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Invited reply

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Evolutionary biology

Response to Packard: make sure we do not throw out the biological baby with the statistical bath water when performing allometric analyses

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Quantifying accurately the relationship between a phenotypic trait and body mass is a long-standing challenge in evolutionary biology and constitutes the core of allometric analyses. The traditional approach to study allometric relationships (expressed as $y = b\ x^a$, [1]) is to fit a linear (or more recently, a quadratic [2]) model on log-transformed data. This allows estimating a, the allometric exponent which corresponds to the growth ratio between y and x, and b the allometric intercept that depends on the initial values of y and x, respectively [1]. Further, the comparison between linear and quadratic models allows the testing for possible changes in the allometric coefficient with increasing size. Using such a standard approach, we have recently shown [3] that the allometric exponent of antler size decreases with increasing body mass in extant cervids larger than 110–120 kg. Our best models, a threshold model and a quadratic model fitted the data particularly well. However, Packard [4] qualified our statistical approach of 'unnecessary and incorrect' and cast doubt on our take-home message that the allometric exponent of antler size changes with body mass.

Packard's criticism falls into the recent debate on using logarithmic transformations in allometric studies (e.g. [5,6]). Packard (e.g. [6,7]) has repeatedly argued that logarithmic transformations are often unjustified, do not meet assumptions of linear models and are misleading. Instead, this author advises to fit a set of power functions on raw data. The expected type of biological variation is a cornerstone in the logarithmic versus arithmetic scale debate [8]. Because it is most probable that biological errors are generated by multiplicative processes similar to those responsible for growth, log-transformations reliably control for this size-dependent variability, and ensure the required normal distribution of the residuals. Fitting a power function assumes that errors are additive rather than multiplicative [8]. Alternatively, Packard [9] argues that the 'multiplicative nature' of any biological trait can be taken into account by controlling for heteroscedasticity when fitting generalized nonlinear models. Using a log–log scale model or a power model with heteroscedastic error should provide similar results. To check whether this is the case, we consider the simple situation of a constant allometric exponent with mass illustrated by the antler size allometry across deer species below 113 kg ($n = 22$). As expected, both estimates of allometric exponent are close (1.326 ± 0.152 for the log–log scale model versus 1.235 ± 0.108 for the power model with heteroscedastic error), leading to the same biological interpretation of a strong positive allometry (the expected exponent for isometry between a mass and a linear measurement being one-third). So, how can we explain the discrepancy observed between the two methods when analysing the whole deer dataset?

To get a model satisfactorily fitting the data, Packard [4] used a three-parameter power function with additive heteroscedastic error ($\hat{y} = -40.536 + 16.414x^{0.399}$). This model hinders any biological interpretation of the parameters. In particular, the exponent in this model does not inform anymore about the value or the change of the allometric exponent (*sensu* Huxley [1]), rendering this model less easily applied in the context of allometric studies. Moreover, the biological meaning of the value -40.536 is unclear. This contrasts with the parameters of a quadratic model $\log(y) = \log(b) + a\log(x) + c(\log(x))^2$ that are relatively straightforward to interpret (e.g. a: the maximum allometric exponent occurring at very low x, and c the strength of the reduction in the allometric exponent with increasing x). This additional parameter leads Packard's model to predict that cervids below 10 kg should not have any antlers, which is not supported by empirical evidence. Indeed, male Northern pudu (*Pudu mephistophiles*) weigh much less than 10 kg but wear antlers [10].

We certainly agree that the three-parameter power model with heteroscedastic error proposed by Packard provides the best fitting line and thus has some merit in a pure statistical sense. His parsimonious model offers a reliable way to describe the allometric relationship. However, allometric analyses do not aim only at fitting lines, and biological inferences are generally looked for, although often overlooked [5]. When it comes to deciphering the complex biological processes underlying the strength and the shape of allometric relationships, the traditional 'log-transformed' methodology should be preferred to Packard's approach because this latter is difficult to interpret in biological terms [11].

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