Comparative Energetics of the Subterranean *Ctenomys* Rodents: Breaking Patterns

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ABSTRACT

Subterranean mammals show lower mass-independent basal metabolic rates (BMRs). Several competing hypotheses were suggested to explain how microenvironmental conditions and underground life affect subterranean mammalian energetics. Two of these are the thermal stress and the cost-of-burrowing hypotheses. The thermal stress hypothesis posits that a lower mass-independent BMR reduces overheating in burrows where convective and evaporative heat loss is low, whereas the cost-of-burrowing hypothesis states that a lower mass-independent BMR may compensate for the high energy expenditure of digging. In this article, we assessed the relationship between BMR of *Ctenomys* and environmental variables through conventional statistics as well as independent contrasts. Moreover, we tested both the thermal stress and the cost-of-burrowing hypotheses at an interspecific level in a very homogeneous genus of subterranean rodents, the South American genus *Ctenomys*. We compared species from different geographic localities that have contrasting habitat conditions. We measured BMR through open-flow respirometry. After conventional as well as independent contrast analyses, our results support neither the thermal stress nor the cost-of-burrowing hypotheses. We observed that only body mass affects the variability in BMR. Contrasting climatic and soil conditions, habitat productivity, and net primary productivity were not correlated with BMR variability. We suggested that, because BMR and maximum metabolic rates (MMRs) are correlated, low BMRs among *Ctenomys* species

could also be determined by factors that affect MMR rather than BMR.

Introduction

One of the central tenets of ecological and evolutionary physiology is the identification of selective factors influencing energy metabolism (McNab 2002; Chappell and Hammond 2004). Energy metabolism is associated with the rate at which materials are acquired and processed. Different studies have evaluated correlations between the rates of metabolism of species or populations and variations in biotic and abiotic factors, and significant correlations have generally been viewed as evidence of adaptation (Bozinovic 1992; Spicer and Gaston 1999).

Among mammals, basal metabolic rate (BMR) is probably the most used predictor of the energetics of individuals because it represents a standardized and comparative measurement of energy expenditure (for discussion about definition and controversies, see Speakman et al. 1993; Speakman 2000; McNab 2002). Since the publication of the article by Kleiber (1932), the main factor proposed to influence BMR is body mass. However, when the effect of body mass is statistically removed, the residual variation could be linked to many ecological and evolutionary factors (McNab 1992). Several hypotheses have been proposed to explain how specific factors affect mass-independent basal rate of metabolism (see McNab 2002). Conventional and phylogenetically based methods show that interspecific comparison of mammalian BMR has been related mainly to food habits (McNab 1992, 2003), habitat productivity (Mueller and Diamond 2001; White 2003), climate (Lovegrove 1996, 2003; Rezende et al. 2004; Withers et al. 2006), and latitude (MacMillen and Garland 1989; Lovegrove 2003).

A special case among mammals is the subterranean species. The convergent evolution of subterranean forms of life among mammals is a fascinating evolutionary phenomenon (Nevo 1999). A subterranean existence has developed in several mammalian orders; subterranean forms include species that live underground and only rarely come to the surface. Interestingly, subterranean mammals often exhibit convergent morphological features, with compact bodies, short tails and necks, microphthalmic eyes, and large and powerful forefeet and pectoral girdle and associated muscles. One of the most interesting physiological features of subterranean species is a low mass-independent BMR compared with that of surface-dwelling species of the same body size. This low BMR has also been associated with a high thermal conductance and a wide range of thermoneutrality (McNab 1966), despite the fact that Gettinger

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Table 1: Habitat characteristics of different species of *Ctenomys*

Species	*n*	Habitat	Locality	Altitude (m asl)	Habitat Productivity (*Q*)	Soil Type	Source
C. australis	3	Coastal grassland	38°37′S, 58°50′W	23	2,422.0	Soft	Busch 1989
C. chasiquensis	3	Shrubland	38°39′S, 63°04′W	10	1,528.6	Medium	This study
C. fulvus	6	Salt flat	23°17′S, 68°05′W	2,240	19.1	Hard	Contreras and McNab 1990; Cortés et al. 2000
C. magellanicus	6	Patagonian steppe	53°18′S, 69°01′W	30	4,522.8	Medium	This study
C. maulinus	…	Andean steppe	36°01′S, 70°32′W	2,183	1,320.6	Medium	Contreras and McNab 1990
C. opimus	5	Andean plateau	19°42′S, 68°52′W	4,602	1,085.3	Hard	This study
C. porteusi	7	Flooding grassland	36°40′S, 62°09′W	119	1,703.5	Medium	This study
C. talarum	14, 4	Coastal grassland	37°45′S, 57°26′W	3	2,912.3	Medium	Busch 1989; Luna and Antinuchi 2007*a*
C. talarum	6	Coastal grassland	38°37′S, 58°50′W	23	2,422.0	Medium	Busch 1989
C. tuconax	5	Highland grassland	26°44′S, 66°46′W	3,042	1,273.2	Hard	This study

(1975) observed the opposite result (see "Discussion"). McNab (1966, 1979) hypothesized that these traits reflect an adaptation to subterranean environments. The abiotic microenvironment experienced by subterranean mammals is relatively stable and humid, with small variations in temperature; as well, it is also hypoxic and hypercapnic (Nevo 1999). Competing hypotheses have been proposed to explain how the subterranean environment affects the energetics of subterranean rodents. The thermal stress hypothesis (McNab 1966, 1979) posits that low BMR could minimize the possibility of overheating in the tunnel system, where convective and evaporative heat loss is restricted, whereas the cost-of-burrowing hypothesis (Vleck 1979, 1981) states that energy intake might be in balance with the extremely high cost of extending the burrow. Concordantly, both hypotheses propose a causal relationship between BMR and body size and the distribution of subterranean species (for an alternative hypothesis, such as food-aridity distribution, see Lovegrove and Wissel 1988). So far, several studies have tested both hypotheses. White (2003) compared the BMR of subterranean and semifossorial species from arid and mesic environments; Luna and Antinuchi (2007*b*) analyzed two species of *Ctenomys* rodents, comparing their basal and digging energy expenditures using different soil types; and Bozinovic et al. (2005) conducted an intraspecific analysis comparing BMRs and digging metabolic rates of *Spalacopus cyanus* from different localities with contrasting soil characteristics. These results failed to support either of the hypotheses. Thus, results indicate that, in some cases, either the cost-of-burrowing hypothesis or the thermal stress hypothesis could drive similar interpretations. Unfortunately, so far no extensive studies have been conducted to test

these hypotheses at the interspecific level; instead, they have been tested only among phylogenetically closely related species sharing similar life forms and structures. Species belonging to the genus *Ctenomys* are a valuable model to explore these hypotheses because (1) they have a large geographical distribution, occurring from 10°S to 55°S, in the southern cone of South America; (2) the species of this genus can be found between 0 and 5,000 m above sea level; and (3) the species are all herbivores and inhabit a variety of habitats and climates. The genus *Ctenomys* represents a rapid and relatively recent radiation (Middle Pleistocene) determining the outburst of the many present species (Reig et al. 1990). Although *Ctenomys* includes more than 60 extant species (Reig et al. 1990), they are relatively morphophysiologically homogeneous but differ markedly in body mass, ranging from 100 g (*Ctenomys pundti*) to more than 1,000 g (*Ctenomys conoveri*). Because we were attempting to understand the physiological strategies of subterranean mammals to cope with subterranean conditions, we first explored the effect of environmental variables (latitude, altitude soil type, habitat productivity) on BMR in a taxonomically homogeneous group through conventional statistics as well as independent contrasts (Felsenstein 1985). Second, we tested the main, commonly used hypotheses, the thermal stress hypothesis and the cost-of-burrowing hypothesis, using ambient temperature and soil type, respectively, as the main factors. As well, as a subrogate model of cost-of-burrowing hypothesis, we evaluated the food-aridity distribution hypothesis, using net primary productivity (NPP) as a variable. This is the first study that provides a blueprint for the effects of different factors on

Table 2: Body mass, basal metabolic rate (BMR), body temperature (T_b), and thermal conductance (C) of species of *Ctenomys*

Species	Body Mass (g)	BMR (mL O_2 g^{-1} h^{-1})	BMR (%)	T_b (°C)	C (mL O_2 g^{-1} h^{-1} °C^{-1})	Source
C. australis	294.1 ± 96.3	.48 ± .10	77.6	37.3 ± .2	.060	Busch 1989; Luna and Antinuchi 2007*b*
C. chasiquensis	140.69 ± 28.68	.80 ± .13	100.7	36.7 ± .4	.093	This study
C. fulvus	275	.64	99.5	35.6	.050	Contreras and McNab 1990
C. fulvus	300	.63	100.8	36.6	.046	Contreras and McNab 1990
C. magellanicus	263.1 ± 72.8	.70 ± .14	109.0	35.6 ± .6	.049	This study
C. maulinus	215	.87	124.5	36.2	.056	Contreras and McNab 1990
C. opimus	218.4 ± 32.6	.59 ± .07	86.3	35.8 ± 1.1	…	This study
C. opimus	214	.65	92.9	36.0	.055	Contreras and McNab 1990
C. porteusi	195.67 ± 35.44	.77 ± .07	107.6	36.5 ± .9	.037	This study
C. talarum	126 ± 5	.95 ± .03	113.7	36.1 ± .1	.085	Busch 1989
C. talarum	116 ± 5	.97 ± .02	113.0	36.1 ± .1	.090	Busch 1989
C. tuconax	325.81 ± 111.37	.64 ± .04	107.1	36.3 ± .3	.037	This study

Note. Habitat productivity (Q) of each locality is evaluated as $Q = \{pp/[(T_{a\,max} + T_{a\,min})(T_{a\,max} - T_{a\,min})]\}1{,}000$, where pp is total precipitation (mm yr^{-1}) and $T_{a\,max}$ and $T_{a\,min}$ are, respectively, the mean maximum and minimum temperature (°C) of each year. BMR (%) = percent expected BMR for burrowing root-eater mammals (BMR $= 4.2M^{-0.337}$; McNab 1988).

BMR through a latitudinal rank in a genus of subterranean rodents.

Material and Methods

BMR and Environmental Data

Data for body mass (M), BMR, body temperature (T_b), and thermal conductance (TC) were obtained from two different sources. First, data for seven species of *Ctenomys* were collected from the literature (Tables 1, 2). Second, BMR of *Ctenomys porteusi*, *Ctenomys chasiquensis*, *Ctenomys magellanicus*, *Ctenomys opimus*, and *Ctenomys tuconax* were estimated for this study (Table 2). In brief, individuals of these species were taken to the laboratory and housed in individual cages (0.30 × 0.40 × 0.25 m) with wood shavings for bedding. The temperature in the animal room was maintained at 24° ± 1°C, and the photoperiod was 12L : 12D (lights turned on at 0700 h). Animals were fed mixed native grasses, carrots, lettuce, corn, alfalfa, and sunflower seeds ad lib. Individuals of these species were maintained in the laboratory for 7 d before any measurements were taken. Although duration of captivity can alter BMR, at least in birds (McKechnie et al. 2006*a*, 2006*b*), no such effect was observed in *Ctenomys* (Meroi 2008). After acclimation, oxygen consumption was measured using a computerized positive-pressure open-flow respirometry system (Sable System, Las Vegas, NV). A cube-shaped chamber (volume, 5.8 L) was used to estimate O_2 consumption. The chamber was constructed of double-wall aluminum with polyurethane between the walls; to observe the animals, the chamber has a 20-mm-thick acrylic window-door (0.19 × 0.14 × 0.22 m) in which an inlet/outlet air-port was included. Heat was interchanged automatically with the outside by way of two Peltier intercoolers (CP-1.4–127-061, Melcor) connected to a PC and controlled by software. T_a inside the chamber was maintained to an accuracy of 0.1°C. The chamber received dry and CO_2-free air between 1 and 1.5 L min^{-1} from a mass flow controller (Sierra Instruments, Monterrey, CA), which was enough to ensure equilibration of the chamber (Lasiewski et al. 1966; Withers 1977). Air was passed through a CO_2-absorbent material (IQB) and a water scrubber (silica gel) before and after passing through the chamber. Excurrent air from the chamber was subsampled at 150 ± 10 mL min^{-1} and oxygen concentration was obtained from an Oxygen Analyzer FC-1B every 1 s by a Datacan V-PC program (Sable System). Oxygen consumption values were calculated using equation (4a) of Withers (1977). Animals were fasted for 12 h before metabolic measurements were taken. To achieve basal metabolism, individuals were left in the chamber for at least 90 min. BMR was measured as the 10-min lowest steady-state values of the experimental trial. *Ctenomys talarum* showed arrhythmic patterns of activity and O_2 consumption (Luna et al. 2000; Meroi 2008). As such, metabolic trials were performed between 0900 and 1700 h; as well, total time trial was chosen to determine the metabolism of individuals (Busch 1989; Zenuto et al. 2002) at any time.

Body mass of individuals was measured using an electronic balance (FX-3000, AND; ± 0.01 g) at the beginning of each trial, and rectal temperature was recorded at the end of each experiment with a YSI probe (93k73545-402) connected to a Cole-Parmer thermistor (8402–10; ± 0.1°C).

Environmental variables such as minimal and maximal am-

bient temperature and annual precipitation were obtained from data summaries from the weather stations nearest the capture sites. Original sources were the Argentine National Weather Forecast Service (http://www.meteofa.mil.ar) and the Chilean Meteorological Agency (http://www.meteochile.cl). Where possible, soil hardness was estimated at the site of capture as the force that must be exerted to penetrate the soil to a given depth (see Luna and Antinuchi 2006); otherwise, soil type was obtained from the geological surveys of Argentina (Secretary of Minery) and Chile (Geology and Minery National Survey). Soil types were characterized in three categories depending on soil hardness. We used categorical data for soil type to exclude any difference in methodology to estimate soil hardness. Habitat productivity Q of each locality was estimated from the relationship between precipitation and ambient temperature as

$$Q = \left[\frac{pp}{(T_{a\max} + T_{a\min})(T_{a\max} - T_{a\min})} \right] 1{,}000,$$

where pp is total precipitation (mm yr^{-1}) and $T_{a\max}$ (°C) and $T_{a\min}$ are the mean maximum and minimum temperature (°C) of each year, respectively (see Tieleman et al. 2003). In brief, Q tends to be low in hot, dry habitats and increases rapidly as the habitat becomes more mesic.

Net primary productivity (NPP; g C m^{-2}) of the location from which each species was captured was obtained from Kicklighter et al. (1999). NPP was an average of estimates from 17 global models, with a spatial resolution of 0.5° longitude or latitude. In those *Ctenomys* species for which diets were evaluated, results indicate that they are generalists in food habits. Thus, NPP is an appropriate proxy of food availability for this genus.

Ctenomys *Phylogeny*

The phylogeny of *Ctenomys* was derived from the tree described in Slamovits et al. (2001) and in Castillo et al. (2005). Additional data for *C. chasiquensis* was used to build the tree (A. Parada, personal communications). Testing hypotheses with independent contrast with an incomplete phylogeny involves the subtraction of 1 df for each polytomy in the tree (Purvis and Garland 1993; Garland and Diaz-Uriarte 1999). Although our tree was completely dichotomous, we subtracted 1 df each time we used two populations of a single species (*C. talarum, C. opimus, Ctenomys fulvus*). Because the subtraction of 3 df did not change our results, our analysis is presented without this subtraction. The arbitrary branch length transformation of Pagel (1992) was used to standardize branch lengths in the tree.

Statistics

We used both conventional and phylogenetically independent contrasts to analyze metabolic data. Independent contrasts (Felsenstein 1985) were computed with the PDAP:PDTREE module (Midford et al. 2003) of the Mesquite program (ver. 1.12; Mad-

dison and Maddison 2006). Before any analysis was performed, BMR, body mass, and NPP were log$_{10}$ transformed. Latitude values were converted to radians and then to arcsines. No transformations were performed on altitude measurements and habitat productivity values. To estimate the effect of soil type, a dummy variable was used. Soil types were ranked on an ordinal scale (2 = hard, 1 = medium, 0 = soft). Allometric equations were estimated by least squares linear regression. Multiple regression analysis was used to test the effect of body mass and the proposed environmental variables (altitude, latitude, soil type, and habitat productivity) on BMR.

After the application of multiple regression analyses, we also conducted an explicit comparison between the proposed hypotheses. The first model was a simple linear relation between BMR and body mass (log BMR = log M). Second, in terms of the thermal stress hypothesis (McNab 1966), we predicted that the best model that explains the BMR of subterranean species is that which includes body mass and maximum ambient temperature (log BMR = log M + $T_{a\max}$). Altuna (1991) found in *Ctenomys pearsoni* a direct relationship between ambient temperature and burrow temperature; therefore, we use $T_{a\max}$ as a proxy of maximal burrow temperatures. Third, in terms of the cost-of-burrowing hypothesis (Vleck 1979), we predicted that the best model is the one that includes M and soil type as predictors of BMR (log BMR = log M + soil type). Finally, we also explored an alternative hypothesis proposed by Lovegrove and Wissel (1988). The food-aridity distribution hypothesis could be proposed to be a determinant of BMR in *Ctenomys* if we found that the best model is the one that includes M and NPP as predictors.

Due to the relatively small sample–estimable parameter relationship, all the models were compared using a second-order Akaike Information Criterion (AIC$_c$; see Burnham and Anderson 2001, 2002). The best model of the set is that with the lowest AIC$_c$ value. We also measured the Akaike weight (ω_i) to estimate the probability that any given model is the best fit compared with the other models.

Results

The slopes of the relationship between body mass (M) and BMR for both (conventional and phylogenetic) analyses were similar. The 95% confidence intervals for the equations obtained using one or the other method overlapped (Fig. 1; Table 3). The standard allometric equation calculated for studied species of *Ctenomys* was

$$\text{BMR (mL O}_2 \text{ h}^{-1}) = 9.34 M^{0.52 \pm 0.03},$$

where M = body mass (g; $R^2 = 0.684$, $F_{1,10} = 21.62$, $P < 0.001$). Because latitude is collinear with the other independent variables, this variable was excluded from the analysis. Conventional multiple regression analyses indicate that body mass appears to be a good predictor for the variation in BMR within *Ctenomys* ($P = 0.01$) but not altitude ($P = 0.31$), habitat productivity ($P = 0.72$), or soil type ($P = 0.23$; Table 4). In the

same way, phylogenetically independent multiple regression analyses indicate that body mass ($P = 0.01$) is the main factor affecting BMR (Table 5).

Concordantly, using AIC_c, the best-fit model explained log BMR in terms of log M, controlling for phylogeny (Table 6). The power of the regressions (both conventional and phylogenetically independent) between log BMR and log M was above 0.90. The probability that this model is better (ω_i) than the other proposed models is presented in Table 6. Moreover, when we order the different models on the basis of their Δ_i values and with their corresponding ω_i values, the second best-fit model is that with log M as a predictor, using conventional data (Table 6).

Discussion

Among subterranean mammals, the thermal stress hypothesis states that a lower mass-independent BMR will reduce the risk of overheating when animals are digging underground burrows (McNab 1966, 1979). Thus, the prediction is that, in subterranean mammals, metabolic rates will be reduced and digging rate will increase in warmer habitats. Alternatively, the cost-of-burrowing hypothesis posits that subterranean mammals exhibit a lower mass-independent BMR to compensate for the extremely high digging-energy demands (Vleck 1979, 1981). This hypothesis predicts low metabolic rates and high digging rates in animals inhabiting hard soils. A recent comparison across species revealed conflicting results between these two variables. BMR values from large (>77 g), truly subterranean mammals from mesic and arid habitats are not different from BMR values of these animals' semisubterranean counterparts, despite expected differences in their foraging costs, a result that is consistent with the thermal stress hypothesis (White 2003). On the other hand, however, small (<77 g) fossorial mammals from arid habitats were found to have lower BMRs than their similarly sized but semisubterranean counterparts, a result that is consistent with the cost-of-burrowing hypothesis (White 2003). These results led White (2003) to conclude that both hypotheses are not mutually exclusive (see also Lovegrove and Wissell 1988; Bozinovic et al. 2005; Luna and Antinuchi 2007b). In addition, Perissinotti (2003) posits that both soil hardness and food quality affects BMR in *Ctenomys talarum*.

In this study, we used several species of the truly subterranean *Ctenomys* genus to evaluate which ecological factors, other than body mass, are coinvolved in BMR variation. Despite the fact that we used species from different altitudes and latitudes, from arid and mesic habitats, and inhabiting soft and hard soil environments with different environmental temperatures, rain regimens, and plant productivity, no variables other than body mass explained BMR variation in this group (Tables 4, 5).

At the interspecific level, it was proposed that animals living in habitats with low availability and/or predictability reveal low BMR values (Lovegrove 2000, 2003; Rezende et al. 2004), whereas high-quality diets allow for high BMRs (McNab 1986). Despite 236-fold variation in habitat productivity and, hence, in energy availability (estimated for the different capture sites by the Q index), we observed no effect of habitat productivity on BMR within *Ctenomys* (Tables 4, 5). This could be attributed to the fact that members of the genus *Ctenomys* behave as
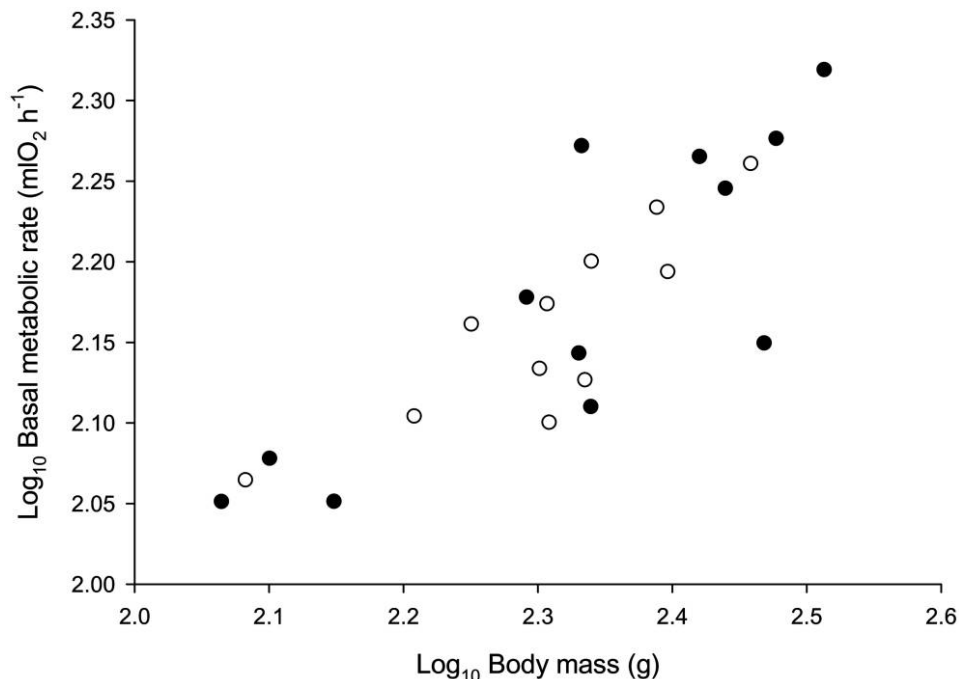

Figure 1. Relationship between $\log_{10}$-transformed basal metabolic rate and $\log_{10}$-transformed body mass using raw data (*open circles*) or independent contrast (*filled circles*).

Table 3: Slopes and intercepts of regressions of basal metabolic rate with body mass obtained with conventional and phylogenetically independent contrast analysis

Measurement	Conventional Regression	Independent Contrast
Slope	−.481	−.498
Minimum 95% CI	−.730	−.736
Maximum 95% CI	−.232	−.260
Intercept	.971	1.001
Minimum 95% CI	.391	.453
Maximum 95% CI	1.550	1.550
R^2	.650	.714

Note. Data are $\log_{10}$ transformed. CI = confidence interval.

generalist and opportunist herbivores, as introduced above (Madoery 1993; Comparatore et al. 1995), consuming the aerial part of plants and as such eating any available food item. Similarly, other studies found that net primary productivity is not a good predictor of BMR in other groups such as birds or surface-dwelling mammal species (Degen et al. 1998; Cruz-Neto and Bozinovic 2004; Rezende et al. 2004; White et al. 2007; but see Bozinovic et al. 2007). On the contrary, on the basis of laboratory experiments, Veloso and Bozinovic (1993) reported for the burrowing *Octodon degus* a relationship between food fiber content and BMR, and Antinuchi et al. (2007) found in *C. talarum* that diet quality affects BMR and other related variables (digestibility and transit time). However, these studies have been performed at an intraspecific level and account for only a plastic variation in BMR rather than an adaptive response.

In regard to soil hardness, differences in BMR between species with similar body masses that are living in hard soils (e.g., *Ctenomys tuconax*) and in soft soils (e.g., *Ctenomys australis*) should be expected. No such relationship was observed, however, when using either phylogenetic or nonphylogenetic analyses (Tables 4, 5). Similar findings were obtained in the subterranean rodent *Spalacopus cyanus* (Bozinovic et al. 2005). Moreover, Luna and Antinuchi (2007b) concluded that soil hardness did not affect digging metabolism in *C. talarum* and *C. australis*, two species inhabiting soils with differences in hardness. Furthermore, Antinuchi et al. (2007) found, for *C. talarum*, that digging costs are only a small part of the daily energy budget (∼8%). The observed pattern could be explained because they would have reached a higher digging efficiency, and soil hardness would not currently represent a challenge to *Ctenomys* distribution (see Luna and Antinuchi 2007b). Nevertheless, is important to note that the cost of burrowing has exerted adaptive pressures on the morphology and physiology of subterranean rodents throughout their evolution (see Nevo 1999). Alternatively, they could choose soil patches with similar properties, mostly sandy soils of different hardnesses, throughout a wide geographical range, where the balance between underground life and their food habits (aboveground foraging)

could reach an equilibrium (Luna and Antinuchi 2003). This alternative hypothesis should be evaluated in future studies.

In regard to the effect of altitude and latitude (hence, P_{O_2} and ambient temperature), no effect of altitude on BMR was observed for two subterranean rodent species by Bozinovic et al. (2005; for *S. cyanus*) or by Broekman et al. (2006; for *Cryptomys hottentotus*). Moreover, minimal metabolism in several subterranean species was not affected by varying experimental P_{O_2} conditions (Contreras 1983; Widmer et al. 1997); this had only a minimal response in semifossorial species (Frappell et al. 2002).

Bergmann (1847) proposed an adaptive physiological relationship that involves the conservation of heat through modification of body mass and that determines a latitudinal variation in body mass (larger species could occupy colder environments). Thus, in a simple interspecific view, if *Ctenomys* species are all affected by temperature in the same way, then a positive relationship between latitude and body mass is predicted. Similarly, because BMR is related to body mass (Tables 4, 5), a relationship between latitude and BMR is also predicted. Recently, and through conventional analysis, Medina et al. (2007) found that the genus *Ctenomys* follows the converse to Bergmann's rule, given that the body size of more than 60 species decreases with increasing latitude. As such, the inverse of the proposed pattern of body mass and latitude rules out the assumption that thermoregulatory constraints affect large-scale distribution of the genus.

Therefore, how can we explain the lack of relationship between BMR and either of the proposed variables—other than body mass—among *Ctenomys* species? Low BMR values were always associated with high thermal conductances; this feature was used to support the thermal stress hypothesis (McNab 1966). However, Gettinger (1975) reanalyzed the data provided by McNab (1966) and found that thermal conductance is low for these animals compared with that of surface-dwelling species of similar body mass, supporting the idea that prevention of hypothermia is more important than overheating. We found that *Ctenomys* species exhibited consistently low thermal conductances (∼80% of the expected value for eutherian mammals; McNab and Morrison 1963). Zelová et al. (2007) proposed that *Heliophobius argenteocinereus* is a good thermoregulator, as it is able to maintain a stable T_b over a wide range of T_a values that are below thermoneutrality even though it has a slightly high thermal conductance. In *C. talarum* exposed to T_a values below 15°C, T_b falls about 4°C (Busch 1989); nevertheless, during digging bouts at this temperature, T_b is maintained at a

Table 4: Results of conventional multiple regression analysis

Model	Sign	Multiple R^2	SE	F	df	P
$\log_{10} M$	−	.755	.422	11.87	1, 11	.011
$M + Q$	+	.435	.001	.012	1, 11	.931
M + soil type	−	.675	.006	.144	1, 11	.769
M + altitude	−	.678	.004	.103	1, 11	.803

Note. M = body mass; Q = habitat productivity.

Table 5: Results of multiple regression obtained with phylogenetically independent contrast (through the origin)

Model	Sign	Multiple R^2	SE	F	df	P
$Log_{10} M$	−	.401	.001	12.02	1, 11	.010
$M + Q$	−	.401	<.0001	<.0001	1, 11	.994
M + soil type	−	.633	.002	.180	1, 11	.185
M + altitude	−	.223	.002	.160	1, 11	.758

Note. Branch length was corrected using the arbitrary method of Pagel (1992). M = body mass; Q = habitat productivity.

constant level as a result of the compensation of heat produced as a by-product of muscular activity (Luna and Antinuchi 2007a). Consequently, it could be a balance between low thermal conductance and low BMR that accounts for the prevention of either hyperthermia at high ambient temperatures or hypothermia at low ambient temperatures. On the other hand, different energy demands to which animals are exposed are not independent. In surface-dwelling species, which are exposed to seasonal variation in values of T_a, a critical point for survival is the combined demand of maintenance, including the costs of maintaining both a constant T_b and locomotor activity, which is covered by an increment of aerobic metabolism. In regard to an evolutionary timescale, Bennett (1991) proposed that changes in aerobic capacity are mainly determined by changes in the maximum capacity of oxygen consumption. The correlation between maximum metabolic rate (MMR) and BMR is a key point in the aerobic capacity model of evolution of endothermy (Bennett and Ruben 1979). Sadowska et al. (2005) established a positive genetic correlation between BMR and MMR in the bank vole *Clethrionomys glareolus*. Because MMR is a function of the metabolism of the skeletal muscles (Tiagen 1983; Bennett 1991) and reflects the limitation of an adequate supply of O_2 from capillary blood during high rates of oxidative metabolism (Weiber and Hoppeler 2005), it could be limited in a hypoxic and hypercapnic environment when an animal digs.

Maximal metabolism in *Ctenomys*, at least in *C. tuconax* and *C. talarum* (F. Luna, personal observation), is lower compared with that observed in surface-dwelling rodent species (Bozinovic and Rosenmann 1989; Bozinovic 1992) and in other subterranean species (Nespolo et al. 2001); however, MMR in *C. talarum* attained a similar value when animals were exposed to low T_a values (cold-induced MMR), when running at high speeds (exercise-induced MMR; F. Luna, personal observation), or during digging activities (Luna and Antinuchi 2006, 2007a). Thus, low basal metabolism among *Ctenomys* species could also be determined by factors that affect MMR rather than BMR.

Hayes (1989) proposed that altitude has only minor effects on MMR in the surface-dwelling rodent *Peromiscus maniculatus*. Thus, low Po_2 values in tunnel systems (independent of altitude) might determine the low MMR. For subterranean species, in fact, an experimental hypoxic atmosphere results in a low MMR in *Spalax ehrenbergi* compared with normoxic conditions (Widmer et al. 1997), even though subterranean species display physiological and morphometric adaptations to low Po_2 values found in the burrows (Busch 1987).

Similarly, in species exposed to burrow temperatures that are buffered from external temperature, as in the case of *Ctenomys fulvus* (Cortés et al. 2000), the summer and winter ranges of burrow T_a values were always below those of the thermoneutral zone. Thus, an increase in O_2 consumption is expected to compensate for the heat loss below thermoneutrality. Therefore, low Po_2 values within burrows could prevent an elevation of the maximal O_2 consumption, but with the consequent risk of hypoxia. Despite the fact that we used proxy variables to evaluate the effects of temperature, plant productivity, and soil characteristics, our results indicate that body mass is the main factor explaining the variation in BMR in the studied species.

In conclusion, other than body mass, habitat productivity, plant productivity, altitude, and soil type do not determine the variation of BMR in this genus of subterranean rodents. Furthermore, our results did not support either the thermal stress hypothesis or the cost-of-burrowing hypothesis within *Ctenomys*. Biogeographical factors that influence BMR in surface-dwelling species appear to have no effect on subterranean species. Burrow microenviromental factors, such as low and high

Table 6: Akaike Information Criterion (AIC$_c$) values, AIC$_c$ differences (Δ_i), and Akaike weights (ω_i) for the proposed models

Parameter, Model	AIC$_c$	Δ_i	ω_i
$Log_{10} M$:			
Phylogenetic	−40.65	…	.52
Conventional	−37.65	2.99	.12
$M + T_{a\ max}$:			
Phylogenetic	−37.18	3.47	.09
Conventional	−34.08	6.57	.02
M + soil type:			
Phylogenetic	−36.53	4.12	.07
Conventional	−33.60	7.05	.02
$M + log_{10}$ NPP:			
Phylogenetic	−36.66	3.99	.07
Conventional	−33.53	7.12	.01

Note: M = body mass; $T_{a\ max}$ = mean annual maximal ambient temperature); NPP = net primary productivity.

extreme ambient temperatures, and/or factors that constrain MMR should be further explored to assess their effect on BMR. Although MMR appears to be infrequently reached, it is an ecologically relevant trait (Bozinovic and Rosenmann 1989; Garland et al. 1990; Garland and Carter 1994), and it is plausible that it is affected by natural selection (Rezende et al. 2004; Sadowska et al. 2005).

Acknowledgments

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