Research Article

Character displacement under influence of Bergmann's rule in *Cerdocyon thous* (Mammalia: Canidae)

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Abstract

In South America, the crab-eating fox *Cerdocyon thous* occurs in sympatry to the ecologically similar, and phylogenetically close *Lycalopex vetulus* to the North, and *Lycalopex gymnocercus* to the South of its range. We studied character displacement in *Cerdocyon* under the effect of Bergmann's rule and the presence (or absence either) of *Lycalopex* within the crab-eating fox range. We performed skull shape analysis on 191 *C. thous* specimens and divided them in three distinct groups, depending on whether *Cerdocyon* occurs in sympatry or in allopatry to *Lycalopex* species. We tested for differences in size and shape between *Cerdocyon* groups and regressed both skull size and sexual size dimorphism against latitude and temperature, while controlling for spatial autocorrelation in the phenotypes. Southern *Cerdocyon* specimens present enlarged temporalis muscle and slender carnassial, both suggestive of a shift towards increased carnivory. Such a niche shift is interpreted as a mean to reduce competition to the larger *Lycalopex* species, which is still smaller than *Cerdocyon*. Consistently with the above, the degree of sexual shape and size dimorphism in *Cerdocyon* increases southward. We found a complex but coherent pattern of size and shape differentiation in *Cerdocyon* groups, which is consistent with the effects of both competition and Bergmann's rule. *Cerdocyon* reduces competition to *Lycalopex* by growing larger in the North. To the South, *Cerdocyon* is still larger, in keeping with Bergmann's rule, but strongly differs in skull shape from both its *Lycalopex* competitor and from any other *Cerdocyon*. Since the Southern *Lycalopex* species is much more similar in size to *Cerdocyon* than its Northern congeneric, this suggests that shape differences serve the goal of reducing competition between *Cerdocyon* and *Lycalopex* to the South, as size differences do to the North. The absence of the hypercarnivorous canid *Speothos venaticus* from the southern range of *Cerdocyon* may have allowed such a pattern to take place.

Introduction

Character displacement is the reduction in phenotypic overlap that occurs where two or more closely related species compete over the same resources, in order to reduce the intensity of competition (Slatkin, 1980; Schluter, 2000; Dayan and Simberloff, 2005; Adams, 2004; Grant and Grant, 2006; Carotenuto et al., 2015). Thereby, species with partly overlapping geographical distributions are expected to diverge in shape or size more where they occur in sympatry than in allopatry (Brown and Wilson, 1956; Loy and Capanna, 1998; Meiri et al., 2011).

Dayan et al. (1992) studied character displacement in carnassial teeth in wolves, jackals and foxes in Israel. They found that the ratios of carnassial lengths in these species hold constant in spite of geographical fluctuation. According to the predictions of community-wide character displacement (Dayan and Simberloff, 2005) this constancy would be evidence that competition shapes morphology in the canid guild. Valkenburgh and Wayne (1994) found character displacement among African jackals, which they related to selection towards improved feeding efficiency in sympatry. By studying the length of the carnassial teeth, which is the main food-processing device in Carnivora, Davies

et al. (2007) generalized claims in favor of character displacement in the entire clade.

Whereas character displacement implies specific trait shifts to occur in sympatry, which is independent from geography, species with wide geographic range are expected to increase in size with latitude, a pattern known as Bergmann's rule (Blackburn et al., 1999; Ashton et al., 2000; Meiri and Dayan, 2003; Meiri et al., 2004; Rodríguez et al., 2008). This implies that Bergmann's rule and character displacement theories predict potentially contrasting patterns (i.e. a species can live in sympatry to a slightly larger competitor at high latitudes and thereby grow smaller whereas, by Bergmann's rule, it would be expected to be larger).

In this theoretical context, the crab-eating fox *Cerdocyon thous* (Linnaeus, 1766) is an ideal case for studying the potential interaction (or conflict) between character displacement and Bergmann's rule. *C. thous* has a wide geographical distribution, ranging over much of the Neotropics, from Colombia to Uruguay (Berta, 1982). In central Brazil, its distribution overlaps to that of hoary fox *Lycalopex vetulus* (Lund, 1842). Still to the South, *C. thous* overlaps with Azara's fox *Lycalopex gymnocercus* (Fischer, 1814). These three phylogenetically-close canids (Perini et al., 2010) have outstanding morphological and behavioral similarities. They are opportunistic and omnivorous feed-

ers preferring open habitats, although *C. thous* may occur in forests (Berta, 1982; Dalponte, 2009; Lucherini and Vidal, 2008). *C. thous* is the largest of the three, followed in size by *L. gymnocercus* and then *L. vetulus* (Vieira and Port, 2007; Lucherini and Vidal, 2008; Dalponte, 2009; Di Bitetti et al., 2009).

By studying *Cerdocyon* cranial morphology, Martinez et al. (2013) found that *C. thous* follows Bergmann's rule south to the equator, that is, its body size increases with the latitude. However, north to the equator, body size follows a reverse pattern in this species, decreasing with latitude (Martinez et al., 2013).

In this study, our main aim is to test whether body size character displacement exists in different groups of *C. thous* living in sympatry with *L. vetulus* and *L. gymnocercus*. We also tested whether cranial shape variation in *C. thous* is conformant with character displacement theory, and whether it shows any latitudinal pattern. We investigated upon these patterns and contrasted shape and size variation of the crab-eating fox both in allopatry and in sympatry with its two *Lycalopex* competitors. If there is character displacement, we predict that *C. thous* should be larger than expected (by Bergmann's rule) to the South, where it occurs in sympatry with the larger species of the *Lycalopex* group. Alternatively, shape differences in cranial features are expected to occur as a form of niche shift in sympatry, to decrease the intensity of competition with *Lycalopex*. In addition we tested whether character displacement shown by *Cerdocyon*, if any, affects the degree of the sexual size and shape dimorphism within the three analyzed groups.

Materials and methods

Sample

Our sample includes pictures taken on museum specimens (skulls) of 191 *C. thous* individuals (62 females, 80 males and 49 unsexed), covering most of the geographic distribution of this species in Brazil, NE Argentina, and Uruguay (see Table S1). We sampled 118 localities overall (Fig. 1). All of the specimens we sampled represent wild-caught adult individuals. We retrieved sex information for most of the specimens as available (see below).
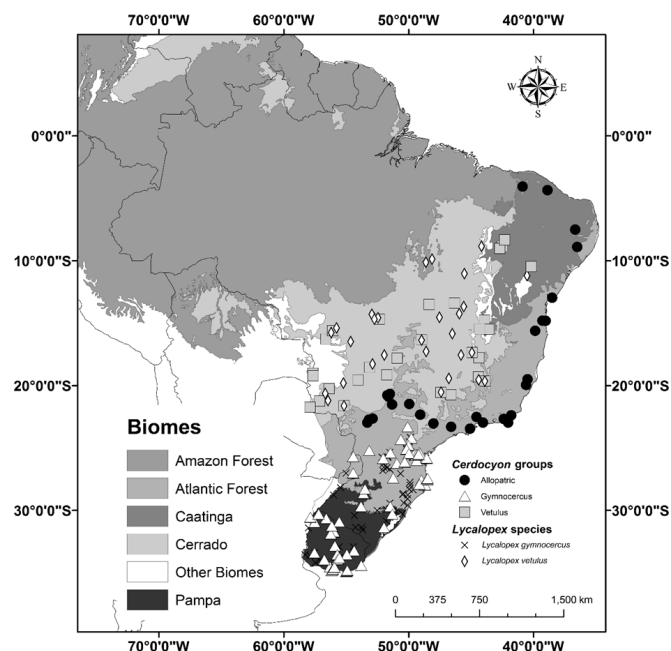

Figure 1 – Map of South America showing the geographical distribution of *Cerdocyon thous* specimens sampled. Each group is labeled in accordance with different symbols.

In order to analyze the effect of sympatry on morphology, we partitioned *C. thous* individuals into three groups according to their distances to *Lycalopex* specimens' geographical coordinates (Fig. 1). We used a dataset gathering 191 *L. vetulus* and *L. gymnocercus* occurrences borrowed from the GBIF database (www.gbif.org) complemen-

ted with specific papers (Sherlock et al., 1988; Persson and Lorini, 1990; Cimardi, 1996; Dalponte and Lima, 1999; Márquez and Ramos, 2001; Juarez and Marinho-Filho, 2006; Michalski and Hasenack, 2002; Rodríguez et al., 2002; Mikich and Bérnils, 2004; Courtenay et al., 2006; Gonçalves, 2006; Rocha et al., 2008; Bocchiglieri et al., 2010; Fernandes and Costa, 2013; Olifiers and Delciellos, 2013; Prevosti et al., 2013). In details, we created a circular buffer area for each *Cerdocyon* sampling locality with a radius of 200 km. For each locality, if a *L. vetulus* sampling locality falled within the buffer area, we ascribed the *Cerdocyon* locality to the "vetulus group". If we sampled a *L. gymnocercus* locality, we ascribed the related *Cerdocyon* locality to the "gymnocercus" group. All those *Cerdocyon* sampling localities that did not sample any *Lycalopex* specimens were assigned to the "allopatric" group. The allopatric group (where the crab-eating fox occurs in allopatry with *Lycalopex*) consists of 42 individuals (19 females, 14 males and 9 unsexed individuals, collected mainly in coastal Atlantic Forest in Brazil, and North of Paraná state). The gymnocercus group consists of 84 individuals (27 females, 35 males and 22 unsexed) collected in areas where *C. thous* is sympatric with *L. gymnocercus* (south of Brazil, Uruguay and NE Argentina). Then, the vetulus group consists of 65 *Cerdocyon* individuals (16 females, 31 males, and 18 unsexed) collected in areas where it is sympatric with *L. vetulus* (Bahia, Goiás, Minas Gerais, Mato Grosso do Sul, Mato Grosso, Piauí, São Paulo states in Brazil). Only specimens with fully erected molars were included in this study. We prepared a database including both digital photographs of skulls and field data for each specimen (species name, sex, and sampling locality, according to museums' specifications). Skull pictures were taken in ventral view at fixed distance (two meters) with a Nikon CoolPix P510 digital camera. This procedure standardizes the sample of digital images and minimizes deformation due to the lenses (Meloro et al., 2011). The palate of *C. thous* is relatively flat so that teeth shape features can be easily recognized. When taking pictures, we set up a scale bar adjacent to the specimen in order to transform digital pixels in linear measurements, and thereby record specimen size. On each picture, we digitized twenty-six homologous landmarks, by using the software tpsDig 2 (Rohlf, 2010a). One single investigator (JMB) performed landmarking to avoid inter-observer error. The chosen landmark configuration (Fig. 2) accurately describes ventral view skull features of *C. thous*, with the temporal muscle insertion area (zygomatic arch), the rostrum area (palate), the auditory bulla area, and the position and size of the teeth. When designing the landmark configuration, we focused on capturing shape information related to feeding We additionally sampled 58 *L. gymnocercus* and 28 *L. vetulus* individuals. Skulls for these species individuals were photographed in ventral view, using the same landmark protocol as for *C. thous*. Our aim was to retrieve body size information on these species, where they occur in overlap with *C. thous* (see Table S2).

Figure 2 – Disposition of 26 landmarks on a skull of *Cerdocyon thous* specimen (MZUSP 3101). 1 = midpoint of central incisors; 2 = posterior-most point of lateral incisor alveolus; 3–5 = canine area; 5–6 = first three pre-molars length; 7–9 = fourth pre-molar (carnassial) area; 10–12 = first molar area; 13–15 = second molar area; 16–19 = temporal muscle insertion area; 20 = most posterior tip of the palatine; 21–23 = auditory bulla area; 24–26 = occipital condyle area.

Geometric Morphometrics

We performed Generalized Procrustes Analysis (GPA, Rohlf and Slice, 1990) to remove from the original data the differences due to scale, position and orientation by superimposing all the landmark configurations and minimizing their differences to the a mean theoretical configura-

tion called "consensus". After this procedure, the "Thin Plate Spline" interpolation method produces a new set of variables (the shape variables) describing the degree of local deformation of landmark configurations on a reference grid (Zelditch et al., 2004). We used Relative Warps analysis (RWA, Bookstein, 1991, a principal component analysis performed over shape variables, Martinez et al., 2013; Cáceres et al., 2014) to explore morphometric variation in *C. thous*, by using the software tpsRelw (Rohlf, 2010b). After GPA, we retrieved information about size of each configuration by computing the Centroid Size, which is the square root of the sum of squared distances of a set of landmarks from their centroid (Rohlf, 2000). For all the analyses we used the natural log-transformed Centroid Size (LnCS) as a proxy of species body mass.

Variation partitionings

Our aim was testing the ecological determinants of *C. thous* phenotypic variability. Although we focus on character displacement as driven by competition as an explanation, the strong geographic component in our data might lead to wrong conclusions (e.g. assuming that *Cerdocyon* groups are different from each other because of competition, or lack thereof, to *Lycalopex* when in fact they differ because they occupy different biomes). Therefore, before directly testing for the effect of competition, we accounted for bioclimatic variation, by using variation partitioning. We obtained climatic information by downloading from worldclim.org 19 bioclimatic variables' maps with a $\sim$ 5 km of resolution. Variation partitioning works by partitioning the variance in a dependent variable Y by the individual contributions of n independent variables $(X_1, X_2 \ldots X_n)$ and all of their interaction terms (Borcard et al., 1992; Borcard and Legendre, 1994; Desdevises et al., 2003). With two independent variables $(X_1$ and $X_2)$ the contribution of X_1 is thus decomposed in two portions: "a", exclusively determined by the effect of X_1 on Y, and "b", which is shared with a second independent variable X_2 (whose exclusive effect on Y variation is "c"). A first regression between Y and X_1 yields an R_1^2 explaining the contribution of X_1 and of that portion of X_1 shared with X_2 ("a"+"b"). Then, the regression coefficient between Y and X_2 (R_2^2) yields the portion "b"+"c". The multiple regression coefficient R^2 gives the total variables contribution ("a"+"b"+"c") to Y variation. By performing subtractions between the three regressions coefficient it is then possible to compute the contribution of "a", "b" and "c" separately. When in a multivariate and/or multiple contexts, variation partitioning performs a redundancy analysis (RDA) to detect the most important vectors in variables' matrices.

To estimate whether the presence of *Lycalopex* matters to *Cerdocyon* skull shape and size, we produced two variation partitioning tests on the sympatric *Cerdocyon* groups. The first test takes *Cerdocyon* skull LnCS as the Y variable. The other takes *C. thous* skull shape variables dependent. In both variation partitionings, the independent variables were the *Cerdocyon* groups, sampling localities' latitude, climate (represented by all the 19 bioclimatic variables) and the mean value of *Lycalopex* LnCS measured in a 50 km diameter search circle around each *Cerdocyon* locality. Since these variation partitions yielded significant contribution of *Lycalopex* sp. LnCS (besides the contributions of all the other explanatory variables) to the Y (*Cerdocyon* LnCS or shape variables, either), the effect of *Lycalopex* was taken as real and further explored.

We performed variation partitioning by using the library "vegan" Oksanen et al. (2015) in the statistical software R 3.2.2 (R Core Team, 2015).

Latitudinal trends in raw and spatially filtered *Cerdocyon* body size

We performed two regressions between *Cerdocyon* LnCS and both the latitude and mean annual temperature recorded at the sampling localities to test for Bergmann's rule in its classic form (as a temperature-related latitudinal cline). As geographical variables may have non-independent values over space (spatial autocorrelation), we aimed to take into account this spatial signal in our analyses. Spatial dependence is a well-known issue when dealing with ecological studies

(Diniz–Filho et al., 2003). This metric is defined as the degree of similarity in a variable as a function of geographical distances between data points (Sokal and Oden, 1978a,b; Griffith, 2013; Legendre, 1993; Rossi and Quénéhervé, 1998). In univariate correlations, the most widely applied autocorrelation index is the Moran's I, which may have either positive or negative values according to direct or indirect spatial dependence, respectively (Diniz–Filho et al., 2003). The degree of autocorrelation is measured for different distance classes. The presence of a significant degree of spatial autocorrelation (i.e. a spatial dependence in the measurements) can lead to an underestimation of the standard errors of a statistic and, thus, inflating Type I errors (Legendre, 1993).

To test for the geographical variation in *Cerdocyon* LnCS, we removed the influence of the spatial autocorrelation and of the mean annual temperature latitudinal trend on LnCS. We took the standardized residuals of a multiple partial regression with LnCS as a response variable and spatial structure and mean annual temperature as predictive variables. To minimize the degree of spatial dependence in our data we used the Eigenvector-based Spatial Filtering (Griffith, 2013). This method uses a distance or connectivity matrix to perform a Principal Coordinate Analysis (PCORD) and detects the orthogonal vectors explaining the structure of the spatial dependence of a variable (called filters in Griffith, 2013). All the filters are used in a partial multiple regression against the chosen response variable (here *Cerdocyon* LnCS). The filters used to remove the spatial dependence are those maximizing the correlation with the response variable and therefore minimizing the spatial autocorrelation in the regression residuals.

To properly compute the LnCS residuals in our models, we additionally introduced the mean annual temperature sampled for each locality as a new predictive variable in the multiple regression with the spatial filters. This more complex model is useful to refine spatial filters if a latitudinal gradient in temperature exists. To avoid multicollinearity, we chose a number of spatial filters that minimized Variance Inflation Factor (VIF) when analyzed in combination with temperature.

We computed spatial filters separately for the whole sample of localities and for those localities restricted to sexed specimens. Residuals were standardized prior to further analysis. All the spatial filtering procedures were performed by using the software SAM (Rangel et al., 2010).

We repeated all the regressions by using temperature-based and spatially filtered LnCS when needed (i.e. when explicitly testing latitudinal trend in filtered LnCS or when not including the mean annual temperature in the model).

Species and groups comparisons

We applied two-way ANOVA to raw LnCS and two-way MANOVA to Relative Warps (RWs), to test for differences between *C. thous* groups (two sympatric and one allopatric). In both analyses, we used sex and the three groups as factors (Machado and Hingst-Zahler, 2009). These analyses were used to test for sexual dimorphism and for size difference between the *C. thous* groups, along with the interaction of these two factors (sex : groups).

We performed the same analyses to test for differences between *C. thous* groups by averaging raw LnCS and RWs for each sampling localities. We performed all the statistical analyses by using R 3.2.2 (R Core Team, 2015).

The ecological character displacement

Latitudinal trends in sexual size dimorphism

By using only the sample of the sexed specimens, we aimed to study the spatial distribution of sexual size dimorphism (SSD) to understand if the ecological interaction between *C. thous* and *Lycalopex* spp. can interplay with the effect of the Bergmann's rule. We considered the SSD as the difference between males and females size, thereby for each locality, we computed the ratio between male and female mean LnCS. Then, we regressed SSD and spatially filtered SSD versus latitude.

Morphological disparity

Morphological disparity is the degree of the shape variance in a group (Foote, 1993). We performed two kind of tests involving this metric to explore whether shape variability in *C. thous* groups is affected by the sympatry with *Lycalopex*. First, we measured the morphological disparity to shape variables of sexed specimens only. We computed the size-corrected multi-group analysis to partition the whole disparity between the three different groups of *C. thous*. To this aim, we computed the grand mean (consensus) of all the specimens. The Procrustes distance of each group mean to the grand mean is the group's contribution to the total disparity, named partial disparity. The confidence intervals were computed by bootstrapping residuals 2000 times (Zelditch et al., 2004). We further computed the size-corrected within group disparity for each group. To measure the degree of sexual shape dimorphism within groups, we computed the bootstrapped pairwise difference in disparity between male and female specimens, whose squared root represents the sexual shape dimorphism, measured as Procrustes distances. In addition, we included a between-groups analysis of shape disparity by computing the differences in disparity between the same sexes of the different groups. We performed all these analyses by using the software DisparityBox v.6.

In addition, as we found a geographic trend in LnCS of sympatric groups, we performed a second procedure to explore the effects of the sympatry with *Lycalopex* species on *Cerdocyon* groups shape disparity by taking into account latitude and bioclimatic variables. To this aim, we performed an additional variation partitioning restricted to the sympatric groups only to exclude the hypothesis that a potential and significant shape disparity could be correlated to climatic variability of the sampling regions only. As for the first variation partitioning, we used shape variables as *Y* and latitude, bioclimatic variables and mean *Lycalopex* LnCS of each sampling locality as *Xs*. Also for this test, a significant contribution of *Lycalopex* LnCS in explaining *Cerdocyon* shape disparity is a result supporting our hypothesis of ecological character displacement.

Results

Shape

Relative warp analysis summarized the variance of 48 shape variables. The Relative Warps from 1 to 26 explained cumulatively 95% of the total variation. The plot showing RW1 (26.34% of the total variance explained) versus RW2 (13.08%) shows the morphological variation within the three groups of *C. thous* skulls (Fig. 3). In the central part of the plot there is a strong overlap between the three groups, and the gymnocercus group show far the higher variability. The RW1 describes a relative changes in the shape of muzzle, the zygomatic arch and teeth occlusal surface. Specimens to the RW1 negative end show proportionally longer muzzle, narrower zygomatic arch, and relatively wider molars and upper carnassial. RW2 describes the relative expansion and contraction of the zygomatic arch, molars, canine and auditory bulla. In the RW2 negative end molars, canine, and auditory bulla reduce their dimensions, while the zygomatic arch and the muzzle expands. We did not detect any significant sexual shape dimorphism (Wilks' Λ=0.674, $F_{26,69}$=1.283, p=0.205), neither the interaction between Group and Sex is significant (Wilks' Λ=0.704, $F_{26,69}$=1.116, p=0.349). However, there was a significant difference between groups (Wilks' Λ=0.602, $F_{26,69}$=1.750, p=0.034). MANOVA using the first 26 RWs with groups as a factor, showed significant difference (Wilks' Λ=0.312, $F_{52,180}$=2.737, p<0.001). Pairwise comparisons (Tab. 1) reveal that all groups are significantly different from each other. For pairwise comparisons we used the R package "RVAideMemoire" (Hervé, 2016), which performs permutational (999 in our case) pairwise comparisons with the "fdr" (Benjamini and Hochberg, 1995) probability correction.

Variation partitioning

Our preliminary test to explore the contribution of abiotic and biological factors explaining *C. thous* groups variability showed that, when
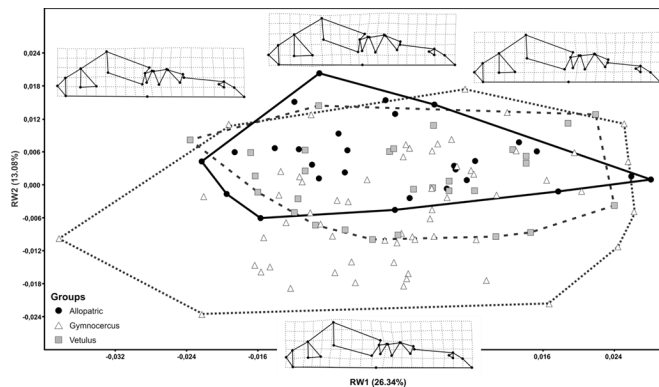
Figure 3 – Scatter plot of RW1 vs. RW2. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of Relative Warps axes. Every *Cerdocyon thous* group is labeled according to different symbols within minimum convex hull superimposed.

Table 1 – Pairwise comparisons between *Cerdocyon thous* groups for skull shape and skull size. Allopatric: in allopatry. Gymnocercus: sympatric to *Lycalopex gymnocercus*. Vetulus: sympatric to *Lycalopex vetulus*. Upper diagonal corresponds to *p* values and lower diagonal corresponds to F values. Significance is highlighted.

	Allopatric	**Gymnocercus**	**Vetulus**
Shape			
Allopatric	-	≪**0.001**	**0.0347**
Gymnocercus	3.717	-	≪**0.001**
Vetulus	1.954	7.568	-
Size			
Allopatric	-	**0.014**	**0.025**
Gymnocercus	6.255	-	0.745
Vetulus	5.276	0.107	-

considering shape variables as response variables, the highest and significant contribution is given by the total fraction of bioclimatic variables, followed by the latitude of sampling localities and by the mean values of *Lycalopex* LnCS (Adj. R^2=0.477, p=0.001; Adj. R^2=0.105, p=0.005; Adj. R^2=0.067, p=0.015). Grouping is not significant (see Table S3 in Supplemental Information). When considering the pure fractions of the same variables (i.e. the contribution of a single variable deprived of the contribution of all the others), no one showed a significant contribution to the total shape variation (Table S3). This indicates that climatic variability and the presence of *Lycalopex* are both significant yet interacting terms affecting *Cerdocyon* phenotype.

Species and groups comparisons

We extracted centroid size data for both *L. vetulus* and *L. gymnocercus* (Fig. 4). *Lycalopex vetulus* is the smallest species (10.3% smaller on average than *C. thous*), followed by *L. gymnocercus*, which is smaller still than *C. thous* (actually 3.5% smaller).

We did not detect sexual dimorphism related to size (F=0.055, d.f.=1, p=0.815). As with shape variables there is no significant interaction between Group and Sex as factors (F=0.372, d.f.=1, p=0.543). Finally, body size of the three groups proved not to be significantly different (F=1.012, d.f.=1, p=0.317; Fig. 4). Therefore, in subsequent analyses we used locality averages including unsexed individuals. One-way ANOVA on LnCS also showed a marginal significant difference between groups when we used all the specimens in the analysis (F=3.839, d.f.=1, p=0.052). Paired comparisons (Tab. 1) revealed that both sympatric groups are different (and larger) than the allopatric group (Fig. 4), in keeping with body size character displacement predictions. For the pairwise comparisons we used the paired t test with the "fdr" (Benjamini and Hochberg, 1995) method for probability correction.
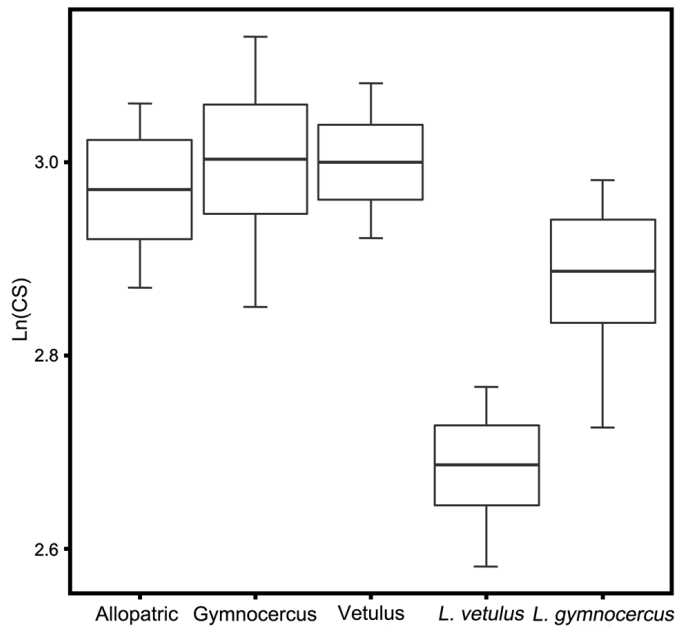
Figure 4 – Box plot with standardized deviation of natural log transformed centroid size (Ln(CS)) across the *Cerdocyon thous* groups and *Lycalopex* species. Black string: median, white box: first interquartile, bar: second interquartile.

Bergmann's rule and sexual size dimorphism

All specimens

Spatial autocorrelation in LnCS is present and significant in several distance classes. We found a significant positive Moran's I mainly for smallest distance classes, whereas largest distance classes were characterized by significantly negative spatial autocorrelation (see Table S3). Due to this degree of spatial dependence, we performed eigenvector spatial filtering to remove spatial autocorrelation from LnCS. We identified two vectors that describe the spatial structure and minimize the spatial autocorrelation (Moran's I) in the first class of distance (R^2=0.201, p<0.001, AICc=-421.75). The chosen vectors are highly correlated with LnCS and VIF in the model including the mean annual temperature as an additional covariate.

For the sample including all specimens, we detected a positive and significant relationship between raw LnCS data and the absolute value of latitude (hereafter AbsLat; slope=0.004, $p \ll 0.001$, Adj. R^2=0.23; Fig. 5), and a significantly negative relationship with the mean annual temperature (slope=-0.005, p=0.0002; Fig. 6). The GLM regression with the spatial and temperature-based residuals of LnCS still yielded a significant and positive latitudinal trend in *Cerdocyon* body mass (GLM slope=0.023, p=0.001, AIC=506.37, Fig. 7).
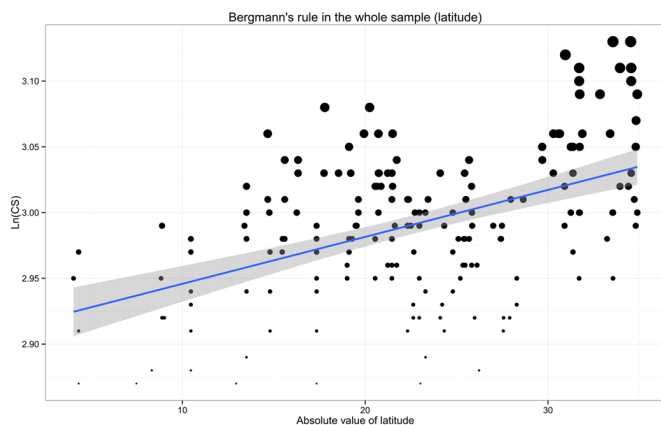

Figure 5 – Natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. absolute value of latitude. Symbols size increase with size.
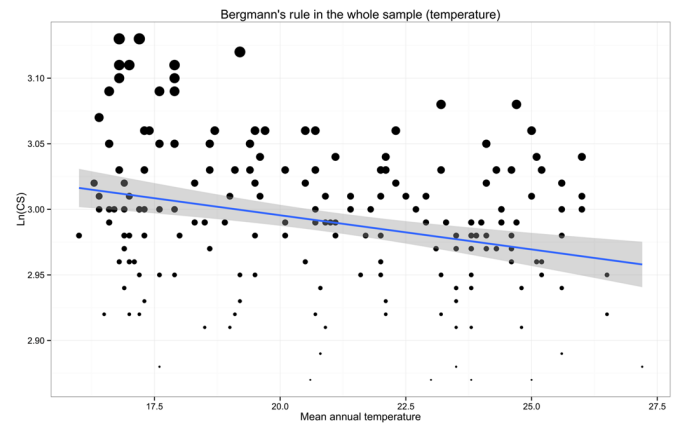

Figure 6 – Natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. mean annual temperature. Symbol size increases with body size.
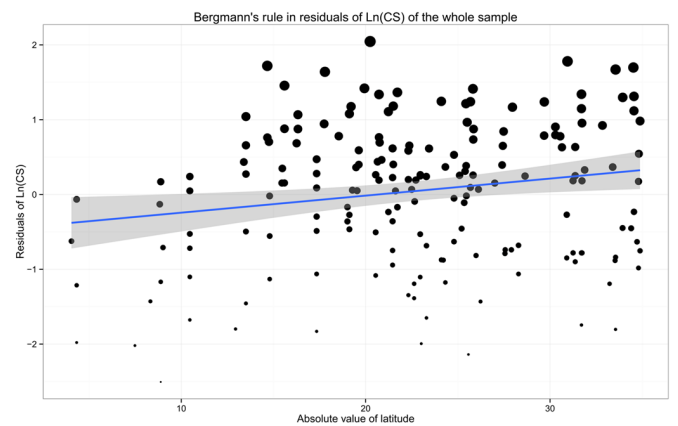

Figure 7 – Filtered natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. absolute value of latitude. Symbols size increase with size.

We investigated Bergmann's rule in each group separately by means of multiple regression. We did not use the temperature based spatially filtered LnCs in within group analyses because these groups are not statistically discriminated by this variable (Kruskal-Wallis χ^2=5.8407, p=0.054). For the allopatric group, the geographical gradient of raw LnCS is positive and significant (slope=0.004, Adj. p=0.002). Yet, the relationship with temperature is no longer significant (slope=0.001, p=0.875; Multiple Adj. R^2=0.1917, p=0.006). For the gymnocercus group, the relationship between raw LnCS and latitude is positive and significant, whereas the relationship with the temperature is also not significant (slope=0.011, $p \ll 0.001$ and slope=0.007, p=0.076, respectively; Multiple Adj. R^2=0.3816, $p \ll 0.001$). Regarding the vetulus group the relationship of raw LnCS is significant and positive with latitude, but not with temperature (slope=0.005, p<0.001; slope=-0.0002, p=0.955, respectively; Multiple Adj. R^2=0.175, p<0.001).

Sexually-determined individuals only

Shapiro-Wilk normality test confirmed that in sexed individuals both LnCS and standardized residuals of LnCS are normally distributed (W=0.990, p=0.459 and W=0.988, p=0.262, respectively). Two-way ANOVA confirmed that, when using LnCS, the whole sample of sexually defined individuals are different if considering the three groups (F=3.97, p=0.021), but no differences are found when taking sex into account (F=0.911, p=0.341). In addition, when using the standardized residuals of LnCS after accounting for spatial autocorrelation, we could not find any significant difference neither when considering the three groups (F=0.69, p=0.503), nor when considering sex as a factor (F=1.545, p=0.216).

We found positive and significant relationship between latitude and both the male-female LnCS ratios (slope=0.002, Adj. R^2=0.370,

p=0.012, Fig. 8), and the male-female differences of the standardized residuals of LnCS (slope=0.133, Adj. R^2=0.410, p=0.008).
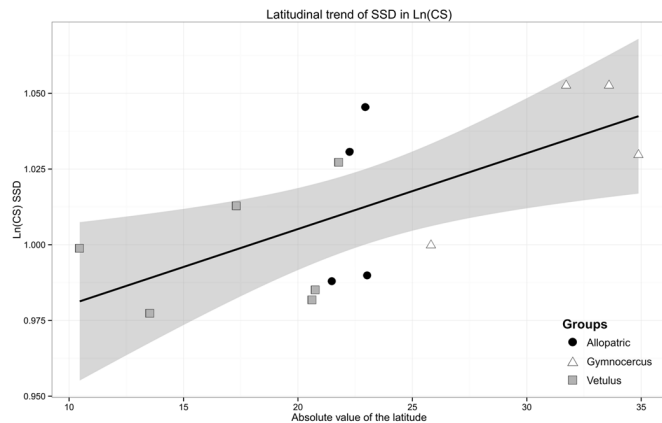

Figure 8 – Sexual size dimorphism (SSD) of *Cerdocyon thous* specimens vs. absolute value of latitude. Every *Cerdocyon thous* group is labeled according to different symbols.

Shape disparity

The size-corrected multi-group analysis indicated that most of total disparity of the whole sexually determined sample is taken by the gymnocercus group (PD=0.0434), followed by the allopatric and vetulus groups (PD=0.0328 and PD=0.0200, respectively). The size-corrected within group analysis unsurprisingly confirmed the gymnocercus group has the largest morphological disparity (MD=0.0007, 95% CI=0.0005 to 0.0008) followed by the allopatric group (MD=0.0006, 95% CI=0.0005 to 0.0008) and by the vetulus group (MD=0.0005, 95% CI=0.0004 to 0.0005). Morphological (Procrustes) distances between sexes of the same group indicated that males and females of the gymnocercus group are the most distant from each other (Procrustes distance=0.0100, 95% CI=-0.0115 to 0.0201). The intra-sex Procrustes distance for the vetulus group is -0.0077 (95% CI=-0.0138 to 0.0109), whereas for the allopatric group is -0.0103 (95% CI=-0.0189 to 0.0129). Thus, the larger sexual shape dimorphism in southern *C. thous* is dependent on males, which are significantly more variable than males in any other group.

We performed the variation partitioning with the averaged variables of the gymnocercus group only as this showed the highest morphological disparity. In this analysis we found that the total fractions of the climatic variability explains most of the gymnocercus group morphological disparity (Adj. R^2=0.188, p=0.01). Also the latitude of the sampling localities and *Lycalopex* LnCS significantly affect the gymnocercus group morphological variability (Adj. R^2=0.140, p=0.001; Adj. R^2=0.094, p=0.002, respectively). No one of the individual fractions (i.e. the contribution a single variable deprived of the contribution of all the others) significantly affect the gymnocercus group morphological disparity (Table S4). All these results suggest that the geographic and ecological factors intermingled in shaping the morphology of this *Cerdocyon* group and bolster the evidence for the ecological character displacement driven by the presence of *Lycalopex* species.

Discussion

Character displacement on body size exists in both sympatric areas. We predicted decreased sexual size dimorphism in sympatric *Cerdocyon* because of competition with *Lycalopex* (Grant, 1975; Dayan and Simberloff, 1994; but see Meiri et al., 2014). Among sympatric carnivorous mammals, differences in body size are especially important for interspecific coexistence (Valkenburgh and Wayne, 1994), since size differentiation between competitors leads to differences in prey size, which reduces competition. However, sympatric omnivorous carnivores often differ in the relative quantities of different food types consumed and such divergences are more likely to be determined by diverging dental morphologies than by body size differences per se (Valkenburgh and

Wayne, 1994). Our results show that interspecific competition influences *C. thous* in shape and size throughout its distributional range, yet Bergmann's rule also applies (Martinez et al., 2013). We deemed that, in the presence of ecologically similar species, latitude is not the only factor influencing species body size. We predicted that Bergmann's rule (as a pattern) loses or gains strength either in sympatric regions, according to the relative size of competitors as a consequence of character displacement.

L. vetulus is a small sized canid (Fig. 4) and its diet mainly includes termites (Dalponte, 2009). As an adaptation to this diet, this species presents large auditory bulla and molar area (Dalponte, 2009). Although we expected that when two related species living in sympatry differ in shape traits, the large body size difference between *C. thous* and *L. vetulus* seems to be the way these two species avoid competition. Groups of *C. thous* also occur in sympatry with the bush dog (*Speothos venaticus*, Lund, 1842). In the north, *S. venaticus* is in sympatry with both the vetulus and the *Cerdocyon* group we defined as "allopatric" (because of not overlapping with any *Lycalopex* species) but does not compete with them because of its hypercarnivorous diet (Perini et al., 2010; Zuercher et al., 2005). To the South, the geographical overlap between the gymnocercus group and the bush dog (*S. venaticus*) is extremely small (De Matteo and Loiselle, 2008). The southern group of *C. thous* is thus living under strongly different competition regimes from the groups living in the north (Cerrado and Northern Atlantic Forest). To the south the presence of *L. gymnocercus*, which is quite similar to *C. thous* in size, calls for stronger competitive effects. In keeping with this, and with the absence of bush dogs, and even under the ubiquitous effect of the Bergmann's rule, *C. thous* in the south presents smaller molars and auditory bulla, but larger temporal muscles and longer muzzle. Such traits suggest a shift towards a certain emphasis on small vertebrate prey consumption (Meloro and O'Higgins, 2003; Meloro et al., 2015). In fact, even the carnassial in this southern group is slender and sharper, indicating a stronger recruitment in prey killing than anywhere else within the *C. thous* geographic range. In keeping with our interpretation, a greater consumption of vertebrates by crab-eating fox has previously been reported also by Pedó et al. (2006) in Southern Brazil. Besides these phenotypic adaptations, *L. gymnocercus* presents behavioral shifts when in the presence of *C. thous*, suggesting one species indeed affects the other at the ecological level. Besides these phenotypic adaptations, *C. thous* in the south tends to be more nocturnal and utilizes more of dense vegetation areas as compared to *Lycalopex* (Vieira and Port, 2007; Di Bitetti et al., 2009). The enlarged temporal muscle is similarly suggestive of a dietary shift for *C. thous* to the south of its range. A large temporalis is related to powerful bite (Valkenburgh and Ruff, 1987). We therefore believe that the shape features in southern *Cerdocyon* are strong indicators that it changes its feeding niche by emphasizing carnivory.

In summary, our results consistently converge on two different means to avoid competition towards *Lycalopex* in *Cerdocyon* groups. To the north (that is towards the equator) body size difference between the two canids is large enough to limit the effect of competitive interactions between them. Therefore, they show some convergent shape features as regard to molar shape (Dalponte, 2009). In keeping with this, *Cerdocyon* in sympatry with *L. vetulus* is significantly larger than in allopatry, although these two *Cerdocyon* groups live at almost the same latitude. This body-size character displacement probably also accounts for the small sexual size dimorphism in the vetulus group. As we predicted, the presence of competitors limits the size variation between the sexes in *Cerdocyon* (Grant, 1975; Dayan and Simberloff, 1994). To the south, *Cerdocyon* is significantly larger (in keeping with Bergmann's rule) but also very different in skull shape from both its *Lycalopex* competitors (Márquez and Fariña, 2003) and from other *Cerdocyon* groups. The enlarged attachment area for the temporalis muscle and slender and sharper carnassial are all suggestive of increased carnivory in this southern group. As a consequence, of these trait shifts, and given the absence of bush dogs there, southern *Cerdocyon* individuals are relaxed from competitive pressures and therefore much more variable in shape (Grant, 1975; Dayan and Simberloff, 1994).

Whereas the effect of Bergmann's rule is evident both at the species level and within groups in *Cerdocyon*, we detected significant and consistent evidence for both body size and skull shape character displacement in *C. thous*. ✍

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 List of *Cerdocyon thous* specimens used in this study with data on group, sex, museum number and geographical coordinates.

Table S2 List of *Lycalopex* specimens used in this study with data on species, sex and museum number.

Table S3 Variation partitioning table.

Table S4 Spatial autocorrelation table.