Letter to Editor

Mass scale and curvature in metabolic scaling

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 $2/3 \leq k \leq 3/4$. 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, 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, 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, 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, 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, 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, 1997).

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 $BMR=P$,}

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

Fig. 1. Natural logarithms of metabolic rate against mass for the marsupials (excluding *Tarsipes rostratus* and *Lasiorhinus latifrons*). Data from McNab (2008).
Suppose now that we choose a different scale $M_0$. Let

$$
\mu = \log(M_0/M_0^0)
$$

Then Eq. (3) becomes

$$
\log \left( \frac{P}{P_0} \right) = \beta_0 - \beta_1 \mu + \beta_2 \mu^2 + (\beta_1-2\beta_2 \mu) \log \left( \frac{M}{M_0^0} \right) + \beta_2 (\log^2 \left( \frac{M}{M_0^0} \right).
$$

(4)

In the simple log-linear, power-law model ($\beta_2 = 0$, $\beta_1 = k$), the $M$-dependence is unaffected by the transformation, and only the constant of proportionality $P_0$ 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 $\mu$, 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 $\beta_2$ 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 $\beta_1$ in Table 1 of Kolokotrones et al. (2010). Further, the significances ascribed to the quadratic terms 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.

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### References


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