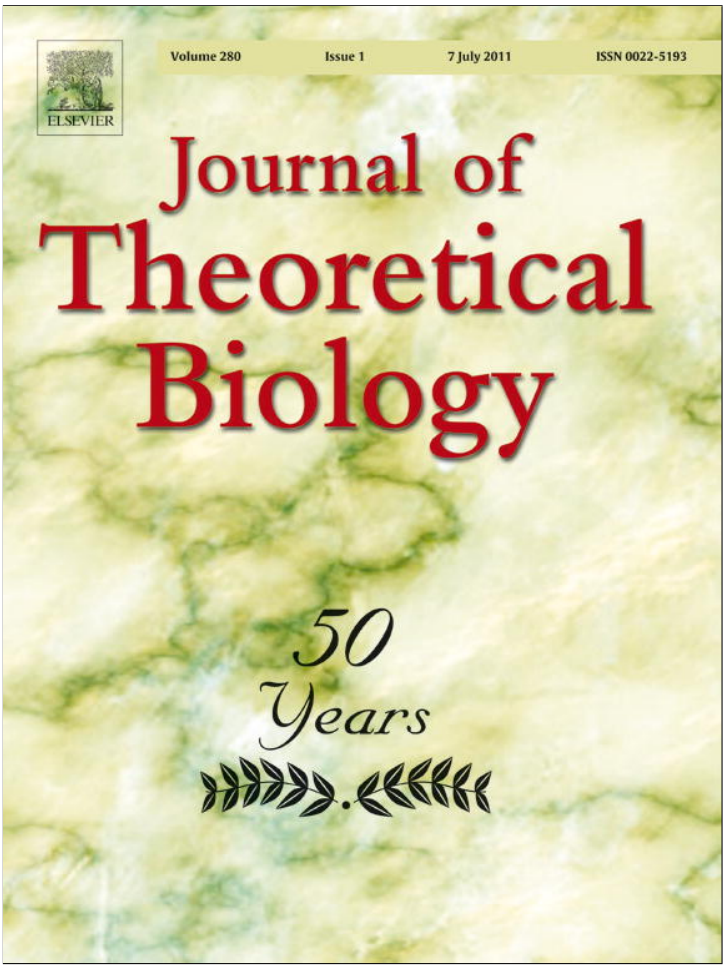

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Letter to the Editor

Curvature in metabolic scaling: A reply to MacKay

The main thread of MacKay's commentary consists of three points. First, he finds no physical rationale for the quadratic form of the relationship between the logarithms of basal metabolic rate (which he denotes P) and body mass (M) that we employ in our fit. Such an objection confuses statistical models aimed at characterizing properties of data with physical models aimed at explaining them. Second, he notes that a (mass) scale transformation of the data makes the linear term of the quadratic model disappear. While this is true, the quadratic term – capturing curvature in the data and therefore representing our primary interest in the fit – is unaffected by scale transformations. This makes the existence of a "natural" mass scale a moot point in assessing curvature. Third, MacKay proposes a two-step procedure that involves first fitting a linear function to the data and then fitting the resulting residuals to a pure quadratic of the "variation of log$M$ about its mean." This procedure will produce an inherently worse fit and, consequently, reduce the significance of curvature. We question the value of a statistical model that is sub-optimal by construction.

We briefly expand our responses to each point below.

1. In our work (Kolokotrones et al., 2010), we analyzed an extensively curated data set on basal metabolic rates in mammals due to McNab (2008) by comparing the fit of a linear relationship between log$P$ and log$M$ to the fit of a quadratic function:

$$\log P = \beta_0 + \beta_1 \log M + \beta_2 (\log M)^2 + \varepsilon. \quad (1)$$

The statistical significance of β_2 in this regression (along with improvement in the residuals) indicated that the quadratic equation provides a much better fit to the data. We found that curvature remained significant even when accounting for other variables such as body temperature, phylogenetic relationships, food sources and habitat, providing strong evidence for curvature in the allometric relationship between log P and log M.

Eq. (1) is a statistical model aimed at capturing and characterizing curvature in the data. Even if "neither physics nor physiology would naturally favor such functional dependence", as MacKay asserts, the lack of theoretical justification for the form of the function is beside the point. We employ model (1) to detect and test for uniform curvature in the data, not to provide a physical reason for it. The latter was the objective of our analysis of the West–Brown–Enquist (WBE) model, a physical theory that can be used to predict the magnitude and direction of curvature for metabolic scaling (Savage et al., 2008). Indeed, in our paper we showed that modified versions of this model could produce convex curvature that fit the data well, despite the fact that the log P vs. log M relationships obtained from the model do not take the functional form of a quadratic (Kolokotrones et al., 2010; Savage et al., 2008).

2. In his second point, MacKay notes that Eq. (1) breaks scale-invariance. Contrary to what MacKay asserts, this observation has no profound implications for our claims.

Given estimates of the parameters in Eq. (1), it is possible to determine a mass scale at which the linear term vanishes. However, the only parameter necessary for the assessment of curvature in the data is β_2, which MacKay himself agrees is scale-invariant (his Eq. (4)). Since our paper is only concerned with curvature, any scale dependence of β_0 or β_1 is irrelevant with regard to the conclusions we draw.

3. In his third point, MacKay claims that 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".

A direct linear regression of Eq. (1) will provide estimates of the parameters such that the sum square of the residuals is minimized. It appears, however, that MacKay would like to fit only scale-invariant models, first obtaining β_1 by a scale-invariant linear fit and then estimating β_2 by fitting a scale-invariant pure quadratic to the residuals from the first step. Yet, taken together, the two steps produce the same scale-dependent functional form for the log P vs. log M relationship as Eq. (1), but with parameters that are now artificially constrained. MacKay thus obtains values for the parameters that differ from the direct fit, and by definition this results in a function with a larger sum square of the residuals. The ansatz appears to confuse the parameter β_1 from the linear model with the parameter β_1 from the quadratic model.

The goal of any statistical model is to provide the best description of the trend in the data. Since MacKay's procedure does not do this, the meaning of the parameters he estimates is unclear, as is the value provided by the analysis of a model that is sub-optimal by construction.

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