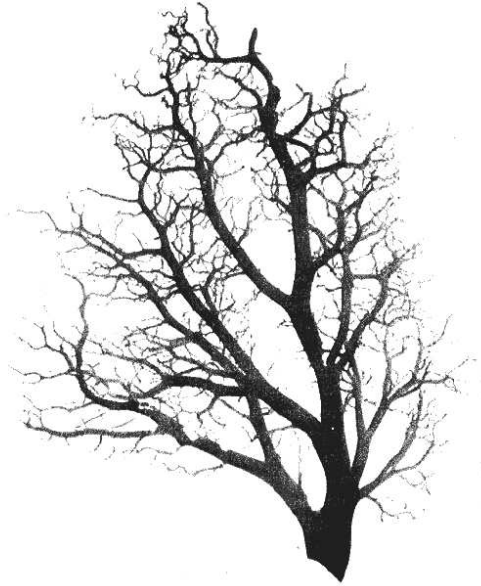


# Allometric Scaling Laws in Nature

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## Abstract

Biological systems of various kinds, from sub-cellular structures like the respiratory complex up to large mammals, seem to exhibit similar scaling behaviour, e.g. regarding their metabolic rates. This review introduces a theory to explain these scaling laws, based on the properties of the underlying biological networks which are needed to distribute resources throughout the corresponding organisms. This leads to a quantitative theory to describe structure, organization and dynamics of living systems.



## 1 Introduction

The philosopher Immanuel Kant (1724 - 1804) once wrote "chemistry was a science but not Science... for that the criterion of true Science lay in its relation to mathematics." [1] By now, inarguably, chemistry has been elevated to true Science, due to the development of "mathematical chemistry" and its blending with physics (based on, for example, Newton's laws).

Whereas chemistry stands on firm mathematical foundations, biology is still lacking in this respect. Although biologists can count on well-founded, general principles, such as Gregor Mendel's laws of inheritance, Charles Darwin's theory of evolution and the principle of natural selection, these hardly help on bringing forth quantitative statements about biological systems. Despite the extraordinary progress biology has made during the last decades, the basic question remains unanswered: "Do biological phenomena obey underlying universal laws of life that can be mathematized so that biology can be formulated as a predictive, quantitative science?" [1]

Most would regard this as unlikely, due to the extraordinary complexity commonly observed in biological systems. Still, it might be reasonable to conclude that at least the coarse-grained behaviour of biological systems is obeying quantifiable laws, which help to "capture the systems' essential features." [1] Characterizing these laws would enable biologists to construct simplified, idealized biological systems, whose average properties can be calculated. These ideal constructs could serve as a first point of departure for quantitatively describing and understanding real biological systems of high complexity.

The high diversity of life makes this search for universal, quantifiable laws a challenging task. The life process covers more than 27 orders of magnitude in mass, from DNA molecules to whales and giant redwoods, whereas "the metabolic power to support life across that range spans over 21 orders of magnitude." [1] Despite this high diversity of forms and dynamical behaviours of biological systems, one can observe that life tends to reuse the same building components over and over again to solve its main problem: The economic and efficient distribution of resources, such as energy, metabolites or information, from macroscopic sources (e.g. food intake) down to the smallest, microscopic subunits of the organism (e.g. cells, mitochondria or chloroplasts) This observation makes it worthwhile to take a look at the scaling behaviour of biological systems.

## 2 Allometric Scaling Laws

Scaling laws deal with measuring and comparing the relation of scale to the parameters which can be observed in a certain system. To put it bluntly, if one considers to construct a ship for sailing, building a little model ship to try out the construction details first might yield most valuable information about the behaviour of the full-size ship. In physics, determining the scaling behaviour of a system is a familiar principle to find out more about its underlying dynamics and geometry. Not only do scaling laws reflect the underlying generic features and physical principles of a system (which are independent of detailed dynamics or specific characteristics), they also help to reveal scale-invariant quantities, which usually point to its fundamental constraints. Considering this, it becomes clear that scaling laws also have relevance for biology.

The interest in scaling behaviour of biological systems brought forth the idea of allometry [greek: *allos* = *different*; *metrie* = *to measure*] [2], which deals with measuring and comparing the relation of body size to different biological parameters. In his work "Die Abhängigkeit des Hirngewichts von dem Körpergewicht und den geistigen Fähigkeiten" (1892), the German psychiatrist Otto Snell coined the classical allometric equation  $Y = Y_0 M^b \Leftrightarrow \log Y = b \log M + \log Y_0$ , where  $Y$  is some observable,  $Y_0$  is the (species-specific) integration constant,  $M$  is body mass and  $b$  the scaling exponent. The case  $b > 0$  is denoted positive allometry,  $b < 0$  equals negative allometry, whereas  $b = 1$  signifies the isometric case. Therefore, in biology, the observed scaling is a simple power law.

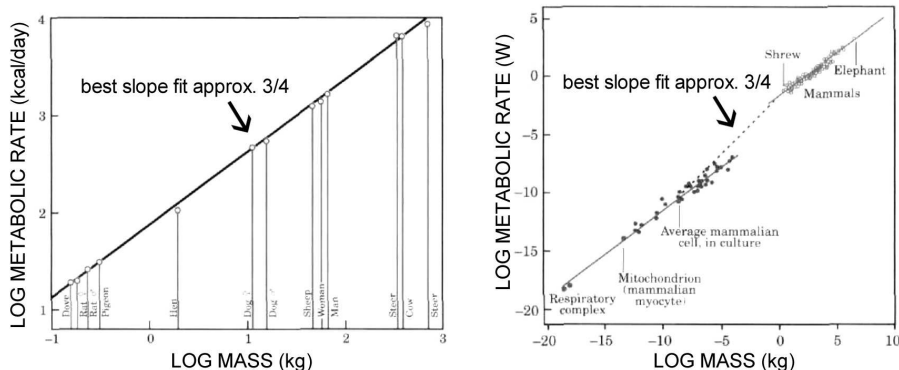


Figure 1: Left: The basal metabolic rate of mammals and birds as described by Kleiber. Right: The extension of Kleiber's work. [1]

One of the most studied observables in biology has probably been the basal metabolic rate, that is, an organism's energy use in respect to time (usually  $kcal/hr$ ). Nearly seventy years ago, the biologist Max Kleiber [3] showed that the metabolic rate of mammals and birds scales as  $M^{3/4}$ , which lead to Kleiber's law  $B \propto M^{3/4}$ , where  $B$  denotes the metabolic rate. While the masses of the animals in his original dataset only extend over four magnitudes in mass, in subsequent studies his finding could be generalized to ectotherms, unicellular organisms, plants and even to the intracellular level, terminating at the mitochondrial oxidase molecules. [1] Therefore, the validity of the metabolic exponent  $b \approx 3/4$  spans over 27 orders of magnitude in mass (see Fig. 1).

The fact that basal metabolic rate scales as  $M^{3/4}$  not only tells us that bigger organisms live more efficiently, it also raises the question why biological systems exhibit quarter-power scaling. A more naive approach might assume that, if an organism doubles its mass, it also would double its energy requirements (therewith  $b \approx 1$ ) or, following a simple surface-to-volume law from geometry,  $b \approx 2/3$ . Taking a look beyond metabolic rates, one realizes that, in biological systems, scaling with multiples of  $1/4$  seems to be a common principle: Heart rate scales as  $M^{-1/4}$ , life span scales as  $M^{1/4}$ , aorta and tree trunk diameters scale as  $M^{3/8}$ , unicellular genome lengths scale as  $M^{1/4}$  and population density in forests scales as  $M^{-3/4}$ . This list may be continued with other examples. As a consequence of quarter-power scaling behaviour, some invariant quantities emerge, that is, quantities that do not change dependent on the system's size.

For example, due to the fact that life span increases as  $M^{1/4}$  while heart rate decreases as  $M^{-1/4}$ , the number of heartbeats per lifetime remains approximately invariant ( $\approx 1.5 \cdot 10^9$ ). Since hearts are not as fundamental for life as the molecular machinery of aerobic metabolism, one might state that the number of ATP molecules produced per lifetime ( $\approx 10^{16}$ ) is an invariant, as well. [1] Another example, on a larger scale, can be observed in forest communities, where population density decreases with individual size as  $M^{-3/4}$ , whereas individual power use increases as  $M^{3/4}$ , which leads to an invariant power use by all individuals in any size class. As mentioned above, these invariant quantities point to the underlying constraints of the corresponding systems.

Now, how can the predominance of quarter-power scaling in nature be explained scientifically? In the following chapter, a popular approach to address this question by West, Brown and Enquist [4] is presented.

### 3 A Modelling Approach

The starting point for West and his fellow scientists was the observation that life, "highly complex, self-sustaining, reproducing, living structures", are dependent on effectively integrating and servicing enormous numbers of microscopic units with resources usually found in macroscopic quantities. To cope with this transport problem, natural selection has evolved biological networks, such as the animal circulatory system, the insect tracheal system, the plant vascular system, the large-scale networks of forest communities, or the microscopical intercellular networks of metabolism. They further concluded that the explanation to quarter-power scaling then has to stem from the structural properties underlying these biological networks. To characterize these properties they made further observations, which sum up to three unifying principles: First, in order to be able to supply the entire volume of the organism, a space-filling, fractal-like branching pattern is required. That means, though every single unit has to be serviced, there still has to be enough room for other internal structures or coexisting networks within the organism's volume. The issue of fractals is rendered more precisely later on. Second, the final branch of the network (such as the capillary in the circulatory system) is a size invariant unit, at least within the corresponding taxon. And third, the energy required to distribute resources throughout the network is minimized, which "is basically equivalent to minimizing the total hydrodynamic resistance of the system." [4] According to West and his colleagues, this energy minimization took place during the course of evolution. Scaling laws of biological systems then arise from the interplay between physical and geometric constraints implicit in these three principles.

The idealized nature of this model is reflected in the fact that non-linear effects such as turbulences in the network flow, or e.g. the deceleration of blood in the capillaries, are not considered crucial for the overall behaviour of the system. Still, using these properties, West and his fellow scientists obtain a strict mathematical derivation of the metabolic exponent  $b \approx 3/4$ , and therewith deliver an explanation for quarter-power scaling in nature. This mathematical derivation is mainly based on the properties of fractals.

## 4 A Short Introduction to Fractals

The term fractal was coined by Benoit Mandelbrot in the 1970s [5] and derives from the latin word *fractus*, which means "broken". Indeed, fractals are fragmented geometric shapes, of artificial or natural origin, whose fragments consist of smaller-sized copies of the whole. This important property of fractals is called self-similarity. Fractals usually can be obtained by using a simple recursive mathematical definition.

The dimensionality of fractals does not obey the laws of classical Euclidean geometry. When a fractal grows in size, this does not necessarily involve the area it is claiming in space, but its "grade of fragmentation" within. Therefore, fractals usually exhibit a non-whole numbered dimensionality, which can intuitively be regarded as an indication of how completely the fractal will fill space. [6] Today, there are various, specific definitions of fractal dimensionality, and none of them can be regarded as the universal one.



Figure 2: Evolution of the Sierpinski triangle, recursion depth four [7]

The Sierpinski triangle (see Fig. 2) is a famous example of a fractal with perfect self-similarity. It can be recursively produced by, in each step, shrinking the original triangle by  $1/2$ , copying it twice, and then placing the new triangles in such a way that each triangle touches the corners of the two other triangles. Therefore, in each step  $k$ ,  $3^k$  new triangles with side length  $(1/2)^k$  will appear. The dimensionality of the Sierpinski triangle can be obtained by using its recursive definition:

$$D = \lim_{\epsilon \rightarrow 0} \frac{\log N(\epsilon)}{\log \frac{1}{\epsilon}} = \lim_{k \rightarrow \infty} \frac{\log 3^k}{\log 2^k} = \frac{\log 3}{\log 2} \approx 1.585,$$

where  $k$  is the recursion depth,  $\epsilon$  is the linear size of self-similar fragments and  $N(\epsilon)$  is the number of self-similar fragments needed to cover the whole original object.

## 5 Derivation of Quarter-Power Scaling

When West and his colleagues observed the biological networks which evolution has brought forth, they realized that these exhibit the fractal-like properties described above. Fractal concepts in nature are not uncommon, as can be observed in the growing patterns of plants like ferns or cauliflower. [5] In general, fractal structures in nature do only show statistical self-similarity, and not the perfect self-similarity of their mathematical counterparts. Therefore, the pattern of vacuoles in a leaf resembles the branching pattern of the tree it came from, but most likely will not represent a perfect copy of it. In addition, the recursion

depth observed in biological fractals is relatively limited, often terminating after four or five steps.

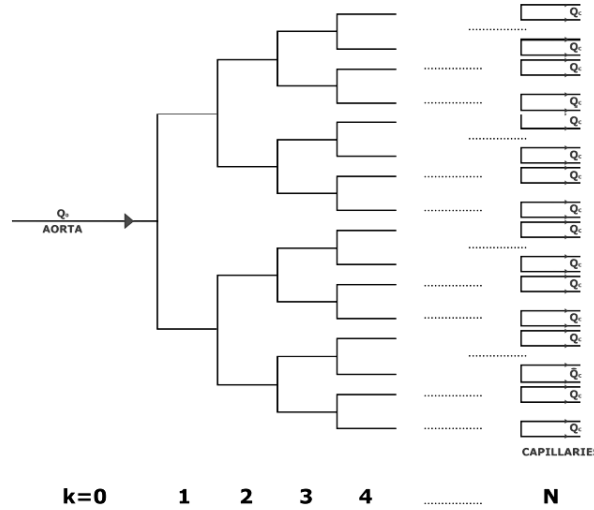


Figure 3: The fractal-like structure of the mammalian circulatory system

Still, the means of using fractal-like structures for describing biological networks is powerful enough to arrive at a derivation of the metabolic exponent,  $b = 3/4$ . West and his fellow scientists concluded that the metabolic rate should be equal to the flow rate through the corresponding network. They further observed that the volume of the flow has to be conserved on all levels of the network, which means that, when one is considering the circulatory system as an example, the capillaries (that, is the final level of the network) have to offer exactly as much volume as level zero, which would represent the aorta. The branching ratio from level to level remains invariant throughout the network, as well as the size of the final unit of the network, the capillaries. Using this knowledge, they then made use of hydrodynamic laws to minimize the total hydrodynamic resistance of their network model. Finally, they arrive at a derivation of the metabolic exponent  $b = 3/4$ , where, intuitively spoken, the three in the numerator refers to the dimensionality of space we live in, whereas the four in the denominator is due to the increase in dimensionality which takes place during the fractal-like space-filling (respectively during the branching process) of the network.

Although this model accepts a variety of simplifications, its predictions are in good compliance with empirical data, at least what concerns the cardiovascular (aorta radii, circulation time, total resistance, ...) and the respiratory system (tracheal radius, volume flow to lung, respiratory frequency, ...). [4] Therefore it can be regarded as a valuable step towards revealing the mathematical foundations underlying biology.

## References

- [1] West, G.B., Brown, J.H. *Life's Universal Scaling Laws*, Physics Today, American Institute of Physics, September 2004
- [2] <http://de.wikipedia.org/wiki/Allometrie>
- [3] [http://de.wikipedia.org/wiki/Kleibers\\_Gesetz](http://de.wikipedia.org/wiki/Kleibers_Gesetz)
- [4] West, G.B., Brown, J.H., Enquist, B.J. *A General Model for the Origin of Allometric Scaling Laws in Biology*, Science, Vol. 276, April 1997
- [5] <http://de.wikipedia.org/wiki/Fraktal>
- [6] [http://en.wikipedia.org/wiki/Fractal\\_dimension](http://en.wikipedia.org/wiki/Fractal_dimension)
- [7] [http://en.wikipedia.org/wiki/Sierpinski\\_triangle](http://en.wikipedia.org/wiki/Sierpinski_triangle)