

CLIMATIC ADAPTATION AND THE EVOLUTION OF BASAL AND MAXIMUM RATES OF METABOLISM IN RODENTS

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Abstract.—Metabolic rate is a key aspect of organismal biology and the identification of selective factors that have led to species differences is a major goal of evolutionary physiology. We tested whether environmental characteristics and/or diet were significant predictors of interspecific variation in rodent metabolic rates. Mass-specific basal metabolic rates (BMR) and maximum metabolic rates (MMR, measured during cold exposure in a He-O₂ atmosphere) were compiled from the literature. Maximum (*T*_{max}) and minimum (*T*_{min}) annual mean temperatures, latitude, altitude, and precipitation were obtained from field stations close to the capture sites reported for each population (*N* = 57). Diet and all continuous-valued traits showed statistically significant phylogenetic signal, with the exception of mass-corrected MMR and altitude. Therefore, results of phylogenetic analyses are emphasized. Body mass was not correlated with absolute latitude, but was positively correlated with precipitation in analyses with phylogenetically independent contrasts. Conventional multiple regressions that included body mass indicated that *T*_{max} (best), *T*_{min}, latitude, and diet were significant additional predictors of BMR. However, phylogenetic analyses indicated that latitude was the only significant predictor of mass-adjusted BMR (positive partial regression coefficient, one-tailed *P* = 0.0465). Conventional analyses indicated that *T*_{max}, *T*_{min} (best), and altitude explained significant amounts of the variation in mass-adjusted MMR. With body mass and *T*_{min} in the model, no additional variables were significant predictors. Phylogenetic contrasts yielded similar results. Both conventional and phylogenetic analyses indicated a highly significant positive correlation between residual BMR and MMR (as has also been reported for birds), which is consistent with a key assumption of the aerobic capacity model for the evolution of vertebrate energetics (assuming that MMR and exercise-induced maximal oxygen consumption are positively functionally related). Our results support the hypothesis that variation in environmental factors leads to variation in the selective regime for metabolic rates of rodents. However, the causes of a positive association between BMR and latitude remain obscure. Moreover, an important area for future research will be experiments in all taxa are raised under common conditions to allow definitive tests of climatic adaptation in endotherm metabolic rates and to elucidate the extent of adaptive phenotypic plasticity.

Key words.—Bergmann's rule, body size, comparative method, diet, endothermy, energetics, temperature.

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Identification of the selective factors that have led to interspecific diversification in metabolic rates has been a major goal of ecological and evolutionary physiology (Garland and Carter 1994; Spicer and Gaston 1999; Walters and Reich 2000; McNab 2002). The most common approach is to correlate species or population differences in metabolic rate with variation in various biotic (e.g., diet) or abiotic (e.g., altitude, latitude, ambient temperature) factors. Mammals have been the most common subjects of such studies, and significant correlations are generally taken as evidence of metabolic adaptation in the genetic, evolutionary sense, although a variety of caveats apply (see Discussion).

Basal metabolic rate (BMR) is the usual estimate of the metabolic floor in mammals. It is generally measured as the rate of oxygen uptake during the inactive part of the 24-h cycle, of a postabsorptive, nonactive, reproductively adult individual (but not in reproductive condition), at an air temperature within its thermal neutral zone (McNab 1988). Since Kleiber (1932), the main factor identified as explaining interspecific variation in BMR has been variation in body mass. Given a large enough body-size range, larger-bodied species have lower mass-specific BMR, although the precise allometric scaling exponent is controversial for a variety of reasons (e.g., Symonds and Elgar 2002; White and Seymour 2003). Clades differences in the elevations of allometric re-

lations (i.e., grade shifts) have been identified by conventional analysis of covariance (ANCOVA), and clade-specific allometric equations have been developed (e.g., MacMillen and Nelson 1969; Dawson and Hulbert 1970; Haysen and Lacy 1985; McNab 1988, 2002; MacMillen and Garland 1989; Koteja and Weiner 1993). However, to our knowledge the clade differences have not been demonstrated with phylogenetically based statistical analyses (e.g., see Garland et al. 1993; Cruz-Neto et al. 2001; with respect to avian metabolic rates, see Garland and Ives 2000; Rezende et al. 2002).

Aside from possible clade differences, several studies have attempted to explain the residual variation in BMR (i.e., after correlations with body size have been controlled statistically) by associations with various biotic or abiotic factors (for reviews, see Leonard et al. 2002; McNab 2002). Interspecific comparisons of mammalian BMR have reported a significant association with diet using conventional statistics (McNab 1992, 2002, 2003), but not with phylogenetically based methods (Degen et al. 1998; Speakman 2000; Cruz-Neto et al. 2001; Genoud 2002). Environmental productivity (as an index of food availability) has also been suggested to influence BMR (Hayes 1989; Mueller and Diamond 2001; White 2003), and a significant positive correlation between mass-independent BMR and net primary productivity was reported for a comparison of five species of *Peromyscus* mice (Mueller and

Diamond 2001, phylogenetic analysis). Comparative studies of small mammals have also reported significant associations between habitat aridity and BMR—that is, species from (hot) deserts have lower BMRs than their counterparts from mesic environments—employing conventional (McNab 1979; Goyal and Gosh 1983; Hulbert et al. 1985) and phylogenetic (Degen et al. 1998) analyses. A significant negative correlation between mean environmental temperatures and mass-independent BMR has also been reported (MacMillen and Garland 1989, nonphylogenetic; Lovegrove 2003, phylogenetic). Mass-corrected BMR was also positively associated with latitude in rodents (MacMillen and Garland 1989; Speakman 2000, both nonphylogenetic; Lovegrove 2003) and birds (Weathers 1979; Ellis 1985, nonphylogenetic), although effects of temperature were not controlled except in MacMillen and Garland (1989; see Discussion).

Maximum metabolic rate (MMR) is typically measured as the highest rate of oxygen consumption in response to cold challenge (often termed summit metabolism) or forced exercise (VO_2max). Although exercise-induced VO_2max can, in principle, be obtained from terrestrial mammals of virtually any size (Seeherman et al. 1981), measurement of cold-induced MMR is typically only attempted with endotherms smaller than about 2 kg (Hinds et al. 1993; but see Fournier and Thomas 1999), especially when the He-O₂ technique is used (see Methods). To our knowledge, only two comparative studies of residual variation in MMR have been published (Bozinovic and Rosenmann 1989; Sparti 1992; see also Taylor 1998).

One limitation of all of the above-mentioned studies is that they have tested for biotic or abiotic correlates of a single measure of metabolic rate. This may be misleading because if the focal trait (e.g., BMR) is genetically correlated with another trait (e.g., MMR), then any correlation observed for the former could actually be the result of selection that has acted on the latter (Lande and Arnold 1983). Indeed, a positive correlation between BMR and MMR is a key assumption of the aerobic capacity model for the evolution of endothermy (Bennett and Ruben 1979; Hayes and Garland 1995; see Discussion). Moreover, the selective factors that act on BMR and MMR are likely to differ. For example, although various authors have suggested that lower BMR would be expected to evolve in hot, arid, low productivity, and/or unpredictable habitats, and often found empirical support for such hypotheses (see above and Discussion), we are not aware of predictions regarding MMR in such habitats.

The purpose of this study was to test for correlations of both BMR and MMR with (1) diet and (2) the climatic and geographic factors of maximum and minimum temperature, precipitation, latitude, and altitude. We also test for a correlation between BMR and MMR. We restricted analyses to rodents to avoid the possibility of comparing “apples and oranges,” for example, if we had included shrews. The point here is that distantly related organisms may differ in many features that have little or nothing to do with the putatively direct association between the independent and dependent variables of interest, and these differences constitute confounding variables (Huey and Bennett 1990; Garland and Adolph 1994; Garland 2001; Rezende and Garland 2003). Several other comparative metabolic studies of mammals

have similarly restricted themselves to particular lineages (e.g., MacMillen and Garland 1989, *Peromyscus*; Hinds and Rice-Warner 1992, rodents; Degen et al. 1998, rodents; Sparti 1992, shrews; Taylor 1998, shrews; Symonds 1999, Insectivora). We discuss our results in the context of geographical distribution and the aerobic capacity model of vertebrate energetics. In addition, we test whether body mass itself is associated with environmental variables or diet. This is important because the most obvious way that selection can alter overall energy budgets is through modification of the size of an organism (Schmidt-Nielsen 1995; Brown and West 2000; McNab 2002, and references therein).

METHODS

Metabolic and Environmental Data

Because BMR has been extensively studied in mammals (e.g., McNab 1988; Lovegrove 2000), our search focused on MMR and was restricted to studies that used cold exposure in a He-O₂ atmosphere to elicit MMR (Rosenmann and Morrison 1974), to avoid potential problems arising from different experimental procedures. We used studies that (1) included both BMR and MMR, measured in the same population and, when possible, in the same individuals; (2) involved animals captured in the field, or were maintained for only a few generations in the laboratory (*Baiomys taylori*, one or two generations in the lab, M. Rosenmann, pers. comm.; *Liomys salvini*, individuals were maintained 12 months in captivity, Hulbert et al. 1985); and (3) reported original collecting sites. Given these criteria, the following species were not included in the analyses, even though their MMR in He-O₂ is available in the literature: *Apodemus sylvaticus* (Hoppeler et al. 1984), *Mesocricetus auratus* (Werner 1992), and *Rattus norvegicus* (Rosenmann and Morrison 1974; Hinds et al. 1993). Values of MMR for porcupines *Erethizon dorsatum* (Fournier and Thomas 1999) were not included because their body mass (5.6 to 6.6 kg) is far beyond the range of the other species (see Appendix online at <http://dx.doi.org/10.1554/03-499.1.s1>), and all individuals measured were winter-acclimatized (see below).

Values of MMR and BMR were recalculated in some cases where the original values of one of the traits was not cited, but traits such as aerobic scope, either the difference or the ratio between MMR and BMR, depending on the study (i.e., Rosenmann and Morrison 1974), were reported, or in cases where metabolic values were given in different units. In acclimatization studies where more than one value of body mass, MMR, and BMR were available, we selected those values that were obtained in seasons other than winter. In addition, one acclimation study was also considered in this review (*Spalacopus cyanus*, Appendix), because the high acclimation temperature employed by these authors closely matches the range of temperatures that this species faces in the field during summer (Begall and Gallardo 2000; Nespolo et al. 2001). Although it would be preferable to control statistically the effects of seasonality in the analyses, such an approach is virtually impossible because some studies did not specify when animals were actually captured and measured (thus we assumed that measurements were not performed during winter).

Although sex differences in metabolism has been documented in some species of rodents (e.g., Scelza and Knoll 1979; Cygan 1985), we could not assess the possible effects of sex because no study in our database reported separate values of MMR and BMR by sex, and few cited the number of males and females used. However, because several different methods have been employed to estimate the minimal metabolism under thermoneutral conditions, we defined BMR as those values obtained from postabsorptive individuals measured in their resting phase for more than three hours. If these requirements were not fulfilled or measurement conditions were unclear in the original studies, then values were considered as resting metabolic rates (RMR), and this distinction was considered in all analyses by use of a 0–1 dummy variable. Each species was also classified into one of three broad diet categories: herbivore, granivore, and omnivore (Degen et al. 1998).

Data on average ambient temperatures, precipitation, altitude, and latitude (see Appendix online) were collected from climatic summaries for the weather station nearest to the collecting locality of each species, from the following sources: Agroclimatological Data for Latin America and the Caribbean (1985), National Climate Data Center (NCDC, <http://lwf.ncdc.noaa.gov/oa/climate/online/ccd/maxtemp.html>, and <http://lwf.ncdc.noaa.gov/oa/climate/online/ccd/mintemp.html>); California Climate Summaries (<http://www.wrcc.dri.edu/summary/climsma.html>); and Pearce and Smith (1984). However, if the altitudes from the collecting sites (when available) and from the stations were considerably different, we obtained the environmental data from a second station near to the collecting site as well, but with a closer altitude value. Normal daily maximum (T_{max}) and minimum temperatures (T_{min}) are the arithmetical average of the maximum and minimum mean temperatures, or the true average temperature based on several temperature observations per day made at representative hours, within a period of not less than 18 years. When climatic data were listed on a monthly basis (e.g., Pearce and Smith 1984), mean maximum and minimum annual temperatures were calculated as the arithmetic averages of all months, whereas mean annual precipitation was calculated as the sum of monthly average values.

Rodent Phylogeny

Our phylogeny (Fig. 1) was derived from the tree described in Lovegrove (2000). Additional literature was used to build the trees within genera *Dipodomys* (Stock 1974) and *Peromyscus* (Stangl and Baker 1984), whereas the tree from Octodontidae was obtained from Gallardo and Kirsch (2001). *Spermophilus beldingi* was placed at the base of the tree following Adkins et al. (2001). *Ellobius talpinus* was included in the phylogeny following Mezhzherin et al. (1995), *Chinchilla lanigera* and *C. brevicaudata* according to the trees in Hugot (2002), whereas *Chroecomys olivaceus* (described in previous studies as either *Akodon olivaceus* or *Abrothrix olivaceus*, and recently classified as *Chroecomys*; Nowak 1999) was incorporated taxonomically.

Additional data from different populations of the same species (e.g., *P. maniculatus*; Appendix) were included as polytomies in the phylogenetic tree (Fig. 1). A conservative

approach when testing hypotheses with independent contrasts with an incomplete phylogeny involves subtracting one degree of freedom for each unresolved branch (Purvis and Garland 1993; Garland and Díaz-Uriarte 1999). This procedure had no qualitative effects on any of our results, thus, for simplicity, we report probability values obtained considering the total degrees of freedom as if the tree had no soft polytomies.

Because “real” branch lengths were not available for the entire phylogeny, three different types of arbitrary branch lengths were considered: all = 1 (constant), Grafen (1989), and Pagel (1992). Statistical adequacy of these was then compared by computing the correlation between absolute values of standardized phylogenetically independent contrasts (Felsenstein 1985) and their standard deviation for all continuous-valued traits (Garland et al. 1992).

Statistical Analyses

Because some of the traits exhibited no statistically significant phylogenetic signal (see Results), we used both conventional statistics and their equivalent with phylogenetically independent contrasts. Independent contrasts were calculated for all variables described above by use of the PDTREE program (Garland et al. 1992; Garland and Díaz-Uriarte 1999; Garland and Ives 2000). (The use of contrasts for environmental variables, which are not inherited in the conventional sense, has been discussed by Garland et al. [1992].) Allometric equations were estimated by least-squares linear regression (95% confidence intervals for the intercepts with independent contrasts were obtained from PDTREE as described in Garland and Ives [2000]). We used multiple regression to test effects of environmental variables and diet on metabolic traits. Because most of the hypotheses and previous evidence regarding environmental predictors focus on temperature as an important factor, we favored models that included temperature (if statistically significant) when building multiple regression models. In addition, because T_{max} and T_{min} were highly correlated (see Results), which can cause problems in estimation and significance testing, we performed separate multiple regression analyses with these variables.

Data for BMR, MMR, and body mass were \log_{10} -transformed prior to all analyses, and we refer to the \log_{10} -transformed data simply as BMR, MMR, and body mass in the following sections. No transformation was performed on temperature, precipitation, absolute latitude, or altitude. To estimate the effect of diet and to control for differences in methods used to measure BMR (see Methods), dummy variables were used. The main effect of diet (three categories) was tested by the partial F for both dummy variables together in the model (granivores were arbitrarily considered as the base group, with 0–1 variables for herbivores and omnivores). For the BMR–RMR dummy variable (0 = BMR, 1 = RMR), independent contrasts were calculated after collapsing the phylogeny to a star with contemporaneous tips. This was done because the methodological distinction is not a biological variable that is inherited; thus, it should not be analyzed on a phylogenetic tree (Wolf et al. 1998; Perry and Garland 2002).

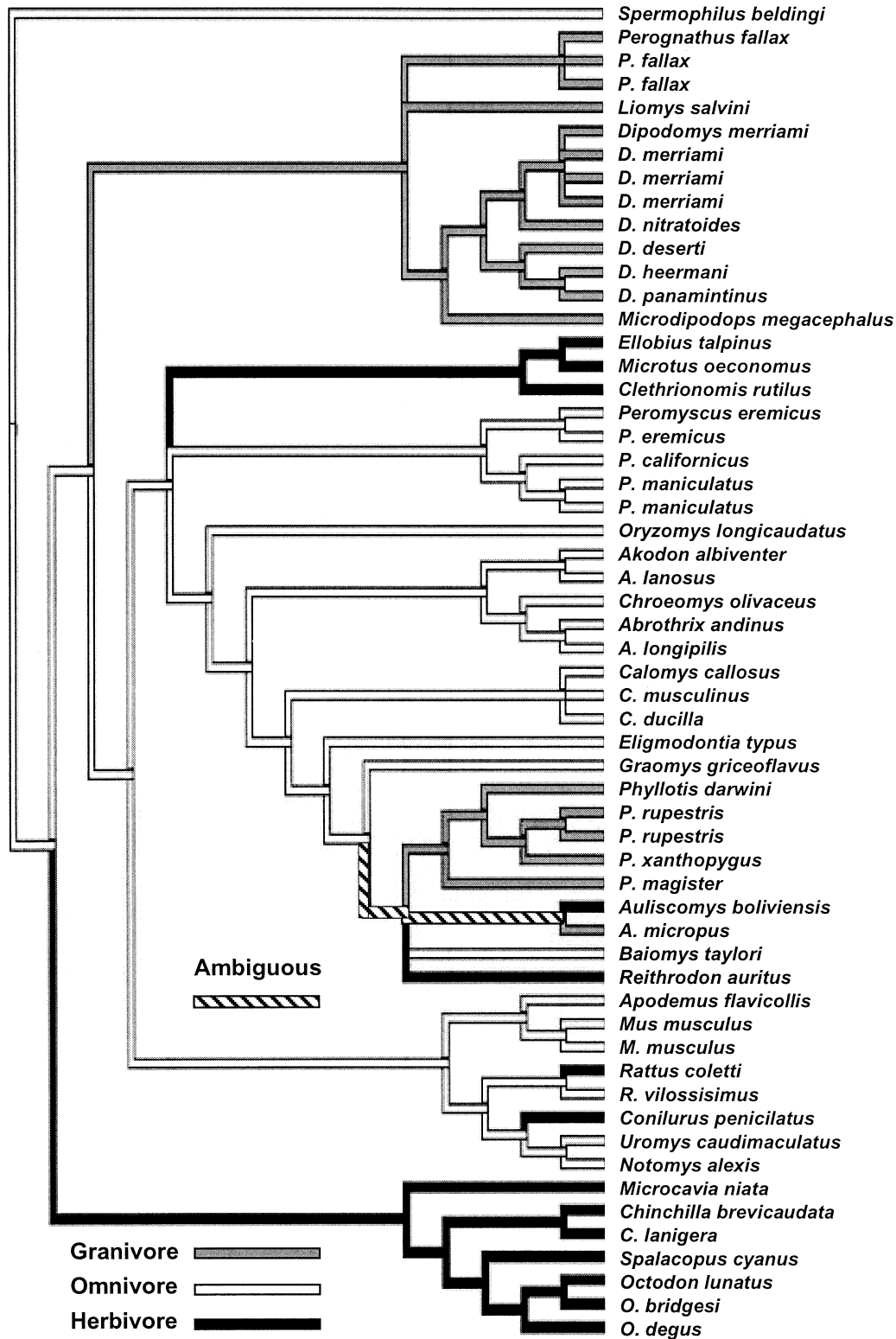


FIG. 1. Topology used for the analysis of independent contrasts performed in this study. Branch lengths are Pagel's (1992) arbitrary; see text for explanation of actual branch lengths used for analyses. Also indicated is unordered maximum parsimony reconstruction of diet evolution. Randomization tests indicate that diet exhibits highly significant phylogenetic signal (see text).

TABLE 1. Tests for adequacy of branch lengths (set equal to unity) for computing phylogenetically independent contrasts (correlations [not through origin] between absolute values of standardized contrasts and their standard deviations: Garland et al. 1992) and for presence of phylogenetic signal (P -value for randomization test and K statistic indicating amount of signal were computed as described in Blomberg et al. 2003, using the program PHYSIG.M). $N = 57$ tips, so 56 contrasts and 54 df for diagnostic r_p [not through origin]; 2-tailed critical value = 0.263 for $P = 0.05$; * indicates $P < 0.05$.

	Diagnostic r_p	Phylogenetic signal P -value	K
log Body Mass for BMR	0.092	<0.001	1.448
log BMR (mlO ₂ /gh)	0.059	<0.001	1.108
log Mass-corrected BMR	-0.089	<0.001	0.347
log Body Mass for MMR	0.092	<0.001	1.499
log MMR (mlO ₂ /gh)	-0.085	<0.001	0.535
log Mass-corrected MMR	-0.106	0.103	0.406
Tmax	-0.140	<0.001	0.383
Tmin	-0.224	0.001	0.371
Latitude	-0.064	<0.001	1.048
Altitude	-0.227	0.784	0.229
Precipitation	-0.290*	0.148	0.288
Precipitation with Pagel (1992) branch lengths	-0.181	0.006	0.289

To analyze the relation between mass-independent BMR and MMR, we first calculated residuals from least-squares linear regressions in both the conventional way and with phylogenetically independent contrasts (through the origin). These residuals were then correlated (through the origin for contrasts: Garland et al. 1992).

Whether conventional or phylogenetically informed analyses are most appropriate for the analysis of comparative data can be approached by testing for phylogenetic signal, or the tendency of related species to resemble each other (recent reviews in Blomberg and Garland 2002; Freckleton et al. 2002). The presence of phylogenetic signal in the continuous-valued traits was tested with the randomization procedure of Blomberg et al. (2003), using the MatLab program PHYSIG.M. For latitude, raw values rather than absolute values were analyzed. For BMR and MMR, body size-corrected data were computed as in Blomberg et al. (2003), which is the same as using "residuals" in the RSD files output from PDTREE (these trees had branch lengths set equal to unity; see Results). As an additional test, we used the PHYSIGOU.M and PHYOH0d.M programs (Blomberg et al. 2003) to estimate the optimal branch length transformation parameter (d) under the Ornstein-Uhlenbeck (OU) model of character evolution and to determine whether it differed significantly from either zero (which implies a star phylogeny) or unity (which implies the original candidate tree). This is similar to the procedure proposed by Freckleton et al. (2002), although their transformation is not based on a specific model of evolution and they use likelihood-ratio tests rather than randomization tests.

To indicate the amount of phylogenetic signal present in the continuous-valued traits, we used the K -statistic of Blomberg et al. (2003). A K of one indicates that a trait has exactly the amount of signal expected under Brownian motion evolution along the specified topology and branch lengths, whereas values less than one indicate less signal than expected, and values greater than one indicate more. For a survey of K -values of different types of traits, see Blomberg et al. (2003).

For diet, we used unordered maximum-parsimony reconstructions and randomizations of the diet character across the

tips of the tree (see Maddison and Slatkin 1991) to test for phylogenetic signal. Branch lengths are assumed to be equal in length by such computations, which were implemented in Mesquite (Maddison and Maddison 2004).

RESULTS

Branch-Length Diagnostics and Phylogenetic Signal

Data on BMR and MMR were obtained for 57 populations of 46 species (Appendix). When branch lengths were set equal to unity, only precipitation showed a statistically significant correlation in the diagnostic test for adequacy of branch lengths (Table 1). With Pagel's (1992) arbitrary branch lengths, significant negative correlations were observed for two traits (altitude and T_{min} ; $r_p \leq -0.341$, $P \leq 0.01$, for both traits). With Grafen's (1989) arbitrary branch lengths, five traits showed negative correlations (altitude, BMR, MMR, T_{min} , and T_{max} ; $r_p \leq -0.279$, $P \leq 0.045$, for all traits). Therefore, equal branch lengths were used for all traits except precipitation, for which Pagel's branch lengths were used.

As shown in Table 1, the randomization test indicated highly significant phylogenetic signal for all continuous-valued traits with the exception of mass-corrected MMR ($P = 0.103$) and altitude ($P = 0.784$). Similarly, when we estimated the optimal transformation under the OU model, d was significantly different from zero (but not significantly different from unity) for body mass, BMR, MMR, T_{max} , and raw latitude; for T_{min} , estimation was unstable and depended on starting value (for discussion of instability on starting trees with constant branch lengths, see Blomberg et al. 2003). For mass-corrected MMR and altitude, d was estimated to be zero, which is consistent with the randomization tests that indicated no significant signal. For precipitation, starting with Pagel's (1992) arbitrary branch lengths, d was estimated to be 0.607, which was significantly different from both zero and unity.

The maximum-parsimony reconstruction of diet evolution (Fig. 1) indicated that nine steps were required. For the 1000 randomized datasets, the number of steps ranged from 19 to 32, with a mean of 26.67 and a median of 27. Therefore, diet

TABLE 2. Pearson product-moment correlations between body mass (log transformed) and environmental variables, and between pairs of environmental variables; df are 55 for both conventional and phylogenetic analyses; 2-tailed critical value = 0.261 for $P = 0.05$; * indicates 2-tailed $P < 0.05$ (not corrected for multiple comparisons).

	Latitude	Altitude	T_{max}	T_{min}	Precipitation
Conventional					
Mass for BMR	-0.209	-0.124	0.152	0.301*	0.114
Mass for MMR	-0.208	-0.124	0.151	0.300*	0.112
Latitude		-0.421*	-0.611*	-0.585*	-0.196
Altitude			-0.228*	-0.436*	-0.070
T_{max}				0.842*	0.057
T_{min}					0.303*
Phylogenetically independent contrasts (constant branch lengths, except precipitation = Pagel 1992)					
Mass for BMR	-0.102	-0.046	0.034	0.165	0.332*
Mass for MMR	-0.100	-0.046	0.033	0.164	0.330*
Latitude		-0.477*	-0.486*	-0.359*	-0.112
Altitude			-0.322*	-0.591*	-0.147
T_{max}				0.794*	0.100
T_{min}					0.329*

also exhibits strong phylogenetic signal (sensu Blomberg and Garland 2002).

Predictors of Body Mass, BMR, and MMR

The predictors of body mass differed between conventional and phylogenetic analyses. The former indicated that T_{min} was a significant positive predictor, but independent contrasts indicated that precipitation was a significant positive predictor (Table 2). In addition, diet was a significant predictor of MMR body mass ($F_{2,54} = 10.86$, $P < 0.001$) in conventional analyses, with the main effect that herbivores are substantially larger than either omnivores or granivores. With diet in the model, T_{max} was an additional positive predictor of body mass ($F_{1,53} = 12.19$, 2-tailed $P = 0.001$). With independent contrasts, the diet effect was not significant ($F_{2,54} = 1.92$, $P = 0.156$). With diet in the model, precipitation was a marginal positive predictor of mass ($F_{1,53} = 3.83$, 2-tailed $P = 0.055$).

As would be expected, several environmental variables were intercorrelated, in particular temperature, altitude, and latitude (Table 2). The strong correlation between T_{min} and

T_{max} ($r = 0.8$) makes it difficult to determine which is actually a better predictor in multiple regression analyses (see below).

Slopes for the independent contrasts allometric equations were slightly shallower than those derived from conventional statistics, but the 95% confidence intervals for both slopes and intercepts overlapped broadly, indicating no statistical difference between the equations for either BMR or MMR (Table 3, Fig. 2). Conventional multiple regressions that included body mass indicated that T_{max} , T_{min} , latitude, and diet were significant additional predictors of BMR, with T_{max} being the best (Table 4). With body mass and T_{max} in the model, no additional variables were significant predictors of BMR (all 2-tailed P to enter > 0.11). With body mass and T_{min} in the model, latitude was an additional significant predictor of BMR (positive partial regression coefficient, 1-tailed $P = 0.047$).

Phylogenetic analyses indicated that only latitude (positive, 1-tailed $P = 0.0465$) was a significant predictor of mass-adjusted BMR (Table 5). With models containing both body mass and latitude, none of the other variables entered as a significant predictor.

Conventional analyses indicated that T_{max} , T_{min} , altitude, and latitude (1-tailed $P = 0.039$) explained significant amounts of the variation in mass-adjusted MMR, with T_{min} being the best predictor (Table 4). With body mass and T_{min} in the model, altitude was the only variable that bordered significance (positive partial regression slope, 2-tailed $P = 0.051$). With body mass and T_{max} in the model, altitude remained as an additional significant predictor (positive, 2-tailed $P = 0.003$).

Phylogenetic contrasts agreed with conventional analyses in indicating T_{max} , T_{min} , and altitude (but not latitude) as significant predictors of mass-adjusted MMR, and again T_{min} was the best predictor (Table 5). With body mass and T_{min} in the model, none of the other variables was significant (all 2-tailed $P > 0.16$).

Finally, we observed a highly significant positive correlation between mass-independent residuals of BMR and MMR in both conventional analyses ($r = 0.534$, $F_{1,55} =$

TABLE 3. Slopes and intercepts of least-squares linear regressions of \log_{10} -transformed MMR and BMR versus \log_{10} body mass (M), obtained with conventional and phylogenetically independent contrasts analysis (all branch lengths = 1). R^2 is not directly comparable between conventional and phylogenetically independent contrasts equations.

	Conventional regression	Independent contrasts
MMR		
Slope	-0.338	-0.296
95% C.I.	-0.403, -0.274	-0.389, -0.204
Intercept	1.450	1.466
95% C.I.	1.338, 1.563	1.215, 1.717
R^2	0.667	0.428
BMR		
Slope	-0.340	-0.311
95% C.I.	-0.398, -0.281	-0.381, -0.241
Intercept	0.697	0.639
95% C.I.	0.595, 0.799	0.449, 0.828
R^2	0.711	0.589

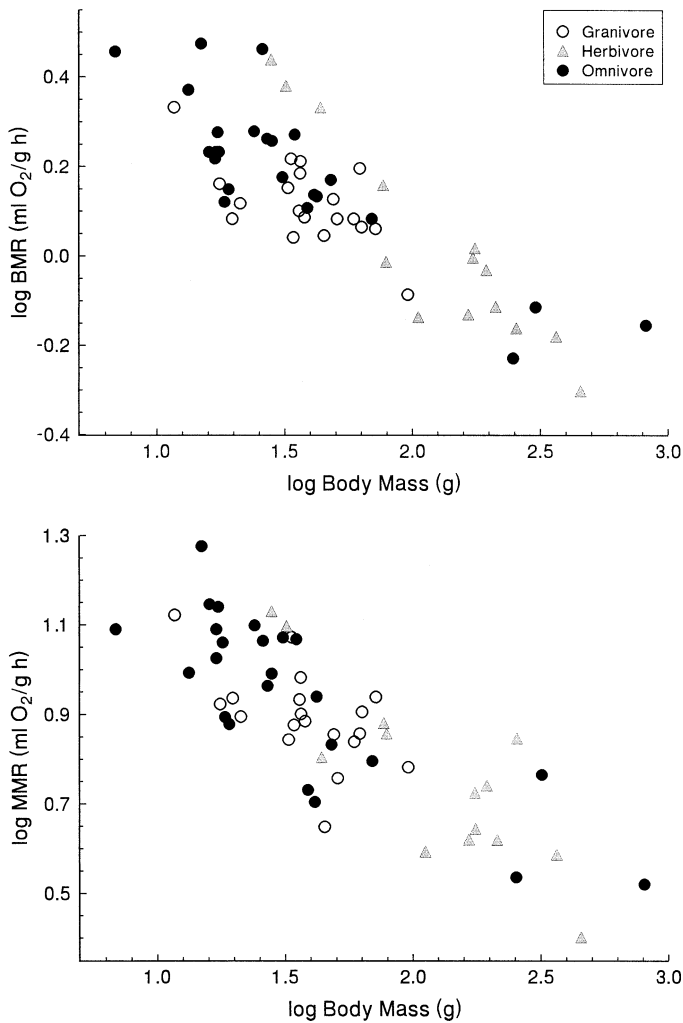


FIG. 2. Relationship of (A) BMR and (B) MMR to body mass (significantly negative for both traits) and diet (nonsignificant). See Tables 3, 4, and 5 for allometric relationships and statistical analyses.

21.99, $P < 0.0001$; Fig. 3) and with independent contrasts ($r_{ic} = 0.500$, $F_{1, 55} = 18.3$, $P < 0.001$).

DISCUSSION

Phylogenetic Signal in Ecological and Physiological Traits

Consistent with the broad empirical surveys presented in Freckleton et al. (2002) and Blomberg et al. (2003), we found statistically significant phylogenetic signal in most—but not all—of the traits that we analyzed. Six of the traits (T_{max} , T_{min} , raw latitude, altitude, precipitation, and diet) may be considered “ecological” rather than physiological or morphological. At any given point in the history of a lineage, latitude should, to some extent, reflect its historical patterns of speciation and vicariance, but this signal may be obscured by some types of dispersal as they interact with geographic barriers and/or unsuitable habitat is encountered. Empirically, latitude seems generally to show phylogenetic signal. In addition to the present study (Table 1), Blomberg et al. (2003) reported significant signal for 15 species of *Drosophila*, and

Freckleton et al. (2002) reported significant signal for five of seven examples of latitude. Altitude did not show significant phylogenetic signal (Table 1), and the previous studies included no other examples. Temperature, which is correlated with both absolute latitude and altitude (Table 3), showed significant signal. Only one other example of environmental temperature has been reported (mean annual temperature in the waters of 15 *Fundulus* fish, $K = 0.324$, P for signal = 0.258; Blomberg et al. 2003). Taken as a whole, existing data on ecological traits indicate that they often do exhibit significant amounts of phylogenetic signal and, thus, phylogenetically based statistical methods will often be appropriate (see also Freckleton et al. 2002).

Body size plays a key role in many aspects of animal ecology (e.g., reviews in Schmidt-Nielsen 1995; Nagy et al. 1999; Brown and West 2000; McNab 2002), and we found highly significant phylogenetic signal for body mass in our sample of rodents, as did Al-kahtani et al. (2004) for a larger sample of rodents. Blomberg et al. (2003) reported significant signal for all 16 studies of vertebrate body size with sample sizes greater than 20 (for which simulations suggest that statistical power should be approximately 0.8 or greater). Freckleton et al. (2002) also reported significant signal (their lambda transformation parameter was different from zero) for all 16 studies of body size (vertebrates and invertebrates) with sample size of 20 or more.

In their literature survey, Blomberg et al. (2003) found that only four of 53 traits with sample sizes greater than 20 showed nonsignificant ($P > 0.05$) phylogenetic signal (based on the randomization test), and one of these was mass-corrected MMR of birds (also measured with the He-O₂ method; $n = 47$; data compiled in Rezende et al. 2002). We found that mass-corrected MMR of rodents also did not exhibit significant phylogenetic signal. These results suggest that endotherm MMR may be relatively adaptive in the genetic, evolutionary sense, such that it often does not retain the imprint of phylogenetic history. Consistent with this hypothesis, we found substantial relations between MMR and environmental variables (especially minimum temperature: see Table 5) in rodents, and it would be of particular interest to test for such correlations with avian MMR.

Aside from adaptation by natural selection, other factors that can lead to low phylogenetic signal are sexual selection, phenotypic plasticity, and measurement error of various types. Errors in topology likely exist in our study, and errors in branch lengths definitely exist given that we used arbitrary values. However, error in the phylogeny should cause a general lowering of the K statistic for all traits, not a specific lowering for one or a few traits. Although the K value of 0.347 for mass-corrected BMR falls below the 95% confidence interval reported for 21 physiological traits by Blomberg et al. (2003), the K value reported for body size (almost 1.5 in Table 1) is above the 95% CI they reported for 24 values of adult body size. Errors related to measurement techniques can, of course, differ among traits, and are presumably greater for metabolic rate than for body size. Several studies have shown that individual differences in MMR elicited by cold exposure in a wind tunnel or employing He-O₂ are highly repeatable over short periods in deer mice (Hayes 1989; Hayes and Chappell 1990), ground squirrels (Chappell et al.

TABLE 4. Results of conventional multiple regression analyses. First line for each dependent variable is for model that contains only body mass, whereas following lines are for models that contain mass and one additional independent variable (or two dummy variables for diet).

Dependent variable	Model	Sign of partial regression coefficient	multiple R^2	Standard error of the estimate	F change	df for F change	2-tailed P for F change	
log BMR	log Body Mass (M)	–	0.711	0.0971	135.32	1, 55	<0.0001	
	$M + Tmax$	–	0.757	0.0883	12.61	1, 54	0.001	
	$M + Tmin$	–	0.761	0.0891	11.28	1, 54	0.001	
	$M + Diet$	herbivore + omnivore +	0.729	0.0932	3.37	2, 53	0.042	
	$M + Latitude$	+	0.758	0.0897	10.55	1, 54	0.002	
	$M + Altitude$	+	0.711	0.0980	0.06	1, 54	0.813	
	$M + Precipitation$	+	0.711	0.0980	0.04	1, 54	0.849	
	$M + BMR_RMR$	–	0.718	0.0968	1.38	1, 54	0.244	
	log MMR	log Body Mass (M)	–	0.667	0.1073	110.35	1, 55	<0.0001
		$M + Tmax$	–	0.734	0.0968	13.47	1, 54	0.001
$M + Tmin$		–	0.776	0.0889	26.04	1, 54	<0.0001	
$M + Diet$		herbivore + omnivore +	0.676	0.1078	0.72	2, 53	0.489	
$M + Latitude$		+	0.686	0.1052	3.23	1, 54	0.078	
$M + Altitude$		+	0.731	0.0973	12.80	1, 54	0.001	
$M + Precipitation$		–	0.668	0.1081	0.12	1, 54	0.727	

1995), junglefowl (Chappell et al. 1996), and porcupines (Fournier and Thomas 1999). We do not know of any studies that have directly compared the magnitude of measurement error in MMR with that of BMR, for which mass-corrected values did show significant phylogenetic signal (Table 1), but we have no reason to believe that they are lower for BMR.

Another complicating factor is that the studies analyzed here were not based on animals that had experienced common rearing conditions (Garland and Adolph 1991, 1994). Thus, for none of the traits do we know how much of the among-species variation is genetically based. Clearly, some of the interspecific variation in body size would remain if all animals had been raised on the same food, etc. (see also Ashton et al. 2000; Al-kahtani et al. 2004), but whether that is true for mass-corrected BMR or MMR is unknown, and compli-

cated effects of genotype-environment interaction are possible. In our opinion, a major goal of future comparative studies (at least for experimentally tractable groups, e.g., see Mueller and Diamond 2001) should be to obtain data from animals born and raised under common conditions, although this obviously does not apply in any simple way for “traits” that are inherently measured in nature, such as home range, latitude, and environmental temperatures (Garland 2001; Garland et al. 1992; Blomberg et al. 2003).

Predictors of Body Mass, BMR, and MMR

Whether body size of mammals or birds is negatively related to temperature (or positively related to absolute latitude) has been debated for over a century and a half (recent reviews

TABLE 5. Results of multiple regressions (through the origin) obtained with phylogenetically independent contrasts. First line for each dependent variable is for model that contains only body mass, whereas following lines are for models that contain mass and one additional independent variable (or two dummy variables for diet). Branch lengths set equal to unity (constant) for all traits, except BMR_RMR (star phylogeny) and precipitation (Pagel’s [1992] arbitrary).

Dependent variable	Model	Sign of partial regression coefficient	multiple R^2	Standard error of the estimate	F change	df for F change	2-tailed P for F change	
log BMR	log Body Mass (M)	–	0.589	0.0613	78.85	1, 55	<0.0001	
	$M + Tmax$	–	0.597	0.0613	1.10	1, 54	0.299	
	$M + Tmin$	–	0.605	0.0606	2.21	1, 54	0.143	
	$M + Diet$	herbivore + omnivore +	0.591	0.0623	0.14	2, 53	0.871	
	$M + Latitude$	+	0.610	0.0603	2.92	1, 54	0.093	
	$M + Altitude$	+	0.590	0.0618	0.14	1, 54	0.710	
	$M + Precipitation$	+	0.590	0.0618	0.17	1, 54	0.683	
	$M + BMR_RMR$	–	0.596	0.0614	0.91	1, 54	0.344	
	log MMR	log Body Mass (M)	–	0.429	0.0806	41.24	1, 55	<0.0001
		$M + Tmax$	–	0.542	0.0729	13.33	1, 54	0.001
$M + Tmin$		–	0.611	0.0671	25.41	1, 54	<0.0001	
$M + Diet$		herbivore + omnivore +	0.452	0.0804	1.13	2, 53	0.331	
$M + Latitude$		+	0.454	0.0796	2.48	1, 54	0.121	
$M + Altitude$		+	0.518	0.0748	9.96	1, 54	0.003	
$M + Precipitation$		–	0.430	0.0812	0.18	1, 54	0.677	

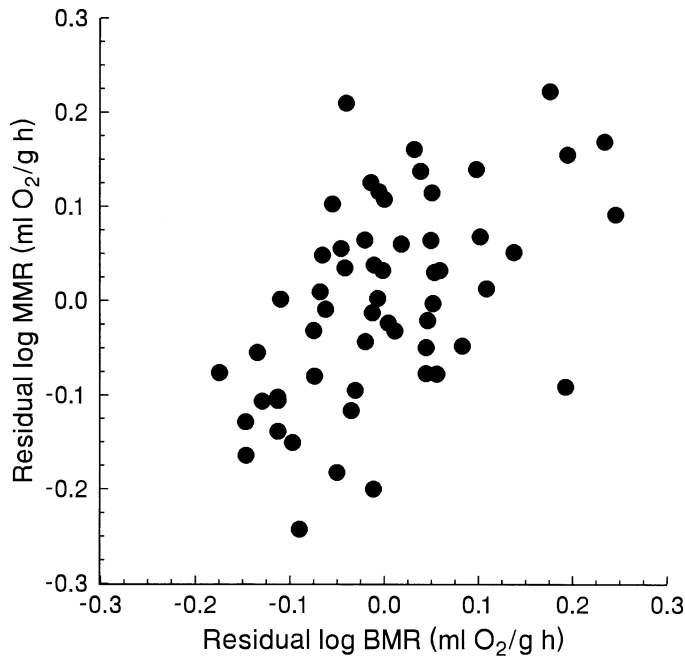


FIG. 3. Relationship between residual (body mass-independent) basal (BMR) and maximum (MMR) metabolic rates. Correlation is significant by conventional correlation, as shown here ($r = 0.534$, $P < 0.0001$), and also in analysis by phylogenetically independent contrasts ($r_{ic} = 0.500$, $P < 0.001$).

in Ashton et al. 2000; Freckleton et al. 2003). For our sample of 57 rodents, body mass was significantly *positively* correlated with T_{min} in the conventional but not the independent contrasts analysis (Table 3). Given the significant phylogenetic signal in both traits (Table 1), the latter result should be more reliable. As body size was *negatively* correlated with latitude in both analyses, although neither was significant, our results offer no support for “Bergmann’s rule,” however it may be defined (Ashton et al. 2000; Freckleton et al. 2003). An apparently novel result is our finding that body mass was significantly positively correlated with precipitation in the phylogenetic analysis, possibly because precipitation reflects variation in primary productivity (e.g., see discussion in Ashton et al. 2000). Silva et al.’s (2001) conventional analysis of 827 populations belonging to 330 different terrestrial mammal species reported that body mass was significantly negatively correlated with latitude, positively correlated with average annual temperature, and uncorrelated ($P > 0.05$) with precipitation or altitude. However, within-species correlations between body size and precipitation have been reported previously for mammals (e.g., Olcott and Barry 2000; Kennedy et al. 2002).

Both theoretical and empirical evidence suggests that diet and body size might coadapt in rodents (e.g., Justice and Smith 1992). Diet was a significant predictor of body mass in our conventional but not phylogenetic analyses, a difference attributable to the strong phylogenetic clumping of diet (Fig. 1). As in the data of Degen et al. (1998, e.g., see their table 5), herbivores are larger than omnivores or granivores, but they apparently did not perform phylogenetic tests of the difference. Although they did not test for a diet effect, Al-

kahtani et al. (2004) reported that body mass was negatively correlated with an index of habitat aridity in both conventional and independent contrasts analyses in a sample of 141 rodents.

The earliest comparative studies of arctic and tropical mammals suggested that BMR remained unchanged while thermal insulation was considerably higher in arctic species (Scholander et al. 1950a,b). Metabolic adaptations as a response to different thermal environments should be more pronounced in small endotherms, not only because they have a relatively high surface/volume ratio, but also because other ways to cope with cold environments, such as burrowing or decreasing thermal conductance by hair or fur, are structurally restricted as body mass decreases (Stuedel et al. 1994; Porter et al. 1994; see also Freckleton et al. 2003). This may also explain why no effect of latitudinal mean annual temperatures on BMR was detected by Scholander et al. (1950b) despite a clear effect on thermal insulation, because small and large mammals were pooled in the same analysis (range from 38 g to 14.5 kg). Moreover, insulation of small arctic mammals did overlap with that of some tropical forms, but this was not the case for larger species (Scholander et al. 1950a).

Two more recent comparative studies have reported significant negative associations between mean environmental temperatures and BMR (or RMR): among 31 populations of *Peromyscus* employing conventional statistics (MacMillen and Garland 1989); on a global scale in small mammals (body mass < 1 kg, $N = 268$) with phylogenetic analyses (Lovegrove 2003). The discrepancy between Lovegrove’s results and ours may be partly related to the difference in sample size, but the small partial r^2 and F change for temperature (Table 5) suggests this is not the entire explanation. In non-phylogenetic analyses, Lovegrove (2003) reported significant negative correlations between temperature and BMR using smaller databases for Nearctic ($n = 94$) and Palearctic ($n = 34$) small mammals, but no significant correlation for Afrotropical ($n = 49$), Australasian ($n = 40$), and Neotropical ($n = 43$) species. Another difference between our analyses is that Lovegrove (2003) computed contrasts for all climate variables on a star phylogeny. This procedure makes sense if the variables do not show phylogenetic signal (see Grafen 1989; Freckleton et al. 2002; Blomberg et al. 2003), but for our data, phylogenetic signal was highly significant for temperature, precipitation, and raw latitude (although not for altitude, Table 1), indicating that it is more appropriate to compute contrasts on a hierarchical phylogeny.

If variation in environmental temperature leads to variable natural selection on BMR, then it could occur in at least two ways (MacMillen and Garland 1989; Lovegrove 2000, 2003; White 2003). First, high temperatures could favor low BMR to avoid overheating and/or for energy or water conservation, given that many habitats with high temperatures also have relatively low primary productivity and water availability (i.e., most deserts). Second, low temperatures could favor high BMR in relation to enhanced thermoregulatory abilities. However, the relationship between thermoregulatory abilities (e.g., ability to withstand cold challenge) and BMR is unclear from first principles. For example, with respect to thermal balance, a high BMR is equivalent to a lower BMR in com-

bination with some amount of non-shivering and/or shivering thermogenesis. Nevertheless, a significant positive phenotypic correlation between BMR and MMR has been reported at the intraspecific level in *Peromyscus maniculatus* (Hayes 1989), so selection on MMR (Hayes and O'Connor 1999) could also impinge on BMR.

In any case, selection in relation to either high or low temperatures could lead to a negative interspecific correlation between BMR and temperature, therefore it is appropriate to test for correlations with one-tailed tests. In principle, the relative importance of the two ends of the temperature continuum could be elucidated by fine-scale analysis of the relationship between mass-corrected BMR and environmental temperatures. Break points in such relationships, if any occurred, could suggest that low-temperature selection is more important than high-temperature selection, or vice versa. Our phylogenetic analyses (Table 5) did not indicate a significant relationship between either T_{min} or T_{max} and BMR, and inspection of conventional partial regression plots of our data did not suggest break points in the overall negative relationships between BMR and temperature (Table 4).

In support of the low-temperature selection hypothesis, rodent species from cold deserts have higher BMRs than predicted for their body mass in nonphylogenetic analyses, despite the aridity, low productivity, and unpredictability of these environments (Weiner and Gorecki 1981; see also Leonard et al. 2002 on human populations). In support of the high-temperature selection hypothesis, several studies of both mammals (e.g., McNab and Morrison 1963; McNab 1979; Hinds and MacMillen 1985; White 2003) and birds (Tieleman and Williams 2000, Tieleman et al. 2003) have reported lower BMR in hot deserts. However, as noted above, hot deserts also have low precipitation and low primary productivity. For example, a reanalysis of Tieleman et al.'s (2003) data for desert larks shows that mass-corrected BMR is negatively correlated with T_{max} , as predicted by the hypothesis (phylogenetically independent contrasts, $n = 12$, partial $r^2 = 0.368$, partial $F_{1,9} = 46.86$, $P < 0.001$), but not with T_{min} ($r^2 = 0.093$, $F_{1,9} = 2.43$, $P = 0.15$), and positively with precipitation ($r^2 = 0.327$, $F_{1,9} = 26.17$, $P < 0.001$). (The strong correlation between T_{max} and precipitation [$r = -0.93$, $P < 0.001$] makes it difficult to determine if both are actually predictors of BMR.) Taken as a whole, comparative studies of whether BMR is related to environmental temperature in small endotherms are inconclusive.

In a phylogenetic multiple regression, absolute latitude was a significant positive predictor of mass-corrected BMR (Table 5, 1-tailed $P = 0.0465$), but none of the other variables entered as a significant predictor. Thus, our results suggest that latitude affects BMR independently of the obvious latitudinal variation in temperature (Table 3). Speakman (2000), using conventional statistics, also reported a significant effect of latitude, and not temperature, on RMR of small mammals (body mass < 4 kg), and an effect of latitude on field metabolic rates (FMR) after the effects of mass and temperature were controlled. Lovegrove (2003) reported a significant correlation between BMR and both latitude and mean temperatures, but did not report results of an analysis with both independent variables in the model. A positive correlation between latitude and mass-independent BMR (or similar in-

stances of resting metabolism) has also been reported for birds in nonphylogenetic analyses (Weathers 1979; Ellis 1985).

Perhaps latitude is actually a better predictor of prevailing (long-term, e.g., thousands of years) temperatures than are temperatures recorded at (nearby) weather stations for tens of years. Alternatively, several other factors may vary with latitude, sometimes in a nonlinear fashion (e.g., see Lovegrove 2003), including primary productivity (and hence food availability), precipitation, seasonality, and environmental unpredictability. Although they did not test for a correlation between BMR and latitude, Mueller and Diamond (2001) found a strong positive correlation between BMR and primary productivity among five species of *Peromyscus*. Basal metabolic rate was not correlated with environmental unpredictability in the same study (calculated as the coefficient of variation of annual precipitation; CVAP). Lovegrove (2003) found a significant negative correlation between mass-corrected BMR and both latitude and \log_{10} CVAP, that is, animals from more "unpredictable" environments had lower BMRs. However, he did not report results of multiple regressions including both independent variables, and, in his data, the relationship between \log_{10} CVAP, and latitude was nonlinear (his fig. 1B).

Seasonality could account for the positive correlation between BMR and latitude if higher metabolic rates facilitate more "accelerated" life histories (McNab 1980), such that selection favors higher BMR where breeding seasons are shorter, for example, at more extreme latitudes (Lovegrove 2003). However, empirical evidence supporting a connection between metabolism and life history is inconclusive. With statistical analyses that included taxonomic affiliation, Harvey et al. (1991) found no significant correlations between 22 life-history traits and BMR in eutherian mammals (see also Read and Harvey 1989), whereas Symonds (1999) reported a negative correlation between residual BMR and gestation length, maximum lifespan, and maximum reproductive lifespan in the Insectivora using phylogenetically independent contrasts (see also Taylor 1998 on shrews; White 2003, p. 126–127).

Our results indicate that MMR has a relatively high evolutionary lability (lack of phylogenetic signal for mass-corrected values) and is negatively correlated with mean minimum environmental temperature. This is a more specific finding than offered by the only two previous comparative studies of MMR in small mammals. In a nonphylogenetic analysis, Bozinovic and Rosenmann (1989) found that rodents from cold climates had high mass-independent values of MMR, whereas the opposite was true for tropical species. In a phylogenetic study of shrews, Sparti (1992; see also Taylor 1998) reported that species from temperate habitats had a higher MMR than their tropical counterparts (see table 1 in Sparti 1992), although these groups were captured and measured at different seasons and no statistical tests were actually performed in this context. Consistent with the comparative studies, Hayes and O'Connor (1999) found that high-altitude *Peromyscus* populations may experience selection for high MMR during winter.

Although many studies have reported that BMR varies with diet (or "food habits") in mammals (e.g., see McNab 2002, p. 95, for a review; McNab 2003), we are not aware of any

TABLE 6. Summary of interspecific correlations between mass-independent (residual) BMR or RMR and maximum metabolic rate elicited with strenuous exercise (VO_2max) or cold exposure (MMR). Statistical analyses are classified as nonphylogenetic (NP) or phylogenetic (P; independent contrasts, Felsenstein 1985).

Taxon	Analysis	Metabolic rate	r	N	1-tailed P	Source
Anurans	NP	VO_2max	0.63	17	0.003	Taigen 1983 ^a
	NP	VO_2max	0.15	9	0.348	Gomes 2002
	NP	VO_2max	-0.48	8	n.a.	Gomes 2002 ^b
	P (gradual)	VO_2max	0.68	15	0.003	Walton 1993 ^c
	P (punctuational)	VO_2max	0.76	15	<0.001	Walton 1993 ^c
Lizards	NP	VO_2max	0.04	9	0.455	Thompson and Withers 1997
Passerines	P	MMR	0.86	10	0.001	Dutenhoffer and Swanson 1996
Birds	P	MMR	0.87	24	<0.001	Rezende et al. 2002
Shrews	P	MMR	0.25	13	0.205	Sparti 1992
	P	MMR	0.29	12	0.180	Sparti 1992 ^b
Rodents	NP	VO_2max	0.44	18	0.034	Hinds and Rice-Warner 1992
	NP	VO_2max	0.64	17	0.003	Hinds and Rice-Warner 1992 ^b
	NP	VO_2max	0.59	8	0.062	Koteja 1987
	NP	MMR	0.70	9	0.018	Hinds and Rice-Warner 1992
	NP	MMR	0.46	29	0.006	Bozinovic 1992a
Mammals	P	MMR	0.50	57	<0.001	this study
	NP	VO_2max	-0.14	18	n.a.	Koteja 1987

^a Correlation performed between ranks.

^b Value reported after removing one influential point.

^c Study reported results for two different sets of branch lengths.

study at the interspecific level that has reported a statistically significant association between BMR and diet by use of phylogenetically based analyses (e.g., this study; Degen et al. 1998; Speakman 2000; Genoud 2002; Cruz-Neto et al. 2001). However, as in any case where independent variables are highly correlated, when diet is strongly related to phylogeny (Fig. 1) it is conceptually and statistically difficult to determine which is actually the better predictor (Garland et al. 1993; Garland and Adolph 1994; McNab 2003).

Correlated Evolution of Vertebrate Metabolic Rates

Interspecific comparative studies testing for correlations between BMR, MMR, and behavioral/ecological traits are one way to address the selective factors associated with the evolution of endothermy. Our results offer some support for two different models that have been proposed. First, the negative correlation between MMR and temperature suggests that selection may act on thermoregulatory performance, which supports the thermal niche expansion model (Block and Finnerty 1994; Hayes and Garland 1995).

Second, the positive correlation between mass-independent BMR and MMR is consistent with the idea that these metabolic states are somehow functionally linked. A positive functional relationship between BMR and exercise-induced VO_2max is a key assumption of the aerobic capacity model (Bennett and Ruben 1979; Taigen 1983; Hayes and Garland 1995). Indeed, significant positive phenotypic correlations between BMR and either VO_2max or MMR in rodents have now been reported at the intraspecific level in *Peromyscus maniculatus* (MMR, Hayes 1989) and *Spermophilus beldingi* (VO_2max , Chappell and Bachman 1995), and at the interspecific level in a variety of vertebrate taxa, especially rodents (Table 6). Of course, a positive interspecific correlation between traits can be the result of a functional relationship, which causes a genetic correlation, and/or selection that has acted on the traits in a parallel fashion. Although the aerobic

capacity model posited positive selection on VO_2max , not MMR, the two measures of maximum aerobic capacity appear to be positively related. For instance, several studies have suggested that small mammals acclimatized to cold may exhibit increased VO_2max (Hart and Jansky 1963; Pasquis et al. 1970), and cold-acclimation significantly increased both MMR and VO_2max in *P. maniculatus* (Hayes and Chappell 1986). In addition, a significant positive correlation between mass-independent residuals of MMR and VO_2max has been reported in *P. maniculatus* (Chappell et al. 2003) and in *S. beldingi* ($r = 0.413$, $n = 157$, 1-tailed $P < 0.0001$, M. A. Chappell pers. comm.; data from Chappell and Bachman 1995). Evidence for a positive genetic correlation between BMR and VO_2max has been reported for laboratory house mice, but only under certain constrained statistical models (Dohm et al. 2001). We know of no estimates of the genetic correlation between BMR and MMR, or between MMR and VO_2max . Moreover, comparative studies of the correlation between MMR and VO_2max are lacking. Another important area for future research will be identification of the mechanistic bases of interspecific variation in metabolic rates, such as whether differences in thyroid function can account for variation in BMR (e.g., see Hulbert et al. 1985; Leonard et al. 2002). Such studies would also help to elucidate if and how BMR and MMR (or VO_2max) are mechanistically related (Hayes and Garland 1995).

Limitations of This Study

Our study suggests that variation in long-term average temperatures leads to variation in selective regimes that causes evolutionary diversification in MMR. However, metabolic traits are plastic and one underlying assumption on our study—as for most comparative metabolic studies (but see Derting and McClure 1989; Mueller and Diamond 2001)—is that metabolic plasticity lies within a limited range for each species/population (Garland and Adolph 1991, 1994).

Rezende et al. (2001) reported differences in MMR of three closely related species of *Phyllotis* after acclimating them to cold and warm temperatures, which supports the assumption of limited metabolic plasticity. However, acclimatization occurring over longer periods of development cannot be ruled out as a major source of among-species variation (e.g., Tracy and Walsberg 2001).

Another limitation arises from the nature of the study itself: comparative studies must trade off precision for generality, and this one is no exception. The use of coarse meteorological variables, for instance, cannot accurately reflect the thermal microclimates that species actually face in nature (MacMillen and Garland 1989; Canterbury 2002). Nevertheless, a highly significant relationship with temperature was detected for MMR. Assuming that the species differences in MMR are at least partly genetically based, this result suggests that behavioral adaptations (e.g., microhabitat selection, huddling) cannot totally compensate for differences in thermal environments as estimated from weather station data.

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APPENDIX. Alphabetical listing of metabolic data compiled from the literature for 57 species or populations of rodents, along with diet and environmental characteristics.

Species	Code	Mass	<i>BMR</i>	<i>BMR</i> _g	Mass	<i>MMR</i>	Diet ^a	Station	Locality	Station	Altitude	Precip-	<i>T</i> _{max}	<i>T</i> _{min}	Source
		<i>BMR</i> (g)	(mlO ₂ /gh)	<i>RMR</i>	<i>MMR</i> (g)	(mlO ₂ /gh)				Latitude	(m)	itation	(°C)	(°C)	
										(°)		(mm/yr)			
<i>Abrothrix andinus</i>	AA	34.6	1.87	<i>RMR</i>	35.0	11.70	o	El Teniente, Chile		-34.10	2134	1073	14.5	5.2	1,2
<i>Abrothrix longipilis</i>	AL	42.3	1.36	<i>RMR</i>	42.0	8.70	o	Santiago, Chile		-33.45	520	335	22.0	7.8	1,2
<i>Akodon albiventer</i>	Aa	31.0	1.50	<i>BMR</i>	31.0	11.80	o	Challapata, Bolivia		-18.87	3720	351	18.2	2.8	3
<i>Akodon lanosus</i>	Al	24.0	1.90	<i>BMR</i>	24.0	12.55	o	Punta Arenas, Chile		-53.03	33	400	10.0	3.4	3
<i>Apodemus flavicollis</i>	Af	25.9	2.90	<i>BMR</i>	25.9	11.60	o	Kracow, Poland		50.08	209	663	12.8	4.4	4
<i>Auliscomys boliviensis</i>	Ab	76.8	1.44	<i>RMR</i>	77.0	7.60	h	Challapata, Bolivia		-18.87	3720	351	18.2	2.8	1,2
<i>Auliscomys micropus</i>	Am	62.3	1.57	<i>RMR</i>	62.0	7.20	g	Talca, Chile		-35.43	97	737	22.1	7.8	1,2
<i>Baiomys taylori</i>	Bt	6.9	2.86	<i>RMR</i>	6.9	12.30	o	Austin, USA		30.00	156	795	26.1	14.6	5
<i>Calomys callosus</i>	Cc	48.0	1.48	<i>RMR</i>	48.0	6.80	o	San Joaquin, Bolivia		-13.07	140	1503	32.1	19.8	5
<i>Calomys ducilla</i>	Cd	16.0	1.71	<i>RMR</i>	16.0	14.00	o	Desaguadero, Peru		-16.65	3850	608	14.6	1.1	5
<i>Calomys musculus</i>	Cm	16.9	1.65	<i>RMR</i>	17.0	10.60	o	San Luis, Argentina		-33.27	713	566	23.8	9.3	2,6
<i>Chroeomys olivaceus</i>	Co	27.0	1.83	<i>RMR</i>	27.0	9.20	o	Santiago, Chile		-33.45	520	335	22.0	7.8	1,2
<i>Chinchilla brevicaudata</i>	Cb	454.4	0.50	<i>BMR</i>	454.4	2.52	h	La Serena, Chile		-29.90	169	78	19.0	11.3	19
<i>Chinchilla lanigera</i>	Cl	365.0	0.66	<i>BMR</i>	365.0	3.86	h	La Serena, Chile		-29.90	169	78	19.0	11.3	7
<i>Clethrionomys rutilus</i>	Cr	28.0	2.75	<i>BMR</i>	28.0	13.50	h	Fairbanks, Alaska		64.85	134	276	2.5	-8.2	8
<i>Conilurus penicilatus</i>	Cp	212.3	0.77	<i>RMR</i>	214.1	4.16	h	Darwin, Australia		-12.47	30	1492	32.6	23.6	9
<i>Dipodomys deserti</i>	Dd	96.0	0.82	<i>RMR</i>	96.0	6.05	g	Daggett, USA		34.87	309	100	27.2	12.4	10
<i>Dipodomys heermanni</i>	Dh	63.3	1.16	<i>RMR</i>	63.3	8.05	g	Bakersfield, USA		35.42	145	145	25.4	11.8	10

<i>Dipodomys merriami</i>	Dm	36.5	1.63	<i>RMR</i>	36.5	7.97	g	Daggett, USA	34.87	309	100	27.2	12.4	10
<i>Dipodomys merriami</i>	DM	33.5	1.65	<i>RMR</i>	33.5	11.82	g	Bishop, USA	37.37	1244	132	23.4	3.2	10
<i>Dipodomys merriami</i>	dM	34.2	1.10	<i>RMR</i>	34.2	7.53	g	Tehachapi, USA	35.13	460	269	19.9	5.3	11
<i>Dipodomys merriami</i>	dm	32.6	1.42	<i>RMR</i>	32.6	6.98	g	Riverside, USA	33.97	469	255	24.6	9.4	11
<i>Dipodomys nitratoides</i>	Dn	37.8	1.22	<i>RMR</i>	37.8	7.68	g	Bakersfield, USA	35.42	145	145	25.4	11.8	10
<i>Dipodomys panamintinus</i>	Dp	71.7	1.15	<i>RMR</i>	71.7	8.69	g	Bishop, USA	37.37	1244	132	23.4	3.2	10
<i>Eligmodontia typus</i>	Et	17.5	1.71	<i>RMR</i>	18.0	11.50	o	Mendoza, Argentina	-32.88	769	194	21.7	10.4	1,2
<i>Ellobius talpinus</i>	ET	43.7	2.15	<i>RMR</i>	43.9	6.37	h	Tomsk, Russia	56.50	122	507	2.7	-5.9	12
<i>Graomys griceoflavus</i>	Gg	69.4	1.21	<i>RMR</i>	69.4	6.25	o	San Luis, Argentina	-33.27	713	566	23.8	9.3	13
<i>Liomys salvini</i>	Ls	45.1	1.11	<i>RMR</i>	45.1	4.45	g	Liberia, Costa Rica	10.60	85	1641	32.9	22.1	11
<i>Microcavia niata</i>	Mn	255.2	0.69	<i>BMR</i>	255.2	7.02	h	Challapata, Bolivia	-18.87	3720	351	18.2	2.8	3,14
<i>Microdipodops megacephalus</i>	Mm	11.7	2.15	<i>RMR</i>	11.7	13.23	g	Bishop, USA	37.37	1244	132	23.4	3.2	10
<i>Microtus oeconomus</i>	Mo	32.0	2.40	<i>RMR</i>	32.0	12.50	h	Fairbanks, Alaska	64.85	134	276	2.5	-8.2	5
<i>Mus musculus</i>	mM	17.3	1.89	<i>RMR</i>	17.3	13.80	o	Cerro de Pasco, Peru	-10.75	4400	969	12.3	-1.2	5
<i>Mus musculus</i>	MM	17.0	1.71	<i>RMR</i>	17.0	12.30	o	Little Rock, USA	35.37	109	1291	22.5	10.6	5
<i>Notomys alexis</i>	Na	38.8	1.28	<i>RMR</i>	38.8	5.38	o	Alice Springs, Australia	-23.63	579	253	28.5	12.9	9
<i>Octodon bridgesi</i>	Ob	176.0	1.04	<i>BMR</i>	176.0	4.40	h	Talca, Chile	-35.43	97	737	22.1	7.8	2,14
<i>Octodon degus</i>	Od	195.0	0.93	<i>RMR</i>	195.0	5.50	h	Santiago, Chile	-33.45	520	335	22.0	7.8	15
<i>Octodon lunatus</i>	OI	173.0	0.99	<i>BMR</i>	175.0	5.30	h	La Serena, Chile	-29.90	169	78	19.0	11.3	2,14
<i>Oryzomys longicaudatus</i>	Or	28.2	1.81	<i>RMR</i>	28.0	9.80	o	Santiago, Chile	-33.45	520	335	22.0	7.8	1,2
<i>Perognathus fallax</i> (San Bernardino Co., CA)	pF	19.7	1.21	<i>RMR</i>	19.7	8.64	g	Tehachapi, USA	35.13	460	269	19.9	5.3	11

<i>Perognathus fallax</i> (Riverside Co., CA)	Pf	21.2	1.31	<i>RMR</i>	21.2	7.86	g	Riverside, USA	33.97	469	255	24.6	9.4	11
<i>Perognathus fallax</i> (Orange Co., CA)	PF	17.6	1.45	<i>RMR</i>	17.6	8.38	g	Riverside, USA	33.97	469	255	24.6	9.4	11
<i>Peromyscus californicus</i>	Pc	41.3	1.37	<i>RMR</i>	41.3	5.06	o	Riverside, USA	33.97	469	255	24.6	9.4	11
<i>Peromyscus eremicus</i>	pE	18.4	1.32	<i>RMR</i>	18.4	7.84	o	Tehachapi, USA	35.13	460	269	19.9	5.3	11
<i>Peromyscus eremicus</i>	Pe	19.1	1.41	<i>RMR</i>	19.1	7.56	o	Riverside, USA	33.97	469	255	24.6	9.4	11
<i>Peromyscus maniculatus</i>	Pm	13.3	2.35	<i>RMR</i>	13.3	9.84	o	Daggett, USA	34.87	309	100	27.2	12.4	10
<i>Peromyscus maniculatus</i>	pM	14.9	2.98	<i>RMR</i>	14.9	18.89	o	Bishop, USA	37.37	1244	132	23.4	3.2	10
<i>Phyllotis darwini</i>	Pd	59.0	1.21	<i>RMR</i>	59.0	6.90	g	Santiago, Chile	-33.45	520	335	22.0	7.8	1,2
<i>Phyllotis magister</i>	PM	50.7	1.21	<i>RMR</i>	50.7	5.72	g	Antofagasta, Chile	-23.43	137	7	20.3	13.8	16
<i>Phyllotis rupestris</i>	Pr	36.0	1.26	<i>RMR</i>	36.0	8.58	g	Arica, Chile	-18.48	100	0	22.9	15.3	16
<i>Phyllotis rupestris</i>	PR	36.4	1.53	<i>RMR</i>	36.4	9.61	g	Challapata, Bolivia	-18.87	3720	351	18.2	2.8	3,17
<i>Phyllotis xanthopygus</i>	Px	49.0	1.34	<i>BMR</i>	49.0	7.17	g	Challapata, Bolivia	-18.87	3720	351	18.2	2.8	3,14
<i>Rattus coletti</i>	Rc	165.7	0.74	<i>RMR</i>	165.7	4.17	h	Darwin, Australia	-12.47	30	1492	32.6	23.6	9
<i>Rattus villosissimus</i>	Rv	247.8	0.59	<i>RMR</i>	253.4	3.43	o	Bourke, Australia	-30.08	110	336	28.2	12.9	9
<i>Reithrodon auritus</i>	Ra	79.0	0.97	<i>BMR</i>	79.0	7.20	h	Evangelistas, Chile	-52.40	52	2569	8.2	4.7	3,14
<i>Spermophilus beldingi</i>	Sb	303.8	0.77	<i>BMR</i>	319.6	5.81	o	Bishop, USA	37.37	1244	132	23.4	3.2	20
<i>Spalacopus cyanus</i>	Sc	105.6	0.73	<i>BMR</i>	112.0	3.92	h	Valparaiso, Chile	-33.03	41	351	18.9	10.6	18
<i>Uromys caudimaculatus</i>	Uc	819.0	0.70	<i>RMR</i>	803.1	3.31	o	Townesville, Australia	-19.23	15	1162	28.1	20.4	9

^a Diet preferences classified as: o = omnivore, g = granivore, h = herbivore.

1.- Bozinovic and Rosenmann (1988a); 2.- Bozinovic and Rosenmann (1989); 3.- Bozinovic (1992a); 4.- Cygan (1985); 5.- Rosenmann and Morrison (1974); 6.- Bozinovic and Rosenmann (1988b); 7.- Cortes et al. (2000); 8.- Rosenmann et al. (1975); 9.- Hinds et al. (1993); 10.- Hinds and Rice-Warner (1992); 11.- Hulbert et al. (1985); 12.- Moshkin et al. (2001); 13.- Caviedes-Vidal et al. (1987); 14.- Bozinovic (1992b); 15.- Rosenmann (1977); 16.- Rezende et al. (2001); 17.- Bozinovic

and Marquet (1991); 18.- Nespolo et al. (2001); 19.- Cortes et al. (2003); 20.- Chappell and Bachman (1995) (only adults were used to calculate average values, Chappell pers. comm.).

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