



Understanding evolutionary variation in basal metabolic rate: An analysis in subterranean rodents



Facundo Luna^a, Hugo Naya^b, & Daniel E. Naya^{c,*}

^a Laboratorio de Ecología Fisiológica y del Comportamiento, Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) - Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

^b Unidad de Bioinformática, Institut Pasteur de Montevideo, Montevideo 11400, Uruguay

^c Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo 11400, Uruguay

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ABSTRACT

Understanding how evolutionary variation in energetic metabolism arises is central to several theories in animal biology. Basal metabolic rate (BMR) –i.e., the minimum rate of energy necessary to maintain thermal homeostasis in endotherms– is a highly informative measure to increase our understanding, because it is determined under highly standardized conditions. In this study we evaluate the relationship between taxa- and mass-independent (residual) BMR and ten environmental factors for 34 subterranean rodent species. Both conventional and phylogenetically informed analyses indicate that ambient temperature is the major determinant of residual BMR, with both variables inversely correlated. By contrast, other environmental factors that have been shown to affect residual BMR in endotherms, such as habitat productivity and rainfall, were not significant predictors of residual BMR in this group of species. Then, the results for subterranean rodents appear to support a central prediction of the obligatory heat model (OHM), which is a mechanistic model aimed to explain the evolution of residual BMR. Specifically, OHM proposes that during the colonization of colder environments, individuals with greater masses of metabolically expensive tissues (and thus with greater BMR) are favored by natural selection due to the link between greater masses of metabolically expensive tissues and physiological capacities. This way, natural selection should establish a negative correlation between ambient temperature and both internal organ size and residual BMR.

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1. Introduction

Understanding how evolutionary variation in energetic metabolism arises is a central topic for several contemporary theories in animal behavior, physiology, ecology and evolution (Kooijman, 2000; Speakman, 2000; Brown et al., 2004; Angilletta, 2009; Careau et al., 2010; White and Kearney, 2012). Among the metabolic rates that can be defined, basal metabolic rate (BMR) –i.e., the minimum rate of energy necessary to maintain thermal homeostasis in endotherms– is a highly informative metric to further our understanding (Hulbert and Else, 2004). This is because BMR can be measured under highly standardized conditions (i.e., on adult individuals within the zone of thermoneutrality, during the normal period of inactivity, and while animals are inactive and in a post-absorptive state), which reduces the sources of variation included in this metabolic rate (McNab, 1988, 2002a; Degen et al., 1998). In addition, BMR is fairly easy to determine, in relation to other energetic variables, and it is the most widely measured metabolic rate in

endothermic animals (Elgar and Harvey, 1987; Koteja, 1991; Hulbert and Else, 2004; Speakman et al., 2004; McNab, 2012).

The two major determinants of BMR are body mass and higher-level taxonomic affiliation (Kleiber, 1932; Haysen and Lacy, 1985; Mueller and Diamond, 2001; McNab, 2012). Nevertheless, once the effect of these two primary factors is excluded, the remaining variation in BMR is still great (ca. 5-fold; McNab, 2008, 2009). Recently, ambient temperature at the site of collection has been identified as the major determinant of mass- and taxa-independent BMR (hereafter “residual BMR”) of a set of several geographic, climatic and ecological factors (Speakman, 2000; Lovegrove, 2003; Rezende et al., 2004; White et al., 2007; Jetz et al., 2008; Naya et al., 2013; Stager et al., 2016). Interestingly, this result comprises the central prediction of the obligatory heat model (OHM), a mechanistic model based on animals' optimal design, to explain the evolution of residual BMR (Naya et al., 2012, 2013). In brief, OHM states that during the colonization of a colder environment, individuals with greater masses of metabolically expensive tissues (and thus with greater BMR) within a given population, are no longer penalized for their “luxurious way of life”, because all the members of the population have to increase the internal production of heat to maintain a constant body temperature in this new environment. In turn, if greater

* Corresponding author at: Departamento de Ecología y Evolución (Piso 6, Ala Norte), Facultad de Ciencias, Universidad de la República, Montevideo 11400, Uruguay.

E-mail address: dnaya@fcien.edu.uy (D.E. Naya).

masses of metabolically expensive tissues are linked to greater physiological capacities (Diamond, 1998), those animals with larger internal organs (and thus with greater BMR) will be now in an advantageous condition with respect to the other members of the population. Natural selection thus establishes a negative correlation between ambient temperature and both internal organ size and residual BMR. Note that, according to OHM, the specific physiological functions that are under stronger selection, and thus the specific internal organs that will be more affected in its size, can vary depending on the attributes of each taxon and the selection pressures acting at each evolutionary moment (Naya et al., 2013, 2016). Even though the former versions of the OHM do not take into account all the potential “solutions” for the thermoregulatory problem caused by a drop in ambient temperature (see Discussion section), empirical evidence for terrestrial rodents appears to support several predictions. For instance, it has been found that: (i) annual mean temperature is the best predictor of residual BMR and also the best predictor of organ size, (ii) residual BMR is correlated with species food habits as expected from their intestinal size, and (iii) herbivorous (large gut) species tend to be more common at high-latitude, cold environments than insectivorous (short gut) species (see Naya et al., 2013).

Within this general framework, this study is aimed at broadening our understanding of how evolutionary variation in BMR arises, through the evaluation of the effect of different environmental factors on residual BMR for subterranean rodents. We focused on this group of species for two different reasons. First, subterranean rodents were not considered in other similar analyses that have been conducted in rodents (e.g., Lovegrove, 2003; Naya et al., 2013). Second, subterranean rodents offer a very interesting biological model for evaluating the central prediction of OHM –i.e., that mean ambient temperature is the major predictor of residual BMR, with both variables inversely correlated–because burrow systems attenuate extreme fluctuations in ambient temperature (McNab, 1966; Cortes et al., 2000). Hence, the effect of other ecological factors, such as habitat productivity, which have a secondary role on residual BMR evolution in other endothermic groups (Jetz et al., 2008; Naya et al., 2013), could be the main factor affecting BMR in subterranean rodents.

2. Material and methods

2.1. Database description

Subterranean rodents live underground and only rarely venture from the burrow to the surface. Even though these species belong to different rodent families (White, 2003), they exhibit several convergent morpho-physiological features (Nevo, 1999). We compiled data on basal metabolic rate (BMR), body mass (mb), and geographical coordinates for 48 populations belonging to 34 subterranean rodent species, which represent ca. 15% of overall extant rodents species that spend most of their life in self-constructed burrows (Begall et al., 2007). To build up this database (Table S1; Fig. 1A) we only considered studies that: (1) included BMR measured in animals captured in the field, and (2) reported geographical coordinates or localities of the collecting sites. We discarded some studies that recorded BMR of animals that were maintained in the laboratory for more than one generation (e.g., Woodley and Buffenstein, 2002), or that did not report the collection site (e.g., Vleck, 1979). For each data point, we downloaded from WorldClim data base (<http://www.worldclim.org/>) the altitude (Altitude, in m) and the following climatic variables: annual mean temperature (Tmean, in °C), minimum temperature of the coldest month (Tmin, in °C), maximum temperature of the warmest month (Tmax, in °C), temperature annual range (TAR: difference between maximum temperature of warmest month and minimum temperature of the coldest month, in °C), temperature seasonality (TS: standard deviation of the mean monthly temperature, in °C), accumulated annual rainfall (Rainfall, in mm), and rainfall seasonality (RS: standard deviation of the

mean monthly rainfall, in mm) (Table S1). These variables were obtained using the free software Diva-Gis (<http://www.diva-gis.org/>). In addition, we downloaded a map of net primary productivity (NPP, in tons of carbon per 0.25° cell) from the Socioeconomic Data and Application Center homepage (<http://sedac.ciesin.columbia.edu/es/hanpp.html>) (based on Imhoff et al., 2004), and used the software ArcGIS version 10 to extract NPP data for each collection site (Table S1).

2.2. Conventional statistical analysis

The relationships between (\log_{10} of) BMR and environmental factors were evaluated through single and multiple regression models, using (\log_{10} of) body mass as a covariate. The absolute value of geographic latitude was used in all regression models. In addition, we estimated the fit of all the 1791 possible models without interaction terms –i.e., the combination of body mass plus ten independent variables, but taking just two of the following three independent variables: Tmin, Tmax, and TAR at a time (because TAR is equal to Tmax minus Tmin)– and used the Bayesian Information Criterion (BIC) to compare them. Specifically, a model was selected as a “good model” if its BIC value did not differ from the overall best model BIC value (which is, by definition, the lowest BIC value) in more than 2.3 units (Raftery, 1995). In addition, to measure the robustness of each “good model” we calculated the number of times that it provided the best fit for residual BMR over 10,000 samples, including different proportions of real data in the dataset used (from 0.5 to 0.95, with a step of 0.05, and sampled with replacement). All these analyses were performed with the R package leaps (Lumley and Miller, 2009; R Core Team, 2011). Conventional analysis were separately conducted for species ($n = 34$) and populations ($n = 48$), but because both data sets gave very similar results, and the same models were selected as “good models” in both cases (Table S2), we present only those results obtained for the species data set.

2.3. Phylogenetically informed analyses

Models selected as “good models” in conventional analyses were evaluated to determine the effect of phylogeny on the relationship between BMR and environmental factors, using a Bayesian Phylogenetic Mixed Model (Bayesian PMM; Naya et al., 2006; Hadfield, 2010) in addition to Bayesian Model Averaging (BMA; Raftery et al., 1997). We developed a topological phylogenetic tree including all the species present in our database (Fig. 1B), by combining two previously published phylogenetic trees (White, 2003, for relationships at the infraorder level; Upham and Patterson, 2012, for the superfamily Octodontoidea). Then, we included phylogenetic uncertainty by generating 1000 trees in which: (i) polytomies were randomly resolved by transforming all multichotomies into a series of dichotomies with one or several branches of length zero, and (ii) branch lengths were randomly sampled from a uniform distribution and the resulting tree was forced to be ultrametric. Informative Inverse-Wishart distributions were used as prior for phylogenetic and residual variances (scale = 0.0015, d.f. = 3), with 3.5×10^6 iterations, 1.5×10^6 of burn-in, and a thinning interval of 20. For each comparative model, the effect of environmental factors on BMR was calculated through linear mixed models, using body mass as a covariate. Then, to estimate the effect of each environmental factor on BMR, we calculated the proportion of posterior estimates larger than zero (gt0). In short, gt0 can be viewed as the probability of observing a positive (if $gt0 > 0.5$) or negative (if $gt0 < 0.5$) association between BMR and each environmental factor. Note that when the dependent variable is not affected by the independent variable this probability is equal to 0.5 (i.e., the distribution of the regression coefficients is centred on zero). All comparative analyses were performed using the software R, through packages “APE” (Paradis et al., 2004) and “bmaMCMCanalysis” (L. Spangenberg, R. Romero and H. Naya; available upon request). Phylogenetically informed analyses were conducted only for the selected

“good models” because it would have been impractical to run phylogenetic analyses for all 1791 models, given the computational costs.

3. Results

As expected, (\log_{10} of) body mass was positively correlated with (\log_{10} of) BMR, explaining 82% of the overall variance in BMR ($r^2 = 0.821$, $BIC = -55.472$). Conventional analysis using single regression

models indicate that two ambient temperatures (T_{min} and T_{mean}) were negatively correlated with residual BMR, while absolute latitude and temperature variability indexes (TS and TAR) were positively correlated with residual BMR (Table 1). However, according to BIC values, only models containing ambient temperatures can be selected as “good models” (Table 1, Fig. 2). Conventional analysis using multiple regressions indicate that four models were selected as “good models”: one including minimum temperature, one including minimum temperature

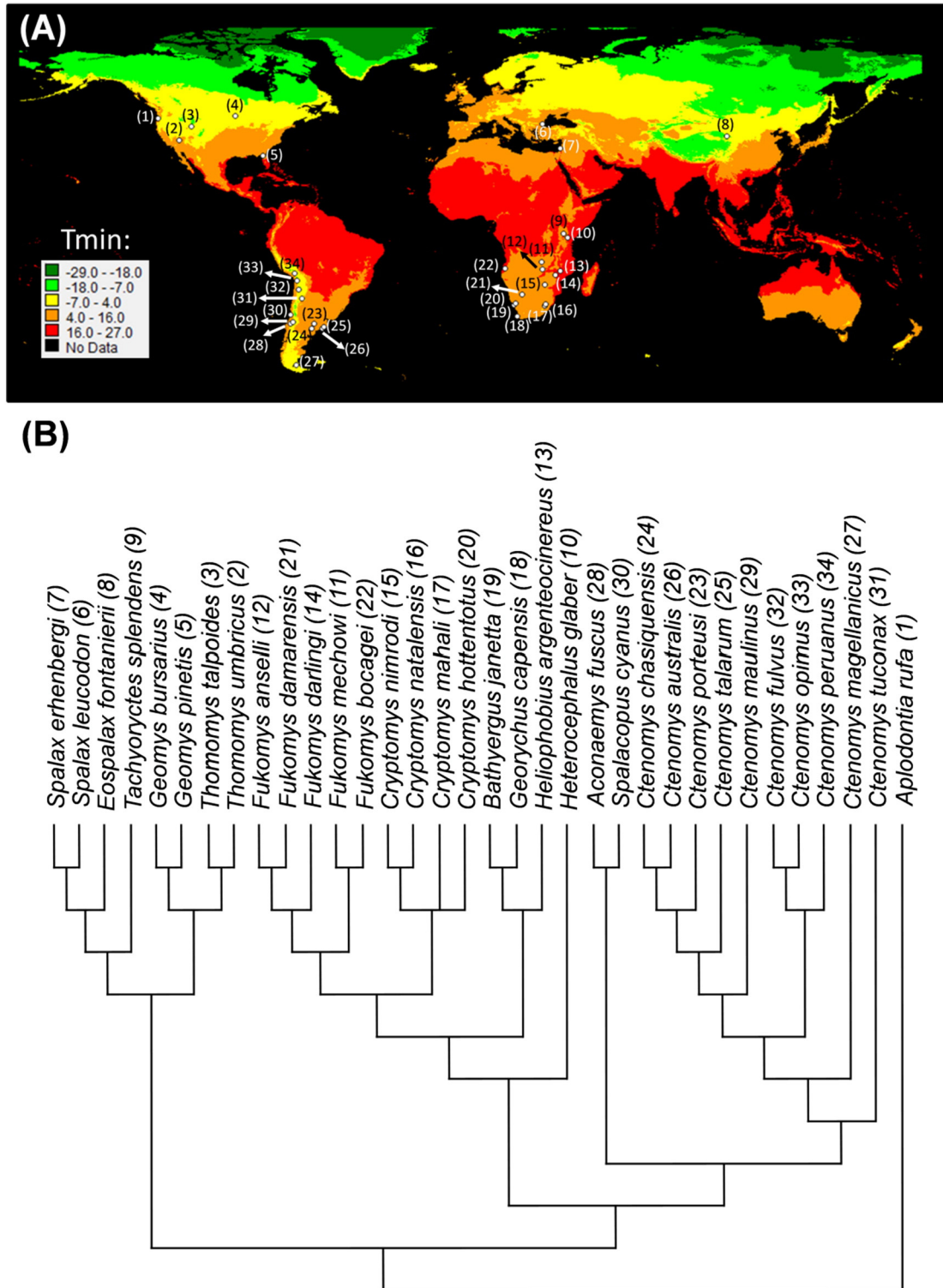


Fig. 1. (A) World map showing the change in minimum temperature of the coldest month (T_{min} , in $^{\circ}C$) and the collection site for each subterranean rodent species included in the analysis, and (B) Phylogenetic tree showing the phylogenetic relationships among these species.

Table 1
Parameters estimation, and associated probabilities, for single regression models with one environmental factor in addition to body mass. B = slope, SE = standard error, P = probability value, r^2 = proportion of the overall variance explained by the model, BIC = Bayesian Information Criterion value, Δ BIC = BIC model – lowest BIC. See Methods for environmental factors abbreviations. NPP is in tons of carbon per 0.25 degree cell.

	Log ₁₀ mb (g)			Environmental factor			Overall model		
	B	SE	P	B	SE	P	r ²	BIC	Δ BIC
Tmin (°C)	0.71	0.06	1.8 E ⁻¹³	-0.006	0.002	0.002	0.864	-62.366	-----
Tmean (°C)	0.68	0.06	3.5 E ⁻¹²	-0.008	0.003	0.005	0.857	-60.709	1.657
Latitude (°)	0.73	0.06	1.7 E ⁻¹³	0.003	0.001	0.01	0.848	-58.684	3.682
TS (°C)	0.77	0.06	2.9 E ⁻¹⁴	0.0002	0.00007	0.02	0.844	-57.834	4.530
TAR (°C)	0.78	0.06	2.6 E ⁻¹⁴	0.005	0.002	0.03	0.842	-57.377	4.989
Tmax (°C)	0.72	0.07	1.8 E ⁻¹¹	-0.004	0.003	0.16	0.827	-54.184	8.168
RS (mm)	0.77	0.06	1.6 E ⁻¹³	-0.0005	0.0004	0.28	0.822	-53.260	9.106
Altitude (m)	0.76	0.06	5.2 E ⁻¹³	0.00001	0.00002	0.51	0.817	-52.422	9.944
NPP	0.76	0.06	3.1 E ⁻¹³	-5.3 E ⁻⁸	8.4 E ⁻⁸	0.53	0.817	-52.383	9.983
Rainfall (mm)	0.78	0.06	3.1 E ⁻¹³	-0.00002	0.00003	0.58	0.817	-52.288	10.078

and rainfall seasonality, one including mean temperature, and one including minimum temperature and latitude (Table 2, Fig. 3). Nevertheless, the amount of the overall variance explained by these models was practically the same in all cases (ca. 86%), and only ambient temperatures (Tmin and Tmean) were significant predictors of residual BMR (Table 2). Finally, phylogenetically informed analyses also indicated

that only ambient temperatures have a significant effect on BMR, after controlling for the effect of body mass and phylogeny (Table 3). Thus, both conventional and phylogenetically informed analyses provide similar results, indicating that, at least in our dataset, minimum and/or annual mean temperature are the major determinants of residual BMR.

4. Discussion

Although metabolic rates have been identified as fundamental variables in animal biology, we still have limited knowledge of their evolution (Hayes, 2010; Burton et al., 2011; Nespolo et al., 2011). We attempted to broaden our understanding of this topic by analyzing the relationship between different environmental factors and residual BMR in subterranean rodents, a group of animals that has been excluded in similar studies previously conducted in rodents (e.g., Lovegrove, 2003; Naya et al., 2013).

The main result of our analysis was that ambient temperature (represented by either Tmin or Tmean) is the best predictor of residual BMR, with both variables inversely correlated. Given the high covariation between minimum and mean ambient temperatures in our data set ($r = 0.90$, $P = 6.4 \times 10^{-13}$), we could not select one of these two temperatures over the other. But, in any case, our results are more in line with the central prediction of the obligatory heat model (OHM) than with other hypotheses proposed to explain the evolution of BMR, such as the “productivity hypothesis” which states that net primary productivity should be the best predictor of residual BMR (Mueller and Diamond, 2001; Bozinovic et al., 2009). Interestingly, similar results were recently found for birds (Jetz et al., 2008) and terrestrial rodents (Naya et al., 2013), suggesting that evolutionary variation in BMR was similarly shaped in endothermic animals. In effect, when we compared data for terrestrial and subterranean we found two interesting results. First, for a given value of ambient temperature, subterranean rodents show a lower residual BMR than terrestrial rodents (Table 4). This result represents a well-established fact and is thought to be related with the hypoxic and hypercapnic conditions inside the burrows, the overheating risk in systems where convective and evaporative heat loss is restricted, and/or the relatively high costs of digging, mainly during foraging activities (McNab, 1966, 1979; Bennett et al., 1994; Buffenstein, 2000; White, 2003; Luna et al., 2009). Second, the slopes of the relationships between residual BMR and ambient temperatures are practically the same for subterranean and terrestrial rodents (Table 4), suggesting that ambient temperature has played a similar role in the evolution of residual BMR in both groups. This last result does not imply that thermal stability inside the burrows and on the surface is similar, but that the geographic change in modal ambient temperature (the fundamental factor driving variation on residual BMR according to the OHM) is similar in both environments when analyzed on a large scale. In this sense, studies

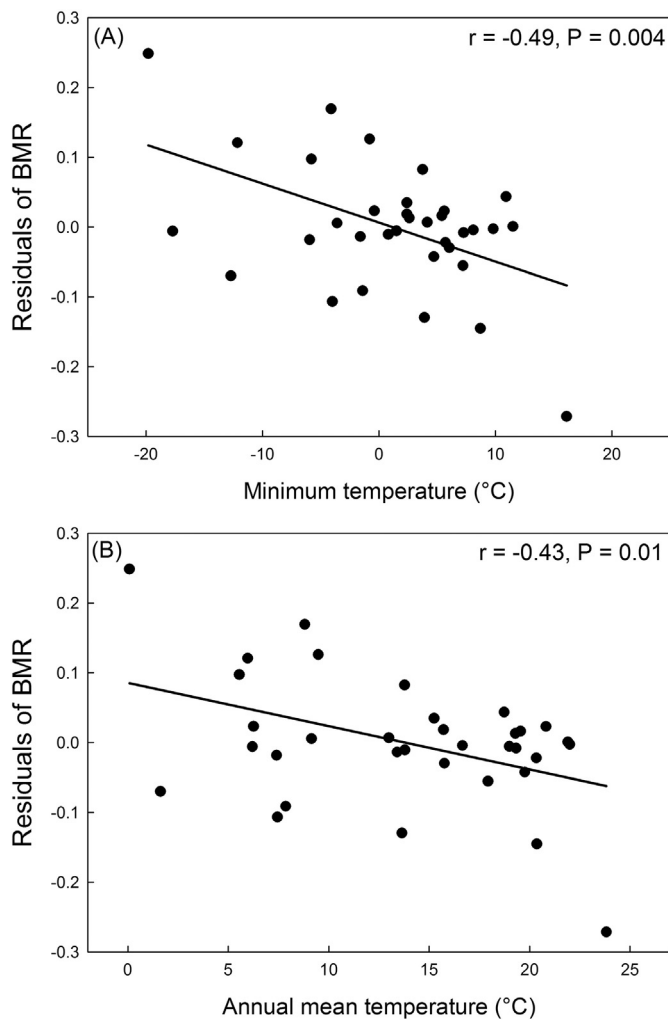


Fig. 2. Relationship between residuals of BMR (with regard to body mass) and (A) minimum temperature of the coldest month, and (B) annual mean temperature, for 34 subterranean rodent species.

Table 2

Parameters estimation, and associated probability, for the four models selected as “good models” according to the Bayesian Information Criterion (BIC). B = slope, SE = standard error, P = probability value, r² = proportion of variance explained by the model, ΔBIC = BIC model – lowest BIC. See Methods for environmental factors abbreviations.

#	Log ₁₀ mb (g)			Tmin (°C)			RS (mm)			Tmean (°C)			Latitude (°)			Overall model		
	B	SE	P	B	SE	P	B	SE	P	B	SE	P	B	SE	P	r ²	BIC	ΔBIC
1	0.71	0.06	1.8 E ⁻¹⁴	-0.006	0.002	0.002	----	----	----	----	----	----	----	----	----	0.864	-62.37	----
2	0.71	0.06	2.2 E ⁻¹⁴	-0.006	0.002	0.002	-0.0005	0.0004	0.20	----	----	----	----	----	----	0.867	-60.71	1.65
3	0.68	0.06	3.5 E ⁻¹³	----	----	----	----	----	----	-0.008	0.003	0.005	----	----	----	0.857	-60.71	1.66
4	0.70	0.06	3.2 E ⁻¹³	-0.005	0.002	0.029	----	----	----	----	----	----	0.0018	0.0014	0.21	0.866	-60.63	1.74

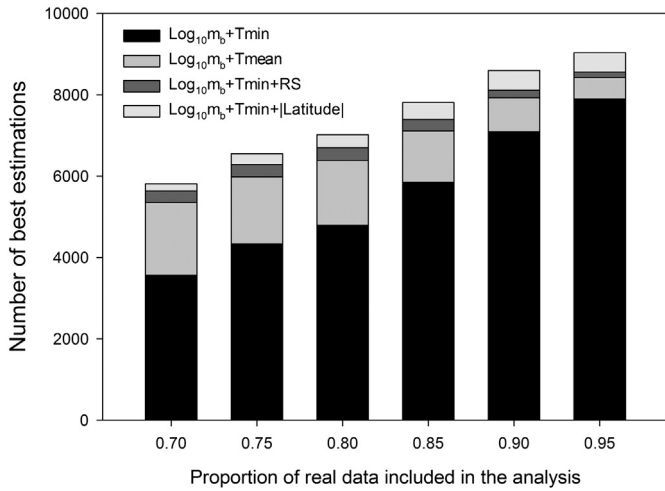


Fig. 3. Number of times (over 10,000 iterations) that each of the four “good models” performed the best as a function of the proportion of real data included in the dataset used. See Methods for environmental factors abbreviations. Note that the overall number of estimations increases with the proportion of real data because at lower proportions several non-selected models gave some of the best estimations.

evaluating seasonal changes in ambient temperature inside the burrow systems indicate that an important temporal (i.e., among-season) variation in temperature usually occurs (Cortes et al., 2000; Cutrer and Antinuchi, 2004). Then, the spatial changes in modal ambient temperature required for OHM to apply are expected to occur also for

subterranean rodents, beyond the attenuation of extreme temperatures offered by burrow systems.

In line with previous studies conducted in birds (White et al., 2007; Jetz et al., 2008; Stager et al., 2016) and rodents (e.g., Rezende et al., 2004; Naya et al., 2012, 2013), our phylogenetic analyses indicate that the effect of ambient temperature on residual BMR remains after controlling for the effect of the phylogeny. This result is similar to those obtained in experiments of artificial selection that indicate that residual BMR in rodents can be noticeably modified after a few generations of positive selection (Sadowska et al., 2009; Swallow et al., 2009; Konarzewski and Książek, 2013). Hence, we do not think that phylogenetic constraints are playing a major role on the evolution of BMR, at least when large temporal scales are considered (see Westoby et al., 1995; McNab, 2009).

Finally, we would like to discuss two different points of the obligatory heat model (OHM) related to our findings. First, it is remarkable that plastic changes in internal organ size and residual BMR observed during an experimental induced drop in ambient temperature, and also during the colder seasons of the year, are in the same direction (i.e., organs are larger in colder environments), as predicted by OHM in an evolutionary timeframe (Tielemans et al., 2003; McKechnie, 2008; Piersma and van Gils, 2010; Zhao et al., 2014). This indicates that phenotypic plasticity may represent the natural link between the putative environmental change (i.e., a fall in ambient temperature) and the observed among-species differences in both organs mass and residual BMR (Fig. 4). Second, there are several, not mutually exclusive, ways animals can cope with a drop in ambient temperature, in addition to an increase in general body size (as stated by Bergmann’s Rule) or in the relative size of metabolically expensive organs (as stated by OHM). These mechanisms

Table 3

Parameters estimation, and proportion of posterior estimates larger than zero (gt0), for each independent variable in each of the four selected models, according to phylogenetically informed analysis. B = slope, SD = standard deviation. See Methods for environmental factors abbreviations.

#	Log ₁₀ mb (g)			Tmin (°C)			RS (mm)			Tmean (°C)			Latitude (°)		
	B	SD	gt (0)	B	SD	gt (0)	B	SD	gt (0)	B	SD	gt (0)	B	SD	gt (0)
1	0.710	0.079	1.0	-0.060	0.0024	0.006	----	----	----	----	----	----	----	----	----
2	0.712	0.079	1.0	-0.062	0.0024	0.006	-4.48 E ⁻⁴	4.84 E ⁻⁴	0.173	----	----	----	----	----	----
3	0.704	0.082	1.0	----	----	----	----	----	----	-7.28 E ⁻³	3.20 E ⁻³	0.013	----	----	----
4	0.711	0.079	1.0	-0.0048	0.0027	0.035	----	----	----	----	----	----	1.9 E ⁻³	1.9 E ⁻³	0.852

Table 4

Mean values of basal metabolic rate (BMR) and body mass (m_b), together with parameters estimation of the regression between residual BMR and ambient temperatures, in terrestrial rodents (from Naya et al., 2013) and subterranean rodents (this study). N = number of species, SE = Standard error.

Group	N	Log ₁₀ BMR (ml O ₂ h ⁻¹) Mean (SE)	Log ₁₀ m _b (g) Mean (SE)	Minimum temperature of the coldest month (°C)		Annual mean temperature (°C)	
				Intercept (SE)	Slope (SE)	Intercept (SE)	Slope (SE)
Terrestrial	194	1.85 (0.02)	1.74 (0.03)	0.017 (0.009)	-0.006 (0.001)	0.148 (0.020)	-0.009 (0.001)
Subterranean	34	2.21 (0.05)	2.08 (0.04)	-0.056 (0.014)	-0.007 (0.002)	0.051 (0.034)	-0.008 (0.002)

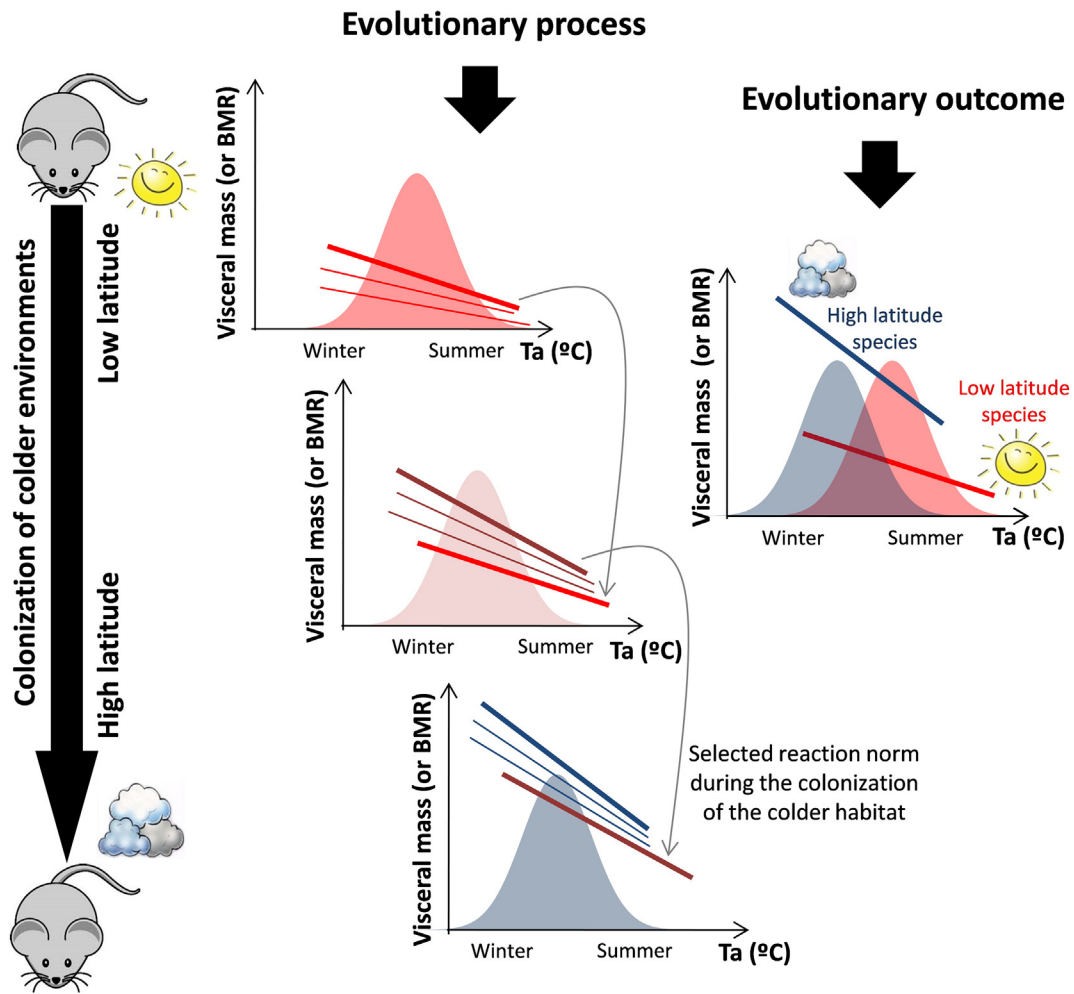


Fig. 4. Hypothetical diagram depicting the evolutionary process resulting in a negative correlation between ambient temperature and internal organ size (and hence residual BMR), established by natural selection via phenotypic plasticity. Note that, as depicted in the diagram, a positive correlation between latitude and both digestive organ size and flexibility in digestive organ size has been previously reported for rodents (Naya et al., 2008, 2013).

can be grouped, from an energetic point of view, into three major categories: (1) those that allow a reduction in the thermal differential with the environment, (2) those that allow a decrease in thermal conductance, and (3) those that allow an increase in the rate of heat production (see McNab, 2002a, 2012; Steegmann et al., 2002; Naya et al., 2016). Mechanisms that permit a reduction in the thermal differential include morphological adjustments, such as changes in body color affecting the absorptivity of solar radiation (and then, the operative temperature of the animal); physiological adjustments, such as the use of torpor; and behavioral adjustments, like the use of shelters and changes in daily activity patterns. Mechanisms that reduce thermal conductance include changes in body shape affecting body surface-to-volume ratio; the circulatory separation of core and shell temperatures; and changes in the subcutaneous fat layer and/or in skin properties. Finally, mechanisms that modify the mass-specific rate of heat production (other than increasing visceral mass) include behavioral adjustments, such as changes in activity levels sustained in nature, and also physiological adjustments, such as changes in active heat production (via the futile cycle and shivering) and the mass-specific activities of some tissues. However, it is important to note that in small animals several of these mechanisms appear to be constrained by internal factors, and/or they could entail important fitness costs by increasing predation risks. For instance, minimal thermal conductance (Stuedel et al., 1994), and circulatory separation between core and shell temperature (McNab,

2002a, b), have been demonstrated to be strongly constrained by body size; changes in body colour (Linnen and Hoekstra, 2010) and activity levels (Berger-Tal et al., 2010) are constrained by predation risk in small sized mammals; and daily activity patterns in rodents have been suggested to be constrained by some rigidity in the mechanisms driving photic cues (Roll et al., 2006). The existence of physiological and ecological constraints does not mean that animals cannot use these mechanisms to some extent (e.g., to conduct seasonal adjustments), but that the adjustments in these variables are not enough to cope with the thermoregulatory problem at large geographic scales. Finally, concerning changes in general body size, it is noteworthy that rodents are one of the few taxonomic groups that have consistently failed to comply with Bergmann's Rule (Ashton et al., 2000; Meiri and Dayan, 2003; Rodríguez et al., 2006; Luna et al., 2015). Thus, current data suggest that an increase in body size was not likely a fundamental mechanism to solve the thermoregulation problem imposed by high-latitude, cold environments in this taxonomic group.

Empirical evaluations of OHM conducted so far have been mostly based on data from small rodents (but see Naya et al., 2016), a taxonomic group that, as explained above, may not have energetic responses representative of other animal groups. Accordingly, further investigation is needed to determine whether the predictions derived from this mechanistic model can be applied to other taxonomic groups, such as small birds.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.cbpa.2017.02.002>.

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References

- Angilletta, M.J., 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford University Press, Oxford.
- Ashton, K.G., Tracy, M.C., de Queiroz, A., 2000. Is Bergmann's rule valid for mammals? *Am. Nat.* 156, 390–415.
- Begall, S., Burda, H., Schleich, C.E., 2007. Subterranean Rodents: News From Underground. In: Begall, S., Burda, H., Schleich, C.E. (Eds.), *Subterranean Rodents: News From Underground*. Springer-Verlag, Berlin, pp. 3–9.
- Bennett, N.C., Aguilar, G.H., Jarvis, J.U.M., Faulkes, C.G., 1994. Thermoregulation in three species of afro-tropical subterranean mole-rats (Rodentia: Bathyergidae) from Zambia and Angola and scaling within the genus *Cryptomys*. *Oecologia* 97, 222–227.
- Berger-Tal, O., Mukherjee, S., Kotler, B.P., Brown, J.S., 2010. Complex state-dependent games between owls and gerbils. *Ecol. Lett.* 13, 302–310.
- Bozinovic, F., Rojas, J.M., Broitman, B.R., Vasquez, R.A., 2009. Basal metabolic rate is correlated with habitat productivity among populations of degus *Octodon degus*. *Comp. Biochem. Physiol. A* 152, 560–564.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, U.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Buffenstein, R., 2000. Ecophysiological responses of subterranean rodents to underground habitats. In: Lacey, E.A., Patton, J.L., Cameron, G.N. (Eds.), *Life Underground*. The University of Chicago Press, Chicago, pp. 62–110.
- Burton, T., Killen, S.S., Armstrong, J.D., Metcalfe, N.B., 2011. What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proc. R. Soc. Lond. B* 278, 3465–3473.
- Careau, V., Réale, D., Humphries, M.M., Thomas, D.W., 2010. The pace of life under artificial selection: personality, energy expenditure, and longevity are correlated in domestic guinea pigs. *Am. Nat.* 175, 753–758.
- Cortes, A., Miranda, E., Rosenmann, M., Rau, J.R., 2000. Thermal biology of the fossorial rodent *Ctenomys fulvus* from the Atacama desert, northern Chile. *J. Therm. Biol.* 25, 425–430.
- Cutrerá, A.P., Antinuchi, C.D., 2004. Fur changes in the subterranean rodent *Ctenomys talarum*: possible thermal compensatory mechanism. *Rev. Chil. Hist. Nat.* 77, 235–242.
- Degen, A.A., Kam, M., Khokhlova, I.S., Krasnov, B.R., Barraclough, T.G., 1998. Average daily metabolic rate of rodents: habitat and dietary comparisons. *Funct. Ecol.* 12, 63–73.
- Diamond, J.M., 1998. Evolution of biological safety factors: a cost/benefit analysis. In: Weibel, E.R., Taylor, C.R., Bolis, L. (Eds.), *Principles of Animal Design*. Cambridge University Press, Cambridge, pp. 21–27.
- Elgar, M.A., Harvey, P.H., 1987. Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecol.* 1, 25–36.
- Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm. *J. Stat. Softw.* 33, 1–22.
- Hayes, J.P., 2010. Metabolic rates, genetic constraints, and the evolution of endothermy. *J. Evol. Biol.* 23, 1868–1877.
- Hayssen, V., Lacy, R.C., 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol. A* 81, 741–754.
- Hulbert, A.J., Else, P.E., 2004. Basal metabolic rate: history, composition, regulation and usefulness. *Physiol. Biochem. Zool.* 77, 869–876.
- Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harris, R., Lawrence, W.T., 2004. Global patterns in human consumption of net primary production. *Nature* 429, 870–873.
- Jetz, W., Freckleton, R.P., McKechnie, A.E., 2008. Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS One* 3, e3261.
- Kleiber, M., 1932. Body size and metabolism. *Hilgardia* 6, 315–351.
- Konarzewski, M., Książek, A., 2013. Determinants of intra-specific variation in basal metabolic rate. *J. Comp. Physiol. B* 183, 24–41.
- Kooijman, S.A.L.M., 2000. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press.
- Koteja, P., 1991. On the relation between basal and field metabolic rates in birds and mammals. *Funct. Ecol.* 5, 56–64.
- Linnen, C.R., Hoekstra, H.E., 2010. Measuring natural selection on genotypes and phenotypes in the wild. *Cold Spring Harb. Symp. Quant. Biol.* LXXIV, 155–168.
- Lovegrove, B.G., 2003. The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *J. Comp. Physiol. B* 173, 87–112.
- Lumley, T., Miller, A., 2009. Leaps: regression subset selection. R Package Version 2, p. 9.
- Luna, F., Antenucci, C.D., Bozinovic, F., 2009. Comparative energetics of the subterranean *Ctenomys* rodents: breaking patterns. *Physiol. Biochem. Zool.* 82, 226–235.
- Luna, F., Bozinovic, F., Antenucci, C.D., 2015. Macrophysiological patterns in the energetics of caviomorph rodents: implications in a warming world. In: Vassallo, A.L., Antenucci, C.D. (Eds.), *The Biology of Caviomorph Rodents: Diversity and Evolution*. SAREM Series A, pp. 245–272.
- McKechnie, A.E., 2008. Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. *J. Comp. Physiol. B* 178, 235–247.
- McNab, B.K., 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology* 47, 712–733.
- McNab, B.K., 1979. The influence of body size on the energetic and distribution of fossorial and burrowing mammals. *Ecology* 60, 1010–1021.
- McNab, B.K., 1988. Complications inherent in scaling the basal rate of metabolism in mammals. *Q. Rev. Biol.* 63, 25–54.
- McNab, B.K., 2002a. *The Physiological Ecology of Vertebrates: A View From Energetics*. Comstock Publishing Associates.
- McNab, B.K., 2002b. Short-term energy conservation in endotherms in relation to body mass, habits, and environment. *J. Therm. Biol.* 27, 459–466.
- McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. *Comp. Biochem. Physiol. A* 151, 5–28.
- McNab, B.K., 2009. Ecological factors affect the level and scaling of avian BMR. *Comp. Biochem. Physiol. A* 152, 22–45.
- McNab, B.K., 2012. *Extreme Measures*. The University of Chicago Press.
- Meiri, S., Dayan, T., 2003. On the validity of Bergmann's rule. *J. Biogeogr.* 30, 331–351.
- Mueller, P., Diamond, J., 2001. Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. *Proc. Natl. Acad. Sci. U. S. A.* 98, 12550–12554.
- Naya, H., Gianola, D., Romero, H., Urioste, J.I., Musto, H., 2006. Inferring parameters shaping amino acid usage in prokaryotic genomes via Bayesian MCMC methods. *Mol. Biol. Evol.* 23, 203–211.
- Naya, D.E., Bozinovic, F., Karasov, W., 2008. Latitudinal trends in physiological flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am. Nat.* 172, E122–E134.
- Naya, D.E., Spangenberg, L., Naya, H., Bozinovic, F., 2012. Latitudinal pattern in rodent metabolic flexibility. *Am. Nat.* 179, E172–E179.
- Naya, D.E., Spangenberg, L., Naya, H., Bozinovic, F., 2013. How does evolutionary variation in basal metabolic rates arise? A statistical assessment and a mechanistic model. *Evolution* 67, 1463–1476.
- Naya, D.E., Naya, H., Lessa, E.P., 2016. Brain size and thermoregulation during Homo evolution. *Comp. Biochem. Physiol. A* 191, 66–73.
- Nespolo, R.F., Bacigalupe, L.D., Figueroa, C.C., Koteja, P., Opazo, J.C., 2011. Using new tools to solve an old problem: the evolution of endothermy in vertebrates. *Trends Ecol. Evol.* 26, 414–423.
- Nevo, E., 1999. *Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Global Convergence*. Oxford University Press.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Piersma, T., van Gils, J.A., 2010. *The Flexible Phenotype. A Body-centred Integrative of Ecology, Physiology and Behaviour*. Oxford University Press.
- Raftery, A.E., 1995. Bayesian model selection in social research. *Sociol. Methodol.* 25, 111–163.
- Raftery, A.E., Madigan, D., Hoeting, J.A., 1997. Bayesian model averaging for regression models. *J. Am. Stat. Assoc.* 92, 179–191.
- R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rezende, E.L., Bozinovic, F., Garland Jr., T., 2004. Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* 58, 1361–1374.
- Rodríguez, M.A., López-Sañudo, I.L., Hawkins, B.A., 2006. The geographical distribution of mammals body size in Europe. *Glob. Ecol. Biogeogr.* 15, 173–181.
- Roll, U., Dayan, T., Kronfeld-Schor, N., 2006. On the role of phylogeny in determining activity patterns of rodents. *Evol. Ecol.* 20, 479–490.
- Sadowska, E.T., Baliga-Klimczyk, K., Labocha, M.K., Koteja, P., 2009. Genetic correlations in a wild rodent: grass-eaters and fast-growers evolve high basal metabolic rates. *Evolution* 63, 1530–1539.
- Speakman, J.R., 2000. The cost of living: field metabolic rates of small mammals. In: Fisher, A.H., Raffaelli, D.G. (Eds.), *Advances in Ecological Research*. Academic Press, California, pp. 178–294.
- Speakman, J.R., Krol, E., Johnson, M.S., 2004. The functional significance of individual variation in basal metabolic rate. *Physiol. Biochem. Zool.* 77, 900–915.
- Stager, M., Pollock, H.S., Benham, P.M., Sly, N.D., Brawn, J.D., Cheviron, Z.A., 2016. Disentangling environmental drivers of metabolic flexibility in birds: the importance of temperature extremes versus temperature variability. *Ecography* 39, 787–795.
- Steggmann, A.T., Cerny, F.J., Holliday, T.W., 2002. Neandertal cold adaptation: physiological and energetic factors. *Am. J. Hum. Biol.* 14, 566–583.
- Studel, K., Porter, W.P., Sher, D., 1994. The biophysics of Bergmann's rule: a comparison of the effects of pelage and body size variation on metabolic rate. *Can. J. Zool.* 72, 70–77.
- Swallow, J.G., Hayes, J.P., Koteja, P., Garland Jr., T., 2009. Selection experiment and experimental evolution of performance and physiology. In: Garland Jr., T., Rose, M.C. (Eds.), *Experimental Evolution*. California University Press, California, pp. 301–351.
- Tieleman, B.I., Williams, J.B., Buschur, M.E., Brown, C.R., 2003. Phenotypic variation of larks along an aridity gradient: are desert birds more flexible. *Ecology* 84, 1800–1815.
- Upham, N.S., Patterson, B.D., 2012. Diversification and biogeography of the Neotropical caviomorph lineage Octodontoidae (Rodentia: Hystricognathi). *Mol. Phylogenet. Evol.* 63, 417–429.
- Vleck, D., 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiol. Zool.* 52, 122–136.

- Westoby, M., Leishman, M.R., Lord, J.M., 1995. On misinterpreting the "phylogenetic correction". *J. Ecol.* 83, 531–534.
- White, C.R., 2003. The influence of foraging mode and arid adaptation on the basal metabolic rates of burrowing mammals. *Physiol. Biochem. Zool.* 76, 122–134.
- White, C.R., Kearney, M.R., 2012. Determinants of inter-specific variation in basal metabolic rate. *J. Comp. Physiol. B.* 183, 27–41.
- White, R.C., Blackburn, T.M., Martin, G.R., Butler, P.J., 2007. Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proc. R. Soc. Lond. B* 274, 287–293.
- Woodley, R., Buffenstein, R., 2002. Thermogenic changes with chronic cold exposure in the naked mole-rat (*Heterocephalus glaber*). *Comp. Biochem. Physiol. A* 133, 827–834.
- Zhao, Z.-J., Chi, Q.-S., Liu, Q.-S., Zheng, W.-H., Liu, J.-S., Wang, D.-H., 2014. The shift of thermoneutral zone in striped hamster acclimated to different temperatures. *PLoS One*, e84396.