

On the Interplay among Ambient Temperature, Basal Metabolic Rate, and Body Mass

Daniel E. Naya,^{1,*} Hugo Naya,² and Craig R. White³

1. Departamento de Ecología y Evolución, Facultad de Ciencias, Universidad de la República, Montevideo 11400, Uruguay; 2. Unidad de Bioinformática, Institut Pasteur de Montevideo, Montevideo 11400, Uruguay; and Departamento de Producción Animal y Pasturas, Facultad de Agronomía, Universidad de la República, Montevideo 12900, Uruguay; 3. Centre for Geometric Biology, School of Biological Sciences, Faculty of Science, Monash University, Clayton, Victoria, Australia

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ABSTRACT: One of the most generalized conclusions arising from studies analyzing the ecological variation of energy metabolism in endotherms is the apparent negative correlation between ambient temperature and mass-independent basal metabolic rate (residual BMR). As a consequence, ambient temperature has been considered the most important external factor driving the evolution of residual BMR. It is not clear, however, whether this relationship is size dependent, and artifacts such as the biased sampling of body masses in physiological data sets could cause us to overstate the ubiquity of the relationship. Accordingly, here we used published data on body mass (m_b), BMR, and annual mean temperature (Tmean) for 458 mammal species (and/or subspecies) to examine the size dependence of the relationship between temperature and BMR. We found a significant interaction between m_b and Tmean as predictors of residual BMR, such that the effect of Tmean on residual BMR decreases as a function of m_b . In line with this, the amount of residual variance in BMR explained by Tmean decreased with increasing m_b , from 20%–30% at body sizes of less than 100 g to almost 0 at body sizes greater than 1,000 g. These data suggest that our current understanding of the importance of broad-scale variation in ambient temperature as a driver of metabolic evolution in endotherms probably is affected by the large number of small species in both nature and physiological data sets.

Keywords: body size, endotherms, energetic, mammals, metabolism.

Introduction

Understanding the sources of variation in energy metabolism is central for several theories in animal behavior, physiology, ecology, and evolution (Kooijman 2000; Brown et al. 2004; Angilletta 2009; Careau et al. 2010; Nespolo et al. 2011; White and Kearney 2012; Rezende and Bacigalupe 2015). This is because metabolic rates represent “physiologi-

cal hubs” in the network of physiological process that underlie life-history traits, connecting them to the pace of life of each species (Lovegrove 2003; Wikelski et al. 2003). Metabolic rates are therefore considered to link processes occurring at the individual scale with processes occurring at higher ecological and evolutionary scales (Sibly et al. 2012).

Among various metabolic measurements, the basal metabolic rate (BMR) represents the minimum rate of energy necessary to maintain homeostasis in endothermic animals, that is, animals that can maintain a relatively constant body temperature over a large range of environmental temperatures through active heat production (McNab 2002a, 2012). One of the most pervasive patterns in comparative studies of metabolic rates in these animals is a negative correlation between ambient temperature and mass-independent BMR (hereafter residual BMR), in such a way that individuals from colder climates have higher rates of energy expenditure. For instance, a significant effect of annual mean temperature and/or minimum temperature of the coldest month on residual BMR has been repeatedly documented in mammals (Speakman 1999; Lovegrove 2003; Rezende et al. 2004; Naya et al. 2012) and birds (White et al. 2007; Jetz et al. 2008; Stager et al. 2016). Moreover, for both taxonomic groups ambient temperature has been identified as a better predictor of residual BMR than other climatic and ecological factors, such as temperature variability, rainfall, rainfall variability, and primary productivity (White et al. 2007; Jetz et al. 2008; Naya et al. 2013a; Luna et al. 2017).

However, to the best of our knowledge, no study has evaluated whether the strength of this negative relationship changes with body mass. This oversight is an important point for at least two reasons. First, the efficiency of several mechanisms involved in thermoregulation and energy balance strongly depends on body mass (McNab 2002a). Second, the distribution of body masses in nature does not follow a uniform or a normal distribution but follows a right-skewed one, even when body mass is expressed in a logarithmic scale

* Corresponding author; email: dnaya@fcien.edu.uy.

ORCID: D. E. Naya, <http://orcid.org/0000-0002-8311-9263>; White, <http://orcid.org/0000-0002-0200-2187>.

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(Brown et al. 1993). For instance, even though the body mass range in mammals spreads over 8 orders of magnitude, more than one-half of extant species weigh less than 100 g (Smith et al. 2003). In addition, this skew in the distribution of body mass could be accentuated in physiological data sets for logistic reasons (e.g., laboratory space constraints might prevent working with larger species). Therefore, it could be possible that—beyond the statistical filters that are commonly used to control for the effect of body mass, such as the use of residual BMR itself—our overall impression about the effect of environmental factors shaping the evolution of physiological variables is compromised by the combination of size-dependent effects and a skewed distribution of body mass. Accordingly, in this study we tested the idea that the effect of ambient temperature on residual BMR changes with the mass of the sampled species. Specifically, we predicted that, to cope with lower ambient temperatures, smaller species will be more dependent on adjustments in BMR than larger species, such that the correlation between ambient temperature and residual BMR should decrease as body mass increases.

Methods

We compiled data on body mass (m_b), BMR, and geographic coordinates of the collection site for 458 mammal species and/or subspecies (hereafter species), from three previous studies: Lovegrove (2003), Khaliq et al. (2015), and Luna et al. (2017; data set S1A in the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.8350667>; Naya et al. 2018). Then, we obtained data on annual mean temperature (Tmean) for each species (i.e., collection site) from WorldClim ([http://](http://www.worldclim.org/)

www.worldclim.org/), using the free software Diva-Gis (<http://www.diva-gis.org/>).

To analyze whether the effect of Tmean on BMR changes with m_b , we estimated the interaction term between m_b and Tmean in a phylogenetic linear regression ($\log_{10}\text{BMR} \sim \log_{10}m_b \times \text{Tmean}$), using the package MCMCglmm (Hadfield 2010) in the free software R (R Development Core Team 2016). Note that by using this approach we are considering a potential bias in the distribution of taxonomic groups along the m_b axis. To visualize size-dependent effects, we also calculated the amount of variance in residual BMR (i.e., residuals of $\log_{10}\text{BMR} \sim \log_{10}m_b$) explained by Tmean, using phylogenetic linear regressions for windows of 1.00 \log_{10} unit of m_b , starting at the interval 0.50–1.50 and sliding successive windows by 0.25 \log_{10} units of m_b (table 1). We pooled data in this way because (1) given the highly skewed distribution of m_b in the data set (more than a half of the species are smaller than 100 g), nonoverlapping windows will result in several windows of very small size and a few of very large size, while a random sampling will result in practically all windows of small size, and (2) we did not conduct any test that assumes data independence among successive windows of m_b . To run these analyses, we first built 16 phylogenetic trees—one including all the species in the data set and one for each of the 15 windows of m_b —using the data set presented by Bininda-Emonds et al. (2007) and the free software Phylomatic v3 (<http://phylodiversity.net/phylomatic/>). Branch lengths were taken from the original source (Bininda-Emonds et al. 2007), and subspecies were entered as species replicates in these trees. In three cases (*Sciurus aberti*, *Ctenomys chasiquensis*, and *Ctenomys porteusi*), we had to use the closest species present in the orig-

Table 1: Sample size (N), mean body mass (m_b), and ambient temperature range (Trange) for each m_b window

Center of window	Interval	N	Mean m_b (g)	Trange (°C)
1.00	.50–1.50	139	17.2	–3.5 to 29.1
1.25	.75–1.75	196	26.0	–12.2 to 29.1
1.50	1.00–2.00	229	40.0	–12.2 to 29.1
1.75	1.25–2.25	230	61.5	–12.2 to 28.2
2.00	1.50–2.50	204	104.4	–12.2 to 27.4
2.25	1.75–2.75	157	166.3	–12.2 to 28.0
2.50	2.00–3.00	127	336.7	–12.2 to 28.0
2.75	2.25–3.25	102	603.3	–12.2 to 28.0
3.00	2.50–3.50	79	1,134.2	–12.2 to 28.0
3.25	2.75–3.75	76	1,912.3	–12.2 to 28.1
3.50	3.00–4.00	56	3,174.1	–11.4 to 28.1
3.75	3.25–4.25	43	5,099.1	–11.4 to 28.1
4.00	3.50–4.50	33	9,038.1	–11.4 to 27.1
4.25	3.75–4.75	20	15,627.3	–6.4 to 26.8
4.50	4.00–5.00	13	19,940.5	4.7–26.8
All data		458	1,286.3	–12.2 to 29.1

Note: Windows of 1.00 \log_{10} unit of m_b were considered, starting at the interval 0.50–1.50 and sliding successively by 0.25 \log_{10} units. The mean temperature was similar for all windows, ranging between 16.2° and 18.7°C.

inal tree (*Sciurus niger*, *Ctenomys azarae*, and *Ctenomys mendocinus*, respectively). Then, we estimated coefficients of phylogenetic linear regressions and the amount of variance explained by the model, using the package MCMCglmm in R. Inferences for each regression model were based on 500,000 samples, obtained after we discarded 100,000 samples as burn-in. In all models, default priors were used for “fixed” effects, while inverse Wishart priors with a scale parameter equal to half of the dependent variable variance (and 3 df) were used for “random” effects. A thinning interval of 200 was used for computing features of the posterior distribution. Convergence diagnostics and statistical and graphical analysis of Markov chain Monte Carlo sampling output were carried out with the CODA package (Plummer 2006) available in R. Finally, to estimate the significance of regression coefficients, we calculated the proportion of posterior estimates greater than 0 (gt0). In our case, gt0 can be viewed as the probability of observing a positive (if $gt0 > 0.5$) or negative (if $gt0 < 0.5$) association between the dependent variable (correlation coefficients) and the independent one (m_b). 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 0).

To test for the effect of potential confounding factors that could be affecting the relationship between BMR, m_b , and Tmean, we downloaded data on minimum and maximum temperature (Tmin and Tmax, respectively), temperature seasonality (TS), annual rainfall (Rain), rainfall variability (RS), and net primary productivity (NPP) for each species included in the data set (data set S1B in the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.8350667>; Naya et al. 2018). Climatic data were downloaded from WorldClim, while NPP data were downloaded from National Aeronautics and Space Administration Earth Observation program (<https://neo.sci.gsfc.nasa.gov/>). In addition, we obtained information on several biological variables, such as species trophic category (herbivorous, omnivorous, and carnivorous), kind of habitat (desert, xeric, mesic, freshwater, and wide-spread), substrate used (fossorial, burrowing and caves, terrestrial, trees, and aquatic), use of hypometabolic responses (daily torpor or hibernation), and occurrence in islands or mountains, for a subset of 428 species (from McNab 2008; data set S1C in the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.8350667>; Naya et al. 2018). Then, we ran three additional phylogenetic regression models: one model with geographic variables (absolute latitude, longitude, and latitude), climatic variables (see above), and NPP as covariates and two models with biological variables (because “diet” was coded in two different forms; data set S1C in the Dryad Data Repository: <http://dx.doi.org/10.5061/dryad.8350667>; Naya et al. 2018) as covariates. We report in the main text only the results obtained for the simplest model ($\log_{10}\text{BMR} \sim \log_{10}m_b \times \text{Tmean}$) because (1) the inclusion of

different covariates did not affect our main result, that is, the significant interaction between m_b and Tmean (tables A1–A3, available online), and (2) although some biological covariates had a significant effect on BMR, the model without covariates was, by far, more parsimonious than the two biological models, according to deviance information criterion values (tables A2, A3).

Results

We found that $\log_{10}m_b$ was positively correlated with $\log_{10}\text{BMR}$ ($r = 0.96$, $P < 1.0E - 34$; fig. 1, *top*), but it was not correlated with ambient temperature ($r = 0.05$, $P = .24$; fig. 1, *bottom*). The interaction term between m_b and Tmean in the phylogenetic regression model was highly significant, indicating that the effect of Tmean on residual BMR changes as a function of m_b (table 2). In line with this, phylogenetic regression models for the sliding windows indi-

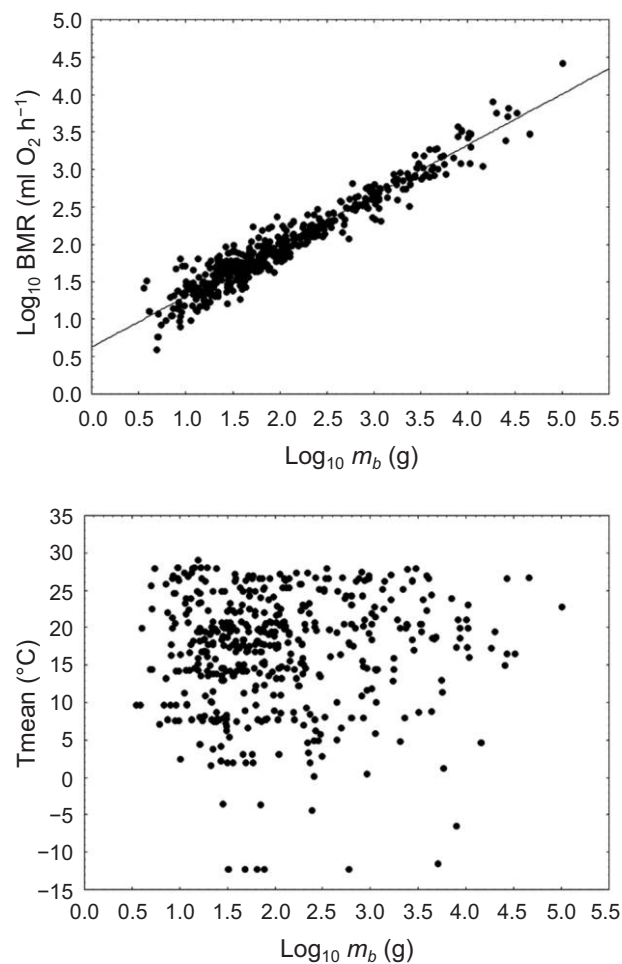


Figure 1: Relationships between $\log_{10}m_b$ (body mass) and $\log_{10}\text{BMR}$ (basal metabolic rate; *top*) and between $\log_{10}m_b$ and annual mean temperature (Tmean; *bottom*).

Table 2: Coefficient values, 95% confidence interval (CI), and proportion of posterior estimates greater than 0 (gt0) from a phylogenetic regression (linear model)

	Coefficient	95% CI	gt0
Intercept	.7300	.5016–.9292	>.9999
$\log_{10} m_b$.6192	.5808–.6635	>.9999
Annual mean temperature	-.0158	-.0205 to -.0112	.0001
Interaction	.0050	.0031–.0070	>.9999

Note: The model uses basal metabolic rate (BMR) as the dependent variable and body mass (m_b) and annual mean temperature (Tmean) as the independent variables ($\log_{10} \text{BMR} \sim \log_{10} m_b + \text{Tmean}$). A significant interaction term indicates that the effect of ambient temperature on residual BMR changes along the m_b axis. Model deviance information criterion value = -755.2. The proportion of variance accounted for by phylogeny, conditioned on the fixed effects, is 0.79 (median), with the highest posterior density 95% ranging between 0.72 and 0.85.

cate that the amount of residual variance in BMR explained by Tmean decreased with m_b , from 20%–30% at body sizes lower than 100 g to almost 0 at body sizes above 1,000 g (fig. 2). Finally, regression coefficients for Tmean were negative and highly significant ($gt0 < 0.001$) from the first m_b window (mean $m_b = 17.2$ g) to the sixth (mean $m_b = 166.3$ g), negative and significant ($gt0 < 0.05$) for the seventh and eighth windows (mean $m_b = 336.7$ and 603.3 g, respectively), and not significantly different from 0 thereafter (fig. 2).

Discussion

The main result arising from our analysis is that the effect of ambient temperature on residual BMR is evident for mammal species smaller than ~100 g, but it rapidly attenuates as m_b increases. For instance, a study including all the species in our data set will conclude that the effect of temperature on residual BMR is markedly and highly significant ($gt0 < 0.0001$, $n = 458$), while a study including only those species larger than 100 g will conclude that this effect is negligible and not significant ($gt0 = 0.14$, $n = 197$). It is important to note, however, that we are suggesting not a particular threshold value of m_b but a transition zone (located at about 100 g) from which the effect of temperature on residual BMR becomes less and less important. The fact that this zone of transition practically does not change with the model used to estimate residual BMR, or with the way in which species were pooled to estimate correlation coefficients (data not shown), strongly suggests that this pattern represents a real phenomenon (and not a statistical artifact), which deserves a biological explanation based on animal energetics (see below).

It would be reasonable, then, to ask what causes determine a change in the metabolic response to ambient temperature as m_b increases. To answer this question, it is important to revisit all the options that animals have to solve the thermoregulatory problem imposed by a fall in ambient

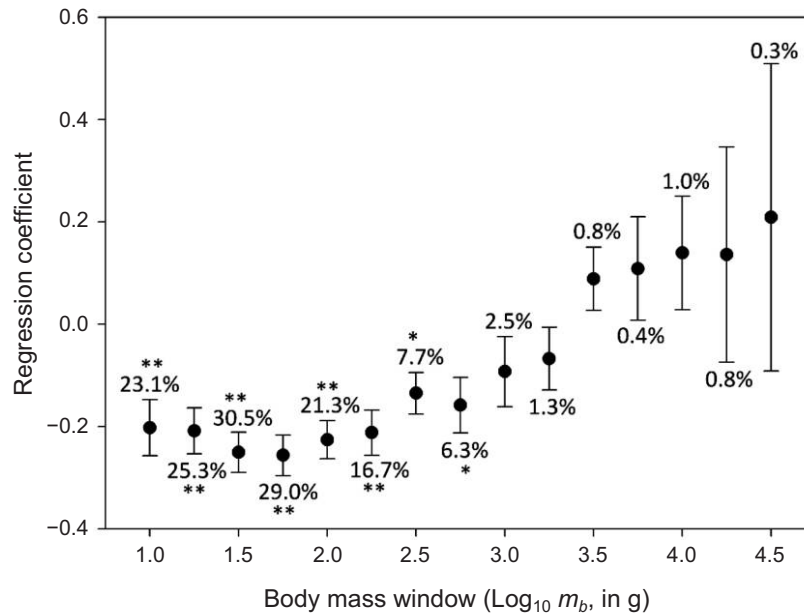


Figure 2: Regression coefficients between basal metabolic rate (BMR) and mean annual temperature (Tmean) for sliding windows of 1.00 \log_{10} units of body mass (m_b), obtained from phylogenetic regressions ($\log_{10} \text{BMR} \sim \log_{10} m_b + \text{Tmean}$). Error bars represent standard deviations. The amount of residual variance in BMR explained by Tmean is provided above (or below) each point. Double asterisks denote a $gt0$ (proportion of posterior estimates greater than 0) value lower than 0.001; a single asterisk denotes a $gt0$ value lower than 0.05.

temperature (i.e., to maintain a constant body temperature at a lower ambient temperature). In brief, as ambient temperature falls, animals can reduce their surface-to-volume ratio by increasing their general body size (the classical argument behind the Bergmann's [1847] Rule) and/or making size-independent adjustments in a range of morphological, physiological, and behavioral traits that affect their energy balance. These size-independent adjustments could be grouped, in turn, into three major categories: avoidance (or, at least, mitigation) of the thermal change, changes in the rate of heat loss, and changes in rate of heat production (McNab 2002a; Naya et al. 2016). Avoidance mechanisms include physiological adjustments, such as the use of torpor and the circulatory separation of core and shell temperatures by peripheral vasoconstriction, and also behavioral adjustments, such as the use of shelters and adjustments in daily activity patterns. Mechanisms that change the rate of heat loss include changes in body shape affecting body surface-to-volume ratio, changes in body color affecting body reflectance and thus the absorptivity of solar radiation, and changes in the subcutaneous fat layer and/or skin properties affecting thermal conductance. Finally, mechanisms that modify the mass-independent rate of heat production include behavioral adjustments, such as changes in activity levels sustained in nature, and also physiological adjustments, such

as changes in active heat production (via futile cycles and shivering), metabolic activities of some tissues, and the relative amount of metabolically active organs (e.g., heart, kidneys, brain, gut, and liver). Several of these mechanisms that allow animals to maintain energy balance at lower ambient temperatures are severely constrained by internal and ecological factors at lower body sizes. For example, adjustments of fur thickness, and thus in minimal thermal conductance, are limited by body size (Steudel et al. 1994; Naya et al. 2013b); body shape at smaller sizes is constrained by a high surface-to-volume ratio and the elevated energetic cost of endothermy (McNab 2002a); circulatory separation between core and shell temperatures is not possible in small species for thermodynamical reasons (Scholander 1955; McNab 2002b). In addition, fur color (Linnen and Hoekstra 2009) and activity levels (St-Pierre et al. 2006; Berger-Tal et al. 2010) have been linked to predation risk avoidance in several mammal species of small size, such that adjustments in these variables for thermoregulatory purposes are probably also restricted. Finally, daily activity patterns have been suggested to be constrained by some rigidity in the mechanisms driving photic cues (Roll et al. 2006). Therefore, internal and external restrictions affecting small species may mean that the basal rate of heat generation represents the most important mechanism to cope with changes in ambient temperature,

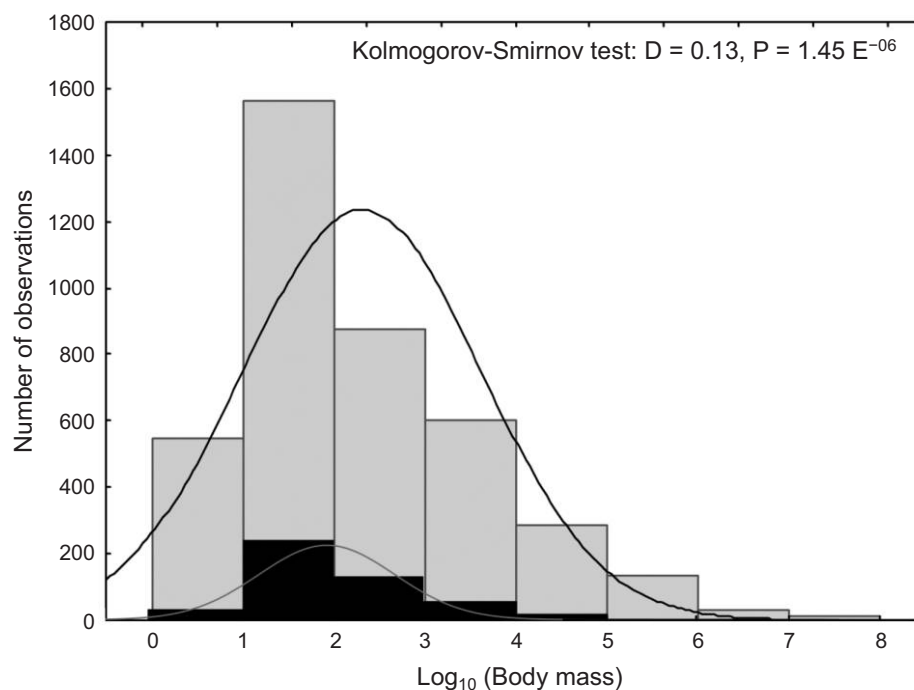


Figure 3: Body size distribution in our data set (black bars and black line) and for all extant mammal species (gray bars and dark gray line; taken from Smith et al. 2003). Note that larger species (e.g., >100 kg) are not included in our data set.

whereas other factors are relatively more important in large endotherms. Consequently, as is empirically demonstrated here, a stronger correlation between residual BMR and ambient temperature should be expected for smaller mammals than for larger ones.

To sum up, our current vision on the relevance of ambient temperature shaping the evolution of mass-independent variation in BMR (e.g., White et al. 2007; Jetz et al. 2008; Naya et al. 2013a; Luna et al. 2017) appears to be strongly biased by the great number of small species in nature, a bias that could be accentuated by logistical constraints in physiological data sets. Indeed, a comparison of species m_b distribution in our data set against the m_b distribution of all extant mammals indicates that there is a significant difference between the curves, reinforcing the idea that larger species (e.g., >100 kg) are underrepresented in the physiological data set (fig. 3). Obviously, this does not deny the relevance of ambient temperature for most of the extant endothermic species, but it argues for a pluralistic approach to explain the evolution of residual BMR. For instance, it could be possible that ambient temperature is the best predictor of residual BMR on the left side of the m_b distribution curve but that other factors (e.g., food availability) could be the best predictors on the right side of this curve. Further studies aimed at collecting more data on metabolic rates (in particular for larger species), as well as reanalyzing existing data sets, are very welcome if we wish to achieve a more comprehensive understanding of the evolution of animal energetics. In particular, evaluating whether the effect of ambient temperature on BMR changes along the m_b axis in birds (i.e., the other major endotherm clade) will be very relevant to understanding the generality of the pattern reported here.

Acknowledgments

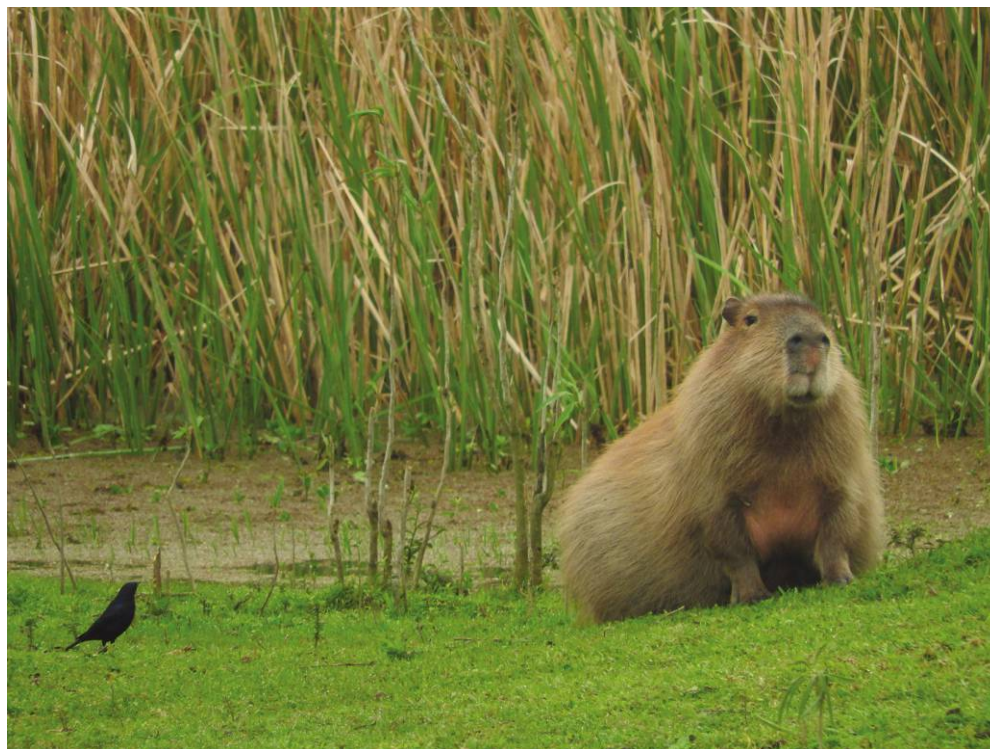
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The *carpincho* or capybara (*Hydrochoerus hydrochaeris*), one of the species analyzed in this study and the largest living rodent in the world. Photo: Daniel E. Naya.