COMMENTARY

Julian Huxley, *Uca pugnax* and the allometric method

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Summary

The allometric method, which often is attributed to Julian Huxley, entails fitting a straight line to logarithmic transformations of the original bivariate data and then back-transforming the resulting equation to form a power function in the arithmetic scale. Development of the technique was strongly influenced by Huxley's own research on growth by the enlarged 'crusher' claw in male fiddler crabs (*Uca pugnax*). Huxley reported a discontinuity in the log–log plot of chela mass *vs* body mass, which he interpreted as an abrupt change in relative growth of the chela at about the time crabs attain sexual maturity. My analysis of Huxley's arithmetic data indicates, however, that the discontinuity was an artifact caused by logarithmic transformation and that dynamics of growth by the crusher claw do not change at any point during development. Arithmetic data are well described by a power function fitted by nonlinear regression but not by one estimated by back-transforming a line fitted to logarithms. This finding and others like it call into question the continued reliance on the allometric method in contemporary research.

Key words: allometry, scaling, crustacea, *Uca pugnax*.

Introduction

Julian Huxley's classic inquiry into the problems of relative growth (Huxley, 1932) introduced biologists everywhere to an engaging theory for constant relative growth by two bodily parts and simultaneously promoted a simple method for computing the ratio for growth rates by the parts in question. Both the theory and the associated computational method were based on observations that (1) the relationship between two bodily parts often can be approximated by a power function of the form $Y=aX^b$ and (2) the aforementioned (allometric) equation can be linearized by logarithmic transformation of the regressor and response variables (*X* and *Y*, respectively). When Huxley plotted logarithms for *X* and *Y* and fitted a line by eye, he was able to estimate the slope and intercept (Huxley, 1927a; Huxley, 1927b; Huxley, 1931; Huxley, 1932), after which parameters *a* and *b* in the power function were computed by back-transforming to the original scale. Huxley believed that he was the first to apply this procedure (Huxley, 1924; Huxley, 1932), but it was actually used on several earlier occasions by investigators who were independently grappling with the general problem of how best to quantify nonlinear scaling relationships (see Gould, 1966; Strauss, 1993; Gayon, 2000). However, none of the earlier workers formulated a general theory for relative growth based on the exponent, *b*, in the allometric equation (Reeve and Huxley, 1945; Strauss, 1993). Under conditions of constant exponential growth by both bodily parts, the exponent in the equation is equal to the ratio of their relative growth rates (Huxley, 1932).

Huxley's theory of constant relative growth was questioned almost from the time his book was published (Pantin, 1932), and the concept had lost much of its initial luster by the 1940s (Reeve and Huxley, 1945). However, his procedure for fitting a statistical model – the allometric method – found favor among a majority of investigators doing research at the time (Reeve and Huxley, 1945). The method was refined during the 1930s with the adoption of

ordinary least squares for fitting lines to log transformations (e.g. Galtsoff, 1931; Brodie and Proctor, 1932; Feldstein and Hersh, 1935), and the method (with minor modifications) has continued to this day to be the primary analytical procedure in the field (e.g. Warton et al., 2006; Glazier, 2010; White, 2011). Nonetheless, the allometric technique has recently been the target of criticism (Packard et al., 2011). Consequently, it is enlightening to re-examine some of Huxley's own research using procedures that were not available at the time of his writing.

Allometric growth in *Uca pugnax*

Huxley's most important contribution to empirical science – and the research in which he first made use of the allometric method – was his investigation of allometric growth by the enlarged 'crusher' claw in males of the fiddler crab *Uca pugnax* (see Huxley, 1924; Huxley, 1927a; Huxley, 1932). He collected 401 male crabs of all sizes from a population at the Woods Hole Marine Biological Station (Woods Hole, MA, USA) and divided the animals into 25 classes (bins) on the basis of live mass. The large chela was then removed from each crab and weighed. Body mass was estimated as live mass less the mass of the amputated chela. Mass of the large chela and mass of the body thus were the two variables (*Y* and *X*, respectively) used for his study. All values for chela mass and body mass were averaged for each of the 25 classes, and means were used in subsequent analyses.

Huxley suspected from the outset that the relationship between chela mass and body mass could be described with a power function (Fig. 1), so he transformed his data and displayed the transformations in a bivariate plot (Fig. 2). The attempt at linearization was largely successful, because the path of the observations followed 'a remarkably straight line' (Huxley, 1924). The only complication in the analysis was said to be a change in slope of the log–log relationship at approximately 30% of maximum mass (Huxley, 1924). The slope was estimated to be 1.62
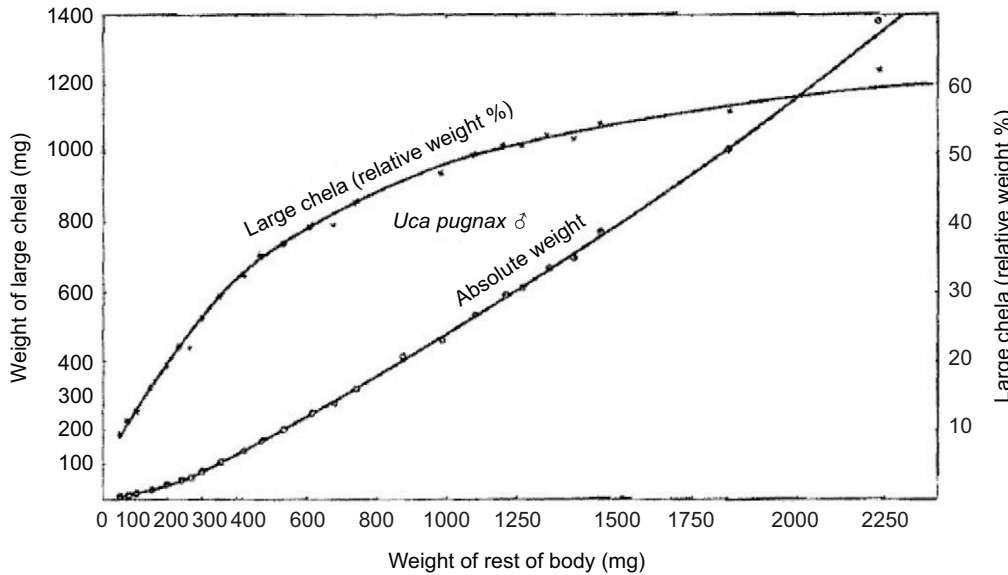
Fig. 1. Mass (left ordinate) and relative mass (right ordinate) of the enlarged claw from male *Uca pugnax* are plotted against body mass in this re-lettered fig. 2 from Huxley's book (Huxley, 1932). The upward trajectory for absolute mass (='weight') of the large chela apparently confirmed Huxley's expectation that his data would follow a power function.

for crabs weighing up to 0.75 g in body mass and 1.255 for all larger animals (Huxley, 1932). Huxley suggested that the putative discontinuity marked the attainment of sexual maturity by crabs and a shifting of nutrient resources from supporting growth by the claw to supporting growth by the gonads (Huxley, 1924; Huxley, 1932). This assertion has important implications for everything from general biology to resource management (Negreiros-Fransozo et
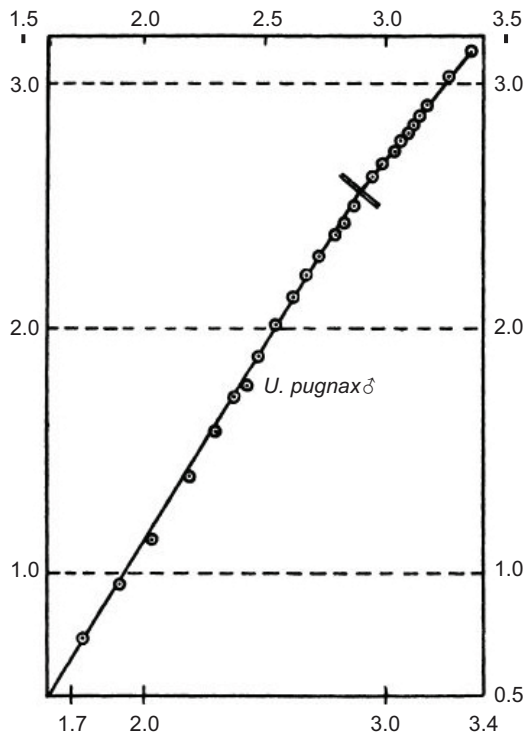

Fig. 2. Logarithmic transformations for chela mass in *Uca pugnax* are plotted against logarithmic transformations for body mass in this re-lettered fig. 3 from Huxley's book (Huxley, 1932). Huxley did not include a graph of transformed data in his original report (Huxley, 1924), but this graph appeared in later summaries (Huxley, 1927a; Huxley, 1932). Note that the graph had a relatively tall, narrow format that may have drawn undue attention to the putative change in slope (identified by a bar) between samples 15 and 16.

al., 2003; Hall et al., 2006). But is the assertion correct (Clayton, 1990)?

Reconsidering allometric growth in *Uca*

Means for both body mass and chela mass were taken from table 1 in Huxley (Huxley, 1932), converted to common logarithms and displayed in a bivariate graph (Fig. 3A). As noted already, Huxley believed that the transformations were described best by two linear segments, one fitted to the 15 observations for small crabs and the other to the 10 observations for large crabs (Huxley, 1924; Huxley, 1927a; Huxley, 1932), so I also identified the putative break-point with a bar (Fig. 3A).

I then fitted several linear and nonlinear models to the transformations (Table 1). Graphical display of the linear model (Fig. 3A) and the associated residuals (Fig. 3B) reveals that the observations deviate somewhat from linearity, so it comes as no surprise that quadratic and three-parameter nonlinear equations are better fits to the observations than the straight line (see scores for the PRESS statistic in Table 1). Although the departure from linearity is problematic, the quadratic and nonlinear models are unacceptable in the context of traditional allometry because neither of these alternatives is amenable to back-transformation to the all-important arithmetic scale (Gould, 1966; Finney, 1989a; Finney, 1989b). The objective of the exercise, after all, is to fit a power function to the original observations (Huxley, 1924; Huxley, 1932), and this cannot be accomplished using the more complex quadratic and nonlinear equations (Table 1). Thus, the linear model, which can be re-expressed in the arithmetic domain, is better than the alternatives despite its imperfect behavior.

I next displayed untransformed data in a bivariate graph (Fig. 4A) and fitted two- and three-parameter power functions by nonlinear regression (Kutner et al., 2004). The models were fitted by the Marquardt–Levenberg procedure in SigmaPlot 10 (Marquardt, 1963). Both the fitted lines are visibly good fits to the data (Fig. 4A), and both the analyses satisfied assumptions for normality and constancy of variances (Table 2). However, PRESS scores indicate that the three-parameter function is a better fit to the observations than the two-parameter model (Table 2). Moreover, standardized residuals from the three-parameter analysis are appropriately balanced (Fig. 4B) whereas those from the two-parameter function are not (Fig. 4C). In neither case, however, do

small and intermediate size but deviates appreciably from the path of the data at the upper end of the size distribution (Fig. 4A). The poor performance by this equation is reflected in the plot of raw residuals, which first follow an upward trajectory and then plunge downward as predictions depart more and more from observations (Fig. 4D). These residuals are neither random (indicative of additive error) nor in the form of a megaphone (indicative of multiplicative error); they confirm, however, the inadequacy of the fitted model.

Discussion

Huxley believed that a break-point in his double-logarithmic plot identified a point in time when the relationship between growth by the large chela and growth by the body changed abruptly. In his view, the attainment of reproductive maturity meant that some nutrients previously allocated to growth by the large chela were being diverted to the gonads, so that instantaneous growth by the chela was diminished as the animal grew larger. A more likely interpretation, however, is that Huxley was simply misled by logarithmic transformations that created the illusion of a break-point, coupled with his use of a graphical format that exaggerated the appearance of the putative change in slope (Fig. 2). Power functions fitted to his original data by nonlinear regression indicate that growth by the claw maintains the same relationship to growth in body mass over the entire range for data in the sample (Fig. 4A).

Consequently, a single straight line fitted to logarithms is better than two lines fitted to limited parts of the distribution, but the power function estimated by back-transformation fails the test of validation in the original scale (see Yates, 1950; Anscombe, 1973; Finney, 1989a; Cox et al., 2008). The re-expressed equation is an acceptable fit to data for crabs of small and intermediate size, but the model is a poor fit to data for the largest animals in the sample (Fig. 4A). The power function fitted by the allometric method consequently fails to yield an accurate view of growth by the large chela in fiddler crabs. In other words, the procedure promoted by Huxley actually worked poorly with his own data!

Why do functions fitted directly to arithmetic values by nonlinear regression perform well whereas the one fitted by back-transformation performs poorly? Jerrold Zar provided the answer more than 40 years ago (Zar, 1968), but his explanation was not fully understood at the time and consequently has gone largely unappreciated by several generations of biologists. To paraphrase Zar, the aforementioned difference between statistical models can be traced directly to the logarithmic transformation, which elicited a fundamental change in the distribution for the observations (see Emerson and Stoto, 1983). When a linear model is fitted to transformations, the equation describes the distribution for
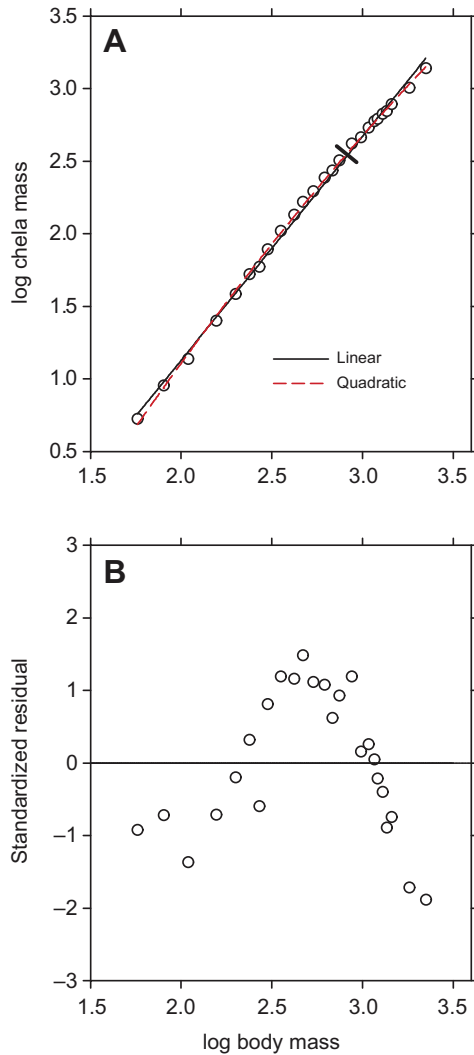

Fig. 3. (A) Linear and quadratic equations were fitted to logarithmic transformations for chela mass and body mass of *Uca pugnax* (Table 1). The bar between observations 15 and 16 marks the break-point identified by Huxley (Huxley, 1924; Huxley, 1927a; Huxley, 1932). (B) The parabolic pattern manifested by standardized residuals from the linear regression confirms that transformation failed to linearize the observations.

residuals assume the megaphone shape that would result from multiplicative error (Kutner et al., 2004).

In contrast, the equation estimated by back-transforming the linear model fitted to logarithms tracks observations for crabs of

Table 1. Diagnostics for statistical models fitted by SigmaPlot 10 to logarithmic transformations of chela mass *vs* body mass in fiddler crabs

Predictive equation	Adjusted R^2	PRESS	Normality test	Constant variance test
			*P*	
Linear: $\widehat{\log Y} = -1.957 + 1.542(\log X)$	0.997	0.036	0.866	0.884
Quadratic: $\widehat{\log Y} = -2.920 + 2.309(\log X) - 0.148(\log X)^2$	0.999	0.018	0.955	0.021
Two-parameter nonlinear: $\widehat{\log Y} = 0.314(\log X)^{1.942}$	0.983	0.224	0.800	0.340
Three-parameter nonlinear: $\widehat{\log Y} = -5.111 + 4.240(\log X)^{0.553}$	0.999	0.022	0.912	0.067

The adjusted R^2 takes into account the number of parameters in the model. The smallest value for the predicted residual error sum of squares (PRESS) identifies the best statistical model (Kutner et al., 2004). The two-parameter nonlinear model is a poor fit because it was constrained to pass through the origin. A generalized linear model also was fitted (SAS 9.2) to obtain an equation that predicts arithmetic means instead of geometric means in the arithmetic domain (Cox et al., 2008), but the resulting equation, $\widehat{\log Y} = -1.958 + 1.543(\log X)$, is virtually indistinguishable from the linear model fitted by ordinary least squares. Tests for constancy of variance raise concerns about the reliability of significance tests for parameters in the quadratic and three-parameter nonlinear models.
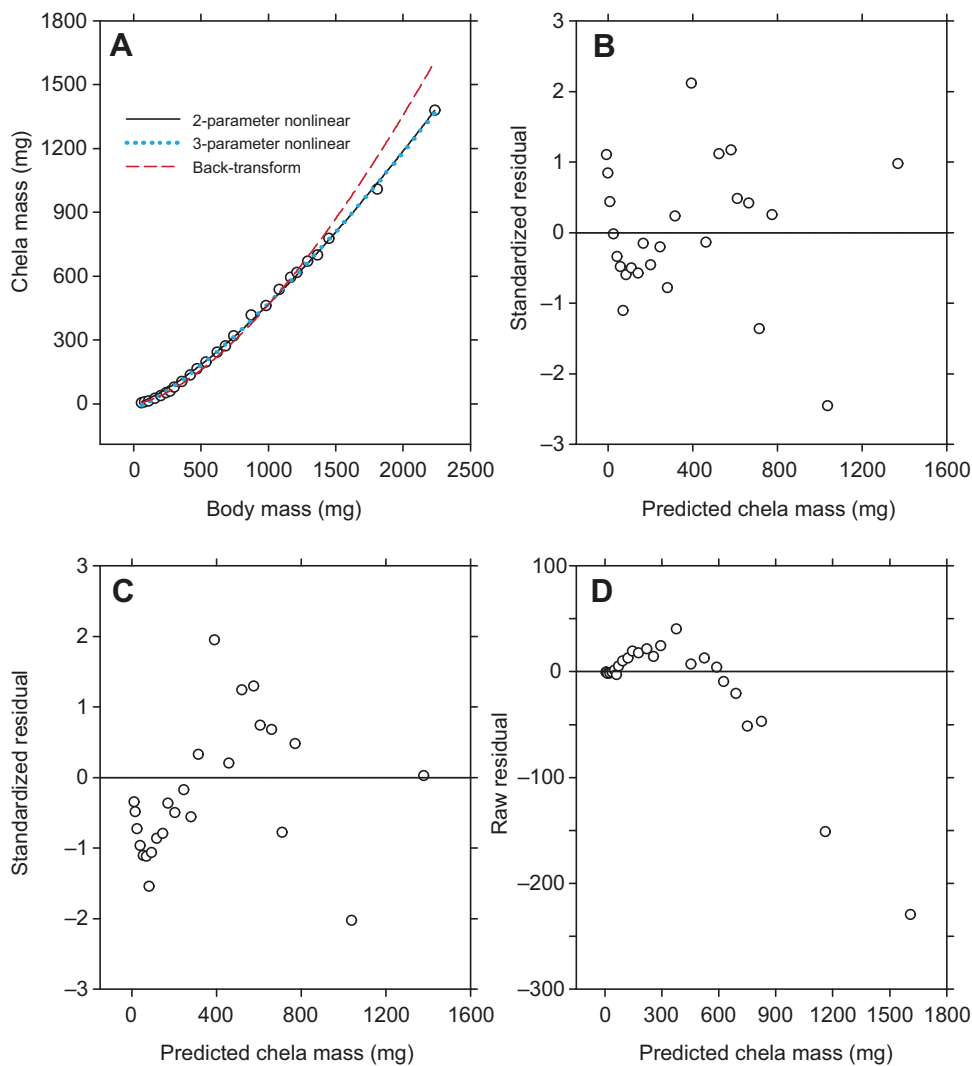
Fig. 4. (A) Two- and three-parameter power functions were fitted to untransformed data for chela mass and body mass of *Uca pugnax* by nonlinear regression (Table 2). Both functions are visibly good fits, but PRESS scores indicate that the three-parameter model is better than the two-parameter model for describing the observations (Table 2). The equation estimated by back-transforming from logarithms, $\hat{Y}=0.011X^{1.542}$, is a poor fit to the largest crabs in the sample. (B) Standardized residuals from the three-parameter nonlinear regression reveal a generally satisfactory distribution, and none of the residuals is so extreme as to be an outlier. (C) Standardized residuals from the two-parameter nonlinear regression reveal uniformly negative values for small claws. The two-parameter model suffered from the requirement that it pass through the origin (Table 2). (D) Raw residuals from the equation estimated by back-transformation exhibit an inexplicable pattern. Raw residuals are presented instead of standardized residuals because the standard error of the estimate for the fitted model was inflated by constraining parameters to $a=0.011$ and $b=1.542$.

observations in log space. But when that linear equation is subsequently re-expressed in arithmetic space, the resulting power function does not describe the arithmetic distribution; the re-expressed model is simply a mathematically equivalent descriptor for the log distribution (see Packard et al., 2010; Packard et al., 2011; Packard, 2011). Thus, unbeknownst to Huxley, the allometric method actually was not a good way to fit a statistical model to data in arithmetic space.

Nevertheless, back-transforming from a linear equation fitted to logarithmic transformations was the only method available in Huxley's time for 'fitting' a power function to nonlinear data (see Snedecor, 1937). Indeed, the absence of an alternative procedure for fitting power functions may explain why Huxley did not attempt to fit three-parameter equations to any of the data available to him: he clearly believed that the three-parameter function is most inclusive and that it should be taken as the starting point in allometric analyses [p. 241 of Huxley (Huxley, 1932)]. Huxley seems simply to have done his best with the tools that were available to him.

Today, however, investigators have ready access to statistical software for fitting nonlinear models directly to arithmetic data (e.g. Motulsky and Christopoulos, 2004; Ritz and Streibig, 2008), so there is no need to resort to the indirect procedure that was so important to Huxley. There is danger, of course, in the uncritical application of nonlinear regression in allometric research. For this reason, nonlinear regression should be performed only after data have been submitted to exploratory analysis to determine general properties of the arithmetic distribution (Behrens, 1997; Zuur et al., 2010). Moreover, future

Table 2. Diagnostics for nonlinear models fitted by SigmaPlot 10 to arithmetic values for chela mass *vs* body mass in fiddler crabs

Predictive equation	Adjusted R^2	PRESS	Normality test	Constant variance test
			*P*	
Two-parameter nonlinear: $\hat{Y}=0.044X^{1.343}$	0.998	5507	0.090	0.795
Three-parameter nonlinear: $\hat{Y}=-19.695+0.067X^{1.288}$	0.999	4934	0.924	0.274

The adjusted R^2 takes into account the number of parameters in the model. The smaller value for PRESS identifies the better statistical model (Kutner et al., 2004). The intercept for the three-parameter model differs significantly from zero ($P=0.002$).

investigations should unfailingly include a graphical display of the fitted model in the arithmetic domain to ensure reliability of the final product (Snee, 1977; Ritz and Streibig, 2008; Zuur et al., 2010).

Acknowledgements

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