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Climbing the *scala energiae*: The cost of growing animals great and small

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Building constructions, whether in technology or in the living world, need work, and work consumes energy. How strongly the energetic perspective matters depends on the cost of energy. The growth of biological populations is limited most of the time, but the limiting resource need not be the one from which the energy is gained. Sailors suffering from scurvy were not necessarily hungry, but they were running low on vitamin C. For a buyer, the energetic efficiency of a car engine may not be of primary concern when fuel is cheap. But, in contrast to living beings, the functioning of cars is neatly separated from production. Cars do not grow, maintain, or repair themselves. Amino acids, lipids, and sugars are needed for constructing the living body, but they also have valuable energy content. Ultimately, heterotrophic organisms live on the energy produced by autotrophs, mostly by photosynthesis. When there is competition for the energy source (as often is), there will be strong selection pressure to increase efficiency (1). In a recent paper, Mike Lynch extends previous work on ciliates (2) and asks how costly is developing metazoan bodies of different sizes (3).

For questions like this, biologists turn to allometric relationships, expressed as $y = a\, x^b$ where y and x are different, measurable trait values, and a is normalization constant. Obviously, this is a power-law formula. Lynch provides new experimental data on planktonic cladoceran (mostly the water flea *Daphnia*) populations and collects data from other taxonomic groups. Body size is easily measured in terms of dry weight, but measuring energy consumption is more indirect. Given that all metazoans considered in his paper are aerobic heterotrophs that obtain energy mostly from terminal oxidation, active respiration rates provide the required information. Lynch also carefully infers the energy requirement in terms of the number of Adenosine triphosphate (ATP) molecules (the main energy currency in all cells) as well.

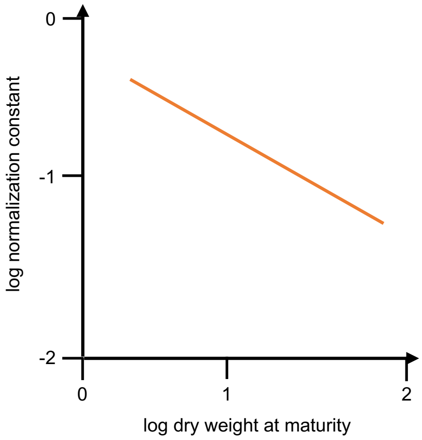

Fig. 1. Scaling of energy consumption per unit body weight with body weight for cladocerans. Energy consumption is cumulative through development. See ref. 3. for data.

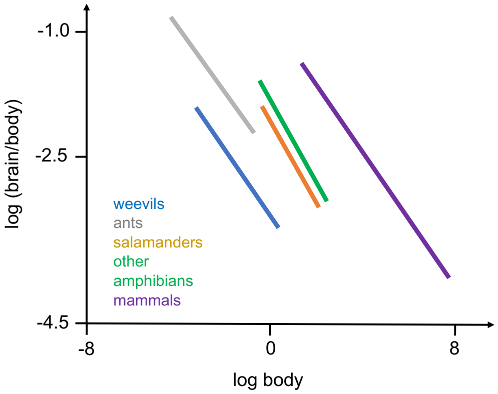

Fig. 2. Scaling of relative brain size with body size across animal taxa. See ref. 8 for data.

When comparing metazoans with protists such as ciliates and amoebae, one is faced with different developmental mechanisms. In the case of protists, we know when a new body has been built because then the cell divides, hence generation times and reproduction rates are readily obtained. Although some metazoans can reproduce by division, for the species considered in Lynch's study the soma (i.e., the body) is disposable, so one must set a criterion when the soma is "ready"—analogous to the time when a piece of product (house or car) can be put on the market. The size at maturity (first reproduction) is a sensible choice.

It is not surprising that other things being equal larger bodies consume more energy. For cladoceran species, the metabolic cost of producing biomass scales with exponent $b \approx 0.038$. The remarkable finding is that across species a is far from constant, as it negatively scales with size at maturity, thus biomass production cost per unit biomass is higher for smaller species, up to by a factor of 10 (Fig. 1). The total cost of development across species scales as $C_{\mathrm{mat}} = 2.38\ B_{\mathrm{mat}}^{0.736}$ where C_{mat} is the cumulative oxygen consumption from birth

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to maturity and B_{mat} is the size at maturity. The slope is parallel to that of ciliates but the cost for metazoans is about 30 times higher. A large protist is much more energetically efficient than a metazoan of the same size, and the cost per dry weight is larger in metazoans with smaller adult body size. What might be the reason? Any answer can only be tentative, since the study is restricted to a restricted sample of aerobic heterotrophs. As Lynch points out, we will need comparison with other taxa that show complex multicellularity (fungi, plants, red and brown algae).

The reason why protists are a lot cheaper energetically may be that they do not invest in nonreproductive tissue and function (support structures, cell adhesion, communication, transport and the nervous system). The question of cell turnover warrants special attention. Cell turnover is important not only in maintaining but also building metazoan bodies: Even during development, there is considerable cell death (4). At the cellular level, starting with bacteria, there is the cost of maintenance, which must be paid even if the cell is not growing. This is universal. But a protist, consisting of one cell, is necessarily not facing the cost of cell turnover. It does happen, but only at the population level—just as there is a population of cells building a metazoan. For cell turnover, this is the right level of comparison. Thus, cell turnover at the level of an individual metazoan entails an energetic cost that is not being paid by a big protist cell of the same size. It will be relevant to estimate in the future the fractional energetic cost of cell turnover.

> **In a recent paper Lynch extends previous work on ciliates and asks how costly developing metazoan bodies of different size is.**

Smaller metazoans may be more costly if they have smaller cells that require more membrane lipids per unit weight (3). Let us ponder about this question a bit more. Perhaps there is a costly body component that cannot be reduced in linear proportion to body size. It seems that the nervous system is a candidate for this. In fact, the nervous system is the specialty of the investigated metazoan species that could be called "neurates" in analogy to the ciliates (sponges and Placozoa do not have a nervous system). The nervous system is built and maintained expensively. The human brain has around 2% of body mass but consumes around 20% of the resting energy production (5). Transmission of just one bit (!) of information through a chemical synapse consumes 10^4 ATP molecules (6).

The logarithm of brain size scales very nearly linearly with body size across several taxonomic groups. Remarkable is what Rensch (7) coined Haller's rule stating that smaller vertebrate animals have bigger brains relative to their body size (Fig. 2). Now we are clear that this rule generalizes to invertebrates, although it is unclear why this must be so (8, 9). It is true for weevils, nematodes, mites, bees, ants, and spiders as well. In some small mites and spiders, the brain grows even into the legs. The slope of the log(brain/body) against log(body) is roughly the same in different taxonomic groups (implying a nearly uniform b), but the corresponding taxonomic lines are shifted from left to right relative to each other (implying different a values, in this context the cephalization quotient, in the allometric relation); the latter phenomenon is referred to as a grade change (figure 1 in ref. 8). For example, for the same body size, the relative brain size increases in the order of salamanders, other amphibia, and mammals. Importantly, the fact that on such a plot the small honeybee is to the left of a somewhat bigger salamander does not mean that it is cognitively inferior to the latter as the former can have the same relative brain size. Small spiders can be as "smart" as big ones, and this may be due to their larger relative brain size (9).

The tendency shown in Fig. 2 is about adult animals, not the whole developmental trajectory. Nevertheless, building a relatively bigger brain also requires more energy throughout development. Nervous tissue appears early in development, and it actively interacts with other body parts, partly guiding their development (10). All this calls for an extension of Lynch's pioneering investigation to look for grade changes in the relative energy consumption versus body size allometry (Fig. 1) across multiple taxa. The fractional energy requirement of the developing nervous system warrants closer scrutiny, since comparison of Figs. 1 and 2 is only suggestive, not decisive.

Energy versus body size considerations literally scale up to our own species. Hominins have gone through the last genetically conditioned major transition enabling them to use natural language for representation, communication, and cooperation (11). Humans and neanderthals have undergone considerable increase in relative brain size. How was this possible if the nervous system is so costly? One suggestion is that cooking allowed for efficient metabolism by the reduction of energy spent on digestion and, consequently, an evolutionary reduction of expensive gut length. This in turn could have allowed selection for larger brain size to be effective without a prohibitive energy cost (12). The hypothesis boldly posits, therefore, that already *Homo erectus* used fire, which squares well with the idea that protolanguage originated with that species (13). This evolutionary version of "Heraclitean fire" is appealing and will become more convincing when evidence for such an early use of fire will be found. This will require, as all serious research, time and energy.

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