Letter to Editor

Mass scale and curvature in metabolic scaling
Comment on: T. Kolokotrones et al., Curvature in metabolic scaling, Nature 464 (2010) 753–756

The relationship between Basal Metabolic Rate (BMR) and mass (M) has long been observed to display approximate power-law scaling, BMR $\propto M^k$, with typically $2/3 \le k \le 3/4$. Scaling of surface area with mass for self-similar animals suggests $k=2/3$, while Kleiber's, 1932's, 1947 (empirical) law is $k=3/4$, and may be related to models of branching networks (West et al., 1997). Arguments for both values continue to be put forward (White and Seymour, 2003; Farrell-Gray and Gotelli, 2005), and the issue remains highly controversial (Agutter and Wheatley, 2004; White and Seymour, 2005; Isaac and Carbone, 2010).

Such simple allometry yields a straight line in the plot of the logarithmic data. However, it has long been noted that a single exponent does not capture all the phenomena. Some 30 years ago it was established (Heusner, 1982; Feldman and McMahon, 1983) that mammalian intraspecific scaling is close to self-similar ($k \simeq 2/3$), while $k \simeq 3/4$ for interspecific scaling. Hayssen and Lacy (1985) noted that goodness of fit is much better for the metatheria than the eutheria, and that better fits are obtained by using separate regression lines for each order. The effects of the conditions under which the measurements are made were investigated in White et al. (2006). The outcome of recent work (Dodds et al., 2001; White et al., 2007; Packard and Birchard, 2008; Glazier, 2005, 2010; Clarke et al., 2010) is that no single exponent can explain the evidence. A recently compiled mammalian data set, in which great pains were taken to isolate *basal* metabolic rates, confirms this (McNab, 2008), noting again however that this effect is almost entirely confined to the eutheria, and ascribing it to ecological factors. Among the marsupials there is an almost-perfect fit for a single exponent. Indeed, if one removes from the combined marsupial data of McNab (2008) just two species (the honey possum *Tarsipes rostratus* and the southern hairy-nosed wombat *Lasiorhinus latifrons*, both of which have known peculiarities of metabolism, Withers et al., 1990; Frappell et al., 2002), the 70 remaining data have BMR $\propto M^k$ with $k=0.75 \pm 0.01$ and $R^2=0.990$, a startlingly good fit for Kleiber's law (Fig. 1). See also Hinds and Macmillen (1985).

In the light of this, the approach of Kolokotrones et al. (2010) is perhaps rather surprising. These authors, noting the curvature of the mammalian metabolic data, described it by introducing a quadratic term in the logarithmic model, which breaks the scale invariance of a simple power-law. However, they failed to understand or explore the consequences of this loss of scale invariance.

The key model of Kolokotrones et al. is the fitting of log BMR to a quadratic polynomial in log M,

$$\log \text{BMR} = \beta_0 + \beta_1 \log M + \beta_2 (\log M)^2, \qquad (1)$$

with M measured in grams. This is claimed to be 'the natural next candidate' on the basis of a Taylor expansion, although neither

physics nor physiology would naturally favour such functional dependence, since it implies

$$\text{BMR} \propto M^{\beta_1} M^{\beta_2 \log M}. \qquad (2)$$

Further, the authors' motivation to choose an 'analytic function' is effectively the desire for a single underlying mechanism which varies smoothly over many orders of magnitude, with no exogenous discontinuities—a strong criterion indeed.

For the mammalian data (McNab, 2008), adding the quadratic term improves R^2 from 0.958 to 0.961, and so accounts for around one-tenth of the residual variance after allometric scaling. The authors of Kolokotrones et al. (2010) emphasize its importance in capturing the data for the megafauna. Fig. 2 shows (a) the logarithmic data for the eutheria (as only among these is the curvature effect to be observed) and (b) the residuals of the best fitting log-linear model, $k=0.722(6)$. The log-quadratic model improves R^2 from 0.959 to 0.962.

However, taking the logarithm of a dimensionful quantity, as in (1), is of course impossible. What is actually being computed is the logarithm of the ratio of the mass to an implicit mass scale of $M_0=1$ g. With a further power scale P_0, the correct, non-dimensionalized form of the equation is, writing BMR$=P$,

$$\log \left(\frac{P}{P_0} \right) = \beta_0 + \beta_1 \log \left(\frac{M}{M_0} \right) + \beta_2 \log^2 \left(\frac{M}{M_0} \right). \qquad (3)$$
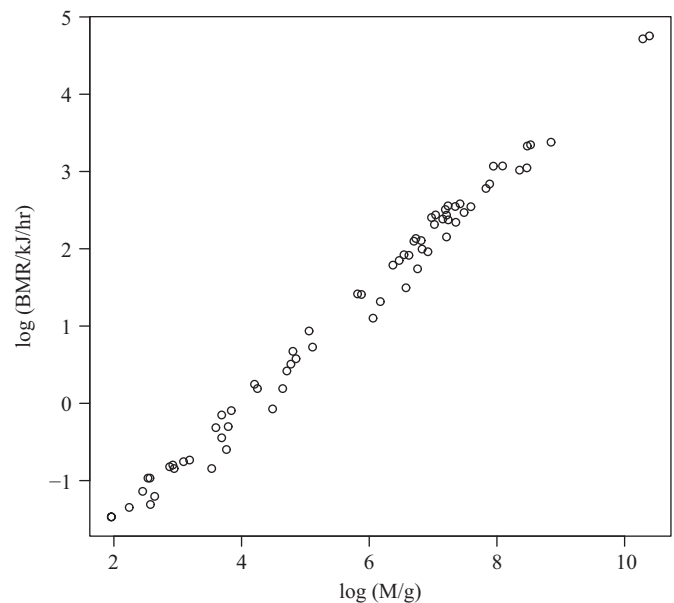

Fig. 1. Natural logarithms of metabolic rate against mass for the marsupials (excluding *Tarsipes rostratus* and *Lasiorhinus latifrons*). Data from McNab (2008).
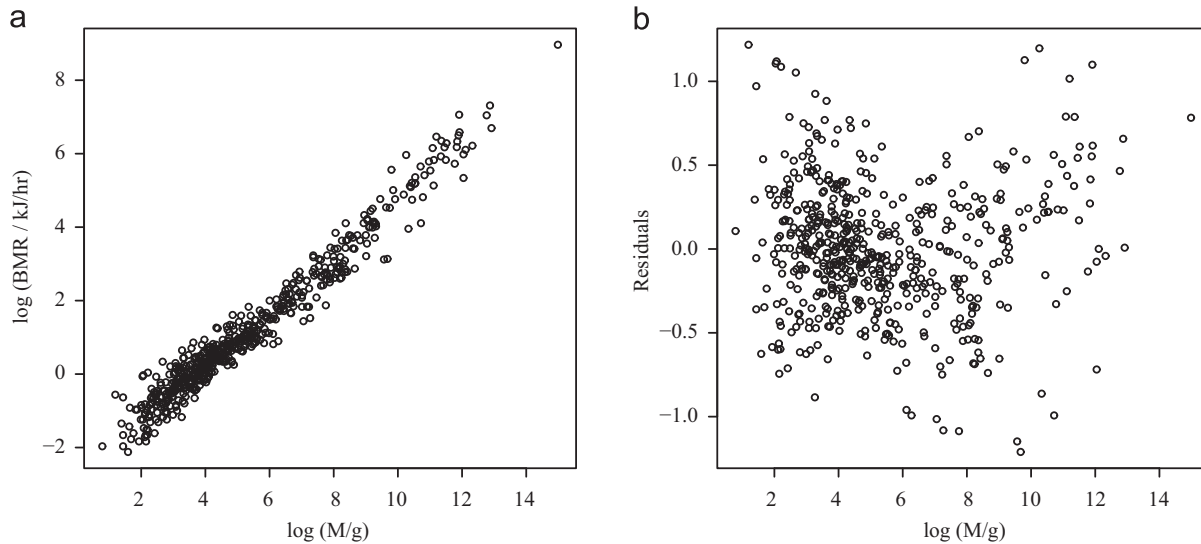
Fig. 2. Natural logarithms of metabolic rate against mass for the eutheria. Data from McNab (2008). (a) Logarithmic eutherian data. (b) Residuals of allometry with $k=0.722$.

Suppose now that we choose a different scale M'_0. Let $\mu = \log(M_0/M'_0)$. Then Eq. (3) becomes

$$\log\left(\frac{P}{P_0}\right) = \beta_0 - \beta_1\mu + \beta_2\mu^2 + (\beta_1 - 2\beta_2\mu)\log\left(\frac{M}{M'_0}\right) + \beta_2\log^2\left(\frac{M}{M'_0}\right). \tag{4}$$

In the simple log-linear, power-law model ($\beta_2 = 0$, $\beta_1 \equiv k$), the M-dependence is unaffected by the transformation, and only the constant of proportionality e^{β_0} is altered. This model is *scale-invariant*: one is fitting a line to the log–log data plot, and a line has no preferred origin, so that the linear model has no preferred mass scale.

The log-quadratic model (3), in contrast, is not scale-invariant: the M-dependence varies with μ, as we see in (4). Only the coefficient of the quadratic term is independent of M_0. The model fits a quadratic curve, a parabola, to the log–log data, and so *does* have a preferred origin. Of the five parameters $\beta_0, \beta_1, \beta_2, M_0, P_0$, only three are independent, and indeed the parabola is specified by three parameters, which might naturally be taken to be β_2 and the coordinates of its turning point. Thus the curve has a unique intrinsic mass scale, that of the turning point, at which the formula for the curve simplifies to become purely quadratic and the linear term vanishes.

This affects the claimed results profoundly. In particular, the values and quoted significances of the linear term are artefacts of the choice of M_0, here 1 g. Thus, and at the risk of pointing out what will be obvious to many readers, no meaning should be imputed to the values (or t-test p values) of β_1 in Table 1 of Kolokotrones et al. (2010). Further, the significances ascribed to the quadratic terms should be treated with caution, precisely because they are invariant under changes of mass scale: the significance is the same as that of a pure quadratic model at its preferred mass scale. Rather the natural approach would be to test for quadratic dependence (in the variation of log$M$ about its mean) of the residuals from the best-fitting linear model. If one does this for all the eutheria, the quadratic term remains significant.

However, precisely the log-quadratic model (1) was fitted to eutherian data 25 years ago in Hayssen and Lacy (1985) (not cited in Kolokotrones et al., 2010), where it was rejected in favour of separate linear models for each Order.[1] The approach of Kolokotrones et al. (2010) is to condition on Order (or other

explanatory environmental or physiological factor) and then test the log-quadratic model. If one instead adopts the approach recommended above, of fitting the residues of the best-fitting linear model to some multiple of the square of the variation of log$M$ about its mean, significances are greatly reduced: of all the mammalian orders, only for the *Rodentia* is a quadratic fit significant at the 5% level (with $p=0.02$), and the quadratic term accounts for only 0.02 of the variance.

In the light of this note, then, claims for descriptive or explanatory worth of the log-quadratic model of curvature in metabolic scaling should be treated with scepticism. Indeed, it should be evident from Fig. 2(b) that any search for a single nonlinear function to explain the residuals of simple allometry is likely to be fruitless.

Acknowledgements

References

Agutter, P.S., Wheatley, D.N., 2004. Metabolic scaling: consensus or controversy? Theoretical Biology and Medical Modelling 1, 13.

Clarke, A., Rothery, P., Isaac, N.J.B., 2010. Scaling of basal metabolic rate with body mass and temperature in mammals. Journal of Animal Ecology 79, 610–619.

Dodds, P.S., Rothman, D.H., Weitz, J.S., 2001. Re-examination of the "3/4-law" of metabolism. Journal of Theoretical Biology 209, 9–27.

Farrell-Gray, C.C., Gotelli, N.J., 2005. Allometric exponents support a 3/4-power scaling law. Ecology 86, 2083–2087.

Feldman, H.A., McMahon, T.A., 1983. The 3/4 mass exponent for energy metabolism is not a statistical artifact. Respiration Physiology 52, 149–163.

Frappell, P.R., Baudinette, R.V., MacFarlane, P.M., Wiggins, P.R., Shimmin, G., 2002. Ventilation and metabolism in a large semifossorial marsupial: the effect of graded hypoxia and hypercapnia. Physiological and Biochemical Zoology 75, 77–82.

Glazier, D.S., 2005. Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biological Reviews of the Cambridge Philosophical Society 80, 611–662.

Glazier, D.S., 2010. A unifying explanation for diverse metabolic scaling in animals and plants. Biological Reviews of the Cambridge Philosophical Society 85, 111–138.

Hayssen, V., Lacy, R.C., 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comparative Biochemistry and Physiology A 81, 741–754.

Heusner, A.A., 1982. Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? Respiration Physiology 48, 1–12.

Hinds, D.S., Macmillen, R.E., 1985. Energy scaling in marsupials and eutherians. Science 225, 335–337.

---

[1] This was principally on the grounds that the former had $R^2=0.85$ and the latter $R^2=0.77$, although Hayssen and Lacy (1985) also incorrectly cited a non-nested F-test in support. Thanks to Walter Fontana for pointing this out.

Isaac, N.J.B., Carbone, C., 2010. Why are metabolic scaling exponents so contro-
versial? Quantifying variance and testing hypotheses. Ecology Letters 13,
728–735.

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

Kleiber, M., 1947. Body size and metabolic rate. Physiological Reviews 27,
511–541.

Kolokotrones, T., Savage, V., Deeds, E.J., Fontana, W., 2010. Curvature in metabolic
scaling. Nature 464, 753–756.

McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of
mammalian BMR. Comparative Biochemistry and Physiology A 151, 5–28.

Packard, G.C., Birchard, G.F., 2008. Traditional allometric analysis fails to provide a
valid predictive model for mammalian metabolic rates. Journal of Experi-
mental Biology 211, 3581–3587.

West, G.B., Brown, J.H., Enquist, B.J., 1997. A general model for the origin of
allometric scaling laws in biology. Science 276, 122–126.

White, C.R., Seymour, R.S., 2003. Mammalian basal metabolic rate is proportional
to body mass$^{2/3}$. Proceedings of the National Academy of Sciences 100,
4046–4049.

White, C.R., Seymour, R.S., 2005. Allometric scaling of mammalian metabolism.
Journal of Experimental Biology 208, 1611–1619.

White, C.R., Phillips, N.F., Seymour, R.S., 2006. The scaling and temperature
dependence of vertebrate metabolism. Biology Letters 2, 125–127.

White, C.R., Cassey, P., Blackburn, T.M., 2007. Allometric exponents do not support
a universal metabolic allometry. Ecology 88, 315–323.

Withers, P.C., Richardson, K.C., Wooller, R.D., 1990. Metabolic physiology of
euthermic and torpid honey possums, *Tarsipes rostratus*. Australian Journal
of Zoology 37, 685–693.

Niall J. MacKay
Department of Mathematics, University of York, York YO10 5DD, UK
E-mail address: niall.mackay@york.ac.uk