Remarks on the article of Packard: Julian Huxley, *Uca pugnax* and the allometric method

Packard (Packard, 2012) restudied Huxley's measurements of *Uca pugnax* and presented not only a two-parameter power function but also a three-parameter power function; this three-parameter model 'is better than the two-parameter model for describing the observations'. The two-parameter model has a biological meaning, as explained by Huxley (Huxley, 1924); the three-parameter model has no biological meaning.

I have shown (Geraert, 2004) that there is a constant change in the relationship (and not a constant relationship) between a small amount of growth of body part *y* compared with that of body part *x*; mathematically speaking, the 'second difference' is constant. This second difference is the growth rate and is present in the quadratic factor of a quadratic equation; the other factors in the equation have no biological meaning but are necessary to position the quadratic curve in a diagram.

In my study (Geraert, 2004), growth is followed from the new-born stage to the adult; in Huxley's study on the fiddler crab, a comparison is made among adult males; as these adults show a very large variation in the development of the claw, Huxley (Huxley, 1924; Huxley, 1932) interpreted this also as 'growth'. An attempt is made to see whether a quadratic parabola can also be used to describe variation in adults, called here 'comparative' growth.

The quadratic equation calculated for the males of *Uca pugnax* is as follows:

$$Y = 0.097X^2 + 0.42X - 0.045\ , \qquad (1)$$

in which Y is the mean mass (in g) of the large chela and X is the mean mass (in g) of the rest of the body after removal of large chela (Huxley, 1932). The calculated values for Y are very near to the observed ones, except for the smallest bodies where a slightly different Y-value is calculated; the overall similarity is obvious in Fig. 1; it is also obvious by the very small value of the sum of (Y measured – Y calculated)^2 being only 4.5 mg. The quadratic factor in the above equation is the growth factor; multiplied by 2, it gives the second difference in the growth of the claw relative to the growth of the rest of the body; e.g. for every additional growth of the body with 100 mg, the differences in the growth of the claw show a constant increase of 1.94 mg (=2×0.97).

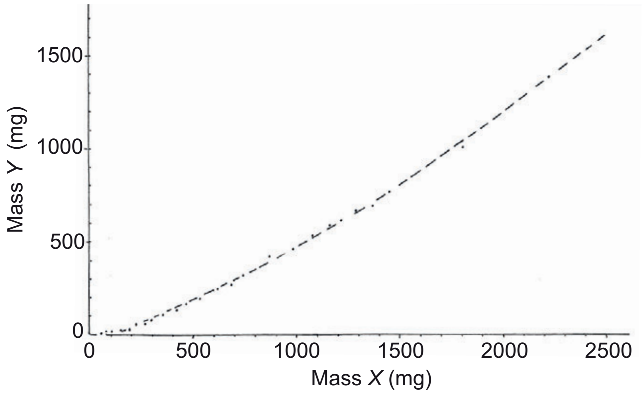

Fig. 1. Diagram representing the measurements obtained by Huxley (modified from Huxley, 1932) of the males of the fiddler crab (*Uca pugnax*); the dashed line is the calculated quadratic parabola.

In the case of *Uca pugnax*, a quadratic curve describes the comparative growth in males in a satisfactory way; moreover, it also has a biological meaning. Power curves with two parameters and three parameters (Packard, 2012) describe the phenomenon as well, but the three-parameter curve has no biological meaning. In my study (Geraert, 2004), the quadratic curve describes real growth in such an impressive way that fare-reaching conclusions could be made; it seems not necessary to introduce similar conclusions for comparative growth.

In a study on comparative growth in adults, if a curved line is obtained it is interesting to evaluate whether a quadratic curve is appropriate to describe the phenomenon; if the match is good enough, the 'growth' rate, indicated by the quadratic factor, could help us to make assumptions about larger and/or smaller values. The term allometry can be continued, although it can be mathematically formulated by a quadratic curve instead of a power curve.

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Response to 'Remarks on the article of Packard: Julian Huxley, *Uca pugnax* and the allometric method'

Professor Geraert and I agree on the importance of examining arithmetic data instead of logarithmic transformations but we disagree on other issues pertaining to the fitting of statistical models in bivariate allometry. The most important of our differences concerns the utility of quadratic equations, which sometimes provide better fits than power functions to observations in bivariate displays. However, a quadratic equation is an unrealistic representation of allometric variation because the quadratic term in the model causes the fitted curve to assume the shape of a parabola (see Finney, 1989) (http://www.mathopenref.com/quadraticexplorer.html). When the coefficient in the quadratic term is positive, the curve has a minimum and both ends point upwards. When the coefficient is negative, the curve has a maximum and both ends point downwards. The problem with a parabolic curve may not be immediately apparent when the tracing is limited to the range of data in the sample (as in the case of *Uca pugnax*), but coefficients in the statistical model are biologically uninterpretable in any case (Gould, 1966; Finney, 1989).

Moreover, a quadratic model is not as good a fit to data for chela mass *versus* body mass in *Uca pugnax* as the two- and three-parameter power functions that were reported in my essay (Packard, 2012a). All

Table 1. Diagnostics for three statistical models fitted to arithmetic values for chela mass *versus* body mass in fiddler crabs

Predictive equation	Normality test	Constant variance test	PRESS
Quadratic polynomial: $\hat{Y} = -45.006 + 0.420X + 0.000097X^2$	P=0.476	P=0.559	5756
Two-parameter non-linear: $\hat{Y} = 0.044X^{1.343}$	P=0.090	P=0.795	5507
Three-parameter nonlinear: $\hat{Y} = -19.695 + 0.067X^{1.288}$	P=0.924	P=0.274	4934

The Kolmogorov-Smirnov test was used to assess normality, and the Spearman rank correlation between absolute values for residuals and observed values for the response variable was used to test for constant variance. The smallest value for PRESS (i.e. the Predicted Residual Error Sum of Squares) identifies the best of the candidate models (Kutner et al., 2004).

three models satisfy tests for normality and constant variance (Table 1), and all three of the mean functions closely follow the path of the observations [see fig. 4A in my study (Packard, 2012a) and fig. 1 in the accompanying Correspondence (Geraert, 2012)]. However, PRESS statistics indicate that both the power functions are substantially better fits than the quadratic model (Table 1). Thus, the quadratic equation in this case is not favored on statistical grounds any more than it is favored on biological grounds.

Professor Geraert also believes that a three-parameter power function has no biological meaning, owing presumably to the term for an intercept. It is worth remembering here that Huxley himself argued in favor of using a three-parameter function as the theoretical starting point in allometric analyses [see p. 241 of Huxley (Huxley, 1932)]. Huxley went on to suggest that the intercept might be relatively unimportant in the scheme of things, so that an investigator might revert to a two-parameter model with minimal loss of fit or relevance. Of course, this argument may have been a convenience for Huxley because he did not have ready access at that time to a procedure for fitting a three-parameter power model to bivariate data.

Professor Geraert is correct when he suggests that I have no biological interpretation to attach to the negative intercept for the three-parameter power function describing the scaling of chela mass to body mass in fiddler crabs. Thus, it might be advisable to revert to the simpler, two-parameter power function (which still shows that the allometric exponent does not change with body size). However, Professor Geraert's assertion that a three-parameter power model generally is meaningless is incorrect, because a non-zero intercept frequently has biological as well as statistical significance when enough is known about the system under study (Bales, 1996; Sartori and Ball, 2009; Packard, 2012b).

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