The Origin of Universal Scaling in Biology

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Fall 2005 Modeling

September 14, 2005

1 Background

Consider the now famous figure reproduced in Figure 1.

Does metabolism scale as mass, taken to the 3/4 power? Or should it, as Euclidean geometry suggests, follow the argument for a sphere:

Since the surface area is $4\pi r^2$ and the volume is $\frac{4}{3}\pi r^3$, then $r = k_1 V^{1/3}$. This tells us that:

$$S.A. \propto V^{2/3}$$

Key factors such as heat dissipation might suggest it...

In the 1980's there was some argument as to whether the exponent was 3/4 or 2/3, and these arguments were based on the statistics used for the data analysis- it was not model based. For example, Heusner (1982) stated that, within a single species, metabolism does indeed scale to 2/3, so the 3/4 scaling factor was simply a statistical artifact[1]. This was followed by a paper by Feldman and McMahon (1983) that stated that, while within a single species, the scaling factor might be 2/3, but between species, 3/4 was not an artifact of the statistics.

So which is correct? We discuss a new model for scaling below, but before doing so, here are some scaling characteristics taken from data analysis for mammals:

- The volume of blood scales with the mass, $V_b \propto M^{1.02}$
- The size of the heart scales with the mass, $M_h \propto M^{0.98}$

[1] See Exercises

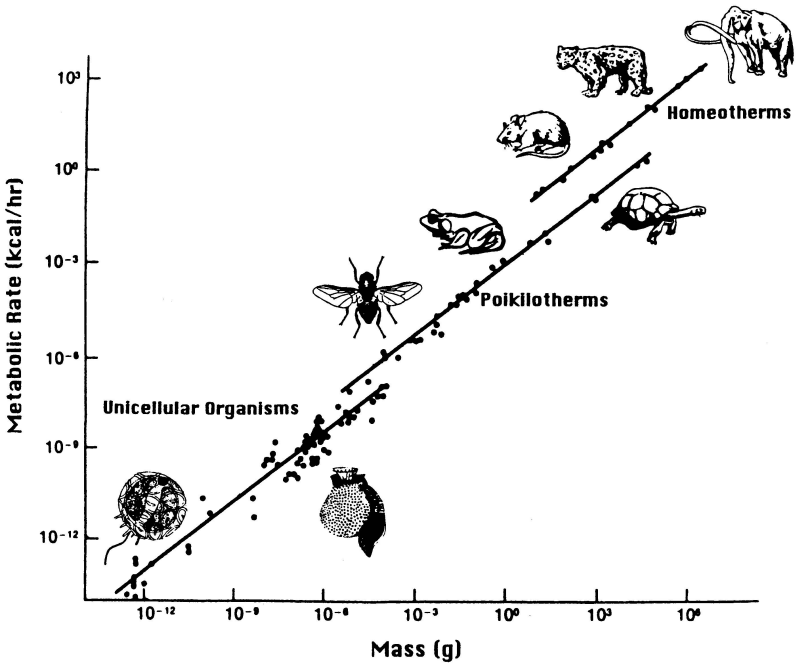

Figure 1: A logarithmic plot of metabolic rate versus body mass. Even though body mass undergoes a 21 order of magnitude difference, we see that the metabolic rate scales quite nicely with mass. (Reproduced from "Scaling in Biology", edited by Brown and West)

- The frequency of the heartbeat scales as: $f_h \propto M^{-1/4}$
- The volume of the lungs scales with mass: $V_l \propto M^{1.04}$
- The tidal volume of the lungs scales as: $V_t \propto M^{1.04}$
- Oxygen consumption scales like $M^{1/4}$
- The following characteristics are independent of mass (scale like M^0): radius of capillaries, velocity and pressure of the blood at both the aorta and the capillaries.

To quote West, Brown and Enquist:

> Allometric scaling laws are special because they express a systematic and universal simplicity in the most complex of all complex systems. They provide rare examples of universal quantitative laws in biology. Their origin presents a major challenge because their very existence, not to mention their common quarter-powers, suggests the operation of a set of principles that are fundamental to all life.

Amazingly enough, it seems that longevity scales as $M^{\frac{1}{4}}$ so that this, taken together with the scaling for the frequency of the heart, means that *the number of heartbeats in a lifetime is the same, about* 1.5×10^9*, for all mammals, regardless of size.* We should note that human beings now live far beyond the age expectancy determined by their body mass (which would be about 40 years)! Here's the equation:

$$\frac{x \text{ beats}}{1 \text{ minute}} \cdot \frac{526032 \text{ minutes}}{1 \text{ year}} \cdot \frac{y \text{ years}}{1 \text{ lifetime}} \approx 1.5 \times 10^9$$

2 Introduction

Recently, a Universal Scaling Law has been introduced by West, Brown and Enquist (2000) for Biology. In this paper, we summarize the model features. As an overview, the basic idea is to use a fractal structure to model the scaling of the circulatory system. This structure will then predict a scaling of metabolism to mass,

$$\text{metabolism} \propto \text{Mass}^{3/4}$$

Since metabolism plays a key role (and a key constraint) in the body, it may not be surprising that other scaling relationships, taken from this one, are multiples of 1/4. We begin with a discussion of the model, and the construction of this scaling model. We will then conclude with some other scaling models built off this.

3 Discussion

The Universal Scaling model (West et. al.) stems from the idea that, when scaling up biological organisms, the key notion is that of a self-similar network (e.g., blood arterial networks). In defining such a network, there are four significant variables:

1. N is the total number of branchings in the network.

2. n is the number of branches at each node (independent of which node, if the network is self-similar).

3. β is the ratio of the radii $\frac{r_{k+1}}{r_k}$, which is independent of the node k if the network is self-similar. We think of r_0 as the radius of the aorta, and r_N as the radius of a capillary. The radius of a capillary, r_N is independent of mass (although N is dependent on mass).

4. γ is the ratio of the lengths $\frac{l_{k+1}}{l_k}$, which is also independent of the node k if the network is self-similar. We think of l_0 as the length of the aorta, l_N is the length of a capillary.

For some benchmark values, in humans $N \approx 22$, $n = 3$, and $\frac{r_0}{r_N} \approx 10^4$.

There are two main scaling arguments that connect the constants together. They are:

$$\gamma = n^{-1/3}, \qquad \beta = n^{-1/2}$$

We will take these first.

Model Assumption 1: Volume Filling
The volume serviced by the blood should fill the entire volume:

$$V = n^N V_N$$

where V is the volume of the animal, V_N is the volume serviced by a capillary.

We make the simplifying assumption that the volume serviced at a capillary, V_N, scales like l_N^3 (versus what it should be, $\pi r_N^2 l_N$). For large N, V_{N-1} should be well approximated by l_{N-1}^3, and

$$\frac{V_N}{V_{N-1}} \approx \left(\frac{l_N}{l_{N-1}}\right)^3 = \gamma^3$$

The authors argue that $V_{N-1} = nV_N$ follows from the volume filling requirement. In that case, we have:

$$\frac{1}{n} = \gamma^3 \text{ so that } \gamma = n^{-1/3}$$

If the service volume was more generally d dimensional, then we could take $\gamma = n^{-1/d}$.

Model Assumption 2: Energy Minimization. This section could be quite technical[2], but the end result is that there is area preservation in the branching so that:

$$\pi r_k^2 = n\pi r_{k+1}^2$$

We will take the area preservation as an assumption. This gives:

$$\beta^2 = \left(\frac{r_{k+1}}{r_k}\right)^2 = \frac{1}{n}$$

or

$$\beta = n^{-1/2}$$

We obtain our last scaling relationship by considering how the blood volume scales. First, we write the total blood volume as the sum of all the blood in the network. Note that at level k, there are n^k branches, each having radius r_k and length l_k.

$$V_b = \sum_{k=0}^{N} \pi n^k r_k^2 l_k$$

In order to write this as a geometric series, recall that γ and β are scaling coefficients so that we can write every length and radius in terms of the length and radius of the aorta:

$$r_1 = \beta r_0, \quad r_2 = \beta^2 r_0, \quad r_3 = \beta^3 r_0, \ldots \Rightarrow \quad r_k = \beta^k r_0$$

[2]We've left off some critical arguments to the full model in this simplification. The interested reader should go to the full reference for all the details.

$$l_1 = \gamma l_0, \quad l_2 = \gamma^2 l_0, \quad l_3 = \gamma^3 l_0, \ldots \Rightarrow \quad l_k = \gamma^k r_0$$

Equivalently, we could write each term in terms of a capillary unit (which is mass independent) rather than in terms of the aorta:

$$r_k = \left(\frac{1}{\beta}\right)^{N-k} r_N, \quad l_k = \left(\frac{1}{\gamma}\right)^{N-k} l_N$$

Finally, recall that the sum of a geometric series is given by:

$$\sum_{k=0}^{N} w^k = \frac{1 - w^{N+1}}{1 - w}$$

Now we can rewrite the blood volume as a geometric series to relate total blood volume to our constants γ, β and n (recall that N is the total number of branchings in the network).

$$V_b = \frac{\pi r_N^2 l_N}{(\beta^2\gamma)^N} \cdot \sum_{k=0}^{N} (n\beta^2\gamma)^k = \frac{V_N}{(\beta^2\gamma)^N} \cdot \frac{1 - (n\beta^2\gamma)^{N+1}}{1 - (n\beta^2\gamma)}$$

The appearance of $\beta^2\gamma$ is rather interesting, since it represents the ratio of the volumes:

$$\beta^2\gamma = \frac{\pi r_{k+1}^2 l_{k+1}}{\pi r_k^2 l_k} = \frac{V_{k+1}}{V_k}$$

Because we assume N to be somewhat large, we can make the approximation:

$$1 - (n\beta^2\gamma)^{N+1} \approx 1$$

so that

$$V_b \approx \left(\frac{V_N}{1 - n\beta^2\gamma}\right) \cdot \left(\beta^2\gamma\right)^{-N}$$

4 Putting it all Together

Now, it seems appropriate that the total volume of blood should scale with the mass,

$$V_b \propto M \text{ and } V_b \propto V_N(\beta^2\gamma)^{-N}$$

However, we assume that V_N is independent of mass[3] , which means that:

$$(\gamma\beta^2)^{-N} \propto M$$

[3]This is the third model assumption

so that:

$$(\gamma\beta^2)^{-Nb} \propto M^b$$

for all $b > 0$. Now suppose that the metabolism rate, B is proportional to some power of mass, M:

$$B \propto M^a$$

Since metabolism is controlled by the cell's fuel, we also have that metabolism scales with the number volumes serviced by the capillaries (n^N),

$$B \propto n^N$$

so that

$$n^N \propto M^a \propto (\gamma\beta^2)^{-Na}$$

which implies that

$$n \propto (\gamma\beta^2)^{-a} = (n^{-1/3} \cdot n^{-1})^{-a} = n^{\frac{4}{3}a}$$

so that $a = \frac{3}{4}$.

5 A Summary of Some Results

- We have shown that metabolism B scales as $M^{3/4}$.
- We can also obtain scaling rules for the aorta:

  $$r_0 = \beta^{-N} r_N, \text{ and } \beta^{-2} = n \Rightarrow \beta^{-N} = (n^N)^{1/2}$$

  Now, $n^N \propto B \propto M^{3/4}$, so the radius of the aorta should scale as mass to the power $\frac{1}{2} \cdot \frac{3}{4} = \frac{3}{8}$, which is in good agreement with the data.
- Similarly, the length of the aorta scales as $M^{1/4}$.
- It seems reasonable to assume that the tidal volume[4], V_h, for an organism is proportional to its mass.

  If we state that the rate of volume change in the blood at the aorta, $\dot{Q}_0$ is equal to the product of the tidal volume, V_h, times the heart rate, ν,

  $$\dot{Q}_0 = V_h \nu$$

  Then, since $\dot{Q}_0 \propto B \propto M^{3/4}$, we get $\nu \propto M^{-1/4}$, which is in good agreement with the data.

[4]The volume of air inhaled and exhaled at each breath.

A final word: This model is still very new and needs to be verified against observed data. However, it seems that the model does explain existing data, and it makes very specific predictions about several other measurements.

6 References:

This article was a summary of the following:

- "The Origin of Universal Scaling Laws in Biology", By G. West, J. Brown and B. Enquist, *Scaling in Biology*, Edited by J. Brown and G. West, Oxford University Press, 2000.

Some items were from:

- *Scaling: Why is Animal Size so Important?*, by K. Schmidt-Nielsen, Cambridge University Press, 1984.