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# Kleiber's law

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Kleiber's law,<sup>[1]</sup> named after **Max Kleiber**'s biological work in the early 1930s, is the observation that, for the vast majority of animals, an animal's **metabolic rate** scales to the <sup>3</sup>/<sub>4</sub> power of the animal's mass. Symbolically: if *q*<sub>0</sub> is the animal's metabolic rate, and *M* the animal's mass, then Kleiber's law states that *q*<sub>0</sub> ∼ *M*<sup>3</sup>/<sub>4</sub>. Thus a cat, having a mass 100 times that of a mouse, will have a **metabolism** roughly 31 times greater than that of a mouse. In plants, the exponent is found to be close to 1.

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## Biography

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Max Kleiber<sup>[3]</sup> was born and educated in **Zurich, Switzerland**. He graduated from the **Federal Institute of Technology** as an Agricultural Chemist in 1920, earned the **ScD** degree in 1924, and became a private dozent after publishing his thesis *The Energy Concept in the Science of Nutrition*.

He came to the Animal Husbandry Department of **UC Davis** in 1929 to construct **respiration chambers** and conduct research on energy metabolism in animals. Among his many important achievements, two are especially noteworthy. In 1932 he came to the conclusion that the <sup>3</sup>/<sub>4</sub> power of body weight was the most reliable basis for predicting the **basal metabolic rate** (BMR) of animals and for comparing nutrient requirements among animals of different size. He also provided the basis for the conclusion that total efficiency of energy utilization is independent of body size. These concepts and several others fundamental for understanding energy metabolism are discussed in Kleiber's book, *The Fire of Life* published in 1961 and subsequently translated into German, Polish, Spanish, and Japanese.

## Reasoning behind the law

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Kleiber's law, as many other biological **allometric laws**, is a consequence of the **physics** and **geometry** of animal **circulatory systems**, according to some authors. Young (i.e., small) organisms respire more per unit of weight than old (large) ones of the same species because of the overhead costs of growth, but small adults of one species respire more per unit of weight than large adults of another species because a larger fraction of their body mass consists of structure rather than reserve; structural mass involves maintenance costs, reserve mass does not.

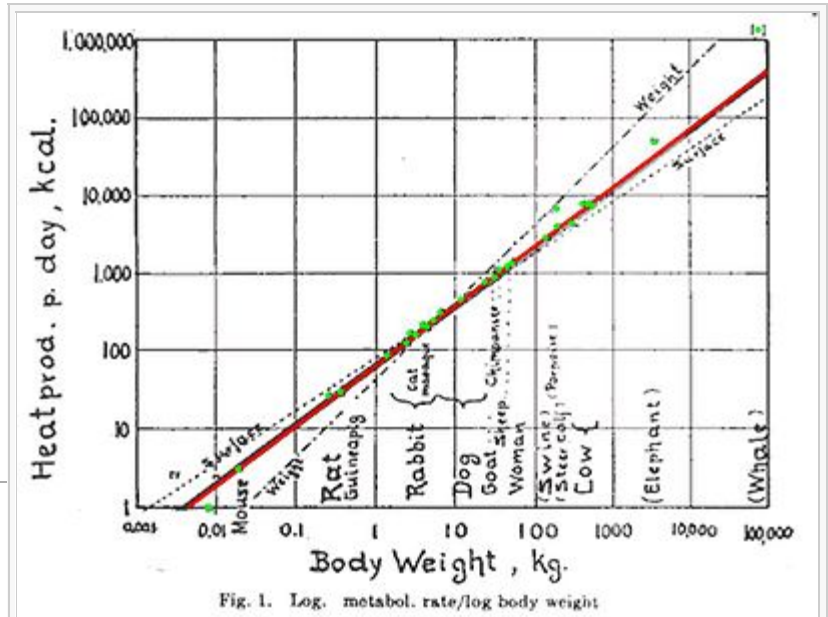


Figure 1. Body size versus metabolic rate for a variety of species<sup>[2]</sup>. Originally published in Kleiber (1947).



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## Value of the exponent

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The exponent for Kleiber's law, which is called a [power law](#), was a matter of dispute for many decades. It is still contested by a diminishing number as being  $\frac{2}{3}$  rather than the more widely accepted  $\frac{3}{4}$ . Because the law concerned the capture, use, and loss of energy by a biological system, the system's metabolic rate was at first taken to be  $\frac{2}{3}$  because energy was thought of mostly in terms of [heat energy](#). Metabolic rate was expressed in energy per unit time, specifically [calories](#) per second. Two thirds expressed the relation of the square of the radius to the cube of the radius of a [sphere](#), with the volume of the sphere increasing faster than the surface area, with increases in radius. This was purportedly the reason large creatures lived longer than small ones - that is, as they got bigger they lost less energy per unit volume through the surface, as radiated heat.

The problem with  $\frac{2}{3}$  as an exponent was that it did not agree with a lot of the data. There were many exceptions, and the concept of metabolic rate itself was poorly defined and difficult to measure. It seemed to concern more than rate of heat generation and loss. Since what was being considered was not necessarily [Euclidean geometry](#), the appropriateness of  $\frac{2}{3}$  as an exponent was questioned. Kleiber himself came to favor  $\frac{3}{4}$ , and that is the number favored today by the foremost proponents of the law, despite that  $\frac{3}{4}$  also does not agree with much of the data, and is also troubled with exceptions. Theoretical models presented by [Geoffrey West](#), [Brian Enquist](#), and James Brown,<sup>[4]</sup> purport to show how the  $\frac{3}{4}$  observation can emerge from the constraint of how resources are distributed through hierarchical branching [networks](#). Their understanding of an organism's metabolic/respiratory chain is based entirely on blood-flow considerations. Their claims have been repeatedly criticized as mistaken given that the role of fractal capillary branching is not demonstrated to be fundamental to the exponent  $\frac{3}{4}$ ; and that blood-flow claims severely limit the relevance of the equation to organisms greater than  $e^{-6}$  ( $\approx .0025$ ) grams when the simultaneous claim is made that the equation is relevant over 27 orders of magnitude, extending from bacteria, which do not have hearts, to whales or forests.

## Concept of metabolic efficiency

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This limit to blood flow considerations is problematic when claims are made that the theoretical models also are relevant to things without blood flow, like bacteria and coral. Moreover, despite assurances that the equation models metabolic efficiency, the term metabolic efficiency (ME) appears nowhere in the equation as expounded upon by its major proponents. When the term is added to the exponent (which becomes  $(4ME-1)/4ME$ , where ME is metabolic efficiency), and the exponent is  $\frac{3}{4}$  or  $\frac{2}{3}$ , ME is 100 or 89%. Efficiencies like these are not found in nature unless thermogenesis is included as part of metabolic rate. This removes the WBE version of Kleiber's Law, upon which the metabolic theory of ecology rests, from having any biological relevance whatsoever. The efficiency that is purported to be modeled is actually assumed.

Attempts to understand the metabolic rate of a multi-cellular organism (field metabolic rate, that includes the activity of the organism) are couched in terms of the product between average basal metabolic rate, and number of cells.<sup>[5]</sup> This, plus capillary terminal size invariance, leaves the equation open to the criticism that it cannot possibly account for spikes in metabolic rate needed for motor activity. Too much blood would be required. This intimates that as proposed and popularly handled, the equation does not have the relevance to biology claimed, and is based upon assumptions that are not part of the equation, like fractality.

In plants, according to a paper in 2006 in *Nature*, the exponent of mass is found to be close to 1.<sup>[6][7]</sup> Mathematically this is not possible since the implication is that ME is greater than 100% in the case of plants. The key problem is the nature of metabolic energy and the extent of what is to be considered as metabolism. The problem is most clearly noticeable in the unit term for metabolic rate, i.e., calories/s. Calories are a measure of heat energy. This leads to the idea that thermogenesis is part of metabolism, Kleiber's original treatment, and rules out that metabolism is all about chemical energy, not heat

energy. The picture is further obfuscated when the idea of respiratory metabolism is introduced to refine and limit the definition of metabolism such that oxygen consumption and synthesis of ATP are its ultimate factors. The data from study of oxygen consumption metabolic rates in cells in vitro suggests that the exponent is not only far less than  $\frac{3}{4}$ , but also becomes negative for things less than one gram in size. Furthermore, glycogenesis is excluded from metabolic consideration on this model since glycogenesis is not included in the respiratory chain, and is itself a reduction reaction not strictly dependent upon the proximity of certain molecules and atoms delivered by capillaries and vibrating from Brownian motion. Energy is required for glycogenesis, and the blood does not deliver energy, just the ingredients for endergonic reactions. The energy comes from redox coupling, what ME is all about.

The term ME amends these problems, and entails the unit term for metabolic rate be watts. Metabolic rate becomes the rate at which a biomass is recharged so that its degeneration is prevented, and its organization is perpetuated. ME is a ratio of the rate of reduction reactions necessary for the maintenance, growth, replication and behavior of the biomass, to the rate of availability of energy to be captured and expended by that biomass. ME is a statement of redox coupling efficiency. ME excludes thermogenesis as part of metabolism, consequently. A graph of Kleiber that includes ME, with ME as the X axis, metabolic rate as the Y axis, and a different curve for each mass, reveals a picture of the relation of biomass to metabolic rate that suggests all of evolution took place at less than 45% ME. Furthermore, this graph models the relation between basal metabolic rate and field metabolic rate, where the latter is the rate for the organism while the former is the rate for its cells. The graph clearly depicts that, contrary to WBE and Savage, biomass for an organism has no affect on basal metabolic rate (BMR); that what influences BMR is the ME of the organism, not its mass. The organism determines ME, and that ME is the same for it and for its cells.

The failure of WBE to parse Kleiber to understand the nature of aging is due to their mishandling of its mathematics. This mishandling results from failure to limit considerations of metabolism to strictly electrochemistry, and to exclude heat generation. Both of these things follow from failure to consider the role of variable ME on that biomass. If metabolic rate (MR) is taken as the recharge rate in watts of an electrolytic biomass, then MR is directly related to the longevity of that biomass. The equation, when graphed, suggests that for creatures operating at over 25% ME, the organism lives longer than its cells. What this indicates is that the organism has a source of new cells that are not initially a part of it, undifferentiated stem cells for example, especially in creatures over one gram mass. Aging appears to be the result of antagonism between BMR and FMR (field metabolic rate), given fluctuations in ME. These fluctuations are driven predominantly by alterations in the denominator of the ratio ME, where that denominator represents the availability of food sources.

## Current debate

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Current discussion and debate in the literature has refrained from consideration of the theoretical foundations for Kleiber's law. The role of thermogenesis in metabolism remains unexplicated, in part because Kleiber's law, as originally formulated, was based upon the idea that metabolic energy was entirely related to measurements of heat generation and loss. This appears in the unit of metabolic rate most favored, calories/s rather than watts (as in the version of Kleiber's law that includes ME, where ME is a ratio of redox amperes), and in the limitation of disputation as to whether ME is 89 or 100%. Others [e.g., Kozlowski and Konarzewski, [John Speakman](#)] have criticized West, Brown, and Enquist on the point that the size-invariance of [capillaries](#), which is the same from leaves to mammalian blood flow, dooms attempts to account for motor activity as part of metabolism.<sup>[8][9]</sup> This is why metabolic rates are almost always associated with the organism at rest, where metabolic rate is figured to be the basal rate for the cell rather than for the rate for the organism in its day-to-day life in the field. West et al. claim that Kleiber's law refers to the basal metabolic rate of an organism's cells, not the field metabolic rate of the organism itself, and regard field metabolic rate to be the product of the average basal metabolic rate and number of cells in the organism. Biologists point out that BMR cannot possibly account for motor activity even by this reckoning, and the equation is therefore of limited value either

way.

That metabolic efficiency should deviate from the favored high values is not part of the current debate, even though it creates inconsistencies within standard models, especially with regard to the nature of aging and the nature of the metabolic relation between the cell and the organism's mass. The standard versions of the equation's exponent (those which do not consider ME) cannot account for the wide variation in the lifetimes between rodents and birds of similar mass. This inconsistency could be explained simply if rodents had an ME less than 25% whereas birds didn't. Nor can the standard exponent explain why primates live so long when mammals of far greater mass do not live correspondingly longer, e.g., humans vs. whales, or chimpanzees vs. buffaloes. This is a simple matter if ME's are 31% vs. 28% in the first case, and 30% vs. 27% in the second. The relation of cell metabolic rate to organism mass, a contentious subject for proponents of the standard exponent, is modeled as non-existent when ME is considered, appearing instead as the relation of the cell's metabolic rate to the organism's ME, where the ME of the organism is the same as for its cells.

Major proponents of the equation, in the form of 'quarter power scaling', always limit themselves to mass specific metabolic rates, where the mass is one gram. The equation shows that at one gram mass, metabolic rate is the same for all MEs. This is why one gram is favored. It eliminates the role of ME in the equation, and makes the exponent  $\frac{3}{4}$  or  $\frac{2}{3}$  at least plausible to the initiate concerned with laboratory rather than mathematical study of metabolism. Gram specific masses limit the understanding of metabolism to the in vitro level, a limitation perpetuated by the unavailability of in vivo metabolic measuring equipment aside from oxygen-use and temperature monitoring. Attention to fundamental principles of the electrochemical nature and dependence of biomass, is deflected in favor of continuing disputation about the equation's relevance, the appropriateness of Euclidean considerations in a fractal world of capillary fluid dynamics, and the whispered depths to its secrets with regard to aging and to cancer, secrets unattainable so far. The inclusion of the term ME in the exponent allows for the energetic basis of biological organization to be modeled, where replication is biomass response to fluctuations in energy availability, and can be seen from bacterial multiplication and [quorum sensing](#), to the relation between mating strategies and food supply in large mammals.

## See also



[[edit](#)]

- [Allometric law](#)
- [Constructal law](#)
- [Evolutionary physiology](#)
- [Metabolic theory of ecology](#)
- [Scaling law](#)

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## External links

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- [Of Mice and Elephants](#) 
- [New Clues to Why Size Equals Destiny](#) 

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