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Scaling of basal metabolic rate with body mass and temperature in mammals

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Summary

1. We present a statistical analysis of the scaling of resting (basal) metabolic rate, BMR, with body mass, B_m and body temperature, T_b, in mammals.

2. Whilst the majority of the variance in ln BMR is explained by ln B_m, the T_b term is statistically significant. The best fit model was quadratic, indicating that the scaling of ln BMR with ln B_m varies with body size; the value of any scaling exponent estimated for a sample of mammals will therefore depend on the size distribution of species in the study. This effect can account for much of the variation in scaling exponents reported in the literature for mammals.

3. In all models, inclusion of T_b reduced the strength of scaling with ln B_m. The model including T_b suggests that birds and mammals have a similar underlying thermal dependence of BMR, equivalent to a Q_{10} of 2·9 across the range of T_b values 32–42 °C.

4. There was significant heterogeneity in both the mass scaling exponent and mean BMR across mammalian orders, with a tendency for orders dominated by larger taxa to have steeper scaling exponents. This heterogeneity was particularly marked across orders with smaller mean B_m and the taxonomic composition of the sample will thus also affect the observed scaling exponent. After correcting for the effects of ln B_m and T_b, Soricomorpha, Didelphimorphia and Artiodactyla had the highest BMR of those orders represented by more than 10 species in the data set.

5. Inclusion of T_b in the model removed the effect of diet category evident from a model in ln B_m alone and widely reported in the literature; this was caused by a strong interaction between diet category and T_b in mammals.

6. Inclusion of mean ambient temperature, T_a, in the model indicated a significant inverse relationship between ln BMR and T_a, complicated by an interaction between T_a and T_b. All other things being equal, a polar mammal living at −10 °C has a body temperature ~2·7 °C warmer and a BMR higher by ~40% than a tropical mammal of similar size living at 25 °C.

Key-words: allometry, bird, diet, energetics, phylogeny, thermal ecology

Introduction

Interest in the relationship between body mass and metabolic rate can be traced back to the seminal study of dogs by Rubner (1883). This was followed by a series of investigations, principally of domesticated or agriculturally important mammals, that suggested scaling exponents for resting metabolism close to 0·75 (Kleiber 1932, 1947, 1961; Benedict 1938; Brody 1945; Hemmingsen 1950, 1960).

More recent work using considerably larger data sets has suggested a range of scaling exponents. Thus Dodds, Rothman & Weitz (2001), White & Seymour (2003, 2005) and White, Phillips & Seymour (2006) have all suggested a scaling exponent ~0·67. In contrast, Savage *et al.* (2004) used a binning procedure and recovered an exponent of ~0·75. Kozowski, Konarzewski & Gawelczyk (2003) fitted individual regressions to six mammalian orders and found a mean value of 0·728, whilst Farrell-Gray & Gotelli (2005) performed a meta-analysis and suggested that a value ~0·75 was the most likely. McNab (2008) determined an intermediate value of 0·72, with the precise value depending on other factors in the model. Whilst these analyses have been concerned with the nature of scaling for mammals overall, it has also been established that there is significant heterogeneity in scaling within mammals (Hayssen & Lacy 1985; Symonds & Elgar 2002;

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Glazier 2005; Duncan, Forsyth & Hone 2007; Sieg *et al.* 2009; White, Blackburn & Seymour 2009).

An intriguing question is why the various studies have reported different scaling exponents for mammals as a group, especially as many of the studies are using essentially the same data. At least five non-exclusive explanations are possible: the choice of data, the statistical protocols employed, the influence of phylogeny, differences between lineages in the level or scaling of resting metabolism and the influence of body temperature on resting metabolism.

In marked contrast to studies of metabolism in ectotherms, relatively few studies of endotherm metabolism make explicit inclusion of body temperature. Whilst some recent studies have noted an association between body temperature and metabolic rate in mammals (Lovegrove 2003; White *et al.* 2006), body temperature has typically been ignored in analyses of the scaling of metabolic rate in mammals. Although most individual mammals regulate their body temperature within a fairly narrow range, recent analyses have shown that the range of body temperatures within mammals as a whole is significant (>10 °C) and moreover varies between lineages (Clarke & Rothery 2008). This suggests that body temperature is sufficiently variable to play a significant role in mammalian resting metabolism and its scaling with body mass.

Here, we present an analysis of the combined effect of body mass and body temperature on resting metabolic rate in mammals. The main thrust of our analysis was to explore the effects of body temperature on the scaling of basal metabolic rate. Several studies, however, have indicated that ecological factors such as diet influence basal metabolic rate in mammals (McNab 1992, 2008; Muñoz-Garcia & Williams 2005) and we therefore also undertook a preliminary analysis of the influence of diet. The aims of the study were:

1. To analyse the joint effects of body mass and body temperature on resting metabolic rate in mammals.
2. To examine the effect of phylogenetic non-independence on the estimate of the scaling exponent (and thereby determine the extent to which the statistical protocol used can explain variation in the scaling parameters reported for mammals).
3. To analyse the influence of environmental temperature and diet on resting metabolic rate in mammals.

Materials and methods

A database of resting (basal) metabolic rate (BMR, W), body mass (B_m, g) and body temperature (T_b,°C) data was constructed, based on previous compilations (White & Seymour 2003; Savage *et al.* 2004; Clarke & Rothery 2008) and augmented with new data from literature searches. As with all such compilations, data quality was variable. Both BMR and T_b should ideally be measured in resting, normothermic, post-absorptive, inactive and conscious individuals (Benedict 1938). However, it can be difficult to achieve these conditions in mammals where the digestive tract supports significant fermentation such as artiodactyls, macropods, or lagomorphs, or in small highly active forms such as shrews.

Since the original databases were compiled, there has been a significant development in mammalian taxonomy with the publication of the third edition of Mammal Species of the World (MSW3) (Wilson & Reeder 2005). This has increased the number of known mammalian species to 5416, in 29 orders. The database was checked against MSW3 to unify the taxonomy and document synonyms. The resultant data set comprised 634 species from 24 orders with data for both BMR and B_m; of these 505 species from 22 orders also had data for T_b. For taxonomic analysis, species were assigned to families and orders from MSW3 and one higher taxon (subclass, infraclass or superorder). The data, taxonomic distribution and higher level taxonomy used in the analysis are shown in the Supporting Information. Data on the mean ambient temperature (for 462 species in the data set) and diet (372 species, eight diet categories) were kindly provided by the PanTheria database team (Jones *et al.* 2009). For comparison of the scaling of BMR in mammals with birds, we used data for BMR, B_m and T_b in birds from White *et al.* (2006).

STATISTICAL ANALYSIS

The body mass and metabolic rate data were highly skewed and were therefore log-transformed (natural logs) before analysis. Temperature data were untransformed, as the regression coefficient b_2 then has a relatively simple interpretation and Q_{10} can be calculated easily: $Q_{10} = \exp[b_2*10]$. The rationale for the transformations and choice of statistical model are given in the Supporting Information.

For the initial analyses we used a General Linear Model (GLM). However, it has long been recognized that much ecological data contain a strong evolutionary signal and that failure to allow for this phylogenetic non-independence can lead to an increase in type I error and erroneous results (Felsenstein 1985). We used two parallel approaches to explore the effect of phylogenetic non-independence in the data. The first was a multi-level mixed effects linear regression model (LMM) which utilizes taxonomic structure as a proxy for phylogeny (Clarke & Rothery 2008) and combines regression (for the trend) with a nested structure (for the random variation). Models were fitted using the method of residual maximum likelihood (REML) (Patterson & Thompson 1971), implemented using the statistical package GENSTAT 5 (GenStat 2005).

The second approach was to use phylogenetically independent contrasts (PIC: Garland, Harvey & Ives 1992). The analysis was based on a phylogenetic supertree containing virtually all extant mammal species (Fritz, Bininda-Emonds & Purvis 2009). Two species in the data set (*Eremitalpa granti* and *Sciurus aberti*) are absent from the supertree, so our phylogenetic analyses were based on 632 species, of which 503 had body temperature data. The λ statistic (Pagel 1999; Freckleton, Harvey & Pagel 2002) for ln BMR had a maximum likelihood estimate of 0·984, indicating strong phylogenetic inertia. All analyses were conducted using the CAIC package (Orme, Freckleton & Petzoldt 2008) in R 2.8.1 (R Development Core Team 2008).

We have thus used three different statistical approaches. The first was a GLM, which ignores phylogenetic effects and is thus liable to underestimate the standard error of the regression slope. LMM and PIC provide two alternatives for estimating this standard error without bias; LMM additionally provides a convenient tool for examining heterogeneity among taxa. We present the results from all three approaches, partly for comparison between them and partly because most previous analyses of the scaling of metabolic rate in mammals have used statistical techniques that assume complete independence among species.

Results

CONVENTIONAL GLM

The data set contains 634 species with values for both body mass (B_m) and basal metabolic rate (BMR), the B_m values ranging from 2·4 g to 407 kg. GLM indicated that for these data the regression coefficient for the log-transformed data had a slope of 0·709 (SE 0·006).

Within these, there are 505 species with data for body temperature (T_b). Confining the analysis to this subset gave a slope of 0·695 (SE 0·007) if T_b was omitted from the model and 0·683 (SE 0·006) for the model including T_b. Whilst most of this variation could be accounted for by the simpler model in ln B_m (Fig. 1a), the effect of T_b was highly significant ($P < 0·001$) (see Supporting Information for the full statistical analysis). The temperature coefficient (Fig. 1b) was equivalent to a Q_{10} of 3·27 over the range 30–40 °C. Although including T_b in the model had only a small effect on the explained variance, the effect size implies that body temperature has a physiologically significant effect on BMR, even within the relatively narrow range of T_b exhibited by mammals.

There was, however, strong evidence from the residuals of curvilinearity in the relationship with ln B_m. Adding the quadratic term in T_b had a negligible effect ($P = 0·55$), but there was small but statistically significant improvement by adding the quadratic term in ln B_m ($P < 0·001$). This means that the relationship between ln BMR and ln B_m across all mammals is significantly nonlinear, even after allowing for T_b (see Supporting Information for a detailed analysis of the various models).

To illustrate the effects of body mass on the scaling coefficient, data were binned by body mass and separate regressions fitted (in ln B_m and T_b) for each bin. The scaling coefficient increased monotonically from $<0·6$ for small mammals (ln $B_m < 3$), approaching an asymptote of $>0·75$ for the largest mammals (Fig. 2a). This result was robust to the choice of bin criteria (see Supporting Information), indicating clearly that the scaling of basal metabolic rate with body mass in mammals depends markedly on size.

A similar analysis binning the data by body temperature showed a much smaller effect of T_b on the scaling coefficient (Fig. 2b).

LINEAR MIXED MODEL

The linear mixed model (LMM) suggested a higher scaling coefficient for ln BMR on ln B_m than did the GLM (Table 1). At the same time, the LMM indicated a lower scaling coefficient for T_b, equivalent to a Q_{10} of 1·99. As with the GLM analysis, incorporation of T_b into the model was significant and

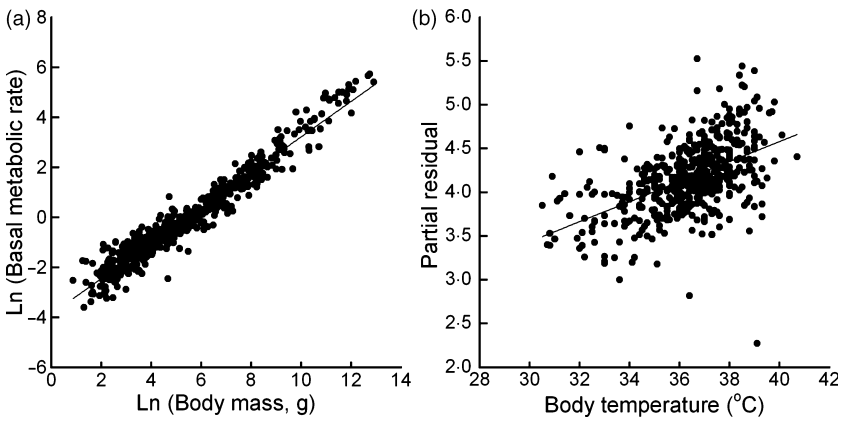

Fig. 1. Scaling of basal metabolic rate (w) in mammals with body mass and body temperature; GLM analysis ($n = 505$ species with data for BMR, B_m and T_b). (a) Scaling of basal metabolic rate with body mass. The slope of this relationship is 0·683 (SE 0·006). (b) Partial residuals from a model in ln B_m and T_b as a function of T_b. The slope of the relationship is equivalent to a Q_{10} of 3·25 over the range 30–40 °C.

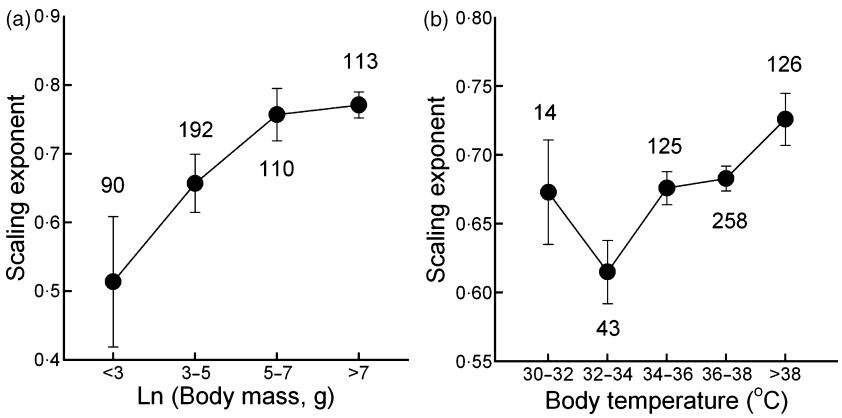

Fig. 2. Variation in the scaling of basal metabolic rate in mammals with body mass and body temperature. Scaling exponents (regression coefficient for ln B_m) taken from a model in ln B_m and T_b, fitted separately to each bin. Data plotted as mean and SE and number of species in each bin shown (see Supporting Information for full details). (a) Data binned by body mass. (b) Data binned by body temperature.

Table 1. Analysis of scaling relationship between basal metabolic rate, BMR, body mass, B_m (both natural log-transformed) and body temperature, T_b, using different statistical methods: general linear model (GLM), linear mixed model (LMM) and phylogenetically independent contrasts with either equal branch lengths (PIC1) or branch lengths proportional to time (PIC2). Analyses based on 505 species with data for BMR, B_m and T_b, all models were fitted with and without the T_b term included. Estimated variance component for linear mixed model in ln B_m and T_b were: order (0·047), family (0·012), genus (0·027) and species (0·052). Coefficients are presented as mean (SE); *n* is the sample size (number of species or contrasts in the analysis)

		Regression coefficient (SE)	
Method	*n*	ln B_m	T_b
GLM	505	0·696 (0·007)	
GLM	505	0·683 (0·006)	0·119 (0·008)
LMM	505	0·719 (0·011)	
LMM	505	0·710 (0·010)	0·069 (0·009)
PIC1	343	0·758 (0·014)	
PIC1	342	0·752 (0·014)	0·065 (0·012)
PIC2	345	0·729 (0·013)	
PIC2	345	0·721 (0·012)	0·082 (0·010)

reduced the value of the scaling coefficient of ln BMR with ln B_m (Table 1). The LMM confirmed the curvilinearity of the scaling relationship for all mammals and also within selected orders (see Supporting Information for the full analysis).

PHYLOGENETIC ANALYSIS

The data set allowed for calculation of 469 independent contrasts for the model in ln B_m and T_b. We estimated the relationship between each trait with phylogenetically independent contrasts, using both branch lengths proportional to time and set equal. Results are reported after outliers and comparisons at polytomies were excluded, in order to satisfy the assumption of constant variance (see Supporting Information for details).

As with both the GLM and LMM analyses, the dominant effect came from B_m. Including T_b in the analysis had only a small effect on the scaling with B_m, but was significant (Table 1). The scaling was, however, affected by the treatment of branch lengths; analysis with equal branch lengths yielded a greater slope than one with branch lengths proportional to time. The temperature coefficients were equivalent to a Q_{10} of 1·68 (branch lengths proportional to time) or 1·92 (equal branch lengths) over the range 30–40 °C. Compared with the GLM analysis, allowance for phylogenetic structure strengthened the scaling with ln B_m, but weakened the temperature dependence. This is an identical qualitative result to the LMM analysis.

VARIATION IN SCALING BETWEEN ORDERS

The variation in scaling parameters with size (Fig. 2a) suggests that there may be systematic differences in scaling parameters across different mammalian lineages. The distribution of variance across the taxonomic levels suggests that the most appropriate level of analysis would be order. MSW3 recognizes 29 mammalian orders but in seven cases there are no species with complete data for BMR, B_m and T_b (see Supporting Information). Adding a code for taxonomic order to the basic model in ln B_m and T_b showed strong evidence ($P < 0·001$) for significant differences in the scaling of basal metabolic rate across orders. There was no evidence for a ln B_m*order interaction ($P = 0·44$), though the analysis is likely to lack statistical power for detecting such interactions because of the small number of species for some orders.

Confining the analysis to the six orders with >20 species indicated a marked order effect ($P < 0·001$), a suggestion of a ln B_m*order interaction ($P = 0·076$) and a significant order*T_b interaction ($P < 0·002$). The quadratic term was statistically significant for Rodentia ($P = 0·017$) and Carnivora ($P = 0·05$), indicating an increase in scaling exponent with B_m within these two orders, but the contribution was relatively small. For the simpler model in ln B_m and T_b, ln B_m showed a marked effect for each order and an effect of T_b was apparent except for Dasyuromorpha ($b = 0·070$, $P = 0·14$). For orders with smaller median B_m values, the scaling exponent was smallest for Soricomorpha, greatest for Chiroptera and intermediate for Rodentia. The estimated coefficients are given in the Supporting Information.

DIFFERENCES IN BMR BETWEEN ORDERS

The significant differences in the scaling of BMR between different mammalian orders raises the question of whether there are also differences in the absolute level of BMR between different lineages of mammals.

Analysis of the residuals from a GLM fitting ln BMR as a function of ln B_m and T_b, including the quadratic term in ln B_m, indicated that there are significant differences in mean BMR between both higher groups ($F_{4,\ 501} = 3·20$, $P = 0·013$) and orders ($F_{8,\ 435} = 5·07$, $P < 0·001$). Among higher groups the lowest median BMR was exhibited by Xenarthra; the highest rates were for Euarchontoglires and Laurasiatheria (Fig. 3a). Among orders represented by more than 10 taxa the highest levels of BMR were for Didelphimorphia, Soricomorpha and Artiodactyla, with the lowest median values for Dasyuromorpha, Primates and Carnivora (Fig. 3b). Fitting a quadratic model is essential for unbiased results, since the distribution of residuals from the simple linear model in ln B_m and T_b (see Supporting Information) would mean that groups dominated by either small or large species would appear to have a high BMR, simply as a result of their mean size.

EFFECT OF AMBIENT TEMPERATURE

Lovegrove (2003) has shown that for small (<1 kg) mammals BMR varies across biogeographic zones and McNab (2008) has established that the resting metabolic rate of

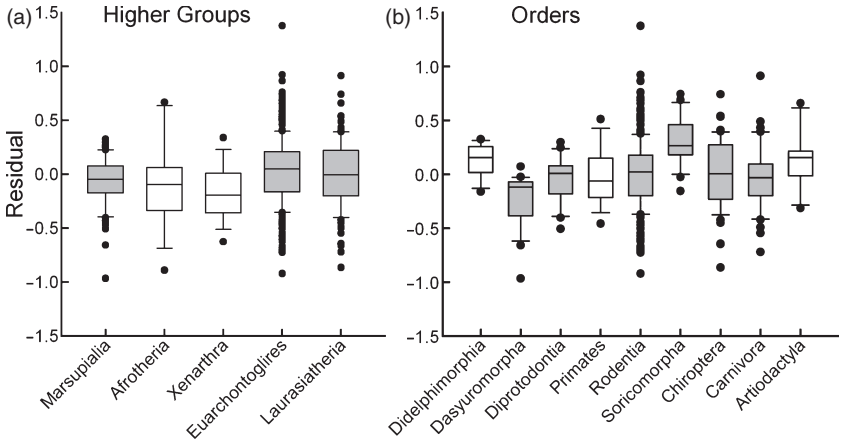

Fig. 3. Box plot of residuals from a model of ln BMR as a function of ln B_m, T_b and (ln B_m)^2. Grey boxes are for taxa with > 20 species, white boxes are for taxa with between 10 and 20 species. (a) Higher Groups. (b) Orders.

mammals is linked to climate. We therefore extended the GLM to include a term for the average environmental temperature experienced within the geographic range of a species, T_a (see Supporting Information for the derivation of this value). The data set contains 462 species with complete data for BMR, B_m, T_b and T_a.

The GLM analysis indicates that after allowing for ln B_m and T_b there was a small but significant decrease in BMR with T_a, although addition of the T_a term to the analysis only explained a further 0·18% of the variance. The slope of the relationship was −0·0097, corresponding to a 10% increase in BMR for a decrease in T_a of 10 °C (Fig. 4a). There was also a clear decrease of T_b with T_a (Fig. 4b); the slope was −0·076, which corresponds to an increase in body temperature of 1 °C for a drop in mean environmental temperature of 13 °C.

Overall the full GLM analysis indicated that the scaling coefficient for BMR in mammals increases with both T_b and T_a, but the effect of T_b decreases with T_a (see Supporting Information). We repeated the analysis with an LMM to allow for the effect of non-independence among taxa. This confirmed the variation in scaling coefficient with both T_b and T_a, but there was little evidence for the T_b by T_a interaction that was evident from the GLM analysis. These analyses indicate that, all other factors being equal, a polar mammal living at −10 °C has a body temperature ∼2·7 °C warmer and a resting metabolic rate higher by ∼40% than a tropical mammal of similar size living at 25 °C.

THE INFLUENCE OF ECOLOGY: DIET

For this analysis we used the eight diet categories from the PanTheria database, including these as a factor in a GLM (model in ln B_m and T_b). Our analysis confirmed previous work (McNab 1992, 2008) showing an effect of diet on ln BMR, after allowing for ln B_m. In contrast, after allowing for both ln B_m and T_b, no effect of diet on ln BMR could be detected; there was, however, an effect of T_b after allowing for ln B_m and diet (see Supporting Information for the full analysis). We conclude that the previously reported effect of diet on BMR in mammals can be accounted for by T_b and its covariation with diet.

Discussion

The analyses presented above indicate that the scaling of basal metabolic rate with body mass is influenced by both body temperature and ambient temperature, that this scaling also varies with body mass and that correction for phylogenetic or taxonomic non-independence among taxa increases the scaling exponent for body mass but decreases the coefficient for body temperature.

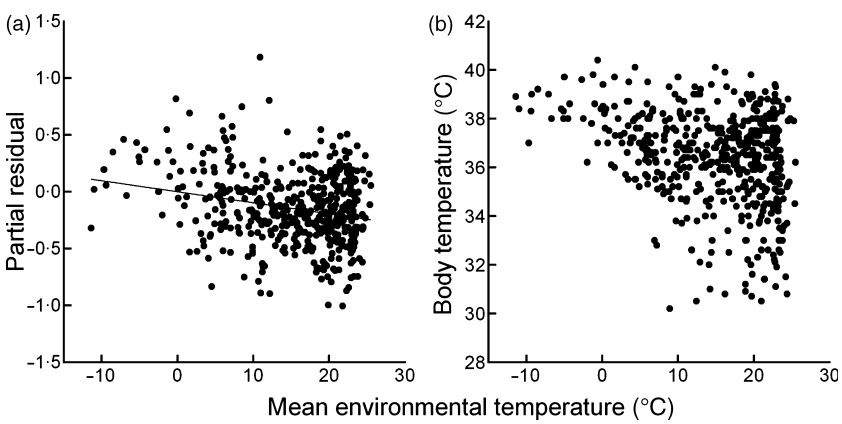

Fig. 4. Effect of environmental temperature on the basal metabolic rate of mammals. (a) Basal metabolic rate (as the partial residual of a model in ln B_m and T_b) as a function of the mean environmental temperature experienced throughout the range for the species (n = 462, one data point per species). (b) Interaction between body temperature (T_b) and mean environmental temperature (Ta) for 462 mammalian species.

THE EFFECT OF BODY MASS ON THE SCALING OF BMR

The dominant factor influencing the resting metabolic rate of mammals is body mass, as has been known since the earliest work on metabolic scaling. In all analyses, including T_b in the model reduced the magnitude of the scaling exponent for ln B_m (Table 1), indicating the importance of including T_b in any analyses of the scaling of BMR in mammals.

Several authors have suggested that the scaling of resting metabolism with body mass may differ between small and large mammals (reviewed by Glazier 2005). The nature of such a nonlinear scaling relationship could theoretically take a number of forms. It could be a single smooth curve (Packard & Birchard 2008), it could be different linear relationships with smaller-bodied taxa having lower exponents (as suggested for domesticated dogs by Heusner 1985, 1991; and White *et al*. 2006, 2009 for all mammals), or it could also be nonlinear within individual taxa (such as mammalian orders) but with the size of the scaling exponent differing across orders. The distribution of residuals from the simple model in ln B_m and T_b (see Supporting Information) suggests that the underlying relationship is a single smooth curve, but our analyses do not rule out alternative explanations.

Binning the data by mass indicated a smooth increase in the scaling exponent with mass (Fig. 2a) and this result was robust to the binning protocol used (see Supporting Information). The shape of this relationship suggests an approach to an asymptotic value of $b_1 \sim 0{\cdot}75$ at larger sizes, whereas in smaller mammals the scaling is around $b_1 \sim 0{\cdot}67$.

This pattern offers a simple explanation for the historical trend in the all-mammal scaling exponent. Early studies (Kleiber 1932, 1947, 1961; Benedict 1938; Brody 1945) were concerned primarily with the energetics of larger mammals, frequently domesticated or agriculturally important species; the scaling exponents observed (0·73–0·74, depending on the species included) reflect the larger size of the species included in the analysis. Kleiber (1961) proposed rounding this exponent to 0·75 for purely pragmatic reasons (ease of computation with a slide rule). Later studies included many more small taxa and this tended to reduce the slope of the scaling relationship (White & Seymour 2003; Glazier 2005; White *et al*. 2006, 2009). This effect can be simulated by sequential removal of data for species with the smallest body mass values; the value of the scaling coefficient for the complete mass range increased from 0·68 (minimum B_m 2·4 g) to 0·75 (minimum B_m 200 g) (see Supporting Information).

The estimate of the scaling coefficient for the smallest size class has low precision because the slope is genuinely heterogeneous at small sizes: bats (Chiroptera) have steep scaling, shrews and allies (Soricomorpha) are shallow and rodents (Rodentia) are intermediate. This finding, combined with the order level analyses reveals that the nonlinearity and heterogeneity among orders are not the same phenomenon, nor is either sufficient to describe the full pattern of scaling of BMR within mammals as a whole. A theoretical prediction that scaling should be less variable at larger sizes emerged from a recent study relaxing the assumptions of the West, Brown & Enquist (WBE) vascular architecture model (Savage, Deeds & Fontana 2008), although this study predicted steeper scaling on average among smaller animals, rather than the shallower scaling we observed.

It thus seems likely that the historical shift in the estimated value of the scaling exponent from $b \sim 0{\cdot}75$ to $b \sim 0{\cdot}67$ results simply from the increased proportion in the data set of species from orders with shallower scaling exponents (especially shrews, didelphids and rodents), which tend to be of smaller size. Glazier (2005) and Duncan *et al*. (2007) also found lower scaling exponents in groups such as rodents and shrews which are predominantly small in size. We would suggest that a major reason for the variation in observed scaling exponent between the many studies of mammalian BMR is simply the taxonomic and size distribution of the taxa included (see Supporting Information for the full analysis).

It would appear that at large sizes, the scaling coefficient for BMR is constrained to be ~0·75, whereas at smaller sizes there are both steep and shallow scaling relationships, although on average they are shallower (Fig. 2a). It is tempting to suggest that a major factor in determining a lower scaling exponent in some smaller taxa is heat flow. Smaller mammals have a higher surface area to volume ratio and all other things being equal, a greater tendency to lose body heat to the environment. This idea underpinned the earliest explanation for the scaling of metabolism in mammals, which was known as the Surface Law (Sarrus & Rameaux 1839).

We suggest that at large sizes the scaling is dominated by factors that dictate $b \sim 0{\cdot}75$ (such as the architecture of vascular systems: Brown *et al*. 2004), whereas at small sizes this factor is overridden by considerations of heat flow and hence $b \sim 0{\cdot}67$. This is analogous to the metabolic boundaries hypothesis of Glazier (2005), though with a different explanation for the upper boundary. Whilst very small mammals show significant heterogeneity in scaling exponents between orders, indicating a complex interplay between T_b and phylogeny, the LMM analysis showed that the significant curvilinearity of the relationship between BMR and B_m (after allowing for T_b) remains after correction for phylogenetic non-independence.

THE EFFECT OF BODY TEMPERATURE ON BMR

The body temperature of an organism is a balance between those processes contributing heat to the organism and those processes removing heat from it. For a terrestrial vertebrate there are two major processes contributing heat (metabolism, absorption of environmental heat) and two major processes removing heat (evaporative cooling during respiration, loss of sensible heat from the body surface). This can be expressed as a simple conceptual model of balanced heat flow (Fig. 5). This model can be applied to both ectotherms and endotherms, as it is simply the relative magnitude of the various heat flows that differs between these two broad ecophysiological groupings.

Among endotherms it has long been recognized that body temperature T_b is influenced directly by metabolism, as this is

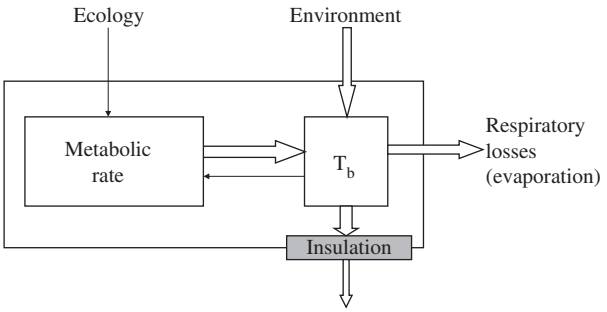

Fig. 5. A conceptual model showing the factors influencing body temperature. Solid arrows show the dominant pathways of heat flow and line arrows indicate influence. Endotherms and ectotherms differ in the balance of importance of metabolism and environmental sources of heat. Reproduced with permission from Clarke & Rothery (2008).

the main source of internal heat. Several authors have explored this relationship, but usually from the perspective that T_b depends on metabolic rate. For example, Lovegrove (2003) used residuals to correct for the effect of body mass and showed a strong positive relationship between T_b and residual BMR in 183 small mammals (<1 kg) from 11 orders; in this study the BMR residual was the independent variable and T_b the dependent variable. By contrast, studies of ectotherms have tended to view the dominant causality as lying in the opposite direction, in that T_b determines the level of BMR; metabolic rate is thus usually plotted as a function of T_b (for example in fish: Clarke & Johnston 1999). The same causality is assumed in the model of Gillooly *et al.* (2001).

Data for ectotherms indicate that whatever the primary source of heat for determining T_b, the resting metabolic rate is influenced by T_b: it costs more to maintain a warm body than it does a cool body (Clarke & Fraser 2004). Thus, whilst the major source of heat that dictates T_b for an endotherm is metabolism, the resultant value of T_b also influences the level of resting metabolism. Despite this important feedback, body temperature has traditionally been ignored in analyses of the scaling of metabolic rate in endotherms, presumably on the assumption that the range of body temperatures involved is relatively narrow. In fact both mammals and birds exhibit a range of ~10 °C in T_b values and T_b varies with body mass (White & Seymour 2003; Clarke & Rothery 2008). To avoid problems from the influence of T_b, White & Seymour (2003) corrected BMR to a common T_b of 36·2 °C. In the analyses presented here we used an alternative approach, namely to include the observed T_b in the statistical model. This has the advantage of estimating the temperature sensitivity of basal metabolism from observation, rather than assuming a theoretical value.

The strength of the temperature sensitivity in mammals is similar to that observed in ectotherm vertebrates (White & Seymour 2003), suggesting that the underlying physiology is similar despite the very different rates of resting metabolism and pointing to a fundamental relationship between T_b and BMR.

If there is a basic underlying relationship between BMR and T_b, then it might be expected that this relationship would be similar in the two endotherm groups, birds and mammals (as suggested by White *et al.* 2006). When BMR is plotted as a function of body mass (Fig. 6a), then the relationships for birds and mammals are significantly different (see Supporting Information for the full analysis): the scaling is similar but birds have a higher BMR than mammals for a given size. However, if T_b is included in the model, then birds and mammals cannot be distinguished statistically and a single relationship describes the thermal sensitivity of resting metabolism in the two groups. Although the inclusion of T_b in the model only explains a small fraction of the variance, its effect is statistically significant and it removes completely the difference between birds and mammals (Fig. 6b).

Birds thus have a higher resting metabolic rate than mammals, mass for mass, but this difference can be explained solely by the fact that birds maintain their bodies at a higher temperature. The underlying thermal sensitivity of resting metabolism in the two groups is indistinguishable, suggesting that there is indeed a common mechanism despite the independent evolution of endothermy and the very different pulmonary systems in the two lineages.

EFFECT OF ENVIRONMENTAL TEMPERATURE AND DIET

Although addition of ambient temperature (T_a) to the model explained only a further 0·18% of the variance, the T_a term was significant. The slope of the relationship indicated a 10%

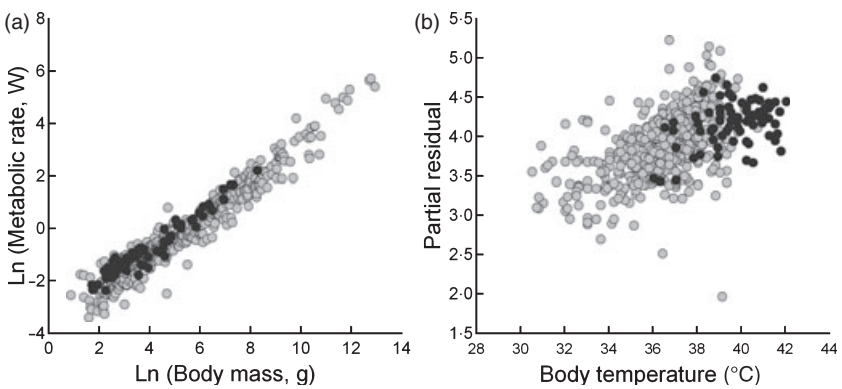

Fig. 6. The temperature dependence of endotherm resting metabolism. (a) Resting metabolic rate in birds (black symbols) and mammals (grey symbols) as a function of body mass; both variables transformed (natural logs). (b) Partial residuals from a model in ln B_m and T_b, as a function of T_b. The slope of the relationships for mammals and birds are statistically indistinguishable and the combined slope is equivalent to a Q_{10} of 2·89.

increase in basal metabolism for a decrease in T_a of 10 °C (Fig. 4a). There was also a clear decrease of T_b with T_a (Fig. 4b), corresponding to an increase in body temperature of 1 °C for a drop in mean environmental temperature of 13 °C.

This result is in broad agreement with previous analyses of resting metabolic rate in mammals in relation to climate (e.g. Lovegrove 2000, 2003) and both results point to the importance of heat flow in the physiology of mammals. All other things being equal, polar mammals have higher body temperatures and an associated higher resting metabolic rate than tropical mammals.

In contrast, our results concerning diet are contrary to previous analyses. Whilst we confirm previous reports of an effect of diet on BMR after correcting for B_m, following inclusion of T_b in the model this effect is no longer discernible. This is caused by an interaction between T_b and diet in mammals, a feature which deserves further exploration.

EFFECTS OF PHYLOGENY

Several previous studies have demonstrated a strong phylogenetic signal in the scaling of mammalian resting metabolism. Symonds & Elgar (2002) used 112 measures of mass-specific metabolic rate in mammals and calculated phylogenetically independent contrasts on the assumption of equal branch lengths. Using this approach they showed that the overall scaling exponent depended on both the evolutionary tree used and the regression model and suggested that the more recent phylogenies tended to steepen the observed scaling exponent. Duncan *et al.* (2007) used a larger data set (625 species) and detected a small influence of phylogenetic structure on the overall scaling, which was 0·71 with ordinary least-squares, but 0·72 with phylogenetic generalized least-squares regression. Although these two studies used different data sets and approaches for testing the influence of phylogeny, both suggested that correcting for phylogeny would increase the overall scaling exponent for mammalian BMR. More recently, Sieg *et al.* (2009) and White *et al.* (2009) used a suite of statistical procedures to correct for phylogenetic non-independence and both studies reported an increase in the overall scaling of ln BMR with B_m after phylogenetic correction. Neither study, however, included the effect of body temperature, or nonlinear effects.

The publication of a virtually complete mammalian supertree (Bininda-Emonds *et al.* 2007; Fritz *et al.* 2009) allowed us to undertake a phylogenetic analysis using the most recent phylogeny and including the effects of both ln B_m and T_b in the model. Our analyses also indicate an increase in the mass scaling exponent for all mammals when phylogeny is allowed for (Table 1). The results must however be treated with some caution because although the mammal supertree is 98% complete at the species level, fewer than 50% of nodes subtending species are resolved (our results are reported with polytomies excluded: see Supporting Information for details). Qualitatively identical results were found with the LMM using taxonomy as a proxy for phylogeny, despite the different assumptions about phylogenetic hierarchy (Table 1).

Clearly neither approach is perfect, both making assumptions about the underlying phylogenetic structure. One conclusion that emerges from both analyses and which therefore would appear to be robust, is that correction for phylogenetic non-independence produces a steeper estimate of the scaling exponent relating BMR to body mass. At the same time both approaches reduced the estimated temperature sensitivity of BMR.

VARIATION ACROSS MAMMALIAN ORDERS

For the orders examined in this study (those with >20 species in the data set) the patterns of variation in the scaling exponent match that established by McNab (2008) and Sieg *et al.* (2009), although the precise values differed because we included T_b in the fitted model (see Supporting Information for the full comparison). Including T_b in the model lowered the scaling exponent in four orders (Dasyuromorpha, Diprotodontia, Rodentia, Chiroptera) and increased it in two (Soricomorpha, Carnivora) when compared with a model in ln B_m alone, but did not change the qualitative pattern.

We also demonstrated significant differences in mean BMR across taxa (Fig. 3). Although the statistical models differ, our results largely matched the results of McNab (2008). In both studies the highest basal metabolic rates were shown by artiodactyls, carnivores and shrews and the lowest by Xenarthra. Including T_b in the model thus does not change the qualitative pattern of variation in BMR across mammalian lineages, though it does change the estimated mean BMR.

Lovegrove (2003), using smaller species (<1 kg), has proposed that the variation around the mean can be viewed as a slow–fast continuum: a relatively high basal metabolism is associated with high latitudes and low mean ambient temperatures, whereas a low basal metabolism is associated with the semi-tropics, low productivity areas or climatically unpredictable habitats such as deserts. The slow–fast continuum has proved a useful approach for subsequent analyses of mammalian physiology and ecology (Sibly & Brown 2007). The inverse association between basal metabolic rate and ambient temperature is confirmed in this study for all mammals (Fig. 4a).

CONCLUDING REMARKS

Previous studies have established the basic features of the scaling of resting metabolic rate in mammals. The key findings to have emerged from this study are:

1. Body temperature has a significant effect on the resting metabolic rate of mammals and the underlying thermal physiology of basal (resting) metabolism is similar in birds and mammals.
2. The scaling of resting metabolic rate with body mass in mammals is significantly nonlinear, approaching $b \sim 0{\cdot}75$

at large size, but with shallower and more heterogeneous scaling in the smaller species that dominate mammals as a class. This result is independent of whether or not T_b is included in the model and remains after correction for phylogenetic non-independence. A simple allometric power law is thus not an appropriate statistical model for describing the scaling of BMR with *Bm* in mammals.

3. The variation of scaling with size, together with the variation of body temperature and metabolic rate with ambient temperature all point to an important role for heat flow in the metabolic physiology of mammals. Heat flow was central to early discussions of mammalian metabolism, but has been largely ignored in more recent models based on vascular architecture. We suggest that any complete physical model of metabolic scaling in endotherms must include explicit consideration of heat flow.
4. The variation in scaling exponents between different studies are explained largely by differences in the taxa selected for analysis and particularly the proportion of smaller species from orders with shallower scaling in the data set.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Data and taxonomy.

Appendix S2. Details of the statistical analysis.

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