



HOW DOES EVOLUTIONARY VARIATION IN BASAL METABOLIC RATES ARISE? A STATISTICAL ASSESSMENT AND A MECHANISTIC MODEL

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Metabolic rates are related to the pace of life. Hence, research into their variability at global scales is of vital importance for several contemporary theories in physiology, ecology, and evolution. Here we evaluated the effect of latitude, climate, primary productivity, habitat aridity, and species trophic habits, on mass-independent basal metabolic rates (BMRs) for 195 rodent species. The aims of this article were twofold. First, we evaluated the predictive power of different statistical models (via a model selection approach), using a dimensional reduction technique on the exogenous factor matrix to achieve a clear interpretation of the selected models. Second, we evaluated three specific predictions derived from a recently proposed hypothesis, herein called the “obligatory heat” model (OHM), for the evolution of BMR. Obtained results indicate that mean/minimum environmental temperature, rainfall/primary productivity and, finally, species trophic habits are, in this order, the major determinants of mass-independent BMR. Concerning the mechanistic causes behind this variation, obtained data agree with the predictions of the OHM: (1) mean annual environmental temperature was the best single predictor of residual variation in BMR, (2) herbivorous species have greater mass-independent metabolic rates, and tend to be present at high-latitude cold environments, than species in other trophic categories.

KEY WORDS: Endothermy, energetic, macrophysiology, organ size, rodents.

Metabolic rates are related to the pace of life, and therefore investigations of their global variability on Earth are of vital importance to gain insight about physiological, ecological, and evolutionary theories (Spicer and Gaston 1999; Kooijman 2000; McNab 2002; Brown et al. 2004; Angilletta 2009). In addition, these studies

could be used in concert with large-scale climatic assessments of species metabolic responses to understand and predict what the near future might hold for a diversity of taxa in a warming world (Helmuth et al. 2005; Deutsch et al. 2008; Bozinovic et al. 2011; Dell et al. 2011). Among various metabolic measurements,

basal metabolic rate (BMR) represents the minimum rate of energy necessary to maintain homeostasis, and is by far the most widely measured energetic variable in endothermic animals (McNab 2002, 2012; Hulbert and Else 2004; Speakman et al. 2004). The two major determinants of BMR are body mass and higher level taxonomic affiliation (Kleiber 1932; Hayssen and Lacy 1985; Daan et al. 1990; Muller and Diamond 2001; McNab 2012). Once these two factors are ruled out, however, the remaining variation in BMR is still large: ca. sixfold in mammals (McNab 1988a, 2008) and ca. fivefold in birds (McNab 2009).

Historically, variation in mass- and taxonomic-independent BMR (hereafter residual BMR) has been associated with several biotic and abiotic factors, such as species trophic habits (McNab 1986, 1988b; Koteja and Weiner 1993; Degen et al. 1998), geographic latitude and climatic variables (MacMillen and Garland 1989; Speakman 2000; Lovegrove 2003; Rezende et al. 2004; White et al. 2007), and environmental aridity (Degen et al. 1998; Lovegrove 2000; McNab 2002; Tieleman et al. 2003). In this sense, one of the most inclusive hypotheses to explain residual BMR is the food habits hypothesis (McNab 1986, 1988b), which identifies three components of the diet that can introduce variability into BMR, namely food quality, availability, and predictability (Cruz-Neto and Bozinovic 2004). According to this hypothesis, species exploiting food with low-energy content and/or low digestibility evolve low residual BMRs, as is also the case of those species occurring in habitats where food availability is low and/or unpredictable (Cruz-Neto et al. 2001; McNab 2002; Cruz-Neto and Jones 2005). The proximal causes for the proposed relationship between metabolic rate and food quality (or availability), however, are not well established and current results showed a mixed support for this hypothesis (for recent reviews, see Cruz-Neto and Bozinovic 2004; Bozinovic and Sabat 2010). Over the last decade, net primary productivity (NPP) has also been claimed as a potential unifying variable that, being related with all the above-mentioned factors, could comprise the major determinant of residual BMR (Mueller and Diamond 2001). Mueller and Diamond (2001) analyzed five species of *Peromyscus* and found evidence for a clear correlation between NPP and residual BMR, whereas Bozinovic et al. (2009) reported the same pattern for four populations of *Octodon degus* (see also Tieleman et al. 2003 for a similar example in birds). Using highly controlled experimental design and protocols, they observed that deer-mice species and degu populations originating from, or inhabiting, more productive habitats, run their metabolic rates “faster” in comparison to species or populations from less-productive habitats. However, a common feature of these two studies is that variation in residual BMR was relatively low (ca. 1.4 times in both cases) in relation to the amount of variation that should be explained (the ca. six times above mentioned). Thus, it could be possible that NPP only became a good predictor of residual BMR when the effects of other

relevant factors have been previously removed (e.g., by choosing species with similar food habits or species that are fairly close in geographical space).

Within this context, we analyzed BMR data for 195 rodent species to simultaneously evaluate the effect of latitude, climate, NPP, habitat aridity, and species trophic habits, on residual BMR. The aims of this study were twofold. First, we evaluate the predictive power of different statistical models via a model selection approach, and using a dimensional reduction technique on the exogenous factors matrix to achieve a clear interpretation of the selected models. To our knowledge, global-scale analyses that simultaneously tested the effect of climatic variables, aridity, and primary productivity have been conducted in birds but not in mammals (White et al. 2007; Jetz et al. 2008). In addition, these studies in birds did not take into account the potential effect of differences in species food habits on residual BMR. Second, we test three predictions derived from a recently proposed hypothesis, here called the “obligatory heat” model (OHM), for the evolution of BMR (Naya et al. 2012). This model states that residual BMR should be adjusted to the modal ambient temperature in such a way that the body temperature increases due to heat generation for tissue maintenance, places organisms near their body temperature set point (Naya et al. 2012; Fig. 1). The rationale behind the OHM is that: (1) endothermic organisms have to maintain, almost all the time, a thermal differential with their environment such that body temperature (T_b) is greater than ambient temperature (T_a); this implies that they have to generate an “obligatory” amount of heat, whose magnitude, averaged over time, depends on the mean temperature in their environment (assuming that body temperature is fairly constant); (2) even though organisms cannot choose to pay for this “obligatory” amount of heat, they can choose how to pay for it; for instance, they can change either the amount of metabolically expensive tissues or the metabolic intensity of these tissues (both affecting BMR), or they can rely on active heat generation mechanisms (and thus not affecting BMR); (3) the generation of an increasing amount of “obligatory” heat as a by-product of the maintenance of larger masses of useful tissues (or the same masses of more active ones) should be favored by natural selection over active heat generation mechanisms, which have no other purpose than heat generation itself (assuming that other nonenergetic costs are negligible); (4) increases in the amount of metabolically expensive tissues, rather than in tissue metabolic intensities, are expected to be favored by natural selection to cope with a rise in the amount of “obligatory” heat; this is because tissue metabolic intensities are thought to be strongly canalized by selective processes, in such a way that a rise in their specific activity cause a drop in the safety margin for the function in which the tissue is involved. As can be seen, the OHM is more a combination of existing ideas concerning the evolution of metabolic rates and organismal design rather than a new idea itself. It is

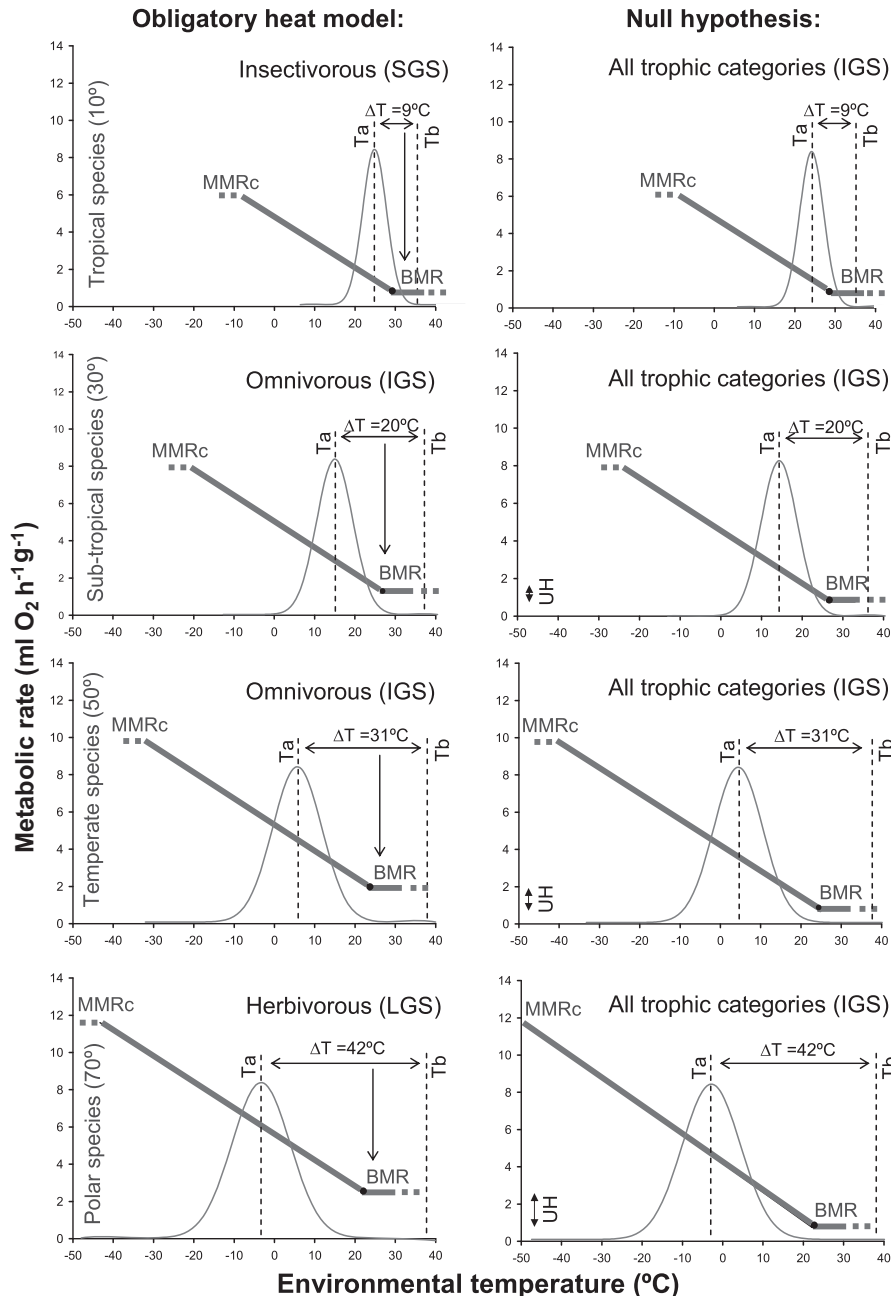


Figure 1. Graphical representation of the obligatory heat model (OHM). Endothermic organisms have to maintain a thermal differential with their environment (ΔT), implying an “obligatory” amount of heat of increasing magnitude as mean environmental temperature (T_a) decreases (from upper to lowest panel). Endothermic organisms can generate this “obligatory” amount of heat by increasing the size of internal organs, that is, affecting BMR (left panels), or by increasing the amount of heat generated by active heat generation mechanisms that have no other purpose than heat generation itself, that is, not affecting BMR (right panels). Given that the second decision implies an unused amount of heat (UH) that could be used for the maintenance of larger organs (e.g., gut), it should be expected that the first option will be favored by natural selection over the second one. Accordingly, the OHM also predicts that (1) shorter gut size (SGS) should be observed at lower latitudes (upper panel), intermediate gut size (IGS) at middle latitudes (middle panels), and larger gut size (LGS) at higher latitudes (lower panel), and (2) an increase in the proportion of herbivorous species at higher latitudes (i.e., from the lower to the upper panel). See the main text for a detailed explanation. Note: For constructing this figure we used real data (i.e., those expected for each latitude) on mean annual temperature (T_a), temperature annual range (i.e., the range of the normal curves), body temperature (T_b), thermal conductance (i.e., the slope of the metabolic functions), and BMR from Lovegrove (2003); maximal metabolic rate during cold exposure (MMRc) from Rezende et al. (2004); and lower critical temperature (i.e., the black dot in the metabolic functions) from Bozinovic and Rosenman (1988).

based in the “heat dissipation limit” theory (Speakman and Krol 2010) and early works (e.g., McNab and Morrison 1963), that highlight the relevance of the thermal differential between organisms and their environment on residual BMR; the “expensive tissue” hypothesis (Aiello and Wheeler 1995) and previous works (e.g., Daan et al. 1990; Bennett 1991; Ruben 1995) that recall the importance of visceral organ size on residual BMR; and the “safety margins” idea (Hammond and Diamond 1992; Diamond 1998), which suggests that tissue mass-specific activities should be canalized by natural selection due to energetic and space constraints. If the OHM is acceptable, we expect that (1) annual mean temperature should be the best single predictor of residual BMR, both variables being inversely correlated, (2) species with greater digestive organ masses (e.g., herbivorous species) should have higher residual BMR than those with smaller ones (e.g., insectivorous species), and (3) species having greater digestive organ masses (e.g., herbivorous species) should be more common at high-latitude cold environments than those having smaller ones (e.g., insectivorous species) (Fig. 1). Even though the general idea of the OHM is not based on a particular metabolically expensive tissue, we note that the second and third predictions are focused on the digestive system. There are practical as well as theoretical reasons for this. First, the well-established link between gut size and diet (Stevens and Hume 1995; Lavin et al. 2008; Lovegrove 2010) allows the use of trophic categories, for which enough data are available, to test model predictions. Second, the digestive system is composed by metabolically expensive tissues, which at the same time represents an important portion of the overall body mass. Indeed, the gastrointestinal tract could represent as much as 40% of the overall BMR (Wang et al. 2006), whereas digestive organs plus the liver could represent more than half of it (Johnson et al. 1990; Aiello 1997). Third, the digestive system is considered one of the most reactive systems to change in environmental conditions (Piersma and Lindstrom 1997; Karasov et al. 2011), and a rise in digestive organ masses in parallel to a fall in environmental temperatures comprises a widespread response among rodent species (Naya et al. 2007, 2008a). Finally, at least at the intraspecific level, it is known that the mass of digestive organs is positively correlated with BMR (Konarzewski and Diamond 1995; Ksiazek et al. 2004).

Materials and Methods

DATABASE DESCRIPTION

To analyze residual variation in BMR, and to test the predictions of the OHM, we used data on BMR, body mass, and geographical coordinates for 195 rodent species compiled by Lovegrove (2003) (Table S1). Methodological details on how these variables were assessed are explained elsewhere (Lovegrove 2003). The following climatic variables for each datapoint were downloaded

from the WorldClim data base (<http://www.worldclim.org/>): annual mean temperature (in °C), minimum temperature of the coldest month (in °C), maximum temperature of the warmest month (in °C), temperature annual range (difference between maximum temperature of warmest month and minimum temperature of the coldest month, in °C), temperature seasonality (standard deviation of the mean monthly temperature, in °C), accumulated annual rainfall (in mm), and rainfall seasonality (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, a NNP map (based on Imhoff and Bounoua 2006) was downloaded from Socioeconomic Data and Application Center homepage (<http://sedac.ciesin.columbia.edu/es/hanpp.html>), and an aridity map (based on Trabucco et al. 2008) was downloaded from the CGIAR Consortium for Spatial Information homepage (<http://csi.cgiar.org/Aridity/>). NPP (in tons of carbon per 0.25 degree cell) and aridity index values (adimensional) were then obtained for each site using the software ArcGis version 10 (Table S1). Aridity index values were multiplied by (−1) to obtain a direct relationship between real aridity and index values; thus, in our scale, values greater than −0.03 represent hyperarid environments, values between −0.003 and −0.2 represent arid environments, values between −0.2 and −0.5 represent semiarid environments, values between −0.5 and −0.65 represent dry subhumid environments, and values lower than −0.65 represent humid environments. Finally, we compiled data on species trophic habits, and assigned each species to one of the following dietary categories: herbivorous (*H*), herbivorous–granivorous (*HG*), granivorous (*G*), omnivorous (*O*), and insectivorous (*I*) (Table S1).

Data on several other geographic and climatic variables (e.g., altitude, rainfall coefficient of variation, temperature, and rainfall of the warmest, coldest, wettest, and driest quarter) were also downloaded, but they were discarded after preliminary analyses due to low explanatory power and/or colinearity with the selected variables. For the sake of simplicity, hereafter the term factors will refer to latitude (*Latitude*), net primary productivity (*NPP*), aridity (*Aridity*), and species trophic habits (*Diet*); climatic variables to mean annual temperature (*Tmed*), minimum of the coldest month (*Tmin*), maximum temperature of the warmest month (*Tmax*), temperature annual range (*TAR*), temperature seasonality (*TS*), accumulated annual rainfall (*Rainfall*), and rainfall seasonality (*RS*); and exogenous factors both to factors and climatic variables indiscriminately.

STATISTICAL ANALYSIS

The relationships between BMR and exogenous factors were evaluated through standard least squares regression techniques, using body mass as a covariate. In regression analyses, species trophic habits were ranked according to their approximate assimilable

Table 1. Parameter estimation (and standard deviation) for the models selected as “good models” according to the Bayesian information criterion (BIC). m_b = body mass, p = number of model parameters, ΔBIC = BIC model—lowest BIC, r^2 = proportion of variance explained by the model. See section Materials and Methods for exogenous factors abbreviations.

No.	Model's parameter	BIC	p	ΔBIC	r^2
1	$\text{BMR} = 42.73(6.78) + 0.59(0.02) m_b - 1.49(0.25) T_{\min} + 0.02(0.005) \text{Rainfall} - 5.08(1.94) \text{Diet}$	1934.0	5	0	0.892
2	$\text{BMR} = 28.14(4.23) + 0.60(0.02) m_b - 1.53(0.25) T_{\min} + 3.93 \times 10^{-5} (1.32 \times 10^{-5}) \text{NPP}$	1935.2	4	1.2	0.888
3	$\text{BMR} = 41.26(7.14) + 0.59(0.02) m_b - 1.44(0.25) T_{\min} + 3.65 \times 10^{-5} (1.31 \times 10^{-5}) \text{NPP} - 4.44(1.96) \text{Diet}$	1935.3	5	1.3	0.891
4	$\text{BMR} = 28.62(4.17) + 0.59(0.02) m_b - 1.57(0.25) T_{\min} + 0.02(0.005) \text{Rainfall}$	1935.7	4	1.7	0.888
5	$\text{BMR} = 63.70(5.58) + 0.59(0.02) m_b - 1.78(0.32) T_{\text{med}}$	1936.1	3	2.1	0.884
6	$\text{BMR} = 74.48(7.29) + 0.59(0.02) m_b - 1.66(0.32) T_{\text{med}} - 4.50(1.99) \text{Diet}$	1936.2	4	2.2	0.887

energy content (see Speakman 2000), and included as an ordinal variable (herbivorous: 1, herbivorous–granivorous: 2, granivorous: 3, omnivorous: 4, and insectivorous: 5). We estimated the goodness of fit of all the possible models (1792 models; Table S2), 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 have a measure of the robustness of each model, we calculated the number of times that it provided the best estimation of residual BMR over 100,000 iterations, 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 using the R package leaps (Lumley and Miller 2009; R Core Team 2012). Finally, to evaluate the covariation among exogenous factors and to explore if this covariation is related to model selection, we conducted a principal component analysis (PCA) on the exogenous factors matrix. This analysis was performed using the module “Multivariate Exploratory Techniques” of the statistical software STATISTICA version 7.0 (Statsoft).

For models selected as “good models,” we evaluated the effect of phylogeny on the relationship between BMR and exogenous 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). The phylogenetic tree published by Lovegrove (2003) was transformed to a Newick formatted tree using the program TreeSnatcherPlus (Laubach and von Haeseler 2007). Using this tree as the starting point, we decided to incorporate phylogenetic uncertainty into the calculations using BMA because: (1) branch lengths are not known for this tree, and (2) there are several soft polytomies associated with (1). In this sense, phylogenetic uncertainty was included by generating 1000 trees in which polytomies were randomly resolved (by transforming all multichotomies into a series of dichotomies with one or several branches of length zero) and branch lengths were randomly sampled from a uniform distribu-

tion (ranging between 0.01 and the maximum branch length). For each comparative model, the effect of exogenous factors on BMR was calculated through linear mixed models, using body mass as a covariate. To estimate the effect of each exogenous factor on BMR, we calculated the proportion of posterior estimates greater than zero (gt0). In short, gt0 can be viewed as the probability of observing a positive (if $\text{gt0} > 0.5$) or negative (if $\text{gt0} < 0.5$) association between the dependent variable (i.e., BMR) and each exogenous factor. Note that when the dependent variable is not affected by the independent variable this probability would be equal to 0.5 (i.e., the distribution of the regression coefficients would be centered on zero). In addition, for each case, the amount of information provided by the phylogeny was evaluated using phylogenetic signal values (Ps), which estimate the proportion of phenotypic variation phylogenetically inherited between species (note that this parameter is also called phylogenetic heritability; Lynch 1991). The Ps value ranges between 0 (i.e., no phylogenetic effect on the inheritance of a character) and 1 (i.e., total dependence between the character state of the ancestor and the character state of the descendent). All comparative analyses were performed using the software R, through the “APE” (Paradis et al. 2004) and “bmaMCMCanalysis” (L. Spangenberg, H. Romero, and H. Naya; available upon request) packages. Phylogenetically informed analyses were only conducted for the selected “good models” for practical reasons (i.e., the inability to run the phylogenetic analyses for all the 1792 models given the computational cost), as well as, conceptual ones (see Discussion below).

Results

STATISTICAL MODELS EXPLAINING RESIDUAL BMR

According to the BIC values, six models were selected as “good models” in conventional analyses (Tables 1, S2). This set of “good models” included those with one (model 5), two (models 2, 4, and 6), or three (models 1 and 3) independent variables, in addition to body mass (Table 1). The independent variables included in these models were minimum temperature of the coldest month or mean

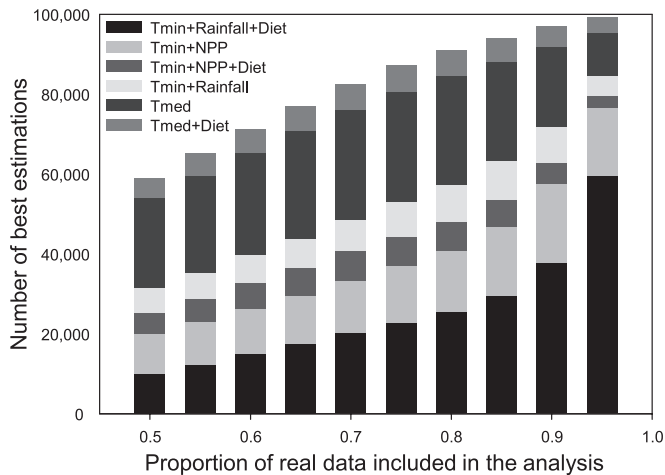


Figure 2. Number of best estimations (over 100,000 iterations) done by each of the six selected models as a function of the proportion of real data included in the dataset used. See section Materials and Methods for exogenous factors abbreviations. **Note:** The overall number of estimations increases with the proportion of real data because at lower proportions several nonselected models gave some of the best estimations.

annual temperature in all the six cases (P -values ranged between 4.9×10^{-7} and 4.6×10^{-9} ; Table S2), rainfall or NPP in four cases (P -values ranged between 0.006 and 0.003; Table S2), and species trophic habits in three cases (P -values ranged between 0.02 and 0.01; Table S2). Robustness analysis indicated that the major change associated with an increasing proportion of real data in the simulations was a reduction in the number of best estimations done by the simplest model (i.e., those that only include mean annual temperature) in parallel to an increase in the number of best estimations done by the overall best model (i.e., those that include minimum temperature of the coldest month, rainfall, and species diet) (Fig. 2). All independent variables included in the selected models also had a significant effect on BMR in the phylogenetic

informed analyses, agreeing with the fact that phylogenetic signals were markedly low (Table 2).

COVARIATION AMONG EXOGENOUS FACTORS

The PCA indicated that the first axis of variation explained 42.72% of overall variance and also that the greater contributions to this axis were done by latitude, mean and minimum temperatures, and thermal variability indexes (Table 3); this axis separated: (1) latitude (with a negative load) from the other three factors, and (2) mean and minimum temperatures (with negative loads) and thermal variability indexes (with positive loads) from the other climatic variables (Fig. 3). The second axis of variation explained 24.85% of overall variance and the greater contributions to this axis were done by primary productivity, aridity, maximum temperature, and rainfall (Table 3); this axis mainly separated: (1) productivity (with a positive load) and aridity (with a negative load) from the other two factors, and (2) annual rainfall (with a positive load) and maximum temperature (with a negative load) from the other climatic variables (Fig. 3). The third axis of variation explained 11.32% of overall variance and the greater contributions to this axis were done by species diet, rainfall seasonality, and maximum temperature (Table 3); this axis separated: (1) species diet (with a negative load) from the other factors, and (2) rainfall seasonality (with positive load) and maximum temperature (with a negative load) from the other climatic variables (Fig. 3). Thus, latitude and associated thermal variables, productivity and rainfall, and species trophic habits, were related, in this order, with greater amounts of variability in the exogenous factors matrix. Note that in our dataset, species body mass did not correlate either with factors (*Latitude*: $r = -0.13$, $P = 0.07$, *NPP*: $r = 0.06$, $P = 0.43$; *Aridity*: $r = -0.06$, $P = 0.42$; *Diet*: $r = -0.02$, $P = 0.75$) or with climatic variables (*Tmed*: $r = 0.03$, $P = 0.65$; *Tmin*: $r = 0.10$, $P = 0.18$; *Tmax*: $r = -0.06$, $P = 0.42$; *Rainfall*: $r = 0.11$, $P = 0.14$; *RS*: $r = 0.10$, $P = 0.17$).

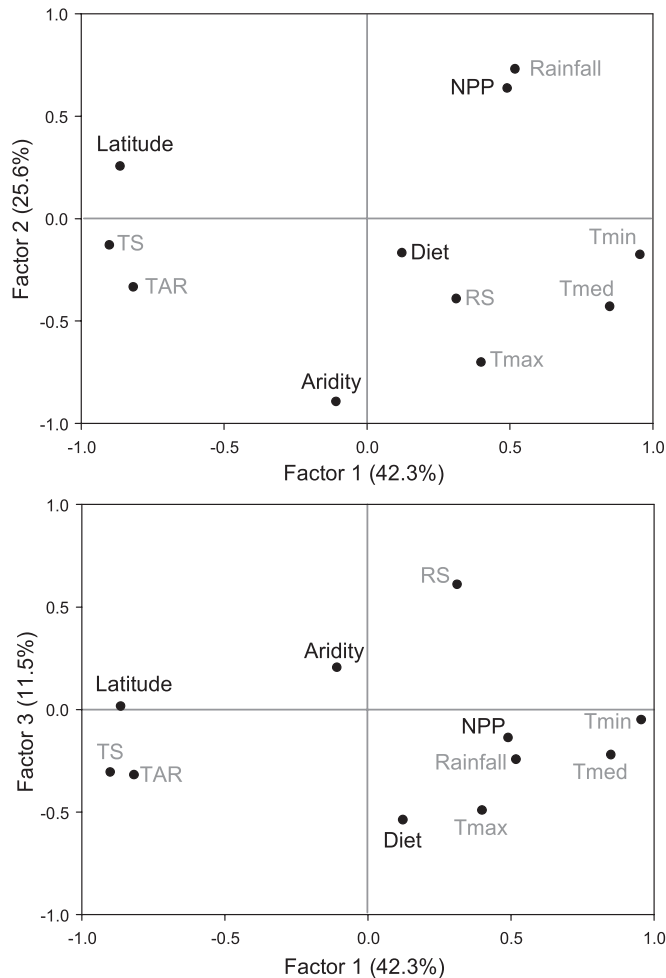
Table 2. Parameter estimation (B), standard deviation (SD), and proportion of posterior estimates greater than zero (gt0) for each independent variable included in each selected model (see Table 1), together with phylogenetic signal value of each model (Ps), according to phylogenetically informed analysis. See section Materials and Methods for exogenous factors abbreviations.

No.	<i>Tmin</i> or <i>Tmed</i>			<i>Rainfall</i> or <i>NPP</i>			<i>Diet</i>			Ps
	B	SD	gt0	B	SD	gt0	B	SD	gt0	
1	-1.486	0.255	0	0.016	0.005	0.999	-5.068	1.955	0.005	1.3×10^{-5}
2	-1.528	0.251	0	3.9×10^{-5}	1.3×10^{-5}	0.998	—	—	—	1.2×10^{-5}
3	-1.442	0.252	0	3.6×10^{-5}	1.3×10^{-5}	0.997	-4.428	1.970	0.013	1.2×10^{-5}
4	-1.561	0.257	0	0.016	0.005	0.998	—	—	—	1.0×10^{-5}
5	-1.779	0.318	0	—	—	—	—	—	—	9.6×10^{-6}
6	-1.656	0.318	0	—	—	—	-4.494	2.002	0.013	8.4×10^{-6}

Note. The intercept and the covariate body mass were highly significant in all the cases (gt0 > 0.9999).

Table 3. Contributions (Cont) and factor loadings (Load) of each exogenous factor to each of the three first axes of variation of the principal component analysis. See section Materials and Methods for exogenous factors abbreviations.

	Factor 1		Factor 2		Factor 3	
	Cont	Load	Cont	Load	Cont	Load
<i>Latitude</i>	0.1604	−0.8641	0.0233	0.2561	0.0002	0.0162
<i>NPP</i>	0.0516	0.4903	0.1438	0.6362	0.0148	−0.1370
<i>Aridity</i>	0.0025	−0.1087	0.2830	−0.8925	0.0332	0.2051
<i>Diet</i>	0.0032	0.1223	0.0099	−0.1668	0.2282	−0.5376
<i>Tmed</i>	0.1550	0.8494	0.0654	−0.4290	0.0384	−0.2205
<i>Tmin</i>	0.1961	0.9553	0.0109	−0.1749	0.0020	−0.0501
<i>Tmax</i>	0.0342	0.3992	0.1746	−0.7010	0.1898	−0.4903
<i>TS</i>	0.1746	−0.9015	0.0058	−0.1281	0.0738	−0.3056
<i>TAR</i>	0.1437	−0.8177	0.0395	−0.3334	0.0799	−0.3182
<i>Rainfall</i>	0.0576	0.5176	0.1896	0.7305	0.0467	−0.2433
<i>RS</i>	0.0210	0.3123	0.0543	−0.3911	0.2930	0.6092

**Figure 3.** Results of the principal component analysis including exogenous factors. See section Materials and Methods for abbreviations.

EVALUATION OF THE OHM

In agreement with the OHM first prediction, the only statistical model with one independent variable (in addition to body mass) selected as a “good model” was that including the mean annual temperature (Table 1; Fig. 4). Moreover, according to BIC values this model was significantly better than any other model with only one independent variable (Table 4). Regarding the second and third predictions, we also found support for the OHM because (1) residual BMR continuously decreased from herbivorous to insectivorous species (Fig. 5A), and (2) herbivorous species tended to occur at high-latitude cold environments, whereas herbivorous–granivorous, granivorous, and omnivorous species did so at intermediate latitudes, and insectivorous species at low-latitude warm environments (Fig. 5B and C).

Discussion

As mentioned in the Introduction, the aims of the present article were twofold. First, we sought to unravel the relationship between residual BMR and several biotic and abiotic factors ascribed as potential drivers in the evolution of residual BMR. Second, we tested for three specific predictions derived from the OHM, that is, a mechanistic model proposed to explain recent evolution of BMR. Thus, in what follows we will discuss these two points in turn.

A STATISTIC EXPLANATION FOR RESIDUAL BMR

The six “good models” explaining residual BMR include mean or minimum environmental temperature—with very high significance levels—in all the cases; rainfall or NPP—with intermediate significance levels—in four cases; and species trophic habits—with a low significance level—in three cases. The PCA indicates

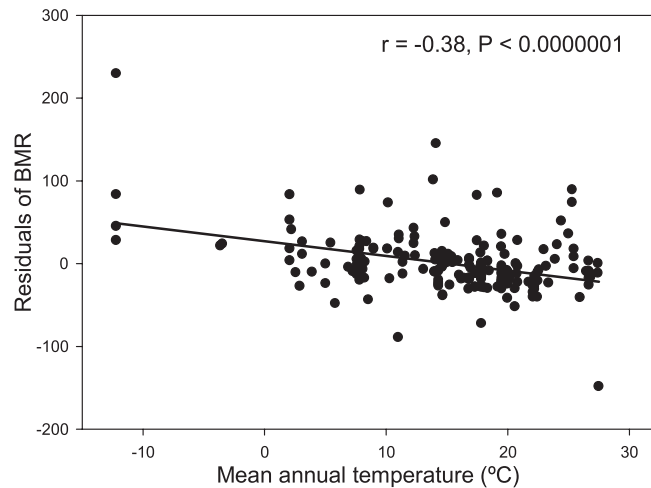


Figure 4. Relationship between residuals of BMR (with regard to body mass) and mean annual temperature.

that mean and minimum temperatures make a great contribution to the first axis of variation in the exogenous factors matrix, rainfall and NPP make a great contribution to the second axis of variation, and, finally, species trophic habits make a great contribution to the third axis of variation. So, there is a good match between the independent variables included in the statistical models and the major sources of variation in the exogenous factors matrix. In addition, robustness analysis indicates that increasing proportions of real data included in the simulations determine a rise in the number of best estimations done by the model including all the three principal axes of environmental variation, and lead to a decrease in the number of best estimations done by the model that includes only the environmental temperature. Thus, obtained results suggest that (1) the amount of variability for each exogenous factor included in each specific dataset could strongly affect the

explanatory power of different statistical models (a very logical point, whose relevance—given the limitation of all physiological datasets—is not always adequately considered); (2) at least for our dataset, environmental temperature, rainfall (or primary productivity), and species trophic habits are, in this order, the main determinants of residual BMR. In other words, our results do not agree with the idea that primary productivity is a unifying variable that comprises the major cause of variation in residual BMR. In line with this, recent studies in birds that evaluated the effect of temperature, aridity, and primary productivity at a global scale also indicate that environmental temperature is a better predictor of residual BMR than primary productivity or rainfall (White et al. 2007; Jetz et al. 2008).

Our analyses also indicate that some of the residual variation in BMR can be related to differences in species trophic habits. To our knowledge, all recent studies (except one, see below) using phylogenetically informed methods fail to detect a significant effect of diet on residual BMR (Degen et al. 1998; Speakman 2000; Cruz-Neto et al. 2001; Genoud 2002; Rezende et al. 2004). Yet, all of these studies have been based on sample sizes that are well below (i.e., less than one-third) the sample size considered here. Interestingly, the only study that detected a significant effect of diet on residual BMR was the one, which quantified diet quality as a continuous variable (i.e., the percentage of animal material), rather than as gross dietary categories (Muñoz-García and Williams 2005). Thus, it could be possible that lower samples size (resulting in a limited statistical power) and/or an inability to achieve fine-grain diet categorizations (resulting in an overestimation of the correlation between diet and phylogeny) do not allow detecting a real effect of diet on residual BMR when phylogenetically informed analyses are conducted. In this sense, our impression is that BMR could be considered a labile trait able to respond to selection in a short evolutionary time (see Swallow

Table 4. Parameter estimation (and standard deviation) for models including only one exogenous factor in addition to body mass (m_b). BIC = Bayesian information criterion values, Δ BIC = BIC model – lowest BIC, r^2 = proportion of variance explained by the model. See section Materials and Methods for exogenous factors abbreviations.

No.	Model's parameter	BIC	Δ BIC	r^2
1	$BMR = 63.70(5.58) + 0.59(0.02) m_b - 1.78(0.32) T_{med}$	1936.1	0	0.884
2	$BMR = 37.37(2.95) + 0.60(0.02) m_b - 1.29(0.24) T_{min}$	1938.9	2.8	0.883
3	$BMR = 91.39(11.75) + 0.58(0.02) m_b - 1.81(0.38) T_{max}$	1943.9	7.8	0.880
4	$BMR = 2.97(7.84) + 0.60(0.02) m_b + 0.97(0.21) Latitude$	1944.8	8.7	0.879
5	$BMR = 17.83(6.05) + 0.60(0.02) m_b + 0.03(0.008) TS$	1952.8	16.7	0.874
6	$BMR = 54.74(6.64) + 0.59(0.02) m_b - 6.32(2.08) Diet$	1956.8	20.7	0.871
7	$BMR = 28.34(4.66) + 0.59(0.02) m_b - 18.29(7.38) Aridity$	1959.8	23.7	0.869
8	$BMR = 14.80(9.49) + 0.60(0.02) m_b + 0.74(0.30) TAR$	1959.8	23.7	0.869
9	$BMR = 33.86(4.51) + 0.59(0.02) m_b + 1.3 \times 10^{-5} (1.4 \times 10^{-5}) NPP$	1965.0	28.9	0.866
10	$BMR = 41.90(6.38) + 0.59(0.02) m_b - 0.07(0.08) RS$	1965.1	29.0	0.866
11	$BMR = 35.03(4.41) + 0.59(0.02) m_b - 0.003(0.005) Rainfall$	1965.6	29.5	0.865

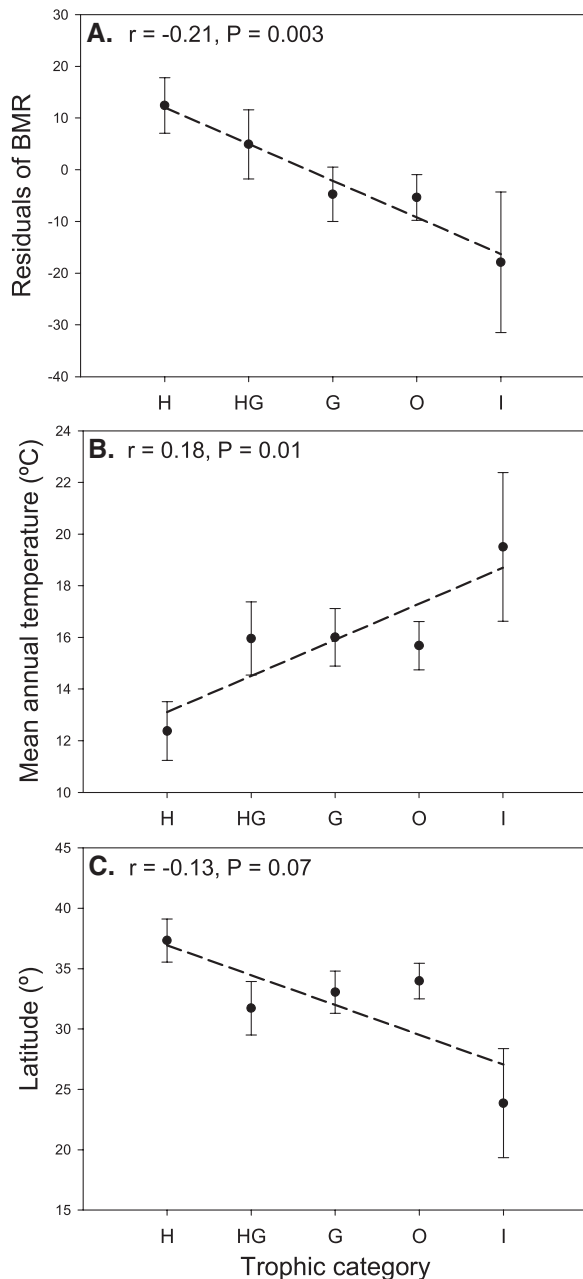


Figure 5. Relationships between species trophic habits and (A) residuals of BMR (with regard to body mass), (B) mean annual temperature, and (C) geographic latitude. Bars represent standard errors. See section Materials and Methods for species trophic habits abbreviations.

et al. 2009), and hence, it is hard to think that phylogenetic constraints are playing a major role when large temporal scales are considered (see Westoby et al. 1995; McNab 2003, 2009). In any case, we hope that the use of more modern techniques to characterize species diet, such as stable isotopic analysis, will help us to definitely solve this point in the near future (see Sabat et al. 2009 for a recent example).

A MECHANISTIC EXPLANATION FOR RESIDUAL BMR

Several models aimed to explain the noticeably high standard metabolic rates of endothermic animals (in relation to ectothermic ones) have been published during the last decades (e.g., the “expanded thermal niche” model [Crompton et al. 1978; McNab 1978], the “aerobic capacity” model [Bennett and Ruben 1979; Else and Hulbert 1985], the “sustained maximal limit” model [Drent and Daan 1980; Daan et al. 1990], the “parental care” model [Farmer 2000], the “assimilation capacity” model [Koteja 2000], and the “muscle power” model [Clarke and Portner 2010]). According to these models, the evolution of higher standard metabolic rates in endotherms is due to genetic and/or functional links with other beneficial traits, such as body temperature, locomotor performance, or parental care. This is simply because higher standard metabolic rates entail a noticeable increase in maintenance costs (and so in food consumption rates) without a direct advantage for the organism. However, given that the evolutionary origin of endothermy is set around 250–200 Mya, it is fairly possible that the genetic architecture of the first endothermic mammals, as well as selection pressures acting on them, have been changing ever since. In this sense, the OHM is an attempt to explain the current evolution of residual BMR (endothermy is a premise of the model) and, thus, to fill the gap between the above-mentioned models and current statistical correlations between environmental factors and residual BMR. According to the OHM, selection for higher BMR is related to an increasing need for heat generation and not to direct selection on other correlated traits. Consequently, the specific physiological function that result enhanced (as a by-product of selection for higher BMR) could change depending on the attributes of each taxon and the selection pressures acting on them at a given evolutionary moment. Moreover, according to the OHM, current evolution of BMR could affect the evolution of other metabolic rates (i.e., not only the other way round is possible), at least in the cases where the genetic architecture underlying these rates allows for an independent evolution (a point under current discussion; see Ricklefs et al. 1996; Ksiazek et al. 2004; Rezende et al. 2004; Gebczynski and Konarzewski 2009; Wone et al. 2009; Nespolo et al. 2011). For instance, if higher BMR values are reached by increasing the size of the digestive (and associated) organs, and if bigger guts allow a more efficient use of high abundance–low-quality dietary items (e.g., plant material) that replace more active prey (e.g., invertebrates), a higher BMR could result in lower maximal metabolic rates in the long term. Note that this hypothetical example is provided to illustrate the potentially complex interplay among metabolic rates; obviously, it does not deny that direct selection on other beneficial traits, genetically or functionally coupled to BMR, could be a key factor in the evolution of residual BMR. From this perspective, the OHM should be considered a

complementary contribution to existing models for the evolution of BMR (see below for further discussion).

Our results support three specific predictions derived from the OHM. First, mean annual temperature—that is, the climatic variable that should be more closely related to the thermal differential between an organism and its environment—was (by far) the best single predictor of mass-independent BMR. Even though the effect of environmental temperature on residual BMR has been widely recognized previously, to date no global scale study includes both mean and minimum temperature (i.e., the second best predictor of residual BMR) in the analyses (e.g., Speakman 2000; Lovegrove 2003; Rezende et al. 2004; White et al. 2007; Jetz et al. 2008). Second, residual BMR was correlated with species trophic habits in the same fashion as should be expected from differences in digestive organ masses; that is, herbivorous and herbivorous–granivorous species showed higher BMR than species in the other trophic categories, especially the insectivorous ones. This result is congruent with data reported for McNab (2008) for 639 mammals species, whereas higher BMR were associated with the consumption of grass and plant leaves, and lower BMR were associated with the consumption of insects. Furthermore, a recent study indicates that desert Otomyinae rodents, which have low BMR, exhibit shorter small intestines, whereas Arvicolidae rodents, which have high BMR, exhibit greater large intestines, without a compensatory reduction in the small intestine, in relation to other rodent species (Lovegrove 2010). Thus, unless it can be accepted that grass and plant leaves are items of greater quality than seeds and insects, all these results do not support a key prediction of the food habits hypothesis (i.e., a positive correlation between diet quality and BMR). Third, herbivorous species tend to be more common at high-latitude cold environments than species in the other four trophic categories, especially than insectivorous species. To our knowledge, the nearest observation to this finding was reported by Koteja and Weiner (1993), who proposed the existence of a “vole strategy” that was characterized by species eating low digestibility food and inhabiting high-latitude regions.

Summarizing, our general interpretation of the obtained results in the context of the OHM is that greater amounts of “obligatory” heat in high-latitude cold environments favors an increase in the size of some metabolically expensive organs, such as the gastrointestinal tract, which, in turn, allows a more efficient use of low quality dietary items (e.g., plant material). In the long term, this creates a bias toward a greater proportion of herbivorous species at higher latitudes (see Sadowska et al. 2009 for preliminary, but promising, results on artificial selection on herbivory). Recall that we visualize this phenomenon as a kind of facilitation process for herbivory at higher latitudes, derived from a physiological factor. We are not claiming that herbivory is the final fate for species colonizing high-latitude environments. The effect of several other phylogenetic (e.g., anatomic features affecting diet

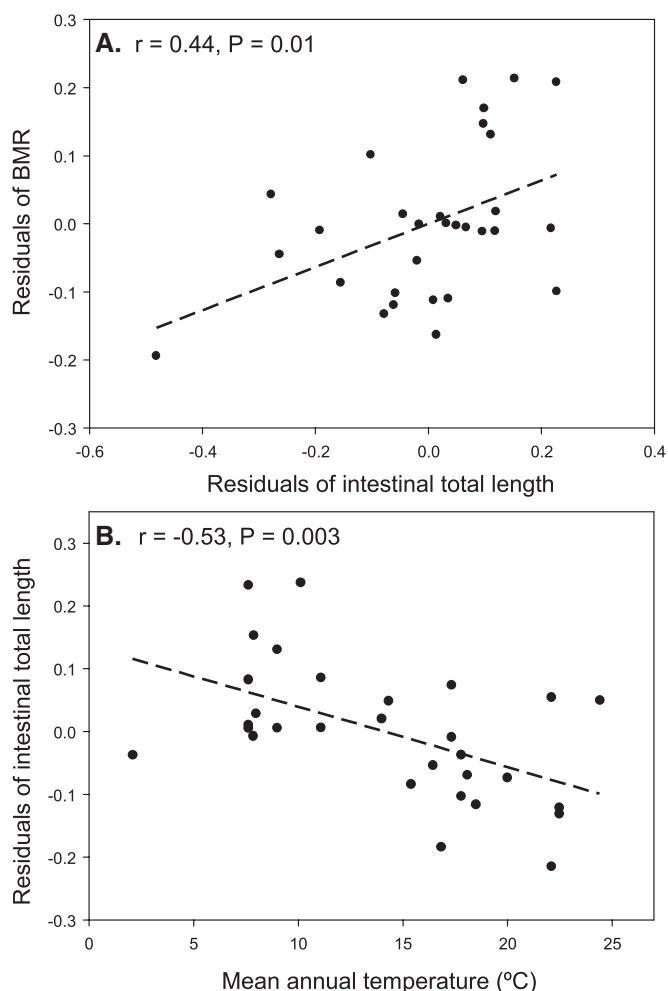


Figure 6. Relationships between (A) residuals of BMR with regard to body mass (both in logarithm) and residuals of intestinal total length with regard to body mass (both in logarithm), and (B) residuals of intestinal total length with regard to body mass (both in logarithm) and mean annual temperature.

selection), biogeographical (e.g., historical processes affecting species distributions), and ecological (e.g., habitat productivity and stability) factors may interact with species physiology, affecting the proposed trend based only on a physiological factor. For instance, the increase in the number of herbivorous species with latitude could be also related to the ecological fact that plant food is easier to find, in relation to animal preys, over the long winters that occur at higher latitudes.

CONCLUSIONS AND PERSPECTIVES

Understanding how evolutionary variation in BMR arises is a central topic for several contemporary theories in physiology, ecology, and evolution (Kooijman 2000; McNab 2002; Brown et al. 2004; Angilletta 2009; White and Kearney 2013). Yet, we still know very little about the evolution of BMR and, more generally, about the evolution of metabolic rates (Hayes 2010; Burton

et al. 2011; but see Nespolo et al. 2011 for new exciting perspectives in the field). According to the review made by Konarzewski and Ksiazek (2013), some recent studies have found a significant narrow-sense heritability of BMR in laboratory and wild mice, as well as, in some non-rodent mammal and bird species. Thus, substantial additive genetic variation in BMR appears to exist in some animal populations, which comprises a fundamental prerequisite for the evolution of this metabolic rate. In addition, artificial selection experiments on rodents were able to achieve a noticeable change in BMR (40%), which is (genetically) correlated with a change in internal organ masses (see Konarzewski and Ksiazek 2013). Moreover, after 31 generations of artificial selection the small intestine was the internal organ that showed the greater change in their size (34%) between the two selected lines (see Konarzewski and Ksiazek 2013).

Regarding selective causes behind current evolution of residual BMR in natural populations, the present study has found support for three predictions derived from the “obligatory” heat model. Further tests of new predictions derived from this model, however, should be conducted before it can be validated, partially validated, or completely discarded. In addition, a deep evaluation of model assumptions should be done. For instance, a key model assumption is that the positive correlation between (residuals of) digestive organs masses and (residuals of) BMR—previously reported in rodents at the intraspecific level (e.g., Konarzewski and Diamond 1995; Ksiazek et al. 2004; Speakman et al. 2004; Naya et al. 2008b)—should also hold at the interspecific level. Interestingly, a preliminary analysis combining data on rodent gut length reported by Lovegrove (2010) with BMR data used here indicates that it appears to be the case (Fig. 6A; Table S3). Furthermore, combinations of these two datasets also reveal another interesting result. Assuming collection sites for the species are the same in both datasets (not reported for gut length dataset), a clear negative correlation between (residuals of) gut length and mean annual temperature is observed (Fig. 6B). Noticeably, this correlation was stronger than those existing for any other exogenous factor in the metabolic database, including species trophic habits ($r = -0.41$, $P = 0.02$, $n = 30$). Thus, the links between mean environmental temperature, residual BMR, and digestive organs size assumed by the OHM appear to have empirical support at least for rodents.

Another important assumption of the OHM is that the benefits of enhanced physiological capacities offset the costs associated with carrying heavier organs. In this sense, a rise in BMR by increasing the gut size may not be expected in some taxonomic groups, such as birds, given the elevated cost of transport and the decrease in manoeuvrability associated with larger guts in these organisms (Lavin et al. 2008). Interestingly, (residuals of) whole-gut mass in birds does not correlate with (residuals of) BMR, but (residuals of) other smaller and metabolically expensive organs, such as heart and kidneys, do so (Daan et al. 1990; Wiersma et al.

2007). This suggests that the second and third predictions of the OHM tested here may not be generalized to all endothermic organisms. In line with this, a study analyzing 58 species belonging to the order Carnivora indicates that residual BMR is positively associated with diet quality (Muñoz-García and Williams 2005), and not negatively as predicted by the OHM. Interestingly, to explain this result the authors propose the “muscle performance” hypothesis, which states that more carnivorous species need to have a greater proportion of slow oxidative muscle fibers, whereas more omnivorous species need to have a greater proportion of fast glycolytic muscle fibers (Muñoz-García and Williams 2005). That is, differences in BMR among species are hypothetically related to variation in the metabolic intensity of muscular tissue (i.e., a relatively cheap but bulky tissue). Altogether these results suggest that—as contemplated by the OHM—those particular changes in tissues composition (or intensity) affecting residual BMR could depend on the specific attributes of each taxon and the strength of different evolutionary processes acting at a particular evolutionary moment.

Our final thoughts contemplate the possibility of developing a model that could explain all aspects of the evolution of BMR, either related to ultimate or proximal causes. Our impression is that it may not be likely to find a unique model, but instead, a combination of models that could provide a good explanation for the evolution of BMR (see Hayes and Garland 1995; Koteja 2004; Kemp 2006; Hayes 2010). For instance, in regard to ultimate causes it could be possible that early stages of the evolution of BMR were dominated by selection for increased locomotion and/or homeothermy, but after millions of years, and once endothermy arose, other factors began to drive the evolutionary dynamics of BMR. From this perspective, the OHM may explain a fine tuning of BMR related with much more recent events (e.g., distributional ranges expansion after glaciations) than those considered by previous models. Furthermore, we believe that the same pluralist approach could be valid in regard to the proximal causes behind the recent evolution of BMR. Perhaps adjustments in gut size affecting BMR were selected in rodents, but changes in muscle metabolic intensity were selected in species of the order Carnivora; adjustments in the size of the heart, kidneys and pectoral muscles could have been relevant for birds, but changes in the brain size occurred in primates. Finally, we want to recall that more studies aimed at understanding the evolution of fundamental biological variables, and particularly how contemporary variability in these variables arises, are highly desirable if we wish to comprehend and predict the potential impacts of human-caused environmental changes on biological diversity.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher’s website:

Table S1. Data on basal metabolic rate and body mass for 195 rodent species, together with data on geographic, climatic and ecological variables.

Table S2. Parameter estimation (and standard deviation) for models including exogenous factors in addition to body mass.

Table S3. Data on basal metabolic rate and intestinal length for 30 rodent species.

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