Commentary: On the Interpretation of the Normalization Constant in the Scaling Equation

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A Commentary on

On the Interpretation of the Normalization Constant in the Scaling Equation
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Many biological size-scaling relationships follow the power function $Y = \beta X^{\alpha}$, where Y is a specific trait, β is the normalization constant (scaling coefficient), X is a measure of size, and α is the slope (scaling exponent). Niklas and Hammond (2019) have argued that, although much investigation has focused on the empirical values and biological meaning of α, comparable attention has not been given to β. They also evaluate four possible reasons for why they think β has been understudied, including a belief by some investigators (e.g., Huxley, 1932) that β has no biological meaning, and that its value is often merely the result of a statistical autocorrelation with α. Their thoughtful argument for increasing investigation of the biological meaning of β is worthwhile reading, but I feel that it leaves out three important points. First, the authors do not mention or even hint at the existence of numerous studies on the scaling of various physiological, anatomical, and life-history traits that show how various factors affect β in biologically meaningful ways. Second, they do not discuss alternative ways of quantifying the elevation of a scaling relationship (conventionally estimated as β) that avoid the autocorrelation problem. Third, they do not recognize previous noteworthy literature concerning the scaling of metabolic rate that has focused on understanding both the elevation and slope, and the relationship between the two. Given space limitations, I can only provide a brief discussion of these three points. Readers can find further details in the cited references, some of which are reviews of relevant theory and empirical data.

First, many studies have examined how various factors affect the elevation (as indicated by β = antilog of the Y-intercept in a log-log plot) of the body-mass scaling of metabolic rate and other traits. For example, much research has shown that temperature and behavioral activity increase metabolic rate at all body sizes, and thus the overall scaling elevation (e.g., Brown et al., 2004; Glazier, 2010). Furthermore, consider that comparative studies of various biological traits often adjust for body-size effects by using analysis of covariance. These countless studies in effect compare the elevations (as indicated by Y-intercepts) of multiple size-scaling relationships, which are assumed to be parallel (i.e., α is constant; see Sokal and Rohlf, 1995). This statistical method thus emphasizes β over α, which is reasonable if α is fixed. Indeed, proponents of the 3/4-power law claim that α is fixed at 3/4 for rates of metabolism and other biological processes, and that variation in these scaling relationships principally involves β (e.g., Brown et al., 2004). An early example was reported by Hemmingsen (1960), whose well-known analysis of metabolic scaling revealed significant differences in β between unicellular ectotherms, multicellular ectotherms, and multicellular endotherms, but no inter-group differences in α ($\sim 3/4$). Several researchers have

discussed biological reasons for not only this variation in scaling elevation (e.g., Phillipson, 1981; Peters, 1983; Glazier, 2014a), but also that of many other kinds of physiological, anatomical, and life-history traits among various taxa (e.g., Peters, 1983; Schmidt-Nielsen, 1984; Hayssen and Lacy, 1985; Zotin, 1990; Sibly and Brown, 2007; Glazier, 2009a, 2018a). Biologically meaningful analyses of β have not been as neglected as claimed by Niklas and Hammond.

Second, although Niklas and Hammond correctly point out that β and α of multiple intersecting scaling relationships may correlate for simple mathematical reasons, this may occur even if the relationships do not intersect. When comparing multiple scaling relationships, if β tends to be less than the geometric midpoint of a scaling relationship, β and α will tend to be negatively correlated, whereas if β tends to be greater than the midpoint, β and α will tend to be positively correlated. Many investigators of scaling relationships have recognized this autocorrelation effect (e.g., Gould, 1966; Peters, 1983; Glazier, 2010, 2018c). To avoid this problem, β can be replaced with another measure of scaling elevation, L, which is $\log(Y/X)$ at the pivotal midpoint of a log-log scaling relationship. For metabolic scaling relationships, this measure of elevation (metabolic level) may relate to the slope in a biologically meaningful way that is not a simple mathematical artifact (e.g., Glazier, 2009b, 2010, 2014b; Killen et al., 2010). However, the L estimate is most useful when comparing non-proximate, non-intersecting scaling relationships with similar body-mass ranges. For example, large variation in the midpoint mass at which one estimates L can potentially confound relationships between the elevation and slope (Glazier, 2009b, 2010). Evidence for biologically significant correlations between the elevation and slope of scaling relationships is strongest when similar results are found for both β and L (Glazier, 2009b, 2010).

Third, several researchers not cited by Niklas and Hammond have explored both the elevation and slope of scaling relationships and their correlation. For example, Heusner (1991) emphasized that metabolic scaling relationships cannot be fully understood without explaining their vertical location in a "mass-power plane." McNab (2008, 2009) showed how several ecological and biological factors affect both the slope and elevation of metabolic scaling relationships in birds and mammals (see also other references cited in Glazier, 2010). Price and Weitz (2012) have examined correlations between the scaling intercepts and slopes of leaf surface area. In particular, Glazier (2005, 2008, 2010, 2014b) proposed the metabolic-level boundaries hypothesis (MLBH), which predicts that the elevation and slope of scaling relationships should be negatively correlated for resting metabolic rate, but positively correlated for active metabolic rate. The MLBH further predicts that any factor that affects the elevation of metabolic scaling relationships (quantified as β or L), including temperature, physiological state, and activity level, will in turn affect the slope via shifts in the relative influence of various metabolic processes that relate to either surface area or volume. Many studies have tested the MLBH, often with confirming results (reviewed in Glazier, 2008, 2009a, 2010, 2014b, 2018b).

Investigations of the biological meaning of both the elevations and slopes of scaling relationships of some physiological, anatomical, and life-history traits are already underway, and similar efforts should be worthwhile for other kinds of biological traits, as advocated by Niklas and Hammond (2019). In so doing, I recommend that researchers become well-versed in the available, widely scattered literature on diverse kinds of organisms to be sure that they do not inadvertently rediscover or miss valuable insights regarding scaling patterns or explanations that have already been reported, a common occurrence in the field of biological scaling (Glazier, 2018c).

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The author confirms being the sole contributor of this work and has approved it for publication.

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