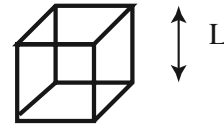
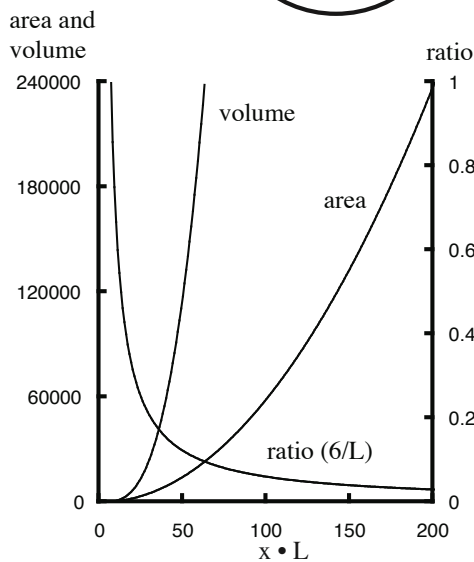
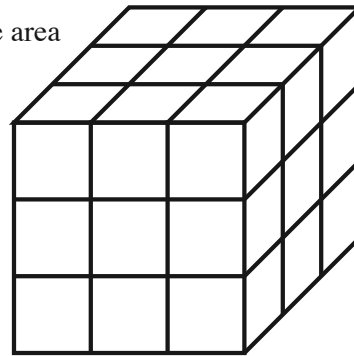
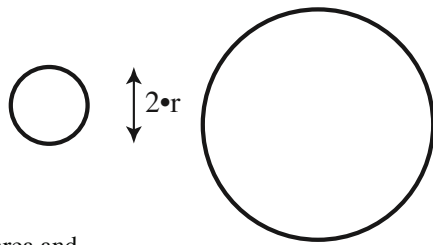


The word Allometry has two roots. *Allo* means ‘other’ and *metric* refers to measurement. The Oxford American Dictionary defines Allometry as “the growth of body parts at different rates, resulting in a change of body proportions.” It is different from either isometry (where *iso* means ‘same’) or anisometry (where *aniso* means ‘not the same’). The emphasis is on a difference in shape or proportions. Allometry may be a term unique to biology, since it is biological organisms that must change their shape (and thus their relative proportions) when their size is changed. To give an example of the differences (and similarities) of allometry and isometry, here is a relatively simple example of isometry that gives insight into why biological organisms tend to be allometric.

A cube has a surface area of $6 \cdot L^2$. Its volume is L^3 . As long as the shape is constant, the ratio of surface area to volume will always be $(6 \cdot L^2) / L^3$, or $6/L$.



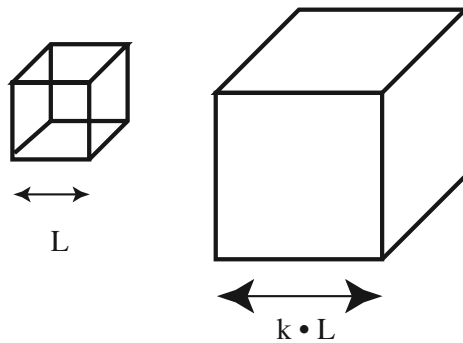
For a sphere, the surface area is $4 \cdot \pi \cdot r^2$, and the volume is $\pi \cdot r^3$; the corresponding ratio of surface area to volume is $4/r$.



The ratio of area to volume scales as the inverse of L with an increase in size. The graph (left) shows the area, volume and ratio as a function of the size of the cube (as a multiple of L).

Nota bene: The decrease in the surface area to volume ratio has an extraordinary impact on biological organisms. Larger organisms have less surface area available for taking up nutrients and radiating heat generated in respiration. That is, both nutrient requirements and heat generation scale with organismal volume, not area. But, nutrient uptake and heat loss scale with area.

Besides nutrient uptake / utilization and metabolic processes / heat loss, another aspect of the consequences of isometry are related to the strength of materials. Re-casting the area / volume of a cube in a different way^[1]:



$$\text{(area) } A_1 = 6 \cdot L^2 \quad A_k = 6 \cdot (k \cdot L)^2 \quad A_k = 6 \cdot k^2 \cdot L^2 \quad (= k^2 \cdot A_1)$$

$$\text{(volume) } V_1 = L^3 \quad V_k = (k \cdot L)^3 \quad V_k = k^3 \cdot L^3 \quad (= k^3 \cdot V_1)$$

The scaling coefficient is different for area (k^2) and for volume (k^3).

Now, suppose you have a swing hanging from a tree, child size, and want to double its proportions (to support an adult). That is $k = 2$.

To double the proportions means that the weight (or volume) is multiplied by 8 ($k^3=2^3$). But, the strength of the rope is proportional to the rope's cross-sectional area. So if $k = 2$, then the cross-sectional area is increased only 4-fold (2^2) when it has to be increased 8-fold to bear the weight of the larger adult.



Simple geometric scaling doesn't always work!

^[1]Inspired by "Galileo on Scaling", lecture notes from a course taught at the University of Virginia (Phys 609 Galileo and Einstein. <http://galileo.phys.virginia.edu/classes/609.ral5q.fall04>)

The problem of area/volume scaling was recognized by Galileo, a while ago. The passage relevant to biology is translated below^[1]:

“...I have sketched a bone whose natural length has been increased three times and whose thickness has been multiplied until, for a correspondingly large animal, it would perform the same function which the small bone performs for its small animal (Fig 27). From the figures here shown you can see how out of proportion the enlarged bone appears. Clearly then if one wishes to maintain in a great giant the same proportion of limb as that found in an ordinary man he must either find a harder and stronger material for making the bones, or he must admit a diminution of strength in comparison with men of medium stature; for if his height be increased inordinately he will fall and be crushed under his own weight. Whereas, if the size of a body be diminished, the strength of that body is not diminished in the same proportion; indeed the smaller the body the greater its relative strength. Thus a small dog could probably carry on his back two or three dogs of his own size; but I believe that a horse could not carry even one of his own size.”

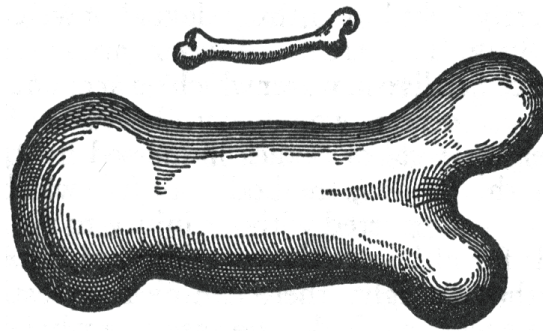
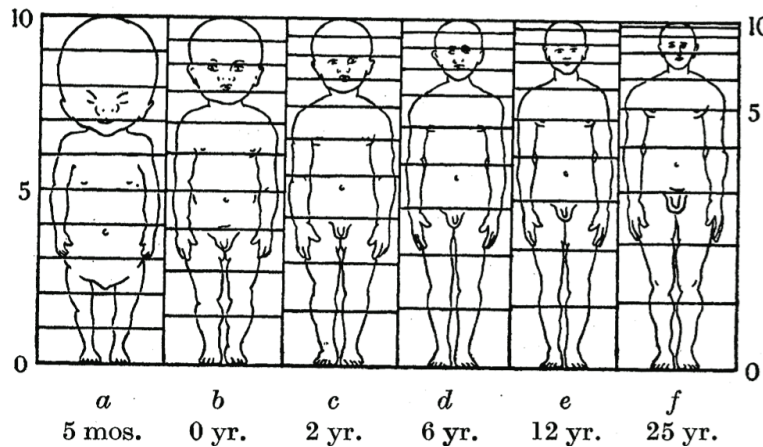


Fig. 27

There is one very important caveat. There may be no mass/area scaling problem at all, if the strength of the material is so great that a change in size is perfectly safe. Furthermore, the kind of strain matters. Think of a masonry bridge, an iron bridge and a suspension bridge. One has strength in compression, the next strength in shear, the last strength in tensility. To various extents, biomaterials offer a similar diversity of strengths (for example, bones offer compressive and shear strength, tendons offer tensile strength).

^[1]From: Dialogues Concerning Two New Sciences by Galileo Galilei. Translated from the Italian and Latin into English by Henry Crew and Alfonso de Salvio.

Because of many physical constraints — of which structural support / weight; metabolic requirements / area available for uptake; metabolic heat generation / radiative heat loss are very important — isometric changes in size are not always viable for a

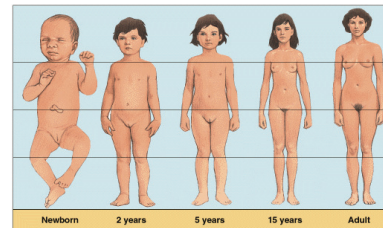


biological organism.

There are many examples of allometric alternatives. Here is an example of changing proportions in a biological context. The figure (left) shows the differences in proportion as a prenatal baby develops into a mature adult human.

It comes from a paper by Peter B. Medawar (1944)^[1] who attributes it to Stratz and obtained it from a human anatomy textbook.

It has been redrawn many times (often replacing the prenatal embryo with a newborn)(right).



Various measures, such as the length of the head, the length of the arms, etc., do not maintain the same ratio from the prenatal baby to the mature adult. That is, it is not isometric because the shape of the organism has changed, hence allometric. Allometry in this sense fits a definition by Gould —the difference in proportions correlated with changes in absolute magnitude of the total organism, or of the specific parts under consideration— as described by Sprent (1972)^[2].

An alternative, and common, definition of allometry is based upon the properties of the power function $y = b \cdot x^a$, in which, if the exponent, $a = 1$, then the function is isometric, otherwise it is allometric^[3] (see next page).

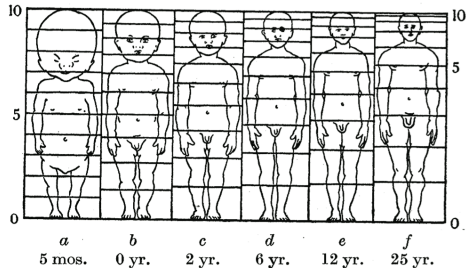
^[1] Medawar PB (1944) The shape of a human being as a function of time. Proceedings of the Royal Society of London. Series B, Biological Sciences 132:133–141.

^[2] Sprent, P (1972) The Mathematics of Size and Shape in Biometrics 28:23–37.

^[3] McMahon TA and JT Bonner (1983) On Size and Life. Scientific American Books Inc. pp. 32

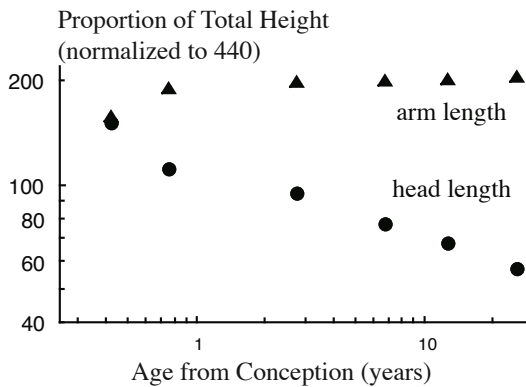
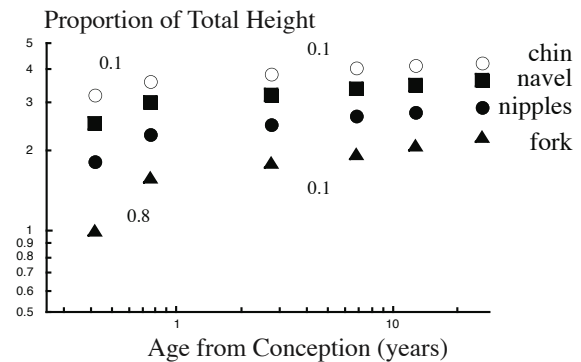
Some of the data presented by Peter B. Medawar (1944)^[1] are tabulated below:

years	fork base-line	navel	nipples	chin	total height
0.42	0.00	1.00	1.81	2.52	3.20
0.75	0.00	1.59	2.29	3.00	3.62
2.75	0.00	1.80	2.50	3.20	3.83
6.75	0.00	1.94	2.67	3.38	4.03
12.75	0.00	2.09	2.77	3.51	4.13
25.75	0.00	2.23	2.90	3.64	4.22



These are normalized to a baseline of zero and a maximum of 4.85, to separate proportions from changes in the length (height) of the organism. The graphs show log-log plots of the data. Thus the power function, $y = b \cdot x^a$, is transformed to $\log(y) = b + a \cdot \log(x)$. The slopes for the chin and fork are shown, for 0–1 and 2–26 years from conception.

For the lower extremities, there is a change in the allometric relation (from 0.8 to 0.1) which is quite striking, while the length to the chin is unaffected (0.1).



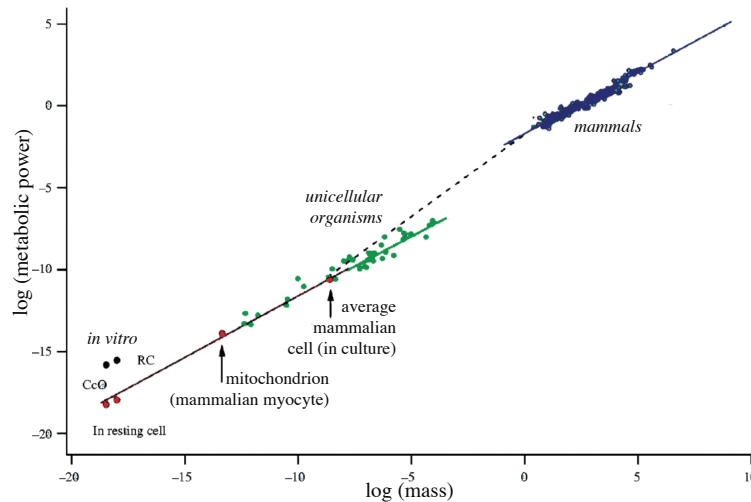
There are other relations. For example, head proportion declines with a slope of -0.22 for all ages, while arm length proportion increases (for 0–1 years, the slope is 0.33, declining to 0.02 for 2–26 years).

Nota bene: Most allometric plots show data in a range of three or more orders of magnitude. With the truncated plots of human proportions, the slopes a , of $y = b \cdot x^a$, are subject to uncertainty.

[1] Medawar PB (1944) The shape of a human being as a function of time. Proceedings of the Royal Society of London. Series B, Biological Sciences 132:133–141.

Allometry can therefore be used to explore the growth and development of a single species, and is easily extended to comparative analysis of related species differing in size. But much of allometric analysis compares unrelated species, since this may reveal general biological principles. One of the most explored relations is that between metabolic rates and the size (mass) of organisms. The graph of metabolic rates *versus* organismal size (mass) —in a log-log plot— (below) comes from a review by West and Brown (2005)^[1]:

“Extension of Kleiber’s 3/4-power law for the metabolic rate of mammals to over 27 orders of magnitude from individuals to mammalian cells, mitochondria and terminal oxidase molecules. In the region below the smallest mammal (the shrew), scaling is predicted to extrapolate linearly to an isolated cell in vitro, as shown by the dotted line. The 3/4-power re-emerges at the cellular and intracellular levels.”^[1]



The slope of the relation approximates to 0.75, the so-called 3/4-power rule originally proposed by Kleiber. The 0.75 slope for multicellular animals (mammals) indicates that large mammals respire proportionally less than smaller animals. One proposed reason is that a large size means less surface area for nutrient uptake and heat radiation. In fact, for mammals of various sizes from mice to whales, a log-log plot of surface area to mass has a slope of 0.63^[2] significantly less, but similar in magnitude to the 0.75 slope of metabolic rate versus size^[3]. Thus metabolic rate (and the concordant requirement for heat dissipation) scale similarly to surface area as a function of organismal mass. Note that metabolic rate normalized to mass would decline with greater organismal mass.

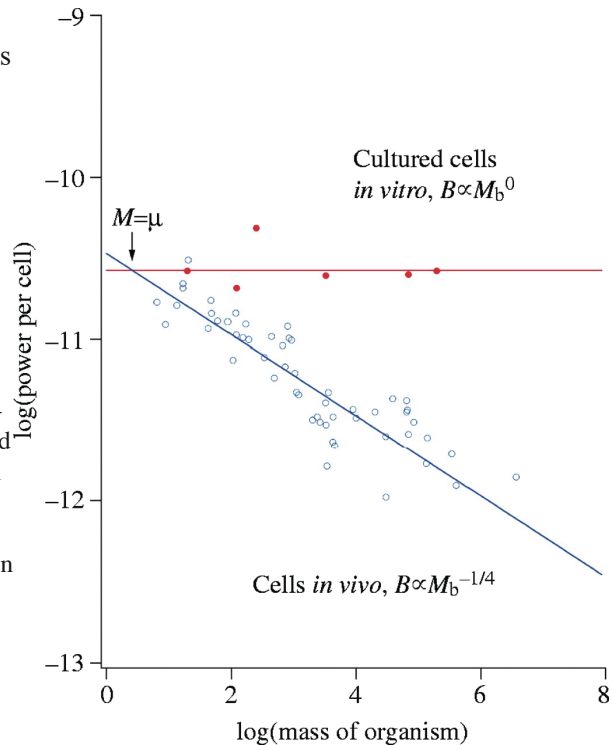
^[1]West JB and JH Brown (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. The Journal of Experimental Biology 208:1575–1592.

^[2]Geometric solids, for example a cube, sphere or dodecahedron, scale to $M^{0.667}$, where M (mass) is considered to be directly proportional to the volume of the solid. Explicitly for the case of a cube (page 1.02): Given that $A_k = k^2 \cdot A_1$ and $V_k = k^3 \cdot V_1$, we can set A_1 and V_1 equal to 1, so that $A_k \propto k^2$ and $V_k \propto k^3$. Now, $V_k^{2/3} \propto (k^3)^{2/3}$, or $V_k^{2/3} \propto k^2$. That is, $V_k^{2/3} \propto A_k$.

^[3]McMahon TA and JT Bonner (1983) On Size and Life. Scientific American Books. pp.130.

West and Brown (2005)^[1] show a graph of metabolic rate per cell (Watts per cell) *versus* organismal mass (right), showing clearly that the two scale as $M^{-0.25}$. Cell grown outside a body (*in vitro*) exhibit no such constraint.

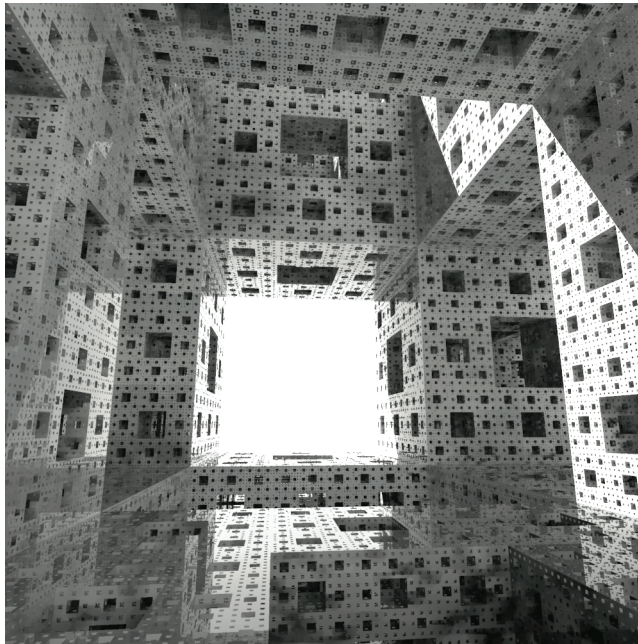
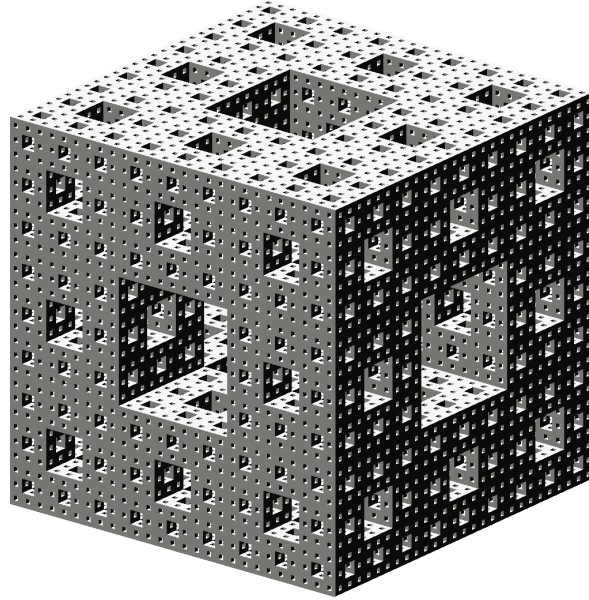
“Metabolic rates (in W per cell) of mammalian cells *in vivo* and cultured *in vitro* plotted as a function of organism mass (M_b in g) on a log–log scale. While still in the body and constrained by vascular supply networks cellular metabolic rates scale as $M_b^{-1/4}$. When cells are removed from the body and cultured *in vitro*, their metabolic rates converge to a constant value.”^[1]



In addition to heat dissipation, another factor that would play a role is the vasculature which supplies nutrients and removes byproducts of metabolism throughout the tissues of the multicellular animal. The size of the arteries etc. of an elephant are significantly larger than those of a small mouse, but would still constrain the metabolic capability of the larger organism. This, in concert with surface area constraints (scaling at $M^{0.63}$), may be one of the factors causing the $M^{0.75}$ scaling of metabolic rate *versus* size.

^[1]West JB and JH Brown (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. The Journal of Experimental Biology 208:1575–1592.

The $M^{0.67}$ scaling of surface area and volume is not a completely accurate model of the scaling in organisms. An interconnected sequence of cylinders is a more accurate shape for many multicellular organisms^[1]. But apart from the accuracy of shape, in animals, intestines, vasculature, lungs (or their equivalent in insects) all serve to increase the surface area relative to organismal mass (or volume) by extending the surface area

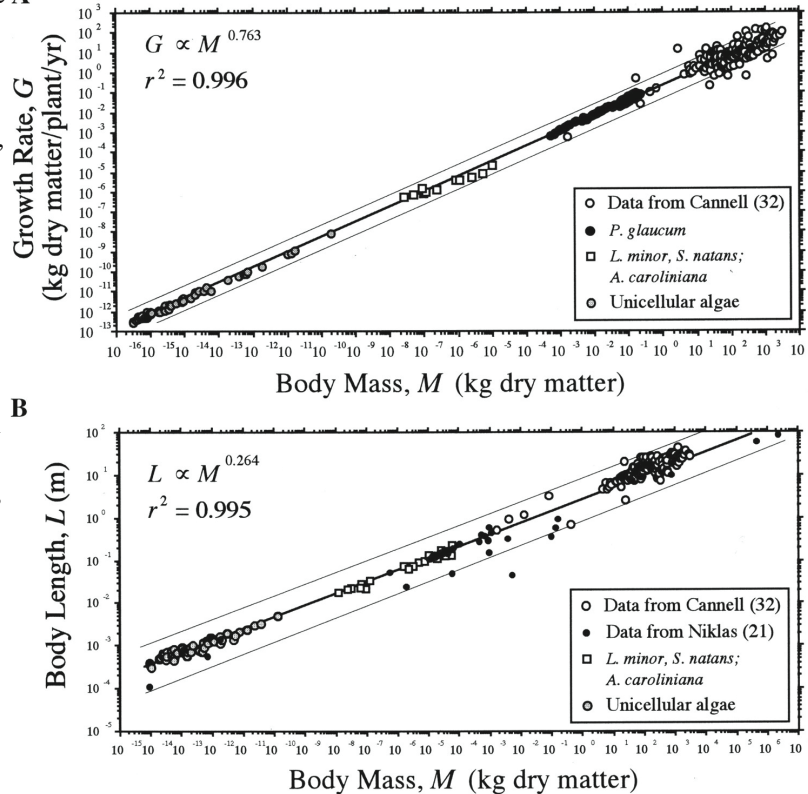


through invaginations that permeate the internal space. In plants, interstitial spaces between the cells and the vasculature of xylem and phloem serve a similar purpose. Both would enhance nutrient uptake. Perhaps a better geometric model of surface area and volume in an organism might be the Menger sponge^[2] of fractal fame, although not taken to the extreme where surface area becomes infinitely larger than the volume.

^[1]McMahon TA and JT Bonner (1983) On Size and Life. Scientific American Books Inc. pp. 128–129.

^[2]http://en.wikipedia.org/wiki/Karl_Menger; and http://en.wikipedia.org/wiki/Menger_sponge.

$M^{0.75}$ scaling of metabolic A rate versus size is not a unique property of animals (whether homeotherms or poikilotherms), but is also observed in plants (Niklas and Enquist (2001)^[1]). In these graphs, biomass production (an indirect measure of metabolic rate) and body length are shown *versus* organismal size. Growth rate scales as $M^{0.763}$. Note that plants exhibit indeterminate growth. That is, it is common for the organism to continue growth indefinitely, constantly accreting biomass.



“Annualized biomass production (growth) rates G (A) and body length L (B) of unicellular and multicellular plants plotted against body mass M . Scaling exponents (upper left) based on \log_{10} -transformed data.”

In summary, allometry and biological scaling can be used to explore the relations of proportions *versus* size, and metabolic rates *versus* size (or mass). The underlying causes can often be attributed to physical constraints of one type or another (but may also be independent of physical constraints). Many other parameters besides proportions and metabolism can also be explored.

^[1]Niklas KJ and BJ Enquist (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc Natl Acad Sci (USA)* 98:2922–2927.

The physics of heat conduction and radiation are relevant to the metabolic rate scaling with respect to organismal size. From *Fundamentals of Physics* by Halliday, Resnick and Walker, heat conduction rates are defined by the relation:

$$P_{\text{cond}} = Q / t = k \cdot A \cdot [(T_a - T_b) / L]$$

where P_{cond} is the rate of conduction (transferred heat, Q , divided by time, t); k is the thermal conductivity; T_a and T_b are the temperatures of the two heat reservoirs a and b ; A is the area; and L is the distance. Thermal conductivities of water and air are about 0.6 and $0.024 \text{ W m}^{-1} \text{ K}^{-1}$, respectively.

Thermal radiation is defined by the relation:

$$P_{\text{rad}} = \sigma \cdot \epsilon \cdot A \cdot T^4$$

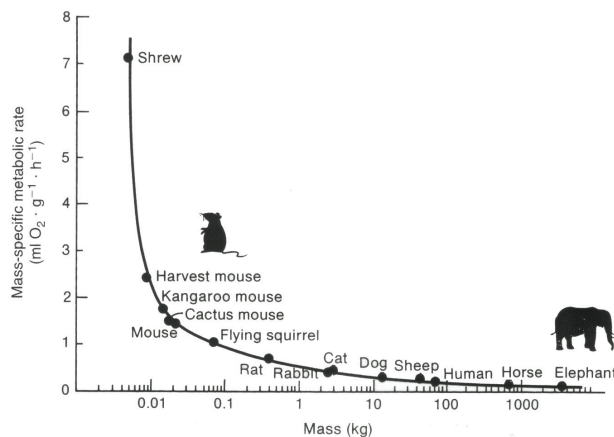
where P_{rad} is the rate of radiation; σ is the Stefan-Boltzmann constant ($5.6703 \cdot 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$); ϵ is the emissivity (varies from 0 to 1, where 1 is for a blackbody radiator); A is the area; and T is the temperature (in Kelvins). The *net* radiative emission or absorption will depend upon the difference in temperature:

$$P_{\text{net}} = \sigma \cdot \epsilon \cdot A \cdot (T_{\text{body}}^4 - T_{\text{ambient}}^4)$$

Advective thermal transport is far more complicated, since it will depend upon mass flow of the media (air or water in the case of biological organisms), in addition to conductive and radiative properties of the system.

Work Problem:

Determine the temperature and radiative heat loss contribution for animals of small and large size, having differing metabolic rates. For example, a shrew of mean weight 8 grams and metabolic rate of $0.75 \text{ ml O}_2 \text{ min}^{-1}$ (1 liter of O_2 consumption is equal to approximately 20.1 kilojoules). By comparison, human mean weight is about 72 kg, the basal metabolic rate is about 1600 kcal/day (1 Joule is equal to 0.2388 cal). How does the heat production balance with radiative temperature loss? Other examples of animals can be drawn from the graph below (source: Echert: Animal Physiology)



Metabolic intensity (mass-specific metabolic rate) is given as O_2 consumption per unit mass, plotted against body mass. Note that the graph is plotted differently from the metabolic rate versus body mass graph central to biological scaling. Values can be taken from the graph, for your animal of choice.

Hints:

Some approaches that may be useful include conversion of energy to temperature increases within an expected ambient range, and modeling the shape of the animal as a cylinder (as a first approximation) when considering of the rate of radiative heat loss required to balance heat production.

Work Problem:

Alexander (1971)^[1] notes that the smallest shrews and hummingbirds are the minimum size possible for an endothermic bird or mammal, because of the high metabolic rate required to maintain their temperature at 40°C (bird) or 37°C (mammal). Contrariwise, West and Brown (2004)^[2] argue that the constricted arteries at small body sizes are the factor limiting body size.

Who is right?

^[1]Alexander RMcN (1971) Size and Shape. section 2.6 (*heat loss by birds and mammals*).

^[2]West JB and JH Brown (2004) Life's universal scaling laws. *Physics Today* (September) 36–42. (*section on metabolic rate*).