

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/259309446>

# A test of Allen's rule in subterranean mammals: The genus *Ctenomys* (Caviomorpha, Ctenomyidae)

Article in *Mammalia* · November 2011

DOI: 10.1515/MAMM.2011.044

CITATIONS

2

READS

244

### 3 authors:



**Claudio Bidau**

Fundação Oswaldo Cruz

117 PUBLICATIONS 1,007 CITATIONS

SEE PROFILE



**Dardo A. Martí**

National Scientific and Technical Research ...

79 PUBLICATIONS 523 CITATIONS

SEE PROFILE



**Alonso Ismael Medina**

National University of Comahue - CONICET

10 PUBLICATIONS 60 CITATIONS

SEE PROFILE

# A test of Allen's rule in subterranean mammals: the genus *Ctenomys* (Caviomorpha, Ctenomyidae)

Claudio J. Bidau<sup>1,a,\*</sup>, Dardo A. Marti<sup>2,4</sup> and Alonso I. Medina<sup>3,4</sup>

<sup>1</sup> Instituto Oswaldo Cruz, FIOCRUZ, Rio de Janeiro, Laboratório de Biologia e Parasitologia de Mamíferos Silvestres Reservatórios, Av. Brasil 4365, Pav. Arthur Neiva, sala 14, Manguinhos, Rio de Janeiro, RJ-21045-900, Brazil, e-mail: bidau47@yahoo.com

<sup>2</sup> Laboratorio de Genética Evolutiva, Facultad de Ciencias Exactas, Químicas y Naturales, Universidad Nacional de Misiones, 3300 Posadas, Argentina

<sup>3</sup> Instituto de Biología Marina y Pesquera "Almirante Storni", 8520 San Antonio Oeste, Rio Negro, Argentina

<sup>4</sup> Consejo Nacional de Investigaciones Científicas y Técnicas, Buenos Aires, Argentina

\*Corresponding author

## Abstract

We tested the applicability of Allen's rule in 47 species and 32 unnamed forms (populations that are probably good species or undefined taxa within a superspecies or species group) of the South American subterranean Hystricomorph rodents of the genus *Ctenomys* (tuco-tucos) (Rodentia: Ctenomyidae) by analyzing tail length in relation with head and body length, and body mass. Tail length allometry was analyzed by Reduced Major Axis regression while the possible correlation of relative tail length with temperature, precipitation and evapotranspiration variables was explored through Simultaneous Autoregression to account for spatial autocorrelations. Our results indicate that tuco-tucos do not follow Allen's rule but its converse, tail proportion relative to body mass increasing with latitude while body size decreases in the same direction (the trend is similar for tail length relative to head and body length but not statistically significant). Regarding climatic variables, the main predictors of relative tail length were temperature and evapotranspiration variables with trends confirming the positive (non-Allenian) correlation of relative tail length with latitude. We conclude that tuco-tucos, being almost fully subterranean, thermoregulate behaviorally by maintaining constant temperatures within their burrows independent of geographic location. The former confirms previous results that indicated that *Ctenomys* follows the converse to Bergmann's rule. Relative tail length variation would be a result of simple allometric growth.

<sup>a</sup> Present address: Universidad Nacional de Río Negro, Sede Alto Valle, Subsede Villa Regina, Tacuarí 669, 8336 Villa Regina, Río Negro, Argentina.

**Keywords:** allometry; body proportions; climate; geographic cline; subterranean rodent.

## Introduction

Allen's rule (Allen 1877, 1905, Mayr 1999) is an empirical geographical pattern according to which, protruding body parts of endothermic animals, such as tails, limbs, ears, bills, etc. tend to be relatively shorter in the cooler parts of the range of a taxon than in its warmer parts. This ecogeographical rule has been considered traditionally as a complement to Bergmann's rule (Bergmann 1847), but has received less attention than the former. Nevertheless, a small number of studies have demonstrated the existence of Allenian clines in endotherms (birds: Snow 1954, Merilä 1977, Raveling and Warner 1978, McGillivray 1989, Bried and Jouventin 1997, Laiolo and Rolando 2001, Cartar and Morrison 2005, Yom-Tov et al. 2006; mammals: Mitchell 1971, Griffing 1974, Ramey and Nash 1976, Stevenson 1986, Lindsay 1987, Ellison et al. 1993, Vrba 1996, Wiggington and Dobson 1999) and also ectotherms (Ray 1960, Salthe and Crump 1977). Both rules as originally interpreted, considered that the increase in body size (Bergmann's rule) and the decrease in the proportions of protruding body parts towards higher latitudes and altitudes conformed to thermoregulation (i.e., heat conservation or the avoiding of heat loss). For Bergmann's rule, a number of alternative explanations other than thermoregulation have been proposed (Ashton et al. 2000, Meiri and Dayan 2003, Medina et al. 2007) many of which could be readily related also to Allen's rule. Both rules, which have been alternatively considered in inter- or intraspecific applications (Blackburn et al. 1999), with exceptions in different animal groups reported.

Classically, natural selection for thermoregulatory adaptation has been invoked as the essential cause of Allen geographical patterns. Experimental evidence of the former hypothesis has recently been obtained for humans (Tilkens et al. 2007). The authors demonstrated that shorter limbs help reduce the metabolic cost of maintaining body temperature, while longer limbs cause greater heat dissipation independent of the effect of mass. Nevertheless, other factors could be involved. Recently, Serrat et al. (2008) demonstrated that in laboratory mice, appendage outgrowth is also markedly influenced by environmental temperature. Vasomotor changes would control limb length indirectly through their effects on appendage temperature. Thus, clinal distributions of limb length following the Allen's rule trend, may represent a complex amalgam of genetic assimilation after generations of selection combined with direct temperature responses in growing cartilage.

Tuco-tucos (genus *Ctenomys* de Blainville, 1826) constitute a useful model to test predictions about relationships between body size and environmental variables. The genus includes at least 62 species, showing a wide variation in body size and an enormous geographic distribution spanning across 45° of southern latitude from ca. -10° in the Peruvian highlands to almost -55° in Tierra del Fuego). Populations are found between 0 m and 5000 m above sea level from the Pacific to the Atlantic coasts (Contreras and Bidau 1999, Bidau 2006, 2011). These rodents are fully subterranean spending more than 95% of their lives underground (Nevo 1999) and are morphologically homogeneous, all species showing the same adaptations for living underground although varying greatly in size (Medina et al. 2007). Furthermore, tuco-tucos inhabit an enormous variety of habitats and climates and although localized populations may be subjected to intense environmental selection resulting from differences in soil texture and depth, available food plants, intensity of predation, etc. their burrows maintain fairly constant temperature and humidity independently of geographic location (Reig et al. 1990, Nevo 1999, Busch et al. 2000, Bidau 2006, Medina et al. 2007). This characteristic probably isolates them quite effectively from the external environment much more than other subterranean rodents (Medina et al. 2007). Finally, it has recently been demonstrated that tuco-tucos follow the converse to Bergmann's rule (Medina et al. 2007).

Similar to other subterranean mammalian taxa, the Ctenomyidae exhibit a complex set of adaptations to the underground milieu that include not only specialized morphological, physiological and biochemical characteristics (Reig et al. 1990, Nevo 1999, Sedláček 2007a,b) but also specialized behaviors regarding burrow construction and maintenance of its internal microclimate (Burda 2007). The aim of this study was to test for Allen's rule across these rodents' wide geographical distribution considering that *Ctenomys* species thermoregulate essentially controlling temperature within their burrows and not by changes in body size.

## Materials and methods

### Study species and morphometric traits

We based this study on 719 specimens of *Ctenomys* belonging to 133 natural populations including 47 named species and 32 unnamed or undescribed forms (the term "form" is used here to denote populations that are probably good species or undefined taxa within a superspecies or species group; see Mirol et al. 2010) from Argentina, Bolivia, Chile, Paraguay and Uruguay sampled by the authors and collaborators (Medina et al. 2007) or obtained from the literature (see Figure 1 and Appendix 1 in Medina et al. 2007). External measurements of all specimens included Total Body (TL) and Head plus Body (HB), and Tail (T) lengths. In most individuals, body mass (BM) was also measured or obtained from the literature. The proportions of TL relative to HB and BM were calculated for all individuals and *arcsin* transformed. Males and females were analyzed separately since all tuco-tuco species exhibit male-biased sexual size dimorphism (SSD) which

decreases significantly towards South following the converse Bergmannian pattern of the genus but conforming Rensch's rule (Bidau and Medina, submitted).

### Independent variables

For each studied locality, latitude (LAT) and longitude (LON) were recorded and transformed to decimal units. Altitude was recorded as metres above sea level. However, one-dimensional analyses have no explanatory power (Hawkins and Diniz-Filho 2004), because size clines may obey to multiple selection pressures that are not only dependent on temperature constraints but also on other climatic and biotic factors that could influence body size as explained above (Jones et al. 2005). Therefore we considered other independent variables as follows. Environmental variables for each locality included: mean annual temperature (TMEA), mean minimal and maximal temperatures (TMIN, TMAX), mean temperature of the dry season (Tdry), total annual precipitation (PANN), minimal and maximal precipitation (PMIN, PMAX) and mean rainfall of the dry season (Pdry) (Cramer and Leemans 2001). To estimate seasonality, we calculated the annual variability of the climatic factors. Annual variability of temperature was estimated through the coefficient of variation ( $CV=SD*100/x$ ) (CVT; where x in this case, is the mean annual temperature of each sampled locality, and SD its standard deviation), and the difference between average maximum and minimum annual temperatures (TM-m). We assessed variability of precipitation by the CV of mean annual precipitation (CVP, calculated from mean monthly precipitation and its SD), and the difference between maximum and minimum average monthly precipitation (PM-m).

Because body size clines may be correlated with primary productivity and ambient energy, two correlates of actual (AET) and potential (PET) evapotranspiration were considered (Rosenzweig 1968, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006). Therefore, we obtained for each geographic point, AET, an estimator of primary productivity (calculated by the Thornthwaite formula), PET, a measure of ambient energy (calculated by the Priestley-Taylor equation), and Water Balance (WB). We used vectors, databases and maps for AET, PET and WB from Ahn and Tateishi (1994a,b). Data analysis was performed with the Geomatica FreeView V. 10.0 software by PCI Geomatics, Ontario, Canada ([www.pcigeomatics.com](http://www.pcigeomatics.com)). All data are in mm/year. Mean annual AET, PET and WB values were calculated for each sampled locality. To analyze tail length allometry we used Reduced Major Axis regression (RMA) to estimate slopes for the relationship between  $\log_{10}$  (TL) and  $\log_{10}$  (HB or BM) employing the software of Bohonak and van der Linde (2004). Clarke's t statistic with adjusted degrees of freedom was used for testing the null hypothesis that  $b_{RMA}=1.0$  for the linear relationship TL/HB, and  $b_{RMA}=0.33$  for TL/BM (Clarke 1980).

Because most environmental variables show a high degree of collinearity, dimensionality of the predictors was reduced by means of Principal Component Analyses (PCA). We established the number of principal components retained and later used as predictors in correlation/regression analyses, by the

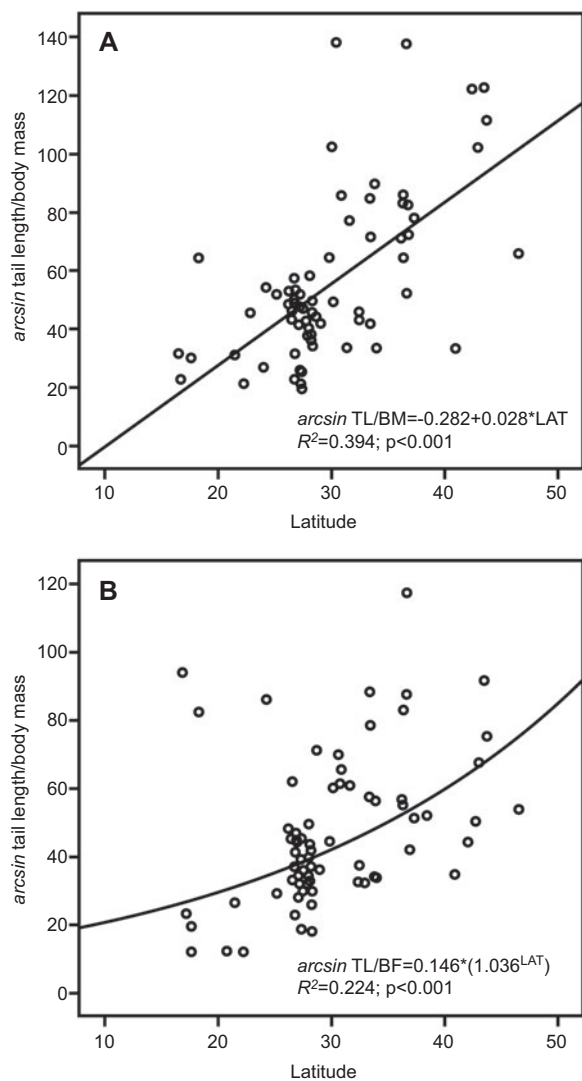


**Figure 1** Geographic distribution of *Ctenomys* populations studied in this paper. See Medina et al. (2007) for references to all localities.

**Table 1** RMA regressions of tail length on head and body length, and body mass for population means of males and females of 112 and 114 *Ctenomys* populations.

Trait 1	Trait 2	Correlation coefficient				RMA slope					RMA intercept	
		r	t	df	p-Value	$\beta$ (SE)	T	df <sup>1</sup>	p-Value	95%CI	a (SE)	95%CI
Male TL	HBL	0.610	8.07	110	<0.001	0.996 (0.075)	0.09	95.99	ns	0.847, 1.145	-0.374 (0.169)	-0.710 -0.038
	BM	0.948	25.67	74	<0.001	0.325 (0.012)	0.30	53.74	ns	0.301, 0.349	1.668 (0.028)	1.613 1.723
Female TL	HBL	0.634	8.50	112	<0.001	1.220 (0.089)	3.02	96.09	0.0032	1.043, 1.397	-0.865 (0.199)	-0.846 0.245
	BM	0.686	8.28	77	<0.001	0.303 (0.025)	0.42	65.13	ns	0.253, 0.353	1.202 (0.056)	1.091 1.313

a, RMA intercept;  $\beta$ , RMA slope; BM, body mass (all variables were log-transformed); CI, confidence interval; df, degrees of freedom; df<sup>1</sup>, adjusted degrees of freedom; HB, head and body length; ns, non-significant; p, probability; r, Pearson's correlation coefficient; SE, Standard error; t, Student's t-statistic; T, Clarke's T-statistic; TL, tail length.



**Figure 2** Regressions between the proportion of tail length to body mass (expressed as  $\arcsin \times 100$ ) and latitude in males (A) and females (B) of *Ctenomys*. For males, the best regression model was linear while for females, exponential.

broken-stick criterion (Legendre and Legendre 1998). To improve interpretation of the principal components, they were rotated to simple structure using VARIMAX criterion (Kline 1994). After identification of the best PCA predictors, the best model (combination of variables with high loadings in that PCA) was identified using Akaike's Information Criterion (Burnham and Anderson 2002).

Most biogeographic and macroecological data are spatially autocorrelated (Legendre 1993, Diniz-Filho et al. 2003, Rangel et al. 2006) thus, special statistical procedures are required for hypothesis testing, such as Simultaneous Autoregression (SAR) with preset coordinate variables (LON, LAT). In this paper, we performed all spatial analyses in SAM v.3 (Spatial Analysis in Macroecology) (Rangel et al. 2006). Finally, independent contrasts (although desirable) were not used because until now, there is not a published comprehensive phylogeny

**Table 2** Principal components analyses of climatic data for species and populations of *Ctenomys*.

Climatic variables	Principal components (broken stick)			
	Male data		Female data	
	PC1	PC2	PC1	PC2
AET	0.907*	-0.018	0.918*	-0.003
PET	0.696*	-0.318	0.675*	-0.347
TMEA	0.879*	-0.076	0.899*	-0.102
Tdry	0.812*	-0.102	0.850*	-0.093
TMIN	0.929*	0.116	0.937*	-0.114
TMAX	0.761*	0.092	0.781	-0.058
CVT	-0.810*	0.255	-0.827*	0.226
TM-m	-0.362	-0.388	-0.430	0.341
PANN	0.877*	0.270	0.872*	0.303
Pdry	0.737*	-0.605*	0.739*	0.605*
PMIN	0.571*	-0.735*	0.553*	0.747*
PMAX	0.778*	-0.276	0.777*	-0.271
CVP	-0.257	0.916*	-0.259	0.923*
PM-m	0.508*	0.681*	0.508*	-0.690*
% Total variance explained	53.90	19.50	55.30	19.60

Factors were extracted and rotated with the VARIMAX procedure with Kaiser Normalization for 15 environmental variables (see Materials and methods for nomenclature of variables). Values correspond to correlation coefficients between variables and factors. Relatively high loadings ( $|r| > 0.5$ ) are marked with an asterisk.

of *Ctenomys* although progress is being made in this sense by CJB and colleagues.

**Results**

The static allometric scaling of TL in relation with HBL and BM of both sexes was investigated by means of RMA regression. Results of the analyses are shown in Table 1 and seem to indicate an isometric scaling of tail length with body size with the exception of the relationship between female TL and HBL where  $\beta_{RMA} > 1.0$  suggesting positive allometry. However, since ontogenetic allometry was not studied due to the lack of enough juvenile individuals (which are usually not captured) it is not possible to know if tail growth is isometric or allometric in either direction.

Raw tail length has a negative correlation with latitude ( $r = -0.374$ ,  $df = 131$ ,  $p < 0.001$ ) as expected because of the converse Bergmann's rule followed by this rodents. We regressed the  $\arcsin$ -transformed proportion of TL respect to body mass against latitude of the sampled localities. In both sexes, the proportion showed a highly significant positive correlation with latitude; that is tuco-tucos show relatively longer tails as latitude increases (Figure 2). No significant correlations were observed between TL/HBL and latitude (females,  $p = 0.822$ ,  $df = 112$ ; males,  $p = 0.629$ ,  $df = 110$ ). Also, no significant altitudinal clines were obtained for either of the analyzed variables.

In order to test the possible relationship of relative tail length to climatic factors we considered 14 temperature, precipitation and evapotranspiration variables as represented by the two first principal components that include almost 75% of the

**Table 3** Standardized partial regression coefficients ( $b$ ) and their respective  $t$ -values for the two principal components (PC1, PC2) derived from 13 environmental variables predicting patterns of tail length proportion distribution in males (M) and females (F) of *Ctenomys*, from a simultaneous autoregressive (SAR) model.

Sex	Trait	Predictor	$b$	$t$	$R^2_{full}$	$R^2_{pred}$	$\rho$	AIC
M	TL/HB	PC1	-0.086	-0.82	0.035	0.022	0.28	-568.1
		PC2	-0.049	-0.46				
F	TL/BM	PC1	-0.311	-2.49*	0.182	0.166	0.47	-215.3
		PC2	-0.059	0.48				
	TL/HB	PC1	-0.212	-2.00*	0.152	0.133	0.51	-626.4
		PC2	-0.127	-1.16				
TL/BM	PC1	-0.332	-2.74*	0.330	0.293	0.64	-228.5	
	PC2	0.226	1.93					

AIC, is the value of Akaike's Information Criterion;  $\rho$ , is the autoregressive coefficient of the SAR model;  $R^2_{full}$  is the total coefficient of determination of the model (predictors+spatially structured error term);  $R^2_{pred}$  refers to the effects of the predictors independently of spatial structure. \*Significant at the 0.05% level.

**Table 4** Standardized partial regression coefficients ( $b$ ) and their respective  $t$ -values for the best univariate models derived from 13 environmental variables predicting patterns of tail length/body mass distribution in males (M) and females (F) of *Ctenomys*, from a simultaneous autoregressive (SAR) model.

Sex	Trait	Predictor	$b$	$t$	$R^2_{full}$	$R^2_{pred}$	$\rho$	AIC
M	TL/BM	PET	-0.277	-2.399*	0.148	0.134	0.467	-429.216
		Tdry	-0.280	-2.452*	0.166	0.144	0.467	-430.116
		TM-m	0.457	4.019**	0.229	0.216	0.467	-440.137
F	TL/BM	AET	-0.314	-2.581*	0.283	0.187	0.643	-446.918
		Tdry	-0.311	-2.799*	0.168	0.141	0.643	-448.900
		TM-m	0.443	4.012**	0.292	0.248	0.643	-448.179

AIC, is the value of Akaike's Information Criterion;  $\rho$ , is the autoregressive coefficient of the SAR model;  $R^2_{full}$  is the total coefficient of determination of the model (predictors+spatially structured error term);  $R^2_{pred}$  refers to the effects of the predictors independently of spatial structure. \*Significant at the 0.05% level; \*\*significant at the 0.001 level.

total variance explained in both samples as shown in Table 2 in which correlations between loadings and the variables are shown. SARs were performed separately for males and females and both tail length proportions. Except for TL/HB of males, the other proportions were significantly correlated with PC1 (Table 3). All regression slopes were negative (Table 3). However, PC1 includes most of the climatic variables considered (Table 2) many of which are colinear and significantly correlated (Appendices 1 and 2) thus, the analyses have not great explanatory power. To explore more thoroughly the relationship between tail proportions and environmental factors, we performed SARs between tail proportions and different combinations climatic variables having the highest and lowest Eigenvector loadings in random combinations of 1, 2, 3 and 4 variables using the Akaike Information Criterion to select the best models that predict variation in tail proportion with respect to body mass in both sexes. The best models are shown in Table 4. In the case of males, PET, Tdry and TM-m were the best univariate models with coefficients for the latter two being the most statistically significant (Table 4). No multivariate model showed higher AIC values. Similarly in females, TL/BM was best explained by three univariate models (Table 4) also including Tdry and TM-m, although AET and not PET was significantly correlated with tail proportion.

The four climatic variables are highly significantly correlated with latitude (see Appendices 1 and 2).

## Discussion

Variation in body size and other morphological traits of animals along geographical gradients is one of the most interesting and least understood patterns in nature (Lomolino et al. 2006a). A number of these trends have been identified and are usually referred to as "ecogeographical rules" (Ashton 2001, Lomolino et al. 2006b, Millien et al. 2006, Gaston et al. 2008). Of these, Bergmann's and Allen's rules refer specifically to body size and body proportions of protruding appendages, respectively (Bergmann 1847, Allen 1877, 1905). We chose to analyze variation in relative tail length for reasons discussed below.

Although Bergmann's rule has received much attention from researchers during more than 160 years and a wealth of information on Bergmannian patterns in endotherms and ectotherms is available (Blackburn et al. 1999, Ashton et al. 2000, Freckleton et al. 2003, Meiri and Dayan 2003, Medina et al. 2007), Allen's rule has been rather neglected despite the fact that the proposed mechanism for explaining the trend to

shorter appendages toward higher latitudes is essentially the same for Bergmann's rule, i.e., conservation or dissipation of heat (Allen 1877, Lomolino et al. 2006a).

Another problem regarding Allen's rule as well as Bergmann's and other ecogeographical rules is whether they apply to inter- or intraspecific variation (Blackburn et al. 1999) and if this is the case, whether mechanisms responsible for the trends are similar or different. In this sense, [Watt et al. \(2010\)](#) have discussed that Bergmann's rule is probably a "concept cluster" ([Peet 1974](#), see also [Lawton 1999](#)) since it has been applied at different taxonomic levels and many underlying mechanisms have been proposed. This may well be applied to Allen's rule too. Most of the published accounts of Allen trends have been intraspecific, tracing relative proportions of protruding body parts across the latitudinal or altitudinal distribution of a species, with few exceptions (e.g., [Cartar and Morrison 2005](#)). By far, the most thorough interspecific study of Allen's rule is that of [Nudds and Oswald \(2007\)](#) in gulls and terns. The authors conclude that the mechanism explaining Allen's rule, is the reduction of thermoregulatory cost during the coldest part of the breeding season of these species. It is interesting to note that variation occurred in the exposed leg bone elements and not in the feathered elements, reinforcing the thermoregulatory interpretation ([Nudds and Oswald 2007](#)).

In rodents, the more important structure involved in thermoregulatory function is the tail, which serves as a heat-loss organ ([Thorington 1966](#), [Hickman 1979](#), [Young and Dawson 1981](#), [Dawson and Keber 2007](#)). For example, the Sciurognath *Geomys* pocket gophers facilitate heat loss during heat stress by increasing blood circulation in their naked tails through which they can lose up to 30% of their heat production ([McNab 1966](#)). Geographic variation in heat loading has produced reduction of body size or increase in tail length in these subterranean rodents ([McNab 1966](#)). Tuco-tucos (*Hystricognathi*) share with pocket gophers many adaptations to the subterranean lifestyle ([Nevo 1999](#)) although less is known about thermoregulatory mechanisms in this genus. Tuco-tucos tail which has sensory functions, is almost hairless and, if it is used in thermoregulation, is a good candidate to show variation in length according to Allen's rule.

The case of tuco-tucos reported here is significant in more than one aspect. First, the observed trend for relative tail length is inverted with respect to Allen's rule expectations. Our first hypothesis was that, being fully subterranean thus being much less affected by surface climatic conditions than cursorial species, Allen's rule should not operate in this genus, and that was the case. However, instead of lacking a geographical trend, tuco-tucos tend to have relatively longer tails at higher latitudes. Tuco-tucos as other subterranean mammals, maintain fairly constant microclimatic conditions of their burrows, within which they spent >95% of the time ([Reig et al. 1990](#)) through specialized behaviors ([Nevo 1999](#), [Burda 2007](#)). The degree of exposure to external environmental conditions is minimal.

Although only three species have been adequately studied in this respect their comparison is revealing. *Ctenomys torquatus* and *C. talarum* were distributed between 25°–35°

and 35°–40°, respectively (0–200 m), and inhabited widely different environments. They maintain constant burrow temperatures of 20°–22°C throughout the year ([Medina et al. 2007](#)). More notorious is the case of *C. fulvus*, which inhabits the Chilean Puna (20°–26°S) in isolated oases up to 4000 m elevation; this species maintains burrow temperatures between 19°C and 25°C, when the above-ground temperature varies from less than 4°C to more than 45°C with a mean thermal amplitude of ca. 38°C during the day and independently of season ([Cortés et al. 2000](#)). Tuco-tuco burrows maintain more constant temperatures than those of other studied subterranean species, such as African bathyergids ([Reichman and Smith 1990](#), [Roper et al. 2001](#), [Sumbera et al. 2004](#), [Burda 2007](#)). It is thus possible that all species maintain similar temperature conditions within their burrows independently of latitude and altitude ([Reig et al. 1990](#)). It has also been reported for *Ctenomys talarum* that seasonal changes in fur length may help thermal stability ([Cutrera and Antinuchi 2004](#)).

This almost independence of external conditions suggests that classical ecogeographic rules based on thermoregulatory mechanisms, such as Allen's, do not need to operate in tuco-tucos but in fact do occur. Furthermore, body size of *Ctenomys* species decreases significantly toward higher latitudes and lower temperatures, opposing Bergmann's rule ([Medina et al. 2007](#)). [Medina et al. \(2007\)](#) explained this inverse pattern by temperature-independent mechanisms, such as geographic variation in resources, seasonality and intensity of predation.

Because the relative tail length trend observed in tuco-tucos also inverts Allen's rule, it is tempting to attribute the pattern as a consequence of the converse Bergmannian pattern. As shown in results, predictors of relative tail length were Tdry, AET, PET (negative) and TM-m (positive). Tail is relatively longer at lower temperatures, lower primary productivity and less ambient energy (two correlates of AET and PET), and high thermal amplitude. This combination of factors indicates progressively higher seasonality, one of the factors suggested to produce the inverse Bergmann's cline ([Medina et al. 2007](#)). It is thus proposed that the inversion of Allen's rule in *Ctenomys* is a consequence of negative allometric growth of the tail, and is probably independent of external ambient conditions. As shown in the results, raw tail length is not correlated with latitude while body length and body mass are strongly negatively correlated with latitude thus, while body size decreases progressively towards south, tail length does not, indirectly suggesting that negative ontogenetic allometry (species attaining larger sizes having a slower tail growth) could be the subjacent cause of the converse Allenian pattern which in turn, would result from the inversion of Bergmann's rule.

## Acknowledgements

We are grateful to all students and colleagues that helped during field work. Financial support from CNPq, FAPERJ, FIOCRUZ and FONCyT through grants to CJB is especially acknowledged. Rocio Hassan read a previous draft of this manuscript and her important contributions were incorporated to the final version. The comments of the Associate Editor and two anonymous reviewers improved the manuscript substantially.

**Appendix**

**Appendix 1** Correlation matrix of all geographic, climatic and morphometric variables considered for males.

Variables	Morphometric variables					Geographic variables					Climatic variables												
	logHB	logWt	Aresin T/HB	Aresin T/Wt		LAT	LON	ALT	TMEA	TMAX	TMIN	CVT	TM-m	Tdry	PANN	PMAX	PMIN	CVP	PM-m	Pdry	AET	PET	
LogHb	-																						
LogWt	0.943	-																					
AresinT/HB			-																				
AresinT/Wt				-																			
LAT					-																		
LON						-																	
ALT							-																
TMEA								-															
TMAX									-														
TMIN										-													
CVT											-												
TM-m												-											
Tdry													-										
PANN														-									
PMAX															-								
PMIN																-							
CVP																	-						
PM-m																		-					
Pdry																			-				
AET																				-			
PET																					-		

Spearman correlation coefficients are represented above the diagonal; Pearson's *r*s, below. All shown coefficients are statistically significant. ns, non-statistically significant correlation.



**Appendix 2** Correlation matrix of all geographic, climatic and morphometric variables considered for females.

Variables	Morphometric variables					Geographic variables					Climatic variables										
	LogHb	LogWt	ArcsinT/HB	ArcsinT/Wt	LAT	LON	ALT	TMEA	TMAX	TMIN	CVT	TM-m	Tdry	PANN	PMAX	PMIN	CVP	PM-m	Pdry	AET	PET
LogHb	-	0.912	/	/	-0.554	ns	ns	0.426	0.383	0.451	-0.462	-0.334	0.376	0.390	ns	0.372	ns	ns	ns	0.370	0.356
LogWt	0.899	-	/	/	-0.496	ns	ns	ns	ns	ns	-0.370	-0.415	ns	ns	0.354	ns	ns	0.389	ns	ns	0.474
ArcsinT/HB	/	/	-	0.562	0.008	0.294	0.233	ns	ns	ns	ns	ns	ns	ns	ns	-0.255	0.224	ns	-0.196	ns	ns
ArcsinT/Wt	/	/	0.554	-	0.516	ns	-0.051	-0.361	-0.241	-0.389	0.471	0.450	-0.322	-0.364	-0.439	ns	ns	-0.565	-0.183	-0.365	-0.467
LAT	-0.541	-0.493	ns	0.629	/	/	/	-0.413	-0.236	-0.488	0.604	0.706	-0.382	ns	-0.494	0.283	-0.490	-0.680	ns	0.303	-0.708
LON	ns	ns	0.258	0.230	/	/	/	-0.732	-0.757	-0.735	0.659	0.285	-0.655	-0.808	-0.431	-0.781	0.650	ns	-0.816	-0.802	-0.346
ALT	ns	ns	ns	ns	/	/	/	-0.496	-0.627	-0.491	0.390	ns	-0.490	-0.637	-0.269	-0.794	0.801	ns	-0.760	-0.637	-0.089
TMEA	0.379	ns	ns	-0.322	-0.544	-0.743	-0.451	-	0.947	0.977	-0.917	-0.426	0.837	0.754	0.697	0.341	ns	0.514	0.553	0.870	0.542
TMAX	0.342	ns	ns	ns	-0.223	-0.721	-0.583	0.940	-	0.909	-0.808	-0.262	0.821	0.707	0.595	0.325	ns	0.481	0.537	0.826	0.362
TMIN	0.401	ns	ns	-0.399	-0.625	-0.750	-0.400	0.979	0.872	-	-0.987	-0.517	0.899	0.779	0.726	0.390	ns	0.512	0.572	0.881	0.605
CVT	-0.388	0.320	ns	0.441	0.751	0.677	ns	-0.896	-0.757	-0.922	-	0.659	-0.877	-0.705	-0.718	-0.281	ns	-0.531	-0.466	-0.836	-0.666
TM-m	-0.278	0.370	0.245	0.501	0.697	ns	-0.223	-0.235	ns	-0.404	0.460	-	-0.480	-0.479	-0.544	-0.229	ns	-0.356	-0.306	-0.470	-0.606
Tdry	0.336	ns	ns	-0.277	-0.425	-0.627	-0.458	0.857	0.732	0.888	-0.736	-0.439	-	0.690	0.666	0.310	ns	0.488	0.461	0.791	0.482
PANN	0.348	ns	ns	-0.427	-0.297	-0.793	-0.487	0.632	0.574	0.680	-0.510	-0.311	0.628	-	0.771	0.752	-0.394	0.376	0.865	0.846	0.498
PMAX	ns	0.361	ns	-0.561	-0.569	-0.491	ns	0.554	0.430	0.599	-0.471	-0.416	0.579	0.780	-	0.273	ns	0.827	0.456	0.802	0.655
PMIN	0.332	ns	-0.272	-0.223	ns	-0.707	-0.486	0.294	0.297	0.348	-0.246	ns	0.304	0.790	0.336	-	-0.852	-0.235	0.929	0.451	0.195
CVP	ns	ns	0.200	ns	-0.420	0.622	0.752	ns	-0.283	ns	ns	-0.209	-0.206	-0.460	ns	-0.786	-	0.577	-0.721	ns	ns
PM-m	ns	0.347	ns	-0.504	-0.675	ns	ns	0.416	0.285	0.434	-0.356	-0.349	0.437	0.380	0.858	-0.196	0.493	-	ns	0.569	0.527
Pdry	ns	ns	-0.208	-0.288	ns	-0.795	-0.533	0.502	0.478	0.556	-0.409	-0.239	0.503	0.903	0.503	0.941	-0.707	ns	-	0.641	0.313
AET	0.331	ns	ns	-0.455	0.470	-0.770	-0.439	0.771	0.695	0.800	-0.661	-0.328	0.703	0.851	0.781	0.501	-0.220	0.540	0.699	-	0.615
PET	0.319	0.410	-0.196	-0.556	-0.752	-0.382	ns	0.530	0.365	0.591	-0.664	-0.520	0.436	0.488	0.607	0.247	0.184	0.498	0.350	0.648	-

Spearman correlation coefficients are represented above the diagonal; Pearson's *rs*, below. All shown coefficients are statistically significant, ns, non-statistically significant correlation.

## References

- Ahn, C.H. and R. Tateishi. 1994a. Development of a global 30-minute grid Potential Evapotranspiration data set. *J. Jpn. Soc. Photogramm. Remote Sens.* 33: 12–21.
- Ahn, C.H. and R. Tateishi. 1994b. Estimation of potential evapotranspiration for global data sets. *Proc. ISPRS Commun. IV Symp. Mapp. Geogr. Inf. Syst.*, May 31–June 3, Athens, Georgia, USA 30/4. pp. 586–593.
- Allen, J.A. 1877. The influence of physical conditions in the genesis of species. *Radical Rev.* 1: 108–140.
- Allen, J.A. 1905. The evolution of species through climatic conditions. *Science* 22: 661–668.
- Ashton, K.G. 2001. Are ecological and evolutionary rules being dismissed prematurely? *Divers. Distrib.* 7: 289–295.
- Ashton, K.G., M.C. Tracy and A. de Queiroz. 2000. Is Bergmann's rule valid for mammals? *Am. Nat.* 156: 390–415.
- Bergmann, C. 1847. Über die Verhältnisse der Warmoeconomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3 Pt.1: 595–708.
- Bidau, C.J. 2006. Family Ctenomyidae. In: (R.J. Bárcquez, M.M. Díaz and R.A. Ojeda, eds.) *Mamíferos de Argentina. Sistemática y Distribución*. Sociedad Argentina para el Estudio de los Mamíferos. Tucumán, Argentina. pp. 212–231.
- Bidau, C.J. 2011. Genus *Ctenomys*. In: (J.L. Patton, ed.) *The mammals of South America*. Vol 3. University of Chicago Press, Chicago, IL. In press.
- Blackburn, T.M., K.J. Gaston and N. Loder. 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Divers. Distrib.* 5: 165–174.
- Bohonak, A.J. and K. van der Linde. 2004. RMA: software for Reduced Major Axis regression. Java version. <http://www.kimvdlinde.com/professional/rma.html>.
- Bried, J. and P. Jouventin. 1997. Morphological and vocal variation among subspecies of the black-faced sheathbill. *Condor* 99: 818–825.
- Burda, H. 2007. Microclimate in burrows of subterranean rodents revisited. In: (S. Begall, H. Burda and C.E. Sleich, eds.) *Subterranean rodents. News from underground*. Springer, Berlin-Heidelberg. pp. 21–33.
- Burnham, K.P. and D.R. Anderson. 2002. *Model selection and multimodel inference: a practical-theoretic approach*. 2nd ed. Springer-Verlag, New York.
- Busch, C., C. Antinuchi, J.C. del Valle, M.J. Kittlein, A.I. Malizia, A.I. Vassallo and R.R. Zenuto. 2000. Population ecology of subterranean rodents. In: (E.A. Lacey, J.L. Patton and G.N. Cameron, eds.) *Life underground. The biology of subterranean rodents*. The University of Chicago Press, Chicago, IL. pp. 183–226.
- Cartar, R.V. and R.I.G. Morrison. 2005. Metabolic correlates of leg length in breeding arctic shorebirds: the cost of getting high. *J. Biogeogr.* 32: 377–382.
- Clarke, M.R.B. 1980. The reduced major axis of a bivariate sample. *Biometrika* 67: 441–446.
- Contreras, J.R. and C.J. Bidau. 1999. Líneas generales del panorama evolutivo de los roedores excavadores sudamericanos del género *Ctenomys* (Mammalia, Rodentia, Caviomorpha, Ctenomyidae). *Ciencia Siglo XXI* 1: 1–22.
- Cortés, A., E. Miranda, M. Rosenmann and J.R. Rau. 2000. Thermal biology of the fossorial rodent *Ctenomys fulvus* from the Atacama desert, northern Chile. *J. Therm. Biol.* 25: 425–430.
- Cramer, W.P. and R. Leemans. 2001. Global 30-year mean monthly climatology, 1930–1960, Version 2.1 (Cramer and Leemans). Data set. <http://www.daac.ornl.gov>. Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA).
- Cutrer, A.P. and C.D. Antinuchi. 2004. Cambios en el pelaje del roedor subterráneo *Ctenomys talarum*: posible mecanismo térmico compensatorio. *Rev. Chil. Hist. Nat.* 77: 235–242.
- Dawson, N.J. and A.K. Keber. 2007. Physiology of heat loss from an extremity: the tail of the rat. *Clin. Exp. Pharmacol.* 6: 69–80.
- Diniz-Filho, J.A.F., L.M. Bini and B.A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecol. Biogeogr.* 12: 53–64.
- Ellison, G.T.H., P.J. Taylor, H.A. Nix, G.N. Bronner and J.P. McMahon. 1993. Climatic adaptation of body size among pouched mice (*Saccostomus campestris*: Cricetidae) in the southern African subregion. *Global Ecol. Biogeogr.* 3: 41–47.
- Freckleton, R.P., P.H. Harvey and M. Pagel. 2003. Bergmann's rule and body size in mammals. *Am. Nat.* 161: 821–825.
- Gaston, K.J., S.C. Chown and K.L. Evans. 2008. Ecogeographical rules: elements of a synthesis. *J. Biogeogr.* 35: 483–500.
- Griffing, J.P. 1974. Body measurements of black-tailed jackrabbits of Southeastern New Mexico with implications of Allen's rule. *J. Mammal.* 55: 674–678.
- Hawkins, B.A. and J.A.F. Diniz-Filho. 2004. 'Latitude' and geographic patterns in species richness. *Ecography* 27: 268–272.
- Hickman, G.C. 1979. The mammalian tail: a review of functions. *Mammal Rev.* 9: 143–157.
- Jones, J., C.E. Gibb, S.C. Millard, J.J. Barg, M.K. Girvan, M.L. Veit, V.L. Friesen and R.J. Robertson. 2005. Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. *J. Biogeogr.* 32: 1827–1833.
- Kline, P. 1994. *An easy guide to factor analysis*. Routledge, London.
- Laiolo, P. and A. Rolando. 2001. Ecogeographic correlates of morphometric variation in the red-billed chough *Pyrrhocorax pyrrhocorax* and the alpine chough *Pyrrhocorax graculus*. *Ibis* 143: 602–616.
- Lawton, J.H. 1999. Are there general laws in ecology? *Oikos* 84: 177–192.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.
- Legendre, P. and L. Legendre. 1998. *Numerical ecology*. 2nd ed. Elsevier, Amsterdam. pp. 870.
- Lindsay, S.L. 1987. Geographic size and non-size variation in Rocky Mountain *Tamiasciurus hudsonicus*: significance in relation to Allen's rule and vicariant biogeography. *J. Mammal.* 68: 39–48.
- Lomolino, M.V., B.R. Riddle and J.H. Brown. 2006a. *Biogeography*. 3rd ed. Sinauer Associates, Sunderland, MA.
- Lomolino, M.V., D.F. Sax, B.R. Riddle and J.H. Brown. 2006b. The island rule and a research agenda for studying ecogeographical patterns. *J. Biogeogr.* 33: 1503–1510.
- Mayr, E. 1999. *Systematics and the origin of species from the viewpoint of a zoologist*. Harvard University Press, Cambridge, MA, London.
- McGillivray, W.B. 1989. Geographic variation in size and reverse size dimorphism of the great horned owl in North America. *Condor* 91: 777–786.
- McNab, B.K. 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology* 47: 712–733.
- Medina, A.I., D.A. Martí and C.J. Bidau. 2007. Subterranean rodents of the genus *Ctenomys* (Caviomorpha, Ctenomyidae) follow the converse to Bergmann's rule. *J. Biogeogr.* 34: 1439–1454.
- Meiri, S. and Y. Dayan. 2003. On the validity of Bergmann's rule. *J. Biogeogr.* 30: 331–351.
- Merilä, J. 1997. Quantitative trait and allozyme divergence in the Greenfinch (*Carduelis chloris*, Aves: Fringillidae). *Biol. J. Linn. Soc.* 61: 243–266.

- Millien, V., S.K. Lyons, L. Olson, F.A. Smith, A.W. Wilson and Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* 9: 853–869.
- Mirol, P.M., M.D. Giménez, J.B. Searle, C.J. Bidau and C.G. Faulkes. 2010. Population and species boundaries in the South American subterranean rodent *Ctenomys* in a dynamic environment. *Biol. J. Linn. Soc.* 100: 368–393.
- Mitchell, G.J. 1971. Measurements, weights, and carcass yields of pronghorns in Alberta. *J. Wildl. Manage.* 35: 76–85.
- Nevo, E. 1999. Mosaic evolution of subterranean mammals. *Regression, progression and global convergence*. Oxford University Press, Oxford.
- Nudds, R.L. and S.A. Oswald. 2007. An interspecific test of Allen's rule: evolutionary implications for endothermic species. *Evolution* 61: 2839–2848.
- Olalla-Tárraga, M.A., M.A. Rodríguez and B.A. Hawkins. 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North-America. *J. Biogeogr.* 33: 781–793.
- Peet, R. 1974. The measurement of species diversity. *Annu. Rev. Ecol. Syst.* 5: 285–302.
- Ramey, C.A. and D.J. Nash. 1976. Geographic variation in alberti squirrel (*Sciurus alberti*). *Southwest. Nat.* 21: 135–139.
- Rangel, T.F.L.V.B., J.A.F. Diniz-Filho and L.M. Bini. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecol. Biogeogr.* 15: 321–327.
- Raveling, D.G. and D.W. Warner. 1978. Geographic variation of yellow warblers killed at a TV tower. *Auk* 95: 73–79.
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.* 106: 85–108.
- Reichman, O.J. and S.C. Smith. 1990. Burrows and burrowing behavior in mammals. In: (H.H. Genoways, ed.) *Current mammalogy*. Plenum Press, New York and London. pp. 197–244.
- Reig, O.A., C. Busch, M.O. Ortells and J.R. Contreras. 1990. An overview of evolution, systematics, population biology, cytogenetics, molecular biology and speciation in *Ctenomys*. In: (E. Nevo and O.A. Reig, eds.) *Evolution of subterranean mammals at the organismal and molecular levels*. Alan R. Liss, New York. pp. 71–96.
- Rodríguez, M.A., L.L. López-Sañudo and B.A. Hawkins. 2006. The geographic distribution of mammal body size in Europe. *Global Ecol. Biogeogr.* 15: 173–181.
- Roper, T.J., N.C. Bennett, L. Conradt and A.J. Molteno. 2001. Environmental conditions in burrows of two species of African mole-rat, *Georchys capensis* and *Cryptomys damarensis*. *J. Zool.* 254: 101–107.
- Rosenzweig, M.L. 1968. The strategy of body size in mammalian carnivores. *Am. Midl. Nat.* 80: 299–315.
- Salthe, S.N. and M.L. Crump. 1977. A Darwinian interpretation of hindlimb variability in frog populations. *Evolution* 31: 737–749.
- Sedláček, F. 2007a. Adaptive physiological mechanisms in the underground dwellers. In: (S. Begall, H. Burda and C.E. Sleich, eds.) *Subterranean rodents. News from underground*. Springer Verlag, Berlin-Heidelberg. pp. 13–19.
- Sedláček F. 2007b. New data on metabolic parameters in subterranean rodents. In: (S. Begall, H. Burda and C.E. Sleich, eds.) *Subterranean rodents. News from underground*. Springer Verlag, Berlin-Heidelberg. pp. 35–47.
- Serrat, M.A., D. King and C.O. Lovejoy. 2008. Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proc. Natl. Acad. Sci. USA* 105: 19348–19353.
- Snow, D.W. 1954. Trends in geographical variation in Palaearctic members of the genus *Parus*. *Evolution* 8: 19–28.
- Stevenson, R.D. 1986. Allen's rule in North American rabbits (*Sylvilagus*) and hares (*Lepus*) is an exception, not a rule. *J. Mammal.* 67: 312–316.
- Sumera, R., W.N. Chitaukali, M. Elichová, J. Kubová and H. Burda. 2004. Microclimatic stability in burrows of an Afrotropical solitary bathyergid rodent, the silvery mole-rat (*Heliophobius argenteocinereus*). *J. Zool.* 263: 409–416.
- Thorington, R.W. Jr. 1966. The biology of rodent tails: a study of form and function. Technical Report (Arctic Aeromedical Laboratory (U.S.) AAL-TR – 65-8, Fort Wainwright, Alaska.
- Tilkens, M.J., C. Wall-Scheffler, T.D. Weaver and K. Stuedel-Number. 2007. The effects of body proportions on thermoregulation: an experimental assessment of Allen's rule. *J. Hum. Evol.* 53: 286–291.
- Urba, E.S. 1996. Climate, heterochrony, and human evolution. *J. Anthropol. Res.* 52: 1–28.
- Watt, C., S. Mitchell and V. Salewski. 2010. Bergmann's rule; a concept cluster? *Oikos* 119: 89–100.
- Wiggington, J.D. and F.S. Dobson. 1999. Environmental influences on geographic variation in body size of western bobcats. *Can. J. Zool.* 77: 802–813.
- Yom-Tov, Y., S. Yom-Tov, J. Wright, C.J.R. Thorne and R. Du Feu. 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos* 112: 91–101.
- Young, A.A. and N.J. Dawson. 1981. Evidence for on-off control of heat dissipation from the tail of the rat. *Can. J. Physiol. Pharmacol.* 60: 392–398.