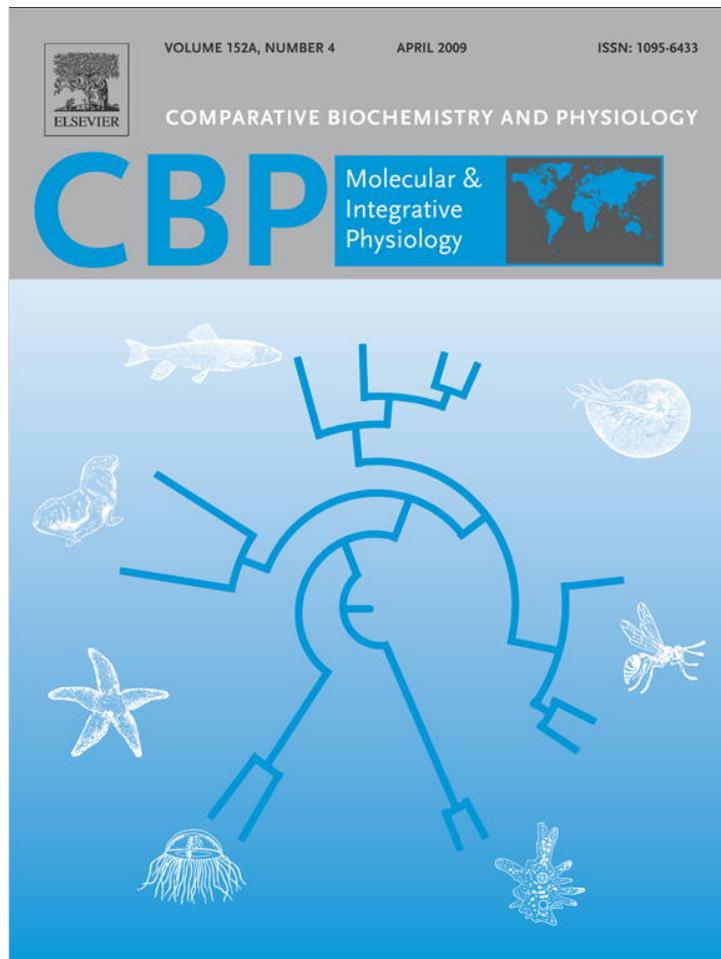


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Basal metabolism is correlated with habitat productivity among populations of degus (*Octodon degus*)

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ABSTRACT

Several competing hypotheses attempt to explain how environmental conditions affect mass-independent basal metabolic rate (BMR) in mammals. One of the most inclusive is the hypothesis that associates BMR with food habits, including habitat productivity. The effects of food habits have been widely investigated at the interspecific level, and variation between individuals and populations has been largely ignored. Intraspecific analysis of physiological traits has the potential to compensate for many pitfalls associated with interspecific analyses and serve as a useful approach for evaluating hypotheses regarding metabolic adaptation. Here we tested the effects of climatic variables (mean annual rainfall=PP, mean annual temperature= T_A), net primary productivity (NPP) and the de Martonne index (DMi) of aridity on mass-independent BMR among four populations of the caviomorph rodent *Octodon degus* along a geographic gradient in Chile. BMR was measured on animals maintained in a common garden acclimation set-up, thus kept under the same environment and diet quality for at least 6 months. Mass-independent BMR was significantly different among degu populations showing a large intraspecific spread in metabolic rates. A very large fraction of interpopulational variability in mass-independent BMR was explained by NPP, PP and DMi. Our results were conclusive about the effects of habitat productivity on setting the level of mass-independent BMR at the intraspecific–interpopulational level.

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1. Introduction

Fundamental to our understanding of physiological responses to different environments is the analysis of mechanisms that cause variation in physiological traits, and the ecological consequences of this variation at different hierarchical levels (Spicer and Gaston, 1999). Metabolic rates are associated with the tempo in which animals acquire and process energy to fuel their existence and therefore affect their fitness. Thus, since metabolic rates set the pace of life, the analysis of their variability in time and space is of vital importance to gain insight about metabolic evolutionary and ecological theories (Kooijman, 2000; Brown et al., 2004).

Among various metabolic measurements, basal metabolic rate (BMR) represents the minimum rate of energy necessary to maintain homeostasis and allostasis, and is by far the most widely measured energetic variable in endothermic vertebrates (McNab, 1992; Hulbert and Else, 2004; Speakman et al., 2004). BMR has been used as a standard to assess the: a) costs of different components of organism energy budgets, b) analyze species-specific variations in rates of energy expenditure during

maximal and sustained activities, c) evaluate scaling effects on rates of energy flux among species, and d) to understand physiological adaptations to the environment (McNab, 2002; van der Meer, 2006).

The dependence of metabolic rates on body mass (M_b) has long been recognized (Kleiber, 1961). Nevertheless, it is well known that M_b alone does not fully explain variation in BMR (McNab, 1992). There are several hypotheses that attempt to explain how biotic and abiotic conditions affect mass-independent BMR in mammals (McNab, 2002). One of the most comprehensive is the food habits hypothesis (FHH), which identifies three components of the diet that can establish variability into mass-independent BMR,—i.e. food quality, food availability, and food predictability or productivity (Cruz-Neto and Bozinovic, 2004). Specifically, the hypothesis predicts that species with diets of low energy content and/or low digestibility evolve low mass-independent BMRs (Cruz-Neto et al., 2001; McNab, 2002). Likewise, the evolution of a low mass-independent BMR is likely to occur in habitats where food availability is low and/or unpredictable (McNab, 2002; Cruz-Neto and Jones, 2005). Even though attractive, several problems have emerged from studies attempting to test the FHH. One main problem is associated with the taxonomic level of analysis. Studies carried out at the interspecific level assume that for any given species all traits are fixed and variation between individuals and/or populations is largely ignored (Bennett, 1987). The

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comparative approach is designed to yield insights into the macro-evolutionary factors responsible for the variability in BMR (Cruz-Neto and Jones, 2005). On the other hand, intraspecific analysis can complement these by giving insights into the proximate factors responsible for this variability and their underlying mechanisms and functional significance. However, interspecific tests of the FHH do not always corroborate the expected patterns, with results differing according to the experimental protocol used and/or with the specific component of the hypothesis being tested (Mueller and Diamond, 2001; Cruz-Neto and Bozinovic, 2004; Speakman et al., 2004). With the exception of some analyses where habitat productivity and/or predictability were directly assessed (Mueller and Diamond, 2001; Speakman et al., 2004; Bozinovic et al., 2007), the precise effects of two components, food availability and food predictability, cannot be separated due to confounding effects from other features of the habitat where the species has evolved (i.e., direct climate effects on food predictability).

Several interspecific studies have analyzed the effects of food availability and predictability on mass-independent BMR by demonstrating that mass-independent BMR is higher in species from mesic habitats when compared with xeric habitats (McNab, 2002; Lovegrove, 2000; Rezende et al., 2004). The effects of food quality have also been extended to a proximate level. For example, it has been hypothesized that within an individual's lifetime, an organism faced with a low quality diet can lower its BMR (Cork, 1994; Bozinovic et al., 2007). Cruz-Neto and Bozinovic (2004) reviewed intraspecific studies that have manipulated diet quality or used natural experiments in order to evaluate changes in BMR, and found mixed support for the FHH (Choshniak and Yahav, 1987; Bozinovic, 1995; Koteja, 1996; Geluso and Hayes, 1999; Rosen and Trites, 1999; Veloso and Bozinovic, 1993, 2000; Silva et al., 2004; Bozinovic et al., 2007). In particular, while intraspecific studies support predictions for changes in food quality and availability, phenotypic plasticity is always confounded by the potential of intraspecific variation in FHH as animals from geographically separated populations may be selected to endure different patterns of environmental variability (Hoffman and Blows, 1994). We investigated the effects of geographic variations in habitat on the BMR of individuals from different populations. We used as a study model the endemic Caviomorph rodent, *Octodon degus*, (Octodontidae; common name: degu; see Methods), in order to test whether the animals exhibit habitat-specific responses. BMRs were measured in lab acclimated animals, i.e. in a common garden experiment where animals endure identical abiotic conditions and diet.

Our main objective was to evaluate one component of the FHH, namely the habitat productivity (food availability and predictability) hypothesis by differentiating between the relative importance of present time and the long-term conditions where individuals originated in determining variability of mass-independent BMR. Because within-species variability can be high and this variability is the raw material upon which natural selection acts, we examined the FHH at the interpopulational (intraspecific) level testing if individuals from habitats with low productivity evolved low mass-independent BMR and vice versa.

2. Material and methods

2.1. Animals and habitats

We used adult males and non-reproductive adult females of the degu, *Octodon degus* (Rodentia: Octodontidae). This species is distributed from the Huasco valley (arid and semi arid habitats; 28°S) to South of Santiago (33°S, Mediterranean habitats). *O. degus* is a small, diurnal, herbivorous rodent that feeds on plant tissue (over 70% of diet) and seeds (Silva, 2005). Animals from different populations comprising entire distribution of the species were captured from May to December 2007, using Sherman live traps. We captured a total of 36 animals (12 males and 24 females). All individuals were ear tagged.

Table 1

Localities of capture, net primary productivity (NPP), de Martonne index (DMi), mean annual rainfall (PP), and mean annual temperature (T_A) among different localities of capture in north-central Chile

	Huasco	Aucó	Ocoa	San Felipe
Coordinates	28.5°S;71.2°W	31.5°S;71.1°W	32.9°S;71.1°W	32.8°S;70.7°W
Habitat description	Costal desert shrubland	Semiarid shrubland	Mediterranean palm-dominated shrublands	Mediterranean montane shrubland
NPP ($\text{g C m}^{-2} \text{y}^{-1}$)	170.0±40.0	290.0±15.0	410.0±18.0	550.0±25.0
DMi	0.80	6.89	11.89	12.17
PP (mm)	20.9	170.0	283.0	310.0
T_A (°C)	16.0	14.7	13.8	15.5

Values are mean±SD.

Animals from all populations were transported to animals facilities and maintained for at least 6 months under common garden acclimation conditions, that is, commercial rabbit food pellet and water *ad libitum*, ambient temperature of 20 ± 3 °C and a photoperiod LD=12:12. The period of capture for each population ranged from one to 3 months. After this acclimation period, BMR was measured (see below).

We obtained estimates of monthly Net Primary Productivity (NPP, $\text{g C m}^{-2} \text{y}^{-1}$) for each habitat (see Table 1) from the Moderate Resolution Imaging Spectroradiometer (MODIS) for January to December 2007 from NASA Land-Process Distributed Active Archive Centers. MODIS estimates of NPP were available at a nominal resolution of $0.1^\circ \times 0.1^\circ$, and from processed images we collected NPP time series at the pixel closest to the location of the field populations where animals were obtained and calculated net NPP as the long-term mean at each site. We also estimated the De Martonne's aridity index (DMi) for each habitat as a second habitat quality estimator. This index is the ratio between mean annual precipitations (PP) and means annual temperature (T_A °C) plus 10 °C as follows:

$$\text{DMi} = (\text{PP}/T_A + 10)$$

A low DMi means a low degree of moisture and a high index means a high degree of moisture, or excessive humidity. Hence, a $\text{DMi} < 20$ corresponds to a Mediterranean habitat; while $\text{DMi} < 10$ is a "desert-like" or a semiarid grassland-cover plain, and finally a $\text{DMi} < 5$, corresponds to extreme aridity or desert (Oury, 1965; Ahmed, 1997; Cavieres and Sabat, 2008). Climatic data were obtained from (<http://www.worldclimate.com>) and diCasteri and Hajek (1976).

2.2. Metabolic measurements

Following acclimation, BMR was measured as the rate oxygen consumption by a computerized open-flow respirometry system (Sable Systems, Henderson, NV). Post-absorptive animals were maintained in plexiglass metabolic chambers (1000 mL) at 30.0 ± 0.5 °C which is within the thermoneutral zone of this species (Veloso and Bozinovic, 1993; Bozinovic, 1992, 1995; Bozinovic et al., 2004). The metabolic chamber received dried air at a rate of 900 mL/min, from mass flow controllers (Sierra Instruments, Monterey, CA, USA), which is enough to ensure adequate mixing in the chamber. Air passed through CO_2 -absorbent granules of Baralyme and H_2O -absorbent granules of Drierite both before and after passing through the chamber and was sampled every 5 s by an upgraded Applied Electrochemistry O_2 -analyzer, model S-3A/I (Ametek, Pittsburgh, PA, USA). Oxygen consumption values were calculated using Expedata[®] data acquisition and analysis program (<http://www.sablesys.com>). Body mass (M_b) was measured prior to metabolic measurements using an electronic balance (± 0.1 g), and colonic body temperature (T_b) was recorded at the end of each measurement using a Digi-Sense copper-constantan thermocouple. Basal metabolic rate was estimated as the lowest steady state period of 3 min, recorded during VO_2 measurements (ca. 2–3 h).

Table 2
Number of individuals studied at each locality, body mass and mass-independent basal metabolic rate of *Octodon degus* from four different habitats in north-central Chile

	Huasco	Aucó	Ocoa	San Felipe	F	P
Number of individuals	10	10	6	10		
Body mass (g)	148.6±24 ^{ab}	138.4±14.4 ^a	178.2±35.3 ^{bc}	182.2±22.7 ^{bc}	4.34	0.04
BMR (mL O ₂ min ⁻¹)	1.92±0.09 ^a (1.91±0.09)	2.18±0.1 ^a (2.17±0.1)	2.45±0.12 ^b (2.45±0.12)	2.56±0.1 ^b (2.55±0.1)	6.98	0.001

Values are mean±SD, similar letters indicate non-significantly differences after an *a posteriori* Tukey test at P=0.05. In parenthesis the least-square means of basal metabolic rate.

2.3. Statistical analysis

Statistical analyses were performed using the Statistica® (StatSoft, 2001) statistical package for the Windows operating system. We performed Pearson product-moment correlations with mass-independent BMR as the dependent variable, and NPP, DMi, PP and T_A as independent variables. Because BMR scales with M_b (Kleiber, 1961) and we found significant differences in M_b among populations (see results) we analyzed BMR by ANCOVA with M_b as covariate. Consequently, all correlation analyses among BMR and environmental variables were conducted using least square-means which is mass-independent BMR (Sokal and Rohlf, 1997). Prior to analyses we tested assumptions of normality and homogeneity of variance test using Shapiro–Wilks W and Levene's tests. An *a posteriori* Tu-

key test was used for multiple comparisons. Results are reported as means±1 SD.

3. Results

Strong climatic differences were observed in PP, which ranged over an order of magnitude, and contrasting plant communities (Table 1). Productivity values estimated from each locality also described contrasting habitats with a steep geographic gradient showing a 3-fold variation over the ~400 km separating the study sites (Table 1).

Body mass of degus differ significantly among populations (one-way ANOVA F_{3,35}=7.49, P<0.001, Table 2). Also, ANCOVA using M_b as a covariate, indicated that mass-independent BMR was significantly different among habitats (F_{3,35}=6.98, P=0.001). Significant and positive correlations between mass-independent BMR and NPP (r²=0.95, P=0.004, Fig. 1a) and between mass-independent BMR and DMi (r²=0.97, P=0.02, Fig. 1b) were found. Also a significant relationships between mass-independent BMR and PP (r²=0.98, P=0.01, Fig. 1c) was observed. Interestingly, no significant relation as observed between mass-independent BMR and T_A (r²=0.22, P=0.52, Fig. 1d).

4. Discussion

Levels of metabolic expenditure in animals are influenced by intrinsic factors, such as body mass, phylogenetic relatedness and activity, ecological factors such as biotic and abiotic habitat conditions, and food habits among others (McNab, 2002). For example, Mueller and Diamond (2001), using a common garden acclimation experiment

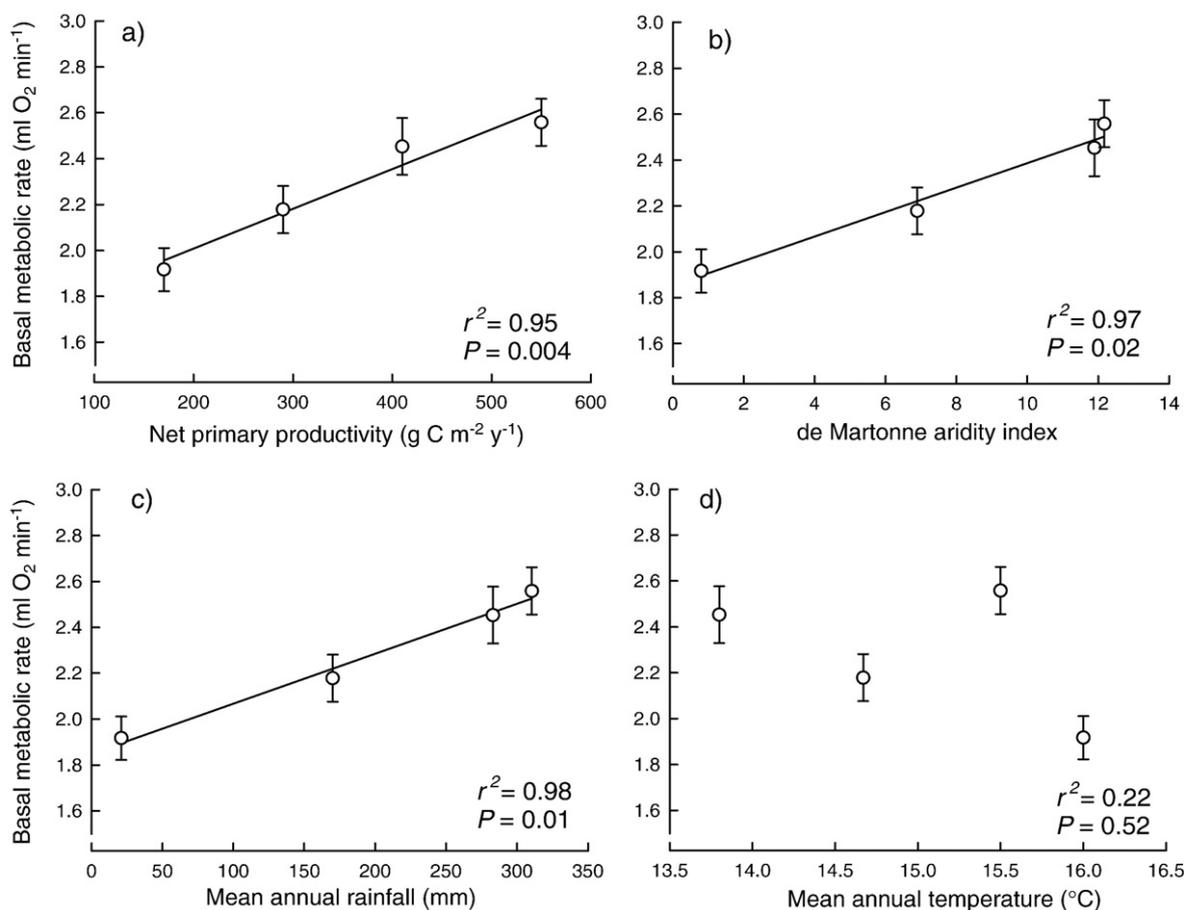


Fig. 1. Relationship between mass-independent basal metabolic rate (BMR) of *Octodon degus* and a) Net primary productivity; b) de Martonne index of aridity, c) mean annual rainfall and d) mean annual temperature at each habitat. The correlation coefficients and their associated significance are indicated on each graph. Each point represents mean BMR±SD of each population. See Table 2 for sample sizes.

found that high-BMR rodent species from high-productivity environments were more active than were low-BMR species from low-productivity habitats, and concluded that BMR is driven by NPP and, hence, food availability, rather than temporal variability in productivity (see also Lovegrove, 2000; Tieleman et al., 2003a,b; Rezende et al., 2004; Muñoz-García and Williams, 2005). At the species level, much of the observed variability in BMR can be directly ascribed to differences in habitat productivity, rather than a direct effect of climate per se. Because their interspecific approaches, those studies in general have focused into the ultimate (i.e. evolutionary) rather than proximate (i.e. ecological–physiological) factors responsible for differences in the rate at which energy is acquired processed and expended. Indeed, the FHH can be explained both by distal and proximal approaches. At the intraspecific–intrapopulational level, in a seasonal study, Bozinovic et al. (2007) demonstrated that when diet quality and availability are analyzed in tandem, habitat productivity emerged as responsible for variations in mass-independent BMR whereas diet quality had no effect on this variable.

To test the FHH, here we followed a mixed approach by studying the same species by examining subjects from populations from different habitats. The broad range of climatic and ecological scenarios that we used comprised a large fraction of the geographic range of distribution of *O. degus*, thus maximizing the range of intraspecific variation that we expected to observe. Our analysis supports the assertion that food productivity indeed affects mass-independent BMR even at a local scale. A pointed out before, interspecific studies have implicitly supported the effects of food availability and predictability on mass-independent BMR (McNab, 2002; Lovegrove, 2000; Rezende et al., 2004). Underlying these analyses was the assumption that climatic variability directly reflects food availability and predictability. Our results show that the mass-independent BMR of degus is lower in habitats with low NPP and PP and it varies positively with PP and NPP. This result supports the prediction that mass-independent BMR is positively correlated with productivity in small rodents, mainly food availability (Mueller and Diamond, 2001). Also, we found that acclimation to temperature could not explain the variability in BMR between degu populations. Thus, a large fraction of the observed variability in BMR can be directly ascribed to differences in NPP, rather than to a direct effect of temperature per se (see also Tieleman et al., 2003a,b). Nevertheless, since we did not observed major differences in T_A among habitats, it seems that a different animal model, with a larger range of distribution, should be used to better test the direct effect of T_A on BMR. Nevertheless a note of caution is necessary since there is always a problem concerning the inability to control for environmental seasonality as well as developmental and parental effects on BMR in free-ranging animals. In essence, there is no way of controlling for these effects other than making the measurements in F1 generation animals that have been raised under identical conditions and which were swapped randomly between parents at birth.

In summary, we found conclusive evidence of NPP effects on mass-independent BMR at the intraspecific–interpopulational level of analysis. Individuals of the same species originating from more productive habitats, run their metabolic rates “faster” in comparison to “slower” individuals from less productive habitats, even though all individuals from all populations were maintained under the same experimental conditions for several months. Here we have shown that a large physiological diversity in receptiveness to different environmental conditions is observed between individuals from different populations, thus providing insights into the evolution of proximal metabolic capacities. We propose that future studies on the fast–slow metabolic continuum hypothesis proposed for small mammalian species by Lovegrove (2003) should be tested among populations. Indeed, and mimicking Lovegrove’s hypothesis at the intraspecific level, we hypothesized that individuals with higher mass-independent BMRs and from high NPP habitats, thus on the “fast” end of the continuum, will mature earlier, show higher reproductive rates and shorter generation

times in comparison to individuals at the “slow” end of the continuum from low NPP habitats and low mass-independent BMR’s.

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