Journal of Biogeography (*J. Biogeogr.*) (2007) **34**, 1439–1454

ORIGINAL ARTICLE

Subterranean rodents of the genus *Ctenomys* (Caviomorpha, Ctenomyidae) follow the converse to Bergmann's rule

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In fond memory of Professor Carlos Alberto Naranjo.

ABSTRACT

Aim We analysed body-size variation in relation to latitude, longitude, elevation and environmental variables in *Ctenomys* (tuco-tucos), subterranean rodents in the Ctenomyidae (Caviomorpha). We tested the existence of inter- and intraspecific size clines to determine if these rodents follow Bergmann's rule, to compare intra- and interspecific size trends and to assess the relevance of the subterranean lifestyle on these trends.

Location South America, south of 15° latitude.

Methods This paper is based on 719 specimens of tuco-tucos from 133 localities of Argentina, Bolivia, Chile, Paraguay, Peru and Uruguay, representing 47 named species and 32 undescribed forms. Intraspecific analyses were performed for *Ctenomys talarum* Thomas, 1898 and the *Ctenomys perrensi* Thomas, 1896 species complex. Head and body length and weight were used for estimating body size. Geographical independent variables included latitude, longitude and altitude. Environmental independent variables were mean minimal and maximal monthly temperature, mean annual temperature, mean minimal and maximal precipitation, and total annual precipitation. To estimate seasonality, the annual variability of the climatic factors was calculated as their coefficients of variation and the difference between maximum and minimum values. Mean annual actual evapotranspiration (AET), and mean annual, January (summer) and July (winter) potential evapotranspiration (PET) values were also calculated for each locality, as well as annual, summer and winter water balance (WB). Statistical analyses consisted of simple and multiple regression and nonparametric correlation.

Results Body size of *Ctenomys* decreases interspecifically from 15°00′ S to 48°15′ S and from 56°33′ W to 71°46′ W, and is positively correlated with ambient temperature and precipitation. The best predictors of body size according to multiple regression analyses were mean annual temperature, the difference between mean maximum and minimum annual temperatures, annual PET, the difference between summer and winter PET, and annual and winter water balance. These patterns are repeated, but not identically, at a smaller geographical scale within the species *C. talarum* and the superspecies *C. perrensi*.

Main conclusions Tuco-tucos follow the converse to Bergmann's rule at the interspecific level. At the intraspecific level some parallel trends were observed, but the smaller scale of these analyses, involving a very reduced variation of environmental factors, necessitates caution in interpreting results. The subterranean lifestyle probably insulates these rodents from the external temperature. The observed latitudinal body-size gradients are more probably related to seasonality, ambient energy, primary productivity and/or intensity of predation.

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doi:10.1111/j.1365-2699.2007.01708.x

Keywords
Bergmann's rule, body size, climatic variables, *Ctenomys*, geographical variation, size clines, South America, subterranean rodent.

INTRODUCTION

Bergmann's (1847) rule was one of the first attempts to correlate morphological variation of organisms with their geographical distribution through a single environmental factor: temperature.

Bergmann's rule, as originally formulated, states that: '(i)f we could find two species of [homeothermic] animals which would only differ from each other with respect to size, …(t)he geographical distribution of the two species would have to be determined by their size…. if there are genera in which the species differ only in size, the smaller species would demand a warmer climate, to the exact extent of the size difference.' (Translation by James, 1970 transcribed by Blackburn *et al.*, 1999.)

de Queiroz & Ashton (2004) have suggested that Bergmann's rule may be ancestral for tetrapods. Blackburn *et al.* (1999) reformulated the rule as: 'Bergmann's rule is the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species'. Temperature is replaced by latitude as a predictor for body size.

The most widely used definition of Bergmann's rule is, however, intraspecific. Rensch (1938, 1959) reformulated the rule to size differences between races of a species, saying that 'within a *Rassenkreis* (*we note: a species composed of several geographical subspecies, a polytypic species*) of warm-blooded animals, the races inhabiting cooler climates are generally larger than those that live in warmer regions'. Mayr (1999) also stated that the smaller (in body size) geographical races within a species occur in the warmer part of the distribution range, while the larger ones occur in the colder regions. Blackburn *et al.* (1999) thus suggested that the notion that Bergmann's rule can be applied intraspecifically is a derived state. However, this apparent controversy may be understood considering that most of Bergmann's 'species' were in fact differentiated populations of a polytypic species in the modern sense. Nonetheless, interspecific and even intra-class analyses have been carried out, despite the mode being intraspecific, but intra- and interspecific geographical body-size patterns may not obey the same mechanisms.

It is unclear if patterns of latitudinal body-size variation for the same group of animals are consistent between biological levels (within and among species). Even if they are, it is unknown if the same mechanisms are responsible for the observed trends. Bergmann (1847) proposed an adaptive physiological process that involved the conservation of body heat through modification of the relationship between body area and body volume. By contrast, Rensch (1938, 1959) and Mayr (1956, 1963, 1999) treated the latitudinal variation in body size as an empirical pattern that could be proved or disproved, regardless of the mechanism that originated the observed distribution. Furthermore, many alternative mechanisms other than thermoregulation have been proposed to account for latitudinal variation in body size of endotherms (Ashton *et al.*, 2000).

Intraspecifically, Bergmann's rule is a common phenomenon in mammals (Ashton *et al.*, 2000; Meiri & Dayan, 2003; Meiri *et al.*, 2004) and birds (Ashton, 2002b; Meiri & Dayan, 2003) when both latitude and/or temperature is the independent variable. Intraspecific Bergmannian trends also occur in vertebrate and invertebrate ectotherms (Ray, 1960; Atkinson, 1994; Atkinson & Sibly, 1997; Ashton, 2002a; Ashton & Feldman, 2003; Blanckenhorn & Demont, 2004; Bidau & Martí, in press).

Reverse patterns have also been revealed in some groups (Belk & Houston, 2002; Ashton & Feldman, 2003; Bidau & Martí, in press). At the interspecific level, evidence for Bergmann's rule is far from clear owing to the scarcity of studies and the complications involved in analyses, including the difficulty of obtaining *bona fide* size data for many species, the occurrence of sexual size dimorphism (SSD), the occurrence of intraspecific geographical size variability, and the lack of phylogenetic information in many cases (Lindsey, 1966; Manly, 1998; Roy *et al.*, 2000). Blackburn & Gaston (1996), Blackburn & Ruggiero (2001), Blackburn & Hawkins (2004) and Rodríguez *et al.* (2006) found some support for Bergmann's rule at the interspecific level in New World birds and northern North American and European mammals, but no such evidence is available for most mammals in the rest of the world. It is thus unknown if interspecific Bergmannian patterns occur within taxa of mammals (genera, families), and if they do, whether interspecific and intraspecific trends are concordant.

Classical Bergmannian gradients are difficult to explain, since temperature alone (Bergmann's original proposal, 1847) is not sufficient to explain all observed trends. A number of alternative mechanisms have been proposed, and these have been reviewed recently by Ashton *et al.* (2000) and Ashton (2002b). Reduction of internal heat loading in warmer environments, instead of minimization of heat loss in cool climates, is one alternative mechanism (Scholander, 1955; McNab, 1979). Changes in insulation could be more important than changes in body size (McNab, 1971; Geist, 1987). The former mechanism could be more important for large mammals, while small mammals would depend more strongly on changes in body size for heat conservation (Steudel *et al.*, 1994); however, the theoretical predictions of Steudel *et al.* (1994) run counter to the empirical evidence (Freckleton *et al.*, 2003; Meiri & Dayan, 2003). Larger

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mammals would have greater fasting endurance during periods of food shortage in seasonal environments (Boyce, 1979; Lindstedt & Boyce, 1985; Millar & Hickling, 1990). Primary productivity, food quality and abundance may influence body size (Rosenzweig, 1968; Erlinge, 1987). Intensity of predation and competition, as well as selection on life-history characteristics correlated with body size, have also been proposed as explanations for Bergmannian clines (McNab, 1971; Ashton *et al.*, 2000).

As some mammal groups with particular adaptations do not follow Bergmann's rule, it has been discussed by McNab (1971), Ashton *et al.* (2000) and Meiri & Dayan (2003) whether lifestyle could be related to geographical body-size variation. Burrowing species of rodents and insectivores are likely candidates because they spend most of the time in favourable and relatively constant microclimatic conditions. Thus it could be expected that body size would be less affected by abiotic environmental variables such as temperature (Mayr, 1963; Rodríguez *et al.*, 2006). Nevertheless, some hibernating or subterranean mammals do seem to follow Bergmann's rule (Panteleev *et al.*, 1998). However, the few available data suggest there are no major differences in size trends between different lifestyles (Ashton *et al.*, 2000; Meiri & Dayan, 2003), and more studies are needed in this respect.

Tuco-tucos (genus *Ctenomys* de Blainville, 1826) constitute an excellent model to test predictions about the geographical distribution of body size. First, the genus has a large geographical distribution, spanning 45° of southern latitude (from *c.* 10°S in the Peruvian highlands to almost 55°S in Tierra del Fuego), and species can be found between 0 and 5000 m a.s.l. from the Pacific to the Atlantic oceans (Contreras & Bidau, 1999). Second, these rodents are fully subterranean and spend more than 95% of their lives underground (Reig *et al.*, 1990; Nevo, 1999). Third, although *Ctenomys* includes *c.* 63 named extant species (Bidau, 2006), these are morphologically homogeneous, showing the same adaptations for living underground, but varying greatly in body size (Contreras & Bidau, 1999; Nevo, 1999).

Finally, 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, etc., their burrows, maintain fairly constant temperature and humidity independently of geographical location (Reig *et al.*, 1990; Nevo, 1999; Nowak, 1999; Busch *et al.*, 2000). This characteristic probably isolates them quite effectively from the external environment. Thus tuco-tucos are a useful model system to test the assumptions of Bergmann's rule when compared with surface-living species.

Here we analyse geographical body-size variation in *Ctenomys* in relation to latitude and other geographical and environmental variables, at both interspecific and intraspecific levels, in order to test: (1) Bergmann's rule (*sensu* Blackburn *et al.*, 1999) in a genus of mammals, (2) Bergmann's rule (*sensu* Rensch, 1938 and Mayr, 1956) within two species of *Ctenomys*, (3) if the subterranean lifestyle has any effects on body-size pattern, and (4) if size trends do occur, whether they are concordant inter- and intraspecifically and what mechanisms can account for them.

MATERIALS AND METHODS

This paper is based on morphological measurements of 530 adult tuco-tucos collected and measured by the authors and collaborators between 1995 and 2003, belonging to 109 localities in Argentina and Paraguay, plus 189 individuals from Argentinian, Bolivian, Chilean, Paraguayan, Peruvian and Uruguayan populations (24 localities), morphological data for which were extracted from Thomas (1919), Thomas & St Leger (1926), Osgood (1943, 1946), Sanborn & Pearson (1947), Barlow (1965), Contreras *et al.* (1977), Pine *et al.* (1979), Lessa & Langguth (1983), Pearson (1984), Pearson & Christie (1985), Kelt & Gallardo (1994) and Anderson (1997) (Table S1 in Supplementary Material; Fig. 1). Specimens not measured by the authors are indicated with an asterisk in Table S1.

The whole sample spans more than 33° of latitude (S), 15° of longitude (W) and from 0 to 4184 m a.s.l., and includes 47 named species and 32 undescribed forms, designated *Ctenomys* sp. followed by a number corresponding to increasing latitude of the respective locality (Table S1; Fig. 1). This is a reflection of the complex and incomplete status of *Ctenomys*

Figure 1 Geographical distribution of 133 populations of tuco-tucos (genus *Ctenomys*) in South America.

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taxonomy (Contreras & Bidau, 1999; Mascheretti *et al.*, 2000). Most species are represented by a single population (especially those of limited geographical distribution), and others by several populations. In almost all cases the unnamed populations can be related to known Linnean species, as indicated in Table S1. For example, in Corrientes province (Argentina) there are three nominal species (*C. dorbignyi* Contreras & Contreras 1984; *C. perrensi* Thomas, 1896; *C. roigi* Contreras, 1988) and numerous discrete populations whose diploid chromosome number varies between 40 and 66, which are morphologically and molecularly close to the three named species (Giménez *et al.*, 2002). The whole assemblage can be better described as a superspecies, but some of the forms are probably good species. These forms are referred to in Table S1 as '*C.* sp. *perrensi* complex'. In other cases the relationships are less clear, especially for a number of recently discovered Patagonian populations, many of which may be species new to science (Montes *et al.*, 2001).

As Bergmann's rule may occur as an empirical pattern both intra- and interspecifically (Blackburn *et al.*, 1999; Ashton *et al.*, 2000), we aimed to perform both kinds of analysis in our sample. In the case of *Ctenomys*, intraspecific analyses are somewhat troublesome. Species limits within this genus are difficult to define because of extensive chromosomal variability and low genetic and morphological differentiation (Giménez *et al.*, 2002). The very reduced geographical ranges of most tuco-tuco species (with few exceptions; see below) make intraspecific analyses of Bergmann's rule practically meaningless because of low variation of environmental variables (Meiri *et al.*, 2004). Thus the following approach was used in the study of geographical body-size patterns: at the supraspecifc level, analyses were performed considering only discrete populations (whether of different or the same species) where body-size estimates were calculated for each sampled population. This approach is valid as the genus *Ctenomys* is undoubtedly a monophyletic taxon and all its species share the same basic morphological, physiological and behavioural adaptations to the subterranean lifestyle (Contreras & Bidau, 1999; Nevo, 1999; Busch *et al.*, 2000).

For intraspecific analyses of geographical body-size patterns, two taxa with a relatively large geographical range were chosen: the *Ctenomys perrensi* species complex from Corrientes province (Argentina), and *Ctenomys talarum* of Buenos Aires and La Pampa provinces. For both assemblages, data for many populations were available. Corrientes province is inhabited by a complex of tuco-tuco populations that include three closely allied nominal species, *C. perrensi*, *C. dorbignyi* and *C. roigi* (Bidau, 2006) and a series of unnamed, chromosomally differentiated populations related to the former (Table S1). The whole group is monophyletic and is better described as a superspecies (Giménez *et al.*, 2002). Populations sampled by us cover the whole range of the complex, which extends between 27°33′ S and 29°11′ S. *Ctenomys talarum* is distributed in Buenos Aires and La Pampa provinces in Argentina (Braggio *et al.*, 2000; Justo *et al.*, 2003). We analysed specimens collected at 15 localities from 35°57′ S to 38°54′ S and 56°40′ W to 65°02′ W, including representatives of the three recognized subspecies (*C. t. talarum*, *C. t. recessus* and *C. t. occidentalis*). In both cases, mean values for body-size estimates were calculated for each population sampled.

All individual measurements employed in the statistical analyses were taken in the field from freshly caught adult tuco-tucos in the case of specimens collected by the authors and collaborators, or obtained from the relevant literature. Mean length of head and body (HB) and mean weight (Wt) were used for estimating body size separately for each sex. Linear measurements were available for all collected specimens and those derived from the literature, while body weight was not obtained for some samples or was not found in the literature examined (27% of localities; Table S1), thus some localities are missing from the body mass analyses. Sexual maturity was assessed through the analysis of the reproductive status of individuals in the specimens collected. In the case of males, only those with scrotal testes were considered. In the case of females, maturity was determined by inspection of vulva, uterus and ovaries. Pregnant females were excluded from the study. Males and females were analysed separately to account for SSD, which occurs in all species of *Ctenomys* (Medina, 2004). All measurements were log-transformed, and latitude (LAT) and longitude (LON) were converted to decimal units.

Latitude was included as an independent variable, since a positive correlation between body size and latitude, or the lack of it, indicates whether or not Bergmann's rule applies to a certain group of organisms (Blackburn *et al.*, 1999; Yom-Tov *et al.*, 2002; Meiri & Dayan, 2003). Longitude was considered because most climatic variables show strong longitudinal gradients in the area surveyed, spanning more than 15° between the Atlantic and Pacific oceans and including the Andes range (Table S1; for a discussion of the relevance of longitudinal clines see Hawkins & Diniz-Filho, 2004; Meiri *et al.*, 2005). Altitude in metres a.s.l. was determined for all localities, and ranged between 0 and 4184 m (Table S1). Altitude (ALT) was included because an increase in elevation is frequently ecologically equivalent to an increase in latitude (Wiggington & Dobson, 1999). However, this kind of unidimensional analysis has no explanatory power (Hawkins & Diniz-Filho, 2004), so as size clines may respond to multiple selection pressures (Jones *et al.*, 2005), other independent variables were considered.

Climatic data for all samples were obtained from Cramer & Leemans (2001). This database is a major update of the Leemans & Cramer (1991) database, recording mean monthly ambient temperature and precipitation over a 30-year period. Temperatures were used as independent variables, as Bergmann's (1847) rule originally relied on a thermoregulation hypothesis. Different precipitation measurements were included because humidity has been hypothesized as relevant to the generation of geographical body-size clines (James, 1970; Aldrich & James, 1991). Mean minimal (TMIN) and maximal (TMAX) monthly temperature, mean annual temperature (TMEA), mean minimal (PMIN) and maximal (PMAX) precipitation and total annual precipitation (PANN) were

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recorded for each locality with an accuracy of 0.5°. Boyce (1979) and Lindstedt & Boyce (1985) proposed that body size should be larger in areas of greater climatic seasonality (the fasting-endurance hypothesis). To estimate seasonality, the annual variability of the climatic factors was calculated. Annual variability of temperature was estimated through the coefficient of variation ($CV = s \times 100/x$) of TMEA (CVT) and the difference between TMAX and TMIN (TM-m). CVT was calculated from average monthly temperatures for each point in Cramer & Leemans (2001), from which the SD of TMEA was obtained. Variability of precipitation was assessed by the CV of mean annual precipitation (CVP, calculated from mean monthly precipitation and its SD) and the difference between maximum and minimum monthly precipitation (PM-m). A further hypothesis pertaining to body-size clines is that of Rosenzweig (1968), who proposes that body size is positively correlated with primary productivity and with such variables as actual evapotranspiration (AET) and potential evapotranspiration (PET) (Olalla-Tárraga *et al.*, 2006; Rodríguez *et al.*, 2006). 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) were obtained for each locality. We used vectors, data bases and maps for AET, PET and WB from Ahn & Tateishi (1994a,b).

Data analysis was performed with the GEOMATICA FREEVIEW ver. 10.0 software by PCI Geomatics, Ontario, Canada (http://www.pcigeomatics.com). All data are in mm year^{-1}. Mean annual AET, mean annual, January (summer) and July (winter) PET values (PET, PETJa and PETJu, respectively) were calculated for each locality, as well as the difference between summer and winter PETs (PETJa-Ju). Annual, January and July water balance (WB, WBJa and WBJu, respectively) were also calculated.

Finally, since in most tuco-tucos external activity is mainly restricted to the dry season (Reig *et al.*, 1990), we calculated mean temperatures and total precipitation for the six drier months of the year in each locality (TDRY and PDRY, respectively) and used them as independent variables in correlation/regression analyses.

In the case of some analyses of body size in *C. talarum* and the *C. perrensi* superspecies, the effect of gender was controlled by the inclusion of a measurement of sex ratio as an independent variable in regressions and correlations. Sex ratio was calculated as the proportion of males (the larger sex) in each studied sample. For evaluating SSD in both taxa, we used reduced major axis (RMA) regression to estimate allometric slopes for the relationship between log10 (female size) and log10 (male size) with the software for RMA (Java version) of Bohonak & van der Linde (2004). Clarke's t statistic with adjusted degrees of freedom was used for testing the hypothesis that $b_{RMA} = 1.0$ (Clarke, 1980).

Normality of data was estimated through the Kolmogorov–Smirnov (Liliefors) test. Since most of the variables tested departed from normality even after log transformation, Spearman's correlation coefficients were calculated (Meiri *et al.*, 2004). Simple linear and nonlinear regression, and multiple stepwise backward regression were performed with SPSS 11.01 software.

RESULTS

Latitudinal, longitudinal and altitudinal variation in body size of *Ctenomys*

A large variation in body size occurs within the genus. In our sample, body mass ranged between 43 g in a female *Ctenomys* sp. 29 from Puerto Madryn (Argentina) and 1200 g in a male *C. conoveri* from Carandayti (Bolivia). Total length ranged from 146 mm in a female *Ctenomys* sp. 12 from Pago Alegre (Argentina) to 680 mm in the same *C. conoveri* male as mentioned above. Females were consistently smaller than males in all species (A.I.M. and C.J.B., unpublished data) and their respective size ranges are: females, body weight 43–420 g; total length 146–374 mm; males, body weight 49–1200 g; total length 149–680 mm. Male body size shows, on the whole, a higher variability than that of females. The coefficients of variation for head and body length for the whole sample were 20.58 for males and 14.53 for females. In the case of body mass, the respective values were 67.99 and 50.73.

Against Bergmann's rule, mean body size of males and females from 112 and 114 population samples, respectively, of the 133 tuco-tuco populations analysed, decreased with latitude along the considered geographical area (Table 1; Fig. 2). Highly significant negative correlations were obtained for both body-size estimators in both sexes, even though body mass was available for only 74 male and 76 female samples (Table S1). In the case of longitude, negative relationships were obtained for body size measurements in both sexes, but only those for males were significant (Table 1). No clear relationships occurred when altitude was the independent variable. Thus in general body size in tuco-tucos decreases with latitude and, to a lesser degree, with longitude (towards W), especially in males, when simple correlations are performed.

Body size and climatic variables

All body-size estimators showed basically the same relationships to climatic variables when simple Spearman's correlations were run (Table 2; Fig. 3). With respect to temperature, body size showed highly significant positive correlations with TMEA, TMIN and TMAX and also with the mean temperature of the six drier months, with the exception of female mean weight, which showed the same tendencies but no significant correlations. Nevertheless, body size decreases as variability in mean monthly temperatures increases, as demonstrated by the negative correlations with CVT and TM-m (Table 2).

Body size increased with the amount of precipitation, the strongest relationship being with PMAX, which generally corresponded to summer at most latitudes, longitudes and altitudes (Table 2). Body size also showed a positive

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Table 1 Spearman's correlation coefficients (r) and their statistical significance (P) between six estimators of *Ctenomys* body size and latitude, longitude and altitude.

	MWt		FWt		MHB		FHB	
	r	P	r	P	r	P	r	P
LAT	**−0.442**	**0.001**	**−0.496**	**< 0.001**	**−0.404**	**< 0.001**	**−0.554**	**< 0.001**
LON	**−0.238**	**0.040**	−0.119	0.302	**−0.244**	**0.010**	−0.093	0.329
ALT	−0.056	0.633	0.075	0.519	0.010	0.915	0.131	0.170

See Materials and methods for abbreviations of variables. Significant correlations are shown in bold type. M, male; F, female.

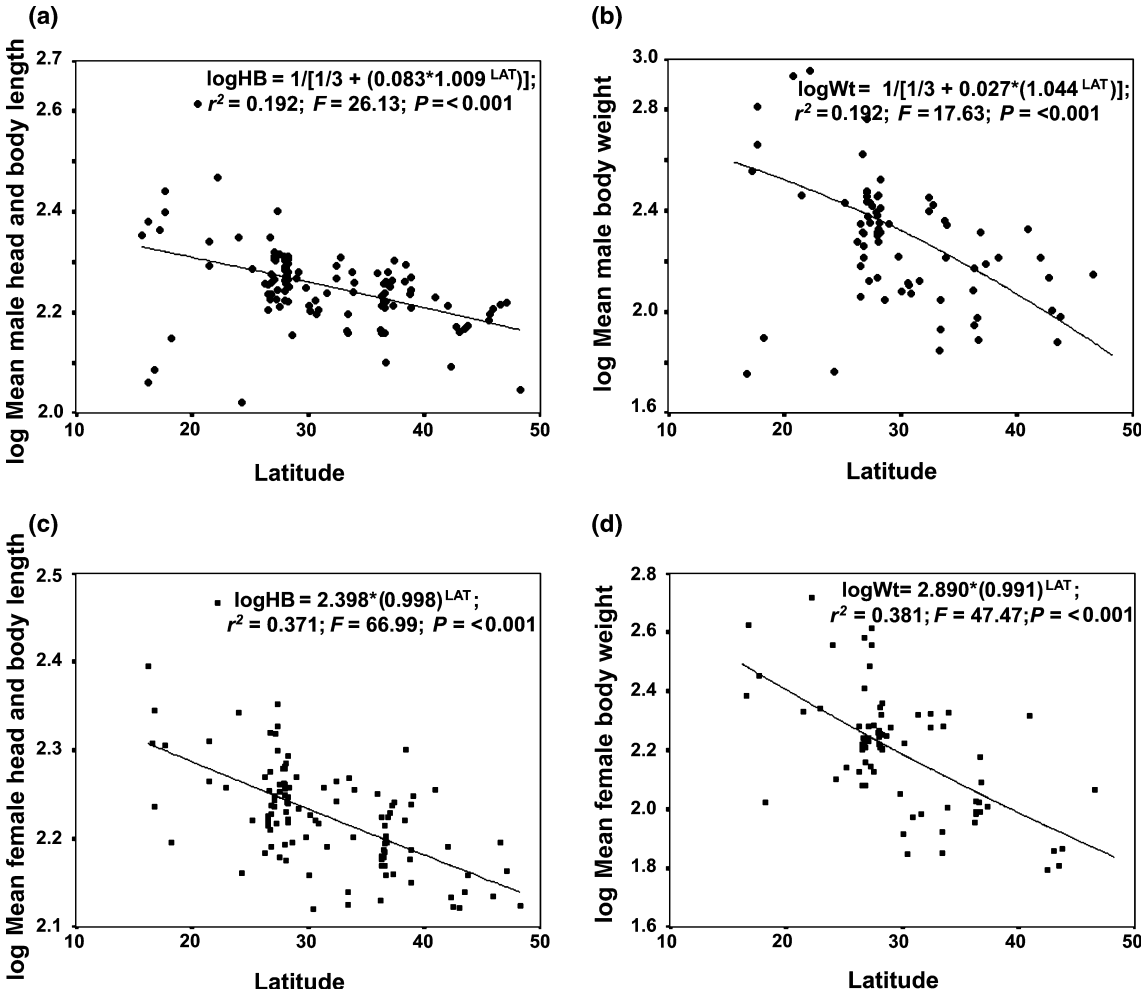

Figure 2 Variation of male (a,b) and female (c,d) *Ctenomys* body size as a function of latitude. Equations represent the best predictive model for each variable. Measurements are in mm (HB) and g (Wt) and transformed to log10.

relationship with variability in monthly local precipitation (PM-m) in the case of females (Table 2).

The amounts of annual, summer and winter PET were significantly and positively correlated with body size (Table 2). Body size was negatively correlated with annual WB values, indicating that larger body sizes tend to be found at more humid localities (Table 2). Also, positive correlations between body-size estimators and AET were observed (Table 2).

Since a number of climatic variables are correlated with latitude, longitude and altitude, causal explanations for body-size trends based on these correlations must be analysed cautiously. Multiple stepwise backward regression was used to explore more thoroughly the environmental factors that may be affecting body size. To reduce collinearity in multiple regressions, we performed an *a priori* selection of the environmental variables to be used by choosing the variable(s) more strongly correlated with body size among those variables that were highly intercorrelated. We also included altitude as a surrogate for mesoclimatic conditions. The results are shown in Table 3 and Fig. 4. It can be seen that TM-m, and the

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Table 2 Spearman's correlation coefficients (r) and their statistical significance (P) between six estimators of *Ctenomys* body size and climatic variables.

	MWt		FWt		MHB		FHB	
	r	P	r	P	r	P	r	P
TMIN	0.453	< 0.001		ns	0.451	< 0.001	0.405	< 0.001
TMAX	0.395	< 0.001		ns	0.383	< 0.001		ns
TMEA	0.447	< 0.001		ns	0.426	< 0.001	0.354	< 0.001
CVT	−0.499	< 0.001	−0.370	0.001	−0.462	< 0.001	−0.472	< 0.001
TM-m	−0.423	< 0.001	−0.415	< 0.001	−0.334	< 0.001	−0.437	< 0.001
TDRY	0.417	< 0.001		ns	0.376	< 0.001	0.338	< 0.001
PMIN		ns		ns		ns		ns
PMAX	0.379	0.001	0.354	0.002	0.372	< 0.001	0.465	< 0.001
PANN	0.384	< 0.001		ns	0.390	< 0.001	0.378	< 0.001
CVP		ns		ns		ns		ns
PM-m		ns	0.389	< 0.001		ns	0.468	< 0.001
PDRY		ns		ns		ns		ns
AET	0.383	0.001		ns	0.370	< 0.001	0.425	< 0.001
PET	0.392	< 0.001	0.474	< 0.001	0.356	< 0.001	0.483	< 0.001
PETJa	0.400	< 0.001		ns	0.389	< 0.001		ns
PETJu	0.461	< 0.001	0.364	0.001	0.426	< 0.001	0.433	< 0.001
PETJa-Ju		ns		ns		ns		ns
WB	−0.374	0.001	−0.340	0.002	−0.380	< 0.001	−0.402	< 0.001
WBJa		ns	−0.488	< 0.001		ns	−0.511	< 0.001
WBJu		ns		ns		ns		ns

See Materials and methods for abbreviations of variables. The Bonferroni correction has been applied to calculate probabilities for Student's t-statistic ($\alpha = 0.0025$). M, male; F, female.

difference between summer and winter PET, two measurements of seasonality, were included in most models, while annual PET and winter WB showed significant partial correlations in two models each.

Body-size variation in the *Ctenomys perrensi* superspecies

The *C. perrensi* superspecies is distributed in Corrientes province along almost 2° of latitude and 2.5° of longitude (Giménez *et al.*, 2002; Bidau, 2006). Body size tended to decrease latitudinally and longitudinally, although Spearman's correlations were non-significant both for each sex separately and when both sexes were pooled, and correlations were controlled for gender except in one case (Table 4).

Multiple regressions including sex as a further explanatory variable revealed that the best predictors of body size in the *C. perrensi* superspecies were PMAX, PM-m, AET, PETJa and WBJu (r^2 for HB = 0.328; r^2 for Wt = 0.315; Table 5). Gender was also a fairly good predictor of body size (Table 5). In the *C. perrensi* complex, a medium-sized group, SSD ranged from 0.98 to 1.07 for head and body length, and from 0.91 to 1.10 for weight. The respective allometric slopes were $b_{RMA} = 1.20$ ($t = 0.99$; d.f. = 25.37; $P = 0.32$) for head and body, and $b_{RMA} = 2.43$ for weight ($t = 5.43$; d.f. = 13.08; $P = 0.0001$), indicating that the difference between males and females increases with increasing size, especially in the case of body mass.

Body-size variation in *Ctenomys talarum*

Ctenomys talarum includes three disjunct population nuclei in Argentina, corresponding to three recognized subspecies (Justo *et al.*, 2003; Bidau, 2006): *C. t. talarum* has a north–south distribution along the Atlantic coast of Buenos Aires province; *C. t. recessus* occupies an east–west strip of the southern Atlantic coast of the same province; and *C. t. occidentalis* is distributed in east-central La Pampa province, probably extending to northern Buenos Aires. The complete range of the species extends for about 3° of latitude and 7° of longitude. We analysed two populations of *C. t. occidentalis*, 12 of *C. t. talarum* and one of *C. t. recessus*. No body-mass estimates were available for most of these samples (Table S1).

When males and females were analysed separately with respect to the geographical variables, no clear trends were observed except a significant negative correlation between female HB and altitude (Table 4). However, when male and female data were pooled and correlations were controlled for sex, highly significant negative relationships between body size and LON and ALT were obtained (Table 4).

With respect to environmental factors, six variables appeared as good predictors of body size as represented by HB. A multiple regression including gender as a further explanatory variable revealed that the best predictors of body size in *C. talarum* were TMAX, TM-m, PM-m, AET, PETJa-Ju and WBJu ($r^2 = 0.921$) (Table 5).

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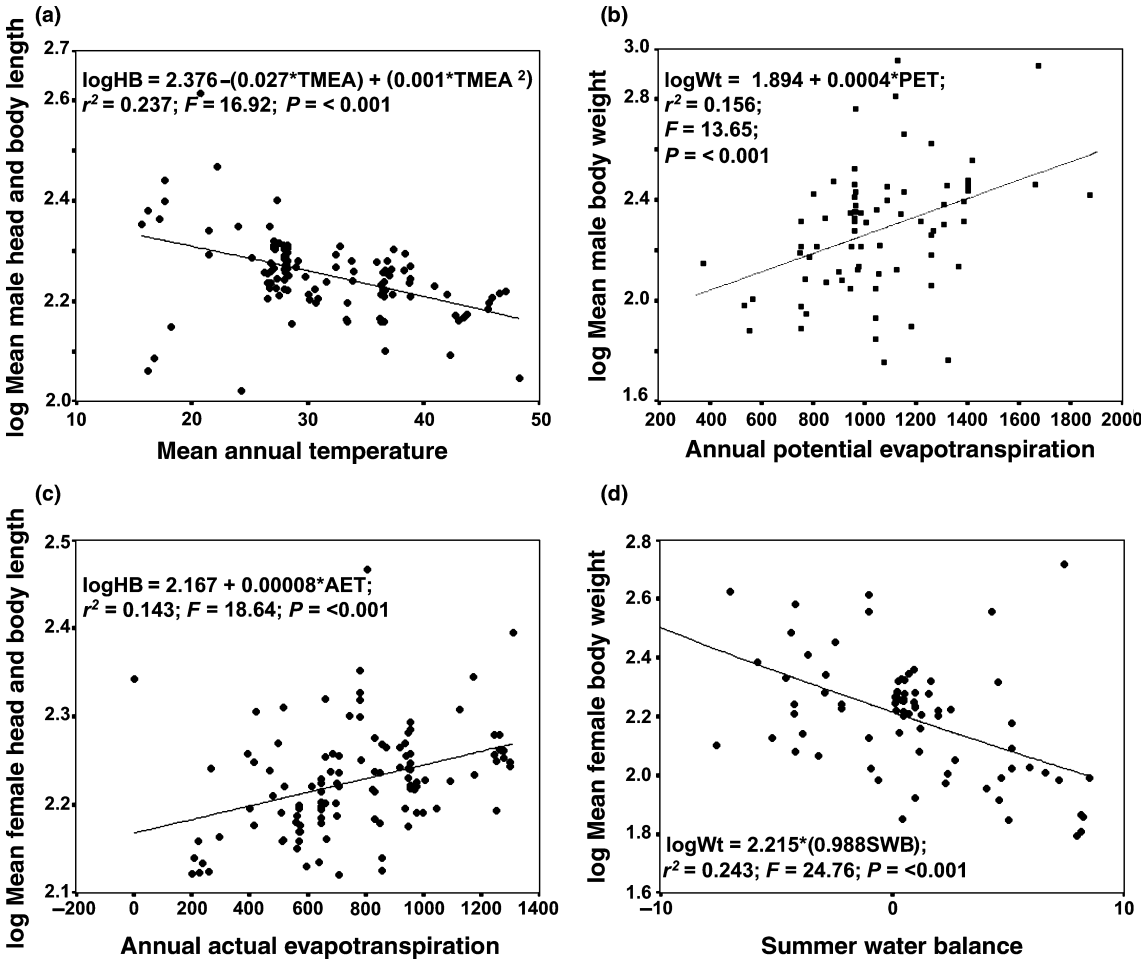

Figure 3 The variation of male (a,b) and female (c,d) *Ctenomys* body size as a function of selected environmental variables. Equations represent the best predictive model for each variable. Measurements are in mm (HB) and g (Wt) and transformed to log10.

In *C. talarum*, one of the smallest species of tuco-tuco, SSD is low, at least for head and body length, ranging from 0.99 to 1.05 in the populations sampled. Furthermore, the allometric RMA slope was not statistically different from 1 ($b_{RMA} = 1.01$; $t = 0.066$; d.f. $= 14.30$; $P = 0.95$), indicating that SSD remains the same, independent of general body size.

DISCUSSION

One of the aims of this study was to test Bergmann's rule interspecifically (*sensu* Blackburn *et al.*, 1999) in a genus of mammals (*Ctenomys*) and, simultaneously, to test for Bergmann's rule intraspecifically (*sensu* Rensch, 1938, 1959; Mayr, 1956, 1963) in selected taxa of the same genus (*C. talarum* and *C. perrensi* species complex) to verify if concordant or discordant patterns of geographical body-size variation occurred at the two levels. In this respect, two results are clear. First, the genus *Ctenomys* follows the converse to Bergmann's rule, since body size of *Ctenomys* species decreases with increasing latitude (and decreasing temperature). Clearly, larger species of tuco-tucos are found at low latitudes, while smaller species tend to have more southern distributions.

Second, in the two intraspecific analyses, the same body size trend was apparent, suggesting that similar evolutionary pressures on body size may be operating at both biological levels. Only one comparable case in endotherms was found in the available literature, that of the leaf warbler *Phylloscopus*, in which a single species showed the converse to Bergmann's rule, similar to the pattern seen across species within this genus (Katti & Price, 2003; see above). Thus intra- and interspecific patterns are concordant, in our case, with tuco-tucos showing the converse to Bergmann's rule within and between species.

Typical Bergmannian body-size gradients may have different explanations. Reverse patterns, such as that of tuco-tucos, are thus more difficult to interpret. Hypotheses for the body-size trends in *Ctenomys* must take into account their subterranean lifestyle. Relative independence of *Ctenomys* species from the external climate would predict that no size trend related to ambient temperature would be found. At least three points of discussion arise from the previous statement. First, independence of ambient temperature could explain a lack of correlation between body size and latitude, but not a negative correlation such as that found in *Ctenomys*. Second, a simplistic hypothesis would predict lack of latitude/temperature

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Table 3 Results of multiple stepwise backward regressions between body-size estimators and environmental variables in *Ctenomys*.

Body-size estimator	Multiple regression			Environmental variables								
				ALT	TMEA	TM-m	PM-m	PET	PETJaJu	WB	WBJu
				Partial correlation coefficients							
	r^2	F	P	r/P	r/P	r/P	r/P	r/P	r/P	r/P	r/P
MWt	0.358	9.917	< 0.001	0.457/< 0.001	0.430/< 0.001	ns	ns	ns	0.269/0.014	ns	−0.361/0.002
FWt	0.297	16.044	< 0.001	ns	ns	−0.314/0.005	ns	0.281/0.013	ns	ns	ns
MHB	0.333	8.739	< 0.001	0.165/0.090	ns	−0.370/< 0.001	ns	0.222/0.022	0.428/< 0.001	0.245/0.011	−0.281/0.003
FHB	0.374	21.953	< 0.001	ns	ns	−0.409/< 0.001	0.255/0.007	Ns	0.157/0.007	ns	ns

r^2, Coefficient of determination; F, F-statistic; r, correlation coefficients; P, statistical significance. See Materials and methods for abbreviations of variables. In the four cases, the results of the best model obtained are shown.

correlations in other fully subterranean mammals; however, most species of fossorial Insectivora and Rodentia (seven out of nine species studied) conform intraspecifically to Bergmann's rule (Ashton *et al.*, 2000; Meiri & Dayan, 2003). The former data do not mean that interspecific patterns should follow the same trend; in a recent study of body size distribution of European mammals, Rodríguez *et al.* (2006) showed that most herbivores (mainly rodents) inhabiting the formerly glaciated region of Europe are burrowers or partial burrowers, and show the weakest correlation of body size with temperature at the interspecific level. Furthermore, the relationship between mean body size and temperature is not necessarily linear at broad scales.

Third, the converse Bergmann's rule pattern may indicate that assumptions about equality of temperature within burrows across sites are wrong. However, data suggest that the hypothesis of stable within-burrow microclimatic conditions regulated behaviourally is correct (Weir, 1974). *Ctenomys torquatus* and *C. talarum* are distributed in eastern South America between 25–35° and 35–40°, respectively, at low elevations (0–200 m). While *C. talarum* inhabits loamy soils with relatively dense vegetation of grasses, perennials and woody shrubs (Justo *et al.*, 2003), *C. torquatus* prefers sandy, rock-free soils in very dry areas (Barlow, 1969). Both species maintain constant burrow temperatures of 20–22°C throughout the year (Barlow, 1969; Weir, 1974). More notable is the case of *C. fulvus*, which inhabits the Chilean Puna (20–26°S) in isolated oases up to 4000 m elevation. It was shown that this species maintains burrow temperatures between 19 and 25°C, when the above-ground temperature vary from less than −4°C to more than 45°C with a mean (Tmax–Tmin) of *c.* 38°C during the day and independently of season (Rosenmann, 1959; Cortés *et al.*, 2000). Tuco-tuco burrows maintain more constant temperatures than those of other studied fossorial species, such as African bathyergids (Roper *et al.*, 2001; Sumbera *et al.*, 2004). It is thus possible that all species maintain similar temperature conditions within their burrows independently of latitude and altitude (Reig *et al.*, 1990). Furthermore, above-ground activity related to feeding, mating or dispersal, which is normally diurnal and restricted to the dry season, is reduced to a minimum (less than 5% of the time) (Reig *et al.*, 1990). The degree of exposure to external environmental conditions is thus minimal.

A further indication that ambient temperature is not the factor behind the observed body-size trends is that, although temperature is negatively correlated with both longitude and elevation, body-size variation of *Ctenomys* along these geographical variables is not coincident with the latitudinal trend. In the case of elevation, no significant correlations were observed. Regarding longitude, negative trends in body size occur for both body-size variables considered, although they were only significant for males and much less strong than with latitude. According to our results, it is possible that a longitudinal decrease in body mass reflects more a decreasing ability for fat accumulation than a real decrease in size.

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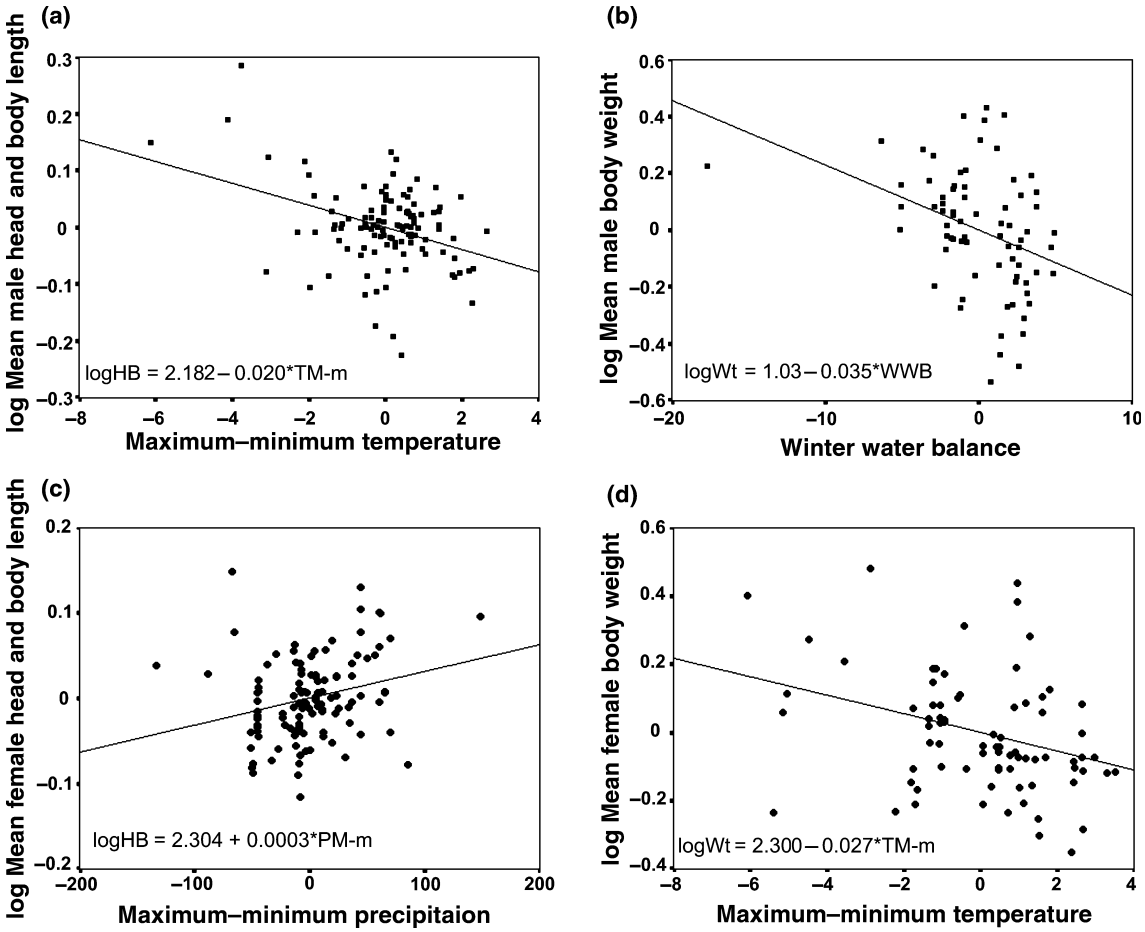

Figure 4 Partial regression plots of body-size estimators in male (a,b) and female (c,d) *Ctenomys* on selected environmental variables. Measurements are in mm (HB) and g (Wt) and transformed to log10.

Constancy of burrow temperature may explain the lack of conformity of tuco-tucos to Bergmann's rule, but not the interspecific and intraspecific gradients in body size, which are probably responding to some environmental factor other than temperature. What is the possible explanation for the negative body-size trend in *Ctenomys*? If it is assumed that, in tuco-tucos, body-size variation is independent of external temperature, the observed positive correlations between body size and temperature would be an indirect consequence of the positive association between temperature and another factor or factors that may be directly affecting body size in the geographical region considered, and that also show latitudinal clines. Furthermore, a strong negative correlation was observed between body size and temperature variability through the year (for example, with CVT or TM-m) but, again, this could be a result of the fact that higher latitudes tend to show wider differences between annual maximal and minimal mean temperatures (they are more seasonal). Seasonality has been suggested as an alternative or indirect mechanism to explain Bergmann's rule, since cooler areas tend to be more seasonal (Ashton *et al.*, 2000; Ashton, 2001a,b). Boyce (1979) and Lindstedt & Boyce (1985) proposed that body size could be larger in more seasonal regions because larger size suggests greater fasting endurance (see also Murphy, 1985). Clearly, this hypothesis is not applicable to *Ctenomys*. Nevertheless, positive relationships exist between body size and two other measurements of seasonality: the variability of precipitation, and the difference between summer and winter potential evapotranspiration. These parameters are inversely correlated with latitude, as body size is, suggesting that humidity may be an important factor in determining body size in tuco-tucos. The fact that humidity influences body size may be related to the digging habits and behaviour of tuco-tucos. In subterranean rodents, body size and metabolic rate are correlated to soil conditions so that larger-bodied species tend to inhabit sandy, friable soils while smaller-bodied species tend to use more compact, harder soils. The former is true of the few tuco-tuco species analysed in this respect (Vasallo, 1998; Busch *et al.*, 2000). Furthermore, the cost of digging through soils moistened by precipitation would decrease in relation to drier conditions (Busch *et al.*, 2000), thus larger-bodied species are probably better adapted to more friable soils in conditions of higher humidity. A further consideration refers to the negative relationship between body size and water balance. Positive values indicate that potential evapotranspiration exceeds precipitation, while negative values show a moisture surplus.

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Table 4 Correlation coefficients between estimators of body size and geographical variables in *Ctenomys talarum* and the *Ctenomys perrensi* superspecies.

Taxon	Body-size estimator	Geographical variable		
		LAT, *r*/*P*	LON, *r*/*P*	ALT, *r*/*P*
C. talarum	HB	−0.220/0.450	−0822/0.000	−0.751/0.002
M	HB	0.349/0.203	−0.178/0.527	−0.228/0.415
F	HB	0.127/0.652	0.052/0.854	−0.593/0.052
C. perrensi	Wt	−0.322/0.166	−0.111/0.640	0.078/0.744
M	Wt	−0.051/0.841	0.160/0.446	−0.225/0.402
F	Wt	0.176/0.457	−0.188/0.428	0.236/0.318
C. perrensi	HB	−0.440/0.024	−0.213/0.297	−0.016/0.940
M	HB	−0.240/0.247	−0.160/0.446	0.035/0.868
F	HB	−0.289/0.135	−0.108/0.586	−0.363/0.057

In all cases the first line represents the results of the joint analysis of male and female data controlled for sex. The other two lines represent separate analyses by gender. For *C. perrensi*, estimates of weight (Wt) and head and body length (HB) were tested. For *C. talarum*, only HB data were available. *r*, correlation coefficient; *P*, statistical significance; M, male; F, female.

The observed negative correlation indicates that larger body sizes tend to occur in regions where the water balance is shifted towards precipitation, reinforcing the previous argument.

An interesting, but not much explored, model explains geographical increase in body size through its positive correlation with food quality, abundance and availability which, in turn, are positively correlated with primary productivity (Rosenzweig, 1968; Erlinge, 1987; Ashton *et al.*, 2000). This could be the explanation for the inverse body-size trends in the semifossorial *Microtus* voles of the northern hemisphere (Ashton *et al.*, 2000). Interestingly mustelids, whose main prey are *Microtus* voles, also do not follow Bergmann's rule, since these carnivores maintain a particular size relative to their prey (Brown & Lasiewski, 1972) although some species (e.g. *Mustela erminea*) do concord with Bergmann's rule (Ralls & Harvey, 1985). According to Brown & Lasiewski (1972), the energetic cost of being long and thin in mustelids is compensated by their ability to find and capture prey, and this explains their deviation from Bergmann's rule. The primary productivity/food-abundance hypothesis has also been applied to Palearctic *Sorex* shrews (Ochocinska & Taylor, 2003) and *Phylloscopus* leaf warblers (Katti & Price, 2003), which follow the converse to Bergmann's rule.

In the case of *Ctenomys*, we believe that trends in body-size geographical variation may also be related, at least to a large extent, to resource availability, thus explaining the observed reverse Bergmannian patterns. Actual evapotranspiration is correlated with net primary productivity, while potential evapotranspiration is considered as a measure of ambient energy input (Rosenzweig, 1968; Churkina *et al.*, 1999; Olalla-Tárraga *et al.*, 2006; Rodríguez *et al.*, 2006), and in *Ctenomys* all estimators of body size were positively and significantly correlated with AET and PET, at least in simple correlations.

Table 5 Results of multiple stepwise backward regressions between body-size estimators and environmental variables in *Ctenomys*.

Taxon	Body-size estimator	r^2	*F*	*P*	TMAX, *r*/*P*	TM-m, *r*/*P*	PMAX, *r*/*P*	PM-m, *r*/*P*	AET, *r*/*P*	PETJa, *r*/*P*	PETJaJu, *r*/*P*	WBJu, *r*/*P*	SR, *r*/*P*
C. talarum	HB	0.921	28.978	< 0.001	−0.771/0.001	−0.854/< 0.001	–	−0.833/< 0.001	0.790/0.001	–	−0.880/< 0.001	−0.849/< 0.001	–
C. perrensi	HB	0.328	3.734	0.025	–	–	–	–	0.430/< 0.001	0.423/0.024	–	–	0.354/0.083
	Wt	0.315	1.840	0.171	–	–	0.491/0.007	−0.494/0.008	–	–	–	0.480/0.044	0.395/0.071

r^2, Coefficient of determination; *F*, *F*-statistic; *r*, correlation coefficients; *P*, statistical significance. See Materials and methods for abbreviations of variables. In the three cases, the results of the best model obtained are shown.

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Tuco-tucos are strictly herbivorous (Reig *et al.*, 1990), and it is reasonable that in areas of higher primary productivity and energy input, diversity and availability of food plants also increases with respect to regions of lower productivity. For example, in *C. mendocinus* Philippi, 1869, from piedmont populations (*c.* 1000 m a.s.l.), where plant coverage reaches 86%, tuco-tucos include 33 plant genera in their diet, while at 3000 m a.s.l. in the Andean Precordillera (plant coverage 36%) the number of plant genera is reduced to 23 (Rosi *et al.*, 2002). Abundance of alimentary resources could thus allow the maintenance of greater body sizes. Plant biomass is another factor likely to influence body size but, given the ample range of plant food items consumed by tuco-tucos, we have considered plant species diversity as a more relevant factor than biomass in this respect.

Another factor that could also be influencing body size is the relative intensity of predation on tuco-tuco populations. Larger animals may avoid predation more efficiently (Ashton *et al.*, 2000). Although these kind of data are lacking for most species of *Ctenomys*, there is some evidence that this mechanism might be of some relevance in body-size distribution of tuco-tucos. Although the subterranean environment has traditionally been viewed as relatively free of intensive predation (Reig *et al.*, 1990), recent field studies have revealed that subterranean rodents, including tuco-tucos, are important diet items for a number of predators including mammals, snakes and, in particular, owls (Kittlein, 1994; Trejo & Grigera, 1998; Busch *et al.*, 2000). Owls and other raptors have been shown to be selective in their rodent prey, depending, among other factors, on their own body mass (Trejo & Guthmann, 2003; Trejo, 2006). Field studies on owl predation, in the only recorded area where sympatry between two tuco-tuco species occur, are revealing in this respect. In southern Buenos Aires province (Argentina), *C. talarum* (a small species) and *C. australis* (a large species) overlap (Vasallo, 1998; Busch *et al.*, 2000) where they are predated by three species of owls (Kittlein, 1994; Vasallo *et al.*, 1994), although *C. talarum* constitutes 16% and *C. australis* only 2% of the prey items of the raptor species. Furthermore, *C. talarum* subadults outnumber adults in owl pellets, while only subadults of *C. australis* are taken by the owls. Also in *C. talarum*, females (the smaller sex) are more often predated than males (Pearson *et al.*, 1968). Trejo & Grigera (1998) and Trejo *et al.* (2005) studied food habits of the great horned owl *Bubo virginianus* and the barn owl *Tyto alba* in southern Argentina. They demonstrated that, within an assemblage of 10 rodent species in a steppe community, *C. haigi*, the largest rodent in the study, constituted a very small portion in numbers of both raptors' diet (although important regarding biomass). In the former case, size in addition to a fossorial habit may be important in avoiding predation with respect to smaller species; however, two other rodents with burrowing habits but of much smaller size (*Chelemys macronyx* and *Geoxus valdivianus*, with about one half and one quarter of *C. haigi*'s body mass, respectively) were almost absent from the diet of *B. virginianus*. Thus in *Ctenomys*, body size might be an important factor in avoiding predation by raptors. Since biodiversity increases as latitude decreases (Hillebrand, 2004), and this has been shown recently for southern Neotropical raptor species (Bellocq & Gómez-Insausti, 2005), it is reasonable to assume that predators will be more abundant at lower latitudes, thus constituting a selective pressure on body size of tuco-tucos. However, as noted above, selectivity of prey by raptors may be influenced not only by prey size, but by prey activities and habitat and by predator energy requirements. Thus the predation hypothesis of Bergmann's rule should, as with other correlations, be regarded with caution until new data are available.

Finally, some differences observed between males and females with respect to body size gradients may be the result of SSD and the fact that Rensch's rule is verified in this genus (Medina, 2004; C.J.B. and A.I.M., unpublished data). The same may be true of the intraspecific analyses, since SSD was of different magnitude in both analysed taxa (see Results). This, along with the reduced variation in environmental conditions across the geographical range studied, could explain, at least in part, the discrepancies in geographical body-size variation between the sexes in the intraspecific analyses.

ACKNOWLEDGEMENTS

The authors are grateful to all the students and colleagues who helped in the collection of tuco-tucos over the years. Special thanks are due to Kyle Ashton for his expert critical revision of the first version of the manuscript, and of course to Julio R. Contreras who introduced us to the fascinating world of subterranean rodents. We are indebted to Enrique Lessa and Rocío Hassan for their extremely helpful comments, and to Lena Geise for allowing C.J.B. and A.I.M. to use the facilities of her laboratory. The detailed and critical comments of Jose Diniz-Filho and three anonymous reviewers were extremely helpful for improving the manuscript. This paper was produced during a visiting professorship of C.J.B. at the Universidade do Estado do Rio de Janeiro, financed by FAPERJ (Fundación de Amparo a Pesquisa do Rio de Janeiro) and completed while a visiting researcher at the Instituto Oswaldo Cruz/FIOCRUZ (Rio de Janeiro), financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico of Brazil (CNPq), thanks to the kindness of Paulo D'Andrea and Pavel Borodin. Wolfgang Cramer kindly authorized us to use his climatic database, Ana Trejo supplied us with extremely helpful information on raptor predation on tuco-tucos, and Carlos Furuti on map projections, and Claudio J. Bidau Jr helped with the statistics software. Collection of specimens was possible through several grants to C.J.B. from CONICET, FONCyT, The Wellcome Trust, The British Council and Fundación Antorchas.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online.

Table S1 Species, populations and localities of tuco-tucos (*Ctenomys*) studied with relation to geographical body-size variation. MHB, FHB, mean head and body length (mm) of males and females respectively; MWt, FWt, mean body weight (g) of males and females respectively. Asterisks indicate specimens not measured by the authors.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01708.x

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Editor: Alexandre Diniz Filho

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