

COMMENTARY

Biological scaling analyses are more than statistical line fitting

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ABSTRACT

The magnitude of many biological traits relates strongly and regularly to body size. Consequently, a major goal of comparative biology is to understand and apply these 'size-scaling' relationships, traditionally quantified by using linear regression analyses based on log-transformed data. However, recently some investigators have questioned this traditional method, arguing that linear or non-linear regression based on untransformed arithmetic data may provide better statistical fits than log-linear analyses. Furthermore, they advocate the replacement of the traditional method by alternative specific methods on a case-by-case basis, based simply on best-fit criteria. Here, I argue that the use of logarithms in scaling analyses presents multiple valuable advantages, both statistical and conceptual. Most importantly, log-transformation allows biologically meaningful, properly scaled (scale-independent) comparisons of organisms of different size, whereas non-scaled (scale-dependent) analyses based on untransformed arithmetic data do not. Additionally, log-based analyses can readily reveal biologically and theoretically relevant discontinuities in scale invariance during developmental or evolutionary increases in body size that are not shown by linear or non-linear arithmetic analyses. In this way, log-transformation advances our understanding of biological scaling conceptually, not just statistically. I hope that my Commentary helps students, non-specialists and other interested readers to understand the general benefits of using log-transformed data in size-scaling analyses, and stimulates advocates of arithmetic analyses to show how they may improve our understanding of scaling conceptually, not just statistically.

KEY WORDS: Allometry, Biological significance, Body size scaling, Logarithms, Proportions, Statistics

Introduction

The magnitude of many biological structures and processes relates strongly to organismal size. Simply knowing how big an organism is can tell us much about what it looks like and how it functions. Therefore, as a first step in attempting to understand variation in a biological trait, comparative biologists often estimate how that variation relates to body size. This undertaking is made simpler if the magnitude of a trait varies proportionately (isometrically; see Glossary) in a 1:1 way with total body size. This may occur for some traits, but often the mass of a body part (e.g. brain mass) or the rate of an activity (e.g. metabolic rate) varies disproportionately (allometrically) with total body mass (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; Hoppeler and Weibel, 2005). That is, as an organism grows in size through development or evolution, the magnitude of a body part or rate process may increase faster or

slower (respectively, hypermetrically or hypometrically; see Glossary) than total body mass. These surprisingly regular body size scaling patterns have invoked debate concerning two major questions. First, why do allometric scaling patterns occur? Second, how should one quantify them mathematically?

The first question has been discussed for decades, especially concerning the scaling of the rate of various biological processes, such as growth and metabolism. This debate has been especially contentious since the recent demise of the classic 3/4 power law, which dictated that the rates of most biological processes of virtually all organisms scale with body mass according to a hypometric 3/4 slope in log–log space. For example, we now know that the body mass scaling of metabolic rate, a major indicator of the pace of life, varies considerably in response to various intrinsic biological and extrinsic ecological factors (e.g. Riisgård, 1998; Bokma, 2004; Glazier, 2005, 2010, 2014, 2018b, 2020; White et al., 2007; DeLong et al., 2010; White and Kearney, 2013, 2014).

The second question has also generated contentious discussion in many scientific journals, including *Journal of Experimental Biology*, and I believe considerable confusion, especially during the last two decades. In my Commentary, I hope to help resolve some aspects of this controversy by clarifying the rationale for the traditional, most commonly used method to quantify scaling relationships. The traditional method involves log-transformation of the data before comparing the magnitude of a specific trait (log Y) against some measure of body size, such as body mass (log X) (e.g. Huxley, 1932; Peters, 1983; Sibly et al., 2012; and several articles in a special issue of *Journal of Experimental Biology* introduced by Hoppeler and Weibel, 2005). This procedure often linearizes the data, allowing one to use linear regression (see Glossary) to calculate the equation $\log Y = \log a + b(\log X)$, where a is the antilog of the Y intercept or scaling coefficient (see Glossary) and b is the slope or scaling exponent (see Glossary). One can also represent this log-linear relationship as a power function $Y = aX^b$. Using log-transformed data in scaling analyses has many additional advantages, as discussed below.

However, some scientists have questioned the traditional method of quantifying scaling relationships and have promoted the use of other methods (e.g. linear or non-linear regression) based on the untransformed arithmetic numbers (see Glossary; i.e. using ordinary Cartesian coordinates) for four major reasons. First, arithmetic scaling analyses may produce better fits to the data, and thus are said to be superior to methods using log-transformed data (e.g. Thompson, 1942; Smith, 1980; Lovett and Felder, 1989; Hui and Jackson, 2007; Packard, 2012; De Giosa and Czerniejewski, 2016; Geraert, 2016; Chen et al., 2020). Second, they may be more appropriate when measurement and (or) biological error is additive, rather than multiplicative (see Glossary; e.g. Xiao et al., 2011; Pélabon et al., 2018). Third, some critics of the traditional scaling method claim that non-linear scaling analyses based on arithmetic data may be more appropriate when scaling relationships are non-linear (curvilinear), as they often are, in either arithmetic or logarithmic space (e.g. Packard, 2012, 2017, 2019). Fourth, some

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Glossary

Additive error (variation)

Arithmetic variation of a trait is unrelated to the mean value of the trait or the size of the system of which it is a part.

Allometric analyses

Analyses of how the magnitude of a trait (structure or process) varies with system size. In biology, system size usually refers to body size, but may also refer to cell size or size of a body part. Typically, allometric analyses involve scaling systems of different size by using proportional (logarithmic, multiplicative or geometric) scales.

Arithmetic number

A counted amount based on simple integers or their fractions. This is the definition understood by the public, and used by most scientists. However, mathematical number theory uses a more complex definition not considered here.

Arithmetic space

A graphical scale of additive arithmetic numbers (mathematical sums).

Geometric space

A graphical scale of multiplicative numbers (mathematical products), often represented by logarithms.

Hypermetric

When the relative magnitude of a trait increases as system size increases, and thus the scaling exponent is >1 (also called 'positive allometry')

Hypometric

When the relative magnitude of a trait decreases as system size increases, and thus the scaling exponent is <1 (also called 'negative allometry')

Isometric

When the magnitude of a trait varies proportionately in a 1:1 way with system size, and thus the scaling exponent is 1.

Isomorphic

Objects with the same shape, regardless of their size.

Logarithmic number

A mathematical figure of how many times a specific base number (e.g. 10) must be multiplied to equal a specific arithmetic number. Logarithms are used to scale quantities in geometric (multiplicative) space, rather than simple arithmetic (additive) space. Logarithms indicate proportional quantities, whereas arithmetic numbers indicate absolute quantities.

Multiplicative error (variation)

Arithmetic variation of a trait increases with the mean value of the trait or the size of the system of which it is a part. Logarithmic transformation converts multiplicative variation in arithmetic space (see Glossary) into additive variation in geometric space.

Regression

Statistical analysis of how a dependent variable (Y) relates quantitatively to an independent variable (X).

Scaling analyses

Proportional comparisons of the magnitude (variation) of a trait (structure or process) among systems of different size.

Scaling coefficient

Y -intercept in a log-linear scaling regression.

Scaling exponent

Slope in a log-linear scaling regression.

Slide rule

A calculator tool that uses a logarithmic scale mainly for multiplication and division of numbers.

Weber–Fechner law

A psychological law concerning the logarithmic relationship between the strength of a stimulus and the intensity of its perception by humans.

numerous, often over-arching general benefits of using scaling analyses based on logarithmic data (including increased theoretical and biological relevance), as I describe next.

Special value of logarithms in biological scaling analyses

A major purpose of my Commentary is to point out the general conceptual advantages of using logarithmic numbers (see Glossary) in scaling studies (for discussions of other issues regarding the use of specific regression techniques, including those that incorporate phylogenetic information, see Riska, 1991; Warton et al., 2006; Smith, 2009; White et al., 2019). These advantages are often forgotten when focusing on finding the best statistical model to fit specific datasets, which often varies idiosyncratically among studies. As McMahon and Bonner (1983, p. 28) remark in their classic, popular book *On Size and Life*, logarithms 'have many worthwhile properties', which distinguishes log-transformation from other kinds of mathematical transformation. Unfortunately, however, confusion about logarithms is common in biology (Gingerich, 2000; Menge et al., 2018). Some or all of the several practical and theoretical advantages of using logarithms are ignored or dismissed without adequate justification by critics of the traditional method (e.g. Lovett and Felder, 1989; Packard, 2017, 2020a,b; Geraert, 2016; Chen et al., 2020). Two widely recognized, statistically important advantages (among others) include normalizing data with multiplicative error (or heteroscedastic variation) and unequal body mass spacing (though it is also possible to incorporate multiplicative error into non-linear analyses based on arithmetic data: e.g. Marshall et al., 2013; Packard, 2017), and converting arithmetic curvilinear relationships into more easily analyzed and comparable log-linear relationships (Gaddum, 1945; Calder, 1984; LaBarbera, 1989; Lovett and Felder, 1989; Keene, 1995; Kerkhoff and Enquist, 2009; Packard et al., 2011; Xiao et al., 2011; Niklas and Hammond, 2014). In addition, log-transformation allows one to compress a huge spread of sizes into a smaller, more easily analyzed and graphed range (Bagnold, 1941; McMahon and Bonner, 1983; Burton, 1998; Mahajan, 2018; Menge et al., 2018), a useful general property exploited by many scientists, including astronomers and geographers faced with quantitative analyses involving immense spatial distances (Clark and Montelle, 2012). Additional important properties of logarithmic data are discussed in more detail below.

Logarithms allow scale-independent comparisons of data

I emphasize here that the most important, often unrecognized or underappreciated useful property of logarithms with respect to scaling analyses is that they facilitate meaningful, scale-independent comparisons of various features of systems that differ markedly in size (also see Gaddum, 1945; Keene, 1995; Kerkhoff and Enquist, 2009). Indeed, they are essential for carrying out scaling analyses (see Glossary) that allow one to analyze small and large systems together in a proportional, scale-invariant way (also see Reich, 2001). Power functions derived from logarithmic data are also well suited for representing scale invariance, where the size of a trait varies in the same relative way with system size for systems of all sizes (Gisiger, 2001; Marquet et al., 2005; Stumpf and Porter, 2012). As Gisiger (2001, p. 165) aptly stated, one can 'zoom in' or 'zoom out' and the form of the functional relationship between Y and X stays the same.

Size variation of small traits in small organisms is not directly comparable in a biologically plausible way to that of large traits in large organisms (Kerkhoff and Enquist, 2009; Cawley and Janacek, 2010; Glazier, 2013; Gingerich, 2019). For example, a young

critics even claim that log-transformation distorts the 'original arithmetic' data, thus creating spurious relationships (Zar, 1968; Sartori and Ball, 2009; Packard, 2012, 2014, 2017, 2019; Packard et al., 2011; Chen et al., 2020). However, although scaling analyses based on arithmetic data may be statistically advantageous in special cases, these specific benefits should be weighed against the

mouse weighing 10 g may grow 1 g in 10 days. By contrast, a young elephant weighing 100,000 g may grow 1000 g in 10 days. The elephant is growing much faster than a mouse in an absolute arithmetic sense. However, this comparison is not biologically meaningful because one has not used proper size-specific scaling. It is impossible for a mouse to grow 1000 g, and it is insignificant for an elephant to grow 1 g. What is biologically relevant is how much a mouse or elephant grows in proportion to its own original body mass, not that of another species with a very different size. One way to do this would be to use ratios or percentages. For example, the mouse grows by 10%, whereas the elephant grows by 1%. Looked at this way, the mouse is actually growing faster than the elephant in a more comparable, scale-independent way than that observed in an absolute sense (see Fig. 1 for an example that uses real data). This kind of relative comparison uses proper scaling.

However, what if one wants to compare growth rate among several mammalian species with different body sizes? One could again use ratios or percentages, but a more sound, convenient method that is amenable to continuous line fitting and also avoids the confounding effect of including the X variable (body mass) in the Y variable (trait magnitude/body mass) is to use logarithms. As Keene (1995, p. 813) stated: ‘A log-transformation weights observations automatically according to a ratio scale’. Indeed, Napier (1614) coined the word ‘logarithm’ to mean ‘ratio number’ or ‘proportional number’, by using the Greek words ‘logos’ (which can mean ratio or proportion) and ‘arithmos’ (number). Therefore, logarithms specifically allow one to compare relative (proportional) changes in the size of a trait as the size of an organism increases in a continuous way, which is what allometric analyses (see Glossary) are fundamentally about (Huxley, 1932; Kerkhoff and Enquist, 2009; Glazier, 2013), at least in the ‘narrow sense’ originally proposed (Pélabon et al., 2014). In fact, Osborn (1925) originally conceived of the ‘principle of allometry’ as referring to proportional

changes in animal evolution. As Gingerich (2019, p. 48) further states: ‘Allometry is the biological equivalent of geometry in mathematics – each is given a name to distinguish it from simple additive arithmetic’. In essence, log-transformation represents a way of making trait variation (differences) in small systems quantitatively equivalent (and thus comparable) to trait variation in large systems. This simple mathematical method of achieving scale independence is comparable to portraying a mouse and elephant as being the same size by using proportional spatial magnification and/or reduction, thus allowing comparisons of trait variation at the same dimensional scale. As such, log-transformation allows scaled (scale-independent) comparisons of growth (or the magnitude of other traits) between systems of different size, unlike non-scaled (scale-dependent) comparisons based on untransformed arithmetic data (Fig. 1). Properly scaled analyses focus on ‘proportions’, not ‘amounts’ (cf. Gingerich, 2000, 2019; Reich, 2001).

Logarithmic transformation can reveal the mechanisms underlying scaling relationships

Another important advantage of log-transformation is that it allows one to compare relative size-dependent changes in a trait with those predicted by geometric or elasticity models, thus increasing our understanding of the mechanistic causes of scaling relationships. For example, surface area tends to scale with body volume to the $2/3$ power for organisms that are isomorphic (see Glossary). Therefore, it is often reasonable to explain scaling relationships with an exponent $\sim 2/3$ in terms of surface area to volume relationships. In fact, surface area scaling was invoked in the first proposed explanation of the body mass scaling of metabolic rate in homeothermic animals. According to the so-called ‘surface law’, because heat loss is proportional to body surface area, which scales to the $2/3$ power, then maintaining a constant body temperature

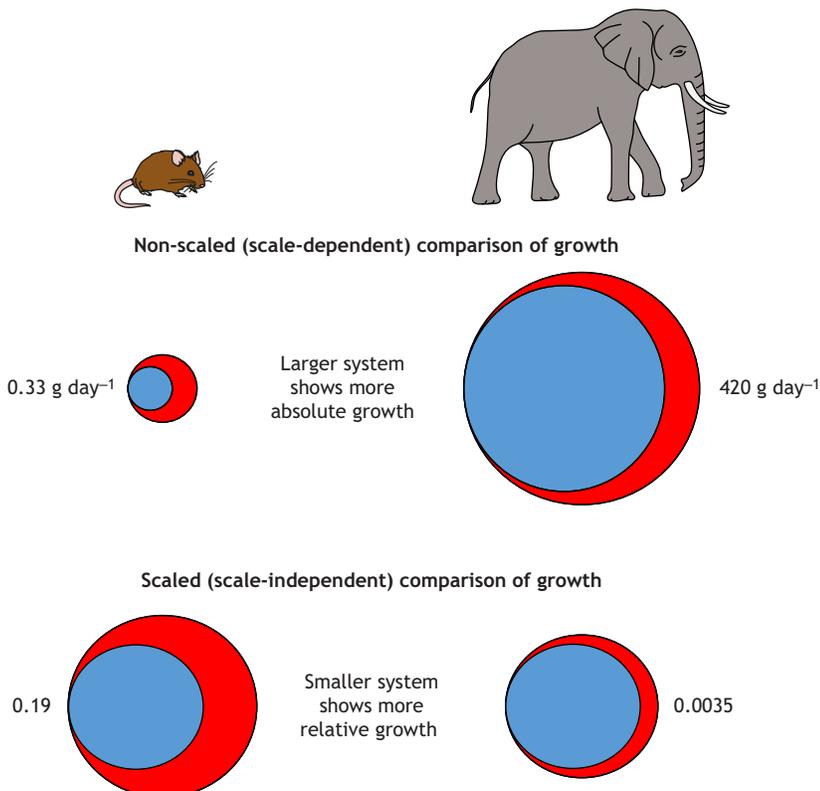


Fig. 1. Schematic depiction of how scaling systems of different size to the same size allows relative (proportional) changes in growth (or other traits) to be readily discerned. Blue areas represent original sizes, whereas red areas represent additional growth in size.

Upper panel, non-scaled comparisons of systems of different size depict differences in absolute growth (or other traits). Lower panel, logarithms allow for scaled comparisons of proportional change. This difference helps to explain why biological (allometric) scaling studies often use log-transformation (see text for other reasons). Numbers refer to actual data for deer mice (*Peromyscus maniculatus*) and female African elephants (*Loxodonta africanus*) taken from Case (1978). Numbers in the upper panel are absolute postnatal growth rates, whereas those in the lower panel are relative growth rates (absolute growth rate divided by birth mass), where the mean birth masses are 1.7 and 120,000 g for the mice and elephants, respectively.

requires that metabolic heat production also scales to the 2/3 power (Sarrus and Rameaux, 1839; Rubner, 1883), as observed in many birds and small mammals (reviewed by Glazier, 2014, 2018a). Other biologists have extended this approach to aquatic skin-breathing animals, where the ontogenetic scaling of metabolic rate relates strongly to the scaling of surface area, which varies with developmental changes in body shape (Hirst et al., 2014; Glazier et al., 2015; Tan et al., 2019). A focus on using non-scaled (scale-dependent) arithmetic data can make it difficult for investigators to see such associations. For example, inspired by critics of the traditional approach, Starostová et al. (2013) improperly tested metabolic scaling theory based on scaled proportional relationships between cell size/number and body mass by using non-scaled (scale-dependent) arithmetic data. Using log-transformed (scale-independent) data would have made a more direct test possible (Glazier, 2013).

Logarithmically transformed data are more biologically relevant

Packard (2012, 2017, 2019) has argued that the traditional method is inapplicable to cases where non-linear scaling occurs in log–log space, even though it has been repeatedly adopted for this purpose by using segmented or polynomial (quadratic) regression techniques (examples cited in Glazier, 2005, 2013; Mascaro et al., 2014). He argues that alternative methods (e.g. non-linear regression) should be used that rely on untransformed arithmetic data. Moreover, he claims that biphasic or other forms of complex logarithmic scaling are a distortion created by the traditional method and that, actually, linear or smooth curvilinear relationships occur when regression methods based on arithmetic data are used (e.g. Packard, 2012, 2017, 2019; Geraert, 2016). For example, by using the traditional method, Tsuboi et al. (2018) showed that brain mass exhibits distinctly biphasic ontogenetic scaling with body mass in many kinds of vertebrate animals. However, Packard (2019) claims that this biphasic scaling is an artifact of log-transformation. Non-linear regression analyses based on untransformed arithmetic data show an approximately continuous curvilinear relationship between brain mass and body mass with no sharp breaks.

However, contrary to Packard's (2019) claims, I argue that his analyses actually validate the traditional method by showing that it is better able to detect biologically significant ontogenetic shifts in size scaling than can alternative methods based on untransformed arithmetic data (see also Glazier, 2013; Tsuboi, 2019). As already noted, regression methods based on arithmetic data do not properly scale systems of varying size. They focus only on absolute, not relative changes in trait sizes (see Fig. 1). Therefore, they are inappropriate for detecting shifts in relative (proportional) scaling relationships that may occur within a species during ontogeny or among species occupying different portions of the body size range of a taxonomic group. By contrast, the traditional method based on log-transformation is well suited for detecting biphasic, curvilinear and other non-linear scaling patterns that represent fundamental breaks or transitions in scale invariance as system size increases. As evidence, ontogenetic scaling shifts in metabolic rate detected by the traditional method often coincide with biologically and/or ecologically significant developmental changes. These discontinuities include shifts from larval to adult life phases, pelagic to benthic lifestyles, prenatal to postnatal development, ectothermy to endothermy, one mode of locomotion to another, and from life inside to outside of a marsupial pouch (e.g. Huxley, 1932; Riisgård, 1998; Glazier, 2005; Glazier et al., 2015; Snelling et al., 2015, 2019; Tsuboi, 2019; Echavarría-Heras et al., 2020).

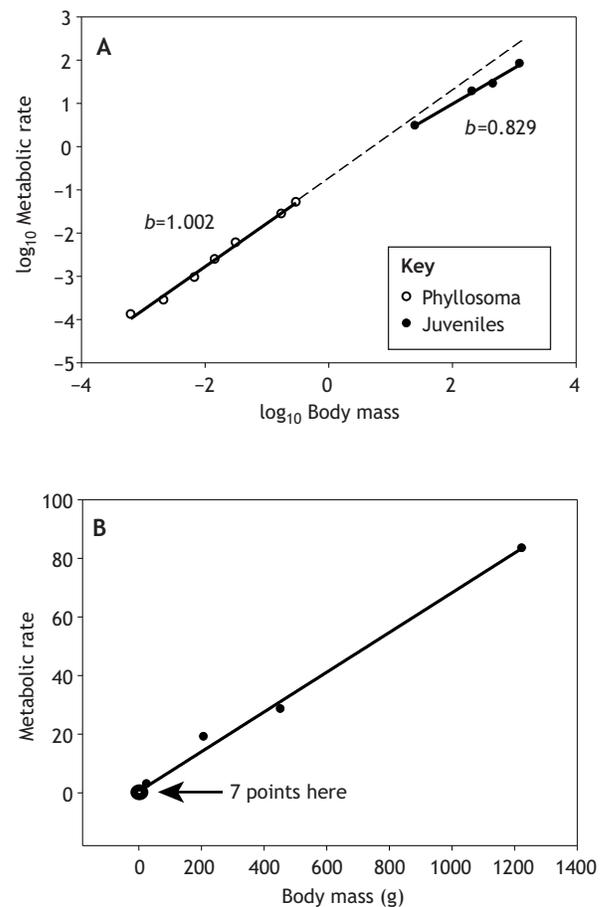


Fig. 2. Comparison of bivariate size relationships using logarithmic versus arithmetic coordinates. (A) Linear relationships between metabolic rate ($\text{mg O}_2 \text{ h}^{-1}$) and wet body mass (g), both \log_{10} -transformed, in phyllosoma larvae and juveniles of the spiny lobster, *Sagmariasus verreauxi* (H. Milne-Edwards 1851) (data from Jensen et al., 2013a,b; Glazier et al., 2015). Each point represents a different size group and is based on 4–11 replicate measurements. Linear regression equations and statistics for phyllosoma and juveniles are, respectively, $Y = -0.773 + 1.002X$, $r^2 = 0.995$, $P < 0.00001$; and $Y = -0.673 + 0.829X$, $r^2 = 0.993$, $P = 0.00353$. The scaling exponents (slopes, b) are significantly different, as the 95% confidence intervals for each ontogenetic stage (± 0.081 and ± 0.157 , respectively) do not overlap the slope of the other (Glazier et al., 2015). This slope difference is also depicted by a linear extrapolation of the phyllosoma relationship, which does not coincide with the juvenile relationship (dashed line). (B) Linear relationship between metabolic rate and body mass using arithmetic coordinates. Linear regression equation and statistics are $Y = 0.468 + 0.068X$, $r^2 = 0.995$, $P < 0.00001$. Comparisons of the relationships in A and B illustrate that logarithmic analyses permit clearer detection of ontogenetic changes in scaling relationships than do arithmetic analyses.

For example, metabolic scaling is isometric (slope ~ 1) in thin, flat phyllosoma larvae of spiny lobsters that grow mainly in two dimensions, whereas it is allometric (slope < 1) in thicker, adult-like juveniles that grow in three dimensions (Fig. 2A), as predicted by surface area theory (Glazier et al., 2015). This biologically significant discontinuity in ontogenetic metabolic scaling (coinciding with a major metamorphic transition: Ventura et al., 2015) goes undetected when a linear regression of the arithmetic data is used (Fig. 2B). Although the arithmetic regression is very tight and highly significant ($r^2 = 0.995$, $P < 0.00001$), using arithmetic coordinates does not allow adequate spacing and scaling of the data, resulting in all of the data points for the

phyllosoma larvae being highly clumped (Fig. 2B). As a result, the data points for the larger juveniles, which are more widely spaced, dominate and thus distort this non-scaled analysis. One could also employ non-linear arithmetic regression analyses on these data, but again, as in the case of the ontogenetic scaling of vertebrate brain mass mentioned above, sharp discontinuities in scaling (i.e. breaks in scaling invariance) would go undetected.

Current evidence supports the view that non-linear biological scaling is not an artifact of log-transformation but rather the result of significant size or age-related changes in various biological properties and (or) ecological influences (see also Mascaró et al., 2014; Tsuboi, 2019). These patterns suggest that not only is the traditional method more appropriate for scaling analyses but also it is more biologically relevant than alternative methods based on simple arithmetic data. Non-linear analyses based on unscaled arithmetic data may be used to show developmental or evolutionary changes in scaling relationships, but they do not readily reveal biologically and theoretically relevant discontinuities in scale invariance shown by proportional, properly scaled, log-transformed data.

Problems with critiques of the traditional method of biological scaling

In my opinion, a narrow focus on statistical line fitting without regard to proper scaling procedures, biological relevance or theoretical significance is not just unproductive but may even be counterproductive to advancing our understanding of biological scaling (also see Kerkhoff and Enquist, 2009; Glazier, 2013; Niklas and Hammond, 2014; Lemaître et al., 2015; Pélabon et al., 2018). I have nothing against the investigation of alternative methods of describing part-whole size relationships, but I do object to studies that propose alternative methods without fairly evaluating their merits and demerits with respect to the traditional method, not only statistically but also conceptually and theoretically. Some recent studies criticizing the traditional approach have one or more of the problems discussed below.

First, they propose alternative methods that do not properly scale systems of different size. Without ensuring scale independence, one cannot compare the magnitude of traits among organisms of different size in a biologically meaningful way (Keene, 1995; Kerkhoff and Enquist, 2009).

Second, they neglect to mention how log-transformation facilitates scaling analyses, not only statistically but also conceptually (especially with regard to ensuring scale independence among the systems compared). Packard (2017) has claimed incorrectly that logarithmic transformation is unnecessary because one can establish proportional relationships by using non-linear regression to calculate power functions from untransformed arithmetic data. Unfortunately, this method does not properly scale the underlying data in geometric (logarithmic) space (see Glossary; Kerkhoff and Enquist, 2009). As a result, power functions derived from arithmetic versus logarithmic data are often quite different (Zar, 1968; Hui and Jackson, 2007; Packard et al., 2011; Xiao et al., 2011; Lai et al., 2013; Starostová et al., 2013; Marchi, 2019; Chen et al., 2020). In my opinion, size-scaling analyses should involve two steps. First, the data should be properly scaled, and log-transformation is an easy, excellent way to do this. Second, a statistical model should be chosen that best fits the data. I see potential problems with skipping the first step and proceeding immediately to the second step. To be sure, non-linear analyses based on arithmetic data may be employed for specific advantageous statistical reasons (including to deal with additive or multiplicative error, by incorporating that error structure in the model used), but the underlying data may still not be properly scaled.

Furthermore, at present, incorporating phylogenetic information into scaling analyses can only be done with linear models, as made possible by log-transformation (e.g. White et al., 2019). Future research is needed to explore whether phylogenetic information can be incorporated into non-linear arithmetic analyses.

Third, critics of the traditional logarithmic approach do not justify their controversial assumption that ordinary arithmetic numbers are inherently more valid than logarithmic numbers, even though they represent the same data. Many scientists, including leaders in biological scaling, regard this assumption as untenable and misguided (e.g. Bagnold, 1941; Gaddum, 1945; McMahon and Bonner, 1983; Peters, 1983; Gingerich, 1993, 2000; Kerkhoff and Enquist, 2009; Glazier, 2013). To quote Bagnold (1941, p. 2): ‘The linear scale, since it was first cut on the wall of an Egyptian temple, has come to be accepted by man almost as if it were the one unique scale with which Nature builds and works. Whereas it is nothing of the sort. Its sole value lies in giving due prominence to the differences and sums of quantities, when these are what we want to display. But Nature if she has any preference, probably takes more interest in the ratios between quantities; she is rarely concerned with size for the sake of size’ (also see McMahon and Bonner, 1983; Gingerich, 1993, 2000).

Indeed, one could argue that logarithmic thinking is more intuitive than arithmetic thinking, because animals and young children think in terms of proportions and not absolute amounts (e.g. Roberts, 2006; Beran et al., 2008; Dehaene, 2009; Yi, 2009; Opfer and Siegler, 2012; Ditz and Nieder, 2016; Kim, 2019). They have a ‘logarithmic sense of approximate numerosity’ (Dehaene, 2009, p. 254), i.e. they assess quantities using a non-linearly compressed logarithmic number scale (Fig. 3). Only later in life do children adopt linear arithmetic thinking, which appears to be culturally imposed by mathematical education (Siegler and Booth, 2004; Merten and Nieder, 2009; Berteletti et al., 2010). Furthermore, people of all ages in some cultures (e.g. Amazonian indigenes) estimate quantities as logarithmic proportions, not as linear amounts (Dehaene et al., 2008; Dehaene, 2011). McMahon and Bonner (1983, p. 30) point out how we naturally perceive our environment in logarithmic ways: ‘when we hold something small up close to our eyes and when we step back to get a whole view of something big. Similarly, our ears are more sensitive to small variations in faint sounds than to small variations in large sounds’. Neuronal activity related to number detection is optimally tuned to operate on a logarithmic scale (Nieder, 2016, 2020), and human memories and time perception appear to be encoded logarithmically as well (Singh et al., 2018; Ren et al., 2020). In other words, the human mind uses an ‘internal slide rule’ (Dehaene, 2003, p. 147; see Glossary). Logarithmic thinking may reduce the risk of perceptual error, and thereby increase evolutionary fitness, as favored by natural selection (Sun et al., 2012). Minimizing relative error may be more important than minimizing absolute error, and neuronal systems tuned to a logarithmic scale do this better than those tuned to an arithmetic scale. For example, ‘being off by four matters much more if the question is whether there are one or five hungry lions in the tall grass around you than if the question is whether there are 96 or 100 antelope in the herd you’ve just spotted’ (Hardesty, 2012). Therefore, one cannot regard arithmetic measures as more fundamental than logarithmic measures. Indeed, logarithmic quantification appears to be more innate in humans and animals than is arithmetic quantification, which is a cultural contrivance.

Unfortunately, however, a belief in the primacy of arithmetic numbers or additive models (implicit or explicit) has engendered the

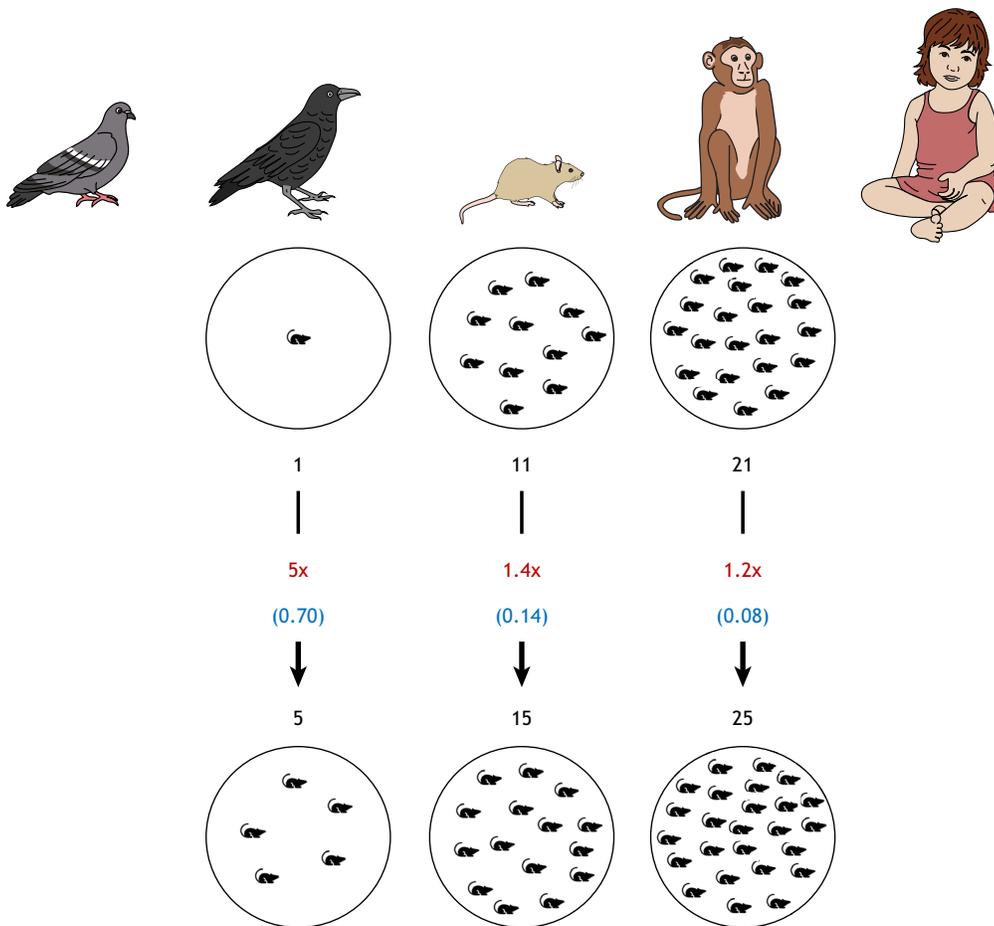


Fig. 3. Birds and mammals have an innate tendency to assess quantity logarithmically, not arithmetically.

The species for which this is shown are pigeons, crows, rats, rhesus monkeys and human children. The depicted self-test shows that mental discrimination of numerical differences depends on the total quantity of points (numerosity). Although the numerical difference is 4 between the top and bottom groups of mice for each vertical pair, this difference is not as readily apparent for groups with larger numbers of mice. Our innate ability to quickly understand amounts is tuned more to ratios or proportions (e.g. 5, 1.4 and 1.2, respectively, for the ratios of number of mice in the bottom group over those in the top group) or equivalent logarithmic differences (0.70, 0.14 and 0.08, respectively) than to absolute amounts.

unjustified view that if back-transformation from logarithmic numbers predicted by traditional (multiplicative) models does not exactly match predictions by arithmetic models, the traditional models must be incorrect. These differences obviously occur because the traditional approach uses scale-independent logarithmic data, thus automatically correcting for multiplicative error, whereas arithmetic models use scale-dependent data that do not (though non-linear arithmetic models may incorporate multiplicative error). As a result, back-transformation from traditional models yields geometric means for Y , whereas arithmetic models predict arithmetic means. This is useful, because geometric means are actually more appropriate than arithmetic means when multiplicative error occurs (Galton, 1879; Gaddum, 1945; Gingerich, 2000; contra Hayes and Scott Shonkwiler, 2006; Packard, 2013), as is typical in scaling relationships (Kerkhoff and Enquist, 2009; Xiao et al., 2011; Niklas and Hammond, 2014; Gingerich, 2019). When measurement and (or) biological error is additive, investigators may wish to use arithmetic data for their scaling analyses (e.g. Xiao et al., 2011; Pélabon et al., 2018), but the benefits of doing so should be weighed against whether this results in the absence of a biologically and theoretically meaningful scaling perspective, otherwise obtained in log-based geometric space.

Given a belief in the primacy of arithmetic numbers, it is also not surprising that some critics assume that practitioners of the traditional method routinely use back-transformed data to derive scaling exponents in the 'original arithmetic' coordinates (e.g. Packard, 2020b). However, this assumption is untrue. One can easily derive scaling exponents (slopes) directly from logarithmic

analyses. In practice, the primary equation that most investigators use to carry out scaling analyses is the relationship between $\log Y$ and $\log X$, not the power function of Y in relation to X (see Gingerich, 2000; contra Packard, 2017). Furthermore, generally adopting the unjustified assumption that arithmetic numbers are superior to logarithms would undermine valuable scientific analyses of many kinds of natural phenomena. These include the quantification of entropy, information content, radioactive decay, voltage amplitudes, sound, sensation–stimulus relationships (Weber–Fechner law; see Glossary), brightness of starlight, magnitude of earthquakes (Richter scale), chemical acidity, relative rates of growth and evolution, relative measures of species abundance, life-table survivorship curves, population growth and economic price elasticity relationships, and many more (also see Burton, 1998; Menge et al., 2018). One cannot regard arithmetic numbers as inherently more foundational than logarithmic numbers, even for measurement units (e.g. consider that decibels, nepers, nats, octaves and pH units are on a log scale) (also see Gaddum, 1945). Their validity depends on the scientific purpose for which they are used (e.g. comparing proportions versus amounts). If one is interested in scaling systems of different size, logarithms are more useful than arithmetic numbers.

Fourth, some critiques misrepresent the motivations and acumen of those who use the traditional scaling method. For example, many investigators (e.g. McMahon and Bonner, 1983; Peters, 1983; Kerkhoff and Enquist, 2009; Cawley and Janacek, 2010; Xiao et al., 2011; Glazier, 2013; Mascaró et al., 2014; Niklas and Hammond, 2014; White and Kearney, 2014; Lemaître et al., 2015; Pélabon

et al., 2018) have not used the traditional method ‘uncritically’ or by ‘rote’, as claimed by some (e.g. Smith, 1980; Lovett and Felder, 1989; Packard, 2013, 2017, 2020a,b). Packard (2017, p. 116) also states without evidence or adequate justification that proponents of the traditional method have used ‘ill-defined arguments’ and ‘misunderstanding of various statistical methods’, merely to protect ‘a large body of published research’.

Fifth, some critiques are based on intraspecific analyses involving relatively narrow body mass ranges (often less than one order of magnitude) that result in large errors in regression parameters (e.g. Smith, 1980; Packard, 2020a,b). These large errors weaken the argument made in these studies that alternative methods based on arithmetic data provide line fits just as good as (or better than) those based on traditional logarithmic analyses. The scaling value of logarithmic transformations increases as the range of sizes considered increases (see also Harvey, 1982).

Sixth, several critiques neglect to cite or fairly evaluate studies criticizing approaches based on untransformed arithmetic data (e.g. Harvey, 1982; Keene, 1995; Kerkhoff and Enquist, 2009; Cawley and Janacek, 2010; Xiao et al., 2011; Glazier, 2013; Lai et al., 2013; Mascaro et al., 2014; Lemaître et al., 2015; Pélabon et al., 2018; Tsuboi, 2019; but see limited attempts made by Packard, 2014, 2017).

Seventh, no recent critiques offer useful, generally applicable theoretical framework(s) supporting or emanating from their idiosyncratic use of alternative methods. In addition, some alternative arithmetic models that have been proposed include parameters with no obvious biological meaning (e.g. Lemaître et al., 2015; Tsuboi, 2019). Without appropriate biological meaning and theoretical frameworks, the arbitrary adoption of alternative methods will result in scientific chaos, and undermine the development of theory in the field of biological scaling. The choice of scaling models should depend on theoretical context and biological relevancy, and not just on statistics (Houle et al., 2011; Tsuboi, 2019). One example of how non-linear analyses based on arithmetic data may be biologically relevant includes the use of a three-parameter power function where the data are not expected to pass through the origin, as for blood pressure in relation to body mass (White and Seymour, 2014, 2015).

Perspectives and conclusions

Many recent studies criticizing the traditional approach to performing scaling analyses have engaged in a largely one-way conversation, whereby specific alternative methods are advocated over the traditional method without adequate justification or attention to valid counterarguments. We shall not have a useful debate about which mathematical methods are best for quantifying scaling relationships until there is a more balanced two-way conversation between critics of the traditional approach and the majority of biologists who routinely use log-transformation in their scaling analyses. This has become an important problem in and of itself, because many kinds of biological journals have published and are continuing to publish one-sided critiques of the traditional method that convey essentially the same negative message, but based on analyses of different published datasets. In the process, these biased critiques have impugned many legitimate studies incorrectly. Interested readers and especially editors and reviewers of biological journals should be aware of this problem.

In conclusion, recent critics of the traditional scaling approach fail to appreciate fully the multiple ‘worthwhile properties’ of logarithms and their critical role in scaling analyses. The ongoing discussion by critics and proponents of the traditional method has

resulted in both positive and negative outcomes. On the one hand, the critiques have prompted practitioners in the field of biological scaling, including myself, to clarify the rationale underlying the methods that they use. On the other hand, the critiques have created some unnecessary confusion about proper methodology, especially for newcomers and others not well versed in scaling analyses. Statistical line-fitting analyses that do not use logarithms or other measures of relative size are not true scaling analyses because they do not allow meaningful scale-independent comparisons among systems of different size. Non-scaled (scale-dependent) methods based on untransformed arithmetic data can produce idiosyncratic results that are not biologically meaningful. The authors who promote these methods should show why they are biologically and theoretically useful, and not merely in a descriptive statistical sense. The scientific significance of a method is just as important, if not more so, than its mathematical significance. As noted by a leader in biological scaling, ‘Highly significant statistics do not signify equally high biological significance’ (Schmidt-Nielsen, 1984, p. 22). By recognizing this, we can then have a more meaningful debate than simply which line fit is best.

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Competing interests

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