UNIVERSIDADE FEDERAL DE SANTA MARIA
CENTRO DE CIÊNCIAS NATURAIS E EXATAS
PROGRAMA DE PÓS-GRADUAÇÃO EM
BIODIVERSIDADE ANIMAL

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FATORES DETERMINANTES DA VARIAÇÃO DO CRÂNIO DE CANÍDEOS SUL-AMERICANOS

Santa Maria, RS

2016

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria, como requisito parcial para obtenção do grau de **Mestra em Ciências Biológicas – Área Biodiversidade Animal.**

Orientador: Prof. Dr. Nilton Carlos Cáceres
Coorientador: Prof. Dr. Carlo Meloro

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Ficha catalográfica elaborada através do Programa de Geração Automática
da Biblioteca Central da UFSM, com os dados fornecidos pelo(a) autor(a).

Bubadué, Jamile de Moura
Fatores Determinantes da Variação do Crânio de Canídeos Sul-Americanos / Jamile de Moura Bubadué.-2016.
110 p.; 30cm

Orientador: Nilton Carlos Cáceres
Coorientador: Carlo Meloro
Dissertação (mestrado) - Universidade Federal de Santa Maria, Centro de Ciências Naturais e Exatas, Programa de Pós-Graduação em Biodiversidade Animal, RS, 2016

1. Carnivora 2. Adaptações Climáticas 3. Clinas Geográficas 4. Competição Interespecífica 5. Macroecologia I. Cáceres, Nilton Carlos II. Meloro, Carlo III. Título.

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Santa Maria, RS
2016

AGRADECIMENTOS

Gostaría de agradecer ao professor **Nilton Carlos Cáceres**, pela orientação e todo o tempo despendido, não somente durante esta dissertação, mas durante toda a minha formação acadêmica. Ao professor **Carlo Meloro**, pela paciência e disponibilidade para ensinar os procedimentos de morfometria geométrica e escrita científica. À **equipe do laboratório do professor Pasquale Raia** da *Università degli Studi di Napoli "Federico II"*, e principalmente ao **Dr. Francesco Carotenouto**, pelo seu comprometimento e auxílio para com o primeiro capítulo desta dissetação. A toda a equipe do **Laboratório de Ecologia e Biogeografia** da Universidade Federal de Santa Maria, pela convivência e por terem me ajudado de diferentes formas ao longo do mestrado. Um agradecimento especial a **Renan S. Carvalho**, que me acompanhou durante as coletas de dados nos inúmeros museus que visitamos. A **Geruza L. Melo** e **Jonas Sponciado**, que se disponibilizaram a coletar dados no Museu Paraense Emílio Goeldi, quando, por questões de logística, não tive oportunidade de ir, bem como todo seu apoio profissional e amizade durante minha formação acadêmica. A **Caroline C. Sartor** e **Cíntia R. N. Ramos** por me ajudarem durante a coleta de dados no Museu Nacional Uruguaio de Historia Natural, e, é claro, pela amizade. A **Bárbara Kuhn** e **George L. S. Polidoro** pela parceria, amizade, momentos de descontração e apoio emocional nos momentos mais difíceis. A **Carla Hendges**, que sempre se dispôs a me auxiliar de inúmeras formas durante este mestrado. Ao Secretário, **Sidnei Cruz** e ao Coordenador do PPGBA, professor **Sandro Santos**, por sempre me ajudarem a resolver os problemas burocráticos.

Agradeço também à **CAPES** – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, pela bolsa de mestrado concedida. Aos curadores e funcionários do Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCNFZB) (**Márcia M. de A. Jardim**), Museu de Ciências e Tecnologia da PUCRS (MCP) (**Carla S. Fontana**), Museu Nacional (MN) (**João A. de Oliveira** e **Sérgio M. Vaz**), Museu Paraense Emílio Goeldi (MPEG) (**Suely A. M. Aguiar** e **José S. Silva Jr.**), Museu de História Natural Capão da Imbuia (MHNCI) (**Vinícius Abilhoa** e **Sebastião C. Pereira**), Coleção Científica do Laboratório de Mamíferos Aquáticos da UFSC (UFSC) (**Maurício E. Graipel**), Museu Nacional Uruguaio de Historia Natural (MNHN) (**Enrique M. Gonzalez**), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) (**David A. Flores** e **Sérgio Lucero**) e Museu de Zoologia da Universidade de São Paulo (MZUSP) (**Mário de Vivo**, **Juliana G. Barros** e **Ismael P. de Jesus**), pela autorização e auxílio no acesso aos espécimens estudados.

Finalmente, agradeço a toda a **minha família** pelo apoio constante. Em especial, agradeço aos meus pais, **Jorge L. Bubadué** e **Sad R. P. de Moura**, e minha avó **Therezinha R. Bubadué** por toda a educação, compreensão, incentivo, amor e convivência. À minha irmã **Renata M. Bubadué**, por todo o auxílio com o inglês, mas principalmente pela amizade, parceria e, muitas vezes, hospedagem durante as fases de coleta.

RESUMO

FATORES DETERMINANTES DA VARIAÇÃO DO CRÂNIO DE CANÍDEOS SUL-AMERICANOS

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Logo após a emergência completa do istmo do Panamá, a família Canidae colonizou a América do Sul, há, aproximadamente, 2.6-2.4 milhões de anos atrás. Embora a radiação dos canídeos seja recente na América do Sul, esta região compõe a maior diversidade atual de espécies desta família no mundo, com mais de 10 espécies viventes. Esta grande biodiversidade também é notável na variação ecomorfológica destes animais. Exemplo disso são os dois extremos desta variação: o lobo-guará (*Chrysocyon thous*), um animal onívoro de grande tamanho corporal; e o cachorro-vinagre (*Speothos venaticus*), espécie hipercarnívora de pequeno porte. Tamanha diversidade de formas pode potencialmente ser explicada tanto por fatores abióticos, como o clima, e bióticos, como a competição. Ambos os fatores podem ter contribuído para a estabilização da comunidade de canídeos sul-americana. Por isso, este estudo se propôs a investigar o que impulsionou esta amplitude ecomorfológica, bem como entender como espécies mais similares coexistem quando em sobreposição distribucional, como o graxaim-do-mato (*Cerdocyon thous*), que possui área simpátrica a *Lycalopex vetulus* e *L. gymnocercus*, duas raposas ecologicamente similares a *Cerdocyon thous.* Para tanto, 431 espécimens foram fotografados em nove museus da América do Sul. Através de procedimentos de morfometria geométrica, foi possível quantificar a variação fenotípica de oito espécies de canídeos (*Atelocynus microtis*, *C. thous*, *C. brachyurus*, *L. culpaeus*, *L. griseus*, *L. gymnocercus*, *L. vetulus* e *S. venaticus*), ao longo de sua distribuição geográfica, e então testar a contribuição dos fatores bióticos e abióticos nesta variação. As evidências deste estudo sugerem que *C. thous* altera sua forma e tamanho corporal quando em simpatria com as duas espécies de *Lycalopex*, padrão descrito pelo "deslocamento de caráter", quando espécies semelhantes alteram seu fenótipo em simpatria, a fim de minimizar a competição. Além disso, *C. thous* também segue a regra de Bergmann, que prevê um aumento de tamanho corporal com o aumento da latitude. Ao considerar a comunidade de canídeos como um todo, o clima foi identificado como o fator que mais contribuiu para a variação fenotípica destes animais. A competição, por sua vez, tem um impacto mais fraco na morfologia do crânio dos canídeos sul-americanos, embora possa ter tido uma maior contribuição no passado, quando a diversidade ecomorfológica no subcontinente era ainda maior.

Palavras-chave: Carnivora; adaptações climáticas; clinas geográficas; competição interespecífica; macroecologia; dimorfismo sexual de tamanho; disparidade morfológica.

ABSTRACT

DETERMINANT FACTORS OF SKULL VARIATION IN SOUTH-AMERICAN CANIDS

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Right after the arising of the Panama isthmus, the family Canidae colonized South America, around 2.6-2.4 million years ago. Although canids radiation in South America is recent, this region holds the largest canid diversity in the world, with more than 10 extant species. This great diversity is also notable when dealing with the ecomorphological variation of these animals. The maned-wolf (*Chrysocyon brachyurus*), a large omnivore, and the bush-dog (*Speothos venaticus*), a small hypercarnivore, are the extreme exemples of this variation. Such shape diversity can be potentially explained by both abiotic, such as climate, and biotic factors, like competition. These factors may have contributed for stabilizing the south-american canids community. Thus, this study aimed to investigate what drives this ecomorphological amplitude, as well as to understand how can similar species coexist when overlapping their distributional ranges, such as the crab-eating fox (*Cerdocyon thous*), which has sympatric areas with *Lycalopex vetulus* and *L. gymnocercus*, two foxes ecologically similar to *Cerdocyon thous.* To answer these questions, 431 especies were photographed in nine South-American museums. Through geometric morphometric procedures, it was possible to quantify the phenotypic variation of eight canid species (*Atelocynus microtis*, *C. thous*, *C. brachyurus*, *L. culpaeus*, *L. griseus*, *L. gymnocercus*, *L. vetulus* e *S. venaticus*) throughout their geographical range and then test the contribution of biotic and abiotic factors driving this variation. The evidences presented in this study suggest *C. thous* alters its shape and body size when in sympatry with two *Lycalopex* species, pattern described by "character displacement", which is when similar species shift their phenotype in order to minimize competition. Besides, *C. thous* also follows the Bergmann's rule, which predicts that body size increases at larger latitudes. When considering the canid community as a whole, climate was identified as the main factor contributing to phenotypic variation in these animals. Competition has a weaker impact in south-american canids skull morphology, although it may have played a larger role in the past, when the ecomorphological diversity in the subcontinent was even larger.

Key-words: Carnivora; climatic adaptations; geographic clines; interspecific competition; macroecology; sexual size dimorphism; shape disparity.

SUMÁRIO

INTRODUÇÃO

Os representantes recentes da ordem Carnivora estão taxonomicamente divididos nas subordens Feliformia (gatos, hienas e afins) e Caniformia (cachorros, ursos e seus parentes). A última é a mais bem representada na América do Sul e também a primeira a colonizar o subcontinente, no começo do Grande Intercâmbio Americano (GABI, do inglês *Great American Biotic Interchange*), a partir do final do Mioceno, mais especificamente há 7,3 milhões de anos atrás (= m.a.a.), muito antes da emergência completa do istmo do Panamá, há 3 m.a.a. (PEDERSEN et al., 2014; VALKENBURGH, 1999). Entre os caniformes, a família Canidae representa uma radiação recente no subcontinente sul-americano, o colonizando durante o Plioceno (2,6-2,4 m.a.a.) (BERTA, 1987; PREVOSTI, 2010; PERINI et al., 2010; WANG et al., 2008). Apesar disso, a região Neotropical possui mais de 10 espécies de canídeos viventes, sendo atualmente a região com a maior diversidade desse clado no mundo (PREVOSTI et al., 2009a; PERINI et al., 2010; SILLERO-ZUBIRI et al., 2004).

Entre os canídeos sul-americanos endêmicos, existe uma grande diversidade de tamanho corporal e ecologia alimentar, como o grande e onívoro lobo-guará, *Chrysocyon brachyurus* (Illiger, 1815), com uma massa média de 25 kg, e o pequeno hipercarnívoro cachorro-vinagre, *Speothos venaticus* (Lund, 1842), com uma massa que varia entre cinco e oito quilos (SILLERO-ZUBIRI et al., 2004). Além disso, a diversidade ecomorfológica de raposas também é notável na América do Sul, a exemplo do cachorro-do-mato, *Cerdocyon thous* (Linnaeus, 1766), amplamente distribuído no subcontinente, e seis espécies de *Lycalopex*, das quais quatro se destacam por sua maior distribuição geográfica – *Lycalopex culpaeus* (Molina, 1782), *Lycalopex griseus* (Gray, 1837), *Lycalopex gymnocercus* (Fischer, 1814) e *Lycalopex vetulus* (Lund, 1842) – e, com a exceção de *L. vetulus*, por coexistirem amplamente no sul da América do Sul, principalmente na Argentina. Essa diversidade era ainda maior no passado (PREVOSTI 2010; PERINI et al., 2010), com formas carnívoras que possivelmente influenciaram a distribuição e ecologia dos taxa menores, hoje em dia dominada por espécies onívoras.

Quando tratamos de uma ampla variação ecomofológica, como o caso dos canídeos sul-americanos, o crânio pode ser uma estrutura especialmente informativa. Por exemplo, os dentes mamalianos trazem adaptações relacionadas, principalmente, à dieta do animal (UNGAR, 2010). Já a complexidade dos ossos turbinados, abrigados dentro do focinho, está positivamente correlacionada com a capacidade olfatória (VALKENBURGH et al., 2014). Quanto maior o tamanho da bula timpânica, uma cápsula óssea que abriga o ouvido médio dos mamíferos, maior é o potencial auditivo do animal (HUNT JR. 2005). E o arco zigomático e o focinho são as principais estruturas do crânio que compõem a fórmula para calcular a força de mordida de um mamífero (DAMASCENO et al., 2013).

Graças a essa relação forma-função, os processos evolutivos associados a diversificação do crânio em mamíferos podem ser influenciados tanto por fatores ambientais como bióticos. Por um lado, espera-se que as forças abióticas, como o clima, apliquem filtros que influenciem a variação intra e interespecífica das espécies (BLACKBURN et al., 1999; MARTINEZ et al., 2013). Enquanto isso, a competição interespecífica pode contribuir para a estabilização das relações dentro das comunidades, resultando em um padrão de diversificação fenotípica conhecido como deslocamento de caráter (BROWN & WILSON, 1956).

Por definição, o deslocamento de caráter é a redução da sobreposição fenotípica que ocorre quando duas ou mais espécies competem pelos mesmos recursos, a fim de reduzir a intensidade da competição e, portanto, serem capazes de coexistir (SLATKIN, 1980; SCHLUTER, 2000; DAYAN & SIMBERLOFF, 2005). Por isso, espera-se que espécies que possuam uma sobreposição parcial na sua distribuição geográfica divirjam em maior escala em tamanho e/ou forma quando em simpatria (BROWN & WILSON, 1956; MEIRI et al., 2011).

DAYAN et al. (1992) estudaram o deslocamento de caráter em dentes carnassiais (4º pré-molar superior e 1º molar inferior) de lobos, chacais e raposas em Israel. Eles descobriram que a diferença de tamanho entre essas espécies permanence constante, apesar da flutuação geográfica. De acordo com as predições de deslocamento de caráter em comunidades (DAYAN & SIMBERLOFF, 2005), essa constante sugere que a competição foi um fator decisivo na divergência morfológica desses canídeos. Ao estudar o comprimento do dente carnassial, uma das características mais marcantes de especialização na ordem Carnivora destinada ao processamento da comida, DAVIES et al. (2007) generalizaram a possível contribuição do deslocamento de caráter na evolução dos carnívoros.

Entre os canídeos sul-americanos, existem evidências diretas do impacto da competição na ecologia e comportamento destes animais. DI BITETTI et al. (2009) registram mudanças comportamentais em cachorro-do-campo, *L. gymnocercus* , devido à competição com cachorro-do-mato. Em simpatria, o cachorro-do-campo altera sua atividade normal para evitar confronto com o maior *C. thous*. Além disso, a predação interespecífica também ocorre intensivamente entre os canídeos sul-americanos, onde espécies maiores, como o lobo-guará tendem a controlar a densidade e comportamento de canídeos menores (DONADIO &

BUSKIRK, 2006; OLIVEIRA & PEREIRA, 2014).

Enquanto que o deslocamento de caráter implica na diferenciação fenotípica que ocorre entre espécies quando em simpatria, e que independe da geografia, espera-se que, devido a relação entre superfície e volume e os efeitos resultantes da termorregulação de animais homeotérmicos, estes tendam a ter um maior tamanho corporal quando habitam áreas de maior latitude (onde o clima é mais frio). Essa predição é conhecida como regra de Bergmann (BLACKBURN et al., 1999; ASHTON et al., 2000; MEIRI & DAYAN, 2003; MEIRI et al., 2004; RODRÍGUEZ et al., 2008; CLAUSS 2013), fenômeno já registrado na raposa vermelha (*Vulpes vulpes*), por exemplo, que fornece evidências claras sobre o impacto do clima no tamanho do crânio, que varia positivamente com a latitude (CHURCHER, 1960; DAVIS, 1977; CAVALLINI, 1995; YOM-TOV & GEFFEN, 2006; MEIRI et al., 2007; YOM-TOV et al., 2007; SZUMA, 2008).

Dentro deste contexto teórico, *C. thous* é uma espécie que se destaca para o estudo da interação entre dois conceitos importantes da macroecologia: o deslocamento de caráter e a regra de Bergmann. Além de ter uma grande distribuição ao longo da América do Sul, *C. thous* entra em sobreposição geográfica no Brasil central com a raposinha-do-campo, *L. vetulus*, e com o cachorro-do-campo ao sul do subcontinente. Essas três espécies de canídeos são filogeneticamente próximas (PERINI et al., 2010) e possuem similaridades morfológicas e comportamentais notáveis. *C. thous* é a maior espécie entre as três, seguida por *L. gymnocercus* e *L. vetulus*, a menor entre elas (VIEIRA & PORT, 2007; LUCHERINI & VIDAL, 2008; DALPONTE, 2009; DI BITETTI et al., 2009). Ao estudar o tamanho do crânio de *C. thous*, MARTINEZ et al. (2013) encontraram um padrão de variação condizente com a regra de Bergmann ao sul do Equador, ou seja, o tamanho corporal aumenta mais ao sul.

Além disso, o crânio de canídeos sul-americanos tem sido usado para esclarescer padrões ontogenéticos e taxonômicos (SEGURA & PREVOSTI, 2012; SEGURA, 2013), adaptações paleobiológicas e ecológicas (PREVOSTI et al., 2005; PREVOSTI et al., 2009a; b), e mais recentemente o impacto do clima sobre a morfologia craniana (MACHADO & HINGST-ZAHER, 2009; MARTINEZ et al., 2013). Apesar disso, pouco se sabe sobre o impacto da competição na variação fenotípica desse grupo. WAYNE et al. (1989) identificaram um grau elevado de divergência morfológica entre as raposas sul-americanas, apesar de o tempo de divergência entre essas espécies ser pequeno (menos de 250.000 anos).

Portanto, usando métodos comumente utilizados em estudos de morfometria geométrica, análises de variância univariada e multivariada, e autocorrelação espacial, dois objetivos principais foram o foco deste estudo: 1) Testar se existe deslocamento de caráter em *Cerdocyon thous* quando em simpatria com *Lycalopex vetulus* e *Lycalopex gymnocercus* e se a primeira espécie segue a regra de Bergmann ao longo de sua ampla distribuição geográfica; 2) Testar a seguinte hipótese: o crânio dos canídeos sul-americanos, como estrutura complexa, e que reflete forte correlação entre forma-tamanho-função (MELORO et al., 2015), varia, ao longo do gradiente geográfico, correlacionando-se com o clima (fator abiótico) e a competição (fator biótico).

Estrutura da dissertação

Esta dissertação está estruturada de acordo com as normas da "Estrutura e apresentação de monografias, dissertações e teses: MDT", da Universidade Federal de Santa Maria (MDT, 2015). Compõem esta dissertação dois capítulos redigidos no formato de artigos científicos, conforme descrição abaixo:

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

Neste capítulo testo e descrevo o efeito da competição (deslocamento de caráter) na variação do crânio de cachorro-do-mato (*Cerdocyon thous*) quando em simpatria com as espécies do gênero *Lycalopex* ao longo de sua distribuição geográfica. Além disso, levo em consideração os possíveis efeitos da latitude e temperatura no tamanho do crânio (regra de Bergmann) e no dimorfismo sexual de tamanho do cachorro-do-mato, controlando o efeito da autocorrelação espacial. Este capítulo foi aceito para publicação no periódico *Hystrix, the Italian Journal of Mammalogy*.

Capítulo II: **Ecogeographical variation in skull shape of South-American canids: abiotic or biotic processes?**

Neste capítulo descrevo e testo os efeitos do clima, alometria, história filogenética e competição na variação do crânio de oito espécies de canídeos Sul-Americanos: *Atelocynus microtis*, *Cerdocyon thous*, *Chrysocyon brachyurus*, *Lycalopex culpaeus*, *Lycalopex griseus*, *Lycalopex gymnocercus*, *Lycalopex vetulus* e *Speothos venaticus*. Este capítulo encontra-se publicado no periódico *Evolutionary Biology*.

CAPÍTULO I

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

Hystrix, the Italian Journal of Mammalogy (2015), no prelo

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.

Keywords: Canidae; crab-eating fox; geometric morphometrics; sexual size dimorphism; shape disparity; South America; Bergmann's rule; character displacement.

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 Capanna1998; 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* (G. Fischer 1814). These three phylogenetically-close canids (Perini et al. 2010) have outstanding morphological and behavioral similarities. They are opportunistic and omnivorous feeders 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 Appendix A in Supporting Information). We sampled 118 localities overall (Figure 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).

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. (Figure 1). We used a dataset gathering 191 *L. vetulus* and *L.*

gymnocercus occurrences borrowed from the GBIF database (www.gbif.org) complemented with specific papers (Sherlock *et al.* 1988; Persson and Lorini 1990; Cimardi 1996; Dalponte and Lima 1999; Marques and Ramos 2001; Juarez and Marinho-Filho 2002; Michalski and Hasenack 2002; Rodrigues *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 (Figure 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 (Gündüz et al. 2007; Schutz et al. 2009; Segura and Prevosti 2012; Cáceres et al. 2014).

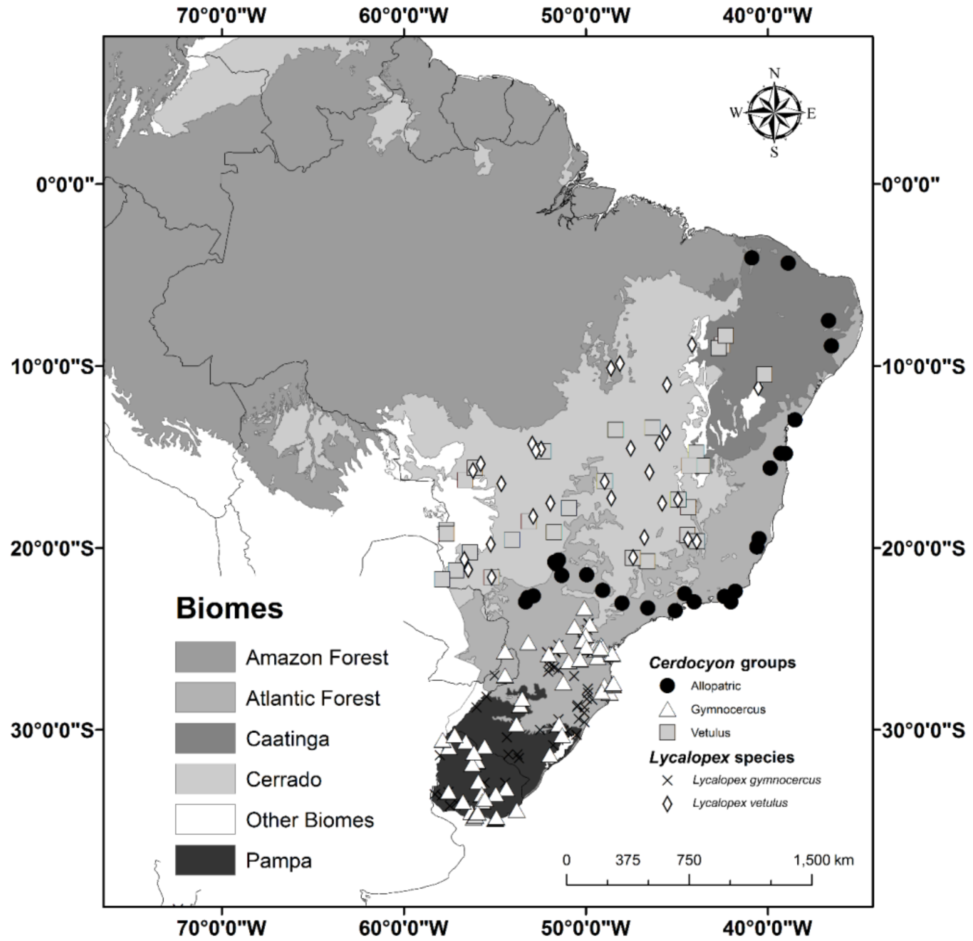

Figure 1. Map of South America showing the geographical distribution of *Cerdocyon thous* specimens sampled. Each group is labeled in accordance with different symbols.

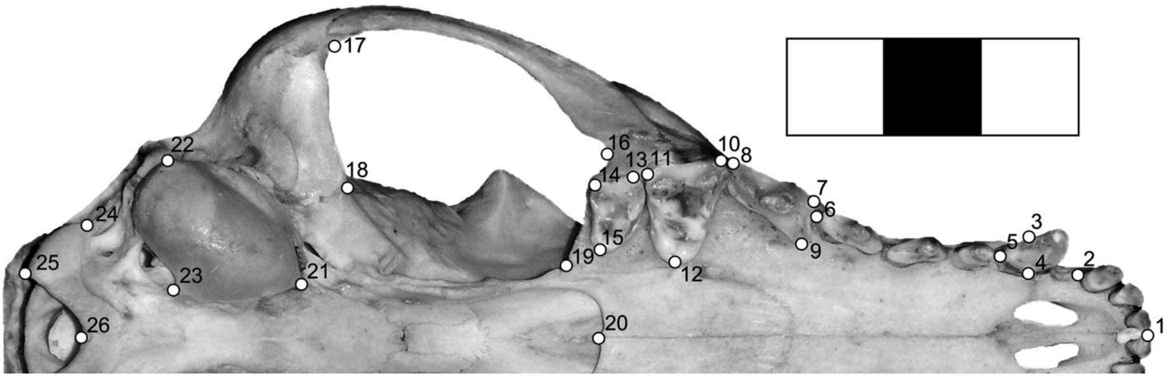

Figure 2. Disposition of 26 landmarks on a skull of *Cerdocyon thous* specimen (MZUSP 3101). 1 = midpoint of central incisors; 2 = posterior-most point of lateral incisor alveolus; 3-5 = canine area; 5-6 = first three pre-molars length; 7-9 = fourth pre-molar (carnassial) area; 10-12 = first molar area; 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.

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 Appendix B).

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 configuration 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 partitioning

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 ~ 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… Xn) and all of their interaction terms (Borcard et al. 1992;

Borcard and Legendre 1994; and 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^2_1 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 1987; 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-Zaher 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 2,000 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 (Figure 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' lambda = 0.674, $F_{26, 69} = 1.283$, $p = 0.205$), neither the interaction between Group and Sex is significant (Wilks' lambda = 0.704, $F_{26, 69}$ = 1.116, p = 0.349). However, there was a significant difference between groups (Wilks' lambda = 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' lambda = 0.312, $F_{52, 180}$ = 2.737, p < 0.001). Pairwise comparisons (Table 1) reveal that all groups are significantly different from each other. For pairwise comparisons we used the R package "RVAideMemoire" (Maxime Hervé 2015), which performs permutational (999 in our case) pairwise comparisons with the "fdr" (Benjamini and Hochberg 1995) probability correction.

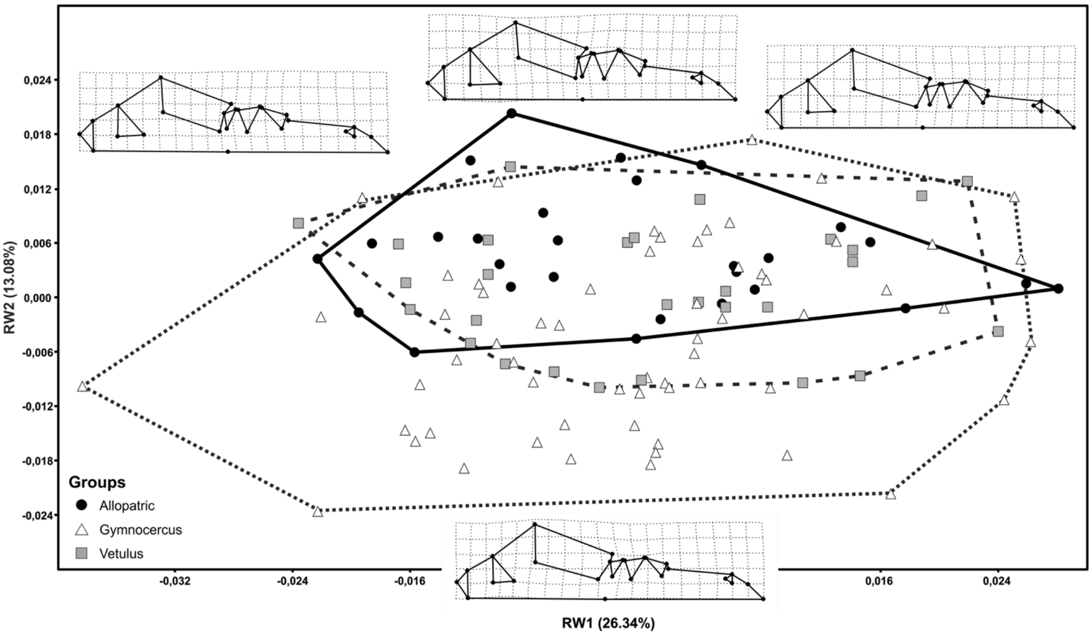

Figure 3. Scatter plot of RW1 vs. RW2. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of Relative Warps axes. Every *Cerdocyon thous* group is labeled according to different symbols within minimum convex hull superimposed.

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	-

Variation partitioning

Our preliminary test to explore the contribution of abiotic and biological factors explaining *C. thous* groups variability showed that, when 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.square = 0.477, *p* = 0.001; Adj.R.square = 0.105, *p* = 0.005; Adj.R.square = 0.067, *p* = 0.015). Grouping is not significant (Appendix C in Supporting 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 (Appendix C in Supporting Information). 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* (Figure 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).

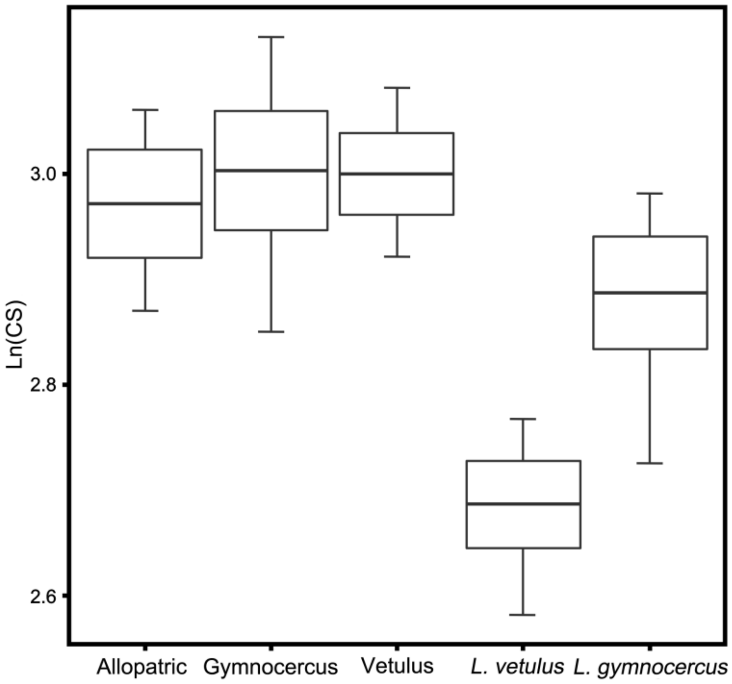

Figure 4. Box plot with standardized deviation of natural log transformed centroid size (Ln(CS)) across the *Cerdocyon thous* groups and *Lycalopex* species. Black string: median, white box: first interquartile, bar: second interquartile.

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; Figure 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 (Table 1) revealed that both sympatric groups are different (and larger) than the allopatric group (Figure 4), in keeping with body size character displacement predictions. For the pairwise comparisons we used the paired t test with the “fdr” (Benjamini & Hochberg, 1995) method for probability correction

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 Appendix C). 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* << 0.001, Adjusted R-squared: 0.23; Figure 5), and a significantly negative relationship with the mean annual temperature (slope = -0.005, *p* = 0.0002; Figure 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, Figure 7).

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 chi-squared = 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 Adjusted $R^2 = 0.1917$, $p = 0.006$). 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, $p << 0.001$ and slope = 0.007, $p = 0.076$, respectively; Multiple Adjusted $R^2 = 0.3816$, $p << 0.001$). 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 Adjusted $R^2 = 0.175$, $p < 0.001$).

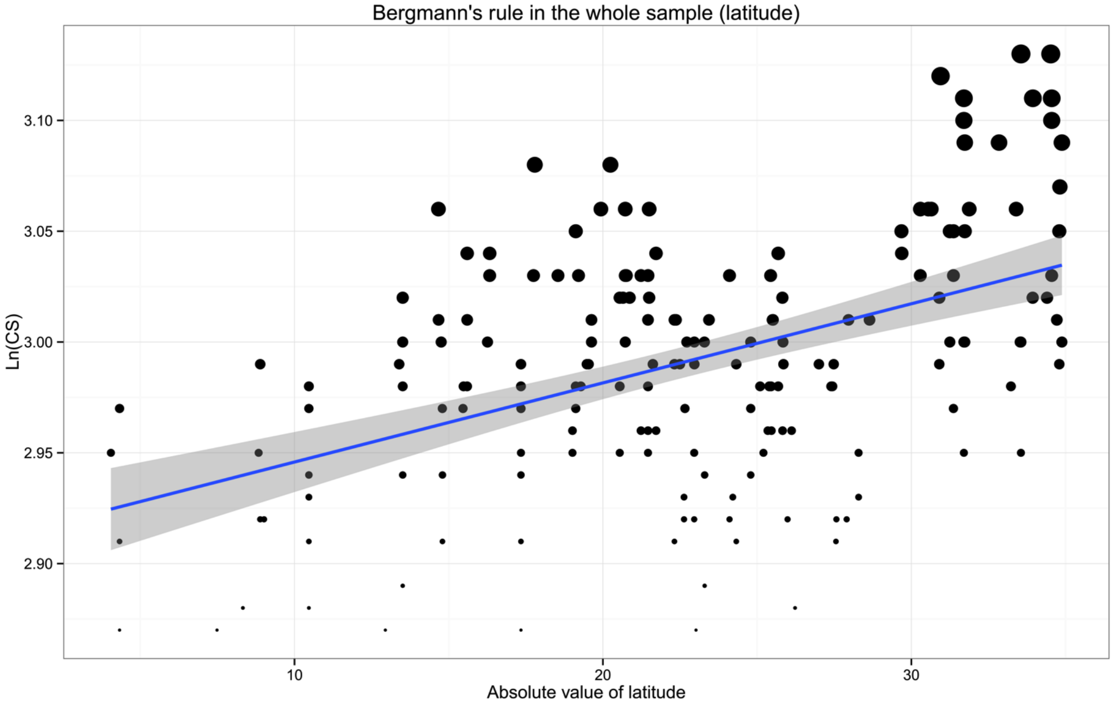

Figure 5. Natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. absolute value of latitude. Symbols size increase with size.

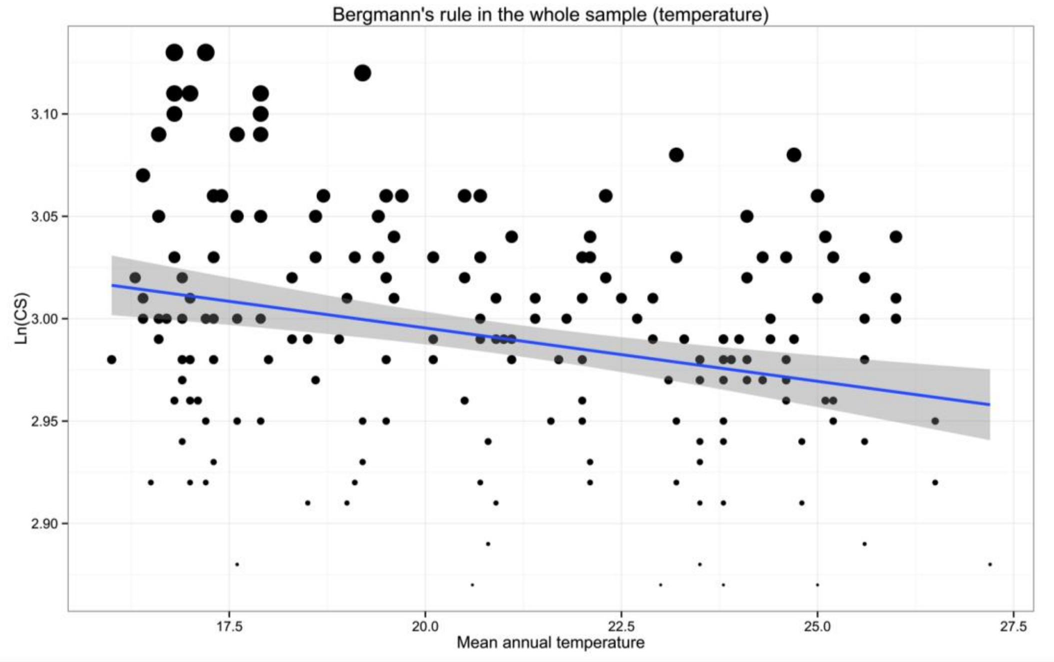

Figure 6. Natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. mean annual temperature. Symbol size increases with body size

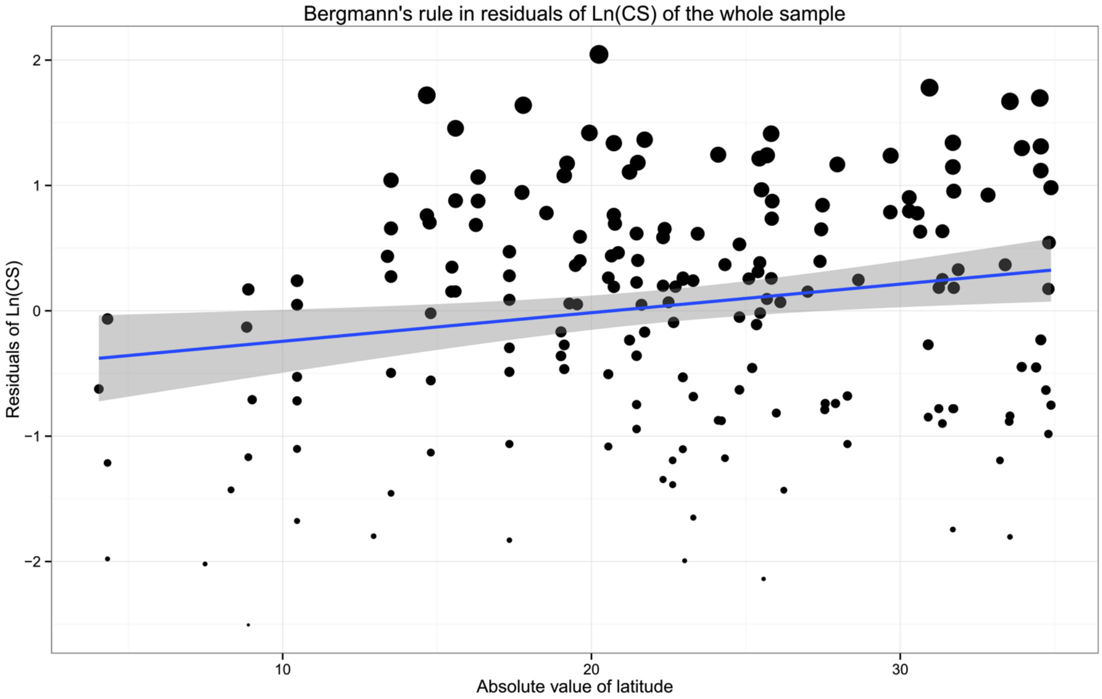

Figure 7. Filtered natural log transformed centroid size (Ln(CS)) of *Cerdocyon thous* specimens vs. absolute value of latitude. Symbols size increase with size.

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

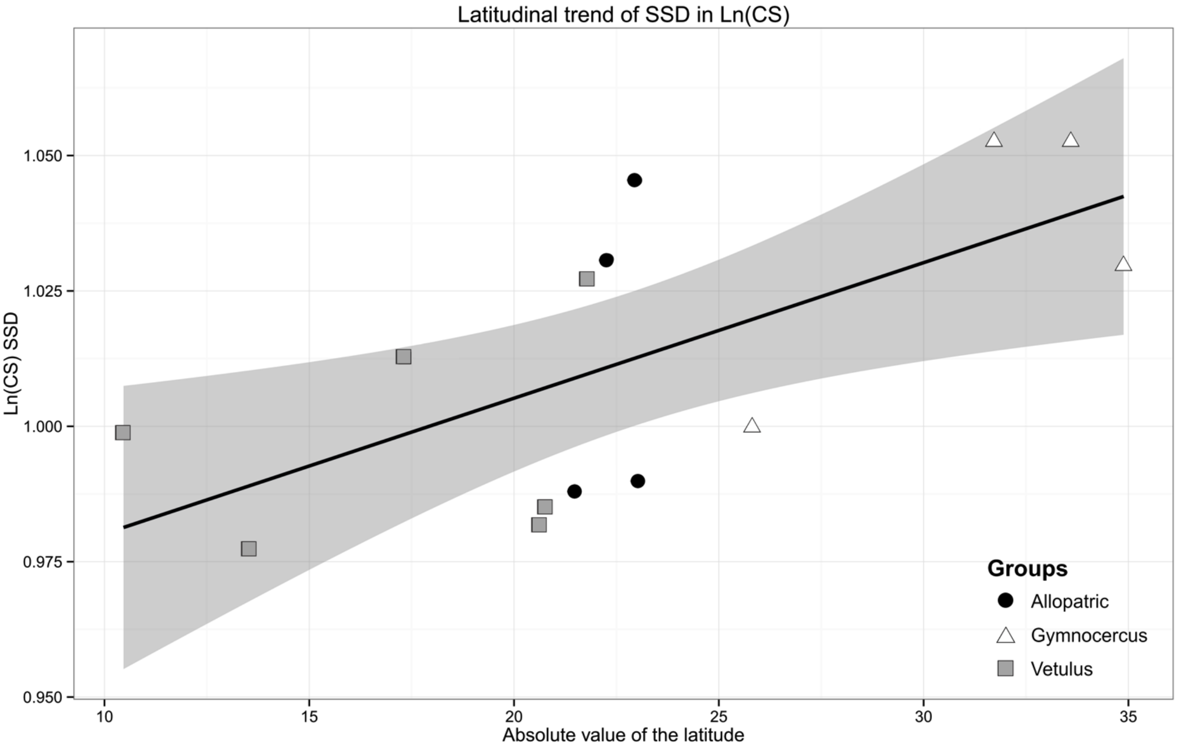

Figure 8. Sexual size dimorphism (SSD) of *Cerdocyon thous* specimens vs. absolute value of latitude. Every *Cerdocyon thous* group is labeled according to different symbols.

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.square = 0.188, *p* = 0.01). Also the latitude of the sampling localities and *Lycalopex* LnCS significantly affect the gymnocercus group morphological variability (Adj.R.square = 0.140, *p* = 0.001; Adj.R.square = 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 (Appendix B in Supporting Information). 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 (Figure 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 2011; 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 (Marquéz 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*.

ACKNOWLEDGEMENTS

We are grateful to the curators and staff of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (FZB) (M.M. de A. Jardim), Museu de Ciências e Tecnologia da PUCRS (MCP) (C.S. Fontana), Museu Nacional (MNRJ) (J.A. de Oliveira and S.M. Vaz), Museu de História Natural Capão da Imbuia (MNHNCI) (V. Abilhoaand S.C. Pereira), Coleção Científica do Laboratório de Mamíferos Aquáticos da UFSC (LAMAQ) (M.E. Graipel), Museu Nacional Uruguayo de Historia Natural (MNHN) (E.M. Gonzalez) and Museu de Zoologia da Universidade de São Paulo (MZUSP) (M. De Vivo and J.G. Barros) for the authorization and support to specimens access. First author (Jamile de Moura Bubadué) was supported by CAPES with a scholarship, Nilton Cáceres by a CNPq-research fellow. Federico Passaro was supported by the “Tefra DISTAR” program, and the corresponding author (Francesco Carotenuto) by the “STAR” program.

Paolo Colangelo, Anna Loy and one anonymous reviewer provided us with fundamental suggestions on an earlier version of this manuscript.

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Appendix A List of 191 *Cerdocyon thous* specimens belonging to group Allopatric, Gymnocercus or Vetulus, representing 118 localities in South America, used for morphometric analyses, with data on species, sex (F, female; M, male; or unknown), museum number and geographical coordinates.

Group	Sex	Museum number	Latitude	Longitude
Allopatric	F	MHNCI 164	– 22.96	– 53.30
Allopatric	F	MHNCI 5235	– 22.63	– 52.88
Allopatric	Unknown	MHNCI 5786	– 22.63	– 52.88
Allopatric	M	MHNCI 60	– 22.72	– 53.17
Allopatric	F	MN 10987	– 14.80	– 39.03
Allopatric	F	MN 11205	– 14.80	– 39.03
Allopatric	Unknown	MN 25570	– 4.33	– 38.88
Allopatric	M	MN 25577	– 4.33	– 38.88
Allopatric	Unknown	MN 25578	– 4.05	– 40.87
Allopatric	M	MN 25583	– 8.89	– 36.50
Allopatric	F	MN 25584	– 8.89	– 36.50
Allopatric	Unknown	MN 25594	– 22.66	– 42.38
Allopatric	F	MN 25597	– 19.93	– 40.60
Allopatric	M	MN 25598	– 19.48	– 40.48
Allopatric	F	MN 25608	– 8.89	– 36.50
Allopatric	Unknown	MN 32370	– 15.60	– 39.86
Allopatric	F	MN 3885	– 22.96	– 44.04
Allopatric	M	MN 3887	– 22.96	– 44.04
Allopatric	F	MN 42800	– 22.50	– 44.56
Allopatric	Unknown	MN 43968	– 22.96	– 42.03
Allopatric	F	MN 5505	– 23.44	– 45.08
Allopatric	Unknown	MN 63471	– 7.49	– 36.66
Allopatric	Unknown	MN 72784	– 22.37	– 41.78
Allopatric	F	MZUSP 1164	– 24.10	– 49.34
Allopatric	M	MZUSP 1165	– 24.10	– 49.34
Allopatric	F	MZUSP 13797	– 23.02	– 48.01
Allopatric	F	MZUSP 1933	– 20.76	– 51.70
Allopatric	M	MZUSP 1935	– 20.65	– 51.50
Allopatric	M	MZUSP 19741	– 20.87	– 51.61
Allopatric	F	MZUSP 2832	– 21.46	– 49.95
Allopatric	F	MZUSP 2833	– 21.46	– 49.95
Allopatric	F	MZUSP 2835	– 21.46	– 49.95
Allopatric	M	MZUSP 3504	– 14.79	– 39.28
Allopatric	F	MZUSP 3762	– 21.50	– 51.32
Allopatric	F	MZUSP 3763	– 21.50	– 51.32
Allopatric	Unknown	MZUSP 3831	– 12.95	– 38.50
Allopatric	M	MZUSP 4135	– 21.46	– 49.95
Allopatric	M	MZUSP 463	– 22.32	– 49.07
Allopatric	F	MZUSP 486	– 22.32	– 49.07
Allopatric	M	MZUSP 487	– 22.32	– 49.07
Allopatric	M	MZUSP 6636	– 23.29	– 46.59
Allopatric	M	MZUSP 8732	– 4.33	– 38.88
Gymnocercus	Unknown	MCNFZB 423	– 28.64	– 53.61
Gymnocercus	M	MCNFZB 598	– 29.69	– 51.47
Gymnocercus	M	MCP 178	– 30.29	– 51.30
Gymnocercus	F	MHNCI 1077	– 25.39	– 51.46
Gymnocercus	M	MHNCI 132	– 24.79	– 50.01
Gymnocercus	M	MHNCI 1708	– 23.30	– 50.07
Gymnocercus	F	MHNCI 1713	– 25.46	– 49.53
Gymnocercus	M	MHNCI 1714	– 23.30	– 50.07
Gymnocercus	M	MHNCI 1717	– 24.21	– 49.78
Gymnocercus	M	MHNCI 252	– 25.85	– 48.64
Gymnocercus	F	MHNCI 2723	– 24.32	– 50.62
Gymnocercus	M	MHNCI 307	– 24.79	– 50.01
Gymnocercus	M	MHNCI 309	– 24.79	– 50.01

Gymnocercus	M	MHNCI 3401	– 25.50	– 49.34
Gymnocercus	M	MHNCI 3728	– 25.99	– 49.34
Gymnocercus	Unknown	MHNCI 3811	– 25.68	– 54.43
Gymnocercus	F	MHNCI 3826	– 25.68	– 54.43
Gymnocercus	M	MHNCI 3850	– 25.68	– 54.43
Gymnocercus	Unknown	MHNCI 3923	– 25.10	– 50.16
Gymnocercus	M	MHNCI 3925	– 25.57	– 49.39
Gymnocercus	M	MHNCI 3941	– 25.35	– 49.16
Gymnocercus	F	MHNCI 3945	– 25.20	– 53.15
Gymnocercus	Unknown	MHNCI 3948	– 25.84	– 52.03
Gymnocercus	F	MHNCI 3972	– 26.23	– 50.93
Gymnocercus	M	MHNCI 4043	– 25.45	– 49.07
Gymnocercus	F	MHNCI 54	– 25.82	– 48.54
Gymnocercus	M	MHNCI 56	– 25.82	– 48.54
Gymnocercus	M	MHNCI 57	– 25.82	– 48.54
Gymnocercus	M	MHNCI 5706	– 25.44	– 49.97
Gymnocercus	F	MHNCI 6184	– 25.51	– 49.20
Gymnocercus	F	MHNCI 6198	– 25.51	– 49.20
Gymnocercus	Unknown	MN 68361	– 24.32	– 50.62
Gymnocercus	F	MNHN 1055	– 29.68	– 53.81
Gymnocercus	M	MNHN 1119	– 31.70	– 55.97
Gymnocercus	M	MNHN 1140	– 31.70	– 55.97
Gymnocercus	F	MNHN 1254	– 32.84	– 55.90
Gymnocercus	F	MNHN 1287	– 34.52	– 56.28
Gymnocercus	M	MNHN 2420	– 31.73	– 55.98
Gymnocercus	F	MNHN 247	– 34.88	– 54.97
Gymnocercus	Unknown	MNHN 249	– 27.00	– 54.44
Gymnocercus	M	MNHN 251	– 31.73	– 55.98
Gymnocercus	Unknown	MNHN 252	– 31.73	– 55.98
Gymnocercus	Unknown	MNHN 253	– 33.94	– 56.75
Gymnocercus	F	MNHN 2538	– 31.70	– 55.97
Gymnocercus	Unknown	MNHN 2540	– 34.82	– 56.16
Gymnocercus	Unknown	MNHN 255	– 33.40	– 57.54
Gymnocercus	F	MNHN 258	– 31.71	– 55.97
Gymnocercus	F	MNHN 260	– 31.88	– 56.24
Gymnocercus	F	MNHN 262	– 30.95	– 57.52
Gymnocercus	F	MNHN 2643	– 33.23	– 54.36
Gymnocercus	M	MNHN 2645	– 30.65	– 56.59
Gymnocercus	M	MNHN 2646	– 34.88	– 54.97
Gymnocercus	F	MNHN 2649	– 33.55	– 55.71
Gymnocercus	M	MNHN 2650	– 33.55	– 55.71
Gymnocercus	F	MNHN 2651	– 33.55	– 55.71
Gymnocercus	Unknown	MNHN 2680	– 33.93	– 55.68
Gymnocercus	Unknown	MNHN 2695	– 33.53	– 54.94
Gymnocercus	Unknown	MNHN 4716	– 30.91	– 55.55
Gymnocercus	Unknown	MNHN 5478	– 34.72	– 56.07
Gymnocercus	M	MNHN 6260	– 34.55	– 55.94
Gymnocercus	M	MNHN 6262	– 34.55	– 55.94
Gymnocercus	M	MNHN 6273	– 34.55	– 55.94
Gymnocercus	Unknown	MNHN 6410	– 34.40	– 53.79
Gymnocercus	Unknown	MNHN 6437	– 30.91	– 55.55
Gymnocercus	Unknown	MNHN 7111	– 34.80	– 54.91
Gymnocercus	Unknown	MNHN 7352	– 34.80	– 54.91
Gymnocercus	M	MNHN 829	– 31.25	– 56.15
Gymnocercus	F	MNHN 869	– 30.55	– 57.86
Gymnocercus	M	MNHN 954	– 33.80	– 55.53
Gymnocercus	M	MNHN 956	– 31.25	– 56.15
Gymnocercus	F	MNHN 965	– 30.29	– 57.20
Gymnocercus	Unknown	MZUSP 3182	– 28.29	– 53.49
Gymnocercus	Unknown	MZUSP 415	– 31.37	– 51.97

Gymnocercus	M	MZUSP 514	– 31.37	– 51.97
Gymnocercus	M	MZUSP 518	– 31.37	– 51.97
Gymnocercus	Unknown	MZUSP 7149	– 28.29	– 53.49
Gymnocercus	F	UFSC 297	– 27.96	– 48.68
Gymnocercus	F	UFSC 298	– 27.56	– 48.49
Gymnocercus	F	UFSC 348	– 27.57	– 48.98
Gymnocercus	M	UFSC 3791	– 27.40	– 51.23
Gymnocercus	F	UFSC 576	– 27.90	– 49.13
Gymnocercus	Unknown	UFSC 762	– 26.12	– 50.31
Gymnocercus	F	UFSC 773	– 27.48	– 48.53
Gymnocercus	M	UFSC 850	– 27.44	– 48.47
Vetulus	Unknown	MN 25005	– 18.54	– 53.12
Vetulus	F	MN 25589	– 20.72	– 46.61
Vetulus	F	MN 25590	– 20.72	– 46.61
Vetulus	M	MN 25591	– 20.72	– 46.61
Vetulus	Unknown	MN 25606	– 21.23	– 57.13
Vetulus	Unknown	MN 25607	– 21.23	– 57.13
Vetulus	Unknown	MN 25612	– 16.33	– 48.96
Vetulus	Unknown	MN 25683	– 14.67	– 52.35
Vetulus	M	MN 29061	– 14.76	– 43.93
Vetulus	M	MN 29062	– 14.76	– 43.93
Vetulus	Unknown	MN 3036	– 19.28	– 44.41
Vetulus	F	MN 4242	– 19.63	– 43.89
Vetulus	M	MN 4243	– 19.63	– 43.89
Vetulus	Unknown	MN 46810	– 15.48	– 43.60
Vetulus	F	MN 4891	– 16.33	– 48.96
Vetulus	Unknown	MN 4908	– 21.62	– 55.17
Vetulus	Unknown	MN 63491	– 8.84	– 42.50
Vetulus	Unknown	MN 63517	– 9.01	– 42.70
Vetulus	M	MN 71092	– 14.67	– 52.35
Vetulus	Unknown	MN 75981	– 8.33	– 42.31
Vetulus	M	MNHN 706	– 21.72	– 57.89
Vetulus	F	MNHN 707	– 21.72	– 57.89
Vetulus	Unknown	MZUSP 19738	– 19.54	– 54.05
Vetulus	M	MZUSP 19742	– 13.51	– 48.36
Vetulus	M	MZUSP 19757	– 10.47	– 40.18
Vetulus	Unknown	MZUSP 19847	– 16.26	– 56.62
Vetulus	M	MZUSP 2594	– 10.47	– 40.18
Vetulus	F	MZUSP 2595	– 10.47	– 40.18
Vetulus	M	MZUSP 2596	– 10.47	– 40.18
Vetulus	F	MZUSP 2598	– 10.47	– 40.18
Vetulus	F	MZUSP 2599	– 10.47	– 40.18
Vetulus	M	MZUSP 2600	– 10.47	– 40.18
Vetulus	M	MZUSP 2601	– 10.47	– 40.18
Vetulus	F	MZUSP 2602	– 10.47	– 40.18
Vetulus	M	MZUSP 2834	– 21.46	– 49.95
Vetulus	M	MZUSP 2917	– 20.55	– 47.41
Vetulus	M	MZUSP 2918	– 20.55	– 47.41
Vetulus	F	MZUSP 2919	– 20.55	– 47.41
Vetulus	M	MZUSP 3031	– 17.34	– 44.92
Vetulus	M	MZUSP 3032	– 17.34	– 44.92
Vetulus	M	MZUSP 3033	– 17.34	– 44.92
Vetulus	F	MZUSP 3034	– 17.34	– 44.92
Vetulus	M	MZUSP 3038	– 17.75	– 44.37
Vetulus	F	MZUSP 3039	– 17.34	– 44.92
Vetulus	F	MZUSP 3042	– 17.34	– 44.92
Vetulus	M	MZUSP 3043	– 17.34	– 44.92
Vetulus	F	MZUSP 3098	– 17.34	– 44.92
Vetulus	M	MZUSP 3101	– 17.34	– 44.92
Vetulus	F	MZUSP 3104	– 17.34	– 44.92

Vetulus	M	MZUSP 3372	– 19.01	– 57.66
Vetulus	M	MZUSP 3373	– 19.01	– 57.66
Vetulus	Unknown	MZUSP 34772	– 19.12	– 51.74
Vetulus	Unknown	MZUSP 34775	– 19.12	– 51.74
Vetulus	Unknown	MZUSP 34776	– 19.12	– 51.74
Vetulus	M	MZUSP 3777	– 20.24	– 56.36
Vetulus	M	MZUSP 4215	– 13.51	– 48.36
Vetulus	M	MZUSP 4216	– 13.51	– 48.36
Vetulus	M	MZUSP 4217	– 13.39	– 46.33
Vetulus	M	MZUSP 4219	– 13.51	– 48.36
Vetulus	M	MZUSP 4220	– 15.46	– 44.32
Vetulus	F	MZUSP 4221	– 13.51	– 48.36
Vetulus	M	MZUSP 6314	– 15.60	– 56.09
Vetulus	M	MZUSP 6315	– 15.60	– 56.09
Vetulus	Unknown	MZUSP 6640	– 17.79	– 50.92
Vetulus	Unknown	UFSC 3728	– 19.21	– 57.65

Appendix B List of *Lycalopex* specimens belonging to either the species *Lycalopex gymnocercus* (58) or *Lycalopex vetulus* (28), used for morphometric analyses (only centroid size), with data on species, sex (F, female; M, male; or unknown) and museum number.

Species	Sex	Museum number
Lycalopex gymnocercus	M	MCNFZB 488
Lycalopex gymnocercus	Unknown	MCP 168
Lycalopex gymnocercus	Unknown	MCP 618
Lycalopex gymnocercus	M	MHNCI 229
Lycalopex gymnocercus	F	MHNCI 231
Lycalopex gymnocercus	M	MHNCI 234
Lycalopex gymnocercus	M	MHNCI 3020
Lycalopex gymnocercus	F	MHNCI 532
Lycalopex gymnocercus	M	MHNCI 55
Lycalopex gymnocercus	F	MHNCI 5583
Lycalopex gymnocercus	F	MHNCI 59
Lycalopex gymnocercus	M	MHNCI 61
Lycalopex gymnocercus	Unknown	MN 2355
Lycalopex gymnocercus	M	MNHN 1014
Lycalopex gymnocercus	Unknown	MNHN 1071
Lycalopex gymnocercus	Unknown	MNHN 1082
Lycalopex gymnocercus	F	MNHN 1091
Lycalopex gymnocercus	F	MNHN 1111
Lycalopex gymnocercus	M	MNHN 1112
Lycalopex gymnocercus	Unknown	MNHN 1144
Lycalopex gymnocercus	Unknown	MNHN 1217
Lycalopex gymnocercus	Unknown	MNHN 1218
Lycalopex gymnocercus	Unknown	MNHN 1219
Lycalopex gymnocercus	M	MNHN 1939
Lycalopex gymnocercus	M	MNHN 1940
Lycalopex gymnocercus	F	MNHN 263
Lycalopex gymnocercus	M	MNHN 2638
Lycalopex gymnocercus	M	MNHN 2648
Lycalopex gymnocercus	F	MNHN 268
Lycalopex gymnocercus	F	MNHN 269
Lycalopex gymnocercus	Unknown	MNHN 2699
Lycalopex gymnocercus	F	MNHN 270
Lycalopex gymnocercus	F	MNHN 271
Lycalopex gymnocercus	M	MNHN 273
Lycalopex gymnocercus	Unknown	MNHN 274
Lycalopex gymnocercus	Unknown	MNHN 275
Lycalopex gymnocercus	Unknown	MNHN 276
Lycalopex gymnocercus	F	MNHN 278
Lycalopex gymnocercus	Unknown	MNHN 281
Lycalopex gymnocercus	Unknown	MNHN 282
Lycalopex gymnocercus	Unknown	MNHN 3125
Lycalopex gymnocercus	M	MNHN 3170
Lycalopex gymnocercus	M	MNHN 3171
Lycalopex gymnocercus	F	MNHN 3172
Lycalopex gymnocercus	F	MNHN 5476
Lycalopex gymnocercus	F	MNHN 6272
Lycalopex gymnocercus	Unknown	MNHN 6280
Lycalopex gymnocercus	Unknown	MNHN 712
Lycalopex gymnocercus	F	MNHN 713
Lycalopex gymnocercus	M	MNHN 881
Lycalopex gymnocercus	M	MNHN 949
Lycalopex gymnocercus	M	MNHN 950
Lycalopex gymnocercus	F	MNHN 953
Lycalopex gymnocercus	F	MNHN 966
Lycalopex gymnocercus	Unknown	MZUSP 651

Lycalopex gymnocercus	Unknown	MZUSP 653
Lycalopex gymnocercus	Unknown	UFSC 329
Lycalopex gymnocercus	F	UFSC 4592
Lycalopex vetulus	Unknown	MN 3037
Lycalopex vetulus	M	MN 3039
Lycalopex vetulus	Unknown	MN 3040
Lycalopex vetulus	Unknown	MN 3044
Lycalopex vetulus	F	MN 4241
Lycalopex vetulus	M	MN 4909
Lycalopex vetulus	F	MN 5151
Lycalopex vetulus	Unknown	MN 651
Lycalopex vetulus	Unknown	MN 655
Lycalopex vetulus	Unknown	MN 656
Lycalopex vetulus	M	MN 68180
Lycalopex vetulus	M	MN 71039
Lycalopex vetulus	M	MN 71045
Lycalopex vetulus	Unknown	MN 71047
Lycalopex vetulus	Unknown	MN 71093
Lycalopex vetulus	F	MN 71112
Lycalopex vetulus	Unknown	MN 71173
Lycalopex vetulus	F	MZUSP 1011
Lycalopex vetulus	Unknown	MZUSP 1012
Lycalopex vetulus	F	MZUSP 1015
Lycalopex vetulus	M	MZUSP 1016
Lycalopex vetulus	F	MZUSP 1018
Lycalopex vetulus	M	MZUSP 1084
Lycalopex vetulus	M	MZUSP 3046
Lycalopex vetulus	Unknown	MZUSP 3047
Lycalopex vetulus	M	MZUSP 3048
Lycalopex vetulus	F	MZUSP 3050
Lycalopex vetulus	F	MZUSP 825

Appendix C Results of Variation Partitioning tests.

Variation partitioning using *Cerdocyon* LnCS as Y

Explanatory tables:
X1: *Cerdocyon* sympatric populations
X2: sampling locality latitude
X3: 19 bioclimatic variables
X4: *Lycalopex* species LnCS

	Df	R.square	Adj.R.square	Testable	p-value
[aeghklno]=X1	1	0.00133	-0.02189	TRUE	0.819
[befiklmo]=X2	1	0.12552	0.10518	TRUE	0.023
[cfgjlmno]=X3	18	0.64273	0.39539	TRUE	0.016
[dhijkmno]=X4	1	0.07322	0.05167	TRUE	0.049
[abefghiklmno]=X1+X2	3	0.3895	0.36043	TRUE	0.001
[acefghjklmno]=X1+X3	20	0.68955	0.45361	TRUE	0.006
[adeghijklmno]=X1+X4	3	0.37655	0.34686	TRUE	0.001
[bcefgijklmno]=X2+X3	19	0.66592	0.41202	TRUE	0.017
[bdefhijklmno]=X2+X4	2	0.13569	0.09453	TRUE	0.046
[cdfghijklmno]=X3+X4	19	0.64275	0.37124	TRUE	0.024
[abcefghijklmno]=X1+X2+X3	21	0.69215	0.4356	TRUE	0.012
[abdefghijklmno]=X1+X2+X4	4	0.45584	0.41603	TRUE	0.001
[acdefghijklmno]=X1+X3+X4	21	0.69807	0.44647	TRUE	0.012
[bcdefghijklmno]=X2+X3+X4	20	0.6685	0.39224	TRUE	0.014
[abcdefghijklmno]=All	22	0.70272	0.43129	TRUE	0.019
Individual fractions					
[a]=X1°|°X2+X3+X4	2		0.03905	TRUE	0.117
[b]=X2°|°X1+X3+X4	1		-0.01517	TRUE	0.535
[c]=X3°|°X1+X2+X4	18		0.01527	TRUE	0.452
[d]=X4°|°X1+X2+X3	1		-0.00431	TRUE	0.377
[e]	0		0.03617	FALSE	
[f]	0		0.08434	FALSE	
[g]	0		0.28245	FALSE	
[h]	0		-0.01547	FALSE	
[i]	0		-0.00283	FALSE	
[j]	0		0.05991	FALSE	
[k]	0		-0.00154	FALSE	
[l]	0		-0.06248	FALSE	
[m]	0		0.31599	FALSE	
[n]	0		-0.05079	FALSE	
[o]	0		-0.24929	FALSE	
[p]=Residuals	0		0.03617	FALSE	
Controlling table X					
[ae]=X1°|°X3+X4	2		0.07522	TRUE	0.059
[ag]=X1°|°X2+X4	2		0.3215	TRUE	0.001

[ah]=X1°|°X2+X3	2	0.02358	TRUE	0.165
[be]=X2°|°X3+X4	1	0.021	TRUE	0.169
[bf]=X2°|°X1+X4	1	0.06916	TRUE	0.017
[bi]=X2°|°X1+X3	1	-0.018	TRUE	0.631
[cf]=X3°|°X1+X4	18	0.0996	TRUE	0.215
[cg]=X3°|°X2+X4	18	0.29772	TRUE	0.047
[cj]=X3°|°X1+X2	18	0.07517	TRUE	0.265
[dh]=X4°|°X2+X3	1	-0.01978	TRUE	0.664
[di]=X4°|°X1+X3	1	-0.00714	TRUE	0.442
[dj]=X4°|°X1+X2	1	0.0556	TRUE	0.043
Controlling table X				
[aghn]=X1°|°X2	2	0.07522	TRUE	0.001
[aehk]=X1°|°X3	2	0.3215	TRUE	0.072
[aegl]=X1°|°X4	2	0.02358	TRUE	0.001
[bfim]=X2°|°X1	1	0.021	TRUE	0.001
[beik]=X2°|°X3	1	0.06916	TRUE	0.191
[befl]=X2°|°X4	1	-0.018	TRUE	0.081
[cfjm]=X3°|°X1	18	0.0996	TRUE	0.006
[cgjn]=X3°|°X2	18	0.29772	TRUE	0.021
[cfgl]=X3°|°X4	18	0.07517	TRUE	0.031
[dijm]=X4°|°X1	1	-0.01978	TRUE	0.001
[dhjn]=X4°|°X2	1	-0.00714	TRUE	0.45
[dhik]=X4°|°X3	1	0.0556	TRUE	0.972

Variation partitioning using *Cerdocyon* shape variables as Y

Explanatory tables:

X1: *Cerdocyon* sympatric populations

X2: sampling locality latitude

X3: 19 bioclimatic variables

X4: *Lycalopex* species LnCS

	Df	R.square	Adj.R.square	Testable	p-value
[aeghklno]=X1	2	0.04225	0.01997	TRUE	0.046
[befiklmo]=X2	1	0.11962	0.09915	TRUE	0.001
[cfgjlmno]=X3	18	0.50376	0.16021	TRUE	0.008
[dhijkmno]=X4	1	0.07131	0.04971	TRUE	0.001
[abefghiklmno]=X1+X2	3	0.17432	0.135	TRUE	0.001
[acefghjklmno]=X1+X3	20	0.52825	0.16972	TRUE	0.002
[adeghijklmno]=X1+X4	3	0.11912	0.07718	TRUE	0.002
[bcefgijklmno]=X2+X3	19	0.52361	0.16155	TRUE	0.006
[bdefhijklmno]=X2+X4	2	0.15623	0.11605	TRUE	0.001
[cdfghijklmno]=X3+X4	19	0.53393	0.17971	TRUE	0.001
[abcefghijklmno]=X1+X2+X3	21	0.54414	0.16425	TRUE	0.004
[abdefghijklmno]=X1+X2+X4	4	0.20688	0.14884	TRUE	0.001
[acdefghijklmno]=X1+X3+X4	21	0.54832	0.17192	TRUE	0.004
[bcdefghijklmno]=X2+X3+X4	20	0.54841	0.17209	TRUE	0.006

[abcdefghijklmno]=All	22	0.56351	0.16497	TRUE	0.01
Individual fractions					
[a]=X1°|°X2+X3+X4	1		-0.00712	TRUE	0.619
[b]=X2°|°X1+X3+X4	1		-0.00695	TRUE	0.612
[c]=X3°|°X1+X2+X4	18		0.01613	TRUE	0.379
[d]=X4°|°X1+X2+X3	1		0.00072	TRUE	0.373
[e]	0		-0.00068	FALSE	
[f]	0		0.07861	FALSE	
[g]	0		0.03991	FALSE	
[h]	0		0.00982	FALSE	
[i]	0		0.00148	FALSE	
[j]	0		0.01312	FALSE	
[k]	0		0.00748	FALSE	
[l]	0		-0.00465	FALSE	
[m]	0		0.04189	FALSE	
[n]	0		-0.00676	FALSE	
[o]	0		-0.01804	FALSE	
[p]=Residuals	0		0.83503	FALSE	
Controlling table X					
[ae]=X1°|°X3+X4	2		-0.00779	TRUE	0.654
[ag]=X1°|°X2+X4	2		0.03279	TRUE	0.01
[ah]=X1°|°X2+X3	2		0.0027	TRUE	0.373
[be]=X2°|°X3+X4	1		-0.00762	TRUE	0.656
[bf]=X2°|°X1+X4	1		0.07167	TRUE	0.001
[bi]=X2°|°X1+X3	1		-0.00547	TRUE	0.565
[cf]=X3°|°X1+X4	18		0.09474	TRUE	0.045
[cg]=X3°|°X2+X4	18		0.05604	TRUE	0.141
[cj]=X3°|°X1+X2	18		0.02925	TRUE	0.27
[dh]=X4°|°X2+X3	1		0.01054	TRUE	0.216
[di]=X4°|°X1+X3	1		0.00219	TRUE	0.358
[dj]=X4°|°X1+X2	1		0.01384	TRUE	0.082
Controlling table X					
[aghn]=X1°|°X2	2		0.03586	TRUE	0.011
[aehk]=X1°|°X3	2		0.00951	TRUE	0.216
[aegl]=X1°|°X4	2		0.02746	TRUE	0.025
[bfim]=X2°|°X1	1		0.11503	TRUE	0.001
[beik]=X2°|°X3	1		0.00134	TRUE	0.378
[befl]=X2°|°X4	1		0.06634	TRUE	0.002
[cfjm]=X3°|°X1	18		0.14975	TRUE	0.008
[cgjn]=X3°|°X2	18		0.0624	TRUE	0.118
[cfgl]=X3°|°X4	18		0.13	TRUE	0.01
[dijm]=X4°|°X1	1		0.0572	TRUE	0.001
[dhjn]=X4°|°X2	1		0.0169	TRUE	0.051
[dhik]=X4°|°X3	1		0.0195	TRUE	0.11

Variation partitioning using shape variables of only "gymnocercus" group as Y

Explanatory tables:

X1: Sampling locality latitude

X2: 19 bioclimatic variables

X3: Lycalopex species LnCS

	Df	R.square	Adj.R.square	Testable	p-value
[a+d+f+g]=X1	1	0.16399	0.13866	TRUE	0.001
[b+d+e+g]=X2	18	0.61789	0.18802	TRUE	0.01
[c+e+f+g]=X3	1	0.12119	0.09456	TRUE	0.002
[a+b+d+e+f+g]=X1+X2	19	0.6462	0.19804	TRUE	0.013
[a+c+d+e+f+g]=X1+X3	2	0.19059	0.14	TRUE	0.001
[b+c+d+e+f+g]=X2+X3	19	0.63521	0.17315	TRUE	0.026
[a+b+c+d+e+f+g]=All	20	0.66494	0.18628	TRUE	0.027
Individual fractions					
[a]=X1°|°X2+X3	1		0.01313	TRUE	0.264
[b]=X2°|°X1+X3	18		0.04628	TRUE	0.27
[c]=X3°|°X1+X2	1		-0.01176	TRUE	0.604
[d]	0		0.03232	FALSE	
[e]	0		0.01311	FALSE	
[f]	0		-0.0031	FALSE	
[g]	0		0.09632	FALSE	
[h]=Residuals			0.81372	FALSE	
Controlling table X					
[a+d]=X1°|°X3	1		0.04544	TRUE	0.009
[a+f]=X1°|°X2	1		0.01002	TRUE	0.284
[b+d]=X2°|°X3	18		0.07859	TRUE	0.153
[b+e]=X2°|°X1	18		0.05939	TRUE	0.216
[c+e]=X3°|°X1	1		0.00135	TRUE	0.351
[c+f]=X3°|°X2	1		-0.01487	TRUE	0.703

Appendix D Spatial autocorrelation table. Results are separated between all the sample and only sex determined sample individuals. Significance is highlighted.

All the sample						
D.Class	Count	DistCntr	Moran's I	P value	I (max)	I/I(max)
1	2350	136.325	0.31	**0.005**	0.967	0.32
2	4534	408.974	0.177	**0.005**	0.457	0.387
3	5016	681.624	0.044	**0.025**	0.402	0.11
4	5994	954.273	-0.073	**0.005**	0.523	-0.14
5	4978	1226.923	-0.068	**0.005**	0.607	-0.112
6	3790	1499.572	0.053	**0.05**	0.619	0.085
7	2600	1772.222	0.086	**0.015**	1.121	0.076
8	2660	2044.871	0.077	**0.02**	1.005	0.077
9	1550	2317.521	-0.02	0.588	1.436	-0.014
10	910	2590.17	-0.148	**0.025**	1.61	-0.092
11	826	2862.819	-0.797	**0.005**	2.488	-0.32
12	630	3135.469	-0.87	**0.005**	2.618	-0.332
13	314	3408.118	-1.046	**0.005**	4.326	-0.242
14	196	3680.768	-1.074	**0.005**	5.521	-0.194
Expected:	-0.005					
Only sex determined						
D.Class	Count	DistCntr	Moran's I	P	I (max)	I/I(max)
1	1632	145.964	0.225	**0.005**	0.88	0.256
2	3046	437.892	0.121	**0.005**	0.488	0.248
3	2724	729.82	-0.04	0.09	0.507	-0.079
4	3706	1021.748	-0.068	**0.005**	0.517	-0.131
5	2734	1313.677	-0.034	0.151	0.685	-0.05
6	1752	1605.605	0.018	0.497	0.822	0.022
7	1464	1897.533	0.087	**0.025**	1.212	0.072
8	1226	2189.461	0.023	0.457	1.212	0.019
9	554	2481.389	-0.141	**0.03**	1.703	-0.083
10	412	2773.317	-0.59	**0.005**	2.587	-0.228
11	248	3065.245	-0.7	**0.005**	2.892	-0.242
12	154	3357.173	-0.962	**0.005**	5.346	-0.18
13	84	3649.102	-0.73	**0.005**	7.799	-0.094
Expected:	-0.007					

CAPÍTULO II

Cerdocyon thous skull, MHNCI 3923

Ecogeographical variation in skull shape of South-American canids: abiotic or biotic processes?

Evolutionary Biology (2015), doi: 10.1007/s11692-015-9362-3

Ecogeographical variation in skull shape of South-American canids: abiotic or biotic processes?

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ABSTRACT

Species morphological changes can be mutually influenced by environmental or biotic factors, such as competition. South American canids represent a quite recent radiation of taxa that evolved forms very disparate in phenotype, ecology and behaviour. Today, in the central part of South America there is one dominant large species (the maned wolf, *Chrysocyon brachyurus*) that directly influence sympatric smaller taxa via interspecific killing. Further south, three species of similar sized foxes (*Lycalopex* spp.) share the same habitats. Such unique combination of taxa and geographic distribution makes South American dogs an ideal group to test for the simultaneous impact of climate and competition on phenotypic variation. Using geometric morphometrics, we quantified skull size and shape of 431 specimens belonging to the eight extant South American canid species: *Atelocynus microtis*, *Cerdocyon thous*, *Chrysocyon brachyurus*, *Lycalopex culpaeus*, *L. griseus*, *L. gymnocercus*, *L. vetulus* and *Speothos venaticus*. South American canids are significantly different in both skull size and shape. The hypercarnivorous bush dog is mostly distinct in shape from all the other taxa while a degree of overlap in shape – but not size – occurs between species of the genus *Lycalopex*. Both climate and competition impacts interspecific morphological variation. We identified climatic adaptions as the main driving force of diversification for the South American canids. Competition has a lower degree of impact on their skull morphology although it might have played a role in the past, when canid community was richer in morphotypes.

Key-words Canidae, Carnivora, climatic adaptations, geographic clines, interspecific competition, macroecology.

INTRODUCTION

Understanding species community assembly is one of the central aims of macroecology (Rosenzwig 1995). For instance, on one side, we expect abiotic forces, such as climate and geographical barriers, to apply filters influencing species distribution and community composition. On the other side, biotic competition might produce unexpectedly stable species assemblages. Such balancing forces are clearly not mutually exclusive and we have strong evidence that the majority of animal groups tend to be quite resilient and less sensitive to abiotic forces than expected by theory (Vrba 1993). In this regards, members of the mammalian order Carnivora received particular attention for being endothermic, ecologically diverse and secondary consumers (Goswami 2010). The red fox (*Vulpes vulpes*), for instance, is the commonest species to provide evidence for the impact of climate on phenotypes, particularly in skull size, which varies with latitude (Churcher 1960; Davis 1977; Cavallini 1995; Yom-Tov and Geffen 2006; Meiri et al. 2007; Yom-Tov et al. 2007; Szuma 2008). Other lines of investigations on carnivorans' skull took direct competition into account for explaining carnivoran assembly rules (Dayan et al. 1989; 1992; Dayan and Simberloff 2005; Meiri et al. 2011).

Carnivora generally exhibit broad range of ecological and phenotypic variation accompanied by behavioural attributes (e.g. predatory/killing behaviour) that makes them particularly sensible to biotic processes (Palomares and Caro 1999; Donadio and Burskik 2006). Here we use South-American canids as model species to test the hypothesis that climate and competition might have a direct impact on species morphological variation at broad geographical scale. South-American canids represent a recent radiation due to their late Pliocene colonization from a restricted pool of North American taxa (Berta 1987; Prevosti 2010; Perini et al., 2010; Wang et al. 2008). Despite this, South America holds more than 10 living canid species, being the largest extant regional diversity found in the world (Prevosti et al. 2009a; Perini et al. 2010; Sillero-Zubiri et al. 2004). Its endemic taxa includes species with a broad diversity of body size and feeding ecology such as the large (average mass = 25 kg) omnivorous maned wolf *Chrysocyon brachyurus* (Illiger, 1815) and the small (mass ranging 5-8 kg) hypercarnivorous bush dog *Speothos venaticus* (Lund, 1842) (Sillero-Zubiri et al. 2004).

Diversity of fox-like ecomorphs is also broad including species such as the widely distributed crab-eating fox (*Cerdocyon thous*) and the four species of *Lycalopex* that share to some extent geographic range, especially in Argentina, and omnivorous feeding habits. Such a high diversity was even higher during the prehistory (Prevosti 2010; Perini et al. 2010) with larger carnivorous wolflike forms possibly influencing ecology and distribution of smaller taxa.

Currently we have direct evidence on the impact of competition on ecology and behaviour of extant South-American canids. Di Bitetti et al. (2009) recorded patterns of behavioural shift by *Lycalopex gymnocercus* due to competition with *C. thous*. In sympatry, *L. gymnocercus* changes its normal activity to prevent confrontation with the larger *C. thous*. Also, interspecific killing occurs quite intensively, with large taxa, such as *C. brachyurus*, generally controlling densities and behaviour of smaller species (Donadio and Buskirk 2006; Oliveira and Pereira 2014).

Skulls of South-American wild dogs received reasonable attention to clarify patterns of growth and taxonomy (Segura and Prevosti 2012; Segura 2013), paleobiological and ecological adaptations (Prevosti et al. 2005; Prevosti et al. 2009a; b), and more recently climatic impact (Machado and Hingst-Zaher 2009; Martinez et al. 2013), but little is known about the impact of competition on their intra and interspecific variation. Wayne et al. (1989) identified high degree of morphological divergence between South-American foxes in spite of their relatively short time of divergence (less than 250,000 years) and we might expect this to occur even strongly when larger taxa are included.

By focusing our investigation on both climate and competition, we aim to provide a fully comprehensive framework to interpret skull morphology of the extant South-American canids at broad, continental scale. We opted to quantify skull size and shape by using geometric morphometrics as a good proxy for phenotypic variation at broad geographical scale (see also Cacéres et al. 2014; Meloro et al. 2014a; b). This method was favoured among others because it allows direct and independent visualizations of size and shape patterns together with higher statistical power with reasonably large sample sizes (Adams et al. 2004; 2013).

More specifically our aim is to test the following hypotheses:

1. South American canids differ in both skull size and shape;
2. Size influences shape differences between species;
3. Skull shape and size co-vary with climatic variables and degree of competition across species;
4. Species follow distinct phenotypic patterns of skull shape changes in relation to broad environmental variables or to different degrees of competition.

Hypotheses 1 concerns the biological paradigm of interspecific differentiation and functional convergence. Functional convergence in the skull of carnivorans has been very often detected in relation to extreme feeding adaptations (e.g. durophagy, Figueirido et al. 2011; 2013 or solitary hunting, Meloro et al. 2015a). Meloro (2011), Meloro and Raia (2010) and Meloro and O'Higgins (2011) identified morphological similarities also between omnivores (i.e., canids and viverrids) and we might expect some overlap between South-American taxa with similar diet. Hypothesis 2 relates to the recent finding by Cáceres et al. (2014) and Meloro et al. (2014a; b) on geographical variation of capuchin and howler monkeys: in these cases a significant allometric component was detected also across geographic localities so that skull shape differences were mostly influenced by size.

Hypotheses 3 and 4 relates to ecogeographical pattern generally identifiable in the mammalian skull (Cardini et al. 2007). If abiotic forces are more relevant to regulate canid community assembly we might expect stronger co-variation between skull morphology and climate then between skull morphology and competition. The opposite might occur if biotic forces are more relevant.

MATERIALS AND METHODS

Raw data and geometric morphometrics

Our sample includes skull pictures in ventral view of 431 wild-caught adult canid specimens of South America (Online Resource). For each specimen we recorded the geographic coordinates of its collection locality resulting in 262 different localities covering seven countries (Fig. 1, see also Table 1).

Skull pictures were taken at fixed distance (two meters). This procedure standardizes the sample of digital images and minimizes deformation due to the lenses (as in Meloro et al. 2008). When taking pictures, we set up a scale bar adjacent to the specimen in order to transform digital pixels in linear measurements (Zelditch et al. 2004).

Ventral view was chosen because the palate of canids is relatively flat and the teeth can be individually recognized. Digital photographs were landmarked by one of us (JMB) using the tpsDig2 ver. 2.16 (Rohlf 2015). Landmarking by only one investigator allowed to minimize inter-observer error and repeated sessions on 10 random specimens were taken to assess landmark repeatability (Cardini and Tongiorgi 2003; Meloro 2011; Meloro et al. 2014a).

In order to describe effectively craniodental morphology, we digitized twenty-nine homologous landmarks (Fig. 2). The landmarks recorded the overall skull shape, zygomatic arch, rostrum (palate), auditory bulla, and position and size of the teeth, being all features generally related to feeding adaptations in Carnivora and Canidae (Schutz et al. 2009; Segura and Prevosti 2012; Meloro et al. 2015b).

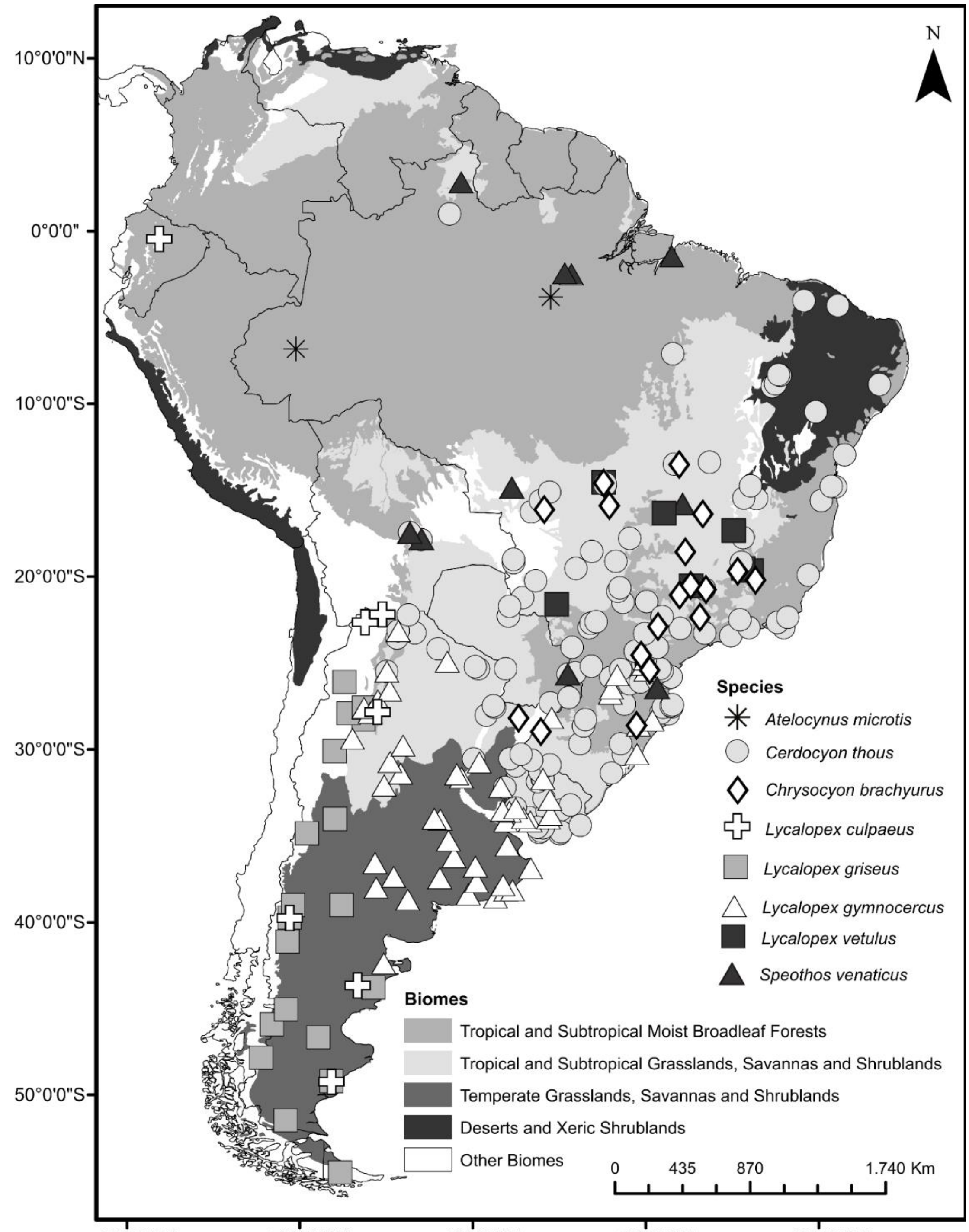

Figure 1. Map of South America showing the geographic distribution of canid skull specimens. Sampling localities of different species are shown by different symbols.

Table 1. Skull sample size for the eight species of canids included in this study.

Species	# specimens	# females	# males	Undet
Atelocynus microtis (Sclater, 1882)	4	1	3	0
Cerdocyon thous (Linnaeus, 1766)	227	71	94	62
Chrysocyon brachyurus (Illiger, 1815)	25	5	7	13
Lycalopex culpaeus (Molina, 1782)	13	5	4	4
Lycalopex griseus (Gray, 1837)	32	9	4	19
Lycalopex gymnocercus (Fischer, 1814)	99	38	28	33
Lycalopex vetulus (Lund, 1842)	16	7	5	4
Speothos venaticus (Lund, 1842)	15	3	10	2
Total	431	139	155	137

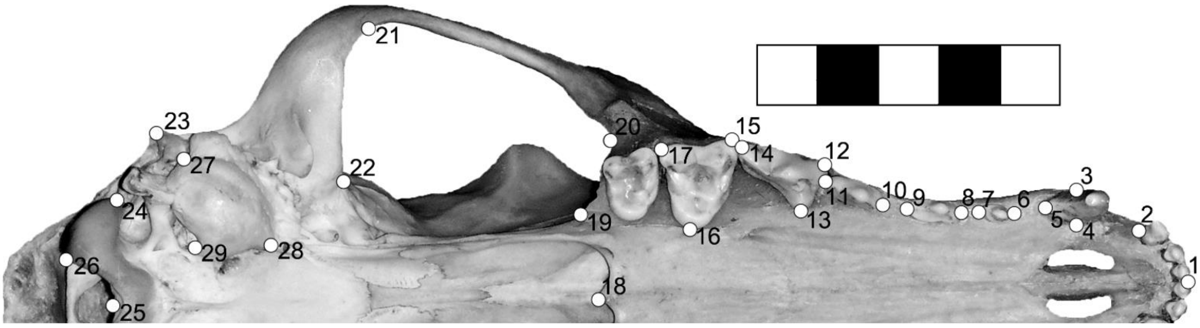

Figure 2. Disposition of 29 landmarks on a skull of *Chrysocyon brachyurus* specimen. 1 = midpoint of central incisors; 2 = posterior-most point of lateral incisor alveolus; 3-5 = canine area; 6-7 = first pre-molar length; 8-9 = second pre-molar length; 10-11 = third pre-molar length; 12-14 = fourth pre-molar (carnassial) area; 15-17 = first molar area; 18=most posterior tip of the palatine; 19-22 = zygomatic arch area; 23 = tip of paracondylar process; 24-26 = occipital condyle area; 27-29 = auditory bulla area.

Generalized Procrustes Analysis (GPA, Rohlf and Slice 1990) allowed us to remove from the original landmark coordinates differences in size, position and orientation. This procedure transforms raw landmarks coordinates into shape variables: the procrustes coordinates. The GPA coordinates were projected into a weight matrix to characterize shape using non-affine (Partial Warps) and affine (uniform) components of thin plate spline. A principal component analysis of the weight matrix (= Relative Warp analysis, RWA) allowed us to visualize shape changes of each specimen relative to the mean shape (Zelditch et al. 2004). Skull size was directly extrapolated from raw landmark coordinates using the centroid size (Rohlf 2000). We used the software tpsRelw version 1.49 (Rohlf 2015) to compute GPA, extract the weight matrix, and to compute a Relative Warp Analysis.

Statistical analyses

Taxonomy and sexual dimorphism

To prevent pseudoreplication and have better estimation of shape and size in each locality, we used the average values of our geometric morphometric results per locality and sex in all statistical analyses (Cardini et al. 2007; Cáceres et al. 2014).

We used ANOVA and MANOVA to test if canid species, used as factor named “taxonomy”, differ in skull size and shape. Sex was also included as factor in the models where taxonomy and sex were tested for interaction (Cardini and Elton 2008). Scores of a selection of Relative Warp axes that explained at least 95% of variance were included as dependent variables in the MANOVA models to reduce degrees of freedom in relation to sample size of particularly small groups (Meloro and O’Higgins 2011).

Allometry

In order to quantify the allometric effects on our sample, we used the natural log transformed centroid size (= lnCS) in all the analyses as an independent variable. The strength of allometric signal was tested separately in the whole (N = 461) and in the locality averaged sample (N = 262) of skulls using MorphoJ (Klingenberg 2011) by performing a multivariate regression of lnCS on skull shape (cf. Cáceres et al. 2014; Meloro et al. 2014a, b). Together with global allometry (that assumes no difference in slope occurs between species subgroups) we also tested for allometry using pooled regression within subgroups (Klingenberg 1996). Using the R environment, version 2.8.1 (R Development Core Team 2013) and the package geomorph (Adams and Otarola-Castillo 2013) we tested for differences in allometric slope between species by running an ANOVA model with interaction using shape (as procrustes distances) as dependent variable, ln CS as covariate and species as factor. We run 9,999 permutations to validate reliability of the P value. Additionally, the global and locality averaged skull sample were subdivided into single species dataset in order to identify the strength of allometry in different taxa and link these results to taxon-specific variation partitioning models (see below).

Ecogeographical variation

To test for the impact of geography on skull shape we employed each specimen collection locality to extract nineteen bioclimatic variables with a resolution of 10’ from the WorldClim raster database (Hijmans et al. 2005) by using the DIVA-GIS 7.5 software (http://www.diva-gis.org/download).

Two block Partial Least Squares (=PLS; Rohlf and Corti 2000) was applied using tpsPLS v.1.18 (Rohlf 2015) to test the relationship between climate and skull shape. PLS extracts vectors from the correlation matrix of each block so that the degree of co-variation between one block and the other is maximized (Rohlf and Corti 2000). In MorphoJ (Klingenberg 2011), we also employed PLS to test the correlation between size (lnCS) and the 19 bioclimatic variables. Although this procedure generates only one pair of vectors, it allows performing comparisons with PLS vectors obtained for shape (see Meloro and Jones 2012).

Competition

To identify the possible impact of competition on skull shape and size we ascribed to each geographic locality the presence/absence of distinct canid species that were characterized according to their diet, body mass, and biome preference (Sillero-Zubiri et al. 2004).

For each focal species recorded at a certain locality we recorded the number of canid taxa that could potentially interact with it due to dietary adaptation, habitat preference and body size. For each locality we recorded the number of canids with the same diet and habitat and standardized these values for the total number of species potentially present. Index for assessing the potential of interspecific killing (here named body size factor) was computed through Donadio and Burskirk (2006) arcsine square root of BSC defined as the body size difference for each species pair, which is calculated through the equation BSD $= (Mb_l - Mb_s)/Mb_l$, where Mb_l is the mass of the larger species and Mb_s the mass of the smaller one. If the result of arcsine $\sqrt{BSD}$ was between 2 to 5.4, than we could consider the pair of species as potential competitors directly influencing each other via interspecific killing (see Donadio and Burskirk 2006 for more details). For example, at locality X we recorded a skull of *Cerdocyon thous*. In this locality the species could potentially interact with *L. gymnocercus* due to habitat preference (open grasslands) and diet overlap (Vieira and Port, 2007), but not by interspecific killing because the pair *C. thous* and *L. gymnocercus* has arcsine $\sqrt{BSD}$ lower than two (see Donadio and Burskirk 2006). *Speothos venaticus* is also present at this locality. This last species is not a potential competitor with *C. thous* in any of our factors because this pair of species arcsine $\sqrt{BSD}$ is lower than 2 (see Donadio and Burskirk 2006). They do not overlap in dietary adaptation due to the fact that *C. thous* presents an omnivorous diet while *S. venaticus* is a specialized meat eater. For habitat preference, *C. thous* prefers open grassland areas (Berta 1982) and *S. venaticus* is primarily a forest dweller (Oliveira 2009). Thus, we have a value of 0 for interspecific killing and 0.5 for diet and 0.5 for habitat (half of the species in that location is a potential competitor due to diet and habitat preferences). We performed this calculation for every specimen, constructing a table that was then used to test competition via PLS between shape or size and the competition data matrix.

Angular comparison

After assessing via PLS the impact of climate and competition vs skull shape, MorphoJ 1.05 (Klingenberg 2011) was used to compare the direction of PLS shape vectors extracted for climate and competition separately. This provides a direct test to assess the impact of these factors on shaping canid communities and phenotypic changes. Such a test was not available for PLS Size for which we opted to simply compare strength of correlation between the samples. If climate impacts size more strongly than competition we might expect higher correlation coefficient (=r) in PLS.

Variation Partitioning

We employed variation partitioning (Diniz-Filho and Bini 2008; Raia et al. 2010; Meloro et al. 2014a) to evaluate the singular contribution to skull shape variance of four distinct components: taxonomy (described by the categorical variable “species”), size (described by lnCS), climate (described by the nineteen bioclimatic indices) and competition (described by the three variables of size, diet and biome overlap between the species). These factors are all considered as predictors (X) of skull shape (Y, described by the 54 shape variables, 2n−4 where n is the number of landmarks, Rohlf and Slice 1990) into multiple multivariate regression models. We tested for the effect of each single factor in isolation and in interaction with each other using the R package vegan 2.0 (Oksanen et al., 2012). We also analyzed the contribution of different predictors into size variation. We performed variation partitioning between all the average per localities (N = 262; using taxonomy, climate and competition as factors). These procedures were employed for the overall sample of South-American canids and nested subsets of the genera *Cerdocyon* and *Lycalopex* that got sufficient data to be considered separately. Since *Lycalopex* is the only genus that is not monophyletic, we also included taxonomy in its model. The other genera were not analyzed separately due to low number of localities.

Comparative Methods

Skull size and shape values together with bioclimatic and competition parameters were averaged across species in order to identify correlation patterns at macroevolutionary (above species) level.

This new dataset included eight data points only. We tested again for allometric patterns in between species as well as impact of climate and competition using Partial Least Squares. Due to species shared ancestry, we firstly produced a molecular phylogeny of our selected taxa using the 10k tree project database (Arnold et al. 2010, Online Resource). This database provided access to all updated molecular data of extant Canidae and generated consensus phylogenetic tree based on a baysean approach using selected taxa only. MorphoJ was employed to test for the presence of a phylogenetic signal in our shape data comparing the observed sum of procustes distances between the eight species averaged shapes and their reconstructed ancestral node values vs the distribution of these sums obtained randomizing tips and node values (cf. Klingenberg and Gidazwiski 2010; Meloro and Jones 2012). Regressions and Partial Least Squares models were eventually repeated on independent contrasts using MorphoJ in order to re-evaluate the influence of allometry, climate and competion on macroevolutionary scale (cf. Meloro et al. 2014).

RESULTS

Canids skull shape

The first twenty five Relative Warps cumulatively explain 95% of total variance. Plotting the first (30.50% of shape variance) versus the second (19.96%) RWs evidence extensive overlap between the different canids' species, although RW1 separates genera, showing some segregation between almost all *Lycalopex* spp. and the others (Fig. 3). Only *Speothos venaticus* did not overlap with others species. RW1 describes changes in the zygomatic arch, occipital condyle, auditory bulla, muzzle and teeth. Species at the extreme negative of RW1 exhibit smaller zygomatic arch, occipital condyle and auditory bulla, more elongated and thinner muzzle, larger first molar and carnassial and smaller canine and incisors. The RW2 describes shape changes related to braincase, zygomatic arch, occipital condyle, auditory bulla, muzzle area and teeth row positioning and size. On the negative scores of RW2 specimens have larger braincase, zygomatic arch, occipital condyle and auditory bulla, shorter and thicker muzzle, small first molar and larger carnassial, canine and incisors.

MANOVA performed using the first 25 RWs evidenced significant shape differences between species (N = 262, Pillai's trace = 4.116; $F_{175, 1652}$ = 13.471; P << 0.001). When only locality average sexed individuals were analyzed (N = 206), two-way MANOVA shows no significant differences between sex (Pillai's trace = 0.173; $F_{25, 165}$ = 1.385; P = 0.118), but confirms significant differences between species (Pillai's trace = 4.146; $F_{175, 1197}$ = 9.936; P <<0.001), with no interaction between the two factors (Pillai's trace = 0.895; $F_{175, 1197}$ = 1.003; P = 0.477). Pairwise comparisons using the first two RWs (50.46% of total variance) revealed that all species differ in skull shape, expect for the pairs *L. culpaeus-L. griseus*, *L. culpaeus-L. gymnocercus* and *A. microtis-L. vetulus* (Table 2).

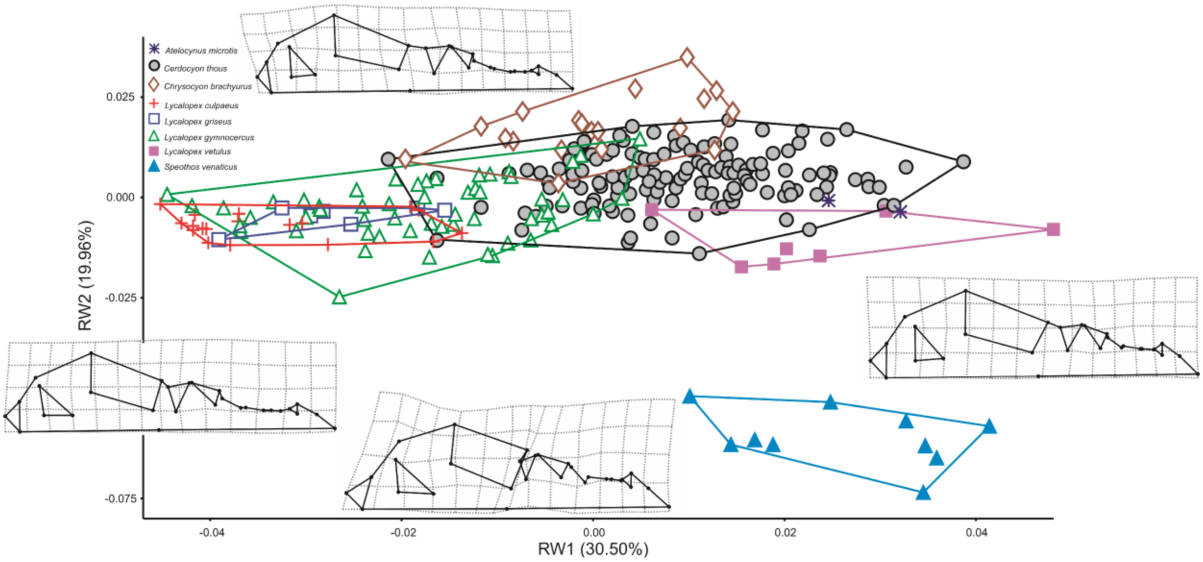

Figure 3. Scatter plot of RW1 vs. RW2. Transformation grids visualize shape deformations relative to the mean at the positive and negative extremes of Relative Warps axes. Every species is labeled according to different color and symbol within minimum convex hull superimposed.

Skull size

Two-way ANOVA (N = 206) revealed canid species to be significantly different in skull size (F = 123.069, d.f. = 7, P << 0.001). Males and females also differ in skull size (F = 7.946, d.f. = 1, P = 0.005) but no interaction occurs between taxonomy and sex in skull size (F = 1.057, d.f = 7, P = 0.393). Therefore, it was possible to use in subsequent analyses the localities averages including those individuals who lacked sex information. One-way ANOVA confirmed species to be significantly different in size after averaging by geographic localities (F = 194.9, d.f. = 7, P << 0.001). Paired comparisons revealed that all species differ in size, except the pairs *A. microtis*-*L. culpaeus* and *L. gymnocercus*-*Speothos venaticus* (Table 3, Fig. 4).

Table 2. Pairwise comparisons between South-American canid species for skull shape. Upper diagonal corresponds to P values and lower diagonal corresponds to F values. Significant is highlighted.

	A. microtis	*C. thous*	*C. brachyurus*	*L. culpaeus*	*L. griseus*	*L. gymnocercus*	*L. vetulus*	*S. venaticus*
A. microtis		**0.008**	<< **0.001**	< **0.001**	<< **0.001**	<< **0.001**	0.275	<< **0.001**
C. thous	4.924		<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**
C. brachyurus	29.160	45.111		<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**
L. culpaeus	40.531	41.745	34.926		0.107	0.142	<< **0.001**	<< **0.001**
L. griseus	38.199	150.730	115.400	2.472		<< **0.001**	<< **0.001**	<< **0.001**
L. gymnocercus	15.378	126.780	63.463	2.0208	14.211		<< **0.001**	<< **0.001**
L. vetulus	1.6110	28.661	84.289	43.912	67.453	48.654		<< **0.001**
S. venaticus	67.480	496.61	447.590	205.290	410.350	390.020	107.510	

Table 3. Pairwise t test between South-American canid species for skull size. Significant P value is highlighted.

	A. microtis	*C. thous*	*C. brachyurus*	*L. culpaeus*	*L. griseus*	*L. gymnocercus*	*S. venaticus*
C. thous	**0.002**						
C. brachyurus	<< **0.001**	<< **0.001**					
L. culpaeus	0.488	<< **0.001**	<< **0.001**				
L. griseus	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**		
L. gymnocercus	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**		
S. venaticus	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	0.140	
L. vetulus	<< **0.001**	<< **0.001**	<< **0.001**	<< **0.001**	**0.043**	<< **0.001**	<< **0.001**

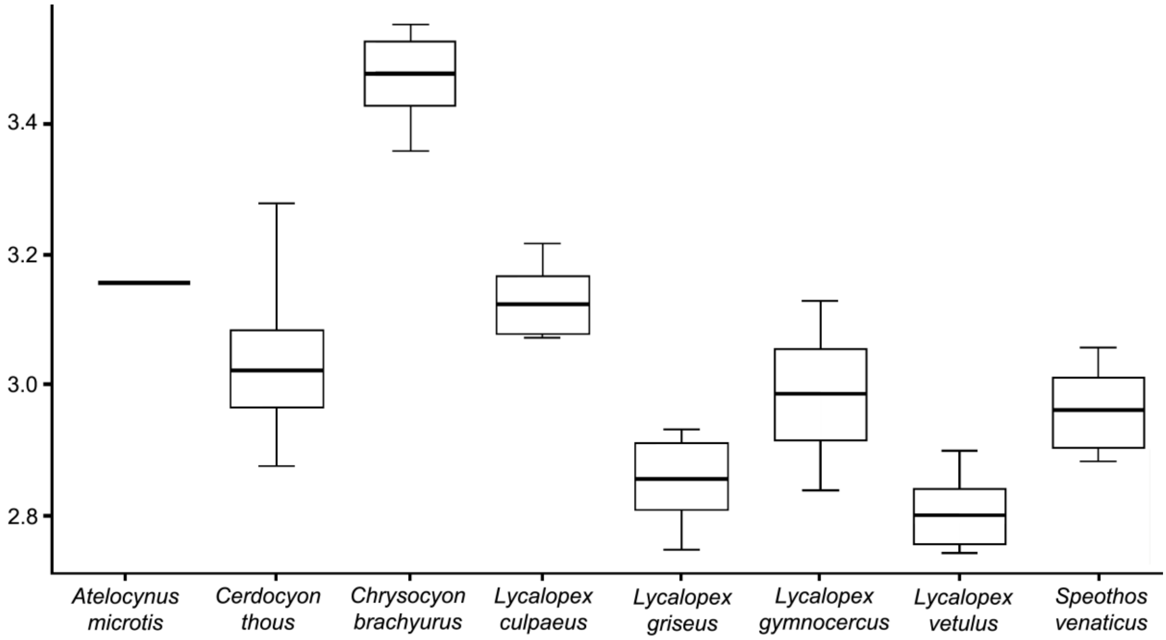

Figure 4. Box plot with standardized deviation of natural log transformed centroid size (lnCS) across the South-American canid species. Black string: median, white box: first interquartile, bar: second interquartile.

Skull allometry

Size had a significant impact on skull shape explaining 7.84% of variance in the global skull sample (N = 431, P <<0.0001, see also Online Resource) and 9.46% of variance in the locality averaged sub-sample (N = 262, P <<0.0001, see also Online Resource). ANCOVA models with permutation demonstrated in all cases that slope differ between species (N = 431, F = 8.713, P < 0.001; N = 262, F = 1.872, P < 0.001). Allometric models using pooled regression within subgroups are also significant in all cases (N = 431, 3.29% variance, P < 0.001; N = 262, 3.77% variance, P < 0.001).

Regression models performed independently for each taxon (Table 4) demonstrates that allometric effect impacts species differently. In the bush dog skull size explains the highest percentage of shape variance when compared to the larger *Chrysocyon* and *Cerdocyon*. Within *Lycalopex* allometric shape changes occurs in *L. gymnocercus* only while they are not statistically detectable in the other taxa (see also Online Resource). However, if all *Lycalopex* species are merged in the same sample, skull size explains almost 9% of shape variance in both complete and locality averaged datasets (Table 4, see also Online Resource).

Table 4. Regressions between skull shape and lnCS in different subsamples of canid taxa. Significance is highlighted.

	Whole sample			Locality averaged		
Species	N	% Var	P	N	% Var	P
Cerdocyon thous	226	**3.85%**	**<0.0001**	143	**4.08%**	**<0.0001**
Chrysocyon brachyurus	25	**9.28%**	**0.0076**	19	**11.52%**	**0.0159**
Lycalopex culpaeus	13	10.85%	0.835	7	25.85%	0.0731
Lycalopex griseus	33	4.86%	0.1003	19	7.19%	0.1881
Lycalopex gymnocercus	99	**4.20%**	**<0.0001**	55	**5.69%**	**0.002**
Lycalopex vetulus	16	6.68%	0.4329	7	26.71%	0.0865
Lycalopex spp.	161	**9.13%**	**<0.0001**	88	**9.02%**	**<0.0001**
Speothos venaticus	15	**13.44%**	**0.0346**	10	**20.81%**	**0.0084**

PLS climate

Two block Partial Least Squares between 19 bioclimatic variables and skull shape extracts 19 pair of vectors of which the first explains 98.33% of covariation between the blocks. Correlation between the first pair of axes is strong (r = 0.720) and significant (P < 0.001). A scatter plot with Singular Warp 1 of the shape block (SW1 shape) vs. SW1 of the climate variables block supports a separation among species along an environmental gradient (Fig. 5). SW1 climate is loaded negatively on Temperature Seasonality (standard deviation *100) (BIO4, r = -0.864) and Temperature Annual Range (BIO 7 = BIO5-BIO6; r = -0.762), while strong positive correlation of SW1 climate scores occurred with Annual Mean Temperature (BIO1, r = 0.864), Min Temperature of Coldest Month (BIO6, r = 0.943), Mean Temperature of Driest Quarter (BIO9, r = 0.794), Mean Temperature of Coldest Quarter (BIO11, r = 0.931), Annual Precipitation (BIO12, r = 0.809), Precipitation of Wettest Month (BIO13, r = 0.891), Precipitation of Wettest Quarter (BIO16, r = 0.896). Therefore, SW1 climate discriminated between seasonal and arid climate (negative scores) versus warm and humid (positive scores).

Species distributed in localities with low precipitation, low mean temperatures and high seasonality exhibited skulls with elongated muzzles, smaller zygomatic arch, larger teeth, narrow auditory bulla and smaller occipital condyle (e.g. *L. griseus*, *L. culpaeus* and most of *L. gymnocercus* representatives). Conversely, *A. microtis*, *S. venaticus*¸ *L. vetulus*¸ *C. brachyurus* and most of *C. thous* representatives showed positive scores in vector SW1 climate (high precipitation and mean temperature and low seasonality) and therefore had antagonistic skull shape (Fig. 5).

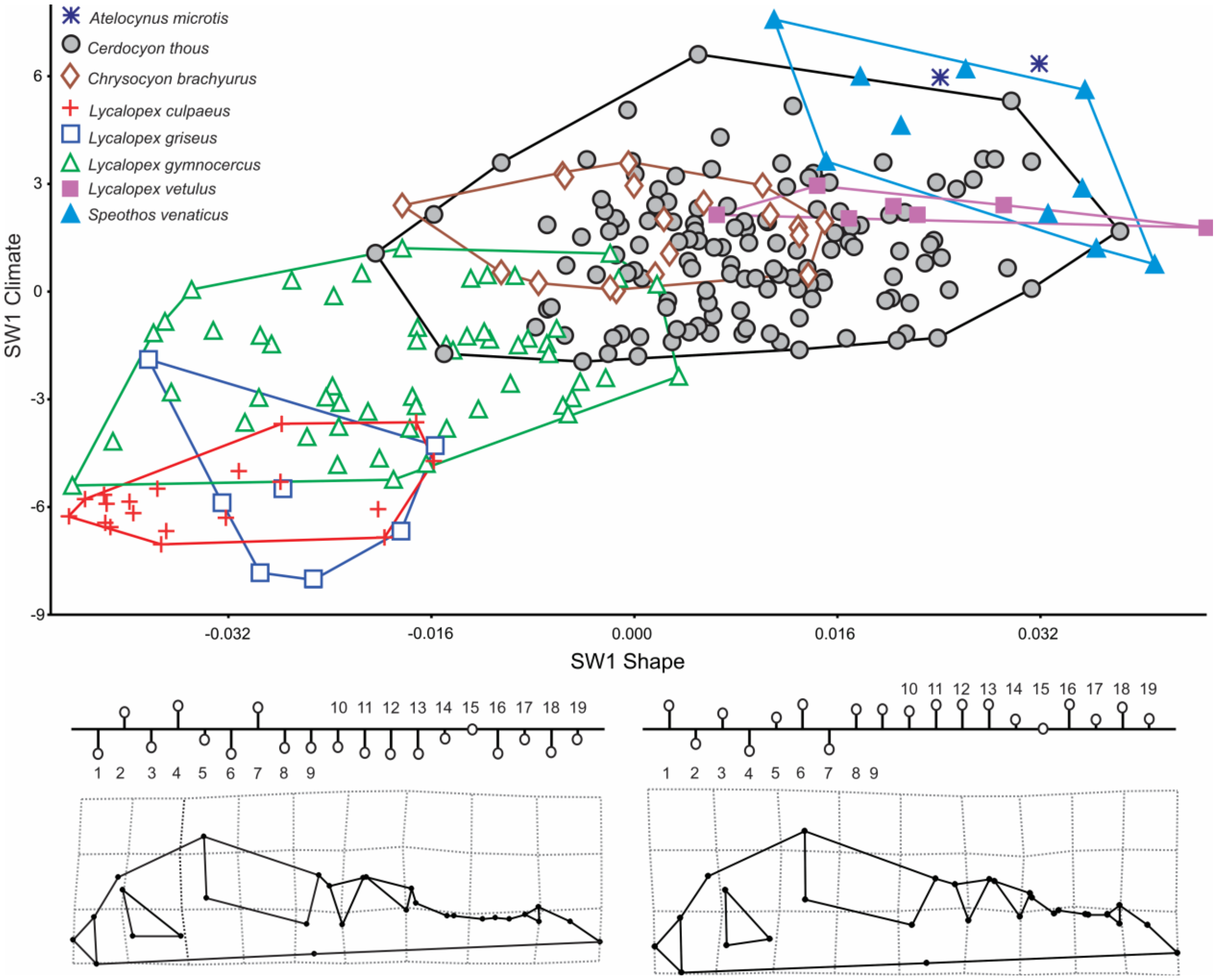

Figure 5. Plot of the first pair of Singular Warps (axis X is block shape, axis Y is block climate). Below deformation grids and variables profile from the most negative to the most positive Singular Warps scores. Every species is labeled according to different color and symbol within minimum convex hull superimposed.

The PLS of size vs climatic variables also extracted a significant pair of axes whose correlation is not particularly strong (r = 0.275; P < 0.001). SW climate is loaded positively with Temperature Seasonality (standard deviation *100) (BIO 4, r = 0.827). All *Lycalopex* species occur in high seasonal environments and are characterized by relatively small size (Fig. 6A).

PLS competition

Two block Partial Least Squares between competition variables (Diet, Size and Biome) and skull shape extracts three pairs of vectors of which the first explains 70.97% of covariation between the blocks. Competition has significant impact on skull shape (PLS1, r = 0.419, P << 0.001). The scatter plot with Singular Warp 1 of the shape block vs. SW1 of competition variables block shows two groups of species that differ among each other the most: the northern group, with *A. microtis*, most specimens of *C. thous*, *C. brachyurus*, *L. vetulus* and *Speothos* and the southern group, with mainly *L. griseus* and *L. culpaeus*. *Lycalopex gymnocercus* is right in the middle, overlapping in shape with both groups (Fig. 7). SW1 competition is loaded positively with all three variables (Diet r = 0.823, Interspecific killing r = 0.578 and habitat r = 0.572). Adaptations in the positive end (*L. griseus*, *L. culpaeus* and *L. gymnocercus*) are related to skulls with a larger bulla, a small temporalis insertion area and relatively larger teeth. On negative scores we find specimens of *C. thous*, *C. brachyurus*, *L. vetulus* and *Speothos venaticus.* These specimens show relatively smaller teeth, bulla and larger muzzle.

Significant association also occurs between size and competition (r = 0.332; P < 0.001). SW competition is loaded negatively on diet (r = -0.662), size (r = -0.036) and biome (r = -0.748). Species with higher impact of competition are smaller (*L. griseus*) and with less impact of competition are larger (*C. brachyurus*) (Fig. 6B).

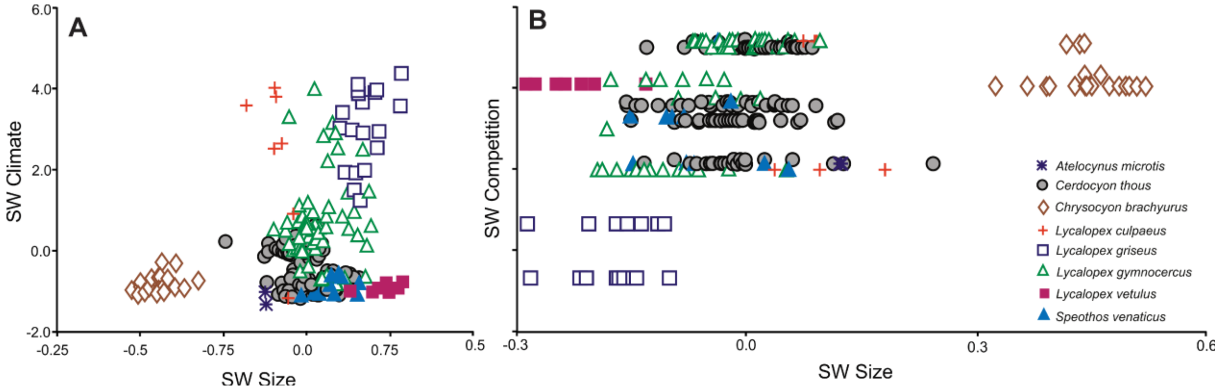

Figure 6. Plot of the pair of Singular Warps. (A) Pls climate plot (axis X is block size, axis Y is block climate). (B) Plot competiton plot (axis X is block size, axis Y is block competition). Every species is labeled according to different color and symbol.

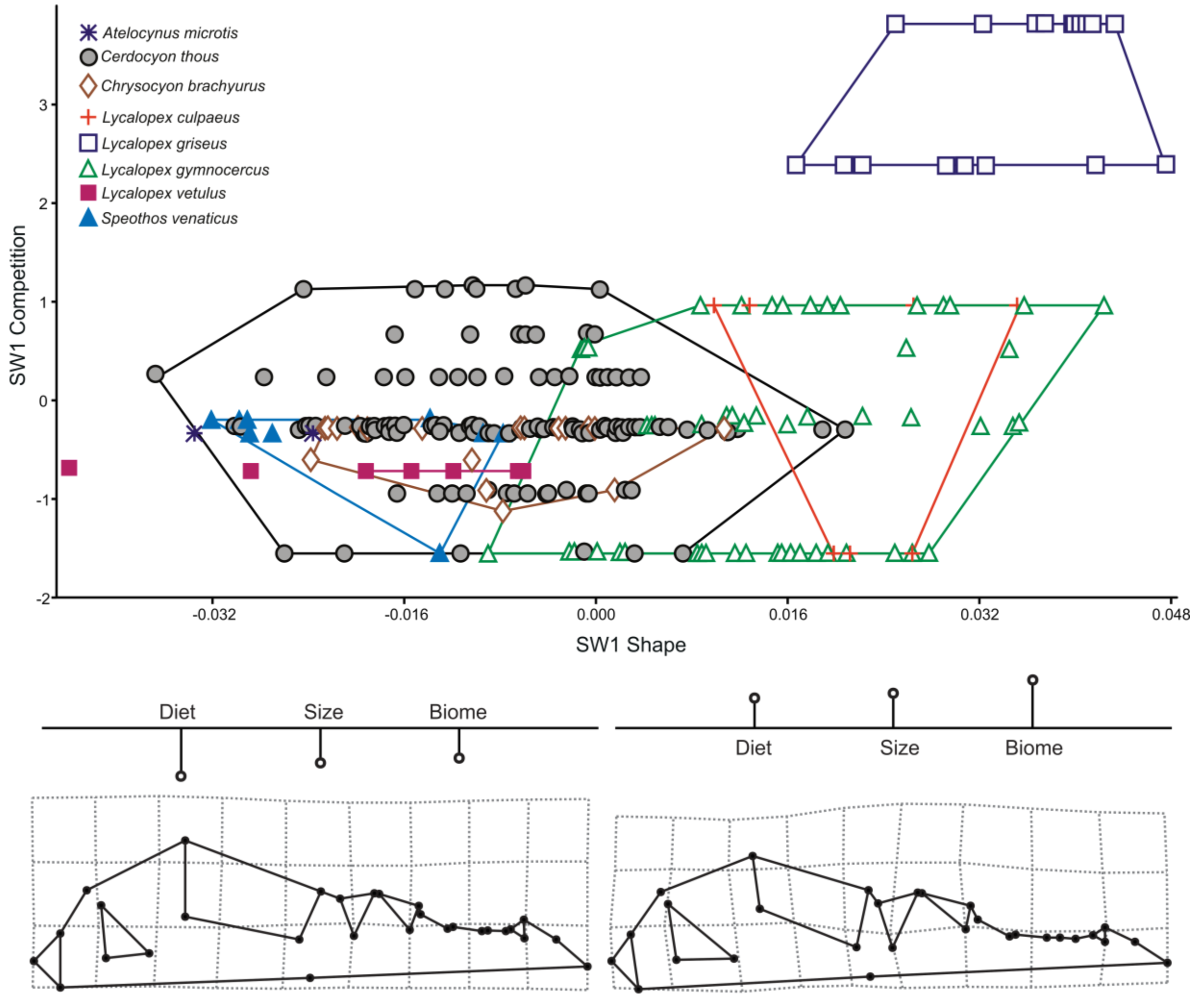

Figure 7. Plot of the first pair of Singular Warps (axis X is block shape, axis Y is block competition). Below deformation grids and variables profile from the most negative to the most positive Singular Warps scores. Every species is labeled according to different color within minimum convex hull superimposed.

Angular comparison

The direction of PLS shape vectors due to climate and competition are significantly distinct from 90 degree thus supporting similarities in patterns of skull shape covariation (Angle = 18.547^{o}; P <0.001).

Pairwise genera angular comparison for PLS climate revealed that only two pairs of species seem to exhibit similar vector directionality: *Chrysocyon* and *Lycalopex*, and *Cerdocyon* and *Speothos* (Table 5A). As to competition, only *Cerdocyon* and *Lycalopex* exhibit an angle significantly smaller than 90 degrees (Table 5B).

Table 5. Pairwise Angular comparisons of SW1 shape vectors of climate (A) and competition (B) between South-American canid genera. Upper diagonal corresponds to P values and lower diagonal corresponds to angles (in degrees). Significant is highlighted.

A: Climate				
	Cerdocyon	*Chrysocyon*	*Lycalopex*	*Speothos*
Cerdocyon		0.576	0.329	**0.001**
Chrysocyon	85.584		< **0.001**	0.365
Lycalopex	82.293	60.375		0.056
Speothos	64.420	82.845	74.994	
B: Competition				
Cerdocyon	-	0.628	**0.013**	0.651
Chrysocyon	86.171	-	0.242	0.449
Lycalopex	70.590	80.763	-	0.314
Speothos	86.427	84.022	82.048	-

Variation partitioning

In a sample of 262 skull shape averages per locality, taxonomy occurs as the most influential variable to explain interspecific shape variation (Adj R^2 Taxonomy = 0.49). This pattern remains consistent if factors are considered as single “pure” components (Adj R^2 Taxonomy “Pure” = 0.22, Fig. 8A). Climate is the second most influential variable when considered together with other variables (Adj R^2 Climate = 0.21) as well as alone (Adj R^2 Climate “Pure” = 0.03, Fig. 8A). Size and Competition have no influence on shape when considered alone (Fig. 8A). Strong interaction occurs between taxonomy and climate and taxonomy and size (Fig. 8A and Online Resource).

The same strong influence of taxonomy occurs when size is considered a predictor (Adj R^2 Taxonomy = 0.84). This pattern remains consistent if factors are considered as single “pure” components (Adj R^2 Taxonomy “Pure” = 0.72, Fig. 8B). After taxonomy, climate is the most influential factor (Adj R^2 Climate “Pure” = 0.03), followed by competition (Adj R^2 Competition “Pure” = 0.01, Fig. 8B). Taxonomy interacts with competition and both together interact strongly with climate (Fig. 8B).

The analyses of nested dataset show distinct partition of variance depending on the genus. In *Cerdocyon* size has no significant influence on skull shape as “pure” component. The impact of climate on skull shape is present and significant (Adj R^2 Climate “pure” = 0.10) while competition explains very little (Adj R^2 Competition “pure” = 0.01, and see Online Resource). When *Cerdocyon* skull size is modelled as dependent variable, competition is more influential in isolation (Adj R^2 Competition “pure” = 0.07) while climate has an impact only due to the interaction with the competition (Adj R^2 Climate x Competition = 0.04, see also Online Resource).

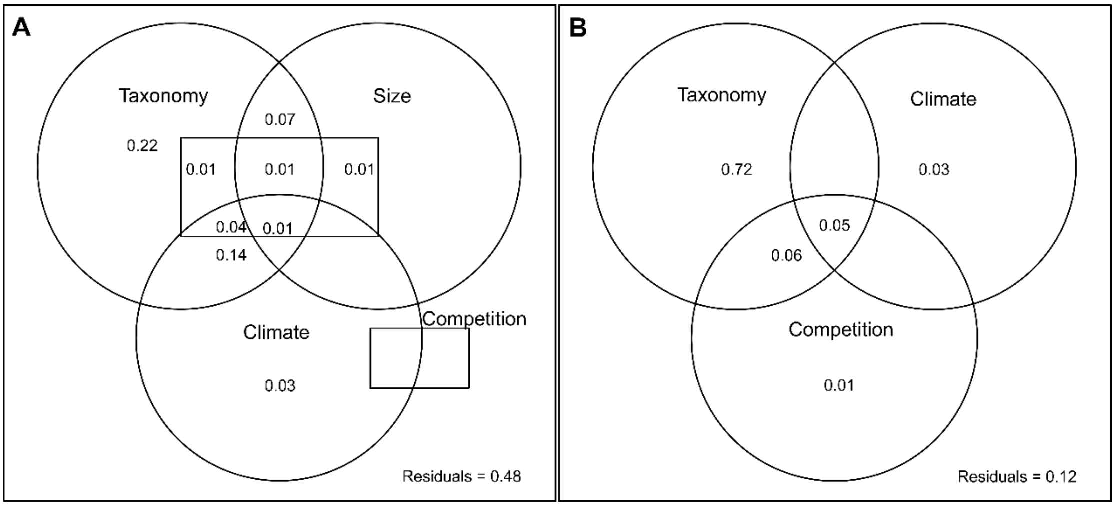

Figure 8. Schematic depiction of the factors analyzed in partition variation meant to illustrate both their individual contribution to shape (A) or size (B) variance and their interaction components. Values < 0 not shown.

For *Lycalopex*, taxonomy is the most influential factor in explaining variance for skull shape (Adj R^2 Taxonomy "pure" = 0.05), followed as pure component by climate (Adj R^2 = 0.04), competition (Adj R^2 = 0.02) and size (Adj R^2 = 0.01). A similar pattern occurs when skull size is considered dependent with taxonomy as pure explaining most of the variance (Adj R^2 = 0.16), followed by climate (Adj R^2 = 0.08) and competition (Adj R^2 = 0.02, see also Online Resource).

Comparative analyses

When using the record of averaged skull shape (N = 8), allometry is not a significant factor anymore even if skull size appears to explain a substantial proportion of shape variance (16.46%; P = 0.332). The Partial Least Squares confirms the impact of climatic variables on skull shape as detectable by the first significant pair of vectors (93.27% of covariation explained, r = 0.957, P = 0.0083). Association between skull shape and competition is not statistically detectable with PLS (SW1, r = 0.8655, P = 0.1954). The test for phylogenetic signal shows that it does not occur in both skull shape (Tree length = 0.0067, P = 0.2063) and size (Tree length = 0.218, P = 0.4438) making it unnecessary the use of comparative methods.

DISCUSSION

Our findings show South-American canids are different in skull shape, with peculiar characters occurring especially in *Speothos venaticus*: large zygomatic arch, big upper carnassial, canine and incisors and short and thick muzzle are all well-established attributes related to its hypercarnivorous diet (Valkenburgh 1991; Kleiman 1972). The tropical hoary-fox (*L. vetulus*) also shows unique skull shape in comparison to other *Lycalopex* southern species. Features such as large auditory bulla and short and thick muzzle make the hoary-fox more similar in skull shape to *Cerdocyon* and *Atelocynus* than to members of its own genus (Fig. 2). In comparison to the southern South-American *Lycalopex*, the hoary-fox is endemic from central Brazil and termites are a large percentage of its diet (Dalponte 2009). The other *Lycalopex* foxes are omnivorous, opportunistic and restricted to colder environments, so this might explain the unusual grouping in cranial shape of *L. vetulus* with other genera (Sillero-Zubiri et al., 2004; Johnson and Franklin 2011).

Skull size also varies considerably among species with *Chrysocyon brachyurus* showing the largest skull. Size differences also occur among members of *Lycalopex* genus confirming and expanding previous observations by Wayne et al. (1989): size differentiation can be interpreted as a mechanism of niche partitioning that eventually allowed these taxa to fulfil different ecological requirements. As such, the role of interspecific allometry in the overall sample is apparent with size explaining almost 10% of variance in skull shape (generally comparable to that from previous studies, Figueirido et al. 2011, 2013 on all Carnivora and Meloro et al. 2015b on canids only). The ANCOVA model suggests that allometric shape variation differ between taxa to the extent that more specialized morphologies show greater percentage of variance explained by size rather than generalists one (Table 4). Indeed, the hypercarnivorous bush dog (*S. venaticus*) exhibits a strong allometric component when compared to the other taxa in relation to its biomechanically demanding predatory behaviour (Slater et al. 2009). We also note that allometry is not significant for many *Lycalopex* species except *L. gymnocerus*. This possibly might be the result of a broader taxonomic differentiation that occurred in the whole genus in relation to size but not shape characteristics (see Table 2, 3). Also localized character displacement in certain members of this genus might have favoured size changes not accompanied by dramatic skull shape changes. Prevosti et al. (2013) supports allometry to occur in a 3D skull shape sample of *L. griseus* and *L. gymnocercus* thus corroborating our general result based on the *Lycalopex* as a coherent taxonomic group.

Clearly allometry is a factor in shape differentiation of South American canids, however the PLS and variation partition analyses support a stronger influence of abiotic factors on skull morphology.

Climate seems to represent a stronger factor than competition in explaining skull shape variation. PLS highlights this and also provides the mechanism to visualize shape and size changes related to these factors. Seasonal environments, such as southern South-America, are occupied by non-specialist canid phenotypes, due to *Lycalopex* dominance. Opposite to that, inside the Amazon we have the co-presence of three distinct morphotypes: *Speothos*, *Atelocynus* and the generalist *Cerdocyon*. The peculiar interaction between these genera occurs only in this biome. Compared to other South-American ecoregions where *S. venaticus* is rarely encountered, its species abundance in the Amazon is higher (Jorge et al. 2013). Meanwhile, *A. microtis* is mainly an Amazonian species whose ecological niche relates strongly with wet environments (e.g. main food source is generally fish, Berta 1986; Sillero-Zubiri et al. 2004). From a macroevolutionary point of view this supports the Amazon as a unique ecosystem hosting an ecologically and morphologically diverse canid community with predominance of carnivorous morphotypes (skulls characterised by large zygomatic arch and short rostrum, Fig. 5). We note still all over South America a general pattern of co-presence involving rather three species in different climatic conditions: far from the equator, the co-existence of fox-like phenotypes increases, suggesting that carnivorous phenotypes went extinct and never replaced; in the savannah-Cerrado environments we record skulls of *Chrysocyon*, *Cerdocyon* and *Lycalopex* (depending on the latitude co-occurrence is with *L. gymnocercus* or *L. vetulus*, Fig. 5). Jácomo et al. (2004) report low degree of ecological overlap between *Chrysocyon*, *Cerdocyon* and *L. vetulus* in Cerrado due to differences in feeding habits and activity patterns. The bush dog is also expected to be part of this guild although no data about its diet in co-existence with the other dogs are available. Zuercher et al. (2005) report high consumption of agouti and paca by *Speothos* in Atlantic Forest of eastern Paraguay. If diet of *Speothos* is consistent across the continent we might expect some possible overlap with the maned wolf and the crab-eating fox, however no report of bush dog killing by larger canids occurs in the literature (Oliveira and Pereira 2014).

The size pattern related to climate is not as strong as with shape and we note generally smaller species in the southern part of South America co-existing together (Fig. 6A). The lack of large carnivorous morphotypes is a relatively recent event in the history of southern South-American canids thus explaining it. Fossil record supports this, since *Theriodictis* and *Protocyon* genera (large hypercarnivores) were recorded in southern South America and went extinct very recently at the end of the Pleistocene (Prevosti et al. 2009b).

The co-presence of three distinct morphotypes in size and shape definitely occurs along an environmental gradient and can be better interpreted after looking at PLS of skull morphology vs competition (Fig. 7). All *Lycalopex* foxes exhibit similar shape morphology and high scores being generally the smallest in the canid guild and showing strong overlap with each other across their range. This co-existence seems interestingly favoured by size differences more than shape (Figs 3 and 4) confirming earlier investigation (Fuentes and Jaksic 1979).

The parallelism observed in the PLS vectors suggests that co-variation between shape with climate and competition gradient are two sides of the same coin. Indeed, canid assemblage rules are definitely controlled by environment and South-American species are no exception (Johnson et al. 1996). The largest canid assemblage ever studied is from central Africa with three species of jackals co-occurring together plus hypercarnivore *Lycaon* and the termite specialist *Otocyon*.

Theoretically the Cerrado (a savannah-like vegetation) could support a similar combination of species and we note again similar niche partitioning with two foxes (*Cerdocyon* and *Lycalopex*) that overlap slightly in skull shape but not in size and feeding habits, then the small hypercarnivore bush dog and the large maned wolf.

Variation partitioning provides strong support for abiotic forces as responsible of interspecific morphological differences in South-American canids as a whole but also in the nested dataset of *Cerdocyon* and *Lycalopex* (Fig. 8, Online Resource). Climate consistently explains 3% of both size and shape variance in isolation, while competition only 1% for size and none for shape.

In *Cerdocyon* the impact of climate on cranial shape is even stronger (10%) although it becomes non-significant to explain skull size variation. It can be argued that size changes in *Cerdocyon* are strongly influenced by co-occurrence with larger taxa that might suppress its spectrum of ecological adaptations via direct killing (Oliveria and Pereira 2010). For *Lycalopex* climate also appears to have stronger influence on skull size (8%) and shape (4%) than competition.

Overall, these results are a bit counterintuitive considering the rapid adaptive invasion of canids in South America (Perini et al. 2010). This explains the lack of phylogenetic signal encountered in macroevolutionary analyses as well as lack of allometry, but still significant influence of climate. Benton (2009) suggests that competition might regulate animal communities on short time scale, while abiotic forces dominate on big temporal scale. We argue that South-American canids show a mix of both phenomena since prehistoric diversity was higher, when competition could have been more relevant than now (Wang et al. 2008). By adapting flexible ecological feeding niches (with the possible exception of hypercarnivorous *Speothos*) South-American canids might have escaped constrains imposed by competition evolving a flexible morphology.

Acknowledgements

Our thanks to colleagues Jonas Sponchiado and Geruza L. Melo of the Laboratório de Ecologia e Biogeografia of the Federal University of Santa Maria for their help in data collection. We are also grateful to curators and staff of the Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCNFZB) (M.M. de A. Jardim), Museu de Ciências e Tecnologia da PUCRS (MCP) (C.S. Fontana), Museu Nacional (MN) (J.A. de Oliveira and S.M. Vaz), Museu Paraense Emílio Goeldi (MPEG) (S.M. Aguiar and J.S. Silva Jr.), Museu de História Natural Capão da Imbuia (MHNCI) (V. Abilhoa and S.C. Pereira), Coleção Científica do Laboratório de Mamíferos Aquáticos da UFSC (UFSC) (M.E. Graipel), Museu Nacional Uruguaio de Historia Natural (MNHN) (E.M. Gonzalez), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) (D.A. Flores and S. Lucero) and Museu de Zoologia da Universidade de São Paulo (MZUSP) (M. De Vivo and J.G. Barros) for the authorization and support to specimens access. Authors Jamile de Moura Bubadué and Renan dos Santos Carvalho were supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior with a scholarship. Nilton Cáceres participated to this study as Conselho Nacional de Desenvolvimento Científico e Tecnológico research fellow in Brazil. Carlo Meloro was supported by British Research Council under the program Research Links (grant no: 127432108).

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EVOLUTIONARY BIOLOGY

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Ecogeographical variation in skull shape of South-American canids: abiotic or biotic processes?

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List of 431 canid specimens used for morphometric analyses, with data on species, sex (F, female; M, male; or unknown), museum number, and geographical coordinates.

Species	Sex	Museum number	Latitude	Longitude
Atelocynus microtis	F	MZUSP 4320	-6.84	-70.24
Atelocynus microtis	M	MZUSP 19753	-3.83	-55.49
Atelocynus microtis	M	MZUSP 19754	-3.83	-55.49
Atelocynus microtis	M	MZUSP 19751	-3.83	-55.49
Cerdocyon thous	F	MACN 14322	-25.49	-64.97
Cerdocyon thous	M	MACN 47402	-23.56	-64.40
Cerdocyon thous	M	MACN 47189	-23.14	-64.32
Cerdocyon thous	F	MACN 30345	-23.14	-64.32
Cerdocyon thous	F	MACN 47190	-23.14	-64.32
Cerdocyon thous	M	MACN 486	-23.14	-64.32
Cerdocyon thous	F	MACN 485	-23.14	-64.32
Cerdocyon thous	M	MACN 4810	-23.14	-64.32
Cerdocyon thous	M	MACN 33344	-22.24	-63.73
Cerdocyon thous	F	MACN 5060	-17.46	-63.66
Cerdocyon thous	F	MACN 5061	-17.46	-63.66
Cerdocyon thous	M	MACN 30481	-23.25	-63.35
Cerdocyon thous	F	MN 5497	-17.87	-63.00
Cerdocyon thous	M	MACN 47116	-24.20	-62.02
Cerdocyon thous	M	MZUSP 9686	0.97	-61.34
Cerdocyon thous	Unknown	MZUSP 9687	0.97	-61.34
Cerdocyon thous	M	MACN 16189	-30.58	-59.95
Cerdocyon thous	Unknown	MACN 24264	-25.22	-59.86
Cerdocyon thous	Unknown	MACN 29839	-25.33	-59.68
Cerdocyon thous	Unknown	MACN 336	-28.04	-59.22
Cerdocyon thous	Unknown	MACN 21228	-27.49	-58.82
Cerdocyon thous	Unknown	MACN 20316	-27.58	-58.75
Cerdocyon thous	Unknown	MACN 24267	-32.22	-58.15
Cerdocyon thous	Unknown	MACN 5045	-25.33	-58.10
Cerdocyon thous	Unknown	MACN 5043	-25.33	-58.10
Cerdocyon thous	Unknown	MACN 5040	-25.33	-58.10
Cerdocyon thous	Unknown	MACN 4534	-22.29	-57.94
Cerdocyon thous	F	MNHN 707	-21.72	-57.89
Cerdocyon thous	M	MNHN 706	-21.72	-57.89

Cerdocyon thous	F	MNHN 869	-30.55	-57.86
Cerdocyon thous	M	MZUSP 3372	-19.01	-57.66
Cerdocyon thous	M	MZUSP 3373	-19.01	-57.66
Cerdocyon thous	Unknown	UFSC 3728	-19.21	-57.65
Cerdocyon thous	Unknown	MNHN 255	-33.40	-57.54
Cerdocyon thous	F	MNHN 262	-30.95	-57.52
Cerdocyon thous	F	MNHN 965	-30.29	-57.20
Cerdocyon thous	Unknown	MN 25606	-21.23	-57.13
Cerdocyon thous	Unknown	MN 25607	-21.23	-57.13
Cerdocyon thous	Unknown	MNHN 253	-33.94	-56.75
Cerdocyon thous	Unknown	MZUSP 19847	-16.26	-56.62
Cerdocyon thous	M	MNHN 2645	-30.65	-56.59
Cerdocyon thous	M	MZUSP 3777	-20.24	-56.36
Cerdocyon thous	F	MNHN 1287	-34.52	-56.28
Cerdocyon thous	F	MNHN 260	-31.88	-56.24
Cerdocyon thous	Unknown	MNHN 2540	-34.82	-56.16
Cerdocyon thous	M	MNHN 829	-31.25	-56.15
Cerdocyon thous	M	MNHN 956	-31.25	-56.15
Cerdocyon thous	M	MZUSP 6314	-15.60	-56.09
Cerdocyon thous	M	MZUSP 6315	-15.60	-56.09
Cerdocyon thous	Unknown	MNHN 5478	-34.72	-56.07
Cerdocyon thous	M	MNHN 2420	-31.73	-55.98
Cerdocyon thous	M	MNHN 251	-31.73	-55.98
Cerdocyon thous	Unknown	MNHN 252	-31.73	-55.98
Cerdocyon thous	F	MNHN 258	-31.71	-55.97
Cerdocyon thous	F	MNHN 2538	-31.70	-55.97
Cerdocyon thous	M	MNHN 1119	-31.70	-55.97
Cerdocyon thous	M	MNHN 1140	-31.70	-55.97
Cerdocyon thous	F	MNHN 1254	-32.84	-55.90
Cerdocyon thous	M	MNHN 6260	-34.55	-55.94
Cerdocyon thous	M	MNHN 6262	-34.55	-55.94
Cerdocyon thous	M	MNHN 6273	-34.55	-55.94
Cerdocyon thous	F	MNHN 2649	-33.55	-55.71
Cerdocyon thous	F	MNHN 2651	-33.55	-55.71
Cerdocyon thous	M	MNHN 2650	-33.55	-55.71
Cerdocyon thous	Unknown	MNHN 2680	-33.93	-55.68
Cerdocyon thous	Unknown	MNHN 4716	-30.91	-55.55
Cerdocyon thous	Unknown	MNHN 6437	-30.91	-55.55
Cerdocyon thous	Unknown	MACN 34676	-27.32	-55.53
Cerdocyon thous	M	MNHN 954	-33.80	-55.53
Cerdocyon thous	Unknown	MN 4908	-21.62	-55.17
Cerdocyon thous	F	MNHN 247	-34.88	-54.97
Cerdocyon thous	M	MNHN 2646	-34.88	-54.97
Cerdocyon thous	F	MNHN 3198	-34.00	-54.96

Cerdocyon thous	Unknown	MNHN 2695	-33.53	-54.94
Cerdocyon thous	Unknown	MNHN 7111	-34.80	-54.91
Cerdocyon thous	Unknown	MNHN 7352	-34.80	-54.91
Cerdocyon thous	M	MACN 20456	-25.66	-54.50
Cerdocyon thous	F	MACN 25802	-25.66	-54.50
Cerdocyon thous	M	MACN 20454	-25.66	-54.50
Cerdocyon thous	F	MACN 20455	-25.66	-54.50
Cerdocyon thous	Unknown	MNHN 249	-27.00	-54.44
Cerdocyon thous	F	MHNCI 3826	-25.68	-54.43
Cerdocyon thous	M	MHNCI 3850	-25.68	-54.43
Cerdocyon thous	Unknown	MHNCI 3811	-25.68	-54.43
Cerdocyon thous	F	MNHN 2643	-33.23	-54.36
Cerdocyon thous	M	MHNCI 489	-24.10	-54.27
Cerdocyon thous	M	MACN 13051	-25.58	-54.07
Cerdocyon thous	Unknown	MZUSP 19738	-19.54	-54.05
Cerdocyon thous	F	MNHN 1055	-29.68	-53.81
Cerdocyon thous	Unknown	MNHN 6410	-34.40	-53.79
Cerdocyon thous	Unknown	MCNFZB 423	-28.64	-53.61
Cerdocyon thous	Unknown	MZUSP 3182	-28.29	-53.49
Cerdocyon thous	Unknown	MZUSP 7149	-28.29	-53.49
Cerdocyon thous	F	MHNCI 164	-22.96	-53.30
Cerdocyon thous	M	MHNCI 60	-22.72	-53.17
Cerdocyon thous	F	MHNCI 3945	-25.20	-53.15
Cerdocyon thous	Unknown	MN 25005	-18.54	-53.12
Cerdocyon thous	F	MHNCI 5235	-22.63	-52.88
Cerdocyon thous	Unknown	MHNCI 5786	-22.63	-52.88
Cerdocyon thous	Unknown	MN 25683	-14.67	-52.35
Cerdocyon thous	M	MN 71092	-14.67	-52.35
Cerdocyon thous	Unknown	MHNCI 3948	-25.84	-52.03
Cerdocyon thous	M	MZUSP 514	-31.37	-51.97
Cerdocyon thous	M	MZUSP 518	-31.37	-51.97
Cerdocyon thous	Unknown	MZUSP 415	-31.37	-51.97
Cerdocyon thous	Unknown	MZUSP 34772	-19.12	-51.74
Cerdocyon thous	Unknown	MZUSP 34775	-19.12	-51.74
Cerdocyon thous	Unknown	MZUSP 34776	-19.12	-51.74
Cerdocyon thous	M	MZUSP 19741	-20.87	-51.61
Cerdocyon thous	M	MZUSP 1935	-20.65	-51.50
Cerdocyon thous	M	MCNFZB 598	-29.69	-51.47
Cerdocyon thous	F	MHNCI 1077	-25.39	-51.46
Cerdocyon thous	F	MZUSP 3762	-21.50	-51.32
Cerdocyon thous	F	MZUSP 3763	-21.50	-51.32
Cerdocyon thous	M	MCP 178	-30.29	-51.30
Cerdocyon thous	M	UFSC 3791	-27.40	-51.23
Cerdocyon thous	F	MHNCI 3972	-26.23	-50.93

Cerdocyon thous	Unknown	MZUSP 6640	-17.79	-50.92
Cerdocyon thous	F	MHNCI 2723	-24.32	-50.62
Cerdocyon thous	Unknown	MN 68361	-24.32	-50.62
Cerdocyon thous	Unknown	UFSC 762	-26.12	-50.31
Cerdocyon thous	Unknown	MHNCI 3923	-25.10	-50.16
Cerdocyon thous	M	MHNCI 1708	-23.30	-50.07
Cerdocyon thous	M	MHNCI 1714	-23.30	-50.07
Cerdocyon thous	M	MHNCI 132	-24.79	-50.01
Cerdocyon thous	M	MHNCI 307	-24.79	-50.01
Cerdocyon thous	M	MHNCI 309	-24.79	-50.01
Cerdocyon thous	M	MHNCI 5706	-25.44	-49.97
Cerdocyon thous	F	MZUSP 2832	-21.46	-49.95
Cerdocyon thous	F	MZUSP 2833	-21.46	-49.95
Cerdocyon thous	F	MZUSP 2835	-21.46	-49.95
Cerdocyon thous	M	MZUSP 2834	-21.46	-49.95
Cerdocyon thous	M	MZUSP 4135	-21.46	-49.95
Cerdocyon thous	M	MHNCI 1717	-24.21	-49.78
Cerdocyon thous	F	MHNCI 1713	-25.46	-49.53
Cerdocyon thous	M	MHNCI 3925	-25.57	-49.39
Cerdocyon thous	F	MZUSP 1164	-24.10	-49.34
Cerdocyon thous	M	MZUSP 1165	-24.10	-49.34
Cerdocyon thous	M	MHNCI 3401	-25.50	-49.34
Cerdocyon thous	M	MHNCI 3728	-25.99	-49.34
Cerdocyon thous	F	MHNCI 6184	-25.51	-49.20
Cerdocyon thous	F	MHNCI 6198	-25.51	-49.20
Cerdocyon thous	M	MHNCI 3941	-25.35	-49.16
Cerdocyon thous	F	UFSC 576	-27.90	-49.13
Cerdocyon thous	M	MHNCI 4043	-25.45	-49.07
Cerdocyon thous	F	MZUSP 486	-22.32	-49.07
Cerdocyon thous	M	MZUSP 463	-22.32	-49.07
Cerdocyon thous	M	MZUSP 487	-22.32	-49.07
Cerdocyon thous	F	UFSC 348	-27.57	-48.98
Cerdocyon thous	F	MN 4891	-16.33	-48.96
Cerdocyon thous	Unknown	MN 25612	-16.33	-48.96
Cerdocyon thous	F	UFSC 297	-27.96	-48.68
Cerdocyon thous	M	MHNCI 252	-25.85	-48.64
Cerdocyon thous	F	MHNCI 54	-25.82	-48.54
Cerdocyon thous	M	MHNCI 56	-25.82	-48.54
Cerdocyon thous	M	MHNCI 57	-25.82	-48.54
Cerdocyon thous	F	UFSC 773	-27.48	-48.53
Cerdocyon thous	F	UFSC 298	-27.56	-48.49
Cerdocyon thous	M	MN 75086	-7.12	-48.45
Cerdocyon thous	M	UFSC 850	-27.44	-48.47
Cerdocyon thous	Unknown	MN 75090	-7.12	-48.45

Cerdocyon thous	F	MZUSP 4221	-13.51	-48.36
Cerdocyon thous	M	MZUSP 19742	-13.51	-48.36
Cerdocyon thous	M	MZUSP 4215	-13.51	-48.36
Cerdocyon thous	M	MZUSP 4216	-13.51	-48.36
Cerdocyon thous	M	MZUSP 4219	-13.51	-48.36
Cerdocyon thous	F	MZUSP 13797	-23.02	-48.01
Cerdocyon thous	F	MZUSP 2919	-20.55	-47.41
Cerdocyon thous	M	MZUSP 2917	-20.55	-47.41
Cerdocyon thous	M	MZUSP 2918	-20.55	-47.41
Cerdocyon thous	F	MN 25589	-20.72	-46.61
Cerdocyon thous	F	MN 25590	-20.72	-46.61
Cerdocyon thous	M	MN 25591	-20.72	-46.61
Cerdocyon thous	M	MZUSP 6636	-23.29	-46.59
Cerdocyon thous	M	MZUSP 4217	-13.39	-46.33
Cerdocyon thous	F	MN 5505	-23.44	-45.08
Cerdocyon thous	F	MZUSP 3034	-17.34	-44.92
Cerdocyon thous	F	MZUSP 3039	-17.34	-44.92
Cerdocyon thous	F	MZUSP 3042	-17.34	-44.92
Cerdocyon thous	F	MZUSP 3098	-17.34	-44.92
Cerdocyon thous	F	MZUSP 3104	-17.34	-44.92
Cerdocyon thous	M	MZUSP 3031	-17.34	-44.92
Cerdocyon thous	M	MZUSP 3032	-17.34	-44.92
Cerdocyon thous	M	MZUSP 3033	-17.34	-44.92
Cerdocyon thous	M	MZUSP 3043	-17.34	-44.92
Cerdocyon thous	M	MZUSP 3101	-17.34	-44.92
Cerdocyon thous	F	MN 42800	-22.50	-44.56
Cerdocyon thous	M	MZUSP 4220	-15.46	-44.32
Cerdocyon thous	F	MN 3885	-22.96	-44.04
Cerdocyon thous	M	MN 3887	-22.96	-44.04
Cerdocyon thous	M	MZUSP 3038	-17.75	-44.37
Cerdocyon thous	Unknown	MN 3036	-19.28	-44.41
Cerdocyon thous	M	MN 29061	-14.76	-43.93
Cerdocyon thous	M	MN 29062	-14.76	-43.93
Cerdocyon thous	F	MN 4242	-19.63	-43.89
Cerdocyon thous	M	MN 4243	-19.63	-43.89
Cerdocyon thous	Unknown	MN 46810	-15.48	-43.60
Cerdocyon thous	Unknown	MN 63517	-9.01	-42.70
Cerdocyon thous	Unknown	MN 63491	-8.84	-42.50
Cerdocyon thous	Unknown	MN 25594	-22.66	-42.38
Cerdocyon thous	Unknown	MN 75981	-8.33	-42.31
Cerdocyon thous	Unknown	MN 63471	-8.36	-42.22
Cerdocyon thous	Unknown	MN 43968	-22.96	-42.03
Cerdocyon thous	Unknown	MN 72784	-22.37	-41.78
Cerdocyon thous	Unknown	MN 25578	-4.05	-40.87

Cerdocyon thous	F	MN 25597	-19.93	-40.60
Cerdocyon thous	F	MZUSP 2595	-10.47	-40.18
Cerdocyon thous	F	MZUSP 2598	-10.47	-40.18
Cerdocyon thous	F	MZUSP 2599	-10.47	-40.18
Cerdocyon thous	F	MZUSP 2602	-10.47	-40.18
Cerdocyon thous	M	MZUSP 19757	-10.47	-40.18
Cerdocyon thous	M	MZUSP 2594	-10.47	-40.18
Cerdocyon thous	M	MZUSP 2596	-10.47	-40.18
Cerdocyon thous	M	MZUSP 2600	-10.47	-40.18
Cerdocyon thous	M	MZUSP 2601	-10.47	-40.18
Cerdocyon thous	Unknown	MN 32370	-15.60	-39.86
Cerdocyon thous	M	MZUSP 3504	-14.79	-39.28
Cerdocyon thous	F	MN 10987	-14.80	-39.03
Cerdocyon thous	F	MN 11205	-14.80	-39.03
Cerdocyon thous	M	MN 25577	-4.33	-38.88
Cerdocyon thous	M	MZUSP 8732	-4.33	-38.88
Cerdocyon thous	Unknown	MN 25570	-4.33	-38.88
Cerdocyon thous	Unknown	MZUSP 3831	-12.95	-38.50
Cerdocyon thous	F	MN 25584	-8.89	-36.50
Cerdocyon thous	F	MN 25608	-8.89	-36.50
Cerdocyon thous	M	MN 25583	-8.89	-36.50
Chrysocyon brachyurus	Unknown	MACN 24043	-28.28	-57.19
Chrysocyon brachyurus	Unknown	MACN 25103	-28.87	-56.33
Chrysocyon brachyurus	Unknown	MACN 24201	-28.87	-56.33
Chrysocyon brachyurus	M	MN 71086	-16.19	-55.94
Chrysocyon brachyurus	M	MN 70999	-14.57	-52.45
Chrysocyon brachyurus	Femea	MPEG 1419	-15.90	-52.24
Chrysocyon brachyurus	M	UFSC 356	-28.63	-50.43
Chrysocyon brachyurus	Unknown	MHNCI 4250	-24.57	-50.27
Chrysocyon brachyurus	M	MHNCI 6087	-25.09	-50.16
Chrysocyon brachyurus	Femea	MHNCI 3522	-25.42	-50.01
Chrysocyon brachyurus	Femea	MHNCI 4246	-25.42	-50.01
Chrysocyon brachyurus	M	MHNCI 4244	-25.42	-50.01
Chrysocyon brachyurus	Unknown	MHNCI 5080	-25.42	-50.01
Chrysocyon brachyurus	F	MZUSP 32042	-22.88	-49.24
Chrysocyon brachyurus	M	MZUSP 32039	-22.88	-49.24
Chrysocyon brachyurus	Unknown	MN 36666	-13.53	-48.21
Chrysocyon brachyurus	Unknown	MHNCI 2699	-21.14	-47.99
Chrysocyon brachyurus	Unknown	MZUSP 3700	-20.54	-47.40
Chrysocyon brachyurus	Unknown	MZUSP 31981	-18.58	-47.87
Chrysocyon brachyurus	F	MZUSP 3025	-22.37	-46.94
Chrysocyon brachyurus	Unknown	UFSC 372	-16.37	-46.85
Chrysocyon brachyurus	M	MN 17501	-20.72	-46.61
Chrysocyon brachyurus	Unknown	MN 1049	-19.73	-44.67

Chrysocyon brachyurus	Unknown	MN 640	-19.73	-44.67
Chrysocyon brachyurus	Unknown	MN 17502	-20.33	-43.56
Lycalopex culpaeus	F	MACN 3159	-0.48	-78.14
Lycalopex culpaeus	M	MACN 15109	-39.75	-70.61
Lycalopex culpaeus	F	MACN 15088	-39.75	-70.61
Lycalopex culpaeus	M	MACN 15102	-39.75	-70.61
Lycalopex culpaeus	M	MACN 15184	-39.75	-70.61
Lycalopex culpaeus	F	MACN 15190	-39.75	-70.61
Lycalopex culpaeus	F	MACN 15183	-39.75	-70.61
Lycalopex culpaeus	Unknown	MACN 19221	-49.21	-68.19
Lycalopex culpaeus	Unknown	MACN 19222	-49.21	-68.19
Lycalopex culpaeus	F	MACN 24210	-43.67	-66.67
Lycalopex culpaeus	M	MACN 3839	-22.66	-66.24
Lycalopex culpaeus	Unknown	MACN 3069	-27.82	-65.50
Lycalopex culpaeus	Unknown	MACN 4155	-22.216667	-65.23
Lycalopex griseus	Unknown	MACN 16322	-47.87	-72.25
Lycalopex griseus	Unknown	MACN 16321	-47.87	-72.25
Lycalopex griseus	Unknown	MACN 15692	-47.87	-72.25
Lycalopex griseus	F	MACN 20208	-45.92	-71.64
Lycalopex griseus	Unknown	MACN 2087	-51.46	-70.83
Lycalopex griseus	F	MACN 20205	-51.46	-70.83
Lycalopex griseus	F	MACN 20206	-51.46	-70.83
Lycalopex griseus	Unknown	MACN 225	-45.04	-70.82
Lycalopex griseus	Unknown	MACN 224	-45.04	-70.82
Lycalopex griseus	M	MACN 20207	-41.13	-70.72
Lycalopex griseus	F	MACN 20278	-41.13	-70.72
Lycalopex griseus	F	MACN 15185	-39.75	-70.61
Lycalopex griseus	F	MACN 15264	-39.75	-70.61
Lycalopex griseus	M	MACN 15265	-39.75	-70.61
Lycalopex griseus	M	MACN 15263	-39.75	-70.61
Lycalopex griseus	M	MACN 15262	-39.75	-70.61
Lycalopex griseus	Unknown	MACN 14902	-39.03	-70.40
Lycalopex griseus	Unknown	MACN 25364	-34.87	-69.60
Lycalopex griseus	Unknown	MACN 20206	-46.67	-68.93
Lycalopex griseus	Unknown	MACN 363	-49.21	-68.19
Lycalopex griseus	F	MACN 13781	-30.12	-68.00
Lycalopex griseus	Unknown	MACN 20829	-34.05	-67.97
Lycalopex griseus	Unknown	MACN 24263	-54.49	-67.67
Lycalopex griseus	Unknown	MACN 2453	-39.03	-67.58
Lycalopex griseus	Unknown	MACN 2452	-39.03	-67.58
Lycalopex griseus	Unknown	MACN 2479	-39.03	-67.58
Lycalopex griseus	Unknown	MACN 25367	-26.11	-67.43
Lycalopex griseus	F	MACN 50420	-27.93	-67.19
Lycalopex griseus	Unknown	MACN 51170	-28.29	-66.34

Lycalopex griseus	Unknown	MACN 50432	-27.60	-66.32
Lycalopex griseus	F	MACN 50419	-27.60	-66.32
Lycalopex griseus	Unknown	MACN 16325	-43.80	-65.75
Lycalopex griseus	Unknown	MACN 2333	-31.66	-64.43
Lycalopex gymnocercus	F	MHNCI 231	-25.42	-50.00
Lycalopex gymnocercus	Unknown	MACN 23290	-31.64	-60.68
Lycalopex gymnocercus	M	MACN 34317	-29.39	-66.98
Lycalopex gymnocercus	F	MACN 50433	-27.60	-66.32
Lycalopex gymnocercus	F	MACN 532	-27.86	-65.95
Lycalopex gymnocercus	F	MACN 15992	-36.57	-65.67
Lycalopex gymnocercus	F	MACN 15938	-36.57	-65.67
Lycalopex gymnocercus	M	MACN 15932	-36.57	-65.67
Lycalopex gymnocercus	M	MACN 15958	-36.57	-65.67
Lycalopex gymnocercus	M	MACN 15966	-36.57	-65.67
Lycalopex gymnocercus	F	MACN 16063	-36.57	-65.67
Lycalopex gymnocercus	M	MACN 15601	-37.99	-65.59
Lycalopex gymnocercus	F	MACN 28182	-27.16	-65.50
Lycalopex gymnocercus	Unknown	MACN 24266	-42.39	-65.17
Lycalopex gymnocercus	Unknown	MACN 2935	-32.08	-65.14
Lycalopex gymnocercus	F	MACN 14323	-25.49	-64.97
Lycalopex gymnocercus	F	MACN 14319	-25.49	-64.97
Lycalopex gymnocercus	F	MACN 30150	-26.59	-64.81
Lycalopex gymnocercus	F	MACN 39194	-30.72	-64.81
Lycalopex gymnocercus	F	MACN 50498	-37.38	-64.60
Lycalopex gymnocercus	M	MACN 50495	-37.38	-64.60
Lycalopex gymnocercus	F	MACN 50491	-37.38	-64.60
Lycalopex gymnocercus	M	MACN 50502	-37.38	-64.60
Lycalopex gymnocercus	F	MACN 50505	-37.38	-64.60
Lycalopex gymnocercus	M	MACN 50494	-37.38	-64.60
Lycalopex gymnocercus	Unknown	MACN 32263	-23.14	-64.32
Lycalopex gymnocercus	M	MACN 24472	-31.40	-64.18
Lycalopex gymnocercus	M	MACN 13313	-29.76	-64.06
Lycalopex gymnocercus	F	MACN 13299	-29.76	-64.06
Lycalopex gymnocercus	F	MACN 49134	-38.69	-63.77
Lycalopex gymnocercus	F	MACN 49160	-38.69	-63.77
Lycalopex gymnocercus	F	MACN 49149	-38.69	-63.77
Lycalopex gymnocercus	M	MACN 49139	-38.69	-63.77
Lycalopex gymnocercus	M	MACN 49148	-38.69	-63.77
Lycalopex gymnocercus	M	MACN 49167	-38.69	-63.77
Lycalopex gymnocercus	Unknown	MNHN 712	-34.01	-62.24
Lycalopex gymnocercus	M	MACN 15389	-37.46	-61.93
Lycalopex gymnocercus	M	MACN 15388	-37.46	-61.93
Lycalopex gymnocercus	F	MACN 15390	-37.46	-61.93
Lycalopex gymnocercus	F	MACN 14386	-34.06	-61.89

Lycalopex gymnocercus	Unknown	MACN 24203	-24.93	-61.48
Lycalopex gymnocercus	Unknown	MNHN 1144	-35.29	-61.42
Lycalopex gymnocercus	M	MACN 15364	-36.23	-61.11
Lycalopex gymnocercus	F	MACN 15363	-36.23	-61.11
Lycalopex gymnocercus	Unknown	MZUSP 653	-31.45	-60.93
Lycalopex gymnocercus	Unknown	MZUSP 651	-31.45	-60.93
Lycalopex gymnocercus	F	MACN 33177	-38.38	-60.28
Lycalopex gymnocercus	Unknown	MACN 2628	-36.78	-59.85
Lycalopex gymnocercus	F	MACN 54133	-37.67	-59.81
Lycalopex gymnocercus	Unknown	MACN 24265	-30.76	-59.64
Lycalopex gymnocercus	F	MACN 14409	-38.56	-58.71
Lycalopex gymnocercus	Unknown	MACN 24208	-32.16	-58.40
Lycalopex gymnocercus	Unknown	MNHN 6280	-33.53	-58.28
Lycalopex gymnocercus	Unknown	MACN 24133	-37.85	-58.26
Lycalopex gymnocercus	Unknown	MACN 24134	-37.85	-58.26
Lycalopex gymnocercus	Unknown	MACN 24140	-37.85	-58.26
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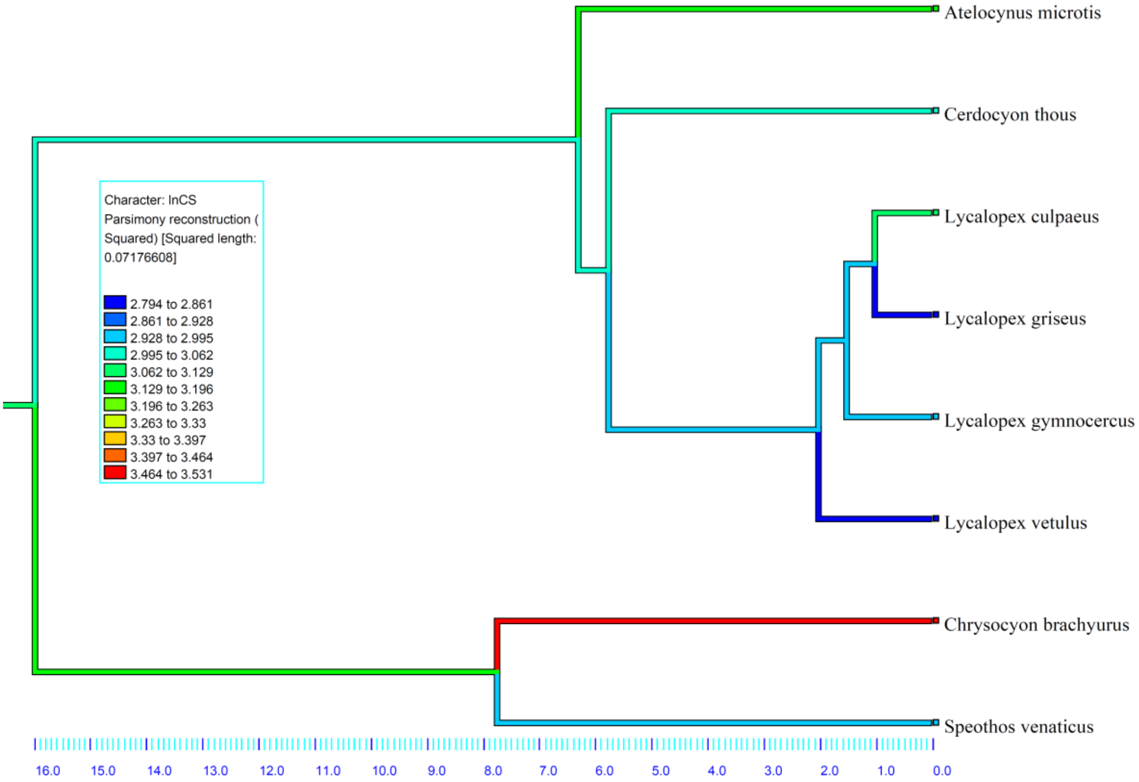
Lycalopex gymnocercus	Unknown	MNHN 3125	-34.18	-58.10
Lycalopex gymnocercus	Unknown	MACN 2448	-38.17	-58.10
Lycalopex gymnocercus	Unknown	MACN 24171	-35.58	-58.02
Lycalopex gymnocercus	Unknown	MACN 266	-38.16	-57.72
Lycalopex gymnocercus	F	MNHN 1111	-33.40	-57.54
Lycalopex gymnocercus	F	MNHN 263	-33.40	-57.54
Lycalopex gymnocercus	F	MNHN 268	-33.40	-57.54
Lycalopex gymnocercus	F	MNHN 269	-33.40	-57.54
Lycalopex gymnocercus	F	MNHN 270	-33.40	-57.54
Lycalopex gymnocercus	Unknown	MNHN 281	-33.40	-57.54
Lycalopex gymnocercus	Unknown	MNHN 282	-33.40	-57.54
Lycalopex gymnocercus	F	MNHN 278	-33.97	-57.08
Lycalopex gymnocercus	M	MNHN 2648	-33.97	-57.08
Lycalopex gymnocercus	M	MNHN 1014	-34.17	-56.68
Lycalopex gymnocercus	Unknown	MACN 26162	-36.88	-56.68
Lycalopex gymnocercus	Unknown	MNHN 2699	-31.70	-55.97
Lycalopex gymnocercus	M	MNHN 881	-33.99	-55.65
Lycalopex gymnocercus	M	MNHN 950	-33.99	-55.65
Lycalopex gymnocercus	M	MNHN 1939	-32.90	-55.55
Lycalopex gymnocercus	F	MNHN 1091	-33.80	-55.53
Lycalopex gymnocercus	F	MNHN 713	-33.80	-55.53
Lycalopex gymnocercus	F	MNHN 966	-33.80	-55.53
Lycalopex gymnocercus	Unknown	MNHN 1071	-33.80	-55.53
Lycalopex gymnocercus	Unknown	MNHN 1082	-33.80	-55.53
Lycalopex gymnocercus	Unknown	MNHN 1217	-33.80	-55.53
Lycalopex gymnocercus	Unknown	MNHN 1218	-33.80	-55.53
Lycalopex gymnocercus	Unknown	MNHN 1219	-33.80	-55.53

Lycalopex gymnocercus	M	MCNFZB 488	-28.17	-55.45
Lycalopex gymnocercus	F	UFSC 4592	-26.78	-52.06
Lycalopex gymnocercus	F	MHNCI 59	-26.48	-51.99
Lycalopex gymnocercus	M	MHNCI 61	-26.48	-51.99
Lycalopex gymnocercus	M	MHNCI 3020	-25.69	-51.65
Lycalopex gymnocercus	Unknown	MCP 168	-30.26	-50.51
Lycalopex gymnocercus	Unknown	MCP 618	-30.26	-50.51
Lycalopex gymnocercus	Unknown	MN 2355	-28.63	-50.43
Lycalopex gymnocercus	F	MHNCI 532	-25.10	-50.16
Lycalopex gymnocercus	M	MHNCI 55	-24.79	-50.01
Lycalopex gymnocercus	F	MHNCI 5583	-25.42	-50.00
Lycalopex gymnocercus	M	MHNCI 229	-25.42	-50.00
Lycalopex gymnocercus	Unknown	UFSC 329	-28.34	-49.63
Lycalopex gymnocercus	F	MNHN 271	-33.60	-57.90
Lycalopex gymnocercus	M	MNHN 273	-33.60	-57.90
Lycalopex vetulus	F	MN 5151	-21.61	-55.17
Lycalopex vetulus	F	MN 71112	-14.56	-52.45
Lycalopex vetulus	M	MN 71045	-14.56	-52.45
Lycalopex vetulus	Unknown	MN 71047	-14.56	-52.45
Lycalopex vetulus	Unknown	MN 71093	-14.56	-52.45
Lycalopex vetulus	M	MN 4909	-16.33	-48.95
Lycalopex vetulus	F	MZUSP 1018	-20.54	-47.40
Lycalopex vetulus	F	MZUSP 1011	-20.54	-47.40
Lycalopex vetulus	F	MZUSP 825	-20.54	-47.40
Lycalopex vetulus	F	MZUSP 1015	-20.54	-47.40
Lycalopex vetulus	M	MZUSP 1016	-20.54	-47.40
Lycalopex vetulus	M	MZUSP 1084	-20.54	-47.40
Lycalopex vetulus	Unknown	MZUSP 1012	-20.54	-47.40
Lycalopex vetulus	M	MZUSP 3046	-17.34	-44.93
Lycalopex vetulus	Unknown	MN 3037	-19.54	-44.38
Lycalopex vetulus	F	MN 4241	-19.65	-43.89
Speothos venaticus	M	MACN 5067	-17.46	-63.66
Speothos venaticus	Unknown	MACN 33154	-17.87	-63.00
Speothos venaticus	M	MPEG 6535	2.82	-60.68
Speothos venaticus	M	MN 3035	-14.85	-57.76
Speothos venaticus	M	MPEG 1042	-2.45	-54.70
Speothos venaticus	M	MACN 16510	-25.66	-54.50
Speothos venaticus	Femea	MPEG 5615	-2.49	-54.30
Speothos venaticus	Femea	MPEG 8794	-2.49	-54.30
Speothos venaticus	M	MPEG 8793	-2.49	-54.30
Speothos venaticus	M	MPEG 5614	-2.49	-54.30
Speothos venaticus	F	MZUSP 2684	-26.44	-49.35
Speothos venaticus	Unknown	MZUSP 2685	-26.44	-49.35
Speothos venaticus	M	MPEG 1778	-1.46	-48.50

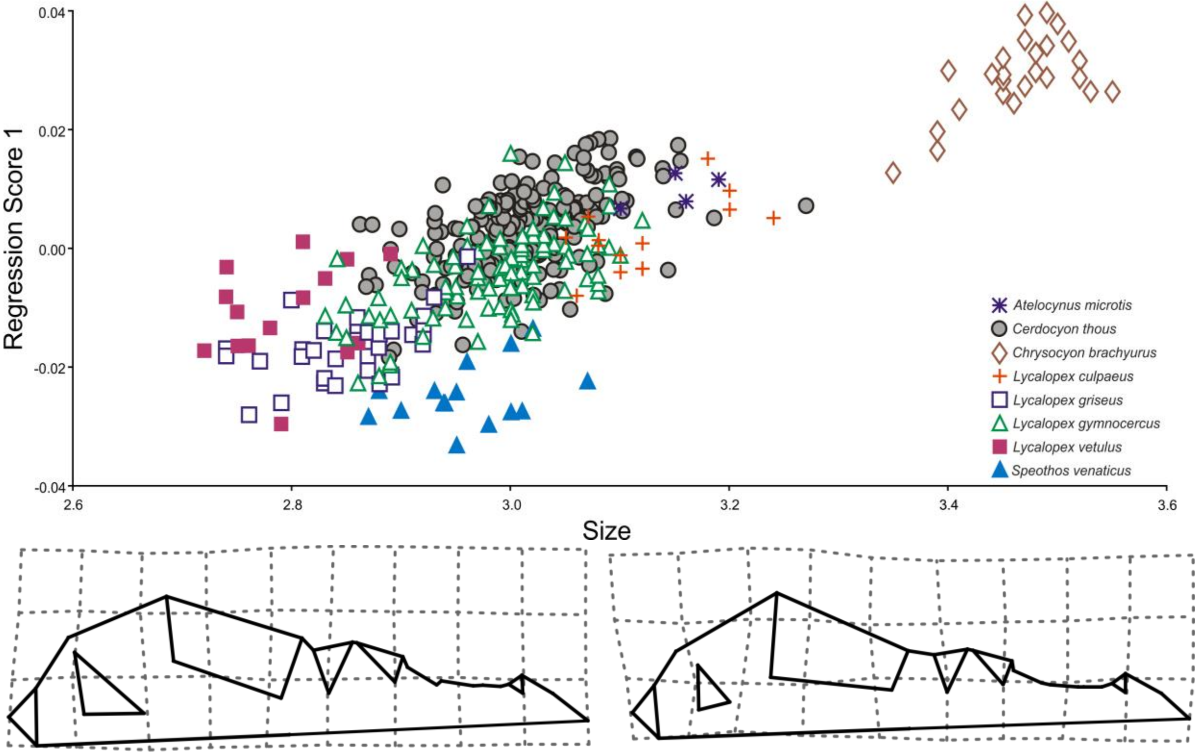
Speothos venaticus	M	MPEG 1780	-1.46	-48.50
Speothos venaticus	M	MN 25668	-15.79	-47.88

South American canid phylogenetic tree generated using the 10K tree project from Arnold et al. (2010). Branch lengths are proportional to million years. Natural log transformed centroid size was also mapped into the tree using squared change parsimony algorithm (Maddison and Maddison 1991) to provide stronger support to the lack of phylogenetic signal in this trait.

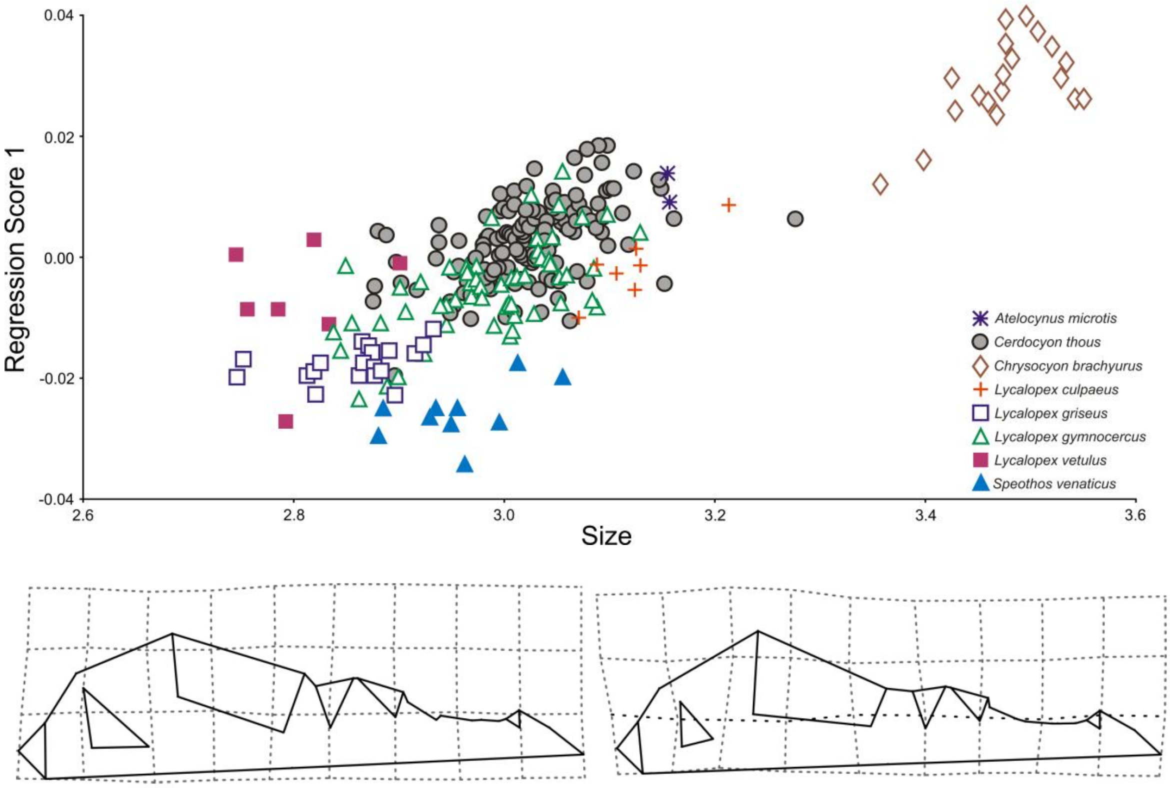


```
#NEXUS
[created by the 10kTree Website - http://10kTrees.fas.harvard.edu]
BEGIN TREES;
translate
1 Atelocynus_microtis,
2 Chrysocyon_brachyurus,
3 Cerdocyon_thous,
4 Lycalopex_culpaeus,
5 Lycalopex_griseus,
6 Lycalopex_gymnocercus,
7 Lycalopex_vetulus,
8 Speothos_venaticus;
tree consensus_8species =
((1:6.255354,(3:5.718385,(((4:0.981755,5:0.981755):0.484353,6:1.466108):0.515162,7:1.981
270):3.737116):0.536969):9.688054,(2:7.698185,8:7.698185):8.245222);
END;
```

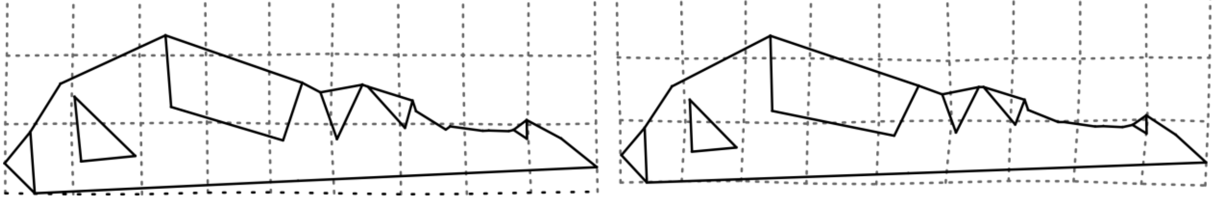
Regression plot showing the effect of size (lnCS) on canid skull shape using 431 specimens. Every species is labelled according to different colour and symbol. Deformation grids show relative shape changes from the smaller (left, lnCS = 2.72) to the larger (right, lnCS = 3.55) individual.



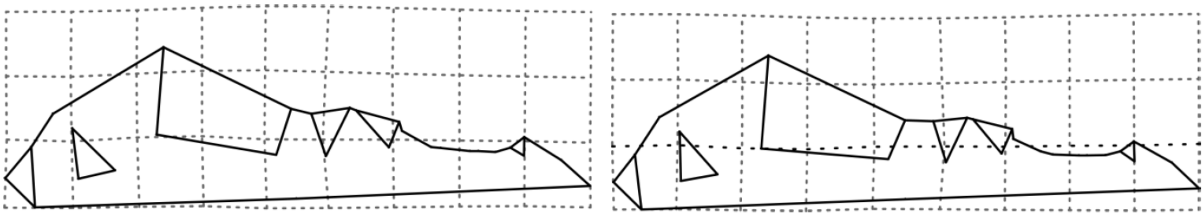
Regression plot showing the effect of size (lnCS) on canid skull shape using 262 locality averaged sub-samples. Every species is labelled according to different colour and symbol. Deformation grids show relative shape changes from the smaller (left, lnCS = 2.74) to the larger (right, lnCS = 3.55) individual.



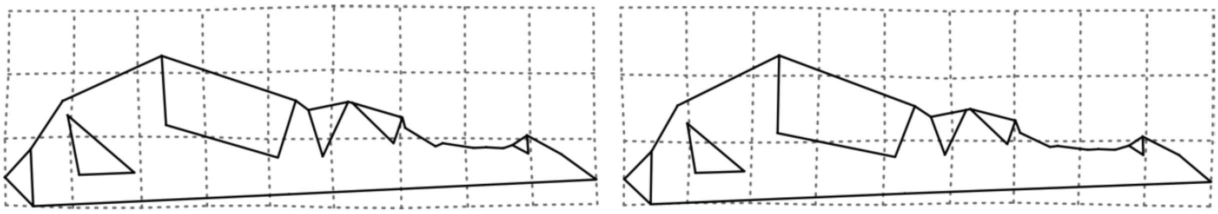
Regression deformation grids showing relative shape changes from the smaller (left, lnCS = 2.86) to the larger (right, lnCS = 3.27) individual of *Cerdocyon thous*.



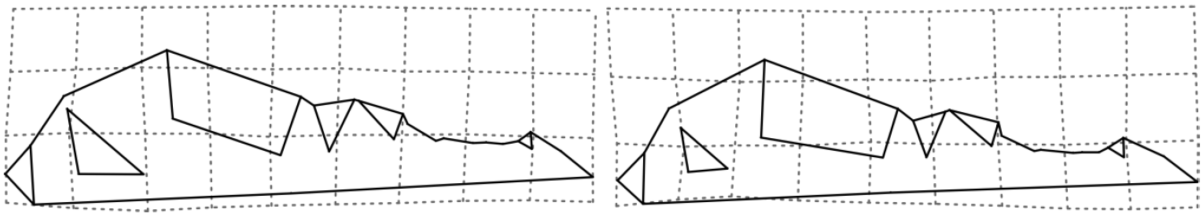
Regression deformation grids showing relative shape changes from the smaller (left, lnCS = 3.35) to the larger (right, lnCS = 3.55) individual of *Chrysocyon brachyurus*.



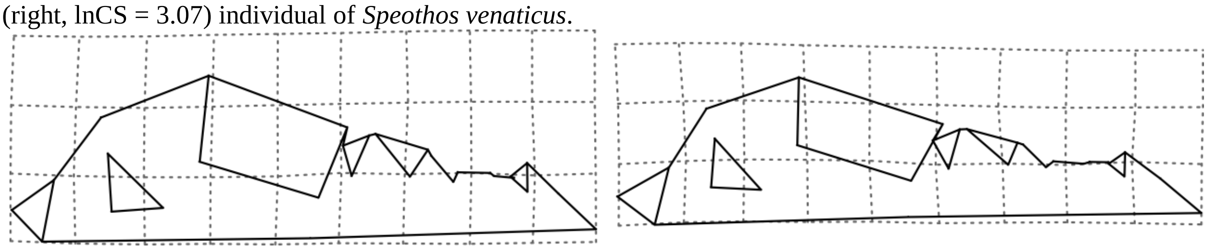
Regression deformation grids showing relative shape changes from the smaller (left, lnCS = 2.83) to the larger (right, lnCS = 3.12) individual of *Lycalopex gymnocercus*.



Regression deformation grids showing relative shape changes from the smaller (left, lnCS = 2.72) to the larger (right, lnCS = 3.24) individual of the *Lycalopex* genera.



Regression deformation grids showing relative shape changes from the smaller (left, lnCS = 2.87) to the larger (right, lnCS = 3.07) individual of *Speothos venaticus*.



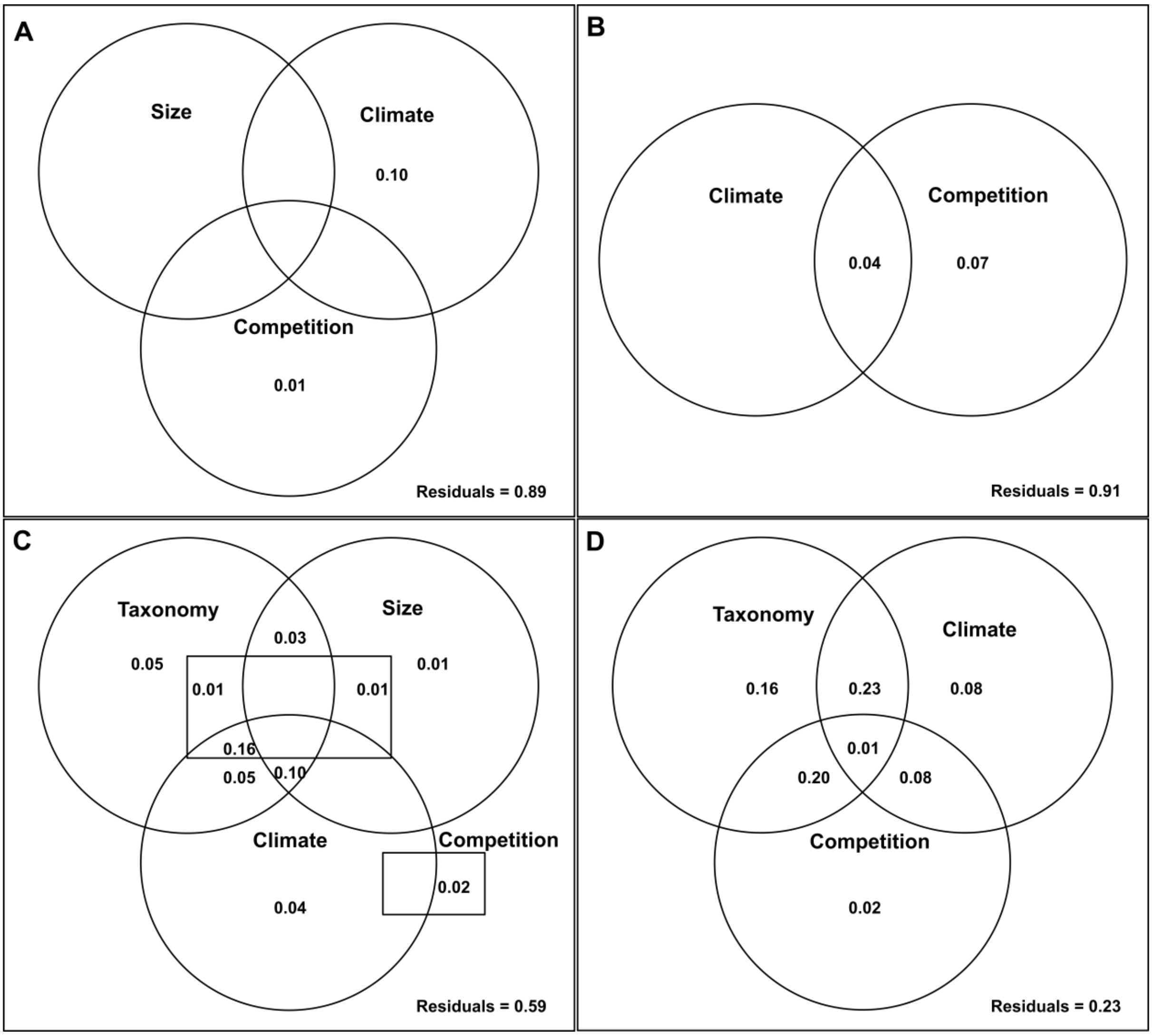
Variation partitioning with skull shape of canids species as dependent variable and taxonomy, size, climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Taxonomy	7	0.49983	0.48604	36.261	**0.005**
Size	1	0.08589	0.08237	24.429	**0.005**
Climate	19	0.26398	0.20619	4.568	**0.005**
Competition	3	0.08386	0.0732	7.872	**0.005**
Taxonomy + Size	8	0.50608	0.49047	32.404	**0.005**
Taxonomy + Climate	26	0.56103	0.51247	11.552	**0.005**
Taxonomy + Competition	10	0.51103	0.49155	26.233	**0.005**
Size + Climate	20	0.3427	0.28815	6.283	**0.005**
Size + Competition	4	0.15128	0.13807	11.452	**0.005**
Competition + Climate	22	0.29931	0.23481	4.640	**0.005**
Taxonomy + Size + Climate	27	0.56575	0.51564	11.291	**0.005**
Taxonomy + Size + Competition	11	0.51608	0.49479	24.238	**0.005**
Taxonomy + Climate + Competition	29	0.57141	0.51783	10.666	**0.005**
Size + Climate + Competition	23	0.36594	0.30467	5.972	**0.005**
All	30	0.57507	0.51988	10.421	**0.005**
Taxonomy “Pure”	7		0.21522	16.241	**0.005**
Size “Pure”	1		0.00205	1.991	**0.035**
Climate “Pure”	19		0.02509	1.688	**0.005**
Competition “Pure”	3		0.00424	1.689	**0.01**

Variation partitioning with skull size of canids species as dependent variable and taxonomy, climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Taxonomy	7	0.84305	0.83873	194.91	**0.001**
Climate	19	0.15318	0.08669	2.3039	**0.005**
Competition	3	0.13405	0.12398	13.312	**0.001**
Taxonomy + Climate	26	0.88041	0.86718	66.54	**0.001**
Taxonomy + Competition	10	0.85391	0.84809	146.72	**0.001**
Competition + Climate	22	0.22998	0.1591	3.2446	**0.001**
All	29	0.89205	0.87856	66.111	**0.001**
Taxonomy “Pure”	7		0.71946	203.28	**0.001**
Climate “Pure”	19		0.03047	4.3141	**0.001**
Competition “Pure”	3		0.01138	8.3417	**0.001**

Schematic depiction of the factors analyzed in partition variation to illustrate both their individual contribution and their interaction components in the variance of shape (A) and size (B) of *Cerdocyon* and shape (C) and size of *Lycalopex* (D). Values < 0 not shown.



Variation partitioning with skull shape of *Cerdocyon* as dependent variable and size, climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Size	1	0.00973	0.00271	1.3856	0.150
Climate	19	0.22307	0.10306	1.8587	**0.005**
Competition	3	0.03016	0.00923	1.441	**0.045**
Size + Climate	20	0.22962	0.10333	1.8182	**0.005**
Size + Competition	4	0.0378	0.00991	1.3554	0.055
Climate + Competition	22	0.25039	0.11297	1.822	**0.005**
All	23	0.25587	0.11204	1.779	**0.005**
Size "Pure"	1		-0.00092	0.8752	0.555
Climate "Pure"	19		0.10213	1.8354	**0.005**
Competition "Pure"	3		0.00871	1.3989	0.085

Variation partitioning with skull size of *Cerdocyon* as dependent variable and climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Climate	19	0.15196	0.02096	1.16	0.300
Competition	3	0.12683	0.10799	6.7303	**0.005**
All	22	0.22843	0.08698	1.6149	**0.035**
Climate "Pure"	19		-0.02101	0.8316	0.670
Competition "Pure"	3		0.06602	3.9645	**0.020**

Variation partitioning with skull shape of *Lycalopex* as dependent variable and taxonomy, size, climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Taxonomy	3	0.35301	0.32963	15.096	**0.005**
Size	1	0.08423	0.07345	7.8176	**0.005**
Climate	19	0.43322	0.27249	2.6954	**0.005**
Competition	3	0.14819	0.1174	4.8133	**0.005**
Taxonomy + Size	4	0.381	0.35081	12.618	**0.005**
Taxonomy + Climate	22	0.53388	0.37365	3.3321	**0.005**
Taxonomy + Competition	6	0.40021	0.35523	8.8967	**0.005**
Size + Climate	20	0.48304	0.32639	3.0836	**0.005**
Size + Competition	4	0.30464	0.27072	8.9811	**0.005**
Competition + Climate	22	0.48695	0.31058	2.7611	**0.005**
Taxonomy + Size + Climate	23	0.5555	0.39323	3.4233	**0.005**
Taxonomy + Size + Competition	7	0.42343	0.37234	8.2881	**0.005**
Taxonomy + Climate + Competition	25	0.57248	0.39726	3.2674	**0.005**
Size + Climate + Competition	23	0.53043	0.359	3.0942	**0.005**
All	26	0.58954	0.41168	3.3146	**0.005**
Taxonomy “Pure”	3		0.05268	2.8803	**0.005**
Size “Pure”	1		0.01441	2.4944	**0.005**
Climate “Pure”	19		0.03934	1.278	**0.025**
Competition “Pure”	3		0.01845	1.6586	**0.025**

Variation partitioning with skull size of *Lycalopex* as dependent variable and taxonomy, climate and competition as dependent variables. P values tests for the significance of F after 1000 permutations. Significance is highlighted.

	Df	R²	Adj. R²	F	P value
Taxonomy	3	0.61023	0.59614	43.316	**0.005**
Climate	19	0.52694	0.39279	3.928	**0.005**
Competition	3	0.32856	0.30429	13.538	**0.005**
Taxonomy + Climate	22	0.81435	0.75053	12.761	**0.005**
Taxonomy + Competition	6	0.71278	0.69124	33.089	**0.005**
Climate + Competition	22	0.71151	0.61234	7.1747	**0.005**
All	25	0.83624	0.76913	12.46	**0.005**
Taxonomy "Pure"	3		0.15679	15.488	**0.005**
Climate "Pure"	19		0.07788	2.4204	**0.01**
Competition "Pure"	3		0.01859	2.7181	0.055

DISCUSSÃO

Nossos resultados demonstram que os canídeos sul-americanos diferem em forma do crânio, especialmente a espécie *S. venaticus*, que possui características peculiares como: arcos zigomáticos, dentes carnassiais superiores, caninos e incisivos mais avantajados e focinho proporcionalmente mais curto e robusto, adaptações características de uma dieta hipercarnívora (VALKENBURGH, 1991; KLEIMAN, 1972). A raposinha-do-campo (*L. vetulus*) também se destaca com uma forma do crânio única, se comparada com as outras espécies do seu gênero. Esta espécie tem uma grande bula auditiva e focinho curto e grosso, tornando-a fenotipicamente mais similar aos gêneros *Cerdocyon* e *Atelocynus* (ver Figura 2, Capítulo 2). A raposinha-do-campo vive em regiões essencialmente quentes e possui uma dieta baseada, principalmente, no consumo de cupins (DALPONTE, 2009). Enquanto isso, as outras raposas do gênero *Lycalopex* são onívoras e mais restritas a ambientes frios. Estes atributos ecológicos são possívelmente a razão para o agrupamento peculiar de *L. vetulus* com outros gêneros de canídeos (SILLERO-ZUBIRI et al., 2004; JOHNSON & FRANKLIN, 2011).

O tamanho do corpo também varia consideravelmente entre a comunidade de canídeos, principalmente no lobo-guará, a maior espécie. Entre os representantes do gênero *Lycalopex* esta diferença de tamanho também é evidente, confirmando e expandindo as observações de WAYNE et al. (1989): a diferença de tamanho pode ser interpretada como um mecanismo de partição de nicho que eventualmente permitiu que estes taxa desempenhassem exigências ecológicas diferentes. Assim, o papel da alometria interespecífica na amostra geral é evidente, com tamanho explicando quase 10% da variância da forma do crânio (comparável ao que foi encontrado em estudos anteriores, FIGUEIRIDO et al., 2011; 2013 em toda ordem Carnivora e MELORO et al., 2015 em canídeos). A ANCOVA sugere que a variação alométrica do crânio difere entre as espécies, onde aquelas mais especializadas demonstram uma maior porcentagem de variação explicada pelo tamanho, se comparada às generalistas (ver Tabela 4, Capítulo 2). Realmente, o cachorro-vinagre (*S. venaticus*) exibe um componente alométrico forte, possívelmente relacionado com a sua demanda biomecânica, por ser um predador especializado (SLATER et al., 2009). A alometria não foi importante para muitas espécies de *Lycalopex*, exceto por *L. gymnocercus.* Isso pode ser resultante da grande diferenciação taxonômica que ocorreu dentro do gênero em relação a características de tamanho, mas não de forma (ver Tabelas 2, 3, Capítulo 2). Além disso, o deslocamento de caráter localizado em alguns membros do gênero pode ter favorecido estas mudanças de tamanho, que não foram acompanhadas por mudanças drásticas na forma do crânio.

De fato, as diferenças no tamanho corporal podem ser especialmente importantes para habilitar a coexistência interespecífica entre mamíferos carnívoros em simpatria (VALKENBURGH & WAYNE, 1994), uma vez que a diferença de tamanho entre competidores pode facilitar a partição de recursos de acordo com o tamanho de suas presas (MCDONALD, 2002). Os resultados deste estudo sugerem que este tipo de estratégia é importante para a manutenção da diversidade dos canídeos sul-americanos, já que a competição significativamente explica uma pequena porção da variação interespecífica do tamanho do crânio nestes animais. Também é plausível que a competição tenha desempenhado um papel mais relevante no passado, quando a diversidade destes animais era maior, sobretudo com relação as formas hipercarnívoras (WANG et al., 2008).

Em escala intraespecífica, a influência da competição na variação do crânio fica mais evidente. *Cerdocyon thous*, quando em simpatria com *L. vetulus*, aumenta de tamanho (contrariamente ao que é esperado pela regra de Begmann). Neste caso, esta estratégia parece ser suficiente para viabilizar a coexistência destas duas espécies no Brasil central. Apesar de também aumentar seu tamanho ao sul da América do Sul (desta vez, em conformidade com a regra Bergmann), quando em simpatria com *L. gymnocercus*, *C. thous* também altera sua forma substancialmente. Por ser maior, é possível que *L. gymnocercus* seja uma competidora mais desafiadora para a população sul de *C. thous*, se comparada a *L. vetulus* para a população mais ao norte. Em resumo, estes três canídeos são onívoros e, por isso, podem diferir quantitativamente no consumo dos diferentes tipos de alimentos disponíveis afim de minimizar a competição (VALKENBURGH & WAYNE, 1994). No geral, os crânios da população de *C. thous* ao sul da América do Sul estão mais adaptados ao consumo de pequenos vertebrados, ou seja, possui pequenos molares, focinho alongado e arcos zigomáticos maiores. PEDÓ et al. (2006) encontraram resultados semelhantes a esta interpretação, quando registraram um grande consumo de vertebrados pelo cachorro-do-mato nesta região.

O clima também é um fator importante para explicar a variação da forma do crânio de *C. thous*, embora não seja significativo para tamanho. Isto foge do esperado, uma vez que *C. thous* segue a regra de Bergmann, ou seja, aumenta em tamanho com o aumento da latitude (MARTINEZ et al., 2013; este estudo). Nas análises interespecíficas contidas nesta dissertação (ver Capítulo 2), o clima aparece como um dos fatores mais importantes para explicar a variação do crânio dos canídeos sul-americanos. Mais especificamente, ambientes sazonais, como o sul da América do Sul, estão, no geral, ocupados por fenótipos não especialistas, graças a dominância do gênero *Lycalopex* na região. Enquanto isso, na Amazônia existe a presença de três morfotipos diferentes: *Speothos*, *Atelocynus* e *Cerdocyon.* A interação peculiar entre estes três gêneros ocorre exclusivamente nesta região. Partindo de um ponto de vista macroevolutivo, isto suporta a Amazônia como um ecossistema único, abrigando uma comunidade de canídeos ecologicamente e morfologicamente diversa, com a predominância de morfotipos carnívoros (crânios caracterizados por grandes arcos zigomáticos e rosto curto, ver Figura 5, Capítulo 2).

Além disso, existe um padrão geral em toda América do Sul de coexistência envolvendo de três a quatro espécies diferentes de canídeos em diferentes condições climáticas: no extremo sul, existe uma dominância de raposas dos gêneros *Lycalopex*, sugerindo que o fenótipo hipercarnívoro foi extinto na região; em ambientes tipo savana, como o Cerrado, crânios de *Chrysocyon*, *Cerdocyon* e *Lycalopex* foram registrados (dependendo da latitude a coocorrência é entre *L. gymnocercus* ou *L. vetulus*). JÁCOMO et al. (2004) reportaram pouca sobreposição ecológica entre *Chrysocyon*, *Cerdocyon* e *L. vetulus* no Cerrado graças às diferenças nos seus hábitos alimentares ou padrões de atividade. Também espera-se que o cachorro-vinagre não possua hábitos substancialmente parecidos às outras espécies de canídeos, por ser hipercarnívoro (OLIVEIRA, 2009).

CONCLUSÃO

Conclui-se que *C. thous* tenha adotado dois diferentes meios para minimizar a competição com espécies dos gêneros *Lycalopex* ao longo de sua distribuição, onde a regra de Bergmann também se aplica:

- Na presença de *L. gymnocercus*, ao sul da América do Sul, *C. thous* altera sua forma em relação a características associadas à predação de pequenos vertebrados. Isso sugere uma mudança no nicho alimentar desta espécie, comumente onívora, enfatizando a carnivoria. Além disso, no sul o deslocamento de caráter fortalesce a regra de Bergmann, uma vez que registramos um considerável aumento do tamanho corporal em latitudes maiores.
- Na presença de *L. vetulus*, na parte central da América do Sul, *C. thous* é maior do que o esperado pela regra de Bergmann, sugerindo que o deslocamento de caráter enfraqueça a mesma. Neste caso, mudanças na forma de *C. thous* não são claramente evidentes, sugerindo que o distanciamento de tamanho corporal entre estas duas espécies seja suficiente para minimizar a competição entre elas.

Ao investigar a variação do crânio dos canídeos sul-americanos ao longo de sua distribuição, pode-se concluir que a taxonomia é o maior contribuinte para explicar a variação fenotípica, seja analisando a forma ou o tamanho do crânio. O próprio tamanho é um fator importante na variação da forma do crânio destes animais, fenômeno conhecido como alometria. Neste caso, a alometria se torna mais importante para algumas espécies do que outras. O cachorro-vinagre, por exemplo, exibe um sinal alométrico forte, padrão comumente encontrado em hipercarnívoros. Enquanto isso, a grande maioria das raposas do gênero *Lycalopex* não tem sua forma afetada pelo tamanho.

Graficamente, a discriminação taxonômica sozinha não exibe diferenças drásticas com relação à forma da maioria das espécies. Porém, quando o clima é adicionado à equação, a história evolutiva deste grupo torna-se mais clara. Existe uma substituição de morfotipos ao longo da variação climática destes animais: em ambientes sazonais, como o sul da América do Sul, existe um domínio de fenótipos não especializados, representado principalmente pelo gênero *Lycalopex*. Enquanto isso, o oposto é encontrado em climas tropicais, a exemplo da Amazônia, onde existe a presença de três fenótipos diferentes, representados pelos gêneros *Speothos*, *Atelocynus* e *Cerdocyon*, destacando aqui o aumento de características ligadas à carnivoria (aumento do arco zigomático e diminuição do rostro) dentro da Amazônia, algo único deste bioma, uma vez que existe uma crescente relação entre latitude e o número de espécies onívoras na América do Sul. A competição também desempenha um papel na variação do crânio dos canídeos sul-americanos, sobretudo no tamanho do mesmo. Entretanto, a relação entre competição e a variação fenotípica é relativamente fraca dentro da comunidade como um todo, diferentemente do padrão encontrado em *Cerdocyon thous*. Por isso, hipotetizamos que este fator possa ter tido uma maior importância no passado, quando a diversidade de canídeos sul-americanos era maior.

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