistic is calculated from the pseudosamples. These statistics (which have a normal distribution) are plotted as a frequency distribution. The hypotheses are tested by comparing the statistic computed on the real sample against the simulated distribution generated by bootstrapping (Noreen 1989). According to the hypothesis being tested, the critical region is represented by either of tails of the simulated distribution.

The samples were bootstrapped 500 times in Minitab (Ryan *et al.* 1985) and pooled *t*-tests (Ott 1988) were computed with a program written for the same statistical package (see Appendix). The critical region for the 5% level was represented by the 25 most extreme values out of the 500 computed (on the upper tail for H_a: $\mu_1 > \mu_2$ and vice versa).

Results and discussion

Data from 9 *D. culpaeus* and 16 *D. griseus* from Aucó and 7 *D. culpaeus* and 36 *D. griseus* from Torres del Paine were analyzed. *D. culpaeus* from Torres del Paine were substantially larger (ie heavier and longer) than those from Aucó (Table 1). *D. griseus* from Torres del Paine were also larger than those from Aucó. These results were consistent for the three body size estimators in all the tests performed (Table 1). The fact that all three body size estimators showed the same pattern should not be surprising because they are probably correlated among each other. Thus, the new data differ markedly from those presented by Fuentes and Jaksić (1979).

Our analysis indicates that both *D. culpaeus* and *D. griseus* increase in size toward the south (Table 1). *D. culpaeus* and *D. griseus* had the same head and body length ratios (Fuentes and Jaksić's size estimator) at the two latitudes examined (1.224 for Aucó and 1.227 for Torres del Paine). For the cubic root of the weights, the ratio for Torres del Paine foxes was somewhat larger than for Aucó foxes (1.408 vs 1.201). Therefore, both foxes diverge in body weight, but only

Table 1. Size relations of sympatric *Dusicyon culpaeus* and *D. griseus* in northern (Aucó) and southern (Torres del Paine) Chile. Comparisons between means were performed by bootstrapping pooled *t*-tests (*p*-values shown). Body length is the length of head + body, total length includes the length of the tail. Length measurements are in mm and weight in g. [a] This paper and Jiménez (1993), [b] this paper and Johnson (1992).

Variable	Aucó[a]			Torres del Paine[b]			H_0: $\mu_1 = \mu_2$ H_a: $\mu_1 > \mu_2$	H_0: $\mu_1 = \mu_2$ H_a: $\mu_1 < \mu_2$
	n	Mean	SE	n	Mean	SE		
D. culpaeus								
Body weight	9	4316.7	207.8	7	10 157.1	848.8		< 0.002
Body length	9	628.3	20.5	7	739.3	50.7		< 0.020
Total length	9	999.4	18.5	7	1152.1	45.4		< 0.008
D. griseus								
Body weight	16	2495.0	86.4	35	3640.0	87.9	> 0.998	< 0.002
Body length	16	513.4	9.4	36	602.4	8.5	> 0.998	< 0.002
Total length	16	824.4	13.6	36	938.6	11.3	> 0.998	< 0.002

because *D. culpaeus* is substantially heavier than *D. griseus* in Torres del Paine. This result is only in partial accord with Fuentes and Jaksić's (1979) report that as *D. culpaeus* increased in size, *D. griseus* decreased.

The increase in body size toward higher latitudes, as shown by *D. culpaeus* and *D. griseus*, is the expected pattern under Bergmann's rule, which states that "... foxes, deer, and other mammals with a wide distribution are often larger in colder areas..." (Begon *et al.* 1990: 65). Therefore, the body size pattern of Chilean foxes may not be a consequence of exploitation competition as previously proposed by Fuentes and Jaksić (1979) but the by-product of their respective adjustments to living in colder regions. Interference competition, however, has been described to occur at both sites, were *D. culpaeus* excludes *D. griseus* from the best (prey-wise) habitat patches (Jiménez 1993, Johnson and Franklin 1994). The hypothesis that the larger southern foxes are faced to a larger spectrum of prey sizes than the smaller northern foxes is appealing and awaits testing.

In order to corroborate the data sets, we surveyed published data on the same species and sent interviews to 31 South American researchers and museum curators. Only 10 (32.3%) responded, all stating that they had no data available at that time.

Few other data could be found in the literature. Body weight data for *D. culpaeus* were found in Crespo and De Carlo (1963; mean = 8177.5 g, n = 195, Neuquén Province, Argentina, 39°33'S), in Jaksić *et al.* (1993; mean = 6520 g, SD = 3019 g, n = 5, Fray Jorge, Chile, 30°38'S), and in Greer (1965; Malleco, Chile, 38°S). Both Crespo and De Carlo's (1963) and Greer's (1965) data, as well as those of one *D. culpaeus* from Cunco (Chile, 39°00'S, 7750 g, B. Guiñez, pers. comm.) were intermediate between the values here reported for Aucó and Torres del Paine. However, *D. culpaeus* data from intermediate localities appear above the lines that connect the extreme values. This suggests that the change in body size may not be a linear function of latitude. An alternative view is that *D. culpaeus* are unexpectedly small for the latitude at Aucó. This speculation is substantiated when calculating the ratio for the cube root of weights between Fray Jorge *D. culpaeus* and Aucó *D. griseus* (1.378), which is surprisingly close to that for Torres del Paine foxes (1.408).

Because *D. griseus* is absent from Fray Jorge (at approximately 150 km NW of Aucó), the large body size of allopatric *D. culpaeus* there compared to *D. culpaeus* at Aucó, is not explained by competition theory. Fray Jorge appears to be an interesting site to study *D. culpaeus* ecology.

Finally, the foxes at Aucó departed from the pattern depicted by Fuentes and Jaksić (1979) in two other ways. First, at Aucó *D. culpaeus* and *D. griseus* are sympatric though not syntopic (ie showed different habitat preferences). Thus, these two foxes are not altitudinally segregated at least in this study site. This scenario of coexisting *D. culpaeus* and *D. griseus* in northern Chile was not contemplated in Fuentes and Jaksić's model. Second, Aucó foxes also differ in their diets (Jiménez 1993), contrary to the predictions of the model. Whether the

sympatric Aucó foxes constitute a unique case, or represent a common situation in northern Chile, remains to be investigated.

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Appendix. Minitab program used for bootstrapping. The program selects n1 and n2 random numbers with replacement from the pooled original data, which were in C1. Each datum was selected with equal probability (1/(n1+n2)) in C2. The program computes a pooled *t*-test. This procedure was repeated 500 times with each data set. The statistics were stored in C6 after being sorted in ascending order. The variables n1 and n2 were the sample sizes.

```
NOECHO
LET K1=n1
LET K2=n2

RANDOM K1 C3;
   DISCRETE C1 C2.
RANDOM K2 C4;
   DISCRETE C1 C2.

LET K3=MEAN(C3)
LET K4=MEAN(C4)
LET K5=K3–K4

LET K6=STDEV(C3)
LET K7=STDEV(C4)
LET K6=K6×K6
LET K7=K7×K7

LET K8=K1+K2-2
LET K9=(K1–1)×K6+(K2–1)×K7
LET K10=K9/K8
LET K11=SQRT(K10)

LET K12=(1/K1)+(1/K2)
LET K13=SQRT(K12)

LET K14=K5/(K11×K13)

STACK K14 C5 C5
SORT C5 C6
END
```