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Is complex allometry in field metabolic rates of mammals a statistical artifact?

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A R T I C L E I N F O

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Recent reports indicate that field metabolic rates (FMRs) of mammals conform to a pattern of complex allometry in which the exponent in a simple, two-parameter power equation increases steadily as a dependent function of body mass. The reports were based, however, on indirect analyses performed on logarithmic transformations of the original data. I re-examined values for FMR and body mass for 114 species of mammal by the conventional approach to allometric analysis (to illustrate why the approach is unreliable) and by linear and nonlinear regression on untransformed variables (to illustrate the power and versatility of newer analytical methods). The best of the regression models fitted directly to untransformed observations is a three-parameter power equation with multiplicative, lognormal, heteroscedastic error and an allometric exponent of 0.82. The mean function is a good fit to data in graphical display. The significant intercept in the model may simply have gone undetected in prior analyses because conventional allometry assumes implicitly that the intercept is zero; or the intercept may be a spurious finding resulting from bias introduced by the haphazard sampling that underlies "exploratory" analyses like the one reported here. The aforementioned issues can be resolved only by gathering new data specifically intended to address the question of scaling of FMR with body mass in mammals. However, there is no support for the concept of complex allometry in the relationship between FMR and body size in mammals.

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1. Introduction

Field metabolic rates (FMRs) of mammals hold the key to understanding energy requirements and turnover of animals living under natural conditions (Nagy et al., 1999; Speakman, 2000; Nagy, 2001, 2005). Although a variety of factors (like habitat and season) doubtless have some influence on metabolism, most of the variation in FMR among species is attributable to variation in body mass (Nagy et al., 1999; Speakman, 2000; Nagy, 2005). Early summaries of the scaling of FMR with body mass in mammals yielded an allometric exponent of ~0.725 (Nagy et al., 1999; Anderson and Jetz, 2005; Nagy, 2005), which is tantalizingly close to the theoretical value of 0.75 for the scaling of basal metabolic rate (Brown and Sibly, 2012) and suggests that the same general constraints may apply to FMR that seemingly apply to the basal rate (West and Brown, 2005). More recent investigations on the scaling of FMR in mammals, however, have detected a slight curvilinear pattern (convex) in log-log plots (Capellini et al., 2010; Müller et al., 2012; Hudson et al., 2013; Bueno and López-Urrutia, 2014), thereby pointing to a pattern of complex allometry (sensu Strauss, 1993) wherein the exponent in the equation of simple allometry

$$y = \mathbf{a} * x^{\mathbf{b}} \tag{1}$$

is an increasing function of body size. Reports of complex allometry have profound implications for the scaling of numerous ecological traits and times (Bueno and López-Urrutia, 2014).

It would be premature, however, to attach undue significance to reports of complex allometry in FMR of mammals. The prior studies relied on statistical procedures that have changed little since the allometric method was first described in detail by Julian Huxley in his monograph on *Problems of Relative Growth* (Huxley, 1932). Unfortunately, Huxley's method was never adequate for dealing with observations that are curvilinear on the logarithmic scale (Reeve, 1940; Reeve and Huxley, 1945; Richards and Kavanagh, 1945), so the appearance of complex allometry may be nothing more than an artifact resulting from inadequate statistical analyses. Newer and more versatile analytical procedures now are available, and application of these procedures to the study of mammalian FMRs has the potential to yield insights that were unattainable heretofore (Packard, 2015, 2016).

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Here I perform a conventional allometric analysis on a large dataset for FMRs of mammals to illustrate the problems and limitations of the traditional method. I then use linear and nonlinear regression, with different assumptions about the nature of random error, to re-examine the same dataset. The regression procedure is a powerful, but underappreciated, tool for use in allometric research because the computational algorithm is not constrained to fitting a narrow range of power functions based on logarithmic transformations. I show that the perception of complex allometric variation in FMRs of mammals is due entirely to inability of conventional approaches to fit descriptive equations with explicit, non-zero intercepts and that the exponent in the best regression model is not a varying function of body size.

2. Conventional allometric analysis

Data for FMR and body mass of 116 species of mammal ranging in size from a 7.3 g bat to a 111,400.0 g sea lion were taken from the online appendix to the article by Capellini et al. (2010), who compiled records for FMRs that were estimated by the method of doubly labeled water. The observations were transformed to logarithms (base 10) and displayed on a bivariate graph, thereby revealing a slight convex curvature in the data (Fig. 1A). Equations for a straight line and a quadratic polynomial then were fitted to the transformations by ordinary least squares to quantify the relationship between the variables. Both models assumed additive, normal, homoscedastic error on the logarithmic scale (Packard, 2014). Normality of the distributions for residuals was assessed with the Shapiro-Wilk test, and constancy of variance was evaluated with the Breusch/Pagan test. Akaike's Information Criterion (AIC) was used to compare the models (Burnham and Anderson, 2002). Generally speaking, models with ΔAICs < 4–7 are plausible alternatives to the "best model" (ΔAIC = 0) whereas models with AICs > 14 have no empirical support (Burnham et al., 2011).

Two potential outliers were identified in a preliminary examination of the full dataset (Fig. 1A). Although neither of these outliers was particularly influential (as judged by Cook's Distance), they were removed from the dataset before proceeding further (removing these observations had no substantive effect on the outcome). The model for the straight line fitted to observations for the remaining 114 species explains > 95% of the variation in log FMR (Table 1). However, the fitted equation does not perform well at the upper and lower ends of the size range, where observations for the response are appreciably higher than expected for a rectilinear model (Fig. 1A). This departure from linearity is confirmed by the curvature in a plot of standardized residuals against fitted values (Fig. 1B). The rectilinear fit also is heteroscedastic (Table 1), owing to greater variability in the response for larger species (Fig. 1B). Back-transforming the deterministic equation is unlikely to yield a good description for the pattern of variation in the original data because the fit to logs failed to satisfy the fundamental requirement for linearity (Reeve, 1940; Reeve and Huxley, 1945; Richards and Kavanagh, 1945).

The quadratic equation explains only 1.3% more of the variation in log FMR than is explained by the rectilinear fit (Table 1), but the mean function for the quadratic successfully captures the curvature in the observations (Fig. 1A) and the model is strongly favored by AIC (Table 1). Although the quadratic seemingly violates the assumption of homogeneity of variance (Table 1), the plot of standardized residuals indicates that the departure from homoscedasticity is trivial and that residuals are satisfactory (Fig. 1C). The quadratic model consequently is accepted here as a reasonable fit to the observations.

How should the quadratic model fitted to logarithms be interpreted? Three problems with the model are major concerns: the first problem is one of general importance to the entire field of biology, namely, the use of quadratic polynomials to describe biological data; the second problem concerns the use of quadratic equations in traditional allometry; and the third problem focuses on the present dataset for FMRs of mammals.

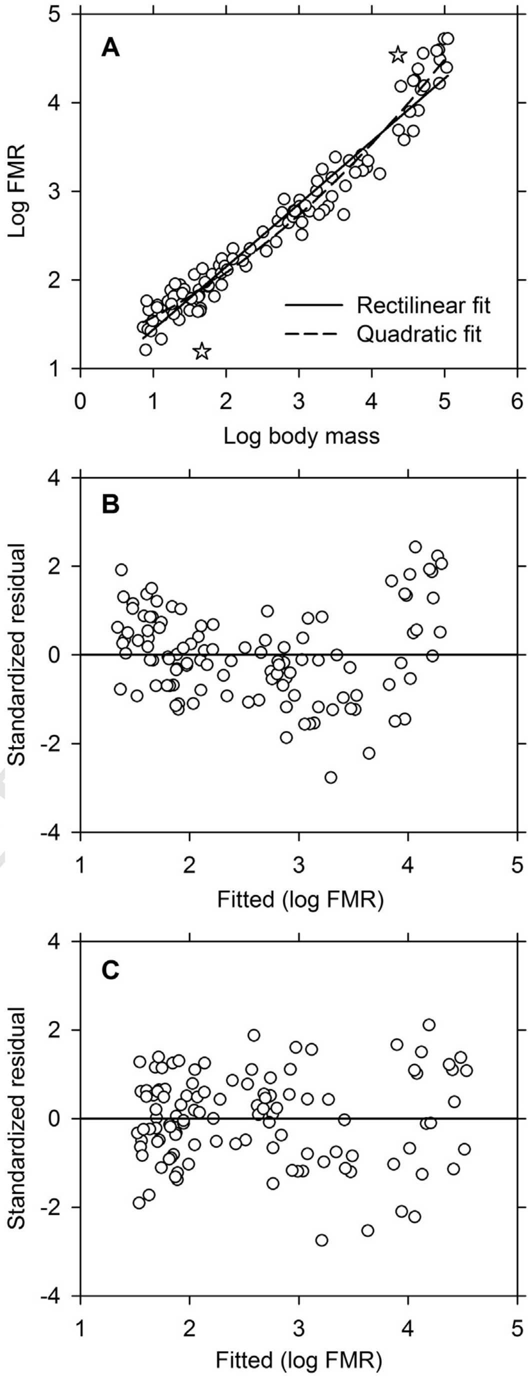

Fig. 1. (A) Rectilinear and quadratic models fitted to logarithmic transformations of data for FMR and body mass of 114 species of mammal. Stars identify possible outliers that were identified in a preliminary examination of the data (Studentized deleted residuals = −3.8 for *Zyzomys argurus* and +3.6 for *Arctocephalus gazella* in the fit of the quadratic model to the full dataset). The outliers were not included in the final analysis. (B) Standardized residuals vs. fitted values from the fit of the straight line to logarithmic transformations. Note the bowl-shaped pattern confirming that transformation failed to linearize the distribution. (C) Standardized residuals vs. fitted values from the fit of the quadratic polynomial to logarithmic transformations.

First, statisticians have tried for years to convince biologists not to resort to quadratic equations (or other polynomials) to describe bivariate data of any kind (e.g., Finney, 1989; Paine et al., 2012). A quadratic equation traces the path of a parabola (http://www.mathopenref.com/quadraticexplorer.html), so a quadratic seldom (if ever) is a realistic representation of pattern in biological data. The fitted model may follow the path of observations quite well over the limited range for the

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