Does Basal Metabolic Rate Contain a Useful Signal? Mammalian BMR Allometry and Correlations with a Selection of Physiological, Ecological, and Life-History Variables

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ABSTRACT

Basal metabolic rate (BMR, mL O_2 h^{-1}) is a useful measurement only if standard conditions are realised. We present an analysis of the relationship between mammalian body mass (M, g) and BMR that accounts for variation associated with body temperature, digestive state, and phylogeny. In contrast to the established paradigm that BMR $\propto M^{3/4}$, data from 619 species, representing 19 mammalian orders and encompassing five orders of magnitude variation in M, show that BMR $\propto M^{2/3}$. If variation associated with body temperature and digestive state are removed, the BMRs of eutherians, marsupials, and birds do not differ, and no significant allometric exponent heterogeneity remains between orders. The usefulness of BMR as a general measurement is supported by the observation that after the removal of body mass effects, the residuals of BMR are significantly correlated with the residuals for a variety of physiological and ecological variables, including maximum metabolic rate, field metabolic rate, resting heart rate, life span, litter size, and population density.

Introduction

Most of the controversy surrounding the relationship between mammalian basal metabolic rate (BMR) and body mass (M, g) focuses on the value of the scaling exponent in the allometric equation BMR $= aM^b$. Empirical support for an exponent of 3/4 is based on species that poorly represent Mammalia and does not unequivocally reject an exponent of 2/3 (Dodds et al.

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2001). Most analyses are compromised by inclusion of gut-fermenting species in which basal conditions are unlikely during measurement and neglect interspecific differences in body temperature (T_b, °C). Incorporation of T_b is important, because it is a primary determinant of metabolic rate (Gillooly et al. 2001) and increases significantly with M for marsupials, eutherians, and mammals in general (White and Seymour 2003). An accurate estimation of the relationship between BMR and M is therefore best obtained by normalising the measured BMRs of all species to a common T_b and eliminating data from suspected non-postabsorptive animals.

White and Seymour (2003) compiled the most comprehensive and representative database so far available for mammals and accounted for variation associated with T_b and digestive state in an allometric analysis of BMR. We found that BMR scaled with M to the power of 0.68 ± 0.01 (95% confidence interval [CI]) and that this conclusion was not affected by phylogeny. In this report we further examine this data set to demonstrate the utility of BMR in relation to other physiological, ecological, and life-history variables. Additionally, because the BMRs of birds are also proportional to $M^{2/3}$ (Bennett and Harvey 1987; Reynolds and Lee 1996; Tieleman and Williams 2000; Frappell et al. 2001), even though birds have higher T_b's and BMRs than mammals (McNab 1966; Calder 1984), a preliminary analysis of the effect of T_b on BMR across mammals and birds is made. This analysis tests the hypothesis that BMR differences between the two major radiations of endothermic homeotherms can be accounted for solely by T_b variation.

Methods

Allometry of Mammalian BMR

M (g), T_b (°C), and BMR (mL O_2 h^{-1}) data for 619 species representing 19 mammalian orders and encompassing five orders of magnitude variation in M were compiled from the literature (Fig. 1). The data set is available in association with White and Seymour (2003). Data were selected according to strictly established guidelines (McNab 1997) and were included only if obtained when animals were inactive, postabsorptive, adult, nonreproductive, and thermoregulating in a thermoneutral environment. No attempt was made to exclude measurements obtained during the active circadian phase. This did not compromise the study, however, because the elevated BMR observed in the active circadian phase (Kenagy and Vleck 1982)
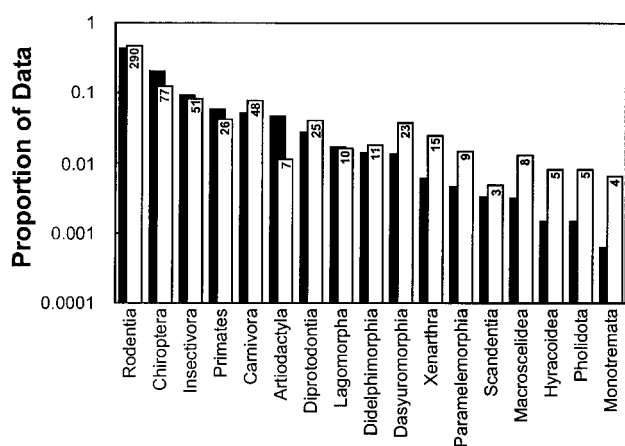
Figure 1. Comparison of contributions of mammalian orders to the present data set (*open bars*; numbers represent sample size) and Mammalia as a whole (*filled bars*; data from Nowak 1999). Notoryctemorphia and Tubulidentata not shown; each includes a single species in the present analysis.

coincides with elevated T_b (Aschoff 1982). Therefore, normalisation of BMR measurements to the mean T_b of species for which measurements are available (36.2°C, $n = 507$; Fig. 2) with the van't Hoff (Q_{10}) principle wholly accounts for circadian variation in BMR, provided that BMR and T_b were measured in the same circadian phase. Least squares regressions of the form $\log(\text{BMR}) = \log(a) + b \log(M)$ were fitted to log-log–transformed data for both the unmodified and Q_{10}-normalised data. Additionally, a hierarchically nested ANOVA (Harvey and Pagel 1991) was used to determine the appropriate taxonomic level at which averages should be calculated to account for the problem of overestimation of degrees of freedom that is inherent in comparative analyses of species data. The order level was found to capture 85% of the variation in M and 86% of the variation in BMR, indicating that this was the appropriate level for analysis, in accordance with previous work (Elgar and Harvey 1987). BMR values for each order were normalised to the mean T_b using the hierarchically nested average T_b of species within the order.

The analysis was then repeated, following exclusion of lineages for which BMR measurements were suspected to be unachievable. Artiodactyls were excluded because microbial fermentation of cellulose may delay or prohibit entrance into a postabsorptive state (McNab 1997); macropods and lagomorphs were excluded for the same reason. Shrews (Soricidae) were excluded because postabsorptive and inactive conditions may be mutually exclusive (Speakman et al. 1993). The absence of some other lineages (e.g., Cetacea, Proboscidae) stems solely from a lack of published BMR measurements. Data selected according to these criteria are henceforth referred to as "conservative BMR" if no Q_{10} normalisation was undertaken and as "conservative Q_{10}-normalised BMR" if it was. Interspecific

allometries were also calculated for each of the orders for which data for more than three species spanning a body mass range greater than an order of magnitude were available and for species from each of the six zoogeographic regions considered by Lovegrove (2000).

Variation in Mammalian BMR

BMR variation was examined at the level of order and infraclass (monotremes were excluded from the infraclass comparison due to small sample size [$n = 4$] relative to eutherians [$n = 546$] and marsupials [$n = 69$]). Allometric exponent heterogeneity was identified using ANOVA (order–log M interaction). The effect of order on BMR was then identified using ANCOVA, and pairs of significantly different orders were identified using BMR residuals [$= \log(\text{measured BMR}) - \log(\text{predicted BMR})$] and the Tukey-Kramer HSD test. Allometric exponent heterogeneity between infraclasses was examined using ANOVA (infraclass–log M interaction), and BMR differences between Eutheria and Metatheria were examined using ANCOVA. For all comparisons, α was set at 0.05.
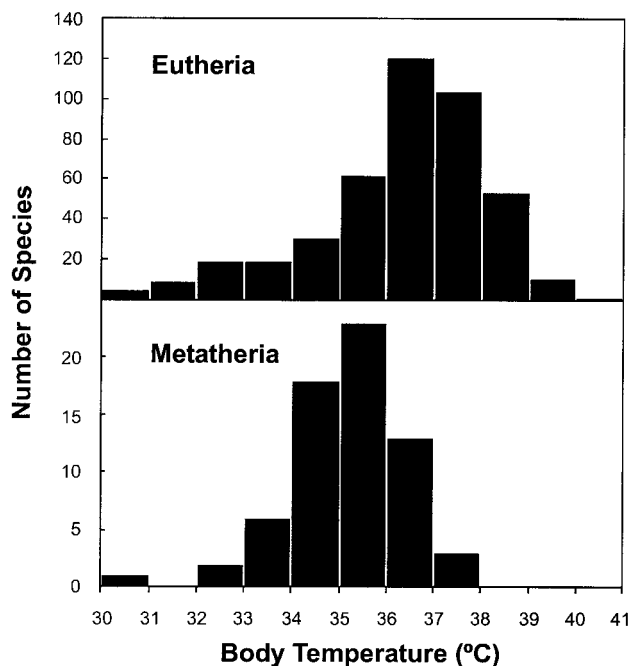

Figure 2. Body temperature (T_b) distributions for eutherians (*top*) and metatherians (*bottom*). Mean ($\pm$SD) mammal T_b is 36.2 $\pm$ 1.9°C ($n = 507$), eutherian T_b is 36.4 $\pm$ 1.8°C ($n = 437$), metatherian T_b is 35.3 $\pm$ 1.2°C ($n = 66$), and monotreme T_b is 31.4 $\pm$ 1.8°C ($n = 4$).
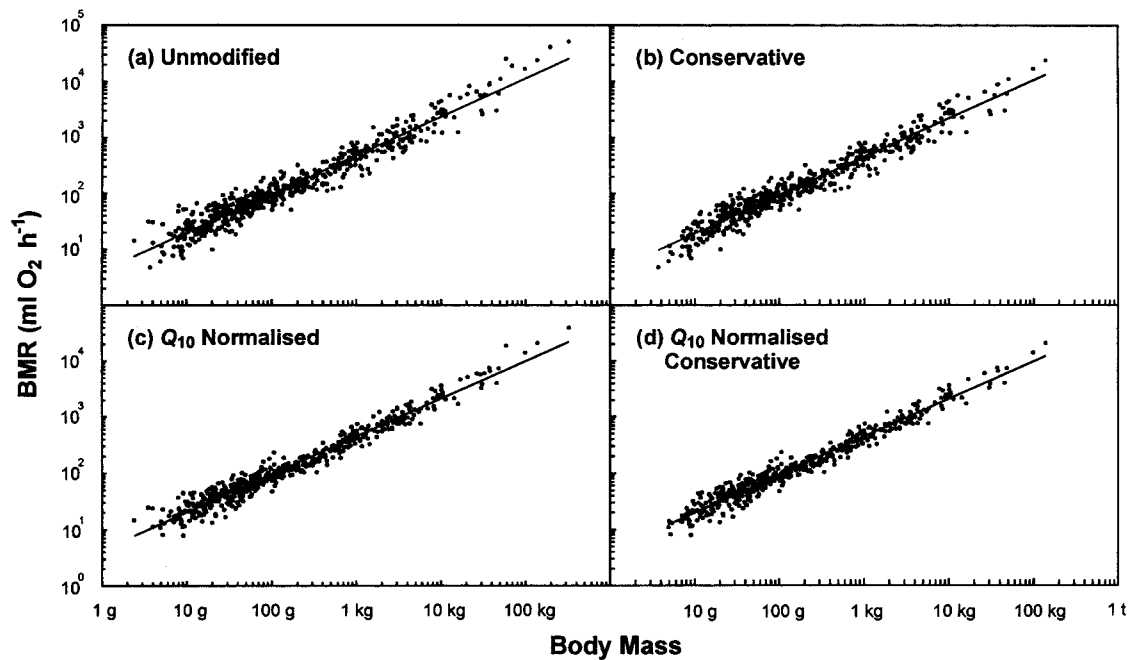
Figure 3. Interspecific relationships between mammalian body mass (M, g) and basal metabolic rate (BMR) for (*a*) all data ($n = 619$), (*b*) conservative data ($n = 571$, see "Methods" for selection criteria), (*c*) all data normalised to a common body temperature of 36.2°C ($n = 507$), and (*d*) conservative data normalised to a common body temperature of 36.2°C ($n = 469$). Equations of the regression lines: (*a*) BMR $= 4.12M^{0.687}$, $r^2 = 0.94$; (*b*) BMR $= 3.98M^{0.686}$, $r^2 = 0.94$; (*c*) BMR $= 4.34M^{0.672}$, $r^2 = 0.96$; (*d*) BMR $= 4.17M^{0.675}$, $r^2 = 0.96$. Exponents for *a* and *b* are significantly different from 2/3 ($P < 0.05$).

Correlations between BMR and Other Physiological, Ecological, and Life-History Variables

Because many biological variables are potentially correlated due only to correlations with body mass (e.g., large animals tend to have both high BMRs and large home ranges), BMR residuals were compared with mass-independent residuals for a variety of variables (body surface area, field metabolic rate [FMR], maximum aerobic metabolic rate [MMR], resting heart rate, fecundity [young per year], litter size, number of litters produced per year, maximum recorded life span, and population density). Data for these variables were obtained from a combination of published allometric analyses and nonallometric studies (sources are provided with Table 4). Wherever possible, the allometric equation used to generate the residuals for the non-BMR variables was the published equation, but in some cases the equation and residuals were calculated from raw data. Comparisons were made both within Mammalia as a group and within those orders for which sufficient data were available.

Results

Allometry of Mammalian BMR

Body mass alone accounts for 94% of the interspecific variation in BMR, but the allometric exponent (0.687) is significantly

different from both 2/3 and 3/4 (Fig. 3*a*; Table 1). However, this finding potentially represents a Type I error, because species values are often not statistically independent, which leads to overestimated degrees of freedom and erroneously narrowed CIs (Harvey and Pagel 1991). This problem is overcome by using average values calculated for each of the 17 orders represented by at least three species. Interestingly, M also accounts for 94% of the interordinal variation in mammalian BMR, but the CI includes both 2/3 and 3/4 (Table 1). T_b is significantly correlated with BMR residuals in both the interspecific analysis ($r = 0.57$, $n = 507$, $P < 0.001$) and the interordinal analysis ($r = 0.87$, $n = 17$, $P < 0.001$; Fig. 4). Normalisation of BMR measurements to a common T_b of 36.2°C ($Q_{10} = 3.0$; White and Seymour 2003) decreases both the interspecific and interordinal BMR scaling exponents: neither is significantly different from 2/3, while only the interspecific exponent is significantly different from 3/4 (Fig. 3*c*; Table 1). Exclusion of suspected nonbasal measurements (Artiodactyla, Macropodidae, Lagomorpha, and Soricidae) also refines the predictions, so that both the interspecific and interordinal exponents are significantly different from 3/4, although the interspecific exponent remains significantly different from 2/3 (Fig. 3*c*; Table 1). When data are normalised to 36.2°C and suspected nonbasal measurements excluded, however, both the interspecific (0.675) and

Table 1: Allometric parameters relating mammalian body mass (M, g) and basal metabolic rate (BMR, mL O_2 h^{-1}) according to the equation BMR = aM^b

Species Combinations	n	a	b	r^2
Interspecific allometry:				
Unmodified	619	4.12 (3.82–4.44)	.687 $\pm$ .007 (.674–.701)	.94
Conservative	571	3.98 (3.69–4.29)	.686 $\pm$ .007 (.672–.700)	.94
Q_{10}-normalised	507	4.34 (4.06–4.63)	.672 $\pm$ .006 (.660–.684)	.96
Conservative Q_{10}-normalised	469	4.17 (3.89–4.47)	.675 $\pm$ .006 (.662–.687)	.96
Interordinal allometry:				
Unmodified	17	3.11 (1.6–6.04)	.71 $\pm$ .05 (.61–.80)	.94
Conservative	15	4.35 (2.57–7.35)	.64 $\pm$ .04 (.56–.72)	.96
Q_{10}-normalised	17	3.57 (2.51–5.07)	.70 $\pm$ .02 (.66–.75)	.98
Conservative Q_{10}-normalised	15	4.58 (3.70–5.66)	.65 $\pm$ .01 (.62–.68)	.99

Note. Data are presented $\pm$ SE. Values in parentheses are 95% confidence limits. Regressions were calculated with the following combinations of species: unmodified, all data ($n = 619$); conservative, data with BMRs for Artiodactyla, Soricidae (Insectivora), Macropodidae (Diprotodontia), and Lagomorpha excluded ($n = 571$); Q_{10}-normalised, all data normalised to a common body temperature of 36.2°C ($n = 507$) according to Q_{10} principles, with a Q_{10} of 3.0; and conservative Q_{10}-normalised, data normalised to a common body temperature of 36.2°C with BMRs for Artiodactyla, Soricidae (Insectivora), Macropodidae (Diprotodontia) and Lagomorpha excluded ($n = 469$).

interordinal (0.65) allometric exponents are significantly different from 3/4 but not significantly different from 2/3 (Fig. 3d; Fig. 5; Table 1).

Variation in BMR between Mammalian Taxa and Zoogeographic Regions

Body mass accounts for 96% of the interspecific variation and 99% of the interordinal variation in Q_{10}-normalised BMR, following exclusion of likely nonbasal measurements (Table 1). At a given body mass, however, variation about the regression line remains considerable (Fig. 6; Table 2). Despite the reduction in variation associated with Q_{10} normalisation, the "bow tie" pattern of residual variation remains (Lovegrove 2000). Maximum BMR variation occurs at the smallest and largest masses, while minimum variation occurs at an intermediate mass, the "constrained body mass" (CBM = 350 g) of Lovegrove (2000; Fig. 7). Regression exponents for each of the 14 orders represented by at least three species are significantly heterogeneous between orders for unmodified data (ANOVA, $F_{16,583} = 6.0$, $P < 0.0001$), but exponents from conservative Q_{10}-normalised data are not (ANOVA, $F_{13,437} = 1.5$, $P = 0.13$). Exponents for small animals ($M < CBM$) and large animals ($M > CBM$) are also not heterogeneous (full-factorial order–CBM–log(M) interactions, $F < 2.0$, $P > 0.16$). After the effect of M is accounted for, order has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{13,453} = 2.1$, $P = 0.02$). However, a Tukey-Kramer HSD test reveals that only Chiroptera and Dasyuromorphia are significantly different from each other (Fig. 8). For small mammals, order has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{9,302} = 2.9$, $P = 0.004$). Post hoc comparison reveals that Chiroptera, Ro-

dentia, and Insectivora each have significantly greater BMRs than Dasyuromorphia (Fig. 8). For large mammals, order has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{11,128} = 2.7$, $P = 0.005$). However, post hoc comparison was unable to identify where these differences lie (Fig.

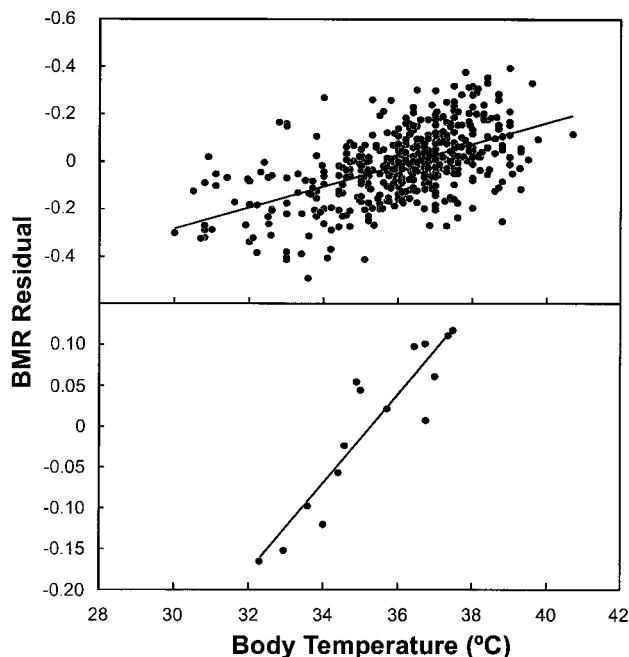Figure 4. Relationship between body temperature and residual variation in conservative basal metabolic rate (BMR; see "Methods") for species (*top*) and order (*bottom*) data. Both correlations are significant ($P < 0.05$).

8). Eutheria and Metatheria show significant allometric exponent heterogeneity when conservative Q_{10}-normalised BMRs are compared interspecifically (ANOVA, $F_{1,461} = 5.4$, $P = 0.02$) but not interordinally (ANOVA, $F_{1,10} = 0.98$, $P = 0.35$). Residuals of Q_{10}-normalised BMRs for Eutheria and Metatheria are not significantly different either interspecifically (ANCOVA, $F_{1,462} = 2.5$, $P = 0.11$) or interordinally (ANCOVA, $F_{1,11} = 0.05$, $P = 0.82$). For small mammals, no significant allometric exponent heterogeneity was identified between zoogeographic regions (ANOVA, region–$\log M$ interaction, $F_{4,304} = 0.73$, $P = 0.6$), and region has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{4,309} = 6.12$, $P < 0.0001$), such that

Neotropical[a] > Nearctic[a,b] > Palearctic[a,b,c] > Afrotropical[c]

> Australian[c] > Indomalayan[b,c],

where regions that do not share superscript characters have significantly different mean mass-independent BMRs (Tukey-Kramer HSD $P < 0.05$). Similarly, when zoogeographic regions are compared within the order Rodentia for small species, there is no significant allometric exponent heterogeneity between regions (ANOVA, region–$\log M$ interaction, $F_{4,188} = 2.4$, $P = 0.052$), and region has a significant effect on conservative Q_{10}-normalised BMR (ANCOVA, $F_{4,192} = 3.4$, $P = 0.01$), such that

Palaearctic[a] > Nearctic[a] > Neotropical[a,b]

> Afrotropical[b] > Australian[a,b]

(Tukey-Kramer HSD $P < 0.05$). For large mammals, however, allometric exponents are significantly heterogeneous between zones (ANOVA, region–$\log M$ interaction, $F_{4,141} = 3.6$, $P = 0.004$). BMR allometric exponents for these groups differ, such that

Palaearctic[a] > Afrotropical[a] > Nearctic[a,b] > Indomalayan[a,b]

> Neotropical[a,b] > Australian[b],

where regions that do not share superscript characters have significantly different exponents (assessed using 95% CI overlap). Only the exponents for Palaearctic and Afrotropical mammals differ significantly from 2/3 (assessed using 95% CI overlap; Table 3).

Correlates to BMR

BMR residuals may be compared to residuals for a variety of physiological, ecological, and life-history variables to test hypothesised correlations. Significant correlations ($P < 0.05$; Table 4) exist between BMR residuals and residuals for FMR (Mammalia and Rodentia), cold-induced MMR (Mammalia and Ro-
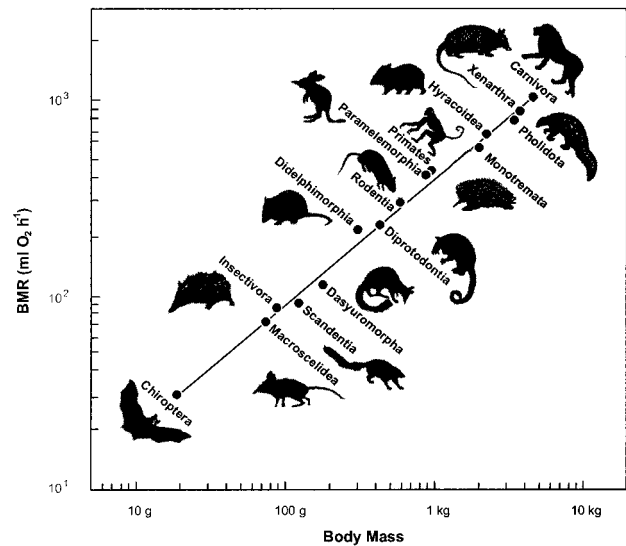

Figure 5. Relationship between body mass (M, g) and Q_{10}-normalised basal metabolic rate (BMR; see "Methods") for orders represented by at least three species. BMR $= 4.58M^{0.65}$, $r^2 = 0.99$.

dentia), resting heart rate (Mammalia and Diprotodontia), population density (Carnivora), life span (Carnivora and Dasyuromorphia), litter size (Mammalia, Dasyuromorphia, and Macroscelidae), litters produced per year (Carnivora), and annual fecundity (Rodentia). Only body surface area and exercise-induced MMR were not significantly correlated with BMR within either Mammalia or at least one of the orders examined ($P > 0.05$; Table 4).

Discussion

Allometry of Mammalian BMR

Body mass accounts for 94% of the variation in mammalian BMR before correction for T_b and digestive state (Table 1). Normalisation to a common T_b cuts the residual variation in BMR in half (Table 2). Following exclusion of likely nonbasal measurements (Artiodactyla, Soricidae, Macropodidae, and Lagomorpha), M accounts for 96% of the interspecific variation and 99% of the interordinal variation in Q_{10}-normalised BMR (Table 1). No significant allometric exponent heterogeneity is evident between orders, and only large Palaearctic and Afrotropical species scale with an exponent different from 2/3. The general conclusion is therefore that the BMR of mammals is proportional to $M^{2/3}$, which is also the case for birds (Bennett and Harvey 1987; Reynolds and Lee 1996; Tieleman and Williams 2000; Frappell et al. 2001).

The usual interpretation of a 2/3 scaling exponent for BMR is that it reflects a balance between the production of heat through metabolic processes and the loss of heat through the body surface, which is also proportional to $M^{2/3}$ (Reynolds
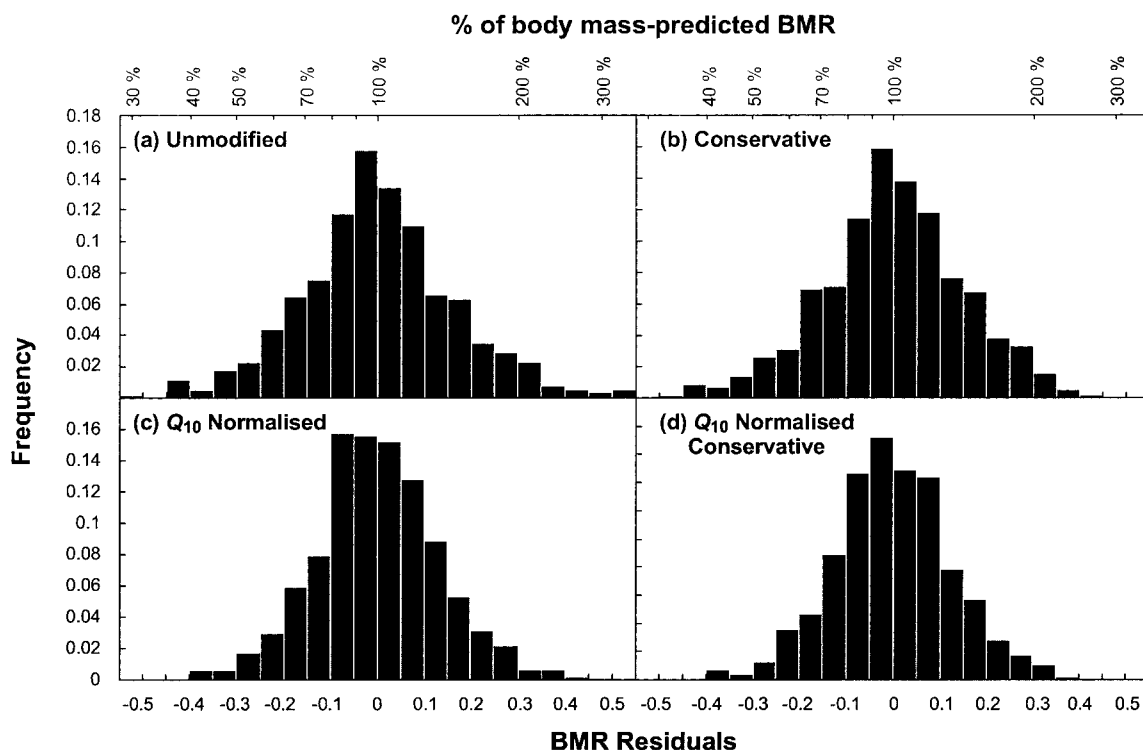
% of body mass-predicted BMR

Figure 6. Residual variation in mammalian basal metabolic rate (BMR) for (*a*) all data (*n* = 619), (*b*) conservative data (*n* = 571; see "Methods" for selection criteria), (*c*) all data normalised to a common body temperature of 36.2°C (*n* = 507), and (*d*) conservative data normalised to a common body temperature of 36.2°C (*n* = 469).

1997). Although this hypothesis cannot be rejected, the lack of a significant correlation between the residuals of BMR and body surface area (Fig. 9) fails to support it. Similarly, Holloway and Geiser (2001) found no difference between the resting metabolic rates (RMRs) of sugar gliders (*Petaurus breviceps*) in helox (79% helium, 21% oxygen) and normal atmospheres, despite observing a significant increase in thermoneutral thermal conductance in the helox atmosphere. They concluded that an animal's rate of basal energy expenditure is not related to heat loss, which suggests that surface area and BMR need not be causally related.

Variation in BMR between Mammalian Taxa

Despite the improvement of allometry, variation about the regression line remains considerable, particularly between species (Fig. 6; Table 2). Despite this variation, scaling exponents do not differ, either between orders or between Eutheria and Metatheria, suggesting that deviations from a BMR scaling exponent of 2/3 that occur at the level of class, infraclass, and order are a result of T_b variation that is correlated with M. Differences in BMR scaling between eutherians and metatherians, for example, can be accounted for by the lower T_b of metatherians, coupled with different relationships between T_b and M (White

and Seymour 2003). Furthermore, across Mammalia only the orders Chiroptera and Dasyuromorphia have significantly different BMRs (Fig. 8). However, small (<350 g) dasyuromorph marsupials have significantly lower BMRs than small primates, rodents, and insectivores (Fig. 8).

Given that avian and mammalian endothermy probably evolved separately, it would be interesting to determine if the BMR differences between mammals and birds can be similarly accounted for by the differences in T_b between these groups

Table 2: Factorial range (upper limit/lower limit) observed in various measures of residual variation unaccounted for in each of four interspecific regression types

Species Combinations	Total	1 SD	95% CI
Unmodified	11.3	1.46	1.030
Conservative	7.8	1.42	1.029
Q_{10}-normalised	6.7	1.35	1.027
Conservative Q_{10}-normalised	5.7	1.33	1.026

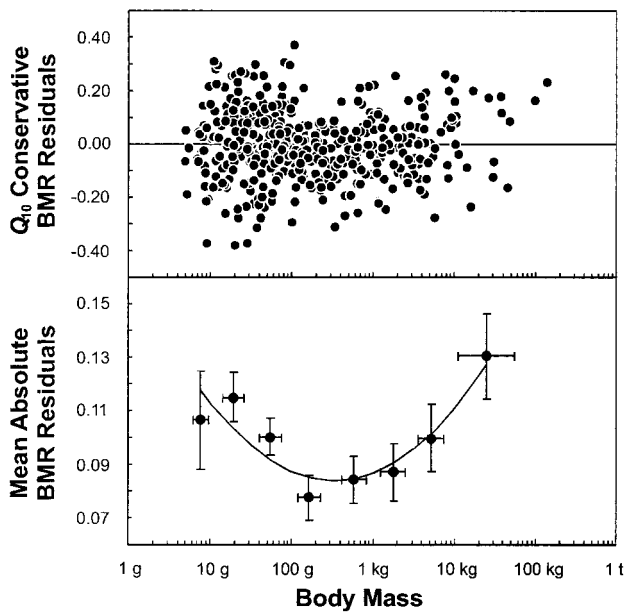Note. Details regarding species combinations are provided in Table 1.

Figure 7. Relationship between body mass (*M*, g) and the residual variation in mammalian conservative Q_{10}-normalised basal metabolic rate (BMR; *top*; see "Methods" for selection criteria). Following Lovegrove (2000), mean absolute BMR residuals (*bottom*) are depicted $\pm$ SE; mean body mass values are depicted ± 1 SD. Variation is maximal at smallest and largest masses. The relationship between log *M* and mean absolute BMR residuals (mean BMR residuals $= 0.0125[\log M]^2 - 0.0632\log M + 0.163$, $r^2 = 0.80$) reaches a minimum at 337 g, which is similar to the 358 g reported by Lovegrove (2000).

(McNab 1966). As a preliminary investigation of this possibility, BMR and T_b data were collated for 66 species of birds (Daan et al. 1989; Thouzeau et al. 1999; McNab 2000, 2003; Tieleman and Williams 2000; Frappell et al. 2001; McKechnie and Lovegrove 2001). As expected, BMR scaling exponents do not differ between mammals and birds, and birds have higher BMRs than mammals (Fig. 10*a*). A Q_{10} of 3.0 was then used to normalise the BMRs of birds and mammals to a common T_b. This Q_{10} was chosen because it minimises variation in mammalian Q_{10}-normalised BMR (White and Seymour 2003). However, mammalian mass-independent conservative BMR (mL O_2 $g^{-0.67}$ h^{-1}) is related to T_b with a Q_{10} of 2.8 (Fig. 11). Q_{10} has a quantifiable effect on the scaling exponent, but the difference between Q_{10} values of 2.8 and 3.0 is minor, and *b* is not significantly different from 2/3 within the range of $2.0 \geq Q_{10} \geq 4.0$ (Fig. 12). When normalised to a T_b intermediate between birds and mammals (38.2°C, $Q_{10} = 3.0$), scaling exponents for these groups do not differ, and birds and mammals do not have significantly different BMRs (Fig. 10*b*). This similarity between the BMRs of birds and mammals further supports the suggestion that a common cause underlies the influence of *M* on BMR for endothermic homeotherms (White and Seymour 2003).

Correlates to BMR

Independent of body mass, high BMR is associated with high MMRs and FMRs, high resting heart rates, production of large numbers of offspring per litter, low population density, and short life spans (Table 4). The number and variety of variables with which BMR is significantly correlated suggests that despite being an unnatural physiological construct that animals rarely show under natural conditions, BMR does indeed contain a useful and meaningful signal.

If BMR is considered to be the minimum energy cost of maintaining the body, its level is likely to be related to the capacity of the body for activity. Animals with higher aerobic capacities have higher mitochondrial volumes (Mathieu et al.
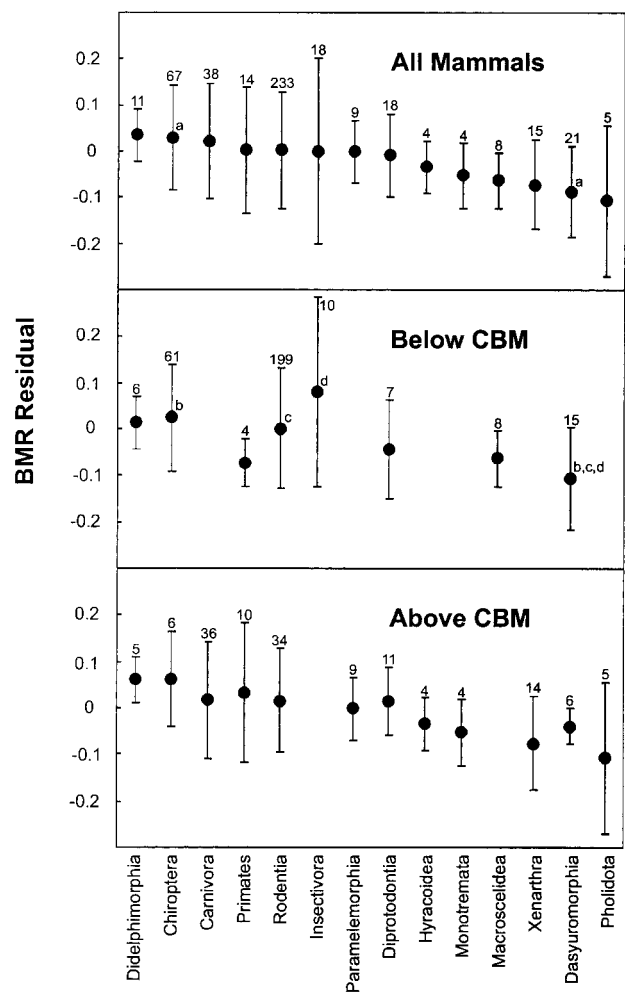
Figure 8. Conservative Q_{10}-normalised basal metabolic rate (BMR) residuals arranged by order as mean $\pm$ SD of mammals of all sizes (*top*) or mammals smaller (*middle*) or larger (*bottom*) than the constrained body mass (CBM) of 350 g (Fig. 7 and Lovegrove 2000). See "Methods" for details of data selection. Numerals show sample size; lowercase characters denote order pairs identified as significantly different (Tukey-Kramer HSD, $P < 0.05$).

Table 3: Allometric relationships between mammalian body mass (M, g) and basal metabolic rate (BMR, mL O_2 h^{-1})

	Small Mammals		Large Mammals		All Conservative Q_{10}-Normalised	
	Relationship	Sample	Relationship	Sample	Relationship	Sample
Interspecific by zoogeographic zone:						
Afrotropical	$3.22M^{71 \pm .12}$	55	$1.57M^{80 \pm .06}$	34	$3.00M^{72 \pm .03}$	89
Australian	$4.70M^{67 \pm .07}$	47	$4.91M^{65 \pm .06}$	34	$3.49M^{70 \pm .02}$	81
Indomalayan	$3.42M^{68 \pm .09}$	11	$3.71M^{68 \pm .15}$	14	$3.20M^{70 \pm .05}$	25
Nearctic	$5.46M^{62 \pm .06}$	90	$2.74M^{74 \pm .09}$	21	$4.52M^{67 \pm .03}$	111
Neotropical	$4.99M^{65 \pm .05}$	77	$3.95M^{68 \pm .07}$	43	$4.96M^{65 \pm .02}$	120
Palaearctic	$5.71M^{61 \pm .14}$	36	$.62M^{94 \pm .20}$	7	$4.71M^{66 \pm .08}$	43
Interspecific by order:						
Carnivora			$1.91M^{77 \pm .07}$	36	$2.84M^{73 \pm .06}$	38
Chiroptera	$4.13M^{70 \pm .07}$	61			$4.10M^{70 \pm .05}$	67
Dasyuromorphia	$3.07M^{70 \pm .16}$	15	$3.07M^{71 \pm .12}$	6	$2.92M^{71 \pm .05}$	21
Didelphimorphia	$2.97M^{76 \pm .09}$	6			$3.29M^{73 \pm .05}$	11
Diprotodontia	$5.65M^{56 \pm .25}$	7	$8.41M^{59 \pm .10}$	11	$3.92M^{68 \pm .04}$	18
Insectivora	$4.36M^{72 \pm .5}$	10			$6.88M^{57 \pm .14}$	18
Monotremata			$1.22M^{82 \pm .19}$	4	$1.22M^{82 \pm .19}$	4
Primates	$12.58M^{44 \pm .35}$	4	$1.21M^{84 \pm .20}$	10	$1.88M^{79 \pm .10}$	14
Rodentia	$5.23M^{62 \pm .05}$	199	$2.48M^{75 \pm .08}$	34	$4.33M^{67 \pm .03}$	233
Xenarthra			$3.14M^{69 \pm .14}$	14	$3.74M^{67 \pm .11}$	15

Note. All regressions are based on BMR data normalised to a body temperature of 36.2°C, with data for Lagomorpha, Artiodactyla, Soricidae (Insectivora), and Macropodidae (Diprotodontia) excluded. Regression exponents are presented ±95% confidence interval. Small mammals are those lighter than 350 g; large mammals are heavier than 350 g, where 350 g is the constrained body mass identified by analysis of BMR residuals (Fig. 7).

1980; Hoppeler 1990), and this in turn is related to greater proton leakage through mitochondrial membranes, which is a significant component of metabolic rate (Hulbert and Else 2000). Similarly, BMR and MMR residuals are positively correlated when elicited by both cold exposure and exercise, although only the former was significant in this analysis (Table 4). Previous work provides mixed support for a correlation between MMR and BMR (reviewed by Hayes and Garland 1995). Significant interspecific and intraspecific correlations have been reported within Mammalia, for both cold-induced and exercise-induced MMR, although such relationships are not ubiquitous and have not been demonstrated for all species or clades so far investigated (Hayes and Garland 1995). This is particularly true of broad, interspecific studies, such as this one, where measurements have been obtained by a variety of experimenters using a range of methodologies (e.g., Koteja 1987). In such cases metabolic data may not be strictly comparable (Hayes et al. 1992b), and elucidation of significant relationships becomes increasingly difficult.

Given that the physiological and biochemical processes that contribute to BMR continue under field conditions and that BMR is equal to around 20%–35% of FMR (calculated using Fig. 3d and Nagy et al. 1999), it is also reasonable to assume that an animal with a high basal energy expenditure would have a high field rate of energy expenditure. In support of this

suggestion, FMR residuals are positively correlated with BMR residuals within both Mammalia and Rodentia (Table 4).

Within Mammalia and Diprotodontia, BMR residuals are significantly positively correlated with heart rate (HR) residuals (Table 4). This original interspecific analysis therefore supports the same pattern shown intraspecifically in studies designed to estimate metabolic rate indirectly by measuring HR with radio telemetry (e.g., Froget et al. 2001; McCarron et al. 2001; Butler et al. 2002). Such correlations are theoretically expected, because they are based on the Fick principle. HR is also thought to be related to life span: large animals live longer than small ones but do so at a slower rate, so the total number of heart beats throughout an animal's life is expected to be roughly independent of body mass (Schmidt-Nielsen 1984, 1990). However, the product of HR and life span scales with a negative exponent, and HR and life span residuals are not significantly correlated ($r = 0.07$, $n = 45$, $P = 0.65$, HR $= 6.4 \times 10^8 M^{-0.29}$ beats yr^{-1}, $r^2 = 0.80$; maximum recorded life span $= 2.0M^{0.22}$ yr, $r^2 = 0.45$; sources presented in Table 4). Large animals therefore experience fewer heartbeats in their lives than small animals, and species with long life spans do not experience a greater number of heartbeats than short-lived ones. This suggests that life span and HR are related only as a consequence of body size. However, maximum recorded life span is a poor measure of natural longevity (Speakman et al. 2002),

Table 4: Interspecific residual (body mass–independent) correlations between basal metabolic rate (BMR) and selected physiological, ecological, and life-history parameters in mammalian groups

	Mam	Car	Chi	Das	Did	Dip	Ins	Mac	Rod	Xen
Body surface area	−.2 (22)	.9 (3)				.81 (4)	.1 (3)		−.1 (7)	
Population density		−.4* (25)		−.6 (3)	.8 (3)	−.5 (8)	−.6 (7)		.3 (70)	−.1 (4)
Fecundity	.2 (78)	−.3 (17)	.6 (5)	−.2 (4)	.8 (3)	0 (4)	−.3 (6)		.4* (28)	.6 (6)
FMR	.7*** (30)		.7 (5)			.92 (4)			.9*** (11)	
Heart rate	.5*** (48)	.2 (11)	−.1 (3)	.7 (5)		.95* (5)			.2 (17)	
Life span	−.1 (225)	−.3* (40)	0 (15)	−.7** (13)	.9 (4)	−.7** (14)	.1 (11)		−.3* (78)	−.4 (11)
Litter size	.2* (198)	.2 (28)	−.5 (5)	.5* (20)	−.1 (10)	−.4 (12)	.2 (21)	−.97* (4)	.2 (66)	.2 (12)
Litters per year	.1 (78)	−.5* (17)	.8 (6)	−.5 (4)	−.3 (3)	−.2 (4)	−.3 (7)		.3 (26)	.4 (6)
MMR, cold	.4** (56)			0 (6)		.84 (5)			.4* (41)	
MMR, exercise	.3 (21)	.3 (4)							.3 (16)	

Note. FMR = field metabolic rate; MMR = maximum aerobic metabolic rate. Data are sorted into the following taxonomic groups: Mam = all mammals; Car = Carnivora; Chi = Chiroptera; Das = Dasyuromorphia; Did = Didelphimorphia; Dip = Diprotodontia; Ins = Insectivora; Mac = Macroscelidae; Rod = Rodentia; and Xen = Xenarthra. Data for some orders are not presented because of small sample size and lack of significance; therefore, n-values may not sum across rows. Data were compiled from published sources: Kinnear and Brown (1967); Dawson and Hulbert (1970); Eisenberg (1981); Seeherman et al. (1981); Taylor et al. (1981); Maloiy et al. (1982); Müller et al. (1983); MacArthur (1984); Damuth (1987); Koteja (1987); Bozinovic (1992); Hinds and Rice-Warner (1992); Van Tienhoven et al. (1993); Chappell and Dawson (1994); Nagy (1994); Purvis and Harvey (1995); Reynolds (1997); Symonds (1999); Carey and Judge (2000); Nagy and Bradshaw (2000); Barros et al. (2001); Holloway and Geiser (2001); Nespolo et al. (2001); White and Seymour (2003). Sample size is in parentheses.
* $P = 0.05$.
** $P = 0.01$.
*** $P = 0.001$.

and the trend for larger animals to show fewer heartbeats in their lifetimes may simply be a reflection of the relative difficulty of obtaining reliable maximum life span data for larger animals (Calder 1984). The failure to identify a significant correlation between BMR and life span residuals across Mammalia may also stem from similar problems (Table 4). Within Carnivora, Dasyuromorphia, Diprotodontia, and Rodentia, however, BMR and life span are significantly negatively correlated (Table 4). In further support of the "rate-of-living," or "live fast, die young," hypothesis (reviewed by Speakman et al. 2002), life span residuals are significantly negatively correlated with residuals for litter size ($r = −0.46$, $n = 153$, $P < 0.0001$), litters per year ($r = −0.36$, $n = 68$, $P = 0.003$), and annual fecundity ($r = −0.59$, $n = 65$, $P < 0.0001$) across Mammalia. Assuming that reproductive life span is related to maximum life span, lifetime reproductive output (calculated as the product of life span and fecundity) is body size invariant (log-log transformed, $r = 0.15$, $n = 65$, $P = 0.22$). Short-lived species therefore compensate for their lack of longevity with an increased rate of offspring production, and thereby produce a similar number of offspring as long-lived species. The product of life span and BMR, on the other hand, scales with an exponent significantly less than 1 ($b = 0.90$, 95% CI = 0.86–0.94, $n = 224$), which suggests that large animals use less energy per kilogram of body mass over their lifetimes than small ones. Once again, this may also reflect the difficulty of obtaining reliable maximum life span data for larger animals (Calder 1984).

BMR and FMR are significantly positively correlated, so a low population density might be expected for animals with high BMRs, because they are likely to require a greater quantity of resources than those with low BMRs. However, BMR and population density residuals are correlated only within Carnivora (Table 4). Nevertheless, home range scaling exponents estimated according to Haskell et al. (2002) are closer to measured values when a BMR scaling exponent of 2/3 is used in preference to 3/4 (White and Seymour 2003).

Studies on the relationship between BMR and other life-history characteristics provide mixed results. Read and Harvey (1989) and Harvey et al. (1991) compared mass-independent
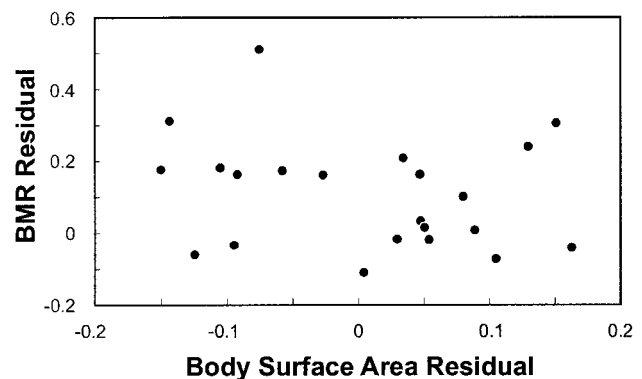

Figure 9. Relationship between mass-independent residuals of basal metabolic rate (BMR) and body surface area. The correlation is not significant ($r = −0.22$, $P = 0.31$, $n = 22$).
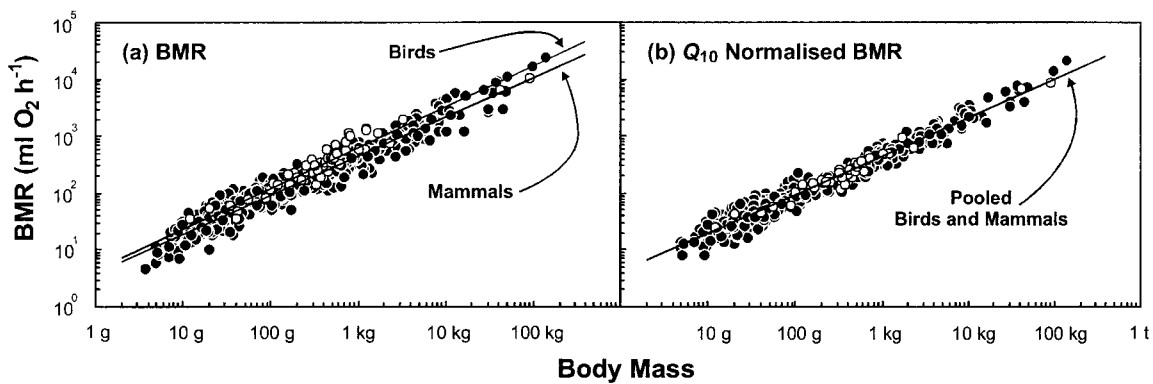
Figure 10. Relationship between body mass and (*a*) basal metabolic rate (BMR) or (*b*) Q_{10}-normalised BMR for birds (*open circles*) and mammals (*filled circles*). Regression lines are extrapolated beyond data ranges to facilitate comparison. The Q_{10}-normalised BMRs were normalised to a body temperature of 38.2°C, which is intermediate between the mean ($\pm$SD) body temperatures of birds (40.1 $\pm$ 1.9°C, $n = 86$) and mammals (36.2 $\pm$ 1.9°C, $n = 507$). A Q_{10} of 3.0 was used for all calculations. Scaling exponents for bird and mammal BMRs do not differ (ANOVA, $F_{1,633} = 0.72$, $P = 0.40$), and birds have higher BMRs than mammals (ANCOVA, $F_{1,633} = 43.5$, $P < 0.0001$). Bird and mammal Q_{10}-normalised BMRs do not have different scaling exponents (ANOVA, $F_{1,512} = 0.11$, $P = 0.74$) or elevations (ANCOVA, $F_{1,513} = 0.11$, $P = 0.74$). Equations of the regression lines: bird BMR $= 4.58M^{0.71}$, $r^2 = 0.91$, $n = 66$; mammal BMR $= 3.98M^{0.69}$, $r^2 = 0.94$, $n = 469$; Q_{10}-normalised BMR $= 4.16M^{0.68}$, $r^2 = 0.96$.

measures of BMR with mass-independent measures of multiple reproductive variables across eutherian orders and found no significant correlations, except one: in accord with this study (Table 4), they found that variation in litter size was positively correlated with BMR. Conversely, Cruz-Neto and Jones (in press) concluded that the evolution of low BMRs within Chiroptera was correlated with faster life histories (earlier age at maturity and higher rates of mortality) and that BMR and fecundity were significantly correlated only if the influence of body mass was not removed. Similarly, Symonds (1999) found that within Insectivora, BMR was significantly negatively correlated with gestation length, the period of maternal investment, maximum life span, and maximum reproductive life span. No significant correlation between litter size and BMR was identified within Insectivora (Symonds 1999). Intraspecifically, BMR and life-history variables are uncorrelated for *Sigmodon hispidus* (Derting and McClure 1989), *Peromyscus maniculatus* (Earle and Lavigne 1990), *Mus musculus* (Hayes et al. 1992*a*; Johnson et al. 2001), *Microgale dobsoni* (Stephenson and Racey 1993), and *Geogale aurita* (Stephenson and Racey 1993). Laboratory-raised lines of mice divergently selected for heat loss measured by direct calorimetry, on the other hand, have shown a positive correlation between RMR and litter size associated with a similar change in ovulation rate (Nielsen et al. 1997). Similarly, mice selected for high rates of food intake have high RMRs (Selman et al. 2001) and high ovulation rates (Brien et al. 1984) and produce large litters (Brien et al. 1984) relative to control lines and lines selected for low rates of food intake. The positive correlation between BMR and litter size observed across Mammalia (Table 4) is therefore also likely to

be associated with a positive correlation between BMR and ovulation rate.

It is clearly unrealistic to expect that BMR can be shown to be correlated with all physiological and ecological characteristics of mammals, but in view of the natural and experimental variation in the available data, the appearance of many significant correlations of residuals shows that BMR contains a relatively high signal-to-noise ratio. Because BMR is a relatively simple measurement to make, it therefore remains a practical metric of metabolic intensity of animals and will continue to be a central benchmark in comparative physiology.
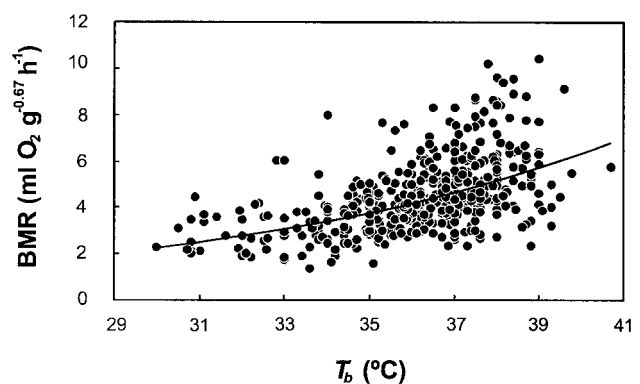

Figure 11. Relationship between body temperature (T_b, °C) and mass-independent conservative Q_{10}-normalised basal metabolic rate (BMR, mL O_2 g$^{-0.67}$ h^{-1}). Equation of the regression line: BMR $= 0.0987e^{0.104T_b}$. Therefore, T_b and BMR are related with a Q_{10} of $e^{0.104 \times 10}$, or 2.8.
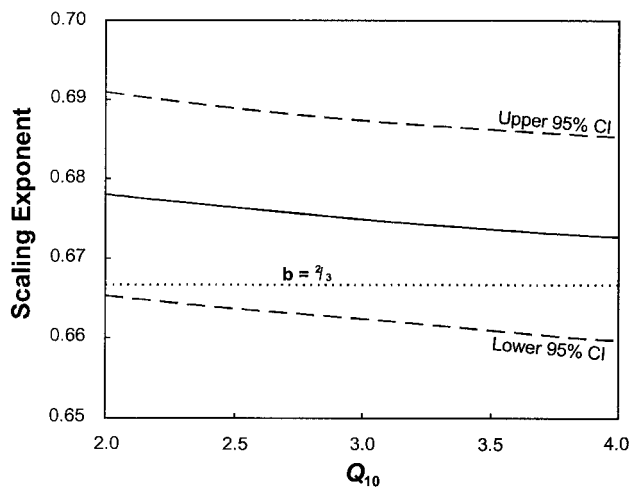
Figure 12. Effect of altering Q_{10} on the scaling exponent (b, where BMR $= aM^b$, BMR is basal metabolic rate, and M is body mass) estimated for mammalian conservative Q_{10}-normalised BMR. Within the range of $2.0 \geq Q_{10} \geq 4.0$, b (*solid line*) is not significantly different from 2/3. Broken lines represent the upper and lower 95% confidence limits of the scaling exponent; the dotted line represents an exponent of 2/3. A Q_{10} of 3.0 was used for normalisation to a common T_b throughout this study (White and Seymour 2003). A Q_{10} of 2.8 is suggested by the relationship between mass-independent BMR and T_b (assuming a b-value of 2/3; Fig. 11).

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