The Zoogeography of Mammalian Basal Metabolic Rate

Barry G. Lovegrove[*]

School of Botany and Zoology, University of Natal, Private Bag X01, Scottsville 3209, South Africa

ABSTRACT: Zoogeographical effects on the basal metabolic rate (BMR) of 487 mammal species were analyzed using conventional and phylogenetically independent ANCOVA. Minimal BMR variance occurred at a "constrained body mass" of 358 g, whereas maximum variance occurred at the smallest and largest body masses. Significant differences in BMR were identified for similar-sized mammals from the six terrestrial zoogeographical zones (Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, and Palearctic). Nearctic and Palearctic mammals had higher basal rates than their Afrotropical, Australasian, Indomalayan, and Neotropical counterparts. Desert mammals had lower basal rates than mesic mammals. The patterns were interpreted with a conceptual model describing geographical BMR variance in terms of the influence of latitudinal and zonal climate variability. Low and high basal rates were explained in unpredictable and predictable environments, respectively, especially in small mammals. The BMR of large mammals may be influenced in addition by mobility and predation constraints. Highly mobile mammals tend to have high BMRs that may somehow facilitate fast running speeds, whereas less mobile mammals are generally dietary specialists and are often armored. The model thus integrates physiological and ecological criteria and makes predictions concerning body size and life-history evolution, island effects, and locomotor energetics.

Keywords: basal metabolic rate, mammals, El Niño–Southern Oscillation, climatic variability, geographical variation, zoogeography.

Basal metabolic rate (BMR), measured during the rest phase of postabsorptive, quiescent mammals, is the most common comparative measure of mammalian metabolic rate (Schmidt-Nielsen 1983). The relationship between BMR and body mass (M_b) is generally approximated with a power equation, $BMR = aM_b^b$, derived as a linear regression ($\log BMR = \log a + b \log M_b$) calculated from $\log_{10}$-transformed empirical data (Schmidt-Nielsen 1983). Sta-

tistically, the strong fit of a power curve implies a functional dependence of BMR on body mass (Kozłowski and Weiner 1997). Interspecific BMR allometries often scale mass with an exponent of 0.75 (Kleiber 1932; Brody 1945).

However, a single regression with a slope of 0.75 often does not adequately predict the BMR of mammals (Hayssen and Lacy 1985; McNab 1988; Heusner 1991). For example, log-transformed BMR data have been described better by two regression lines (data outside and within 95% confidence intervals) with similar slopes of 0.67 but different intercepts (Heusner 1991). Also, taxon-specific exponents are often significantly different from 0.75 (Hayssen and Lacy 1985), and exponents may differ significantly between small and large mammals (Harvey and Elgar 1987; Jürgens 1989). Last, the residual variation of BMR may exceed one order of magnitude at the same body mass (McNab 1988). These observations have called into question any direct functional relationship of BMR with body mass and ask for explanations of BMR variance based on underlying mechanisms (Kozłowski and Weiner 1997).

The residual variance of BMR has been correlated with biotic factors, such as taxonomic arrangement (Hayssen and Lacy 1985), life-history parameters (Harvey et al. 1991), and food habits (McNab 1986), and with abiotic factors, such as ambient temperature (MacMillen and Garland 1989) and habitat, specifically aridity (McNab and Morrison 1963; Hulbert and Dawson 1974; Shkolnik and Schmidt-Nielsen 1976; Lovegrove 1986; Lovegrove et al. 1991). Generally, abiotic associations are less common than biotic explanations, perhaps because early studies emphasized the lack of correlation with broad-scale geographic influences such as latitudinal temperature gradients (Scholander et al. 1950). Nevertheless, apart from mechanisms that predict low BMRs in desert mammals (Parsons 1991), plausible mechanisms accounting for the evolution of BMR have not been forthcoming.

Lately, optimal resource allocation models have probed the evolutionary relationship, not only between metabolism and body size, but also between both of these traits and life-history parameters (see Chown and Gaston 1997 for overview). Two contrasting models in particular, by

[*] E-mail: lovegrove@nu.ac.za.

Brown et al. (1993) and Kozłowski and Weiner (1997), highlight the dichotomous views on the functional dependence of physiological traits on body size.

Brown et al. (1993) predict that a single, optimal taxon-specific body mass can be determined by the rate of resource acquisition from the environment and, hence, the amount and rate of energy that can be partitioned to reproduction. The model assumes that allometric exponents remain constant among different kinds of organisms and that the rate of energy acquisition from the environment scales with the same exponent (0.75) as that of "individual metabolism." The model therefore implicitly assumes a functional relationship between metabolism and body size. The validity of several other assumptions of the model have been questioned (Blackburn and Gaston 1994; Kozłowski 1996; Chown and Gaston 1997).

Kozłowski and Weiner (1997), on the other hand, argue that within-species dependencies of physiological parameters, such as respiration, assimilation, and production, and life-history parameters, such as mortality rates, determine intraspecific optimal body sizes. They show that interspecific allometries are by-products of body size optimization and the distributions of intraspecific production and mortality parameters. Using randomly generated constants and exponents to simulate intraspecific allometries of assimilation and respiration, they obtained significant interspecific allometries of various physiological traits as well as strong correlations between age at maturity and life expectancy after body size effects were removed (Kozłowski and Weiner 1997).

One novelty of the Kozłowski and Weiner (1997) model is that the within-species variance of physiological traits used to generate a plausible relationship between age at maturity and life expectancy may be indicative of an underlying "slow-fast" continuum of metabolic rate associated with the variation of life-history parameters. The model emphasizes that physiological variance is not random noise surrounding a functional power relationship but probably reflects selective processes that optimize body size for production. Therefore, their model highlights more than ever before the urgent need to identify the selection processes/mechanisms associated with within-species variance of traits such as BMR.

One approach is to establish whether the variance of metabolic traits can be associated with environmental variability. Generally in the quest for modelling simplicity, resource allocation models tend to model optimality in "saturated" (Brown et al. 1993) or "aseasonal, constant" environments (Kozłowski and Weiner 1997). Thus, the likelihood that the evolution of physiological traits may be influenced by spatial and temporal resource availability is seldom considered.

In this article, I provide empirical evidence of an as-sociation of BMR variance with broad-scale, global latitudinal and zonal climate patterns that influence the temporal and spatial reliability of resources. I argue that rainfall variability in particular may be very important in selection of BMR and show that mammalian BMR varies significantly among the six terrestrial zoogeographical zones. I interpret these patterns with a conceptual model that argues that the evolution of BMR and the energetic perspective on life histories should not be considered in isolation of resource predictability gradients and predation and related size-dependent parameters, such as home range, dispersal ability, and running speed.

Broadscale Global Climatic Patterns

Latitudinal Patterns

The most obvious latitudinal climate gradient on Earth is the general decrease in the mean annual temperature from the Tropics to the higher latitudes (Budyko 1986; Mann et al. 1998). Rainfall patterns are less generalized, but three principal latitudinal zones of ground-level air divergence and convergence determine yearly and seasonal rainfall patterns within both hemispheres (Barry and Perry 1973; Perry and Walker 1977; Tyson 1986; fig. 1).

The Tropics (0°–20° south or north) and temperate latitudes (40°–60° south or north) are dominated by low-pressure, convergent circulation systems, whereas the semitropics (20°–40° north and south) are dominated by
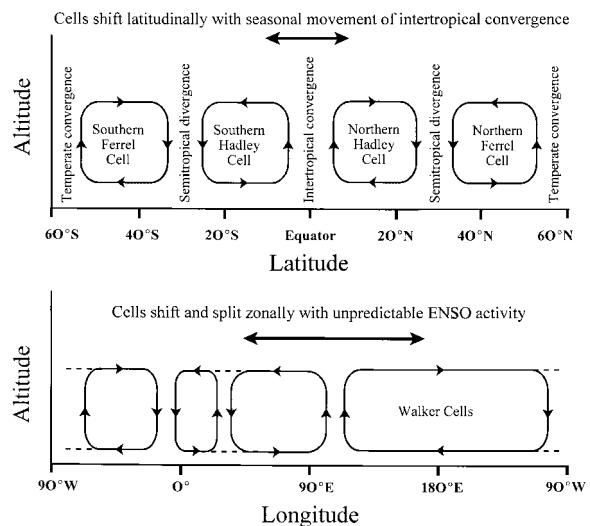

Figure 1: Simplified schematic representation of the major latitudinal and zonal (longitudinal) atmospheric circulation systems showing the major zones of ground level convergence (low pressure) and divergence (high pressure) that influence spatial and temporal rainfall patterns globally. Simplified and redrawn from Tyson (1986).

high-pressure, divergent systems (fig. 1). The zones of convergence and divergence are determined by the location of Hadley and Ferrel cells of circulating air masses (Barry and Perry 1973; Perry and Walker 1977; Tyson 1986). Seasonal north-south movements of the equatorial intertropical convergence zone (ITC) influence the geographical position of these latitudinal cells accounting for most of the predictable seasonal patterns of climate (Perry and Walker 1977). As a broad generalization, dominating high-pressure systems generate unpredictable low rainfall (semiaridity and aridity), whereas dominating low-pressure systems generate moderate to high predictable rainfall (Tyson 1986; Stone et al. 1996).

Zonal Effects

Latitudinal weather systems are also influenced by east-west zonal circulation cells (fig. 1). Arguably, the most important of these in terms of anomalous rainfall is the tropical Walker Circulation (fig. 1; Tyson 1986; Allan et al. 1996). The temporal geographical location of the Walker cells is determined by the prevailing tropical easterlies, the strength and direction of which is influenced by the El Niño–Southern Oscillation (ENSO; Tyson 1986; Glantz et al. 1991; Allan et al. 1996). Resultant ENSO-induced zonal shifts in the Walker cell bring about periodic El Niño and La Niña events that cause marked rainfall anomalies over vast geographical regions (Tyson 1986; Allan et al. 1996; Stone et al. 1996).

Although any particular geographical region may be dominated, for example, by a convergent low-pressure zone (e.g., the Tropics), and hence would theoretically be considered a zone of reliable seasonal rainfall, temporal effects of ENSO can cause extended periods of subsidence and drought during the rainy season. This is particularly pertinent in parts of the Indomalayan zoogeographical zone where ENSO causes regular failures of the monsoon rains (Harger 1995; Stone et al. 1996; Chang 1997; Gopinathan 1997).

Zoogeographical Zones

Of the six terrestrial zoogeographical zones of the world (sensu Udvardy 1975), four zones, the Indomalayan, Australasian, Afrotropical, and, in certain regions, the Neotropical zones, are strongly influenced by temporal shifting of zonal circulation systems (NOAA 1994; Allan et al. 1996; Stone et al. 1996). The frequency of negative rainfall anomalies is generally high in these zones, as are indices of long-term rainfall variability (Allan et al. 1996; Stone et al. 1996).

On the other hand, the Nearctic and the Palearctic zones fall within predominantly convergent climate zones, and both are highly seasonal. ENSO is not associated with widespread negative rainfall anomalies in these zones, and hence, rainfall is more predictable relative to ENSO-afflicted regions (Stone et al. 1996). The predictability of exceeding the median rainfall can be low in regions of Europe and North America following the "rapid fall" phase of the Southern Oscillation index (SOI), but typically, rainfall is predictable during the low SOI phases, that is, during the peak of El Niño events, except at the very highest latitudes (Stone et al. 1996).

Methods

Data for the BMR (mL O_2/h) and body masses (g) of 487 nondomesticated mammalian species were taken from the literature. They are available from the author on request and in the online edition of the *American Naturalist*. A taxonomic summary of the data is provided in table 1. Data published as resting metabolic rates (RMR) were accepted as basal if authors argued that their measured rates were realistic estimates of BMR or a minimum observed metabolic rate in resting animals at thermoneutrality. Where more than one BMR measure for a species was available, the mean BMR and M_b was calculated. Species were classified as either mesic or desertic. Desert species were defined as those for which at least 95% of the distribution range occurred within the 500-mm mean annual rainfall isohyet. Species were also assigned to one of the six zoogeographical zones of the world. Species inhabiting more than one zone were excluded.

Conventional and phylogenetically independent (PI) ANCOVA were used to test for zone differences in BMR. However, PI ANCOVA were restricted to rodents because these were the only data represented sufficiently within zones (see table 1) that also revealed homogeneous slopes of the regressions of BMR and M_b among zones (shown in "Results"). The latter condition is a requirement for subsequent analysis of variance (Zar 1984). To minimize the number of unresolved polytomies in the rodent phylogeny (data are available from the author on request and in the online edition of the *American Naturalist*), I used mean BMR and body mass data for 105 genera rather than species data. Although this procedure theoretically defeats the purpose of independent species data, Harvey and Pagel (1991, p. 193) have shown that the relationship between BMR and body mass in mammals does not differ at different taxonomic levels. Unresolved polytomies are especially troublesome within genera represented by many species for which phylogenetic relationships are either obscure or completely unknown. This procedure introduced the problem of a few shared genera among zoogeographical zones. Rather than discard these genera, that is, the procedure followed for species common to more than one

Table 1: Number of mammal species used in the analyses of BMR and body mass for six zoogeographical zones

Mammal order	Afrotropical	Australasian	Indomalayan	Nearctic	Neotropical	Palearctic	Total
Artiodactyla	6	7	1	3	0	2	19
Carnivora	9	0	4	6	4	1	24
Chiroptera	1	0	3	4	29	0	37
Dasyuromorphia	0	20	0	0	0	0	20
Didelphimorphia	0	0	0	0	9	0	9
Diprodontia	0	22	0	0	0	0	22
Hyracoidea	4	0	0	0	0	0	4
Insectivora	20	0	1	8	0	11	40
Lagomorpha	0	0	0	6	0	1	7
Macroscelidae	7	0	0	0	0	0	7
Monotremata	0	4	0	0	0	0	4
Peramelemorphia	0	6	0	0	0	0	6
Philodota	1	0	2	0	0	0	3
Primates	10	0	1	0	6	0	17
Rodentia	53	12	3	96	56	28	248
Scandentia	0	0	3	0	0	0	3
Sirenia	0	0	0	0	1	0	1
Tubulidentata	1	0	0	0	0	0	1
Xenarthra	0	0	0	0	15	0	15
Total	112	71	18	123	120	43	487

zone, I regarded shared genera as separate data points for each respective zone. The genera involved were *Heteromys*, *Liomys*, *Peromyscus*, *Pitymys*, and *Sigmodon* (Nearctic and Neotropical); *Arvicola*, *Clethrionomys*, and *Microtus* (Nearctic and Palearctic); and *Gerbillus* and *Mus* (Afrotropical and Palearctic).

The significance of *F* statistics calculated from ANCOVA was tested against PI null *F* distributions generated by 1,000 Monte Carlo simulations using the program PDSIMUL and PDANOVA (Garland et al. 1993). Three evolutionary models were used, assuming Brownian motion as the null process of evolution: gradual, gradual with bounds, and speciational (Garland et al. 1993). For each model, the critical value for $\alpha = 0.05$ (95th percentile) of the null *F* distribution was determined and compared with that of conventional tables. The phylogeny of rodent genera was constructed with PDTREE (Garland et al. 1993). Sufficient branch length information was not available for all 105 rodent genera, and hence, branch lengths were chosen arbitrarily according to the method of Pagel (1992). A value of Grafen's (1989) $\rho = 0.8$ was used to standardize branch lengths adequately (see Garland et al. 1992). Adequacy was indicated by nonsignificant correlations ($P > .05$) between standardized contrasts and the square root of the sum of branch lengths for both body mass (two-tailed test; $r = 0.170$, $t = -1.732$, df = 102) and BMR ($r = 0.145$, $t = -1.495$).

For two models (gradual and speciational), the correlation between body mass and BMR was set to 0. Starting values of BMR and body mass were set to values equal to input values, and no bounds were set. For the third model (gradual with bounds), body mass and BMR bounds were set, and the correlation of variables was set to that obtained from the regression of independent linear contrasts of the variables ($P < .05$, $t = 2.228$, df = 103, $r^2 = 0.826$, slope = 0.677 ± 0.060). The bounds algorithm was set to "replace." The lower body mass limit was $\log_{10} M_b = 0.176$ (i.e., 1.5 g) and the upper limit $\log_{10} M_b = 5$ (i.e., 100,000 g). The upper limit was based upon estimates of the size of *Telicomys*, an extinct caviomorph rodent from the Late Miocene and Pliocene (Benton 1990). The lower BMR limit was $\log_{10} BMR = 0.867$ (i.e., 7.36 mL O_2/h), and the upper limit $\log_{10} BMR = 3.872$ (i.e. 7,441 mL O_2/h). These BMR limits were calculated from the allometric equation for rodents calculated from conventional regression analysis of species data; that is, it was assumed that the BMR of the ancestral rodents was not significantly different from that of the extant species. No trends were set.

Results

Residual BMR: The Bowtie Effect

The linear regression of $\log_{10} BMR$ as a function of $\log_{10} M_b$ for all ($n = 487$) mammal species was $\log_{10} BMR = 0.614 + 0.690 \log_{10} M_b$ ($F = 7304.7$, df = 1, 486, $r^2 = 0.938$, $P < .001$) The residual BMRs calculated from this regression revealed an unexpected pattern of large residuals at the smallest and largest body masses and of the smallest

residuals at intermediate body masses (fig. 2*A*). For ease of subsequent discussion, I term this observation of low variances at intermediate log body masses the "bowtie effect." Absolute residuals within 10 body-size classes ($\log_{10} = 0.5$ intervals) were significantly different (ANOVA: $F = 10.46$, df = 9, 477, $P < .001$; fig. 2*B*). A polynomial quadratic equation fitted to mean absolute residuals and mean $\log_{10}$ body masses of each size class ($y = 0.0324x^2 - 0.1655x + 0.313$; $r^2 = 0.941$) gave a minimum at $\log_{10}$ body mass $= 2.554$ (i.e., 358 g; fig. 2*B*). Again, for ease of reference, I term this body mass associated within minimum BMR variance the "constrained body mass" (CBM) and "small" and "large" mammals refer to mammals either smaller or larger than the CBM, respectively.

I investigated the residuals further to verify that the bowtie effect was not an artifact of either body size or sample size (fig. 3). Large variances may occur at large body sizes because of the high quantitative values of BMR at the largest body sizes or in size classes with small sample sizes.
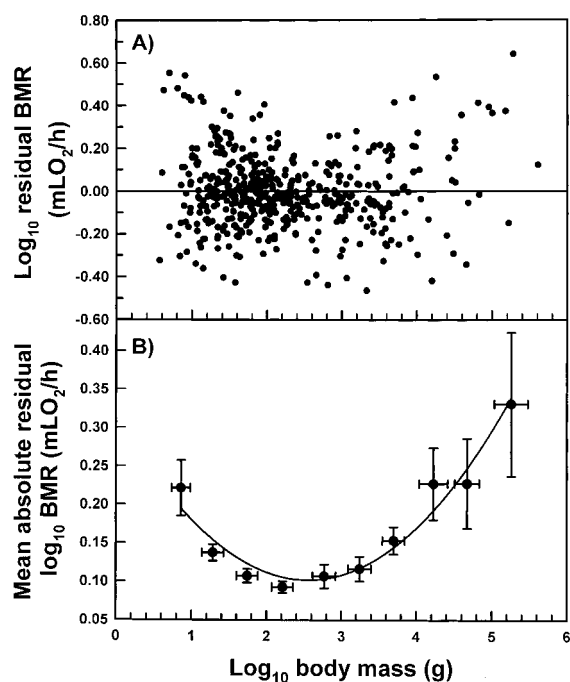

Figure 3: BMR variance calculated for the same data in figure 2*B* showing the number of species within each size class. *A*, Simple linear regression of BMR variance within each size class as a function of sample size. *B*, Variances calculated from residual BMR values of 25 species subsampled at random from each size class. Data for mammals $> \log_{10} = 4.0$ were pooled because of small sample sizes.

A correlation of the variance of each size class with its sample size revealed, as expected, a significant negative linear relationship ($F = 11.69$, df = 9, $r = 0.77$, $P < .05$; fig. 3*A*). To test whether the bowtie effect was, thus, sample-size dependent, I calculated the variances for 25 species chosen randomly from each size class (the last three size classes were pooled because of low species numbers). This analysis also revealed maximum BMR variances at the smallest and largest body sizes and the bowtie effect at intermediate size classes (fig. 3*B*). Hence, the bowtie effect cannot be explained by either sample size or the quantitative value of BMR. In the latter respect, the smallest size class with the lowest theoretical quantitative BMR values had high subsampled BMR variances equal to those of the largest size class (fig. 3*B*).

Figure 2: *A*, Residuals of mass-specific $\log_{10}$ BMR (mL O_2/h) calculated from the linear regression of $\log_{10}$ BMR and $\log_{10}$ body mass (g) and expressed as a function of $\log_{10}$ body mass. The data for 487 species of mammals representing six zoogeographical zones were taken from the literature. *B*, Mean $\pm$ SE absolute residual BMR (mL O_2/h) calculated for 10 body size classes (bin interval: $\log_{10} = 0.5$). The body mass error bars are $\pm$ 1 SD. A quadratic polynomial equation fitted to the data ($y = 0.032x^2 - 0.167x + 0.313$; $r^2 = 0.94$) gave a minimum at $\log_{10} = 2.554$ g (i.e., 358 g).
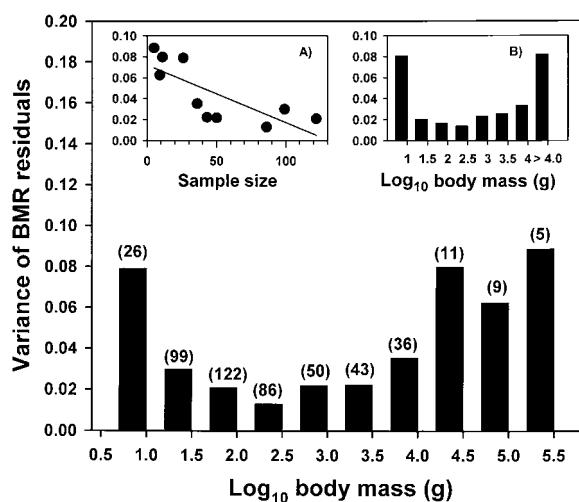
Aridity Effects

For mammals of all sizes, the slopes of regressions for desert and mesic species were not significantly different, although basal rates differed significantly (table 2). Overall, desert species have a lower BMR than mesic species. On average, the BMR of a 10-g desert mammal is 24.31% lower than that of its mesic counterpart. The difference decreases with increasing body size to 6.2% at 10 kg. To control for this habitat effect, in subsequent ANCOVA mesic and desert mammals were analyzed separately.

Table 2: Statistics of conventional linear regression and ANCOVA of species data of $\log_{10}$ body mass and $\log_{10}$ BMR for mesic mammals and desert mammals within six zoogeographical zones

Source of variation	df	a	b	SS	MS	F
Desert	109	.505	.710	...	...	2,518[*]
Mesic	376	.657	.679	...	...	5,341[*]
Slopes	1	...	...	.064	.009	2.26[a]
Error	483	...	...	13.68	.017	...
Habitats	1	...	...	.670	.670	23.61[*]
Body mass	1	...	...	68.62	68.62	7,436[*]
Error	484	...	...	13.74	.028	...
Total	486	...	...	231.53	.476	...

Note: Constants a and b represent the y-intercept and the slope of the equation $\log_{10}BMR = a + b\log_{10}M_b$, respectively; $\log_{10}$ body mass = g, and $\log_{10}$ BMR = mL O_2/h. Mesic mammals, $n = 377$; desert mammals, $n = 110$.

[*] $P < .05$.
[a] Not significant ($P > .05$).

General Effects

A small sample size ($n = 2$) precluded the Indomalayan desert species from analysis, and the Afrotropical large desert mammal regression was not significant (table 3). All other conventional ANCOVA revealed significantly different slopes ($P < .05$) among zones for habitat (mesic and arid) and body size (small and large). Although all analyses also revealed significantly different BMR among zones, heterogeneous slopes render the test for BMR differences meaningless (Zar 1984).

Regression slopes varied markedly among zones within the small- and large-mammal guilds (table 3; see fig. 4 for mesic mammals plots). The Palearctic mammals had the lowest slope (0.417) for small mammals, as well as the highest slope (1.026) for small, desert mammals. The slopes for large mesic mammals often exceeded the 0.75 exponent. For example, the Palearctic, Afrotropical, and Nearctic zones had the highest slopes of 0.957, 0.900, and 0.830, respectively (table 3; fig. 4).

In the Palearctic and Afrotropical mesic mammal regressions there was a marked difference in the slope between small and large mammals (table 3). The Afrotropical slope for mesic mammals changed from 0.639 to 0.900, whereas, in the Palearctic, it virtually doubled from 0.489 to 0.957 (fig. 4). In short, the largest mammals within these zones have high basal rates. The Palearctic data are perhaps influenced by a small sample size ($n = 4$), but the Afrotropical data set was not ($n = 33$). Of the 15 largest Afrotropical mammals, 11 are either artiodactyls ($n = 6$) or carnivores ($n = 5$). The slope for the large Nearctic mammals was also high (0.830; table 3). Again, like the Afrotropical zone, the six largest Nearctic mammals were either artiodactyls ($n = 2$) or carnivores ($n = 4$).

Heterogeneous regression slopes, coupled with the present lack of a resolved mammal phylogeny for 487 species, unfortunately precluded PI ANOVA on the complete mammalian data set to further test for geographical effects on BMR. In any event, PI analyses are unlikely to alter the conclusion of heterogeneous slopes by conventional analysis because PI regressions of independent linear contrasts generally do not produce regression slopes significantly different from those of conventional regression models (Ricklefs 1996). This problem can be overcome, however, by restricting further analysis to subsets of the total mammalian data set.

Small Rodents

The rodents are a convenient group with which to analyze geographic BMR effects because they are better represented within all zones than any other group (table 1) and their small body sizes avoid the bowtie effect that contributes to slope heterogeneity (fig. 5). The modal body size of the frequency distribution of 215 species smaller than the CBM occurred between 20–40 g, with 85% of species ($n = 182$) less than half the size of the CBM (fig. 5). Again, the Indomalayan zone was excluded because of small sample size ($n = 2$).

The regression slopes for species pooled for habitat (mesic and arid) of the five remaining zones were not significantly different among zones, but basal rates were (table 4). The lowest intercept value for the regression occurred for the Afrotropical zone, whereas the highest occurred for the Palearctic zone (table 5). The mean Afrotropical residual BMR was significantly lower than those of the Nearctic, Neotropical, and Palearctic zones, whereas the Palearctic mean was significantly higher than those of the Afrotropical, Australasian, and Neotropical zones (Tukey test; fig. 6A). The mean residual BMR values for the Afrotropical and the Australasian zones were both nega-

Table 3: Statistics of conventional linear regression analyses of mammal species data of $\log_{10}$ body mass (g) and $\log_{10}$ BMR (mL O_2/h) for various habitat (desertic and mesic) and body size categories for the six zoogeographical zones

	All				Small				Large			
Zone	df	*a*	*b*	*F*	df	*a*	*b*	*F*	df	*a*	*b*	*F*
Mammal:												
Afrotropical	110	.503	.773	2,680[*]	72	.496	.718	330[*]	36	−.080	.899	626[*]
Australasian	69	.668	.698	2,637[*]	35	.494	.706	338[*]	32	.658	.656	263[*]
Indomalayan	16	.707	.681	423[*]	6	.157	.890	232[*]	8	.664	.640	56[*]
Nearctic	121	.602	.728	1,856[*]	99	.753	.637	357[*]	20	.317	.821	345[*]
Neotropical	118	.737	.667	2,978[*]	76	.498	.752	686[*]	40	.747	.630	264[*]
Palearctic	41	.858	.641	357[*]	33	1.201	.417	36[*]	6	−.080	.884	193[*]
Common	485	.614	.690	7,305[*]	331	.697	.643	1,020[*]	152	.292	.780	1,232[*]
Mesic mammals:												
Afrotropical	86	.418	.765	2,178[*]	53	.661	.639	219[*]	31	−.074	.900	503[*]
Australasian	49	.569	.680	1,370[*]	22	.514	.706	232[*]	26	.266	.774	362[*]
Indomalayan	14	.515	.683	340[*]	4	.157	.891	153[*]	8	.664	.640	56[*]
Nearctic	90	.680	.707	1,309[*]	70	.808	.625	277[*]	17	.287	.830	254[*]
Neotropical	96	.610	.676	2,504[*]	61	.472	.762	558[*]	33	.794	.620	214[*]
Palearctic	30	.893	.667	352[*]	26	1.143	.489	57[*]	2	−.201	.957	264[*]
Common	376	.657	.679	5,341[*]	247	.768	.615	732[*]	128	.328	.773	865[*]
Desert mammals:												
Afrotropical	22	.352	.764	213[*]	17	.110	.926	131[*]	3	−1.062	1.260	4.65[a]
Australasian	18	.434	.719	1,497[*]	11	.523	.660	91[*]	5	.262	.765	192[*]
Nearctic	29	.478	.756	761[*]	26	.644	.640	147[*]	1	.477	.776	224[*]
Neotropical	19	.861	.571	605[*]	13	.780	.613	261[*]	5	1.048	.510	9.30[*]
Palearctic	9	.407	.734	308[*]	5	−.100	1.026	40[*]	2	−.008	.824	304[*]
Common	106	.505	.710	2,471[*]	81	.485	.730	410[*]	20	.204	.791	463[*]

Note: Variables *a* and *b* represent the *y*-intercept and the slope of the equation $\log_{10}\text{BMR} = a + b\log_{10}M_b$, respectively. Small and large mammals are smaller and larger than the CBM (358 g), respectively.

[*] $P < .05$.

[a] Not significant ($P > .05$)

tive, indicating lower than average BMR values compared with all rodents (fig. 6*A*).

The species data for desert rodents, on the other hand, showed significantly different slopes among zones (table 4). The notable regressions were those for the Afrotropical and Palearctic, which respectively had very steep slopes (0.908 and 1.026) and low *y*-intercept values (0.118 and −0.064; table 5).

The species analysis of mesic rodents was similar to that for pooled rodent species, namely, homogeneous slopes but significantly different BMR values among zones (table 4). The mean Afrotropical residual BMR was again significantly lower than those of the Nearctic, Neotropical, and Palearctic zones (Tukey test; fig. 6*B*). Moreover, the mean Australasian and Neotropical residual BMR values were significantly lower than that of the Palearctic (fig. 6*B*). In this analysis, however, the mean residual BMR value for the Neotropical zone was, like those for the Afrotropical and the Australasian zones, negative, indicating slightly lower-than-average BMR values (fig. 6*B*).

Like the pooled rodent species analysis, the rodent genera analysis revealed homogeneous regression slopes among zones and significantly different BMRs (table 6;slopes and intercepts in table 5). Again, the mean Afrotropical residual BMR was significantly lower than those of the Nearctic, Neotropical, and Palearctic zones (Tukey test; fig. 6*C*). The mean residual BMR values for the Afrotropical and the Australasian zones were also negative (fig. 6*C*).

The PI analysis of rodent genera confirmed the statistical conclusion of the conventional species ANCOVA, namely, homogeneous slopes but significantly different BMR among zones. The critical values ($\alpha = 0.05$) of the *F* statistic for the zone effect on BMR calculated from null *F* distributions generated by all three evolutionary models (gradual Brownian, gradual Brownian with bounds, and speciational) were lower than the observed *F* statistic calculated using conventional ANCOVA ($F = 11.66$; table 6).

Quantitative Differences in BMR between Zoogeographical Zones

Heterogeneous slopes among zones limit options for evaluating the BMR for all mammals to comparisons of BMR
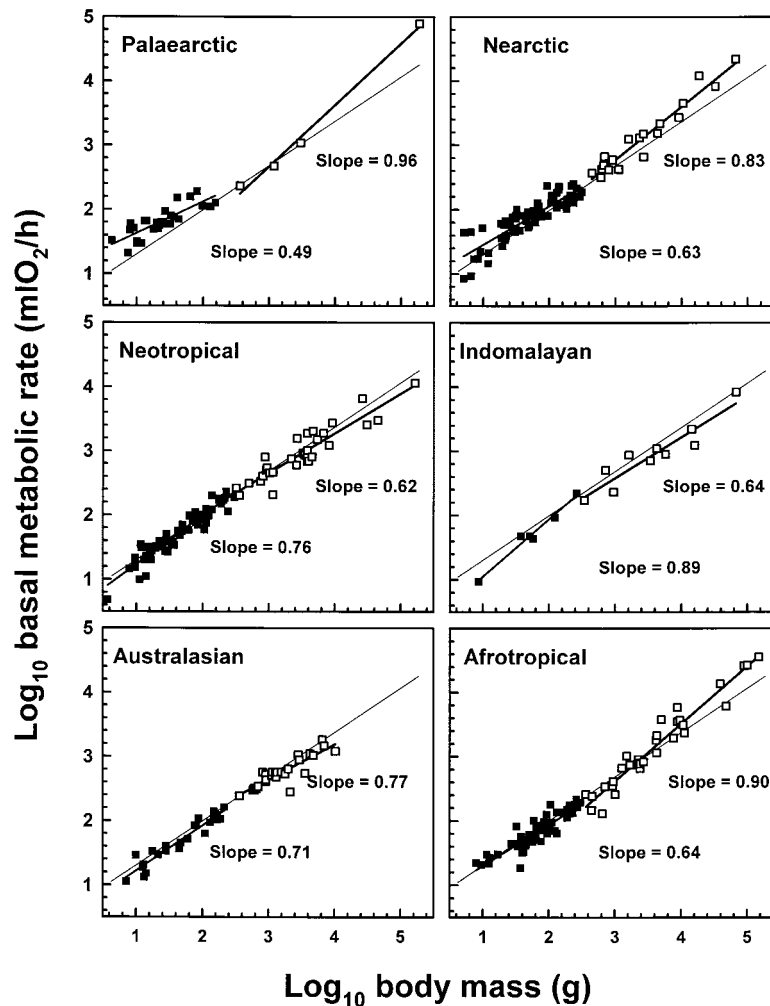
Figure 4: Linear regressions of $\log_{10}$ BMR (mL O$_2$/h) and $\log_{10}$ body mass (g) for small mesic mammals (<358 g; *filled squares*) and large mesic mammals (>358 g; *open squares*) for six zoogeographical zones. For regression statistics, see table 3. The thin line in each graph represents the regression for all 487 mammals (slope = 0.690).

predicted from regression equations for various habitat and body size categories. As a guide to the magnitude of average differences in BMR, I calculated the BMR predicted for hypothetical 10-g and 10-kg mammals and listed the values in order of increasing BMR (table 7).

The predicted BMR of small (10-g) mesic mammals varied by approximately 3.8-fold between the lowest value (Indomalayan zone) and the highest (Palearctic mammals; table 7). Small mesic mammals in the four ENSO zones had the lowest BMRs, whereas counterpart Nearctic and Palaearctic mammals had the highest basal rates (table 7). This disparity of basal rates is generated in part by the high basal values for soricid shrews in the Palearctic and

Nearctic, but the shrews certainly do not determine the overall pattern of BMR differences among zones because the rodent analyses revealed similar patterns (fig. 6A–6C).

The lowest BMRs for small desert species occurred in specialist desert species from some of driest deserts of the world (see Mares 1999): the Sahara (Palearctic); Namib, Kalahari, and Karoo (Afrotropical); and the interior deserts of Australia (table 7). Seven gerbil species (*Gerbillurus*, *Meriones*, and *Jaculus*) from the Sahara Desert have the lowest basal rates of the Palearctic desert species—all other small Palearctic mammals tend to have very high basal rates (table 7). Ten of the 19 Afrotropical small desert mammals are also specialist desert rodents (*Gerbillurus*,
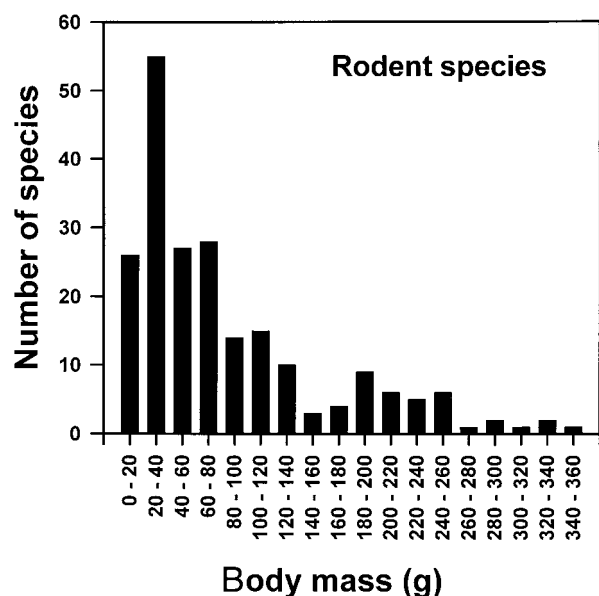
Figure 5: Body-size frequency distribution of rodents (used in this study) smaller than the constrained body mass of 358 g.

Malacothrix, Desmodillus, Parotomys, Otomys, and *Thallomys*) from the Namib and Kalahari Deserts contributing to the low average BMR predicted for this zone.

There was roughly a 2.5-fold difference between the lowest (Indomalayan) and the highest (Palearctic) predicted BMR of a large 10-kg mesic mammal (table 7). This difference presumably increases further at larger body sizes because of the increasing divergence of regressions at larger body masses (fig. 4). Generally, large mesic mammals in the ENSO zones have lower basal rates than Nearctic and Palearctic mammals.

Discussion

Heterogeneous slopes of BMR regressions among zoogeographical zones confirm that a single allometric relationship does not meaningfully predict BMR over all mammalian body sizes. They also highlight the considerable and significant BMR variance surrounding a common allometry, especially at the smallest and largest body sizes. However, the most unexpected observation was that a minimum BMR variance occurred at intermediate body sizes on a logarithmic scale (bowtie effect).

The lack of a common scaling exponent even within zones can be illustrated by data for Palearctic mesic mammals (fig. 4). Small-mammal BMR scaled with a slope of 0.49, large mammals with a slope of 0.96, and the common regression with a slope of 0.67. The small- and large-mam-

mal regressions converge at the CBM, and both indicate basal rates higher than the regression for all mammals. None of these slopes is equal to, or even close to, the 0.75 exponent, and the common slope (0.67) simply represents the average slope for small and large mammals. It has minimal predictive value.

Although the difference in the exponents between small and large mammals is admittedly maximal in the Palearctic zone, which has a small sample size, the disparity is common to all zones. Two general patterns are apparent. First, high slopes for small mammals (i.e., low BMRs) are generally restricted to the ENSO zones (especially the Indomalayan, Australasian, and Afrotropical zones), whereas low slopes (high BMRs) characterize the Palearctic and Nearctic zones (table 7; fig. 4). Second, high slopes for large mammals generally occur in those zones represented by high proportions of Artiodactyla and Carnivora (Afrotropical, Palearctic, and Nearctic).

On the other hand, homogeneous slopes and significantly different BMRs between mesic and desert regressions confirm the strong global influence of aridity on BMR (see introductory paragraphs). In addition, a strong geographical effect on BMR is particularly evident within mesic small mammals (rodents). Although abiotic factors, such as rainfall unpredictability, may explain these zone effects fairly well (see "A Predictive Model"), additional factors are needed to explain the apparent taxonomic influence (e.g., high BMRs of artiodactyls and carnivores) on BMR variation in large mammals. The model presented below attempts to elucidate these factors, as well as those associated with the bowtie effect.

A Predictive Model

Attempts to model latitudinal effects on mammalian BMR face the problem of separating latitudinal or regional temperature effects from those involving temporal and spatial resource availability. Scholander et al. (1950), however, made the early observation that the BMR of mammals is not influenced by latitudinal mean annual temperature. These authors argued that insulation rather than BMR in birds and mammals is the principal adaptation to temperature. On the other hand, MacMillen and Garland (1989) reported significant ambient temperatures effects on the BMR of *Peromyscus* species from various habitats. However, species with low BMRs in their study occurred in hot deserts with unpredictable rainfall, a pattern consistent with the predictions of this study.

For the purposes of the model, I have assumed that temporal and spatial resource availability, and not temperature, represent the principal latitudinal forces involved in BMR selection. Nevertheless, I do not discount the possibility that the magnitude of BMR differences among

zones may be either directly or indirectly associated with mean annual temperature. The role of mean annual temperature clearly requires further investigation beyond the scope of this article.

The model hinges on the assumption that the global effect of aridity in selecting for low BMRs is indicative of an underlying mechanism or selection process common in all habitats. I assume that the low BMRs of desert mammals represent the slow end of a slow-fast metabolic rate (and life history?) continuum determined by the reliability of resource availability (fig. 7). In essence, I argue that BMR is determined by the lowest resource availability in time and space, but may be influenced in addition by size-dependent predation and mobility parameters (fig. 7).

Generally, low basal rates in desert animals are thought to offset the high energetic costs of maintaining physiological homeostasis in response to aridity stresses such as heat and cold, and food and water scarcity (MacMillen and Hinds 1983; Hinds and MacMillen 1985; Parsons 1991). However, it is questionable whether evolutionary novelties, such as low BMR, evolve in direct response to such stresses (Dobson and Crawley 1987; Seely 1989; Ward and Seely 1996). The alternative is that episodic and unpredictable spatial and temporal flushes of resources select for the overall physiological machinery of desert animals (Dobson and Crawley 1987). Thus, I argue that the low BMRs of desert mammals confirmed in this study are evidence of ultimate evolutionary responses to unpredictable resource availability.

Resource availability in deserts is determined primarily by rainfall (Noy-Meir 1973; Louw and Seely 1982; Southgate et al. 1996), which is typically low with a high annual variability (Lovegrove 1993; Mares 1999). However, high rainfall variability is not necessarily restricted to arid zones. It also occurs in mesic zones subject to temporal zonal perturbations (e.g., ENSO) that generate different magnitudes and frequencies of rainfall anomalies with respect

Table 5: Statistics of conventional linear regression analyses of $\log_{10}$ body mass and $\log_{10}$ BMR data of all rodent species and genera smaller than the CBM for five zoogeographical zones

Zone	df	*a*	*b*	*F*
All rodent species:				
Afrotropical	42	.420	.753	137[*]
Australasian	8	.733	.599	110[*]
Nearctic	86	.725	.652	369[*]
Neotropical	39	.694	.669	622[*]
Palearctic	25	1.021	.519	29[*]
Common	209	.757	.623	621[*]
Desert rodent species:				
Afrotropical	10	.118	.908	75[*]
Australasian	2	.729	.601	1,041[*]
Nearctic	24	.664	.650	139[*]
Neotropical	13	.780	.613	260[*]
Palearctic	5	−.064	1.026	40[*]
Common	62	.561	.696	317[*]
Mesic rodent species:				
Afrotropical	30	.595	.671	69[*]
Australiasian	4	.782	.577	5.88[*]
Nearctic	59	.880	.589	229[*]
Neotropical	24	.671	.685	376[*]
Palearctic	18	.969	.592	52[*]
Common	143	.901	.563	368[*]
Rodent genera:				
Afrotropical	26	.376	.774	99[*]
Australasian	2	.686	.635	82[*]
Nearctic	29	.719	.672	201[*]
Neotropical	25	.702	.663	309[*]
Palearctic	13	1.020	.528	29[*]
Common	103	.749	.630	325[*]

Note: Here, $\log_{10}$ body mass = g, and $\log_{10}$ BMR = mL O_2/h. All rodent species, $n = 209$; all genera, $n = 105$. Separate species analyses are shown for mesic ($n = 146$) and desert rodents ($n = 64$). The variables *a* and *b* represent the *y*-intercept and the slope of the equation $\log_{10}BMR = a + b\log_{10}M_b$, respectively. The Indomalayan zone was excluded because of a small sample size ($n < 3$).

[*] $P < .05$.

Table 4: Conventional ANCOVA of species data of $\log_{10}$ body mass and $\log_{10}$ BMR for all rodents, desert rodents, and mesic rodents smaller than the CBM, for five zoogeographical zones

Source of variation	All rodent species				Desert rodents				Mesic rodents			
	df	SS	MS	*F*	df	SS	MS	*F*	df	SS	MS	*F*
Slopes	4	.108	.027	1.652[a]	4	.103	.026	3.343[*]	4	.037	.010	.624[a]
Error	200	3.277	.016	...	54	.417	.008	...	135	2.024	.015	...
Zones	4	.788	.197	11.866[*]	4	.191	.048	5.338[*]	4	.723	.181	12.188[*]
Body mass	1	13.090	13.090	788.79[*]	1	3.295	3.295	367.48[*]	1	7.732	7.732	521.32[*]
Error	204	3.385	.017	...	58	.520	.009	...	139	2.062	.015	...
Total	209	16.636	.080	...	63	4.348	.070	...	144	9.943	.069	...

Note: All rodents, $n = 209$; desert rodents, $n = 64$; mesic rodents, $n = 145$. The Indomalayan zone was excluded. See table 5 for statistics of regression analyses; $\log_{10}$ body mass = g, and $\log_{10}$ BMR = mL O_2/h)
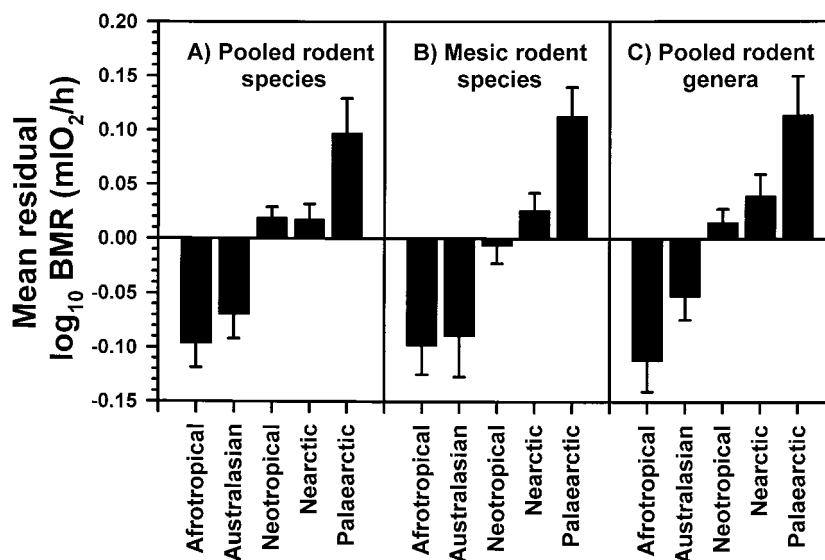
[*] $P < .05$.

[a] Not significant ($P > .05$).

Figure 6: Mean $\pm$ SE residual $\log_{10}$ total BMR (mL O_2/h) calculated from the linear regression of $\log_{10}$ BMR and $\log_{10}$ body mass (g) for (*A*) all rodent species (*n* = 210), (*B*) mesic rodents (*n* = 145), and (*C*) all rodent genera (*n* = 105), from five zoogeographical zones.

to the long-term rainfall average (Allan et al. 1996; Stone et al. 1996). Hence, selection for low BMRs associated with unpredictable rainfall caused by ENSO should "mimic" those of arid habitats to some extent. Selection in mesic ENSO zones may differ from those in true deserts only in terms of temporal scale; low resource availability may occur less frequently and for shorter sustained periods in nondesert ENSO zones but may be unpredictable, often aseasonal, and of severe magnitude nevertheless, for example, Indomalayan zone.

The fast end of the slow-fast metabolic rate continuum (high BMRs) would be represented by mammals inhabiting predictable environments in which rainfall is spatially and temporally predictable and influenced little, if at all, by ENSO-induced negative rainfall anomalies. In predictable environments, selection for high BMR may be favored if it optimizes production and reproduction. On the other hand, low BMRs in unpredictable environments may optimize survival and longevity over production and reproduction if equitable long-term reproductive output is to be achieved. Although the model does not pursue these predictions here, I allude to their relevance in terms of life-history predictions in closing.

Predictions for nonflying small mammals are likely to be most realistic using the single criterion of a resource predictability gradient because these mammals do not migrate but nevertheless face high mass-specific metabolic demands (Kleiber 1932). Migration is assumed to be constrained by various body size correlates, namely, daily movement distance (DMD; km/d) that scales positively

with body mass (1.038 mass$^{0.25}$; Garland 1983*b*), and a high cost of transport (COT; J/km; fig. 7; Taylor et al. 1970). Note, however, that the ecological cost of transport (ECT) of small mammals, expressed as a percentage of daily energy expenditure (DEE; J/d), is lower than that of large mammals (Garland 1983*b*). For example, the ECT of a 10-g mammal is 0.26% of its DEE, compared with 13% for a 10,000-g mammal (Garland 1983*b*). However, a low ECT may be irrelevant for small mammals in terms of migration benefits because physical and predation constraints may be more important in precluding migration.

Small mammals inhabiting regions with predictable, highly seasonal climates should display high basal rates because the energetic demands of a high mass-specific metabolism are not constrained by limited resource availability, despite a predictable harsh winter (fig. 7). On the other hand, small mammals in climatically unpredictable environments should display low basal rates. The lowest basal rates should occur in the smallest animals because they are most severely constrained by high mass-specific metabolic rates (fig. 7).

Although the above arguments may apply reasonably well at the very smallest body masses and explain the large residual BMR variance at these body sizes, at least two size-dependent factors should minimize BMR variance as body sizes approach the CBM; the capacity for heterothermy and constraints concerning predation.

First, the amplitude of circadian fluctuations of BMR and body temperature between the rest and active phase of the animal (RT curve in fig. 7) decreases with increasing

Table 6: ANCOVA of $\log_{10}$ body mass and $\log_{10}$ BMR of rodent genera with a body mass <358 g (CBM) from five zoogeographical zones (Afrotropical, Australasian, Nearctic, Neotropical, and Palearctic)

| Source of variation | SS | df | MS | F | Conventional tables | | Brownian | | | | | |
| | | | | | | | Gradual[a] | | Speciational[b] | | Gradual with bounds[c] | |
					Critical value	P	Critical value	P	Critical value	P	Critical value	P
Slopes	.078	4	.020	1.478	2.46	>.05	4.72	>0.05	5.92	>.05	4.84	>.05
Error	1.258	95	.013	...	...	...	...	...	...	...	...	...
Zones	.630	4	.157	11.66	2.46	<.001	8.47	<.05	10.75	<.05	8.85	<.05
Body mass	6.440	1	6.440	477.02	3.94	<.001	20.82	<.001	31.24	<.001	764.76	>.05
Explained	6.826	5	1.365	101.12	2.31	<.001	9.35	<.001	12.68	<.001	174.32	>.05
Error	1.336	99	.013	...	...	...	...	...	...	...	...	...
Total	8.162	104	.078	...	...	...	...	...	...	...	...	...

Note: Indomalayan zone was excluded because of a small sample size ($n < 3$); $\log_{10}$ body mass = g, and $\log_{10}$ BMR = mL O_2/h. Rodent genera, $n = 105$. Critical values of F statistics (95% percentile) for three models of character evolution were calculated from null-distributions of F generated by 1,000 computer simulations of data along a rodent phylogeny with the program PDSIMUL of Garland et al. (1993). The branch lengths of the phylogeny were arbitrarily chosen using Pagel (1992) and transformed with Grafen's (1989) value of $\rho = 0.8$ to standardize branch lengths.

[a] Correlation set to 0, starting values equal to final values, no bounds.

[b] Correlation set to 0, starting values equal to final values, no bounds.

[c] Correlation of input distributions (0.909), bounds algorithm = "replace," lower bounds ($\log_{10}M_b = 0.176$, $\log_{10}$BMR = 0.867), upper bounds ($\log_{10}M_b = 5.0$, $\log_{10}$BMR = 3.872), no trend.

body mass (Aschoff 1982). Reductions of metabolic rate during the rest phase reduce DEE (Lovegrove and Heldmaier 1994), a benefit maximized through daily torpor (Lyman et al. 1982). Large mammals, though, are effectively precluded from employing large circadian metabolic rhythms (Aschoff 1982) or daily torpor (Heldmaier 1989) as a means of conserving DEE. The constraint on torpor in large mammals often manifests at body sizes around 1,000 g, that is, close to the CBM (Aschoff 1982; Heldmaier 1989).

Second, predation risk is influenced by home-range size, distance to cover, foraging distance, and the size and dispersion pattern of foraging patches (Lima and Dill 1990; Morton 1990; Hughes and Ward 1993). I also assume that it may be minimized by increased running speed and running endurance. Running speed (MRS in fig. 7) scales positively with body mass (mass$^{0.17}$) before reaching an asymptote at a body mass of approximately 119 kg (Garland 1983a). Hence, although the smallest mammals are the slowest runners, their small home range requirements (HR in fig. 7) minimize the need to break cover to move between foraging patches relative to larger mammals (Morton 1990). They should, therefore, be exposed to lower predation risks than those whose increasingly larger body sizes and DEE require increased DMD between foraging patches and hence cover (Morton 1990). These latter intermediate-sized mammals may thus face the highest risks of predation because of their low running speeds and running endurance relative to larger predators, and their need to forage away from cover.

As body size approaches or slightly exceeds the CBM,

a mammal can be considered to be energetically "too small to be big and too big to be small." Minimum BMR variance at the CBM may be predicted from various opposing selection pressures. On the one hand, selection for low BMR should conserve energy if resource availability is unpredictable and there is decreased capacity for adaptive heterothermy. A lower BMR may also minimize home range and DMD requirements. However, this selection may be opposed by selection for high BMR to maximize running speed in response to increasing predation pressure (an assumption discussed further in "Running Speed and BMR").

If these selection pressures balance each other, the net result should be minimal BMR variance at or near the CBM. If the selection pressures are unbalanced, above- or below-average BMRs may result. For example, if predation pressure is weak (e.g., in predator-free environments) or offset by antipredator adaptations (e.g., morphological or behavioral defenses), weak selection for fast running speeds could result in very low basal rates. However, if predation pressure is intense and cannot be countered other than by fast running speeds, selection for above-average running speeds, and BMR may result.

Large, highly mobile mammals (e.g., migratory and nomadic species) are not constrained by local resource unpredictability because of their high DMD (fig. 7) and running endurance. They should, therefore, display high or average basal rates (fig. 7).

Large herbivores are capable of exploiting the temporal availability of cellulose resources, for example, perennial grasses, over vast regions of any continent. Cellulose is the

Table 7: Average basal metabolic rates (mL O_2/h) predicted from various categorical allometric equations for mammals (see table 3)

Zone	Predicted BMR
10-g mammals:	
All:	
Indomalayan	11.14
Australasian	15.85
Afrotropical	16.37
Neotropical	17.78
Nearctic	24.55
Palearctic	41.50
Mesic:	
Indomalayan	11.16
Australasian	16.62
Neotropical	17.14
Afrotropical	19.95
Nearctic	27.10
Palearctic	42.85
Desert:	
Palearctic	9.16
Afrotropical	10.86
Australasian	15.24
Nearctic	19.23
Neotropical	24.72
10-kg mammals:	
All:	
Indomalayan	1,674
Neotropical	1,849
Australasian	1,914
Palearctic	2,871
Afrotropical	3,274
Nearctic	3,990
Mesic:	
Indomalayan	1,675
Neotropical	1,882
Australasian	2,301
Afrotropical	3,356
Nearctic	4,045
Palearctic	4,240
Desert:	
Neotropical	1,225
Palearctic	1,941
Australasian	2,099
Nearctic	3,810

Note: In each category, the zoogeographical zones are listed in order of increasing average BMR.

Figure 7: *Top,* conceptual model of the variation of mammalian BMR (mass-specific or total) expressed as arbitrary residual BMR units. Residuals are calculated from the allometric relationship between $\log_{10}$ BMR and $\log_{10}$ body mass. Basal metabolic rate is assumed to be determined by gradients of rainfall variability, and hence resource variability, in small mammals, and in addition by mobility (e.g., migration potential), predator-prey interactions, and habitat and dietary specialization in large mammals. The constrained body mass (CBM) represents the intermediate body mass at which minimum metabolic variance has evolved as a consequence of hypothesized opposing selection for low BMR to minimize existence costs, and a high BMR to maximize running speed and mobility. Maximum BMR variance occurs at the smallest and largest body sizes. *Bottom,* typical allometries of various parameters that may influence BMR selection. All curves have been scaled to the same range of independence values. BMR (mL O_2/g/h) = 4.11 $M_b^{-0.31}$ (this study); COT (cost of transport, kJ/g/km) = 10,678 $M_b^{-0.30}$ (Taylor et al. 1970); MRS (maximum running speed, km/h; polynomial equation in Garland 1983*a*); DMD (daily movement distance, km/day) = 1.038 $M_b^{0.25}$; Garland 1983*b*); HR (home range, ha) = 14.9 $M_b^{1.083}$ (Garland 1983*b*); R_t (circadian amplitude of body temperature, °C) = 4.762 $M_b^{-0.197}$(Aschoff 1982).

most abundance organic material on Earth, and hence, most zoogeographical zones could, historically speaking, accommodate high abundances and biomass of mobile herbivores. High herbivore abundances should promote intense predator-prey interactions and "arms races" selecting for fast runners. In terms of the aerobic capacity
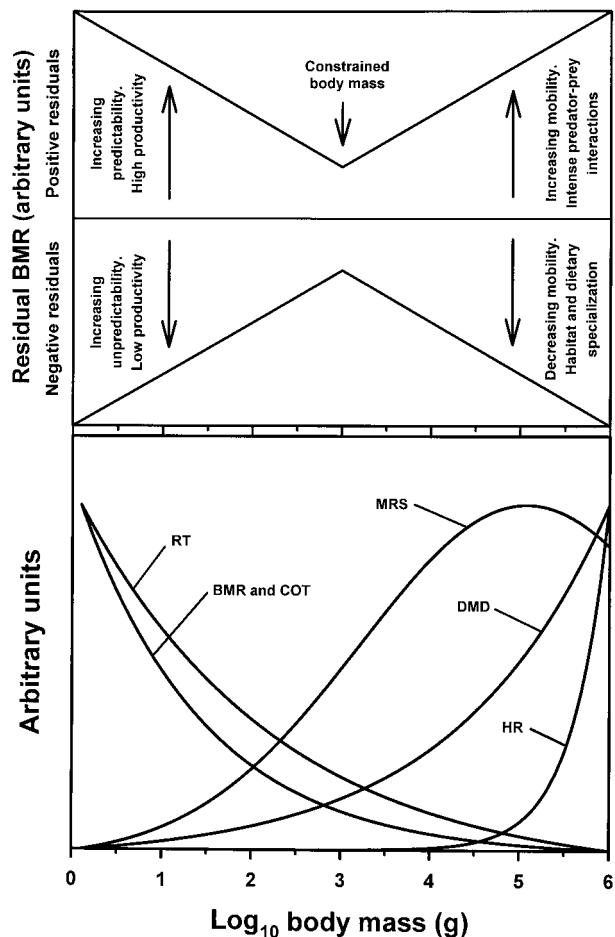
model (Bennett and Ruben 1979; Hayes and Garland 1995), the high aerobic capacity necessary for fast running speeds may, in turn, necessitate elevated basal rates of metabolism (see closing discussion under "Running Speed and BMR"). In this respect, their high ECT may be irrelevant in light of intense predator pressure and the capacity for mobility.

Large mammals that are not highly mobile should display low basal rates and tend toward habitat and dietary specialization (fig. 7). They do not, or cannot, migrate from their specialist habitats when resource availability is low. In many cases, morphological specialization to certain lifestyles, for example, burrowing and arboreality, preclude cost-effective long distance movement (Garland 1983a). The lowest BMRs should evolve in response to the lowest resource availability likely to occur in time and space. Relative to mobile large mammals, abundance and biomass are likely to be lower, and consequently predator-prey interactions should be less intense or may be reduced by morphological adaptations other than running speed.

Existing Zoogeographical Support for the Model

Although the bowtie model invokes an abiotic gradient of resource predictability as the primary determinant of a mammal's BMR, it also integrates biotic considerations related to size-dependent predation pressure and mobility that may be more important for large mammals than for small mammals. Predictions in this regard are presented in closing. Here I outline some immediate quantitative support for the model based upon the zoogeographical BMR data.

In general, the comparatively low BMRs of small mammals of deserts and ENSO zones and the high BMRs of species in the climatically predictable Palearctic and Nearctic zones support the model well. The Indomalayan and the Australasian zones, as predicted, display the lowest rates (table 7) possibly because these two zones are influenced by ENSO-generated, negative rainfall anomalies in both winter and summer, whereas the Afrotropical is affected by failed summer rains only (NOAA 1994). However, the high BMRs of Nearctic and Palearctic small mammals appear to be linked to highly seasonal, predictable environments (see also McNab 1992).

In most analyses, the Neotropical BMR data were intermediate between those of the Afrotropical-Australian-Indomalayan grouping and the Palearctic-Nearctic grouping. First, ENSO events may not necessarily cause strong negative rainfall anomalies throughout the Neotropics (Philander 1990; Stone et al. 1996). Certainly, on the coast of Chile, ENSO events appear to generate favorable rainfall conditions, rather than prolonged droughts, which stimulate reproduction in small-mammal populations (Mes-

erve et al. 1995). Negative rainfall anomalies are restricted to the northeastern shoulder of the continent and to Middle America, for example, Mexico (NOAA 1994; Stone et al. 1996).

Second, the invasion of South America from North America by eurytopic mammals via land bridges formed during the Pleistocene <3 million years ago coincided with extensive extinction of diverse Neotropical mammals, especially the xeric-adapted mammals (Mares 1985). Whereas some of the extinction may have resulted from competitive interactions with northern invaders, they most probably resulted from the reduction and/or fragmentation of xeric habitats following major climate changes at that time (Mares 1985). The diversity of the current xeric-adapted fauna is, thus, very poor compared with other zoogeographical zones, and many mammals occurring in Neotropical deserts are eurytopic.

Those zones with high proportions of highly mobile Artiodactyla and Carnivora (Nearctic, Palearctic, and Afrotropical) with high BMRs seem to support the model predictions for large mammals. The Artiodactyla and Lagomorpha, the two most important prey taxa for carnivores larger than the CBM, have the highest residual BMRs of any mammalian group (Hayssen and Lacy 1985; Lovegrove 1996). The Carnivora have the next highest mean residual BMR value (Lovegrove 1996). The majority of these mammals are highly mobile, and many species of Artiodactyla are well known for their ability to undertake predictable long-range seasonal migrations. Some of the smaller carnivores, such as badgers and skunks, which are relatively slow runners for their size (Garland 1983a), are exceptions to this generalization.

Notwithstanding the poor understanding of the relationship between maximum running speed and BMR discussed in "Running Speed and BMR," several trends suggesting evidence of an evolutionary arms race between carnivores and their prey at body masses greater than the CBM are worth noting. First, the Artiodactyla, Lagomorpha, and Carnivora include the fastest runners of all mammalian taxa (Garland 1983a). Second, maximum running speed is mass independent within the Artiodactyla and the Carnivora; many small artiodactyls and carnivores can run as fast as their larger counterparts (Garland 1983a). Thus, for these groups, casual observation does point to an association between fast maximum running speeds and high BMR values.

The low BMRs of the large Xenarthra agree with the predictions for large mammals that are not highly mobile. Apart from the Monotremata, the Xenarthra display the lowest basal rates of all mammals (McNab 1984; Hayssen and Lacy 1985; Lovegrove 1996). They also have the longest history of dietary specialization of any mammalian lineage (Eisenberg 1981). Presumably their specialized

feeding habits brought them into minimal competitive conflict with Nearctic invaders because they appear not to have been displaced as dramatically as many other Neotropical mammals (Mares 1985). They may not need to migrate during periods of resource variability provided that sufficient resources exists to sustain their comparatively low energetic requirements. Moreover, as discussed shortly, selection for high BMRs in response to predation pressure (i.e., fast running speeds) may also be offset by the evolution of body armor in many species in this group.

The other large mammals characterized by low BMRs are the Australian macropod marsupials. The model predicts that large mobile herbivores should display high BMRs, but two factors unique to Australia may have promoted selection for low BMRs: hopping locomotion and very low soil nutrients (Flannery 1994). It has been argued (Flannery 1994) that the evolution of a hopping gait alternative to quadrupedal locomotion in macropods guarantees running speeds equal to those of similar-sized quadrupeds (Garland et al. 1988), but at the lowest COT yet measured in terrestrial mammals (Dawson and Taylor 1973). A low COT is achieved by attaining running speeds in excess of those normally determined by an animal's maximum oxygen consumption during running (V_{O_2}max). Hence, macropods can theoretically move considerable distances rapidly and cheaply without the attendant requirement for a high BMR, a novel evolutionary solution to low and unpredictable resource and nutrient availability on the Australian continent (Flannery 1994).

Further Testable Predictions

Although largely qualitative at this stage, the bowtie model should provide a fresh basis for unifying physiological and ecological concepts associated with resource allocation and the energetic basis of life-history evolution. Of course, the underlying cause and effect of geographic variation in BMR cannot be identified definitively using the approach adopted in this study. However, this should not restrict the development of hypotheses aiding a future experimental or eclectic approach. In closing, I outline several obvious, but not exhaustive, approaches that may assist in quantitatively testing various predictions and assumptions of the model.

Selection against the CBM. Minimal BMR variance and predation, locomotor, and energetic constraints associated with the CBM, should lead to detectable selection against body sizes surrounding the CBM. For example, I would predict lower-than-expected extant species numbers especially in unpredictable environments, lower-than-expected extinct species numbers in the fossil record, and high rates of extinction in unpredictable environments dis-

turbed in historical time, for example, those badly fractionated through habitat degradation, those subjected to altered fire regimes, or those in which alien predators have been introduced. These predictions are relatively easy to test with zoogeographical body mass frequency distribution data. However, geographical scale may be an important consideration in the outcome of such tests (see "The 'Island Rule'").

The "Island Rule." The bowtie model argues that large mobile mammals can avoid unpredictable environments by migration, whereas small mammals cannot. The potential for migration is, however, limited on small land masses, for example, large islands. If, in addition to limited migration potential predation risks are also low, as they often are on smaller land masses, we should expect deviations from the predictions of the model. For example, I would predict selection for lower-than-average BMRs in both small and large island mammals, but also a tendency toward gigantism in small mammals and dwarfism in large mammals, relative to mainland counterparts. Under reduced predation pressure, gigantism increases DMD and HR and decreases the COT, whereas dwarfism reduces DEE and the need for high MRS (fig. 7). Although these body size predictions are consistent with the island rule (Foster 1963; Van Valen 1965; Lomolino 1985), the bowtie model provides an alternative explanation for the patterns. It is noteworthy that the switch from gigantism to dwarfism in Lomolino's (1985) data occurs at the CBM. It may be possible to resolve these alternative explanations by quantitatively comparing BMR and body mass trends in terms of the relative rainfall unpredictability of small, insular land masses.

The Aridity-Mimic Effect. The basic tenet of the bowtie model is that the selective influence of ENSO-induced rainfall variability in mesic habitats mimics the selection that occurs in arid zones, especially in small mammals. This assumption can be easily tested by comparing the BMR of counterpart mesic and arid mammals from zoogeographical zones in which the severity of association between ENSO and rainfall variability in mesic zones differs. For example, I would predict marked differences in the BMR of arid and mesic Nearctic and Palearctic small mammals but marginal differences in Afrotropical and Australasian species.

Running Speed and BMR. The relationship between maximum running speed and BMR in large mammals is an important assumption in the bowtie model, yet what we currently understand is little more than speculation or circumstantial observation. Garland (1983*a*) has suggested that, on average, the maximum running speed a mammal

can attain is roughly twice its maximum aerobic speed (the maximum speed at Vo_2max). Hence, mammals with a high Vo_2max should presumably attain faster maximum running speeds. However, Vo_2max is also generally about tenfold greater than the basal metabolic rate in mammals (Taylor et al. 1970). Small marsupials (<3 kg), though, display a greater aerobic scope between minimum and maximum cold- or exercise-induced metabolism than eutherians (Hinds et al. 1993), but this capacity has not been investigated in large mammals. Selection for high BMR may therefore be positively correlated with Vo_2max and hence maximum running speed, or conversely, selection for a high Vo_2max may be correlated with high BMRs. Ultimately, elucidating physiological adaptation in this regard will require more rigorous testing of the Aerobic Capacity Model (Hayes and Garland 1995), possibly by integrating mechanistic and phylogenetic performance approaches (Autumn et al. 1999).

Unbalanced Selection Surrounding the CBM. Two circumstantial observations of potential unbalanced selection surrounding the CBM are worthy of further testing. First, eight of the 10 mammals with the lowest BMR residuals (excluding the aquatic platypus) in the body size range 200–4,000g (132 species) surrounding the CBM possess body armor either in the form of spines (two tenrecs, three hedgehogs) or dermal armor (three armadillos). These data may support the prediction that, if predation pressure on mammals that cannot run fast is reduced, in this instance by morphological defenses, unbalanced selection for low BMR in response to other constraints concerning resource availability and energy expenditure should evolve.

In this regard, it is also noteworthy that vigilance sociality has evolved in response to predation pressure in several ground-dwelling mammals (e.g., suricate, dwarf mongoose) in this body size range (Skinner and Smithers 1990). The suricate (*Suricatta suricata*) also has a comparatively low BMR residual (this study), but this could also be attributed to its arid habitat.

On the other hand, the 10 mammals with the highest BMR residuals within the same size range include four of the seven lagomorphs in the data set (1,563–3,250 g). The Lagomorpha are the fastest runners for their size of all mammals; they have a maximum running speed four times higher than predicted by their body mass (Garland 1983*a*). This observation supports the prediction that selection for fast running speeds and high BMRs may be the only alternative to defense or vigilance mechanisms immediately beyond the CBM.

However, these observations are biased by species relatedness and hence shared inherited traits. Adequate testing of the speed-versus-defense association with BMR requires an independent PI analysis of correlated traits.

BMR and Life-History Parameters. It is implicit in the bowtie model that, if life history parameters (e.g. age and size at maturity) are correlated with physiological variables (Harvey et al. 1991; Kozłowski and Weiner 1997), then the model should provide a basis for life-history predictions based upon resource predictability, mobility and predation criteria. For example, if the high BMR of small mammals in predictable environments optimizes production rather than longevity, we should expect these mammals to grow fast, reach maturity quickly, and produce large and frequent litters. Yet, the empirical relationship between mammal metabolism and life-history parameters remains unresolved (Read and Harvey 1989; Yom-Tov 1989; Harvey and Pagel 1991; Harvey et al. 1991; Stearns 1992; Stephenson and Racey 1995). Harvey et al. (1991) questioned early attempts to correlate variables using species data and conventional statistical procedures. Their PI analysis failed to establish a consistent relationship between metabolic rate and 22 life-history characteristics. Only one trait, the number of offspring per litter, was positively correlated.

I am cautious about inferring too much from Harvey et al.'s (1991) analysis in light of several implications of the bowtie model that may render past analyses unrealistic. First, the evolutionary dichotomy between small and large mammal guilds has not been previously recognized. Body size cannot continue to be treated merely as a troublesome covariate. The bowtie model would argue that small mammals should not be compared with large mammals in terms of the evolution of metabolic and life-history traits. The life-history traits of large mammals may be less predictable on energetic grounds than they are for small mammals because relative mobility and predator-prey pressures may be more important in their evolution than spatial resource variability. Second, data sets may be biased by disparate zoogeographical representation. It is unrealistic, for example, in analyzing data sets predominantly from Holarctic mammals, as is often the case. Holarctic species are likely to display similar energetic adaptations in response to highly seasonal, predictable environments and are, therefore, unlikely to vary much in terms of life-history traits. Tests of the association between life-history traits and BMR analyses must ensure balanced representation of mammals from all zoogeographical zones and separate analyses for small- and large-mammal guilds.

Literature Cited

Allan, R., J. Lindesay, and D. Parker. 1996. El Niño Southern Oscillation and climatic variability. CSIRO Australia, Collingwood.

Aschoff, J. 1982. The circadian rhythm of body temperature as a function of body size. Pages 173–188 *in* C. R. Taylor, R. Johansen, and L. Bolis, eds. A companion to animal physiology. Cambridge University Press, Cambridge.

Autumn, K., D. Jindrich, D. DeNardo, and R. Mueller. 1999. Locomotor performance at low temperature and the evolution of nocturnality in geckos. Evolution 53: 580–599.

Barry, R. G., and A. H. Perry. 1973. Synoptic climatology: methods and applications. Methuen, London.

Bennett, A. F., and J. A. Ruben. 1979. Endothermy and activity in vertebrates. Science (Washington, D.C.) 206: 649–654.

Benton, M. J. 1990. Vertebrate palaeontology. Unwin Hyman, London.

Blackburn, T. M., and K. J. Gaston. 1994. Animal body size distributions: patterns, mechanisms and implications. Trends in Ecology & Evolution 9:471–474.

Brody, S. 1945. Bioenergetics and growth. Reinhold, New York.

Brown, J. H., P. A. Marquet, and M. L. Taper. 1993. Evolution of body size: consequences of an energetic definition of fitness. American Naturalist 142:573–584.

Budyko, M. I. 1986. The evolution of the biosphere. Reidel, Dordrecht.

Chang, W. Y. B. 1997. ENSO: extreme climate events and impacts on Asian deltas. Journal of the American Water Resources Association 33:605–614.

Chown, S. L., and K. J. Gaston. 1997. The species-body size distribution: energy, fitness and optimality. Functional Ecology 11:365–375.

Dawson, T. J., and C. R. Taylor. 1973. Energetic cost of locomotion in kangaroos. Nature (London) 246: 313–314.

Dobson, A. P., and M. J. Crawley. 1987. What's special about desert ecology. Trends in Ecology & Evolution 2: 145–146.

Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. Athlone, London.

Flannery, T. 1994. The future eaters. Braziller, New York.

Foster, J. B. 1964. The evolution of mammals on islands. Nature (London) 202:234–235.

Garland, T. 1983a. The relation between maximal running speed and body mass in terrestrial mammals. Journal of Zoology (London) 199:157–170.

———. 1983b. Scaling the ecological cost of transport to body mass in terrestrial mammals. American Naturalist 121:571–587.

Garland, T., F. Geiser, and R. V. Baudinette. 1988. Comparative locomotor performance of marsupial and placental mammals. Journal of Zoology (London) 215: 505–522.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41: 18–32.

Garland, T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology 42:265–292.

Glantz, M., R. Katz, and N. Nicholls. 1991. ENSO teleconnections linking worldwide climate anomalies: scientific basis and societal impacts. Cambridge University Press, Cambridge.

Gopinathan, C. K. 1997. Impact of 1990–'95 ENSO/WEPO event on Indian monsoon rainfall. Indian Journal of Marine Science 26:258–262.

Grafen, A. 1989. The phylogenetic regression. Philosophical Transactions of the Royal Society of London B, Biological Sciences 326:119–157.

Harger, J. R. E. 1995. Air temperature variations and ENSO effects in Indonesia, the Philippines and El Salvador: ENSO patterns and changes from 1866 to 1993. Atmospheric Environment 29:1919–1942.

Harvey, P. H., and M. A. Elgar. 1987. In defense of the comparative method. Functional Ecology 1:160–161.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Harvey, P. H., M. D. Pagel, and J. A. Rees. 1991. Mammalian metabolism and life histories. American Naturalist 137:556–566.

Hayes, J. P., and T. Garland. 1995. The evolution of endothermy: testing the aerobic capacity model. Evolution 49:836–847.

Hayssen, V., and R. C. Lacy. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of

BMR and body mass. Comparative Biochemistry and Physiology 81A:741–754.

Heldmaier, G. 1989. Seasonal acclimatization of energy requirements in mammals: functional significance of body weight control, hypothermia, torpor and hibernation. Pages 130–139 *in* W. Wieser and E. Gnaiger, eds. Energy transformations in cells and organisms. Thieme, Stuttgart.

Heusner, A. A. 1991. Size and power in mammals. Journal of Experimental Biology 160:25–54.

Hinds, D. S., and R. C. MacMillen. 1985. Scaling of energy metabolism and evaporative water loss in heteromyid rodents. Physiological Zoology 58:282–298.

Hinds, D. S., R. V. Baudinette, R. E. MacMillen, and E. A. Halpern. 1993. Maximum metabolism and the aerobic factorial scope of endotherms. Journal of Experimental Biology 182:41–56.

Hughes, J. J., and D. Ward. 1993. Predation risk and distance to cover affect foraging behavior in Namib Desert gerbils. Animal Behaviour 46:1243–1245.

Hulbert, A. J., and T. J. Dawson. 1974. Standard metabolism and body temperature of perameloid marsupials from different environments. Comparative Biochemistry and Physiology 47A:583–590.

Jürgens, K. D. 1989. Allometrie als Konzept des Interspeziesvergleiches von Physiologischen Grössen. Parey, Hamburg.

Kleiber, M. 1932. Body size and animal metabolism. Hilgardia 6:315–353.

Kozłowski, J. 1996. Energetic definition of fitness? yes, but not that one. American Naturalist 147:1087–1091.

Kozłowski, J., and J. Weiner. 1997. Interspecific allometries are the by-products of body size optimization. American Naturalist 149:352–380.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lomolino, M. V. 1985. Body size of mammals on islands: the island rule reexamined. American Naturalist 125:310–316.

Louw, G. N., and M. Seely. 1982. Ecology of desert organisms. Longman, London.

Lovegrove, B. G. 1986. The metabolism of social subterranean rodents: adaptation to aridity. Oecologia (Berlin) 69:551–555.

———. 1993. The living deserts of southern Africa. Fernwood, Cape Town.

———. 1996. The low basal metabolic rates of marsupials: the influence of torpor and zoogeography. Pages 141–151 *in* F. Geiser, A. J. Hulbert, and S. C. Nicol, eds. Adaptations to the cold. Tenth International Hibernation Symposium. University of New England Press, Armidale.

Lovegrove, B. G., and G. Heldmaier. 1994. The amplitude of circadian body temperature rhythms in three rodents (*Aethomys namaquensis*, *Thallomys paedulcus* and *Cryptomys damarensis*) along an arboreal-subterranean gradient. Australian Journal of Zoology 42:65–78.

Lovegrove, B. G., G. Heldmaier, and M. Knight. 1991. Seasonal and circadian energetic patterns in an arboreal rodent, *Thallomys paedulcus*, and a burrow-dwelling rodent, *Aethomys namaquensis*, from the Kalahari Desert. Journal of Thermal Biology 16:199–209.

Lyman, C. P., J. S. Willis, A. Malan, and L. C. H. Wang. 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.

MacMillen, R. E., and T. Garland. 1989. Adaptive physiology. Pages 143–168 *in* J. N. Lane and G. L. Kirkland, Jr., eds. Advances in the study of *Peromyscus* (Rodentia). Texas Technical University Press, Lubbock.

MacMillen, R. E., and D. S. Hinds. 1983. Water regulatory efficiency in heteromyid rodents: a model and its application. Ecology 64:152–164.

Mann, M. E., R. S. Bradley, and M. K. Hughes. 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature (London) 392:779–787.

Mares, M. A. 1985. Mammal faunas of xeric habitats and the Great American interchange. Pages 489–520 *in* F. Stehli and D. Webb, eds. The Great American biotic interchange. Plenum, New York.

———. 1999. Encyclopedia of deserts. University of Oklahoma Press, Norman.

McNab, B. K. 1984. Physiological convergence amongst ant-eating and termite-eating mammals. Journal of Zoology (London) 203:485–510.

———. 1986. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56:1–19.

———. 1988. Complications inherent in scaling the basal metabolic rate of metabolism in mammals. Quarterly Review of Biology 63:25–54.

———. 1992. The comparative energetics of rigid endothermy: the Arvicolidae. Journal of Zoology (London) 227:585–606.

McNab, B. K., and P. Morrison. 1963. Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. Ecological Monographs 33:63–82.

Meserve, P. L., J. A. Yunger, J. R. Gutierrez, L. C. Contreras, W. B. Milstead, B. K. Lang, K. L. Cramer, et al. 1995. Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580–595.

Morton, S. R. 1990. The impact of European settlement

on the vertebrate animals of arid Australia: a conceptual model. Proceedings of the Ecological Society of Australia 16:201–213.

NOAA (National Oceanic and Atmospheric Administration). 1994. El Niño and climate prediction—reports to the nation on our changing planet. National Oceanic and Atmospheric Administration Award NA27GP0232-01. University Corporation for Atmospheric Research, Boulder, Colo.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Pagel, M. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology 156:431–442.

Parsons, P. A. 1991. Evolutionary rates: stress and species boundaries. Annual Review of Ecology and Systematics 22:1–18.

Perry, A. H., and J. M. Walker. 1977. The ocean-atmosphere system. Longman, London.

Philander, S. G. 1990. El Niño, La Niña, and the Southern Oscillation. Academic Press, San Diego, Calif.

Read, A. F., and P. H. Harvey. 1989. Life history differences among the eutherian radiations. Journal of Zoology (London) 219:329–353.

Ricklefs, R. E. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. Oikos 77:167–172.

Schmidt-Nielsen, K. 1983. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge.

Scholander, P. F., R. Hock, V. Walters, and L. Irving. 1950. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. Biological Bulletin (Woods Hole) 99:259–271.

Seely, M. K. 1989. Desert invertebrate physiological ecology: is anything special? South African Journal of Science 85:266–270.

Shkolnik, A., and K. Schmidt-Nielsen. 1976. Temperature regulation in hedgehogs from temperate and desert environments. Physiological Zoology 49:56–64.

Skinner, J. D., and R. H. N. Smithers. 1990. The mammals of the southern African subregion. University of Pretoria.

Southgate, R. I., P. Masters, and M. K. Seely. 1996. Precipitation and biomass changes in the Namib Desert dune ecosystem. Journal of Arid Environments 33:267–280.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stephenson, P. J., and P. A. Racey. 1995. Resting metabolic rate and reproduction in the Insectivora. Comparative Biochemistry and Physiology 112A:215–223.

Stone, R. C., G. L. Hammer, and T. Marcussen. 1996. Prediction of global rainfall probabilities using phases of the Southern Oscillation index. Nature (London) 384:252–255.

Taylor, C. R., K. Schmidt-Nielsen, and J. L. Raab. 1970. Scaling of energetic cost of running to body size in mammals. American Journal of Physiology 219:1104–1107.

Tyson, P. D. 1986. Climatic change and variability in southern Africa. Oxford University Press, Cape Town.

Udvardy, M. D. F. 1975. A classification of the biogeographical provinces of the world. IUCN Occasional Papers 18:1–50.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 104:589–590.

Ward, D., and M. K. Seely. 1996. Adaptation and constraint in the evolution of the physiology and behavior of the Namib Desert tenebrionid beetle genus *Onymacris*. Evolution 50:1231–1240.

Yom-Tov, Y. 1989. Environmental predictability and life history traits in arid environments. Journal of Arid Environments 17:193–197.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, N.J.