LETTERS

Curvature in metabolic scaling

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For more than three-quarters of a century it has been assumed[1] that basal metabolic rate increases as body mass raised to some power *p*. However, there is no broad consensus regarding the value of *p*: whereas many studies have asserted that *p* is 3/4 (refs 1–4; 'Kleiber's law'), some have argued that it is 2/3 (refs 5–7), and others have found that it varies depending on factors like environment and taxonomy[6,8–16]. Here we show that the relationship between mass and metabolic rate has convex curvature on a logarithmic scale, and is therefore not a pure power law, even after accounting for body temperature. This finding has several consequences. First, it provides an explanation for the puzzling variability in estimates of *p*, settling a long-standing debate. Second, it constitutes a stringent test for theories of metabolic scaling. A widely debated model[17] based on vascular system architecture fails this test, and we suggest modifications that could bring it into compliance with the observed curvature. Third, it raises the intriguing question of whether the scaling relation limits body size.

In 1932, Max Kleiber found that basal metabolic rate (B)—the power produced by a fasting, inactive organism—scales with body mass (M) across animal species[1]. Based on 13 data points, Kleiber concluded that this relationship was well described by a 3/4-power law:

$$B = B_0 M^{3/4} \quad (1)$$

This apparently simple relationship underlies and constrains an extensive web of scaling relationships, ranging from growth rates to lifespans to trophic dynamics[18–20].

Since 'Kleiber's law' was first proposed, significant amounts of data have been collected and analysed[4,7,8,13,15], fuelling debate about the value of the exponent[19,21–23], a quantity that is crucial for understanding the physical origins of metabolic scaling. An exponent of 2/3 has often been suggested[5–7,15,24] based on a simple surface-to-volume argument. In contrast, a 3/4 exponent emerges from a theory proposed by West, Brown and Enquist based on the properties of optimized resource distribution networks, such as the cardiovascular system[17]. Additionally, some investigators have noted deficiencies in the overall fit of the power law and suggested that the exponent itself might vary with factors such as taxonomic group or environment[6,8–16].

We show that the widely held assumption of a scale-free power law is incorrect. In our analysis, we utilize McNab's recently compiled data set[8] of measurements made reliably under basal conditions (inactive, thermoneutral, post-absorptive adults). It contains measurements of mean metabolic rate from 637 species of mammals spanning 6 orders of magnitude, making it one of the largest such collections yet assembled. To estimate the effect of body temperature on metabolic rate, we extracted temperature measurements from the original papers used in McNab's compilation. The resulting data set of 447 species spans 5 orders of magnitude in mass (Supplementary Information) and was used for those fits that take into account temperature effects. We excluded the orca because its large size has the potential to disproportionately influence the fit, though we found that this is not the case (Supplementary Information). We repeated our analysis using data from Savage[4] and Sieg[16]. Both data sets give essentially the same results as the analysis presented below (Supplementary Information). In all regressions, we use units of grams for mass, watts for basal metabolic rate, and kelvin for temperature.

On a logarithmic scale, a power law, like equation (1), but with an arbitrary scaling exponent β_1, becomes:

$$\log_{10}B = \beta_0 + \beta_1 \log_{10}M + \varepsilon \quad (2)$$

where β_0 is the logarithm of B_0 in equation (1), and ε is the error term. A fit to equation (2) accounts for a significant amount of the trend, but poorly describes the data for both small and large mammals (Fig. 1a, Supplementary Information). This suggests considering a nonlinear model (on the logarithmic scale). As every analytic function can be expanded as a power series, the natural next candidate is a quadratic model:

$$\log_{10}B = \beta_0 + \beta_1 \log_{10}M + \beta_2 (\log_{10}M)^2 + \varepsilon \quad (3)$$

This model results in a visibly better fit for mammals with $M > 50$ g (Fig. 1a, Supplementary Information), which is confirmed by the extremely small P value for β_2 of 9.0×10^{-10} (Table 1). Although the quadratic term explains only an additional 0.3% (96.1% versus 95.8%) of the total variation (7% of the unexplained variation), its impact is clearly seen in both residual and partial residual plots (Supplementary Information). The quadratic term is also necessary to correctly predict the metabolic rate of megafauna such as the orca and elephant (Fig. 1a). Importantly, the addition of higher-order terms beyond the quadratic does not significantly improve the fit (Supplementary Information), suggesting that the scaling relationship for the mammals in this data set is well approximated by a quadratic function of $\log_{10}M$.

Despite the improved fit, there is still considerable residual variation in the data (Supplementary Information). Several studies have demonstrated that temperature affects metabolic rate[7,14,25,26]. We attempt to capture this effect by including a Boltzmann–Arrhenius factor, that is, $B = f(M)\exp(-E/RT)$, where R is the gas constant and T is body temperature in kelvin. When f is a pure power law, equation (2), this new model fits significantly better, but still poorly describes the data for small and large mammals (Supplementary Information). However, when f is given by equation (3), the resulting temperature-corrected quadratic model:

$$\log_{10}B = \beta_0 + \beta_1 \log_{10}M + \beta_2 (\log_{10}M)^2 + \frac{\beta_T}{T} + \varepsilon \quad (4)$$

shows dramatically improved fit over the entire range of the data (Supplementary Information). A plot of the residuals (Supplementary Information) shows that the fit for mammals of intermediate size (between 25 g and 10 kg) is extremely good and that the deviation in the upper tail is small, though still increasing. All of the terms in the

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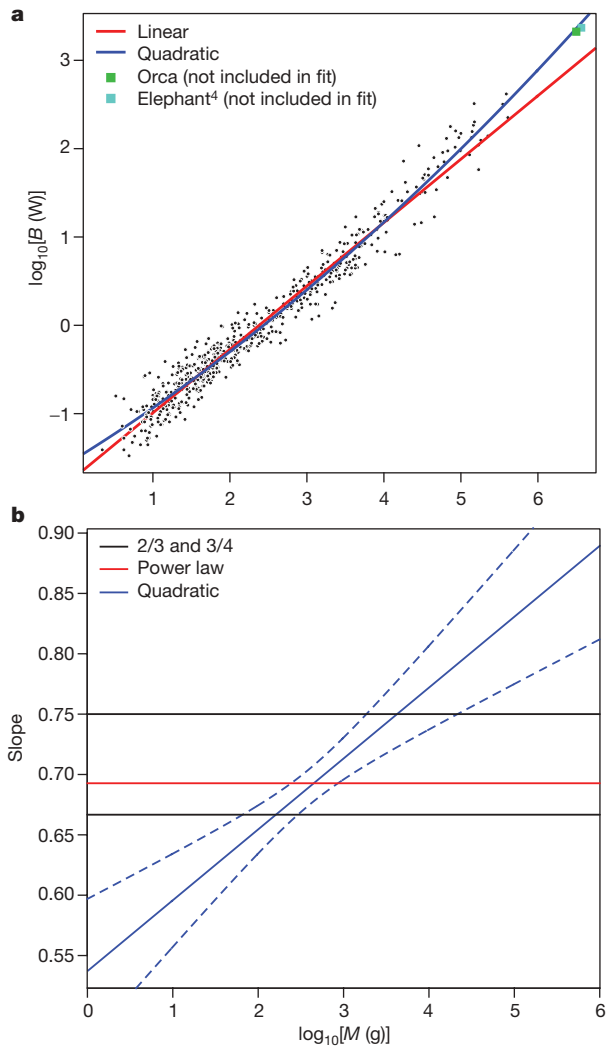

Figure 1 | Curvature in metabolic scaling. a, Linear (red) and quadratic (blue) fits (not including temperature) of $\log_{10}B$ versus $\log_{10}M$. The orca (green square) and Asian elephant (ref. 4; turquoise square at larger mass) are not included in the fit, but are predicted well. Differences in the quality of fit are best seen in terms of the conditional mean of the error, estimated by the lowess (locally-weighted scatterplot smoothing) fit of the residuals (Supplementary Information). See Table 1 for the values of the coefficients obtained from the fit. **b**, Slope of the quadratic fit (including temperature) with pointwise 95% confidence intervals (blue). The slope of the power-law fit (red) and models with fixed 2/3 and 3/4 exponents (black) are included for comparison. This panel suggests that exponents estimated by assuming a power law will be highly sensitive to the mass range of the data set used, as shown in Fig. 2.

Table 1 | Regression coefficients without and with temperature correction

Regression coefficient	Estimate	Standard error	*P* value
Without temperature correction*			
β_0	−1.5078	0.0377	$<2\times10^{-16}$
β_1	0.5400	0.0295	$<2\times10^{-16}$
β_2	0.0322	0.0053	8.9560×10^{-10}
With temperature correction†			
β_0	14.0149	1.1826	$<2\times10^{-16}$
β_1	0.5371	0.0305	$<2\times10^{-16}$
β_2	0.0294	0.0057	2.5680×10^{-7}
β_T	−4,799.0	362.22	$<2\times10^{-16}$

Regression coefficients, standard errors, and *P* values for quadratic models without and with temperature correction (for mass in grams, basal metabolic rate in watts, and temperature in kelvin). The former use the full McNab data set (minus the orca) of 636 species; the latter use a subset of 447 species for which we obtained temperature data. All coefficients are highly significant.

* $\log_{10}B = \beta_0 + \beta_1\log_{10}M + \beta_2(\log_{10}M)^2 + \varepsilon$.

† $\log_{10}B = \beta_0 + \beta_1\log_{10}M + \beta_2(\log_{10}M)^2 + \beta_T/T + \varepsilon$.

regression are extremely significant ($P<3\times10^{-7}$ or better), suggesting that both the temperature and quadratic terms are important predictors of metabolic rate. From the value of β_T (the coefficient of the inverse temperature term) obtained from the quadratic fit, we calculate an effective activation energy of 21.9 ± 3.2 kcal mol^{-1} or 0.95 ± 0.14 eV (95% confidence intervals). This value is less than the free energy of the full hydrolysis of ATP to AMP under standard cellular conditions (26 kcal mol^{-1} or 1.13 eV; ref. 27), indicating that the model produces a biologically realistic coefficient.

In addition to temperature, previous studies have attempted to control for other factors that may affect metabolic rate, such as shared evolutionary history[16,28], habitat, climate and food type[8]. To account for these potential effects, we analyse the data using phylogenetic generalized least squares regression[29] and by conditioning on categorical variables (Supplementary Information). For both analyses, we find that the quadratic and temperature terms remain significant, with some changes in the magnitude of the coefficients (Supplementary Information). We also find that no single study or group of points is responsible for the curvature in the data, and that the quadratic and temperature terms remain significant across a variety of subsets of the data (Supplementary Information). These results suggest that the nonlinearity of the relationship between basal metabolic rate and mass on a logarithmic scale is highly robust.

The local scaling exponent, defined as the derivative of the scaling relationship (equation (4)) with respect to $\log_{10}M$, increases significantly—from 0.57 to 0.87—over the range of the fitted data (Fig. 1b). This stands in sharp contrast to the constant exponent of a pure power law, and indicates that the relationship between metabolic rate and mass is quite different for large and small animals. This finding explains the long-standing disagreement regarding the value of the scaling exponent, because assuming a power law at the outset results in linear fits to curved data. Carrying out such fits yields scaling exponents similar to the slopes of tangent lines at the mean of the $\log_{10}M$ distribution of the underlying data sets (Supplementary Information). Indeed, performing linear fits over partial mass ranges confirms this increasing trend and reveals different regions of the data that are consistent with either 2/3 or 3/4 (Fig. 2). Using the values of β_1 and β_2 from the fit of the full model (equation (4)), we can predict the scaling exponents obtained in previous studies using only the first three moments of their $\log_{10}M$ distributions (Fig. 2d, Supplementary Information). In general, we find that data sets with fewer large mammals[7,14] tend to exhibit smaller exponents than ones weighting large mammals more heavily[1,4]. Together, these results indicate that curvature in the data is a major factor underlying the historical variation in estimates of the scaling exponent (Supplementary Information).

Our findings have critical implications for theories of metabolic scaling. The West, Brown and Enquist (WBE) model[17] derives equation (1) as a consequence of the relationship between the volume of a vascular network (which is proportional to mass) and the number of capillaries (which is proportional to metabolic rate). However, it predicts pure 3/4-power scaling only as an asymptotic law in the limit of infinite body mass. For animals of finite size, the model instead yields an (implicit) scaling relation that exhibits curvature on a logarithmic scale[30]:

$$M = c_0B + c_1B^{4/3} \quad (5)$$

Under the assumptions of West *et al.*, both coefficients in the extended model (equation (5)) are positive, predicting concave curvature—not the convex curvature found in the data—and resulting in a relatively poor fit (Fig. 3a and Supplementary Information). This raises the question of whether the theory can be adapted to agree with the data.

The WBE model posits that evolution resulted in a hierarchical vascular system that minimizes energy loss in the transport of blood. This assumption appears as an energy minimization criterion that

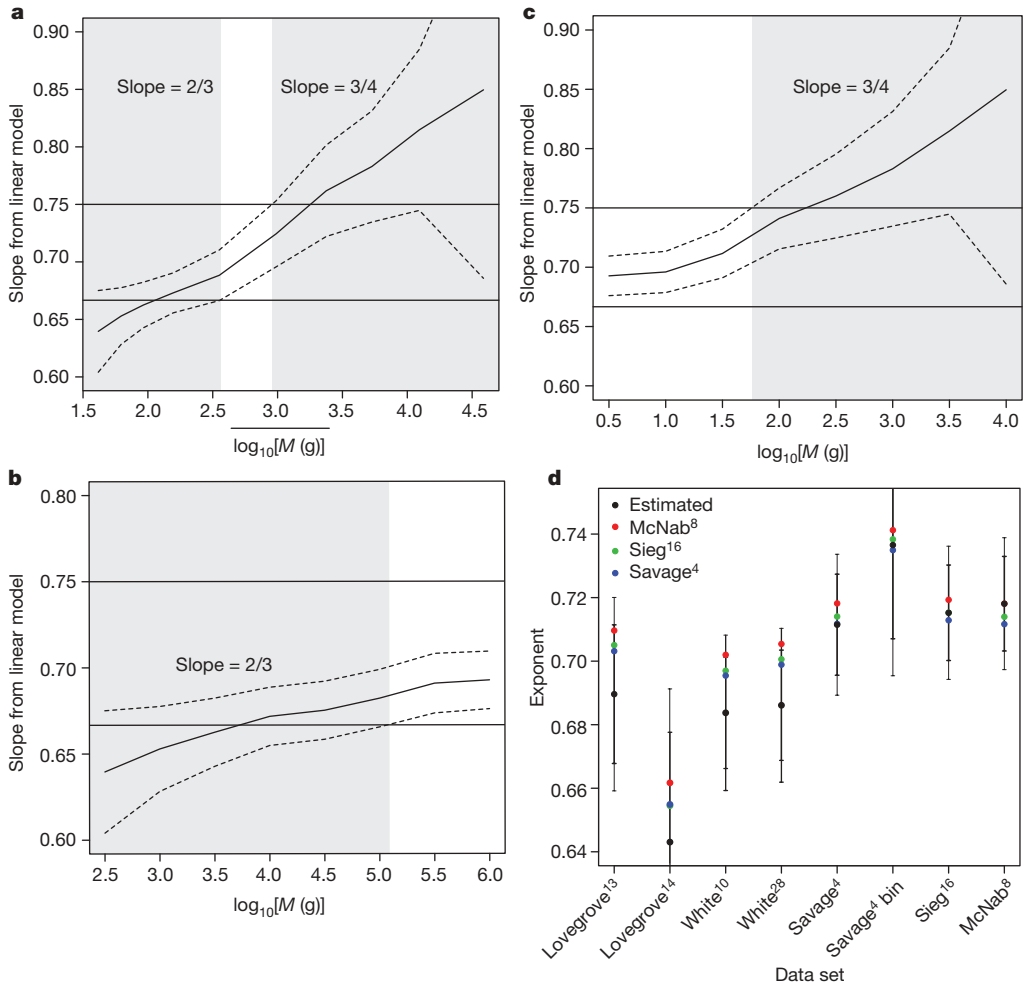

Figure 2 | Scaling exponent depends on mass range. **a**, Slope estimated by linear regression within a three log-unit mass range (smaller near the boundaries). Values on the abscissa denote mean $\log_{10}M$ within the range. When the 95% confidence regions (dashed lines) include the 2/3 or 3/4 lines, the local slope is consistent with a 2/3 or 3/4 exponent, respectively. These cases are indicated by the shaded regions (2/3 on the left and 3/4 on the right). **b**, Slope estimated by using all data points with $M < x$. The shaded region is consistent with 2/3 slope estimates. **c**, Slope estimated by using all data points with $M > x$. The shaded region is consistent with 3/4 slope estimates. **d**, Exponents estimated for eight historical data sets using linear regression (black filled circles): Lovegrove[13], Lovegrove[14], White[10], White[28], Sieg[16], McNab[8], and Savage[4] using species average data ('Savage[4]') and binned data ('Savage[4] bin'). Exponents predicted using coefficients from quadratic fits to McNab's (red), Sieg's (green), or Savage's (blue) data and the first three moments of $\log_{10}M$ (Supplementary Information). Thick lines represent uncorrected 95% confidence intervals. Thin lines are multiplicity corrected intervals.

fixes the vessel geometry (Supplementary Information). In the model, the vascular system is composed of two parts: large vessels with pulsatile blood flow and small vessels with smooth blood flow. The transition between these regions happens abruptly a constant number of levels from the capillaries. Together, these assumptions yield equation (5) (Supplementary Information). However, the calculation neglects physical effects, such as the attenuation of pulses as they travel away from the heart, which may affect the behaviour of large vessels and the position and nature of the transition between vessel types. This suggests several modifications to the model (Supplementary Information).

We first relax the assumptions about vessel geometry (model RG, 'relaxed geometry') in the pulsatile regime, resulting in a version of equation (5) in which the asymptotic exponent is no longer 3/4, but c_0 and c_1 are still positive, thus failing to produce convex curvature. Next, we modify the location of the transition between flow regimes. In one possibility, the transition occurs a constant number of levels from the heart (model FH, 'from heart'), rather than from the capillaries. In another possibility, the transition occurs a constant fraction of levels from the heart (model PT, 'proportional transition'). Both modifications lead to models that predict convex curvature, as detected in the data (Fig. 3a and b). However, the fit of the FH model is almost as poor as the original WBE model (Fig. 3a, Supplementary Information). In contrast, the PT model fits nearly as well as the quadratic model, suggesting that it merits further investigation. These modifications demonstrate that the WBE model can, in principle, be brought into agreement with the observed curvature, while still preserving core assumptions, such as the primacy of resource distribution networks. A more detailed energy minimization calculation should help to determine if these adaptations represent physically realistic cases or suggest alternative corrections.

The WBE model and its variants necessarily predict an asymptotic scaling exponent, suggesting that metabolic rate does not limit animal size without additional assumptions, such as the existence of a minimal cellular metabolic rate. On the other hand, the quadratic model with temperature (equation (4)), which provides the best fit to the data, predicts that the slope of the scaling function increases without bound (though this apparent behaviour may be due to the paucity of data for large animals). If this is correct, the metabolic scaling relationship may directly determine maximum animal size. This limit might occur at the mass at which the slope equals 1. Beyond this point, bigger is no longer better, meaning that an x% increase in

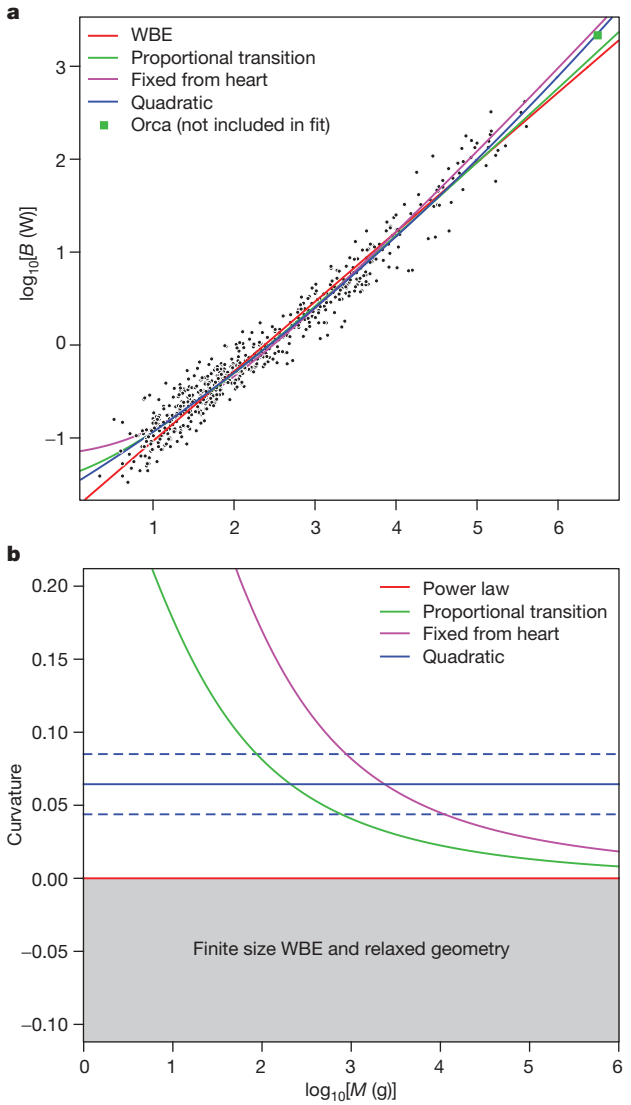

Figure 3 | Modified WBE models. a, Fits of the 'proportional transition' (PT, green) and 'from heart' (FH, magenta) models. Fits of the quadratic (blue) and WBE (red) models are included for comparison. The FH model posits that the transition from large to small vessels occurs a fixed number of levels from the heart. This is in contrast to the WBE model, which assumes that this transition occurs a fixed number of levels from the capillaries. The PT model represents another possibility, in which the transition occurs a fixed fraction of levels from the heart. **b**, Curvatures, as measured by the second derivative, achievable by the models considered in the main text. The quadratic model (blue) provides an estimate of the empirical curvature of the data itself. Dashed lines represent 95% confidence intervals. Pure power-law models (red) have no curvature, which is inconsistent with the data. The finite-size corrected WBE and 'relaxed geometry' (RG) models (the latter is the variant with relaxed geometry for large vessels) exhibit negative or concave curvature (not shown in **a**), which is also inconsistent with the data. The PT (green) and FH (magenta) variants of WBE have mass-dependent positive or convex curvature, consistent with the data, and asymptotically have no curvature (meaning that they become pure power laws for very large animals).

body mass requires a greater than x% increase in metabolic rate. Our fit suggests that this point occurs around 10^8 g (100 t): intriguingly, this is about the size of the blue whale, which is believed to be the largest animal that has ever lived.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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