

Power laws in biology.*

Between fundamental regularities and useful interpolation rules.

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Why live larger mammals longer than smaller ones? Why is the energy consumption per body mass of a mouse six times higher than that of a human? These questions and many others dealing with biological *allometry*[‡] kept and keep biologists busy since the second half of nineteenth century and as it seems, the ultimate answers have not yet been given. Analyzing allometry is particularly attractive since the biomass of organisms varies over more than twenty orders of magnitude from approximately 1 pg = 10⁻¹² g (mycoplasma, a very small bacterium) to 2 × 10⁸ g (blue whale), and in case of mammals the lower limit by mass is provided by the Etruscan Shrew with about 1 g thus still leaving eight orders of magnitude variation in body mass. The wide range of animal sizes makes body mass related properties an ideal test ground for scaling relations, in particular for power laws, and this is the reason why body mass allometry is chosen here as a representative and data rich example for other power laws. The number of papers dealing with attempt to scale body mass dependent relations in log/log-plots is indeed enormous.

The physiologist Max Rubner was presumably the first who addressed allometric scaling in his paper on body size and metabolism.¹ He suggested a power law

$$B = \beta M^\alpha \quad \text{or} \quad \log B = \log \beta + \alpha \log M$$

relating the whole-organism metabolic rate B to body mass M . From his data he found an exponent $\alpha = 2/3$, which meets the intuition that the metabolic rate should be related to the surface-to-volume ratio in order to sustain temperature regulation: Heat loss is proportional to the body surface and lost heat has to be compensated by metabolic energy dissipation. About fifty years later the Swiss biologist Max Kleiber reported that the consumption of oxygen of a resting mammalian body fulfilled a power law with a different exponent of $\alpha = 3/4$, which is often called Kleiber's law.² Ever since his publication more than seventy years ago a great number of scientists have tried either to question the relation or to provide an explanation for it. Jacob Blum provided a somewhat naïve solution to the problem: Biological organisms are four dimensional and the (hyper)volume to hyper(surface) ratio is then 3/4.³ John Speakman argues in response that heat exchange occurs across the two-dimensional body surface no matter what the (highest) dimension of the creature is and mass is proportional to volume and therefore "... the relationship 3/4 has absolute no bearing on the relationship between energy expenditure, body mass and the surface law..." and thus $\alpha = 2/3$ remains to be expected for four-dimensional organisms as well.⁴ We dispense here from all other historic details

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[‡] Allometry is the study of the relationship between size and shape. The original meaning of the term has been extended to all kinds of size and body mass related properties.

and mention only the more recent approaches beginning with the West-Brown-Enquist model published in 1997.⁵

The model by Geoffrey West, James Brown, and Brian Enquist (WBE model)⁵ is based on the assumption that metabolism is limited by transport of essential materials through a space-filling (near) optimal fractal network of branching tubes. In particular, the model is based on three principles: (i) The transport network supplies the entire organism, (ii) the final branches of the transport system, e.g. the capillaries of the blood circulation system, are size invariant, and (iii) the energy dissipation accompanying the distribution of resources is minimized. Because of the fractal nature of many biological transport systems – respiratory, cardiovascular, tracheal, xylem (for water) and phloem (for organic molecules) transport in plants – a formal fourth internal dimension in organisms is postulated. A fractal built from hierarchically structured one-dimensional objects may indeed have a Hausdorff-dimension of $d_H=2$ like, for example, the Peano curve does.⁶ Other examples are the Sierpiński curve, the Hilbert curve as well as probabilistic curves.^{8,7} The Hilbert curve is particularly interesting because the *Hilbert acinus* has some topological properties in common with the real acini.^{**},⁸ Consequently, biology of metabolic transport in organisms would not be three- but four-dimensional and this could explain intuitively the appearance of exponents in the power laws, which are multiples of $1/4$.⁹ In contrast to the Blum's explanation the 'fourth'-dimension of the WBE model is embedded in three-dimensional space in form of an area filling fractal. Many examples of scaling relations are known in which the scaling exponents are $n/4$ with n being some integer between -3 and 4.^{5,10} For some properties multiples of fractions of $1/4$, $1/6$, $1/8$, and $1/12$ are predicted and observed. The metabolic rate per gram body mass in mammals is easily shown to scale with $-1/4$:

$$b = \frac{b}{M} = \beta M^{\alpha-1} \quad \text{or} \quad \log b = \log \beta + (\alpha - 1) \log M \quad \text{with} \quad \alpha - 1 = -1/4$$

The cells in larger mammals metabolize more slowly and this fact is reflected by cardiac frequency and life span, which scale approximately with $-1/4$ and $1/4$, respectively.^{5,11} The final conclusion for the WBE scaling of the metabolic rate B boils down to the result:

$$B = \beta M^{(2+\varepsilon_A)/(3+\varepsilon_A+\varepsilon_L)},$$

with ε_A and ε_L being exponents describing the contributions of the effective surface area, through which metabolic resources are exchanged, and the characteristic length, respectively. Optimization of the exponents with respect to minimal energy dissipation eventually yields $\varepsilon_A = 1$ and $\varepsilon_L = 0$.^{9,12} A convincing argument for the validity of the interpretation based on fractal networks results from a comparison of size-scaling in non-fractal and fractal objects: combustion engines and electric motors exhibit the ordinary geometric, i.e. third power scaling. The WBE model thus seemed to have solved the debate on allometry that had lasted already for longer than a century.

[§] For a proof concerning the existence of probabilistic area filling curves of Hausdorff dimension $d_H = 2$ see, for example, Vincenz Beffara⁶.

^{**} A pulmonary acinus is the ending of a tiny airway in the lung where the air sacs called alveoli are attached.

In the review of the book ‘Scaling in Biology’¹³ Karl Niklas raises the question whether WBE theory because of its unifying explication of size-dependent organic phenomena is potentially as important to biology as Newtonian mechanics is to physics.¹⁴ Fair enough I would put Darwin’s principle of selection closer to Newton because it is in the core of biological thought but the following argument holds for both Darwin and WBE: Newton’s success was based on the existence of a celestial mechanics where all predictions of gravity could be studied without the perturbation by terrestrial side phenomena, friction and air resistance, spatial extension and plasticity of moving bodies for example. There is no celestial biology and therefore an ideal reference system that is accessible to observation and precise measurement is missing. Personally, I doubt that the laws of gravity would have been detected so fast without the simple celestial reference system together with the wealth of several thousand years of astronomic observations. Maybe they would not have been detected at all.

Despite the enthusiastic comments to the WBE model by part of the scientific community several criticisms were raised too. Already in 2001 it was argued that available data as well as the theoretical background for $\alpha = 3/4$ are unconvincing for rejecting the “null hypothesis” that $\alpha = 2/3$.¹² In particular, various deviations from the value $3/4$ are observed but the theory cannot account for such deviations although they are remarkable – the maximal metabolic rate (MMR), for example, scales with exponents as large as 0.92.^{11,15} A year later, in 2002 followed the suggestion to distinguish carefully between basal and maximal metabolic rates and to accept multiple causes for allometry that manifest themselves in a multi-exponential relationship:¹⁵

$$MR = \beta \sum_i \gamma_i M^{\alpha_i} ,$$

where MR stands for the metabolic rate in some given state, β is the intercept of the metabolic rate / body mass plot, and γ_i and α_i are weighting factor and scaling exponent of the i -th contribution to the metabolic rate. Almost all analyses of metabolic scaling involved data from different species. An extensive analysis of data from fish belonging to the same species¹⁶ revealed different α -values for different species and thus provided strong arguments against a single, universal value of α . Temperature dependence of metabolic rates has been taken into account but the scaling exponents for fish, amphibians, reptiles, and mammals remained significantly heterogeneous after normalization to a temperature of 38°C.¹⁷ Eventually, Douglas Galzler made an attempt to derive a unifying explanation for differences in metabolic rate scaling by broadening the focus of the analyses from considering average tendencies to understanding the variation between extreme boundary limits and from considering primarily internal factors like body design to explaining the influence of both, internal and external (ecological) factors.¹⁸ The inclusion of extreme situations, like sleep and in particular hibernation, suggests an interesting systematic extension of the ranges of scaling exponents at metabolic levels between the extremes of minimal and maximal metabolic rates where demand is much smaller than supply and demand is much larger than supply, respectively: The scaling exponent is supposed to be $\alpha = 1$ in the two limits and smaller in between. Variation of α is thought to follow a “U”-shaped curve with a minimum

value at $\alpha = 2/3$. The idea of Douglas Glazier called the metabolic level boundaries (MLB) hypothesis certainly is appealing but more data and further theoretical support are required for making it a serious alternative to WBE theory.

Finally, we mention extensive studies based on the WBE model and its amendments, which correct for finite size effects – because the scaling exponent $\alpha = 3/4$ is valid only in the limit of infinitely large body mass – and temperature differences.^{19,20} In addition, a quadratic rather than a linear fit is used yielding an equation of the form:

$$\log B = \log \beta + \alpha \log M + \gamma (\log M)^2 + \frac{\beta_T}{T} + \varepsilon .$$

The fit of data over the entire range is dramatically improved and the quadratic relation makes one more interesting prediction. Since power laws are necessarily linear they predict an asymptotic scaling exponent and there is no limit put on animal size by the metabolic rate. The quadratic model, however, suggests that the scaling exponent would increase without a bound. Then, metabolic scaling may define a maximal animal size, which might be at the mass where the local slope reaches the value $\alpha + 2\gamma \log M = 1$. Above this value further increase in body size would not allow for saving on metabolism. Interestingly, this limit lies around 10^8 g (100 t) and this is close to the size of the blue whale, the largest animal known.

The expressions for allometric scaling have increased in complexity from the first to the last equation shown here and purists might argue that the beauty of a simple power law has been lost eventually and what remains is little more than an interpolation formula based on some theory. This, however, is to be expected when one aims at fitting real data, which encapsulate the impacts of largely different influences on metabolism. It remains a task for the future to show whether or not more insight into metabolic mechanisms will provide hints for the choice of suitable conditions – internal and environmental – that will allow for a return to simpler relations.

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