

Bergmann's rule across the equator: a case study in *Cerdocyon thous* (Canidae)

Pablo A. Martinez^{1*}, Dardo A. Marti², Wagner F. Molina¹ and Claudio J. Bidau³

¹Departamento de Biologia Celular e Genética, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brazil; ²Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, Posadas, Argentina; and ³Sede Alto Valle, Universidad Nacional de Rio Negro, Villa Regina, Argentina

Summary

1. The variation in cranial size of the crab-eating fox *Cerdocyon thous* was analysed in relation to latitude and several environmental variables throughout its distribution in South America.

2. We tested the existence of clines to determine whether this canid follows Bergmann's rule to the north and south of the Equator. Also, using niche modelling, we analysed whether the climatic changes during the last glaciation could have influenced Bergmann's rule in this species. We quantified the size of the cranium of *C. thous* ($n = 300$). The data were divided into two groups: (i) south of the Equator ($n = 163$) and (ii) north of the Equator ($n = 137$). We performed correlations, OLS regressions and simultaneous autoregressions to analyse the relationship between the variation in size and different geographic and environmental variables. Data of occurrence ($n = 594$) together with ambient variables from the present and the last glacial maximum (LGM) were used to predict the occurrence of *C. thous* with the implementation of the maximum entropy method. Present-day and historical distribution maps were obtained.

3. The variation in the size of the cranium of *C. thous* showed two trends. In the south of Equator, we observed that the size of the skull shows an inverse relationship with temperature-related variables and a positive one with precipitation, while in north of the Equator, we observed the opposite relationship. Populations south of the Equator follow Bergmann's rule showing increasing size with increasing latitude. To the north of the Equator, a non-Bergmannian pattern occurs because size decreases with increasing latitude.

4. Niche modelling showed two present-day groupings in South America, one north of Amazonia and the other south. However, for the period of the LGM, four groups emerged, possibly related to the four subspecies presently described for *C. thous*. Therefore, it is possible that the observed pattern – southern populations following Bergmann's rule while northern populations reflecting the opposite – has been influenced by the events that occurred during the LGM that could have led to the differentiation of populations.

Key-words: canids, ecological rules, last glacial maximum, precipitation, South America, subspecies, temperature

Introduction

Macroecology has provided new perspectives through which we can examine geographic distribution patterns of species, notably analyses of latitudinal/altitudinal gradients and of ecogeographic rules (Gaston, Chown & Evans 2008). One of the first and more well-known

generalizations in ecology was suggested by Bergmann (1847) and establishes that homeothermic animals inhabiting higher latitudes and colder climates tend to have larger body sizes than related species living in warmer environments. This hypothesis, known as 'Bergmann's rule', postulates that this pattern is due to the fact that larger animals have a smaller surface area in relation to body volume, thus allowing better heat retention (or less heat loss) than smaller animals. However, classic Bergmannian patterns (or converse ones) are not always easy to explain,

*Correspondence author. E-mail: pablo_sc82@hotmail.com

because in many cases, ambient temperature alone is not sufficient to account for all observed trends. Different ecological and evolutionary mechanisms have been put forward to complement or refute Bergmann's original thermoregulatory explanation. Body size clines could follow geographic differences in primary productivity (Rosenzweig 1968; Geist 1987); in seasonality and ambient predictability, leading to improved survival of larger animals in higher latitudes (Calder 1984; Lindstedt & Boyce 1985; Millar & Hickling 1990; McNab 1999); in differential predation (Medina, Martí & Bidau 2007); and others.

Clearly, many selective forces can affect body size in different species or populations, and regional- or global-scale deviations of Bergmann's rule may occur (Dayan *et al.* 1991), but independently of the driving mechanism leading to Bergmannian patterns, the rule is an empirical generalization whose meaning depends on its prevalence in homeothermic organisms (Meiri & Dayan 2003). Such mechanisms have been amply debated in the last six decades (i.e. Mayr 1956; Scholander 1956; Irving 1957), and the ecogeographic pattern has received wide support from studies of mammals (Ashton, Tracy & de Queiroz 2000; Meiri & Dayan 2003; Diniz-Filho *et al.* 2007) and birds (Ashton 2002).

Besides ambient factors that may presently influence body size, several other effects must be considered such as life history (Brown 1995; Haskell, Ritchie & Olf 2002; Angilletta *et al.* 2004; Shelomi 2012), interactions between species (Dayan *et al.* 1989), evolutionary history (Renaud, Benammi & Jaeger 1999; Blois, Feranec & Hadly 2008) and anthropic effects (McCoy 2012; Yom-Tov, Yom-Tov & Zachos 2013; and references therein). Recent advances in geographic information systems (GIS) allow species niche modelling on the basis of environmental attributes (Guisan & Thuiller 2005). These models have been successfully applied to several animal groups (Luoto, Kuussaari & Toivonen 2002; Raxworthy *et al.* 2003), in different ecosystems and temporal intervals (Werneck *et al.* 2011), producing reliable results (Elith *et al.* 2006) and generating useful information on historical processes.

Several lines of evidence have been used to assess the relevance of climatic fluctuations and the changes in vegetation in the biological diversification of the Neotropical region (Moritz *et al.* 2000; Carnaval *et al.* 2009; Werneck *et al.* 2011). The model known as 'refugia theory' was centred in the tropical forests and suggested that climatic changes during the Pleistocene, especially during the last glacial maximum (LGM) about 21 000 years ago, led to fragmentation of the tropical forests creating refugia separated by savannas and other open and dry formations. This could have promoted the expansion or retraction of the distributional ranges of species leading to diversification, fuelled by forest fluctuations (Haffer 1969; Pennington, Prado & Pendry 2000). Meanwhile, the open formations could have served as corridors for connecting populations to the north and south of Amazonia during this period (Pennington, Prado & Pendry 2000; Pennington *et al.* 2004).

The effects of climate change have had a great influence on flora and fauna and have been well documented in mammalian evolutionary history (Patterson & Pascual 1972; Janis 1993; MacFadden 2000). The canids reached South America after the formation of the Panama isthmus about 2.3 mya through at least two independent colonization events, producing the origin of the two present-day groups of canids of the continent. Thus, a rapid radiation seems to have occurred, which could be related to the retraction and expansion of the glaciers and to the climatic changes in the Andes at the culmination of the Pleistocene (Markgraf 1989; Perini, Russo & Schrago 2010).

Cerdocyon thous (Linnaeus, 1766) is a South American endemic, and the genus is usually considered as monotypic (Berta 1982; Tedford, Taylor & Wang 1995). It is a generalist species, and its diet varies according to the time of the year and the inhabited region being one of the more plastic species within the Neotropics, thus having a large geographic distribution (Trovati, de Brito & Duarte 2007). *Cerdocyon thous* has a disjunct distribution in South America with two large dispersion areas, north and south of the Equator, showing a clear preference for open habitats (Bisbal 1989; Sillero-Zubiri *et al.* 2004; Trovati, de Brito & Duarte 2007). Its geographic distribution in the north of the Equator extends on northern Colombia and almost all Venezuela with the exception of the southern Amazonia state and north of Guyana and Surinam. South of the Equator, the species is found in the north-eastern, central and southern Brazil, Paraguay, central-northern Argentina, Bolivia and Uruguay (Sillero-Zubiri *et al.* 2004). Five subspecies have been recognized within its distributional range: *C. t. germanus*, restricted to the high savannas of central Colombia; *C. t. aquilus*, in savannas and forests of Colombia and Venezuela; *C. t. thous*, found in the Guyanas, eastern Amazonia and northern Brazil; *C. t. azarae*, in north-eastern and central Brazil; and *C. t. entrerrianus*, in southern Brazil, northern Argentina, Paraguay, western Bolivia, and Uruguay (Cabrera 1931, 1958; Tate 1939; Berta 1982; Bisbal 1988). However, this subspecific classification is not without criticism, once many diagnostic characters were mainly based on differences in fur colour, which shows a wide intraspecific variation. Nevertheless, evident morphological differences have been observed between both subspecies isolated by the Orinoco river in Venezuela (Bisbal 1988), as well as between populations from northern, eastern and southern South America (Machado & Hingst-Zaher 2009).

Although a vast literature analysing Bergmann's rule in carnivores exists, there is a clear bias towards studies of taxa in the northern hemisphere, especially those with temperate climates, in relation to tropical ones (Meiri, Dayan & Simberloff 2004). Furthermore, very few investigations have focused on tropical taxa with distributions in the north and south of the Equator (e.g. Graves 1991; Brumfield & Remsen 1996); thus, *C. thous* represents an excellent mammalian model to assess the effects of

ambient variables and historical processes influencing body size across the Equator.

In the present work, using geometrical morphometric procedures, we studied whether the body size of *C. thous*, as represented by cranial measurements, follows Bergmann's rule across its geographic distribution north and south of the Equator; further, through ecological niche modelling, we studied the possible historical effects of the LGM in structuring populations and influencing Bergmannian patterns.

Material and methods

OBTENTION OF DATA FOR GEOMETRIC MORPHOMETRICS

A total of 300 crania of *C. thous*, covering most of its geographic distribution, were analysed (Fig. 1). Individuals were identified at the species level on the basis of discrete morphological characters *sensu* Berta (1982, 1988) and Tedford, Taylor & Wang (1995). Adult individuals were identified using global skull size, the state of the cranial sutures and tooth eruption. The specimens were obtained from several museum collections: Argentina, Fundación Félix de Azara, Museo de Ciencias Naturales 'Florentino Ameghino', Museo de Ciencias Naturales de La Plata, and Universidad Nacional de Salta; Brasil, Museu de Zoologia da Universidade de São Paulo, Museu Nacional do Rio de Janeiro, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Bolivia, Museo de Historia Natural 'Noel Kempff Mercado', Museo Nacional de Historia Natural de La Paz; Venezuela, Museo de la Estación Biológica de Rancho Grande, Museo de Ciencias Naturales de Caracas.

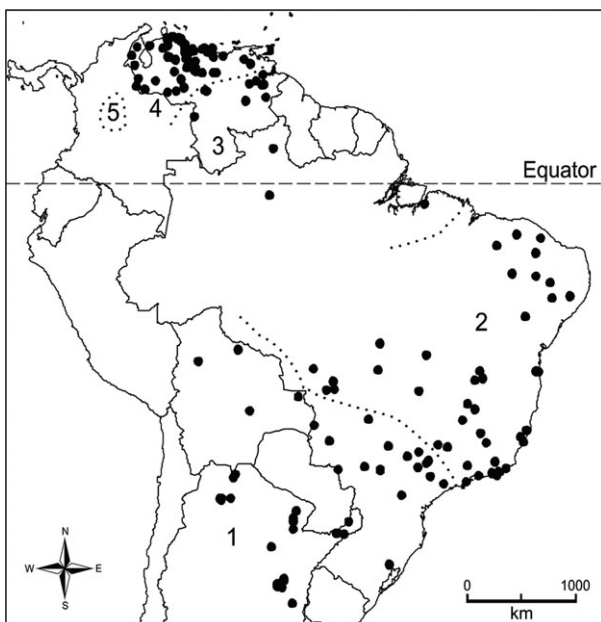


Fig. 1. Geographic distribution of the individuals of *Cerdocyon thous* in South America. The dotted line separates the different subspecies proposed by Cabrera (1931). (1) *C. t. enterrrianus*, (2) *C. t. azarae*, (3) *C. t. thous*, (4) *C. t. aquilus* and (5) *C. t. germanicus*.

The skulls were photographed in dorsal view with a Digital Sony DSC-H10 8.1 mp camera (Sony, Japan). The support on where they were photographed as well as the camera, were always levelled, and all the photographs were taken by the same person, as to minimize possible effects of distortion. A total of 27 landmarks in two dimensions were digitalized on the obtained images with the TPSDIG v2.16 software (Rohlf 2010; Fig. 2). Procrustes superposition (Dryden & Mardia 1998) was performed with the software MORPHOJ (Klingenberg 2008). Centroid size (Cs), a measurement of landmark dispersion around their centre of gravity, was used as size estimator. It is calculated as the square root of the sum of the squared distances of all landmarks from their centroid (for details of mathematical procedures and applications, see Bookstein 1991 and Zelditch *et al.* 2004). To evaluate possible photographic errors, the value of the Cs was preliminarily analysed separately on the right and left sides of the dorsal view using 16 landmarks and also the length of skull (cm). Both sides produced similar results between different size estimators (Fig. 3); thus, the final analysis of Cs involved 27 landmarks as shown in Fig. 2.

DATA ANALYSIS

To test the possible existence of sexual size dimorphism that could affect our results, we performed ANOVA analyses of Cs between females, males and sexually undetermined individuals in each subspecies. No significant differences within subspecies were observed ($P > 0.05$); thus, all individuals were analysed jointly regardless of sex. Results are shown in Fig. 4.

For ecogeographic variation, a total of 23 variables, 22 climatic and one topographic, obtained from Cramer & Leemans (2001) and the WORLDCLIM data base (available: www.worldclim.com). Because the proximity to large human settlements can influence the quantity and quality of available food for the species and thus affect body size (McCoy 2012), we obtained population density values for the year 2000 of the relevant geographic areas to test possible anthropic effects using the data base at International Earth Science Information Network (CIESIN), Columbia University, and Centro Internacional de Agricultura Tropical (CIAT; available at <http://sedac.ciesin.columbia.edu/>

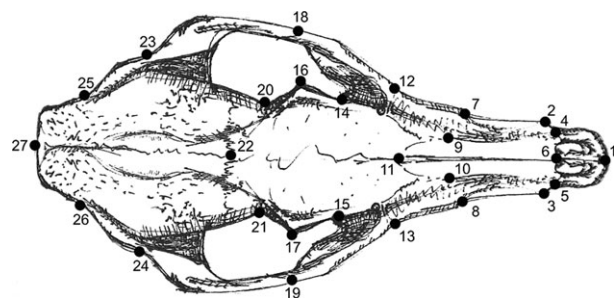


Fig. 2. Twenty-seven landmarks selected for analysis shown on the image of the cranium of *Cerdocyon thous* in dorsal view. Landmark (1) end of premaxilla; (2–3) premaxilla–maxilla suture; (4–5) lateral point of the nasal; (6) point of the nasal; (7–8) curve corresponding to the end of P2; (9–10) premaxilla–nasal–maxilla suture; (11) nasal–frontal suture; (12–13) jugal–maxilla suture; (14–15) interorbital constriction; (16–17) end of the postorbital process; (18–19) point of the frontal process; (20–21) postorbital constriction; (22) frontal–parietal suture; (23–24) end of the squamosal; (25–26) end of the occipital crest; (27) inion. Illustrated by my friend Marcelo Ribaya.

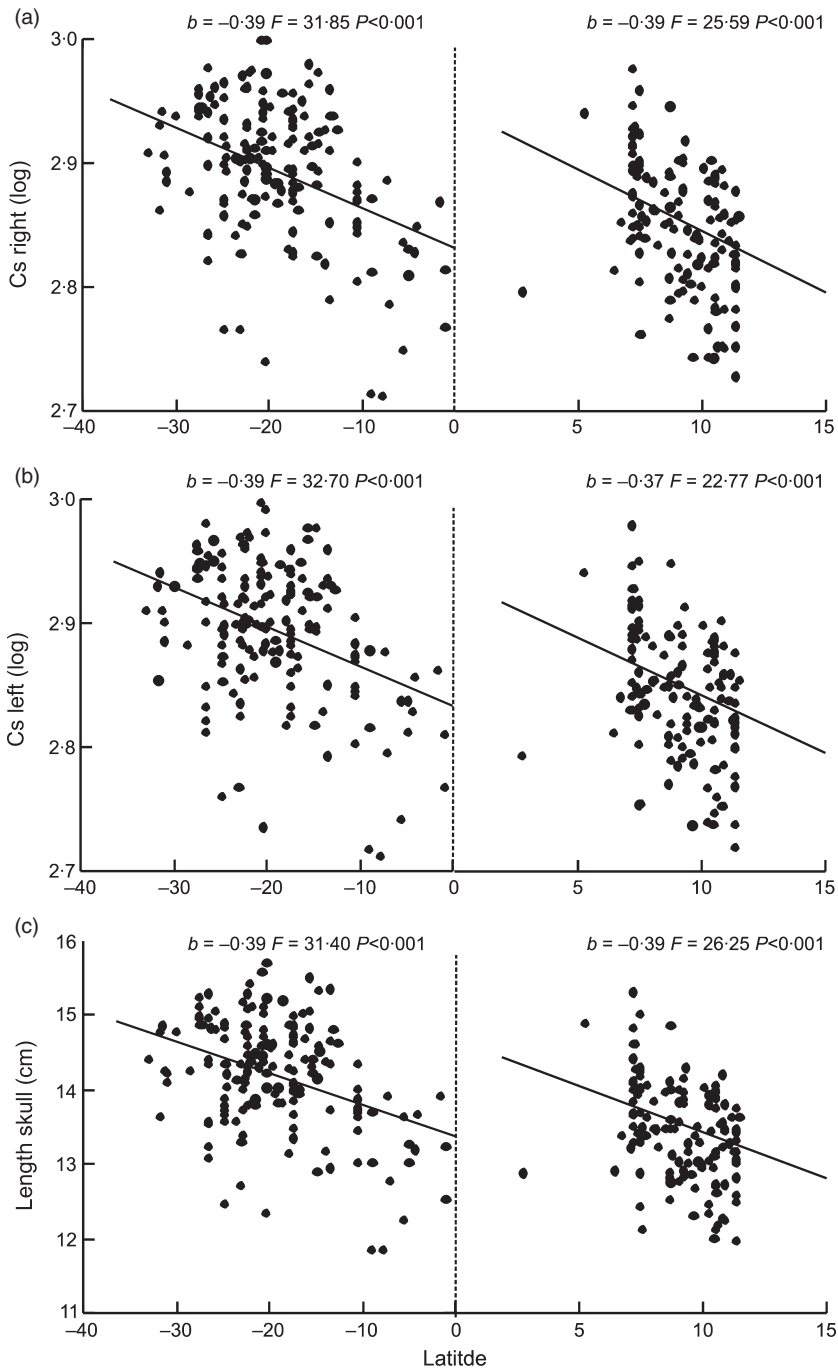


Fig. 3. Regressions of the greatest length of skull (a), of right-side landmarks (b) and of the left-side landmarks (c) on latitude. Significance of the regression slopes is indicated. The dotted line represents the Equator and separates both linear regressions.

gpw; Table 1). To process the data base the DIVA-GIS 7.1 software was used (<http://www.diva-gis.org/download>).

Because *C. thous* is present in two great geographically isolated areas, the samples were separated into two groups: (i) comprising all individuals south of the Equator ($n = 163$) and (ii) those north of the Equator ($n = 137$) with the aim of assessing whether different trends in size variation occur in both groups. To analyse geographic variation in size, linear regressions between log-transformed Cs and latitude were performed. A series of parametric (Pearson) and nonparametric (Spearman) correlations between log Cs and the geographic, ambient and anthropic variables were carried out to discard those that were not correlated with Cs, which left seven useful variables (Table 2). Conventional statistical analysis assumes that all observations are independent.

However, the possible spatial autocorrelation among data may produce an overestimation of the number of independent observations in spatial studies (Peres-Neto 2006) that may lead to the rejection of H_0 (type I error), assuming a false correlation between morphological and climatic variables. Different models tend to decrease the effect of spatial autocorrelation, but caution is always recommended when interpreting the results (Bini *et al.* 2009). In this study, we used univariate and multivariate simultaneous autoregression (SAR) between log Cs and the seven chosen climatic variables using Akaike's Information Criterion (AIC) to select the best model fitting the data, with the SAM 4.0 software (Rangel, Diniz-Filho & Bini 2006; <http://www.ecoevol.ufg.br/sam>). Comparisons were made between the north and south of the Equator.

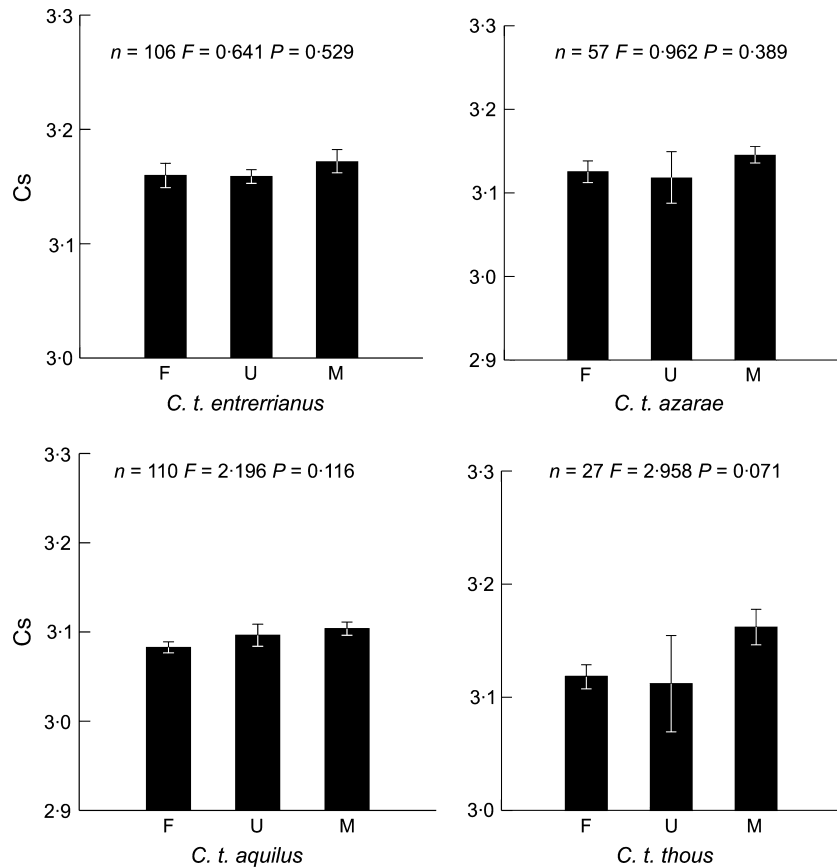


Fig. 4. ANOVA tests of sexual size dimorphism between females (F), males (M) and sexually undetermined individuals (U) of the subspecies *C. t. entrerrianus*, *C. t. azarae* and *C. t. aquilus* y *C. t. thous*, respectively. Results of the statistical analyses are indicated.

NICHE MODELLING

Data on the presence of *C. thous* were obtained from the different surveyed museum collections, from the 'species link' data base (available online at: <http://splink.cria.org.br>) and from personal observations and communications. A total of 237 localities covering most of the species distribution were recorded. Recent climatic variables (1960–1990) were downloaded from WORLDCLIM. Climatic data for the LGM (21 mya Kb) were obtained from the Community Climate System Model (CCSM). Original data were downloaded from the Paleoclimate Modeling Intercomparison Project (PMIP; available online at: <http://www.ncdc.noaa.gov/paleo/model.html>) with a resolution of 2.5 arcmin (*c.* 5 km). Highly correlated variables ($r > 0.9$) were maintained in the model on the basis of their biological relevance following the procedure described by Rissler & Apodaca (2007). Ten variables of 20 available in WORLDCLIM were used, including elevation (Table 1). The bioclimatic slices were cut to include latitudes from 12N°54' to 40S°21', and longitudes from 82W°22' to 33W°28', which represent all zones with bioclimatic conditions compatible with the occurrence of *C. thous*. The modelling of *C. thous* distribution during the LGM and the present was performed with the method of maximum entropy with the MAXENT software (Phillips & Dudík 2008), which has proved to be superior to other modelling algorithms used traditionally to produce predictions about distribution maps (Elith *et al.* 2006). In the present work, the precision of the model was estimated from the area under the curve (AUC) method, which is considered an effective indicator of the performance of the model and

frequently used to assess the consistency of the model's projections on the distribution of species (Manel, Williams & Ormerod 2001; Pearson *et al.* 2006). More details are given in the study by Phillips (2008).

Results

CLINAL BODY SIZE VARIATION

The analysis of body size variation regarding latitude both sides of the Equator, revealed two distinct trends: Individuals south of the Equator showed a significant increase in size with increasing latitude ($F = 32.44$; $r^2 = 0.16$; $P < 0.01$) according to the expectations of Bergmann's rule. However, those populations north of the Equator showed the opposite trend, a significant decrease in body size with increasing latitude ($F = 22.17$; $r^2 = 0.14$; $P < 0.01$), thus following the converse to Bergmann's rule (Fig. 5).

When partial SARs were performed, significant correlations between body size and the climatic variables MDR, ISO, TSE, MTDQ, MTCQ and PWQ were verified south of the Equator, while populations in the north showed significant correlations between body size and the climatic variables AMT, ISO, TSE, MTDQ, MTCQ and PWQ, indicating that some climatic variables differ in their effects on populations north and south of the Equator. Two different trends were observed: south of the Equator,

Table 1. List of geographic, topographic, anthropic (A–D) and environmental (1–22) variables used for correlation–regression analyses [ordinary least squares (OLS) and spatial autoregression (SAR)] and ecological niche modelling (ENM)

Variable	Code	OLS and SAR	ENM
A. Latitude	LAT	X	
B. Longitude	LON	X	
C. Elevation	ELE	X	X
D. Human Population Density	HPD	X	
1. Annual Mean Temperature	AMT	X	
2. Mean Diurnal Range	MDR	X	
3. Isothermality	ISO	X	X
4. Temperature Seasonality	TSE	X	X
5. Maximum Temperature of Warmest Month	MTWM	X	
6. Minimum Temperature of Coldest Month	MTCM	X	
7. Temperature Annual Range	TAR	X	X
8. Mean Temperature of Wettest Quarter	MTWQ	X	
9. Mean Temperature of Driest Quarter	MTDQ	X	
10. Mean Temperature of Warmest Quarter	MTQ	X	X
11. Mean Temperature of Coldest Quarter	MTCQ	X	X
12. Annual Precipitation	ANP	X	
13. Precipitation of Wettest Month	PWM	X	
14. Precipitation of Driest Month	PDM	X	X
15. Precipitation Seasonality	PSE	X	X
16. Precipitation of Wettest Quarter	PWW	X	X
17. Precipitation of Driest Quarter	PDQ	X	X
18. Precipitation of Warmest Quarter	PWQ	X	
19. Precipitation of Coldest Quarter	PCQ	X	
20. Actual Evapotranspiration	AET	X	
21. Potential Evapotranspiration	PET	X	
22. Water Balance	WB	X	

Crosses indicate the variables used for each type of analysis.

temperature variables MTDQ and MTCQ showed a negative correlation in relation to body size according to Bergmann's rule. However, both parameters showed a positive correlation with body size north of the Equator, opposing Bergmann's pattern. The analysis of the precipitation variable PWQ also showed opposite trends in the populations north and south of the Equator: body size was positively correlated with PWQ in the southern populations, which could be related to ambient productivity and resource availability, while a negative correlation occurred for the north of the Equator (Table 3). From multivariate SARs, it can be seen that the model that best predicts body size south of the Equator includes MDR, ISO and PWQ, which significantly explains *c.* 20% of the variation. In the north of the Equator, the best model includes AMT, ISO, MTDQ, MTCQ and PWQ. MTDQ was significantly explaining 20% of the total variation in body size (Table 4).

When comparing body size variances as estimated by Cs north and south of the Equator, a difference is

observed even considering that the northern region is smaller in area. However, when comparing the variances of the climatic variables, a clear difference is apparent: a higher variance occurs in the populations south of the Equator (Table 5).

ECOLOGICAL NICHE MODELLING

The distribution of *C. thous* predicted by the niche model for the present climatic conditions showed a good performance with AUC = 0.886. Two geographic regions can be distinguished: (i) comprising the Dry Diagonal (Cerrado, Caatinga and Chaco), and (ii) comprising the *llanos* of northern Venezuela, the Caribbean coast of Venezuela and Colombia, and part of the Guyanas (Fig. 6a). Besides these zones, small spots were observed in the savanna region of northern Brazil and Bolivia, suggesting a reduction in the distribution potential through the Amazonian basin. Precipitation during the wet season was among the variables that most influenced the distribution of the species, indicating that high levels of rainfall may limit the range of *C. thous*. High thermal amplitude also decreases the probability of occurrence of the species.

Furthermore, the projection of the present niche in the climatic scenario of the LGM showed four main groupings: (i) northern Venezuela and western Colombia, (ii) northern Brazil, (iii) north-eastern Brazil, corresponding to the Caatinga region and (iv) Chaco. It is important to note the existence of a corridor connecting the Chaco and Caatinga blocks (Fig. 6b).

Discussion

CLINAL VARIATION IN BODY SIZE

Despite the vast literature on Bergmann's rule since its formulation in 1847, there is a notorious paucity of studies addressing the variation in body size of species or higher taxa both sides of the Equator. Gay & Best (1996) analysed the size variation in *Puma concolor* (Felidae) in North and South America, observing an increase in the size at higher latitudes, both north and south of the Equator. Likewise, two intraspecific studies in Andean Passeriformes, the grey-bellied Flowerpiercer *Diglossa carbonaria* (Icteridae) and the yellow-billed Cacique, *Amblycercus holosericeus* (Thraupidae), showed that Bergmann's rule is verified in both sides of the Equator, with birds becoming progressively larger as distances north and south of 0° latitude increase (Graves 1991; Kratter 1993). However, Brumfield & Remsen (1996) studying four Andean species of *Cinnycerthia* wrens (Troglodytidae) found a converse pattern both north and south of the Equator: birds showed a negative correlation between body size and latitude.

However, the case of *Cerdocyon thous* is very different from what other studies have shown. The species shows a significant amount of body size variation throughout its geographic distribution. In this investigation, we aimed to

Table 2. Parametric (Pearson) and nonparametric (Spearman) correlations between \log_{10} skull centroid size of *Cerdocyon thous* and geographic and climatic variables

Area	Variable	d.f.	Pearson's r	F	P	Spearman's r	t	P
Total	LAT	299	-0.487*	93.06	<0.001	-0.533*	-10.94	<0.001
	LON	299	0.228	16.53	<0.001	0.309	5.63	<0.001
	AMT	299	-0.203	12.85	<0.001	-0.234	-4.18	<0.001
	MDR	299	0.393	54.76	<0.001	0.460	7.93	<0.001
	ISO	299	-0.427	66.87	<0.001	-0.484	-9.60	<0.001
	TSE	299	0.402	57.72	<0.001	0.478	9.43	<0.001
	MTDQ	299	-0.393	30.24	<0.001	-0.316	-5.79	<0.001
	MTCQ	299	-0.293	28.18	<0.001	-0.297	-5.39	<0.001
	PWQ	299	0.351	42.09	<0.001	0.354	6.57	<0.001
South	LAT	161	-0.377*	26.85	<0.001	-0.295*	-3.94	<0.001
	LON	161	-0.267	2.94	<0.001	-0.292	-3.90	<0.001
	AMT	161	-	-	NS	-	-	NS
	MDR	161	0.311	17.38	<0.001	-0.292	-3.89	<0.001
	ISO	161	-0.242	-10.11	0.002	-0.207	-2.71	0.002
	TSE	161	0.225	8.61	0.004	0.237	3.11	0.004
	MTDQ	161	-0.237	9.60	0.002	-0.238	3.14	0.002
	MTCQ	161	-0.183	5.61	0.019	-0.182	-2.37	<0.019
	PWQ	161	0.369	25.48	<0.001	0.305	4.09	<0.001
North	LAT	137	-0.426	30.20	<0.001	-0.401	-5.13	<0.001
	LON	137	-	-	NS	-	-	NS
	AMT	137	0.341	17.88	<0.001	0.408	5.24	<0.001
	MDR	137	-	-	NS	-	-	NS
	ISO	137	-0.217	6.74	0.01	-0.227	-2.73	<0.001
	TSE	137	-	-	NS	-	-	NS
	MTDQ	137	0.369	21.40	<0.001	0.405	5.18	<0.001
	MTCQ	137	0.334	17.09	<0.001	0.396	5.04	<0.001
	PWQ	137	-0.260	9.90	0.002	-0.324	-4.01	<0.001

Only those variables that produced statistically significant results are shown. For abbreviations of variables, see Table 1. Total: whole *C. thous* sample; south: subequatorial sample; north: supra-equatorial sample; d.f., degrees of freedom; *F*, Fisher-Snedecor statistic; *t*, Student's statistic; *P*, probability; NS, non-significant. Note that correlation coefficients for LAT are marked with an asterisk; this is because in our analysis, and negative values were assigned to southern latitudes. Thus, they represent truly Bergmannian trends. The negative correlations north of the Equator indicate a converse Bergmannian pattern.

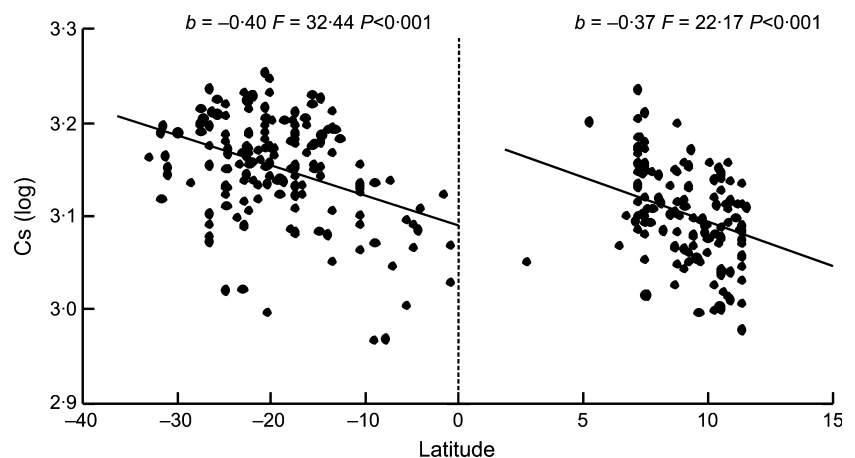


Fig. 5. Variation in cranium size of *Cerdocyon thous* in relation to latitude. Centroid size (Cs) was log-transformed. The dotted line represents the Equator and separates both linear regressions.

identify the main responsible factors for such wide variation. The most intriguing observation was that the individuals distributed south of the Equator followed the canonical Bergmann's rule (Tables 3 and 4), that is, animals from higher latitudes are larger in relation to those nearer the Equator, but this was not true for populations north of the Equator (Ashton, Tracy & de Queiroz 2000;

Meiri & Dayan 2003). Since the formulation of Bergmann's rule, the main mechanism proposed to explain the observed patterns was thermoregulation; larger bodies allowed for better heat conservation (Rensch 1938; Mayr 1956).

However, this mechanism has not received complete support. Although many studies have stressed the

Table 3. Univariate simultaneous autoregressions (SARs) between centroid size (Cs) and different environmental variables (predictors) in the groups of *Cerdocyon thous*, north and south of the Equator

Region	Variable	Coefficient OLS	Coefficient SAR	Predictor (r^2)	Predictor + space (r^2)	F	P
South	AMT	-0.227	-0.293	0.017	0.032	2.745	0.099
	MDR	0.960	1.037	0.096	0.116	17.159	<0.001
	ISO	-1.670	-1.775	0.059	0.077	10.007	0.002
	TSE	0.010	0.012	0.050	0.071	8.463	0.004
	MTDQ	-0.330	-0.352	0.056	0.074	9.467	0.002
	MTCQ	-0.270	-0.290	0.033	0.051	5.523	0.020
	PWQ	0.140	0.129	0.136	0.134	25.253	<0.001
North	AMT	0.780	0.763	0.116	0.135	17.742	<0.001
	MDR	-0.070	-0.282	<0.001	0.022	0.014	0.908
	ISO	-2.040	-1.922	0.047	0.060	6.670	0.011
	TSE	0.050	0.041	0.021	0.038	2.916	0.090
	MTDQ	0.750	0.724	0.136	0.150	21.200	<0.001
	MTCQ	0.770	0.742	0.111	0.129	16.939	<0.001
	PWQ	-0.130	-0.115	0.067	0.077	9.740	0.002

Table 4. Multivariate Simultaneous Autoregressions (SARs) between Centroid Size (Cs) and different environmental variables (predictors) in the groups of *Cerdocyon thous*, north and south of the Equator. The best model for each region was chosen from the lower value of Akaike's Information Criterion (AIC)

Region	Variables	OLS coefficient	SAR coefficient	Predictors (r^2)	Predictors + space (r^2)	F	P
South	Model (3 predictors)			0.210	0.220	13.730	<0.001
	MDR	0.620	0.720				<0.01
	ISO	-1.030	-1.120				<0.01
	PWQ	0.110	0.100				<0.01
North	Model (5 predictors)			0.190	0.200	6.260	<0.001
	AMT	2.990	3.270				0.180
	ISO	2.880	2.640				0.070
	MTDQ	3.200	2.760				0.030
	MTCQ	-5.570	-5.390				0.050
	PWQ	-0.080	-0.080				0.130

Table 5. Variance of the centroid (Cs) and the correlated environmental variables of *Cerdocyon thous*, north and south of the Equator

	Variance							
	Cs	AMT	MDR	ISO	TSE	MTDQ	MTCQ	PWQ
South	1.58	701.31	313.9	63.66	1213077	1599	1428	22592
North	1.27	466.56	75.92	28.05	23735	591	461	10466
South/North	1.24	1.50	4.13	2.26	51.10	2.71	3.09	2.15

importance of temperature on body size clinal variation in birds and mammals (e.g. Smith & Betancourt 1998; Ashton, Tracy & de Queiroz 2000), other studies suggest that factors such as precipitation, primary productivity, seasonality or resource availability may be equally or more important in generating Bergmann-like patterns (James 1970; Murphy 1985; Yom-Tov & Yom-Tov 2005; Yom-Tov & Geffen 2006). As indicated, populations north of the equator showed a significant decrease in size with increasing latitude (Fig. 5), showing a converse Bergmannian trend. Thus, both groups of populations have completely opposite geographic patterns of body size distribution.

We used SARs to discriminate the effects of space and the environmental predictors that could explain the geographic patterns shown for *C. thous* on both south and north of the Equator. Again, two different trends were observed, suggesting not only that different variables are probably involved in body size variation in both groups, but also that variables could be acting in contrasting ways (Tables 3 and 4).

For the populations south of the Equator, it was observed that the mean temperatures of the driest and coldest periods have a negative correlation with body size, that is, a higher mean temperature during these periods predicts smaller size, which agrees with Bergmann's rule.

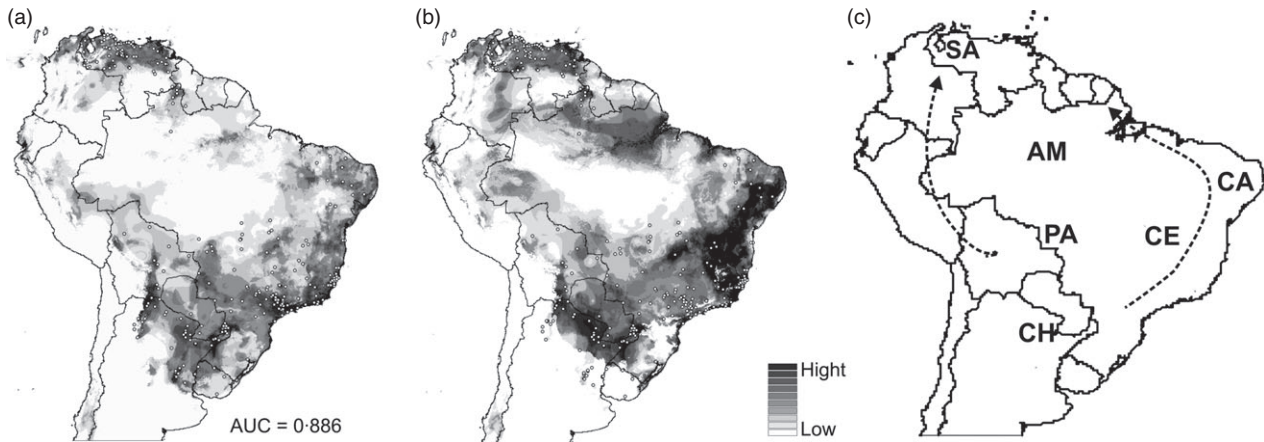


Fig. 6. Modelling of the distributional ranges of *Cerdocyon thous* for the climatic scenarios of (a) present-day, (b) Last glacial maximum (LGM) and (c) the bioregions of the South America, Chaco (CH), Cerrado (CE), Pantanal (PA), Caatinga (CA), Amazonas (AM) and savanna (SA). The dotted arrows show the possible corridors that linked the north and south populations of Equator during the LGM. The localities of presence are indicated by white circles, and the MAXENT probability values are listed as a scale of greys. Black corresponds to the logistic result of higher probability of occurrence of *Cerdocyon thous*. AUC refers to the area under the curve, an indicator of the performance of the model.

A strong correlation with seasonality was also observed: there exists a positive correlation with mean diurnal range and a negative one with isothermality [(MDR/TAR) * 100], indicating that the high variability of daily temperatures may act as a selective force on the evolution of body size, because in less predictable environments, larger individuals would be positively selected (Meiri, Dayan & Simberloff 2005). Seasonality is a plausible alternative or complementary mechanism to explain Bergmann's rule, because colder regions tend to be more seasonal (Ashton, Tracy & de Queiroz 2000; Ashton 2001a,b).

An increase in precipitation during the warmer season had also a positive correlation with body size. This fact was observed in previous studies (James 1970; Wigginton & Dobson 1999; Yom-Tov & Geffen 2006) and could reflect the relevance of primary productivity and resource availability as having a positive effect on body size, more than a direct impact of precipitation on organisms (Blois, Feranec & Hadly 2008). Primary productivity generally impacts carnivores only indirectly, but may have a direct effect on the omnivorous *C. thous*; fruits are an important element of its diet (Bisbal & Ojasti 1980; Facure & Monteiro-Filho 1996; Macdonald & Courtenay 1996).

In the populations north of the Equator, the situation is completely different. Mean annual, autumn and winter temperatures show a positive relationship with body size, while summer rainfall shows a negative one. Converse Bergmannian patterns are rare in endothermic animals (Katti & Price 2003; Meiri & Dayan 2003; Ochocinska & Taylor 2003; Medina, Martí & Bidau 2007) and are even more difficult to explain. It would be expected that populations north of the Equator had less body size variation than those south of the Equator, because of the difference in the geographic range. A smaller range reduces the probability of size clines (Meiri & Dayan 2003). Neverthe-

less, when comparing Cs variances, it was observed that body size variation is high and similar in both sides of the Equator, while the environmental variance is much lower north of the Equator. This suggests that environmental variables may not be the main factor influencing Cs among these northern populations.

North of the Equator, there exist two subspecies, *C. t. aquilus* and *C. t. thous*, which are probably allopatric and which show differences in body size (Bisbal 1988). *C. t. thous* is larger than *C. t. aquilus*, which leads to a non-Bergmannian pattern. Two main forces may have driven the subspecies to diverge in body size: genetic drift and natural selection. When the genetic flux becomes limited between populations, as it seems to be the case for these two subspecies isolated by the formidable barrier of the Orinoco river, rapid morphological differentiation and local adaptation may occur (Thompson 1998), and natural selection would thus be a powerful force driving phenotypic divergence (Ogden & Thorpe 2002). Another factor that could be affecting body size is resource availability. Bisbal & Ojasti (1980) showed that different populations of *C. t. aquilus* feed preferentially on small vertebrates, insects and fruits and that the diet composition varies in the dry and wet seasons, while *C. t. thous* eats mainly fruits and, to a less extent, small vertebrates, without showing great variations in diet along the year. However, these authors were not able to correlate size with diet. The present-day climatic factors and feeding habits do not seem to explain body size variation north of the Equator. The observed great phenotypic variation between geographically close populations that are isolated (at least partially by the Orinoco river) suggests that natural selection has a central role in size variation. However, a role of genetic drift in morphological differentiation cannot be disregarded (see Historical Factors). We also did not find

evidence that food availability was related to anthropic interference as suggested for other carnivores (Yom-Tov, Yom-Tov & Zachos 2013, and references therein).

HISTORICAL FACTORS

The prediction of the geographic distribution of *C. thous* for present-day climatic conditions indicates a high probability of occurrence in open habitats of South America (savannas and seasonal dry forests), agreeing with the proposals of several authors (Bisbal 1989; Trovati, de Brito & Duarte 2007), having two clear distribution areas, isolated by the Amazonian Forest. The consensual opinion is that these two regions were connected during the cold and dry periods of the LGM in the recent past, when savannas expanded and the Amazonian forest retracted (Mayle, Burbridge & Killeen 2000). Three corridors connecting the northern and southern savannas during the LGM have been proposed: (i) the Andean corridor, connecting the southern savannas with Colombia and Venezuela; (ii) the central Amazonian corridor, connecting the southern savannas with those of northern Amazonia; and (iii) the coastal corridor that would connect south with north through spots of savanna along the Atlantic coast (Haffer 1997; Cardoso da Silva & Bates 2002).

The data of the present study shed light on the possible historical distribution of *C. thous*. The modelling of the paleodistribution showed four main groupings with two groups in the north and two in the south, potentially connected south of the Equator, that could be related to the subspecies *C. t. aquilus* and *C. t. thous*, and *C. t. azarae* and *C. t. entrerrianus*, respectively, and agreeing with the proposal of Cabrera (1931). Our data do not support the hypothesis of a central corridor through Amazonia and is consistent with connections of the populations through the coastal corridor and the Andes (Fig. 6c).

The climatic changes associated with events of retraction and expansion of the Amazonian forest during the quaternary have been postulated by several biogeographers as an important factor in the speciation of South American tropical organisms (Whitmore & Prance 1987; Haffer & Prance 2001). Phylogeographic studies in *C. thous* have shown that populations from north-eastern Brazil exhibit a certain degree of genetic differentiation when compared with those of southern Brazil and Paraguay, while those from the Cerrado and Pantanal share haplotypes with both regions (Tchaicka *et al.* 2007). These data are consistent with the niche modelling performed by us: two groupings of high occurrence probability, one in the Caatinga and the other in Chaco, were observed with an intermediary contact zone during the LGM. The existence of two groupings north of the Equator during the LGM shows that a possible isolation that occurred in the past could have produced the differentiation of the subspecies *C. t. aquilus* localized in the north of Venezuela and Colombia, and *C. t. thous* localized in the north of Brazil and southern Guyanas.

The idea of isolation is reinforced by the fact that both subspecies show substantial differences in shape and size, *C. t. thous* being larger than *C. t. aquilus*. Both subspecies occur in allopatry, separated by the Orinoco river basin (Bisbal 1988).

Future research of population genetics will allow us to meet the levels of genetic diversity within subspecies, which will be important to detect possible population bottlenecks during the LGM. Likewise, phylogeographic studies comprising the entire distribution of the species will help to confirm or refute that these two subspecies have been isolated since the LGM. They will also indicate the level of divergence between the different subspecies, to determine whether *C. thous* is a single species or a species complex.

Factors affecting body size such as climatic conditions, resource availability and the composition of communities may vary frequently in the continent along time (Raia & Meiri 2011). The potential populations of *C. t. thous* during the LGM were possibly exposed to selective pressures different to those existing nowadays, which could have led to an increase in body size of this subspecies. Separate from the niche modelling, it can be observed that the potentially habitable area for *C. thous* was larger during the LGM than in the present (Fig. 6) and that the climatic change and the concomitant expansion of the forest have produced a reduction in open areas in South America (Werneck *et al.* 2011), which are suitable for the species. This situation would explain the presence of populations of *C. t. thous* in northern Brazil isolated from populations of the same subspecies in Venezuela (Sillero-Zubiri *et al.* 2004). Under this perspective, it may be expected that population bottlenecks have occurred for *C. t. thous*, and given that genetic drift has an important effect in fixating phenotypic characteristics in small populations (Stern & Orgogozo 2009), a larger size in *C. t. thous* could be the result of drift.

The mechanisms that produced the inversion of Bergmann's rule north of the Equator are still obscure, but the situation of the present geographic isolation of *C. t. aquilus* and *C. t. thous*, driving these subspecies to fixate unique adaptive characteristics, plus possible genetic drift events in *C. t. thous* could help to explain the unusual observed pattern.

In conclusion, two opposite trends with regarding geographic variation in body size were observed for *Cerdocyon thous*. First, populations south of the Equator show a strong Bergmannian pattern of spatial (clinal) body size variation negatively correlated with temperature. The positive correlations of body size with seasonality and precipitation also suggest a dependence on resource availability. Conversely, populations north of the Equator, comprising two subspecies, showed a completely opposite pattern. We consider that this deviation from Bergmann's rule in northern populations must have been influenced by historical factors, local adaptation and genetic drift.

Acknowledgements

We would like to thank Shai Meiri and Miguel Angel Olalla-Tarraga for their helpful criticism of a previous version of this manuscript. We are also extremely grateful to Dakota McCoy, Graham Slater, and an anonymous reviewer for their expert comments and suggestions. The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES-REUNI) and the Postgraduate Ecology Course of the Universidade Federal do Rio Grande do Norte are gratefully acknowledged for their support.

References

- Angilletta, M.J. Jr, Niewirowski, P.H., Dunham, A.E., Laeche, A.D. & Porter, W.P. (2004) Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. *The American Naturalist*, **164**, 169–183.
- Ashton, K.G. (2001a) Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions*, **7**, 289–295.
- Ashton, K.G. (2001b) Body size variation among mainland populations of the Western rattlesnake (*Crotalus viridis*). *Evolution*, **58**, 2523–2533.
- Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505–523.
- Ashton, K.G., Tracy, M.C. & de Queiroz, A. (2000) Is Bergmann's rule valid for mammals? *The American Naturalist*, **156**, 390–415.
- Bergmann, C. (1847) Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**, 595–708.
- Berta, A. (1982) *Cerdocyon thous*. *Mammalian Species*, **186**, 1–4.
- Berta, A. (1988) Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). *University of California Publication Geological Sciences*, **132**, 1–149.
- Bini, L.M., Diniz-Filho, J.A.F., Rangel, T.F.L.V.B., Akre, T.S.B., Albaladejo, R.G. & Albuquerque, F.S. *et al.* (2009) Coefficient shifts in geographical ecology: an empirical evaluation of spatial and non-spatial regression. *Ecography*, **32**, 193–204.
- Bisbal, F.J. (1988) A taxonomic study of the crab-eating fox, *Cerdocyon thous*, in Venezuela. *Mammalia*, **52**, 181–186.
- Bisbal, F.J. (1989) Distribution and habitat association of the carnivores in Venezuela. *Advances in Neotropical Mammalogy* (eds K.H. Redford & J.F. Eisenberg), pp. 339–362. The Sandhill Crane Press, Inc., Gainesville, FL.
- Bisbal, F.J. & Ojasti, J. (1980) Nicho trófico del zorro *Cerdocyon thous* (Mammalia, Carnivora). *Acta Biológica Venezuelica*, **10**, 469–496.
- Blois, J.L., Feranec, R.S. & Hadly, E.A. (2008) Environmental influences on spatial and temporal patterns of body-size variation in California ground squirrels (*Spermophilus beecheyi*). *Journal of Biogeography*, **35**, 602–613.
- Bookstein, F.L. (1991) *Morphometric Tools for Landmark Data*. Cambridge University Press, Cambridge.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago.
- Brumfield, R.T. & Renssen, J.V. Jr (1996) Geographic variation and species limits in *Cinnycerthia* wrens of the Andes. *Wilson Bulletin*, **108**, 205–277.
- Cabrera, A. (1931) On some South American canine genera. *Journal of Mammalogy*, **12**, 54–67.
- Cabrera, A. (1958) Catálogo de los mamíferos de América del Sur. Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'. *Ciencias Zoológicas*, **4**, 1–307.
- Calder, W.A. (1984) *Size, Function and Life History*. Harvard University Press, Cambridge, MA.
- Cardoso da Silva, J.M. & Bates, J.M. (2002) Biogeographical patterns and conservation in the South American cerrado: a tropical savanna hotspot. *BioScience*, **52**, 225–233.
- Carnaval, A.C., Hickerson, M.J., Haddad, C.F.B., Rodrigues, M.T. & Moritz, C. (2009) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. *Science*, **323**, 785–789.
- Cramer, W.P. & Leemans, R. (2001) *Global 30-Year Mean Monthly Climatology, 1930–1960, Version 2.1. Data Set*. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. Available online from <http://www.daac.ornl.gov>.
- Dayan, T., Tchernov, E., Yom-Tov, Y. & Simberloff, D. (1989) Ecological character displacement in Saharo-Arabian *Vulpes*: outfoxing Bergmann's rule. *Oikos*, **55**, 263–272.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1991) Calibrating the paleothermometer: climate, communities, and the evolution of size. *Paleobiology*, **17**, 189–199.
- Diniz-Filho, A.F., Bini, L.M., Rodríguez, M.A., Rangel, T.F.L.V.B. & Hawkins, B.A. (2007) Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography*, **30**, 598–608.
- Dryden, I.L. & Mardia, K.V. (1998) *Statistical Shape Analysis*. Wiley Press, New York, NY.
- Elith, J., Graham, C.H., Anderson, R.P., *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Facure, K.G. & Monteiro-Filho, E.L.A. (1996) Feeding habits of the crab-eating fox, *Cerdocyon thous* (Carnivora: Canidae), in a suburban area of southeastern Brazil. *Mammalia*, **60**, 147–149.
- Gaston, K.J., Chown, S.L. & Evans, K.L. (2008) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, **35**, 483–500.
- Gay, S.W. & Best, T.L. (1996) Relationships between abiotic variables and geographic variation in skulls of pumas (*Puma concolor*: Mammalia, Felidae) in North and South America. *Zoological Journal of the Linnean Society*, **117**, 259–282.
- Geist, V. (1987) Bergmann's rule is invalid. *Canadian Journal of Zoology*, **65**, 1035–1038.
- Graves, G.R. (1991) Bergmann's rule near the equator: latitudinal clines in body size of an Andean passerine bird. *Proceedings of the National Academy of Sciences USA*, **88**, 2322–2325.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, **165**, 131–137.
- Haffer, J. (1997) Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiversity and Conservation*, **6**, 451–476.
- Haffer, J. & Prance, G.T. (2001) Climatic forcing of evolution in Amazonia during the Cenozoic: on the refuge theory of biotic differentiation. *Amazoniana*, **16**, 579–607.
- Haskell, J.P., Ritchie, M.E. & Olff, H. (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, **418**, 527–530.
- Irving, L. (1957) The usefulness of Scholander's views on adaptive insulation of animals. *Evolution*, **11**, 257–259.
- James, F.C. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365–390.
- Janis, C.M. (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics*, **24**, 467–500.
- Katti, M. & Price, T.D. (2003) Latitudinal trends in body size among over-wintering leaf warblers (genus *Phylloscopus*). *Ecography*, **26**, 69–79.
- Klingenberg, C.P. (2008) *MorphoJ*. Faculty of Life Sciences, University of Manchester, Manchester. http://www.flywings.org.uk/MorphoJ_page.htm.
- Kratter, A.W. (1993) Geographic variation in the yellow-billed cacique, *Amblycercus holosericeus*, a partial bamboo specialist. *The Condor*, **95**, 641–651.
- Lindstedt, S.L. & Boyce, M.S. (1985) Seasonality, fasting endurance, and body size in mammals. *American Naturalist*, **125**, 873–878.
- Luoto, M., Kuussaari, M. & Toivonen, T. (2002) Modeling butterfly distribution based on remote sensing data. *Journal of Biogeography*, **29**, 1027–1037.
- Macdonald, D.W. & Courtenay, O. (1996) Enduring social relationships in a population of crab-eating zorros, *Cerdocyon thous*, in Amazonian Brazil (Carnivora, Canidae). *Journal of Zoology*, **239**, 329–355.
- MacFadden, B.J. (2000) Cenozoic mammalian herbivores from the Americas: reconstructing ancient diets and terrestrial communities. *Annual Review of Ecology and Systematics*, **31**, 33–59.
- Machado, F. & Hingst-Zaher, E. (2009) Investigating South American biogeographic history using patterns of skull shape variation on *Cerdocyon thous* (Mammalia: Canidae). *Biological Journal of the Linnean Society*, **98**, 77–84.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- Markgraf, V. (1989) Palaeoclimates in central and South America since 18,000 BP based on pollen and lake-level records. *Quaternary Science Review*, **8**, 1–24.
- Mayle, F.E., Burbridge, R. & Killeen, T.J. (2000) Millennial scale dynamics of southern Amazonian rain forests. *Science*, **290**, 2291–2294.

- Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.
- McCoy, D.E. (2012) Connecticut birds and climate change: Bergmann's rule in the fourth dimension. *The Northeastern Naturalist*, **19**, 323–334.
- McNab, B.K. (1999) On the comparative ecological and evolutionary significance of total and mass-specific rates of metabolism. *Physiological and Biochemical Zoology*, **72**, 642–644.
- Medina, A.I., Martí, D.A. & Bidau, C.J. (2007) Subterranean rodents of the genus *Ctenomys* (Caviomorpha, Ctenomyidae) follow the converse to Bergmann's rule. *Journal of Biogeography*, **34**, 1439–1454.
- Meiri, Y. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.
- Meiri, S., Dayan, T. & Simberloff, D. (2004) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, **81**, 579–588.
- Meiri, S., Dayan, T. & Simberloff, D. (2005) Biogeographical patterns in the Western Palearctic, the fasting endurance hypothesis and the status of Murphy's rule. *Journal of Biogeography*, **32**, 369–375.
- Millar, J.S. & Hickling, G.J. (1990) Fasting endurance and the evolution of mammalian body size. *Functional Ecology*, **4**, 5–12.
- Moritz, C., Patton, J.L., Schneider, C.J. & Smith, T.B. (2000) Diversification of rainforest faunas: an integrated molecular approach. *Annual Review of Ecology and Systematics*, **31**, 533–563.
- Murphy, E.C. (1985) Bergmann's rule, seasonality, and geographic variation in body size of house sparrows. *Evolution*, **39**, 1327–1334.
- Ochocinska, D. & Taylor, J.R.E. (2003) Bergmann's rule in shrews, geographic variation in body size in Palearctic *Sorex* species. *Biological Journal of the Linnean Society*, **78**, 365–381.
- Ogden, R. & Thorpe, R.S. (2002) Molecular evidence for ecological speciation in tropical habitats. *Proceedings of the National Academy of Sciences USA*, **99**, 13612–13615.
- Patterson, B. & Pascual, R. (1972) The fossil mammal fauna of South America. *Evolution, Mammals, and Southern Continents* (eds A. Keast, F.C. Erk & B. Glass), pp. 247–309. State University of New York Press, Albany.
- Pearson, R.G., Thuiller, W., Araujo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P. & Lees, D.C. (2006) Model-based uncertainty in species range prediction. *Journal of Biogeography*, **33**, 1704–1711.
- Pennington, R.T., Prado, D.E. & Pendry, C.A. (2000) Neotropical seasonally dry forests and quaternary vegetation changes. *Journal of Biogeography*, **27**, 261–273.
- Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K. & Butterworth, C.A. (2004) Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both tertiary and quaternary diversification. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **359**, 515–538.
- Peres-Neto, P.R. (2006) A unified strategy for estimating and controlling spatial, temporal and phylogenetic autocorrelation in ecological models. *Oecologia Brasileira*, **10**, 105–119.
- Perini, F.A., Russo, C.A.M. & Schrago, C.G. (2010) The evolution of South American endemic canids: a history of rapid diversification and morphological parallelism. *Journal of Evolutionary Biology*, **23**, 311–322.
- Phillips, S.J. (2008) Transferability, sample selection bias and background data in presence-only modeling: a response to Peterson et al. (2007). *Ecography*, **31**, 272–278.
- Phillips, S.J. & Dudík, M. (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.
- Raia, P. & Meiri, S. (2011) The tempo and mode of evolution: body sizes of island mammals. *Evolution*, **65**, 1927–1934.
- Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, **33**, 46–50.
- Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Peterson, A.T. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature*, **426**, 837–841.
- Renaud, S., Benammi, M. & Jaeger, J.J. (1999) Morphological evolution of the murine rodent *Paraethomys* in response to climatic variations (Mio-Pleistocene of North Africa). *Paleobiology*, **25**, 369–382.
- Rensch, B. (1938) Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London*, **50**, 275–285.
- Rissler, L.J. & Apodaca, J.J. (2007) Adding more ecology into species delimitation: ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Systematic Biology*, **56**, 924–942.
- Rohlf, F.J. (2010) *TpsDig, ver 2.16*. Department of Ecology and Evolution, State University of New York, Stony Brook. <http://life.bio.sunysb.edu/morph/>.
- Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *The American Naturalist*, **102**, 67–74.
- Scholander, P.F. (1956) Climatic rules. *Evolution*, **10**, 39–40.
- Shelomi, M. (2012) Where are we now? Bergmann's rule sensu lato in insects. *The American Naturalist*, **180**, 511–519.
- Sillero-Zubiri, C., Hoffmann, M. & Macdonald, D.W. (2004) *Canids: Foxes, Wolves, Jackals and Dogs*. Status Survey and Conservation Action Plan. IUCN/SSC Canid Specialist Group, Gland, Switzerland and Cambridge, UK.
- Smith, F.A. & Betancourt, J.L. (1998) Response of bushy-tailed woodrats (*Neotoma cinerea*) to late quaternary climatic change in the Colorado Plateau. *Quaternary Research*, **50**, 1–11.
- Stern, D.L. & Orgogozo, V. (2009) Is genetic evolution predictable? *Science*, **323**, 746–751.
- Tate, G.H.H. (1939) The mammals of the Guiana region. *Bulletin of the American Museum of Natural History*, **76**, 151–229.
- Tchaicka, L., Eizirik, E., de Oliveira, T.G., Cândido, J.F. & Freitas, T.R.O. (2007) Phylogeography and population history of the crab-eating fox (*Cerdocyon thous*). *Molecular Ecology*, **16**, 819–838.
- Tedford, R.H., Taylor, B.E. & Wang, X. (1995) Phylogeny of the Caninae (Carnivora: Canidae): the living taxa. *American Museum Novitates*, **3146**, 1–37.
- Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends in Ecology and Evolution*, **13**, 329–332.
- Trovati, R.G., de Brito, B.A. & Duarte, J.M.B. (2007) Área de uso e utilização de habitat de cachorro-do-mato (*Cerdocyon thous* Linnaeus, 1766) no cerrado da região central do Tocantins, Brasil. *Mastozoologia Neotropical*, **14**, 61–68.
- Werneck, T.P., Costa, G.C., Colli, G.R., Prado, D.E. & Sites, J.W. Jr (2011) Revisiting the historical distribution of seasonally dry tropical forests: new insights based on palaeodistribution modeling and palynological evidence. *Global Ecology and Biogeography*, **20**, 272–288.
- Whitmore, T.C. & Prance, G.T. (1987) *Biogeography and Quaternary History in Tropical America*. Oxford Monograph on Biogeography 3. Clarendon Press, Oxford.
- Wigginton, J.D. & Dobson, F.S. (1999) Environmental influences on geographic variation in body size of western bobcats. *Canadian Journal of Zoology*, **77**, 802–813.
- Yom-Tov, Y. & Geffen, E. (2006) Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia*, **148**, 213–218.
- Yom-Tov, Y. & Yom-Tov, J. (2005) Global warming, Bergmann's rule and body size in the masked shrew *Sorex cinereus* Kerr in Alaska. *Journal of Animal Ecology*, **74**, 803–808.
- Yom-Tov, Y., Yom-Tov, S. & Zacos, F.E. (2013) Temporal and geographical variation in skull size of the red fox (*Vulpes vulpes*) and the Eurasian badger (*Meles meles*) in Austria. *Biological Journal of the Linnean Society*, **108**, 579–585.
- Zelditch, M.L., Swiderski, D.L., Sheets, H.D. & Fink, W.L. (2004) *Geometric Morphometrics for Biologists: A Primer*. Elsevier Academic Press, San Diego.

Received 29 November 2012; accepted 22 February 2013

Handling Editor: Shai Meiri