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Dimensional analysis and allometric equations concerning Cope's rule

Análisis dimensional y ecuaciones alométricas en relación a la regla de Cope

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ABSTRACT

Cope's law deals with the phyletic increase in body size, both in invertebrates and vertebrates, and is based on paleontologic evidences and the qualitative morpho - functional advantages of living beings with greater body mass. In the present study we have applied dimensional analysis, allometric equations, and a theory of biological similarity to submit Cope's rule to a quantitative test. When the allometric exponent is equal or greater than unity ($b \geq 1.0$) the corresponding functions increase at a greater rate than body mass, implying that larger species have a greater advantage for survival (fight or flight). On the other hand, biological functions with allometric exponents lesser than unity ($b < 1.0$) are of vital importance when the corresponding function implies an economy of matter or energy. The survival of living beings of different body size under extreme environmental conditions is determined by functional reserves, such as water, salts, and calories, which could also be defined in a quantitative manner by means of allometric exponents (b). Finally, it is necessary to emphasize that the present mechanistic approach of Cope's rule has a limited validity since it ignores the incidence of many biological factors, such as population dynamics, evolutionary and ecological processes.

Key words: body mass, quantitative analysis, survival, morphometry, physiometry.

RESUMEN

La regla de Cope se refiere al incremento filético del tamaño corporal, tanto en invertebrados como en vertebrados, basándose en evidencias paleontológicas y en el análisis cualitativo de las ventajas morfofuncionales de las especies que tienen un mayor tamaño corporal. En el presente trabajo se intenta realizar un análisis cuantitativo de dicha regla en base al análisis dimensional, a ecuaciones alométricas empíricas, y en una teoría de similitud biológica.
Las ecuaciones alométricas con exponentes iguales o mayores que la unidad ($b \geq 1,0$) indican que la función correspondiente crece mas rápidamente que la masa corporal, lo que implica que las especies más grandes tienen ventajas en la supervivencia de cada individuo (ataque o fuga). Por otra parte, las funciones biológicas con exponentes alométricos menores que la unidad ($b < 1,0$) también pueden ser de importancia vital cuando ellas significan una economía de materia o de energía. Finalmente, la supervivencia de los seres vivos en condiciones ambientales extremas está condicionada por las reservas funcionales, tales como agua, sales y calorías, las que también se pueden evaluar en forma cuantitativa en base al correspondiente exponente alométrico (b). Finalmente, es necesario señalar que el presente enfoque mecanicista de la regla de Cope necesariamente tiene una validez restringida, ya que ignora factores biológicos importantes como la dinámica de poblaciones, procesos evolutivos y ecológicos.

Palabras clave: masa corporal, análisis cuantitativo, supervivencia, morfometría, fisiometría.

INTRODUCTION

The American paleontologist Edward Drinker Cope (1840 - 1897) established in 1885 a pattern concerning the phyletic increase in size, both in vertebrates and invertebrates (Peters 1983). This assertion was denominated initially as Cope's law, but the increasing number of exceptions justifies the denomination of Cope's rule (Brown & Maurer 1986). In general, large species tend to appear later in a group's phylogeny, as

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has been corroborated empirically by the fossil record (Simpson 1985).

Up to the present, Cope's rule has been interpreted only from a "qualitative" point of view, as has been summarized by Peters (1983, pp. 111), in the sense that large species:

1) are usually dominant in interspecific aggressions;
2) have better homeostatic mechanisms;
3) have greater mobility;
4) are more capable to adapt to a wider range of environmental conditions;
5) can seek out more favorable locations within local environments;
6) spend lesser energy per unit biomass on maintenance;
7) are more efficient at extracting usable energy from low-quality foods;
8) are more efficient in avoiding predators;
9) dominate resource use and consequently leave more offsprings than smaller relatives.

It is well known that the increase in body mass (M) is not due to a corresponding increase in cell size. On the contrary, cell diameter is almost constant in vertebrates (Thompson 1917, Maldonado et al. 1974, Ocquetau et al. 1989, Morgado et al. 1990) and in consequence, any increase in body mass (M) is correlated with a greater number of cells and additionally with a wider spectrum of cell types (McMahon & Bonner 1983). This is particularly significant for the central nervous system (Haldane 1956, Went 1968, Jerison 1961), where an increase in the number of neurons means a huge increase in connectivity, thus providing a over-whelming selective advantage for all vertebrates of greater size. In the present paper we have tried to emphasize the necessity of a "quantitative" study of Cope's rule by means of dimensional analysis, theories of biological similarity, and the corresponding empirical allometric equations.

A QUANTITATIVE ANALYSIS OF COPE'S RULE

For interspecific comparisons of morphological or physiological variables, Huxley's (1932) allometric equations are commonly applied, both for empirical data, as well as for theoretical inferences.

Huxley's allometric equation reads as follows:

$$Y = a \cdot M^b \qquad (1)$$

where
Y is the dependent variable
a is an empirical parameter
M is body mass (kg); and
b is the allometric exponent

All empirical values of the allometric exponent (b_E) which are mentioned in the present study were obtained form the pertinent literature (Peters 1983, Calder 1984, Schmidt-Nielsen 1984). On the other hand, the theoretical reduced exponent (b_R) was calculated in accordance with the corresponding theory of biological similarity (Günther et al. 1992), which are only based on the dimensional analysis (MLT-system) of each function (Günther 1975). The calculated reduced exponent (b_R), as shown in Table 1, is the result of the product of three power functions concerning mass, length, and time ($Y = a \cdot M^{\alpha} \cdot L^{\beta} \cdot T^{\gamma}$), and the coefficients of the corresponding exponents (α, b, and γ) were obtained by means of the statistical analysis of 203 empirical allometric equations (Günther et al. 1992):

$$b_R = 0.96 \cdot \alpha + 0.35 \cdot \beta + 0.30\,\gamma \qquad (2)$$

The comparison of these two allometric exponents (b_R vs. b_E) yielded very similar values (items 2, 3 and 7, Table 1) for those variables whose allometric exponents are almost equal or greater than unity ($b \geq 1.00$). These variables are relevant for the quantitative analysis of Cope's rule, in the sense that they are increasing in proportion to body mass (M), as can be deduced from the theory of biological similarity (b_R) and confirmed empirically (b_E) in five instances.

TABLE 1

Seven functions whose allometric exponent (b) are equal or grater than unity ($b \geq 1$). The reduced exponents (b_R) were calculated in accordance to eqn. 2 and the empirical allometric exponents (b_E) were obtained from the literature.

Siete funciones cuyos exponentes alométricos (b) son iguales o mayores que la unidad ($b \geq 1$). Los exponentes reducidos (b_R) fueron calculados de acuerdo a la ecuación 2 y los exponentes empíricos (b_E) se obtuvieron de la literatura.

Item	Function	Definition	Mass M (α)	Length L (β)	Time T (γ)	Allometric exponents b_R	b_E	Organ or function	References
1	Action	Product of work by time	1	2	- 1	1.40	ND*		
2	Energy; work	Capability of doing work	1	2	- 2	1.06	1.06	Cardiac work	Peters, p. 260
3	Mass	Quantity of matter	1	0	0	0.96 0.96	0.99 0.98	Lung mass Heart mass	Calder, p. 49 Calder, p. 49
4	Momentum	Product of mass and velocity	1	1	- 1	1.01	ND*		
5	Moment of inertia	Effectiveness of mass in rotation	1	2	0	1.70	ND*		
6	Torque	Turning movement	1	2	- 2	1.10	ND*		
7	Volume	Three dimensions of space	0	3	0	1.05 1.05	1.04 0.98	Tidal volume Blood volume	Peters, p. 255 Peters, p. 257

* ND: no data available

DISCUSSION

The mechanical advantages of being large, as illustrated in Table 1, are complemented with other advantages of metabolic nature (Table 2), as for instance, body surface ($b_R = 0.70$) is advantageous –increases less than body mass– in large animals when the ambient temperatures are extreme (item 2). With regard to item 3 (Table 2), the negative sign of the allometric exponents (b) for frequency, means that in large animals the heart rate is significantly lower, and in consequence the oxygen consumption per unit mass of the heart is markedly smaller in large specimens.

The empirical allometric exponent of the total peripheral resistance (Table 2, item 5) is $b_E = -0.76$, which indicates that the impedance of the arterial branching system (arterioles and capillaries) is progressively decreasing– in a nonlinear fashion – in homeotherms of increasing body mass (M), indicating lesser cardiac power for maintaining blood circulation at invariant arterial pressure (Table 2, item 4).

Furthermore, it is worth mentioning that both, the metabolic rate (Table 2, item 9) and the volume-flow of the heart (item 8), have very similar empirical allometric exponents ($b_E \cong 0.75$); when they are expressed per unit body mass, the corresponding specific functions have a negative allometric exponent ($b \cong - 0.25$).

We will briefly analyze in Table 3 some other advantages which can be associated with Cope's rule, as for instance the variables specified in the items 1 - 6, whose allometric exponents are equal or greater than unity ($b \geq 1$). With regard to item 7, the dissication endurance, when expressed per unit body mass, yields an allometric exponent of $b = - 0.12$, and in consequence, a larger animal has a better chance to survive during severe water deprivation due probably to a smaller relative body surface. Item 8 results from the ratio of items 2 and 9 of Table 2, yielding the metabolic endurance (turnover time) with $b = 0.45$, which means that the metabolic endurance is roughly proportional to the square root of

TABLE 2

Nine functions whose allometric exponent (b) are smaller than unity ($b < 1$). The reduced exponents (b_R) were calculated in accordance to eqn. 2 and the empirical allometric exponents (b_E) were obtained from the literature.

Nueve funciones cuyos exponentes alométricos (b) son menores que la unidad ($b < 1$). Los exponentes reducidos (b_R) fueron calculados de acuerdo a la ecuación 2 y los exponentes empíricos (b_E) aparecen en la literatura.

Item	Function	Definition	Mass M (α)	Length L (β)	Time T (γ)	Allometric exponents b_R	b_E	Organ or function	References
1	Length	Basic unit of the metric system	0	1	0	0.35	0.32	Aorta	Calder, p. 110
						0.35	0.40	Trachea	Calder, p. 111
2	Area	Square of a length	0	2	0	0.70	0.78	Trachea	Calder, p. 111
						0.70	0.67	Aorta	Peters, p. 259
3	Frequency	Rate of oscillation	0	0	-1	- 0.30	- 0.27	Heart	Peters, p. 257
						- 0.30	- 0.28	Respiration	Peters, p. 255
4	Pressure; stress	Force distributed over a surface	1	- 1	- 2	0.01	0.032	Arterial	Peters, p. 260
						0.01	0.004	Pleural	Peters, p. 256
5	Resistance	Ratio of pressure and volume-flow	1	- 4	- 1	- 0.74	- 0.76	Total peripheral resistance	Peters, p. 260
6	Tension	Force per unit length	1	0	- 2	0.36	0.35	Aortic wall	Peters, p. 260
7	Velocity	Time rate of motion in a fixed direction	0	1	- 1	0.05	0.07	Blood in the aorta	Peters, p. 259
8	Volume-flow	The volume of a cube per unit time	0	3	- 1	0.75	0.74	Cardiac output	Peters, p. 258
						0.75	0.72	Inulin clearance	Peters, p. 261
9	Power	Time rate at which work is done	1	2	- 3	0.76	0.78	Breathing	Peters, p. 256
						0.76	0.7518	Metabolic rate	Peters, p. 239

TABLE 3

Allometric parameters (a & b) concerning body composition, energy reserves and different endurances in mammals.

Parámetros alométricos (a & b) concernientes a la composición corporal, a las reservas energéticas, y a diferentes formas de resistencia en mamíferos.

Item	Function	Reserve of	Allometric parameters a	b	References
1	Total body water (%)	water	60.5	1.00	Calder, p. 136
2	Total fat content (kg): skin, viscera, carcass	calories	0.075	1.19	Calder, p. 48
3	Carcass fat (kg)	calories	0.11	1.02	Calder, p. 215
4	Muscle mass (kg)	proteins	0.45	1.0	Peters, p. 264
5	Skeleton mass (kg)	calcium & phosphorus	0.061	1.09	Calder, p. 49
6	Total blood volume (kg)	water & oxygen	0.069	1.02	Calder, p. 49
7	Dissication endurance (g/day)	water loss by evaporation	38.8	0.88	Calder, p. 217
8	Turnover time (s): metabolic endurance	amount of fat/metabolic rate	-	0.45	Calder, p. 145
9	Practical migratory distance (km/day)	energy	172	0.25	Calder, p. 194

body mass. Finally, the practical migratory distance (item 9) is proportional to $M^{1/4}$, which represents another advantage of large size.

The biological relevance of the present study is obvious when one considers that the size span of living organisms is of 21 orders of magnitude, and consequently the relationship between body size and physiology must be of paramount importance. Recently, West et al. (1997) developed a general model of allometry and biological scaling laws, based on three general assumptions, which allowed the prediction of numerous cardiovascular and respiratory allometric exponents, in close agreement with the empirically obtained values. The latter authors utilized exclusively a fractal geometry to establish the three unifying principles for their model concerning the origin of allometric scaling laws in biology, which is primarily of microscopic nature, whereas the whole animal is a macroscopic entity. Cope's rule is correlated with the whole body mass, and consequently the Euclidean approach is the most adequate one. A comparison between both geometries, as applied in biology can be found in Günther & Morgado (1996). It is important to note, that the body mass distribution of the number of species in nature is right skewed (Brown et al. 1993), which seem to indicate that Cope's rule is not the predominant factor which determines biological success, since the optimal size peaks at body mass of about 100 grams in mammals (Marquet et al. 1995). In essence, Cope's rule, which in the present paper was analyzed in a quantitative manner by means of dimensional analysis imposes numerous mechanical advantages at the individual level. Nevertheless, evolutionary history and the ecological settings wherein individuals interact are also of paramount importance and should be taken into account. However, this is beyond the scope of the present study.

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