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Biological similarity theories: a comparison with the empirical allometric equations

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Twelve biological variables were submitted to dimensional analysis in accordance with the MLT-system of physics (M, mass; L, length; T, time). Each of these variables has a characteristic numerical value for the exponents α for mass, β for length, and γ for time. By means of Newton's reduction coefficient (χ), the three dimensions (MLT) can be expressed as power functions of body mass (M^b); the exponent (b) is the result of the combination of the three dimensional exponents (α, β, γ).

By linear regression analysis of 203 allometric exponents (b_E) obtained from the literature, the following equation was found for the regression exponent ($\hat{b}_R$)

$$\hat{b}_R = 0.96\alpha + 0.35\beta + 0.30\gamma$$

The estimated numerical coefficients (k_i) for the three exponents (α, β, γ) of the basic dimensions (MLT) do not agree with those of the prevailing theories of biological similarity.

INTRODUCTION

Three and one-half centuries ago Galileo extrapolated the principle of similarity from the realm of the physical sciences to the study of form and function in animals and plants. Dimensional analysis, on the other hand, is associated with the names of Newton, Fourier, and Maxwell, and in modern times with those of Bridgman and Buckingham. These two concepts (similarity and dimensionality) were introduced into biology in 1917 by D'Arcy Thompson (29), and in 1927 Lambert and Teissier (20) formulated the first "theory of biological similarity". Since that time, several authors have proposed other biological similarity criteria (5-8, 10-17, 23-25). However, it is mandatory that any morphometric or physiometric prediction, which might be deduced from a given theory, should be confronted with the empirical findings. Fortunately, this comparative analysis is now feasible due to the impressive quantitative information which can be found in four recent monographs on the subject (3, 25, 27, 28). Another favorable circumstance for this analysis is the fact that the great majority of these studies have utilized Huxley's (18) allometric equation to express the numerical results as functions of body mass (M) or of body weight (W), both of which can be considered as an holistic reference system for each organism.

GLOSSARY

A. *Symbols:*

- b = canonical allometric exponent;
- b_P = postulated allometric exponent (reduced), in accordance with any theory of biological similarity;
- b_E = experimentally obtained allometric exponent, mentioned in the literature;
- $\bar{b}_R$ = mean values of the empirical data (b_R) for each function;
- $\hat{b}_R$ = estimated exponent, obtained from regression analysis;
- $\hat{b}_i$ = allometric exponents corresponding to the four subdivisions of the body mass of 1-kg terrestrial mammal;
- k_i = numerical values for each of the parameters of exponents (α, β, γ);
- Q = any biological function, defined by means of MLT-system of physics.

B. *Greek Letters:*

- α = mass exponent;
- β = length exponent;

γ = time exponent;
μ = mass ratio (M_p/M_m), between prototype (p) and model (m)*, in order to be able to cancel the corresponding physical dimensions and to exclude from the presents analysis the influence of parameter (a) of the allometric equation (eqn. 9);
λ = length ratio (L_p/L_m);
τ = time ratio (T_p/T_m); and
χ = Newton's reduction coefficient (Q_p/Q_m)

DIMENSIONAL ANALYSIS IN THE BIOLOGICAL SCIENCES

Whenever structures or functions of individual members of the same, or of different, species are compared, one member is defined as the prototype (p) and the other as the model (m), and when this is done, a comparison can be made in terms of mass (M), length (L), and time (T). The formal analysis begins with the adimensional ratios of mass ($\mu = M_p/M_m$), length ($\lambda = L_p/L_m$), and time ($\tau = T_p/T_m$). Since the great majority of the biological functions (Q) can be defined in accordance with the MLT-system of physics

$$Q = M^{\alpha} L^{\beta} T^{\gamma} \quad (1)$$

the ratio of a given function (Q), between prototype (p) and model (m), yields Newton's reduction coefficient

$$\chi = Q_p/Q_m \quad (2)$$

Substituting the corresponding dimensional rations (μ, λ, τ), we obtain

$$\chi = \mu^{\alpha}\ \lambda^{\beta}\ \tau^{\gamma} \quad (3)$$

THE ALGORITHM FOR A THEORY OF MECHANICAL SIMILARITY

With the aim of establishing formal relationships among the three fundamental ratios (μ, λ, τ) for a "mechanical" similarity (21), at least two postulates must be established:

1. body density (ρ) is assumed to be constant ($\rho = ML^{-3}$); and

2. the acceleration of gravity (g) on earth is also invariant ($g = LT^{-2}$).

In the first postulate we assumed that $\rho_p/\rho_m = 1.0$, and in the second that $g_p/g_m = 1.0$. The introduction of the ratios μ, λ, τ into the first postulate gives

$$\mu\lambda^{-3} = 1.0 \quad (4)$$

and from the second we obtain

$$\lambda\tau^{-2} = 1.0 \quad (5)$$

Since the first postulate is equivalent to $\mu = \lambda^3$, and the second to $\tau = \lambda^{1/2}$, then eqn. 3 can be expressed as

$$\chi = \lambda^{3\alpha}\ \lambda^{\beta}\ \lambda^{1/2\gamma} \quad (6)$$

On the other hand, $\lambda = \mu^{1/3}$, and when this equivalence is introduced into eqn. 6, we obtain

$$\chi = \mu^{\alpha + 1/3\beta + 1/6\gamma} \quad (7)$$

Thus, the "reduced" mass-ratio exponent ($b\rho$) can be defined as follows

$$b_p = \alpha + 1/3\beta + 1/6\gamma \quad (8)$$

THE ALLOMETRIC EQUATION

In 1932 Huxley (18) introduced the allometric equation into the biological sciences

$$Y = aM^{b} \quad (9)$$

in which *Y* is any morphological, physiological or ecological variable, *M* is body mass, while *a* and *b* are the mass-coefficient and the mass-exponent, respectively. The advantage of this apparently simple formula is that its logarithmic form represents the equation of a straight line.

$$\log Y = \log a + b \log M \quad (10)$$

which allows for the statistical treatment of biological data after their log-log transformation.

* Prototype (p) means a large or small scale organism to which a model (m) organism is geometrically, chemically, or physically related.

TABLE I

Comparison of different theories of similarity, based on the numerical values of the coefficients (k_1, k_2, k_3) for the three exponents (α, β, γ) of the MLT-system

Items	Similarity	Exponents α k_1	β k_2	γ k_3	References
1	Mechanical	1	1/3	1/6	Galileo (1638)
2	Biological	1	1/3	1/3	Lambert & Teissier (1927)
3	Elastic	1	1/4	1/4	McMahon (1973)
4	Empirical coefficients	1	1/3	1/4	Present study (1992)

COMPARISON BETWEEN THEORETICAL AND EMPIRICAL EXPONENTS

For the different theories of similarity, Yates (31) has suggested the following algebraic equation

$$b = p\alpha + q\beta + r\gamma \quad (11)$$

The three coefficients (p, q, r) are unknown, whereas the values α, β and γ are defined by the dimensional analysis of the biological variable involved.

In order to obtain a numerical solution of eqn. 11 for a given theory of similarity, we employed the following model

$$b_R = k_1\alpha + k_2\beta + k_3\gamma + \varepsilon \quad (12)$$

As a result of the multiple linear regression analysis of 203 empirical allometric exponents (b_E), found in the literature (3, 27), we obtained the following adjusted equation

$$\hat{b}_R = 0.958\alpha + 0.346\beta + 0.296\gamma \quad (13)$$

in which the corresponding standard errors (SE) for k_1, k_2 and k_3 are 0.0102, 0.0023 and 0.0051. The determination coefficient for eqn. 13 was $r^2 = 0.993$.

The estimated values for k_1, k_2 and k_3 (eqn. 13) can now be compared with the corresponding values of the prevailing theories of biological similarity:

1. Mechanical Similarity

This physical similarity (21) was postulated by Galileo, in 1638, on the basis of two assumptions:

i) the density (ρ) of prototype (p) and model (m) should be identical;

ii) the relationship between length (L) and time (T) can be defined by means of the characteristics of a physical pendulum, where $T = 2\pi\ (L/g)^{1/2}$, g is the acceleration of gravity on earth.

It is interesting to note, that this theory of "mechanical similarity" was applied by Galileo to interpret forms and functions in animals and plants of different sizes.

The respective numerical values for k_1, k_2 and k_3 are shown in Table I (item 1).

2. Biological Similarity

This theory was postulated by Lambert and Teissier (20) in 1927, and was also based on two assumptions:

i) the constancy of body density (ρ), a statement which is corroborated by the fact that all organisms are on the verge of flotation when placed in water; and

ii) that time (T) and length (L) must vary proportionally (T α L); unfortunately, this postulates is only an *a priori* assumption.

The numerical values for k_i are given in Table I (item 2).

3. Elastic Similarity

With regards to McMahon's (23) "elastic" similarity, it is noteworthy that this approach was based on animal proportions and on the buckling and bending loads, which the weight-bearing structures must support in animals of different size. This particular theory is based on the stability and flexure of bony structures, which are both important in animal locomotion and muscular dynamics.

For the numerical values of k_i see Table I (item 3).

DISCUSSION

One of the main problems of biological scaling is to decide which reference system should be chosen to compare morphometric and physiometric data obtained from animals of different size. These prospective reference systems must have one characteristic in common, namely, that they should be of an integrative nature, *i.e.*, they must represent an holistic approach. Among the best candidates, one could mention:

A. body mass (M), which represents the sum of all cells, together with the weight-bearing system (bones and ligaments), and the extracellular fluid compartment (plasma plus interstitial fluid);
B. the metabolic rate (m), which corresponds to the oxygen consumption (V_{O2}) per unit time, or to the total heat production per unit time (thermogenesis), since both functions are associated with the aerobic metabolism of all mitochondria.

The great majority of biologists have preferred body mass (M) as a convenient reference system for interspecies comparisons.

The remainder of the discussion will be concerned with the analysis of the three parameters (k_1, k_2 and k_3) from eqn. 12, and how they correlate to each other.

A. About the Coefficient (k_1) of the Mass Exponent

From a physical or a chemical point of view, mammalian organisms cannot be defined as homogeneous compartments, since they are characterized by multifarious structures and functions. Among the major subdivisions of body mass (Pace *et al.*, 26), one should consider:

1. the weight-bearing musculo-skeletal system;
2. the internal organs or viscera;
3. the containment integument, represented by the skin; and
4. the blood as a transport system of aqueous nature.

The corresponding proportions of these four compartments were studied in a 1-kg terrestrial mammal (26), whose respective fat-free masses can be defined by means of the allometric parameters, which are summarized in Table II. It is noteworthy, that only in the present case (W = 1 kg), the four allometric equations can be summated, despite the fact that the exponents ($\hat{b}_i$) differ from unity, with the exception of item 3 (skin), in which case the allometric exponent ($\hat{b}_3$ = 1.010) is probably not significantly different from unity. However, the comparison between carcass skin, and viscera (Table II), should be interpreted as a zero-sum solution for the organism as a whole.

TABLE II

Relative distribution of the fat-free masses of the four subdivisions of the body mass of small terrestrial mammals (Pace *et al.*, 28)

Subdivisions	Parameter ($\hat{a}_i$)	Exponent ($\hat{b}_i$)
1. Carcass	0.625	1.043
2. Viscera	0.148	0.880
3. Skin	0.141	1.010
4. Blood	0.081	0.952
Total	0.995	

Besides this subdivision of a mammalian organism into four main structures (Table II), one should consider that, as summarized by Peters (27), for instance, among the visceral organs the allometric exponents are not always equal to the mean value $\hat{b}_2 = 0.88$ (Table II); since, for the spleen $b_E = 1.06$; for the heart and the lungs $b_E = 0.98$; for the gut $b_E = 0.94$; for the kidneys $b_E = 0.84$; and for the brain $b_E = 0.66$. Whith regards to the allometric exponent for the brain-mass of mammals (27), we must add that these values were excluded in the present analysis, due to the fact that the brain is not a visceral organ, but a processing center of the sensory input from the surface of the body and from numerous peripheral sense organs. The numerical value of the allometric exponent for the brain ($b = 2/3$) is the same as the relationship between the surface and the volume of any geometric body.

In sum, and as shown in Table III (items 3 and 5), the allometric exponent (b) for the volume (V) and the mass (M) functions are close to unity (1.036 and 0.975), and in consequence the mean density (ρ) of mammalian bodies is practically constant, in agreement with the first postulate of all theories of biological similarity.

Finally, with regards to body mass (M) as a universal reference system, several authors (1,2) have denied the possibility of utilizing the body-mass exponent for metabolic scaling based on dimensional analysis, but this specific problem is beyond the aim of the present study.

B. Concerning the coefficient (k_2) for the length exponent

With regard to the biological length functions, it is interesting to compare the theoretically expected value ($b_P = 1/3$) with the 20 empirical values: $\hat{b}_R = 0.314 \pm 0.0094$ (Table III, item 1).

Economos (4) on the other hand, obtained an allometric exponent $\hat{b}_R = 0.314$ for the body-head lengths of 240 mammalian species. This value is identical with our data (see Table III, item 1). Heusner (17) has digitized Economo's data ($n = 240$), and obtained a slightly different mean value ($\hat{b}_R = 0.325 \pm 0.003$), which is significantly different ($p < 0.001$) from the value ($b_P = 0.25$) proposed for length functions (L) by McMahon (23), as indicated in Table I, item 3.

C. The coefficient (k_3) for the exponent of time

For biological time functions we obtained a mean value of $\hat{b}_R = 0.251 \pm 0.0099$ (Table III, item 12). On the other hand, Lindstedt and Calder (25), in their extensive study on physiological time and body size, studied 15 different time functions in homeothermic animals, which included a wide range of chronological functions, *i.e.*, from the fast muscle contraction to the lifespan of mammals in captivity, and found that the 95% confidence intervals (0.227-0.278) included $b_P = 0.25$ as the most likely body mass exponent ($mass^{1/4}$) for biological scaling, a power function which agrees with McMahon's theory of elastic similarity (Table I, item 3).

D. About the length-time-mass relationship (k_1, k_2, k_3)

The significant difference (eqn. 13) between length ($k_2 = 0.346 \pm 0.0023$) and the time coefficient ($k_3 = 0.296 \pm 0.0051$) seems to indicate that the "length-time" relationship cannot be described adequately (see Table I) by means of Galileo's simple pendulum mode ($k_2 = 1/3$; $k_3 = 1/6$), nor with Lambert and Teissier's biological similarity theory ($k_2 = 1/3$; $k_3 = 1/3$), nor by McMahon's elastic similarity criterion ($k_2 = 1/4$; $k_3 = 1/4$).

More recently, through the use of dimensional analysis, similarity criteria and allometry, it has been possible to establish terrestrial locomotion (30) and a physical law for a wrist-pendulum system in humans (19). The periodic time (τ_o) could be correlated with mass (M) and length (L) of the wrist-pendulum system, such that

$$\tau_o = a\,(M^{1/16}L^{1/2})^c \qquad (14)$$

where

a means the corresponding allometric parameter, and

c is the exponent for this twice-scaled law, which can be referred as pertaining to the "moment" class.

TABLE III

Dimensional analysis of 12 biological functions and mean allometric exponents calculated from the literature (3, 27)

Item	Functions	Dimensions			Allometric Exponents	
		M	L	T		
		α	β	γ	n	$b_R \pm SE$
1	Length	0	1	0	20	0.314 ± 0.0094
2	Area	0	2	0	7	0.687 ± 0.0129
3	Volume	0	3	0	41	1.036 ± 0.0086
4	Minute–volume	0	3	–1	27	0.768 ± 0.0115
5	Mass	1	0	0	29	0.975 ± 0.0177
6	Concentration	1	–3	0	6	–0.0675 ± 0.0186
7	Energy; work	1	2	–2	6	1.066 ± 0.0302
8	Pressure	1	–1	–2	8	–0.010 ± 0.0169
9	Power	1	2	–3	33	0.746 ± 0.0066
10	Resistance	1	–4	–1	4	–0.752 ± 0.0427
11	Compliance	–1	4	2	5	0.960 ± 0.0510
12	Period	0	0	1	17	0.251 ± 0.0099
					$\Sigma n = 203$	

The non-linear character of eqn. 14 is noteworthy, and the degree of curvature of the Gaussian coordinate system (c) can be measured by the slope in a log by log plot.

On the other hand, it is generally assumed that the metrics of living organisms belong to an Euclidean space (c = 1.00), and that any point inside the organism can be defined by means of Cartesian coordinates. Nevertheless, this simplified assumption is not necessarily true, because the prevalent form in living beings is approximately spherical or cylindrical. For this reason, a spherical or a cylindrical geometry should be applied to the biological realm, and in consequence, any distance should be measured in a manner similar to the geodesics on earth, *i.e.*, depending upon the curvature of the intrinsic (biological) geometry. For the sake of simplicity, let us assume that all terrestrial mammals have a spherical shape, such that the curvature (c) is inversely proportional to the mean body radius (r), which in turn is a function of the cubic root of body volume (V) or of body mass (M), provided that body density (ρ = M/V) remains constant. Thus, the corresponding body radii (r_i) must vary in accordance with the body mass range (M) of terrestrial mammals (from a 3-g shrew to a 3-ton elephant), which represents a body radii scope of 10^2. But, if we take into account the radii (curvatures) of all living beings (25), from my-

coplasmas (10^{-13} g) to whales (10^{8} g), then the corresponding radii scope will be 10^{7}.

When quadrupedal locomotion of mammals of different sizes was studied at the trot-gallop transition point, Heglund *et al.* (9) found the allometric exponents for stride frequency (b_E = -0.14), and for stride length (b_E = 0.38), two values which are consistent with the theory of "elastic similarity" (24), whose predictions were b_P = -1/8 or -0.125 for stride frequency, and b_P = 3/8 or 0.375 for stride length. Curiously enough, the mechanical similarity (Table I, item 1) already predicted a value of b_P = -1/6 for stride frequency and b_P = 1/3 for stride length, both based on a simple pendulum-mode similarity.

Finally, we would like to emphasize that in order to interpret form and function of living beings, the present study was based on an Euclidean geometry and on a Newtonian dimensional analysis. Nevertheless, it is very likely that the prevailing geometry in all organisms is mainly of "fractal" nature, that the corresponding functions are not linearly correlated, and that almost all biological variables are of a "non-linear" nature. However, as a first approach, we can say that the general regression equation (eqn. 13) is a valuable tool to obtain reasonable figures for at least 12 variables of biological interest (see Table III).

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