Allometric Scaling Laws and the Derivation of the Scaling Exponent

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Abstract

Allometric scaling relations abound in nature. Examples include the power law relating the metabolic rate of organisms to their masses and the power law describing the dependence of the size. In Kleiber's Law, the metabolic rate scales as the three-quarter power of body mass. These relations are the characteristic of all organisms and are here derived from a general allometric scaling model using the concept of fractals. The crucial point (i.e. the source of the 3/4 scaling exponent) is that however the size of terminal tubes does not depend on the body size. The model provides a complete analysis of scaling relations for mammalian circulatory systems. Furthermore, it predicts structural and functional properties of vertebrate circulatory and respiratory systems, plant vascular systems, insect tracheal tubes, and many other distribution networks.

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1 Introduction

Many relations between sizes of nature can be described through scaling laws. In biology the relationship of body size and metabolisms is a particularly prominent example of it: Large animals have - relatively seen - a lower metabolic rate than small animals. The first accurate measurements of body mass versus metabolic rate in 1932 shows that the metabolic rate R for all organisms follows exactly the 3/4 power-law of the body mass, i.e., $R \propto M^{3/4}$. This is known as the Kleiber's Law. It holds good from the smallest bacterium to the largest animal (see Figure 1). The relation remains valid even down to the individual components of a single cell such as the mitochondrion and the respiratory complexes. It works for plants as well. This is one of the few all-encompassing principles in biology.
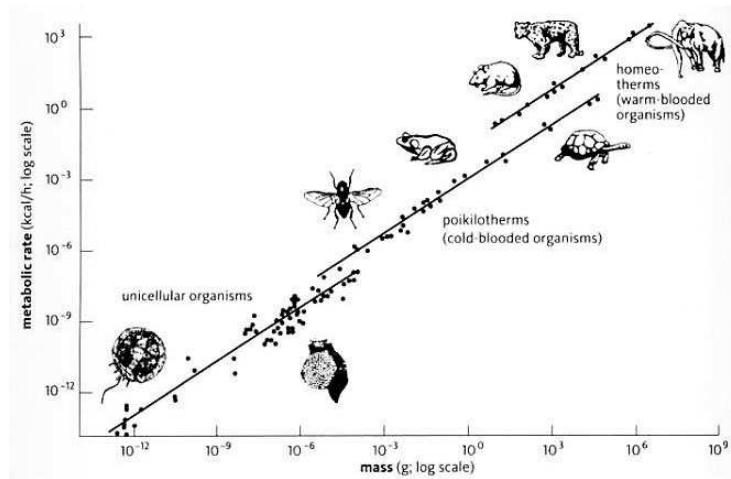

Figure 1: Allometric scaling of metabolic rate for a selection of homeotherms (birds and mammals), poikilotherms (fish, reptiles, amphibians, and inverte-brates), and unicellular organisms. The solid lines all have a slope of .75. (1; 8)

The dependence of a biological variable Y on the body mass M is typically characterized by an allometric scaling law of the form

$$Y = Y_0 M^b \tag{1}$$

where b is the scaling exponent and Y_0 a constant that is characteristic of the kind of organism. Most biological phenomena scale as quarter rather than third powers of body mass. For example, metabolic rates B of entire organisms scale as $M^{3/4}$; rates of cellular metabolism and heartbeat scale as $M^{-1/4}$, and times of blood circulation, embryonic growth and development, and life-span scale as $M^{1/4}$. Sizes of biological structures scale similarly. For example, the cross-sectional areas of mammalian aortas and of tree trunks scale as $M^{3/4}$. No general theory explains the origin of these laws.

Then in 1997, a couple of scientists around the physicist Geoffrey B. West of the Los Alamos National Laboratory in New Mexico successfully derive the

3/4 power-law using the concept of fractals (a more realistic geometry for organisms). Fractals are natural or artificial structures or geometrical samples, which exhibit a high degree of scale invariance and/or self similarity. That is for example the case, if an object consists of several reduced copies of its. Scale invariance is a feature of objects or laws that do not change if length scales are multiplied by a common factor. One of the basic examples of self-similar sets is the Sierpinski triangle (see Figure 2).
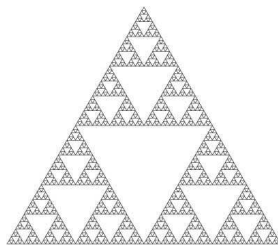

Figure 2: Sierpinski triangle (11)

West *et al.* (1) developed a quantitative model that explains the origin and ubiquity of quarter-power scaling. The model predicts the essential features of transport systems, such as mammalian blood vessels and bronchial trees and also plant vascular systems, and insect tracheal tubes. It is based on fundamental principles or assumptions: At all scales organisms are sustained by the transport of energy and essential materials through hierarchical branching network systems in order to supply all local parts. These networks are space-filling fractal-like branching pattern. The terminal branches of the network are invariant units. Finally, the energy required to distribute resources is minimized and this final restriction is basically equivalent to minimizing the total hydrodynamic resistance of the system. In particular, scaling and their exponents arise from an interplay between the physical and geometrical constraints inherent in these principles.

Most distribution systems can be described by a branching network in which the size of tubes regularly decrease. One version is exhibited by mammalian circulatory and respiratory systems, another by the the vessel-bundle structure of multiple parallel tubes, characteristic of plant vascular systems (Figure 3).

2 Derivation of 3/4 Exponent

The circulatory system (or cardiovascular system) is an organ system that moves substances to and from cells. The main components of the system are the heart, the blood and the blood vessels, namely, aorta, arteries, arterioles and the capillaries. In the general case the network has N branching levels from the aorta (level 0) to the capillaries (level N) (see Figure 3C). A typical tube at the kth level has length l_k, radius r_k, and pressure drop $\triangle p_k$ (see Figure 3D). The volume flow rate is $Q_k = \pi r_k^2 \bar{u}_k$ where $\bar{u}_k$ is the flow velocity averaged over the cross section and/or over time. Each tube branches into n_k smaller ones and so the total number of branches at level k is $N_k = n_0 n_1 ... n_k$. Because the fluid is
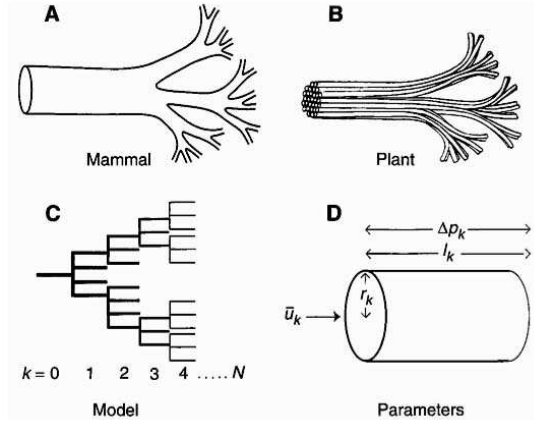
Figure 3: Examples of segments of biological distributed networks: (A) mammalian circulatory and respiratory systems composed of branching tubes; (B) plant vessel-bundle vascular system composed of diverging vessel elements; (C) topological representation of such networks, where k specifies the branching level, beginning with the aorta (k=0) and ending with the capillary (k=N); (D) parameters of a typical tube at the kth level. (1)

conserved as it flows through the system and so the volume flow rate through the aorta

$$Q_0 = N_k Q_k = N_c Q_c = N_c \pi r_c^2 \bar{u}_c \qquad (2)$$

which holds for any level k. N_c is the number of capillaries and the Q_c is the volume flow rate in the average capillary. The next important assumption is that the terminal units (capillaries) are invariant, i.e. $r_c, l_c, \bar{u}_c$ and $\triangle p_c$ are independent of body size.

Since the fluid (blood) transports oxygen, nutrients, metabolites and other materials from the aorta to the capillaries for metabolism, the volume flow rate through the aorta is proportional to the metabolic rate ($Q_0 \propto B$); thus , if $B \propto M^a$ (*Recall*: Kleiber's Law; a will be determined later), then $Q_0 \propto M^a$. Capillary is an invariant unit (*Recall*: scale invariance); thus, the number of capillaries (N_c) must scale in the same way as the metabolic rate: if $B \propto M^a$, then $N_c \propto M^a$. So, if $B \propto M^{3/4}$ then the number of capillaries $N_c \propto M^{3/4}$. But the number of cells fed by a single capillary increases with M ($N_{cell} \sim M \rightarrow linear$). This "mismatch" means that the number of cells fed by a single capillary increases as $M^{1/4}$ (not $N_{cell} \sim M$). This is another manifestation that efficiency increases with size, and important implications for growth and death.

In order to characterize the branchings and to answer the question, how do radii and length of tubes scale through the network we introduce scale factors $\beta_k = r_{k+1}/r_k$ and $\gamma_k = l_{k+1}/l_k$. Because the terminal branches of the network are invariant units, the network must be a conventional self-similar fractal, i.e., $\beta_k = \beta, \gamma_k = \gamma$ and $n_k = n$ (branching ratio), all independent of the branching level k. For a self-similar fractal, the number of branches increase in geometric proportion ($N_k = n^k$) as their size geometrically decrease from level 0 to

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level N. Because $N_c = n^c$, the number of generations of branches scales only logarithmically with size

$$N = \frac{(a)ln(M/M_0)}{ln(n)} \tag{3}$$

where M_0 is a normalization scale for M. Thus, a whale is 10^7 times heavier than a mouse but has only about 70 percent more branchings from aorta to capillary.

The volume of fluid in the network ("blood" volume V_b) is

$$V_b = \sum_{k=0}^{N} N_k V_k = \sum_{k=0}^{N} \pi r_k^2 l_k n^k \propto (\gamma\beta^2)^{-N} V_c \tag{4}$$

where the last expression reflects the fractal nature of the system ($V_k \equiv$ volume of tube and $V_c \equiv$ volume of average capillary). From assumption that capillaries are invariant units, it follows that $(\gamma\beta^2)^{-N} V_c \propto M$. Using this relation in Eq. 3 then gives

$$a = \frac{ln(n)}{ln(\gamma\beta^2)} \tag{5}$$

To understand or to set the scaling exponent "a" it requires knowledge about the scale factors γ and β. The condition, that the fractal be volume-preserving from one generation to the next, can therefore be expressed as $N_k l_k^d \approx N_{k+1} l_{k+1}^d$, where l_k^d is the d-dimensional volume of space filled by branch at size l_k. This relation gives

$$\gamma_k = \frac{l_{k+1}}{l_k} = (\frac{N_k}{N_{k+1}})^{1/d} = \frac{1}{n^{1/d}} \tag{6}$$

showing that $\gamma_k \approx n^{-1/3} \approx \gamma$ (for d=3) must be independent of k. The 3/4 power law arise in the simple case of the classic rigid-pipe model, where the sum of the cross-sectional areas of daughters branches equals that of the parent, so $\pi r_k^2 = n\pi r_{k+1}^2$, where $r_k^2 \equiv$ x-sectional area of parent branch and $r_{k+1}^2 \equiv$ x-sectional area of each daughter. Thus,

$$\beta_k = \frac{r_{k+1}}{r_k} = \frac{1}{n^{1/2}} = \beta \tag{7}$$

independent of k.

When the area-preserving branching relation, $\beta = 1/n^{1/2}$, is combined with the space-filling relation, $\gamma = 1/n^{1/3}$, Eq. 5 yields $a=3/4$, so $B \propto M^{3/4}$, where "3" represents the dimensionality of the space and "4" (3+1) increases in dimensionality due to fractal-like space filling.

3 Further Scaling Laws

There are many other scaling laws. For example, for the aorta, the radius $r_0 = \beta^{-N} r_c = N_c^{1/2} r_c$ and the length $l_0 = \gamma^{-N} r_c = N_c^{1/3} l_c$, yielding $r_0 \propto M^{3/8}$ and $l_0 \propto M^{1/4}$. The hydrodynamic resistance of the network is proportional to $1/M^{3/4}$. This means that total resistance decreases with size (*Small may be*

beautiful but large is more efficient!).

The mammalian respiratory system is quite similar to the circulatory system. For instance, the tracheal radius is proportional to $M^{3/8}$ (like the aorta radius), the oxygen consumption rate $\propto M^{3/4}$ (like the metabolic rate) and the total resistance of the respiratory network decrease with size, too ($\propto 1/M^{3/4}$).

The derivation of the a=3/4 law is a geometric one, strictly applying only to systems like the cardiovascular or respiratory system that exhibits area-preserving branchings. A further consequence of this property is that the fluid velocity must remain constant throughout the network and be independent of size. It follows from Eq. 2. In the idealized vessel-bundle structure of plant vascular systems, the area-preserving branchings arises automatically because each branch is assumed to be a bundle of n^{N-k} elementary vessels of the same radius. Pulsative mammalian vascular systems do not conform to this structure. So we must look for the origin of quarter-power scaling laws. (1)

There is a more general 1/4 power-law applicable to many physiological variables y as shown in the table of Figure 4. It seems that all these physiological variables have something to do with the nutrient distribution networks and the dimensional dependence. For example, the life span is proportional to the linear dimension L, and the heart beat rate is related to the inverse L^{-1}. The other variables simply follow the same 3/4 power-law or L^3 as for the case of metabolic rate. It is obvious that the various physiological variables are determined primarily by the dimensional dependence.

Physiological variables	Dimension	Scaling exponent
Heart Beat Rate	-1	-¼
Period of Heart Beat	1	¼
Life Span	1	¼
Diameter of Tree Trunks	3	¾
Diameter of Aortas	3	¾
Brain Mass	3	¾
Metabolic Rate	3	¾

Figure 4: Examples of quarter-power scaling laws

4 Results and Conclusion

The allometric model of the form $Y = Y_0 M^b$ (b is the scaling exponent and Y_0 a constant that is characteristic of the kind of organism) accurately predicts the known scaling relations of mammalian circulatory system and the minor variant of the model describes the mammalian respiratory system, too. (see table in Figure 5)

Cardiovascular			Respiratory		
Variable	Exponent		Variable	Exponent	
	Predicted	Observed		Predicted	Observed
Aorta radius r_0	3/8 = 0.375	0.36	Tracheal radius	3/8 = 0.375	0.39
Aorta pressure Δp_0	0 = 0.00	0.032	Interpleural pressure	0 = 0.00	0.004
Aorta blood velocity u_0	0 = 0.00	0.07	Air velocity in trachea	0 = 0.00	0.02
Blood volume V_b	1 = 1.00	1.00	Lung volume	1 = 1.00	1.05
Circulation time	1/4 = 0.25	0.25	Volume flow to lung	3/4 = 0.75	0.80
Circulation distance l	1/4 = 0.25	ND	Volume of alveolus V_A	1/4 = 0.25	ND
Cardiac stroke volume	1 = 1.00	1.03	Tidal volume	1 = 1.00	1.041
Cardiac frequency ω	−1/4 = −0.25	−0.25	Respiratory frequency	−1/4 = −0.25	−0.26
Cardiac output $\acute{E}$	3/4 = 0.75	0.74	Power dissipated	3/4 = 0.75	0.78
Number of capillaries N_c	3/4 = 0.75	ND	Number of alveoli N_A	3/4 = 0.75	ND
Service volume radius	1/12 = 0.083	ND	Radius of alveolus r_A	1/12 = 0.083	0.13
Womersley number α	1/4 = 0.25	0.25	Area of alveolus A_A	1/6 = 0.083	ND
Density of capillaries	−1/12 = −0.083	−0.095	Area of lung A_L	11/12 = 0.92	0.95
O_2 affinity of blood P_{50}	−1/12 = −0.083	−0.089	O_2 diffusing capacity	1 = 1.00	0.99
Total resistance Z	−3/4 = −0.75	−0.76	Total resistance	−3/4 = −0.75	−0.70
Metabolic rate B	3/4 = 0.75	0.75	O_2 consumption rate	3/4 = 0.75	0.76

Figure 5: Values of allometric exponents for variables of the mammalian cardiovascular and respiratory systems predicted by the model compared with empirical observations. Observed values of exponents are taken from (4; 5; 6); ND denotes that no data are available. (1)

The presented model provides a theoretical, mechanistic basic for understanding the central role of body size in all aspects of biology. Non-fractal systems (e.g. electric motors) exhibits geometric (third-power) rather than quarter-power scaling. Because the fractal network must still fill the entire D-dimensional volume. In general case, the scaling exponent a=D/D+1 and organisms are three-dimensional, which explains the 3 in the numerator of the 3/4 power law. The model can potentially explain how fundamental constraints at the level of individual organisms lead to corresponding quarter-power allometries at other levels. Organisms of different body size have different requirements for resources and operate on different spatial and temporal scales, quarter-power allometric scaling is perhaps the single most pervasive theme underlying all biological diversity. (1)
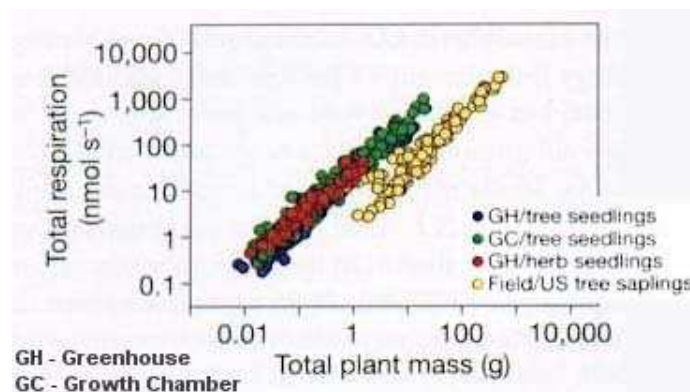

Figure 6: Plot with respiration (metabolic rate) against plant mass (3; 7)

A report in the January 26, 2006 issue of Nature indicates that the 3/4 power law is not observed in plants. The new experiment involved 500 individ-

ual plants, across 43 species, from varying environments, and covering six orders of magnitude variation in plant mass. It is found that the slope for a plot with respiration (metabolic rate) against plant mass is close to 1 (see Figure 6). The differences in the intercepts between the indoor and outdoor groups disappears if plant nitrogen mass is used instead of the total plant mass. This new result can be explained by the theory if the metabolic rate of plants is proportional to L^4 so that the metabolic rate is proportional to the body mass. (3; 7)

List of Figures

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