

Improved approximations to scaling relationships for species, populations, and ecosystems across latitudinal and elevational gradients

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Abstract

Historically, allometric equations relate organismal traits, such as metabolic rate, individual growth rate, and lifespan, to body mass. Similarly, Boltzmann or Q_{10} factors are used to relate many organismal traits to body temperature. Allometric equations and Boltzmann factors are being applied increasingly to higher levels of biological organization in an attempt to describe aggregate properties of populations and ecosystems. They have been used previously for studies that analyse scaling relationships between populations and across latitudinal gradients. For these kinds of applications, it is crucial to be aware of the “fallacy of the averages”, and it is often problematic or incorrect to simply substitute the average body mass or temperature for an entire population or ecosystem into allometric equations. We derive improved approximations to allometric equations and Boltzmann factors in terms of the central moments of body size and temperature, and we provide tests for the accuracy of these approximations. This framework is necessary for interpreting the predictions of scaling theories for large-scale systems and grants insight into which characteristics of a given distribution are important. These approximations and tests are applied to data for body size for several taxonomic groups, including groups with multiple species, and to data for temperature at locations of varying latitude, corresponding to ectothermic body temperatures. Based on these results, the accuracy and utility of these approximations as applied to biological systems are assessed. We conclude that approximations to allometric equations at the species level are extremely accurate. However, for systems with a large range in body size, evaluating the skewness and kurtosis is often necessary, so it may be advantageous to calculate the exact form for the averaged scaling relationships instead. Moreover, the improved approximation for the Boltzmann factor, which uses the average and standard deviation of temperature, is quite accurate and represents a significant improvement over previous approximations.

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1. Introduction

There is a rich history of research on allometric scaling relationships for the biological rates and times of individuals (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984), and there has been a resurgence of interest in the last few years (West et al., 1997, 1999, 2001; Banavar et al., 1999, 2002; Dodds et al., 2001; Gillooly et al., 2001, 2002; White and Seymour, 2003). Recent work has begun to extend these scaling relationships for

individuals to ones describing entire populations and ecosystems (Peters, 1983; West et al., 2001; Enquist and Niklas, 2001, 2002; Allen et al., 2002; Brown et al., 2003; Savage et al., 2004b). Savage et al. (2004b) develop a framework for predicting the mass and temperature dependence for life history parameters such as the intrinsic rate of increase and mortality rates for populations. This gives a deeper understanding of the pace of life for different populations within the same ecosystem and is relevant to concerns regarding the introduction of new species into an ecosystem. Such efforts have the eventual goal of quantifying how energy and nutrients flux through entire ecosystems. The accomplishment of this goal should aid in addressing

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questions regarding carbon sequestration, species diversity (Allen et al., 2002), and the ability of species to respond to anthropogenic changes. The work of Allen et al. (2002) provides an energetic explanation, linked to metabolic rates, for latitudinal differences in species diversity. In that study the average body temperature for ectotherms was taken to be the average temperature at various latitudes. These average temperatures were then substituted into Boltzmann factors to calculate average metabolic rates at those latitudes. It is just such approximations that the present paper addresses. Additionally, many important studies on the effects of the rapid climate changes associated with global warming and the ability of species to respond have focused on single species (e.g. Visser et al., 1998; Visser and Holleman, 2001). Combining scaling relationships with the work of Norberg et al. (2001) may provide a more comprehensive framework for studying such problems; preliminary results are encouraging. Since studying the effects on every species is not practical, more general approaches are greatly needed.

The most fundamental allometric equation expresses an individual's metabolic rate, B , in terms of its body size, M , and temperature, T ,

$$B \propto M^a e^{-E/kT}, \quad (1)$$

where M is the body mass, a is the allometric scaling exponent, T is the body temperature, E is an activation energy associated with biochemical reactions used for metabolism, and $k = 8.62 \times 10^{-5}$ eV/K is Boltzmann's constant. It is widely accepted that $a = \frac{3}{4}$ (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; West et al., 1997), although some contend either that $a = \frac{2}{3}$ (White and Seymour, 2003) or that $a = \frac{2}{3}$ is statistically more favored than $a = \frac{3}{4}$ (Dodds et al., 2001). There is a forthcoming paper (Savage et al., 2004b) that argues that the majority of data support a value of $a = \frac{3}{4}$ and that addresses the concerns of White and Seymour (2003) and Dodds et al. (2001). Eq. (1), with $a = \frac{3}{4}$, has been shown to hold for unicells, amphibians, reptiles, fishes, mammals, and plants (Gillooly et al., 2001). The power per unit mass is obtained after dividing by M

$$\bar{B} = \frac{B}{M} \propto M^{a-1} e^{-E/kT}. \quad (2)$$

Since this is a characteristic rate, it has been argued that all characteristic biological rates will scale in this way (Gillooly et al., 2002). When $a - 1 = -\frac{1}{4}$, many biological rates for individuals, including heart rates (West et al., 1997), ontogenetic growth rates (West et al., 2001), and feeding rates (Peters, 1983) have been shown to exhibit this mass dependence, and in some cases it has been shown that they also exhibit this temperature dependence. The inverse of Eq. (2) can be interpreted as a biological time

$$t_B \propto M^{1-a} e^{E/kT}. \quad (3)$$

When $1 - a = \frac{1}{4}$, it has been shown that biological times for individuals, including lifespans (Gillooly et al., 2001) and times to first reproduction (Gillooly et al., 2002), follow this scaling relationship.

In applying Eqs. (2) and (3) to biological systems, average values for mass, $\langle M \rangle$, and temperature, $\langle T \rangle$, are often used in place of M and T . For endotherms $\langle T \rangle$ is roughly constant, but for ectotherms $\langle T \rangle$ is dictated by the environmental temperature. Note that throughout this paper $\langle y \rangle_p$ denotes the average value of the variable y over some distribution p , and $\langle y \rangle$ denotes the average value of the variable y with respect to an arbitrary distribution. For example, when comparing across species, the average value of mass for a given species, $\langle M \rangle_{\text{species}}$, is frequently used in place of M (Savage et al., 2004a). Moreover, in applying Eqs. (2) and (3) to population growth rates (Savage et al., 2004a) and patterns of biodiversity (Allen et al., 2002), the average value of T over an entire year, $\langle T \rangle_{\text{year}}$, is often calculated and substituted for T . Characterizing biological rates and times for entire ecosystems is an eventual goal, and the natural and most easily estimated parameters are $\langle M \rangle_{\text{eco}}$ and $\langle T \rangle_{\text{eco}}$. (For a discussion of the use of total biomass versus average biomass when studying self-thinning relationships in mono-specific stands, see Petraitis, 1995.)

An exact calculation of the average biological rate or time for some distribution is the average over the functions, rather than the parameters. The problem of simply substituting in the average of the parameters is known as the "fallacy of averages" (Wagner, 1969). Medel et al. (1995) discuss problems with the "fallacy of averages" in relation to the allometry of energy use in ecosystems and demonstrate that substituting in the average of the parameters often leads to spurious results. It has recently come to the attention of this author that similar debates over the analysis of aggregate data are present in the literature of statistics and epidemiology. In particular, Greenland and Robins (1994) discuss problems with individual- versus ecologic-level analyses. They construct several epidemiological examples that convincingly show that data at the ecologic level can be misinterpreted if nonlinear effects at the individual level and other confounds are not accounted for. Richardson and Guihennuec-Jouyaux (1996) derive a second-order approximation to exponential dependencies at the individual level that gives satisfactory results for the examples constructed by Greenland and Robins (1994). In the limit of small variance, it can be shown that their approximation for an exponential is tantamount to that obtained by retaining the first two terms in Eq. (10) of the present paper. Furthermore, Guthrie and Sheppard (2001) derive a more general method for dealing with confounds and nonlinear effects that may be useful for more complicated distributions. However, their method

can be technically challenging and requires numerical simulations. The methods in this paper provide more easily calculable and sufficiently accurate approximations for the mass and temperature distributions of many biological systems.

For metabolic rate the average of the functions is explicitly given by

$$\langle B \rangle = \langle M^a e^{-E/kT} \rangle = \langle M^a \rangle \langle e^{-E/kT} \rangle = \left(\frac{1}{N_1} \sum_{i=0}^{N_1} M_i^a \right) \left(\frac{1}{N_2} \sum_{j=0}^{N_2} e^{-E/kT_j} \right), \tag{4}$$

where N_1 and N_2 are the number of data points for M and T respectively, and we assume that M and T are uncorrelated. Eq. (4) does not equal $\langle M \rangle^a e^{-E/k\langle T \rangle}$ unless all higher-order moments are zero. However, when the variance and other higher-order moments are small, this is a good approximation. In this paper, we answer the questions of whether

$$\langle M^\gamma \rangle \sim \langle M \rangle^\gamma \tag{5}$$

for any power γ and whether

$$\langle e^{-E/kT} \rangle \sim e^{-E/k\langle T \rangle} \tag{6}$$

are accurate approximations. We also derive corrections to these two equations that often allow us to make very accurate approximations to Eq. (4). Further, we specify under what conditions Eqs. (5) and (6) are accurate approximations and thus, provide tests for their accuracy. By adding just one more term to Eq. (6), we obtain an approximation that is excellent for almost any geographic location. Through these findings we make explicit the connection between Eq. (4) and Eqs. (5) and (6). This allows us to express all calculations in terms of the average of the physically measurable variables.

In Section 2 we develop the necessary theory for tests and approximations. In Section 3 we apply the theory to relevant biological examples involving body size and temperature, and in Section 4 we study the combination of these two effects. We conclude in Section 5 by reviewing these results and discussing how they can be implemented in future work.

2. Theory

In this section we take an arbitrary, analytic function, $f(x)$, and Taylor expand it around the average value of its argument, $\langle x \rangle$. After taking the average of $f(x)$ with respect to an arbitrary distribution, we obtain a moment expansion for $\langle f(x) \rangle$. We then show that this moment expansion can be used to provide approximations to $\langle f(x) \rangle$. These approximations are obtained by truncating the expansion after some finite number of terms. Therefore, calculating the magnitude of the neglected terms relative to that of the terms used in the

approximation tests the validity of the approximation. Since each term is directly related to a central moment, there is a geometric interpretation for each approximation scheme. Usually, calculating only the magnitude of the lowest-order term that has been neglected relative to that of the terms used in the approximation is a sufficient test, but there exist distributions for which this is not true. We study this further in the next section by analysing mass and temperature data for several biological systems.

Given a function $f(x)$ and N values of x , $\{x_i\}$, the average value of f is calculated by

$$\langle f(x) \rangle = \frac{\sum_{i=0}^N f(x_i)}{N}. \tag{7}$$

As long as $f(x)$ is an analytic function, a condition satisfied by all functions discussed thus far and to this author’s knowledge, all functions discussed in the literature on allometry, it can be Taylor expanded around $\langle x \rangle$

$$f(x_i) = \sum_{j=0}^{\infty} \left. \frac{d^j f(x_i)}{dx^j} \right|_{x=\langle x \rangle} \frac{(x_i - \langle x \rangle)^j}{j!} \equiv \sum_{j=0}^{\infty} f^{(j)}(\langle x \rangle) \frac{e_i^j}{j!}, \tag{8}$$

where $e_i = x_i - \langle x \rangle$ are the residuals of the data around the average. Substituting Eq. (8) into Eq. (7), interchanging the order of summation, expanding out the first three terms, and factoring constants from sums, we have

$$\langle f(x) \rangle = \frac{1}{N} (f(\langle x \rangle) \sum_{i=0}^N 1 + f^{(1)}(\langle x \rangle) \sum_{i=0}^N e_i + \frac{1}{2} f^{(2)}(\langle x \rangle) \sum_{i=0}^N e_i^2 + \sum_{j=3}^{\infty} \frac{1}{j!} f^{(j)}(\langle x \rangle) \sum_{i=0}^N e_i^j). \tag{9}$$

By definition $\sum_{i=0}^N e_i = 0$ and $\sigma^2 = \sum_{i=0}^N e_i^2 / N$, where σ is the standard deviation in x . In general, $M_j = \sum_{i=0}^N e_i^j / N$ is the j th central moment. Therefore, Eq. (9) can be further simplified to give the moment expansion

$$\langle f(x) \rangle = f(\langle x \rangle) + \frac{1}{2} f^{(2)}(\langle x \rangle) \sigma^2 + \sum_{j=3}^{\infty} \frac{M_j}{j!} f^{(j)}(\langle x \rangle). \tag{10}$$

Note that M_3 is a measure of the skewness of the distribution (how symmetrical it is), and M_4 is a measure of the kurtosis (how rapidly the distribution decays away from its peak). Eq. (10) is an exact expression for $\langle f(x) \rangle$. If the terms in the series decrease in magnitude as a function of j , then by keeping only the

first few terms we have a good approximation to $\langle f(x) \rangle$. Often, just the first term provides a good approximation. As we will show, however, there are cases, especially across latitudinal gradients and for populations and ecosystems, where the second term and sometimes even the third and fourth terms are needed in order to provide a good approximation to $\langle f(x) \rangle$.

Consequently, Eqs. (5) and (6), which are equivalent to

$$\langle f(x) \rangle \sim f(\langle x \rangle) \tag{11}$$

are good approximations if all terms beyond the first in Eq. (10) are small in comparison to $f(\langle x \rangle)$. Hence, a simple test for the accuracy of this approximation is

$$\frac{1}{2}|f^{(2)}(\langle x \rangle)|\sigma^2 \ll |f(\langle x \rangle)|. \tag{12}$$

If Eq. (12) is violated, then Eq. (11) is an invalid approximation. If Eq. (12) holds, then Eq. (11) will usually be a good approximation. There are examples of distributions, however, where this is not true. One example of a distribution where application of just Eq. (12) will lead to incorrect conclusions is when derivatives of $f(x)$ have zeros at the average value of x . Consequently, it could happen that $f^{(2)}(\langle x \rangle) = 0$ but there exists a large, non-zero $f^{(n)}(\langle x \rangle)$ for $n > 2$. In this case, the first non-zero term in $\sum_{j=3}^{\infty} (1/j!)f^{(j)}(\langle x \rangle) \sum_{i=0}^N e_i^j/N$ should be calculated and compared with $f(\langle x \rangle)$. For example, if $f(x) = \sin(x) + 1$ and $\langle x \rangle = 0$, $\sum_{i=0}^N e_i^3/6N$ must be compared with 1.

One can also interpret the validity of this approximation in terms of the size and shape of the distribution. Since the second-order term in Eq. (10) corresponds to the second central moment of the distribution, i.e., the standard deviation, the approximation is good when the width of the distribution is narrow, where narrow is defined by Eq. (12). Similarly, the third-order term, M_3 , is negligible when the skewness is small and the distribution is highly symmetrical. Finally, the fourth-order term, M_4 , is negligible when the kurtosis is small, and the distribution has a slow decay, similar to that of a Gaussian. These arguments correspond to the statements and mathematical equations given above but provide a more geometric, intuitive interpretation of the equations that can be used to guide the approximation scheme.

We can also define a function $g(x) = \langle x \rangle^2 f^{(2)}(x)/f(x)$, so that the condition in Eq. (12) becomes

$$\frac{1}{2}r^2|g(\langle x \rangle)| \ll 1, \tag{13}$$

where $r \equiv \sigma/\langle x \rangle$ is the relative standard deviation. Using $g(x)$ to re-express the first two terms on the right side of Eq. (10), we have

$$\langle f(x) \rangle \sim f(\langle x \rangle)(1 + \frac{1}{2}r^2g(\langle x \rangle)). \tag{14}$$

Expressions similar to Eqs. (12) and (13) can be derived to test the validity of keeping the first two terms in Eq. (10), and in fact, for keeping j terms. For individual rates and times, it is rare that terms beyond the second order (standard deviation) need to be kept, as we will show, but when applying allometric equations to entire ecosystems, the third and fourth terms are often necessary.

In the above, it is assumed that either N data points for x or just estimates of an average and a variance that are supposed to represent a continuous function $f(x)$ are available. For example, body temperature has a value at every time during the year, but it is only measured and taken as data at certain intervals. If the data poorly represent the distribution, then the above analysis is incorrect, but that will be true of any analysis that is performed on that data. To understand how the above formulation works for analytic functions and probability distributions over some continuous interval, we realize that in this limit Eq. (7) becomes

$$\langle f(x) \rangle = \int f(x)p(x) dx, \tag{15}$$

where $p(x)$ is the probability distribution of x . Employing the Taylor expansion in Eq. (8), noting that $\sigma^2 = \langle x^2 \rangle - \langle x \rangle^2$, and identifying the central moments of the distribution as $M_j = \int (x - \langle x \rangle)^j p(x) dx$, we are again led to Eq. (10). Therefore, Eqs. (11)–(14) are the same as before and are the general expressions.

3. Examples for average body size (species and other taxonomic groups) and temperature (latitudinal gradients)

We now apply these equations to allometric scaling relationships using existing data for species and other taxonomic groups, as well as data for temperature at locations of varying latitude.

We begin with Eq. (5). For the function M^γ , we have $f^{(2)}(\langle M \rangle) = \gamma(\gamma - 1)\langle M \rangle^{\gamma-2}$ and therefore, $g(\langle M \rangle) = \gamma(\gamma - 1)$, so Eq. (13) reduces to the condition

$$|F_1(r_M, \gamma)| \equiv \left| \frac{\gamma(\gamma - 1)}{2} r_M^2 \right| \ll 1. \tag{16}$$

To disentangle the effects of mass and temperature, we evaluate this equation using data for endotherms. If we consider the average value of M for each species, $\langle M \rangle_s$, then r_M appears to be roughly constant across species of mammals (private communication with Morgan Ernest). Plotting $\ln \sigma$ versus $\ln \langle M \rangle$ for 53 species of mammals, ranging in size from 1 to 160 g, gives a slope of 0.996 ($r^2 = 0.90$). The average value for r_M is approximately 0.23. This gives values of $F_1(0.23, -\frac{1}{4}) = 0.0083$ and $F_1(0.23, \frac{3}{4}) = F_1(0.23, \frac{1}{4}) = -0.0050$. For third-power scaling $F_1(0.23, -\frac{1}{3}) = 0.0118$

and $F_1(0.23, \frac{2}{3}) = F_1(0.23, \frac{1}{3}) = -0.0059$. Correcting for these miniscule effects does not help resolve the debate of quarter- versus- third-power scaling because there are other, larger sources of error. Moreover, studies that attempt to address these issues mostly use data for which the metabolic rate and body size were measured for a single individual from each species (Dodds et al., 2001; White and Seymour, 2003). Thus, there is no averaging effect, and the equations in this paper are not applicable.

Given these results we conclude that the approximation in Eq. (5) is excellent for biologically relevant choices of γ . In Table 1 we show the relevant parameters for the approximation for three mammals of different sizes. In every case, the approximation is extremely accurate. Another way to state this is that Eq. (5) is a good approximation when $|F_1(0.23, \gamma)| = |0.0529\gamma(\gamma - 1)/2| \ll 1$. Using this equation, we find γ must equal -3.877 or 4.877 before $|F_1(0.23, \gamma)| > 0.5$.

When averaging M over an ecosystem, $\langle M \rangle_{eco}$, or some taxonomic grouping with a large range in mass, the values of σ_M and r_M are substantially larger.

Requiring $|F_1(r_M, \gamma)| \leq 0.5$ for the biologically relevant value of $\gamma = -\frac{1}{4}$ gives a maximum value of $r_M = \pm 1.79$ and for $\gamma = \frac{3}{4}$ or $\frac{1}{4}$ gives ± 2.31 . We can simplify calculations for groups with multiple species by considering each species to have an average mass, M_i , and a population size of N_i individuals. This allows the averages and standard deviations to be expressed as

$$\langle M \rangle_{ECO} = \frac{\sum_{i=0}^{N_S} N_i M_i^\gamma}{\sum_{i=0}^{N_S} N_i} \tag{17}$$

and

$$\sigma = \sqrt{\frac{\sum_{i=0}^{N_S} N_i (\langle M \rangle_{ECO} - M_i)^2}{\sum_{i=0}^{N_S} N_i}}, \tag{18}$$

where the sum is over all species and N_S is the total number of species. Consequently, if there is a function that relates N_i to M_i , the calculation and the number of free parameters are reduced even further.

We consider two types of distributions. First, we consider the case $N_i = N$, where N is some constant, independent of mass, e.g., there are as many elephants

Table 1

Values of the average mass, $\langle M \rangle$, standard deviation of the mass, σ_M , relative standard deviation of the mass, r_M , and the second-order correction terms, $F_1(r_M, -\frac{1}{4})$, $F_1(r_M, \frac{1}{4})$, $F_1(r_M, \frac{3}{4})$ for the scaling exponents $-\frac{1}{4}$, $\frac{1}{4}$, and $\frac{3}{4}$ respectively, computed for three mammals

Mammal	$\langle M \rangle$ (kg)	σ_M (kg)	r_M	$F_1(r_M, -\frac{1}{4})$	$F_1(r_M, \frac{1}{4}); F_1(r_M, \frac{3}{4})$
American shrew mole	0.011	0.003	0.29	0.0131	-0.0078
Western lowland gorilla	205	70	0.34	0.0182	-0.0109
African elephant	4800	1200	0.25	0.0098	-0.0059

We chose three mammals of very different sizes to demonstrate that r_M is roughly constant, independent of body size. The standard deviation was taken as half the difference between the maximum mass and the minimum mass of the range of masses for these mammals as reported in Animal Diversity Web, University of Michigan. This is an overestimate of the standard deviation, and this is why the r_M values are all greater than the value of 0.23 given in the text. Hence, neglecting the first-order correction terms are even better approximations than the results of this table suggest. Note that the values for the first-order correction terms in columns 5 and 6 are much less than 1, confirming Eq. (16). That is, for these mammals, including the first-order correction term will have at most a 1.09% effect on the first-order approximation calculated by substituting $\langle M \rangle$ into an allometric relationship with an exponent of $\frac{3}{4}$ and that effect is negligible.

Table 2

Values of the average mass, $\langle M \rangle$, standard deviation of the mass, σ_M , relative standard deviation of the mass, r_M , and the second-order correction term, $F_1(r_M, \frac{3}{4})$, for a scaling exponent of $\frac{3}{4}$ computed for six different groupings of organisms, assuming that all species have an equal number of individuals

Group	$\langle M \rangle$ (kg)	σ_M (kg)	r_M	$F_1(r_M, \frac{3}{4})$
Birds of the Boreal Forest	0.307	0.675	2.199	-0.453
Mammals of the Boreal Forest	27.081	84.637	3.115	-0.910
Birds of the Boreal Prairie	0.405	0.696	1.716	-0.276
Mammals of the Boreal Prairie	28.163	89.045	3.162	-0.937
Pelagic Birds of Northwest North America	1.007	1.063	1.056	-0.099
Antelopes of the African Savanna	145.786	211.206	1.449	-0.197

The data for each group are taken from Holling (1992) and include an average mass for each species but not a standard deviation of the mass for each species. Thus, this is a slight underestimate of the standard deviation for each group as a whole. Note that the values in column 5 are often not significantly less than 1, thus violating Eq. (16). For these examples, including the first-order correction term will have between a 9.9% and a 93.7% effect on the first-order approximation calculated by substituting $\langle M \rangle$ into an allometric relationship with an exponent of $\frac{3}{4}$, and that is not negligible.

as mice. This allows the simplest possible calculations, but it is not biologically realistic for groups with a large range in mass. In Table 2 we apply our formulae to six groups, using data compiled by Holling (1992). These tables show that Eq. (5) is usually not a good approximation when applied to taxonomic groupings that have a large mass range. Since the number of organisms in a population for each species is unlikely to be constant, we can easily modify the above calculations to account for different biomass distributions. As a second case, we consider the energetic-equivalence rule of Damuth (1987), which maintains that $N_i = N_0 M_i^{-3/4}$. Therefore, the number of individuals of a given species decreases with the average size of that species. In Table 3 we again apply our formulae to the data from Holling (1992). Comparing Tables 2 and 3, we find that the values of the quantities depend greatly on the functional form of N_i . Moreover, the corrections are often vastly more important for the energetic-equivalence case than the case where all populations have equal numbers, and thus, using only $\langle M \rangle^{3/4}$ is indeed a very poor approximation to the exact expression. Since the energetic-equivalence case is more biologically realistic, this is especially notable. Apart from cases where a few species of similar body size, and thus, similar values of

M_i , dominate the community, Eq. (5) is always a poor approximation for communities of multiple species.

Returning to the case $N_i = N$, we now include the second-order correction

$$\langle M^{\gamma} \rangle \sim \langle M \rangle^{\gamma} (1 + F_1(r_M, \gamma)) \equiv F_2(\langle M \rangle, r_M, \gamma). \quad (19)$$

The results are given in Table 4, and except for pelagic birds of northwest North America and antelopes of the African Savanna, they are not very accurate approximations to the exact calculation. If we use higher-order terms in Eq. (10), we could obtain more accurate approximations. This is because M_3 , corresponding to the skewness (symmetricality), and M_4 , corresponding to the kurtosis (measure of decay rate), are large in this case (see Fig. 1). Note that for the data used in Table 4, including the second-order term actually exacerbates the approximation for mammals of the boreal forest and mammals of the boreal prairie. Furthermore, for the case of energetic equivalence, the results corresponding to those in Table 4 will be considerably worse, and the skewness and kurtosis will also be large. For the distribution of masses of plants in forests, there is even larger variation in size, so in forest systems, the problems associated with these approximations will be even greater.

Table 3

Values of the average mass, $\langle M \rangle$, standard deviation of the mass, σ_M , relative standard deviation of the mass, r_M , and the second-order correction term, $F_1(r_M, \frac{3}{4})$, for a scaling exponent of $\frac{3}{4}$ computed for six different groupings of organisms, assuming that Damuth's energetic-equivalence rule (1987) determines population size

Group	$\langle M \rangle$ (kg)	σ_M (kg)	r_M	$F_1(r_M, \frac{3}{4})$
Birds of the Boreal Forest	0.034	0.139	4.077	-1.559
Mammals of the Boreal Forest	0.082	2.709	32.915	-101.570
Birds of the Boreal Prairie	0.047	0.170	3.646	-1.246
Mammals of the Boreal Prairie	0.109	3.138	28.702	-77.231
Pelagic Birds of Northwest North America	0.449	0.598	1.330	-0.567
Antelopes of the African Savanna	30.408	74.792	2.460	-0.125

The data for each group are taken from Holling (1992) and include an average mass for each species but not a standard deviation of the mass for each species. Thus, this is a slight underestimate of the standard deviation for each group as a whole. Note that the values in column 5 are not significantly less than 1 and often are significantly greater than 1, thus violating Eq. (16). For these examples, including the first-order correction term will have between a 12.5% and a 10,157.0% effect on the first-order approximation calculated by substituting $\langle M \rangle$ into an allometric relationship with an exponent of $\frac{3}{4}$. Consequently, including higher-order terms is crucial.

Table 4

Columns 2, 3, and 5 are values for the exact calculation, $\langle M^{3/4} \rangle$, the first-order approximation, $\langle M \rangle^{3/4}$, and the second-order approximation, $F_2(\langle M \rangle, r_M, \frac{3}{4})$, respectively, computed for six different groupings of organisms, assuming that all species have an equal number of individuals. Column 4 gives the percent error of the first-order approximation in column 3 compared with the exact calculation in column 2. Column 6 gives the percent error of the second-order approximation in column 5 compared with the exact calculation in column 2

Group	$\langle M^{3/4} \rangle$ (kg ^{3/4})	$\langle M \rangle^{3/4}$ (kg ^{3/4})	% Error	$F_2(\langle M \rangle, r_M, \frac{3}{4})$ (kg ^{3/4})	% Error
Birds of the Boreal Forest	0.056	0.073	30.9	0.040	28.4
Mammals of the Boreal Forest	1.373	2.111	53.8	0.190	86.1
Birds of the Boreal Prairie	0.074	0.090	21.5	0.065	12.0
Mammals of the Boreal Prairie	1.417	2.174	53.4	0.137	90.4
Pelagic Birds of NW North America	0.165	0.179	8.4	0.160	3.0
Antelopes of the African Savanna	6.431	7.461	16.0	5.993	6.8

The data for each group are the same as in Tables 2 and 3 and are taken from Holling (1992).

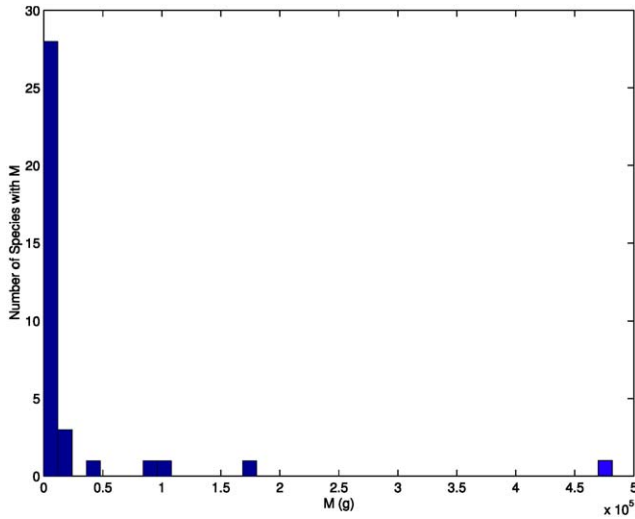


Fig. 1. The mass distribution for mammals of the boreal forest. The mass for each species, which ranges from 3.685–481,828.100 g, as taken from [Holling \(1992\)](#), has been binned into 40 groupings of equal size. The y-axis is the number of data points in each bin, and the x-axis is the mass, M . Note that many bins have zero entries. Further, note the large standard deviation and skewness (lack of symmetry) of this distribution. Additionally, the decay from the peak is quite rapid, leading to large values of the kurtosis. This results in higher-order terms in Eq. (10) being of significant magnitude.

As a second example, consider Eq. (6). For the function $e^{-E/kT}$, we find

$$f^{(2)}(\langle T \rangle) = \left(\left(\frac{E}{k\langle T \rangle^2} \right)^2 - \frac{2E}{k\langle T \rangle^3} \right) e^{-E/k\langle T \rangle} \quad \text{and}$$

$$g(\langle T \rangle) = \frac{E}{k\langle T \rangle} \left(\frac{E}{k\langle T \rangle} - 2 \right),$$

so that Eq. (13) becomes

$$|G_1(r_T, \langle T \rangle)| \equiv \left| \frac{E}{k\langle T \rangle} \left(\frac{E}{2k\langle T \rangle} - 1 \right) r_T^2 \right| \ll 1, \quad (20)$$

where $E \approx 0.6$ eV ([Gillooly et al., 2001](#)). Since endotherms have a roughly constant body temperature, r_T is very close to 0, and Eq. (6) is always a good approximation. For ectotherms, e.g. amphibians, reptiles, fishes, and plants, we must consider the variation in environmental temperatures that dictate the body temperatures of these organisms. [Table 5](#) lists the relevant parameters for various locations around the world. These values are based on average monthly temperatures taken from [Hoare \(1996\)](#) and [The British Antarctic Survey \(2002\)](#). Using average daily temperatures would increase σ_T , implying our estimates are conservative, but these effects will be small. From [Tables 5 and 6](#) we see that Eq. (20) is indeed a good test of the accuracy of the approximation. Moreover, [Tables 5 and 6](#) show that Eq. (6) is often a valid approximation in equatorial regions like Quito, Ecuador and Paya Lebar, Singapore. However, there are certainly regions

Table 5

Values of the average monthly temperature, $\langle T \rangle$, and the standard deviation, σ_T , for the locations listed in the first column were taken from [Hoare \(1996\)](#) and [The British Antarctic Survey \(2002\)](#). The corresponding latitudes for these locations are given in column 2. We then computed the relative standard deviation of the temperature, r_T , and the second-order correction term, $G_1(r_T, \langle T \rangle)$

Location	Latitude	$\langle T \rangle$ (°C)	σ_T (°C)	r_T	$G_1(r_T, \langle T \rangle)$
Quito, Ecuador	0°	13.5	0.20	1.10	0.0001
Paya Lebar, Singapore	1°N	26.9	0.47	0.91	0.0006
Albuquerque, USA	35°N	13.4	8.5	0.98	0.2410
Memphis, USA	35°N	16.6	8.0	0.97	0.2040
Minneapolis, USA	45°N	6.8	11.7	1.01	0.4954
London, UK	51°N	9.6	4.6	0.98	0.0727
Berlin, Germany	53°N	8.9	6.9	0.99	0.1689
Oslo, Norway	60°N	5.6	7.6	1.01	0.2117
Baker Lake, Canada	64°N	-12.1	15.7	1.11	1.1877
Reykjavik, Iceland	64°N	4.6	4.1	1.00	0.0639
Fairbanks, USA	65°N	-2.8	14.6	1.06	0.8919
Inuvik, Canada	68°N	-9.4	15.7	1.10	1.1507
Murmansk, Russia	69°N	0.3	8.0	1.03	0.2576
Alta, Norway	70°N	1.0	7.2	1.02	0.2072
Resolute, Canada	74°N	-16.4	13.6	1.12	0.9557
Alert, Canada	83°N	-18.0	13.4	1.12	0.9476
South Pole	90°S	-49.7	11.8	1.28	1.2772

Note that three values in column 6 are greater than 1, thus strongly violating Eq. (20) and implying that the first- and second-order terms are of comparable magnitude. Consequently, just substituting $\langle T \rangle$ into the Boltzmann factor, i.e., the first-order approximation, will give very poor results for these cases. In fact, the second-order correction term should probably be employed whenever $G_1(r_T, \langle T \rangle) \geq 0.1$, corresponding to a 10% or greater correction to the value obtained using the first-order approximation.

where Eq. (6) is not valid, most notably Fairbanks, United States; Dawson, Baker Lake, Inuvik, Resolute, and Alert, Canada; and the South Pole. Minneapolis, United States is also a questionable region for application of Eq. (6). One trend is that the nearer the location is to the poles the worse the approximation, but even this is often a wrong conclusion due to the stabilizing effect of proximity to large bodies of water, as evidenced by London, United Kingdom and Reykjavik, Iceland. This suggests that Eq. (6) is a good approximation at certain high-latitude locations, and that it is likely to apply to marine organisms at extreme latitudes because σ_T and r_T will be small. It is expected that elevational effects will also be significant.

The Q_{10} factor, an approximation to the Boltzmann factor, is often used to describe biological rates and times. The functional form of this temperature dependence is given by $Q_{10}^{T_c/10}$, where Q_{10} is typically a number between two and three and T_c is the temperature in degrees Centigrade. The second derivative of this is $Q_{10}^{T_c/10} \ln^2 Q_{10}/100$. Taking the simple example of $Q_{10} = e$, Eq. (13) becomes

$$\left| \frac{\sigma_T^2}{200} \right| \ll 1. \quad (21)$$

Table 6

The yearly averages of the Boltzmann factor, $\langle e^{-E/kT} \rangle$, are given in column 3 for the locations listed in column 1. These locations are the same as in Table 5. The corresponding latitudes for these locations are given in column 2. The fourth column is the Boltzmann factor evaluated at the yearly average temperature, $e^{-E/k\langle T \rangle}$, and the fifth column is the percent error between the exact calculation in the third column and the first-order approximation in the fourth column. The sixth column is the second-order approximation to the yearly average of the Boltzmann factor, $G_2(r_T, \langle T \rangle)$, and the seventh column is the percent error between the sixth and third columns

Location	Latitude	$\langle e^{-E/kT} \rangle$ (10^{-11})	$e^{-E/k\langle T \rangle}$ (10^{-11})	% Error	$G_2(r_T, \langle T \rangle)$ (10^{-11})	% Error
Quito	0°	2.81	2.81	0.01	2.81	0.0001
Paya Lebar	1°N	8.35	8.34	0.06	8.35	0.0003
Albuquerque	35°N	3.48	2.78	20.1	3.45	0.89
Memphis	35°N	4.39	3.63	17.2	4.37	0.34
Minneapolis	45°N	2.38	1.57	34.1	2.35	1.38
London	51°N	2.17	2.02	6.98	2.16	0.21
Berlin	53°N	2.22	1.89	14.86	2.20	0.49
Oslo	60°N	1.73	1.41	18.30	1.72	1.01
Baker Lake	64°N	0.65	0.26	60.32	0.56	13.20
Reykjavik	64°N	1.37	1.29	6.25	1.37	0.26
Fairbanks	65°N	1.30	0.65	50.26	1.22	5.90
Inuvik	68°N	0.84	0.34	59.72	0.73	13.4
Murmansk	69°N	1.11	0.87	21.77	1.09	1.62
Alta	70°N	1.13	0.92	18.46	1.12	1.56
Resolute	74°N	0.37	0.17	55.09	0.32	12.16
Alert	83°N	3.21	1.40	56.4	0.27	15.13
South Pole	90°S	0.01	0.003	71.22	0.007	34.46

The second-order approximation gives much smaller percent errors than the first-order approximation and is the correct approximation to use.

This demands $\sigma_T \ll 14.14$. Based on column 4 in Table 5, we see that this condition is violated even more strongly than for the Boltzmann factor. Thus, using average values for the temperature in a Q_{10} is an even worse approximation, and second-order corrections will be even more important.

Consequently, one must be extremely aware of location when applying Eq. (6) to ectotherms in temperate regions or at high elevations, and therefore, when using approximations of the type in Eq. (6) to conduct latitudinal or elevational studies. In addition, it is likely that these approximations do not apply when averaging T over ecosystems in temperate regions that contain both endotherms and ectotherms because the temperature variation across species will be large.

Keeping the second-order term in the series for Eq. (6)

$$\begin{aligned} \langle e^{-E/kT} \rangle &\sim e^{-E/k\langle T \rangle} (1 + G_1(r_T, \langle T \rangle)) \\ &\equiv G_2(r_T, \langle T \rangle) \end{aligned} \tag{22}$$

gives a better approximation to the exact answer. Table 6 displays the values of the exact expression $\langle e^{-E/kT} \rangle$, the first-order approximation $e^{-E/k\langle T \rangle}$, and the second-order approximation in Eq. (22). It also shows the percent error of the first- and second-order approximations compared with the exact values. Note that including the second-order approximation in Eq. (22) greatly reduces the percent error compared with that obtained by using Eq. (6). Except for the South Pole, the maximum percent error obtained using Eq. (22) is

15.13%, so Eq. (22) is a good approximation for virtually *all* geographic locations. Similar results hold for Q_{10} factors, but as explained previously, the percent errors will be slightly larger than those obtained for the Boltzmann factor. Therefore, including the second-order term for temperature data always leads to a very good approximation. Initially, this may seem surprising since including the second-order correction does not improve the results obtained for the mass distributions used in Tables 2–4. However, this is easily explained by the fact that temperature distributions are symmetrical, while mass distributions are often highly skewed. Therefore, the skewness, which corresponds to M_3 and the third-order term in Eq. (10), is large for the mass distributions considered, but not for the temperature distributions. That is, the symmetrical nature of the temperature distribution, as seen in Fig. 2 (compare with Fig. 1), results in all terms beyond the second in Eq. (10) being small. Consequently, the skewness of a distribution is important for mass distributions of large taxonomic groupings but not for temperature distributions across latitudes. Standard deviations are possible to estimate without detailed knowledge of an ecosystem, but skewness and kurtosis are more difficult. Thus, including higher-order terms to improve the approximation to the mass distribution of ecosystems may not be much easier than calculating the exact expression in Eq. (4). We conclude, however, that the approximation for the Boltzmann factor given in Eq. (22) should prove very useful.

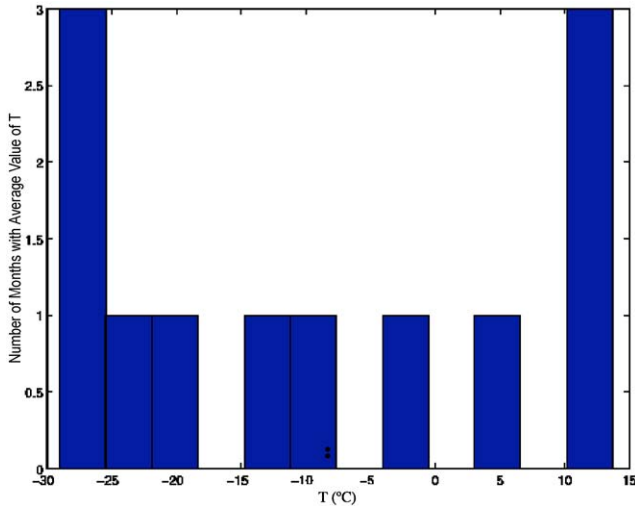


Fig. 2. The temperature distribution throughout the year for Inuvik, Canada. The monthly average of the temperature, which ranges from -29.0°C to 13.7°C , as taken from Hoare (1996), has been binned into twelve groupings of equal size. The y-axis is the number of data points in each bin, and the x-axis is the temperature, T . Note the large standard deviation but the relatively small skewness (corresponding to a high degree of symmetry) of this distribution. This results in the second-order term in Eq. (10) being of significant magnitude and in the third- and higher-order terms in Eq. (10) being negligible.

4. Combined effects for mass and temperature

In many instances the combined effects of mass and temperature must be analysed simultaneously. Based on the previous section, the error in the approximation is straightforward to derive

$$\begin{aligned} \langle M^{\gamma} \rangle &\langle e^{-E/kT} \rangle \\ &\sim \langle M \rangle^{\gamma} e^{-E/k\langle T \rangle} (1 + G_1(r_T, \langle T \rangle) \\ &\quad + F_1(r_M, \gamma) + F_1(r_M, \gamma)G_1(r_T, \langle T \rangle)). \end{aligned} \quad (23)$$

When averaging mass for each species, $F_1(r_M, \gamma) + F_1(r_M, \gamma)G_1(r_T, \langle T \rangle)$ will be small compared with $G_1(r_T, \langle T \rangle)$, so the test reduces to Eq. (20). Once again, this approximation is good in the tropics but poor in inland parts of the temperate zones. Retaining $G_1(r_T, \langle T \rangle)$ will significantly improve the results. When studying ecosystems all terms should be evaluated, and often, approximations will not be valid. If the ecosystem does not have a large variation in body size and is in the tropics, where there is not a large distribution of temperatures across ectotherms and endotherms, then Eqs. (5) and (6) should be quite accurate. Elsewhere, if the mass distribution is small or has little skewness, then a good approximation will be given by Eq. (23). Otherwise the exact expression in Eq. (4) should be used.

5. Discussion and conclusions

In this paper we have analysed whether the allometric approximations given in Eqs. (5) and (6) are valid when applied to biological systems. We have provided simple tests for the validity of these approximations, Eqs. (16) and (20). Moreover, we have provided improved approximations to allometric equations, Eqs. (19), (22), and (23).

We found that substituting $\langle M \rangle_{species}$ into allometric equations is a good approximation. Further, we found that inserting $\langle T \rangle_{year}$ for ectotherms is a good approximation in the tropics or near a large body of water but often, it is not accurate for inland locations in temperate zones or possibly at high elevations. We also showed that inserting $\langle M \rangle_{eco}$ is not a good approximation, and similarly, we argued that inserting $\langle T \rangle_{eco}$ outside of the tropics will not be accurate because the average has to be done over ectotherms and endotherms, creating a large standard deviation in the distribution. Thus, when studying the combined effects of mass and temperature, it will likely become difficult to use Eq. (5) together with Eq. (6). Therefore, Eq. (23) plus higher-order terms or the methods of Guthrie and Sheppard (2001) might be well suited for these cases.

Perhaps, the most important result of this study is that the second-order approximation to the Boltzmann factor given in Eq. (22) is virtually always an excellent approximation, whereas the commonly used approximation in Eq. (6) is not. If these scaling relationships are to be used to quantify the flux of energy and nutrients through ecosystems or the response of species to climate change, a high degree of accuracy is crucial. Due to the significant improvement in accuracy and the relative ease with which the average value and standard deviation of temperature are obtained, it seems Eq. (22) should be used when performing elevational or latitudinal studies.

It is often easy to estimate $\langle M \rangle$ and $\langle T \rangle$ as well as the standard deviations for each with very little data, and the form of the allometric equations are much simpler when these values can just be inserted. Moreover, this provides a direct connection between Eq. (4) and Eqs. (5) and (6), where the latter are more intuitive quantities. That is, expressing calculations in terms of the average values of the physically measurable quantities is a more natural approach. Together, these are the great utility of the approximations that are so often used in Eqs. (5) and (6), but as this paper has demonstrated, these approximations must be used with care. When Eqs. (5) and (6) do not work and estimates for the standard deviation are available, then the improved approximations in Eqs. (19), (22), and (23) will often be useful. As we have demonstrated, Eq. (22) is especially useful. If skewness and kurtosis are non-negligible and easily estimated, it is straightforward to use Eq. (10) to

derive a higher-order approximation scheme. For entire ecosystems good approximations to the allometric equations require knowledge about the skewness and kurtosis of the distribution, and that often requires detailed knowledge about the entire ecosystem. In those cases it may be as easy and will be more accurate to calculate Eq. (4) directly; when there is an abundance of data, this is always the safest choice.

This paper provides a means to test whether previous approximations to allometric equations were in fact valid and derives a framework for expressing equations in terms of average values of physically measurable quantities. More importantly, it provides improved approximations to Boltzmann factors and to allometric relationships, as well as tests for the accuracy of these approximations, that can be used in future work.

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