Nutrient-Flow Model for 3/4 Metabolic Scaling

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The West, Brown and Enquist (WBE) 1997 paper provided a new approach to understanding allometric metabolic scaling, $B \propto M^a$, commonly supposed in ecology. Through a series of assumptions, they provided a theoretical basis for the exponent value $a = 3/4$. Criticized on both empirical and mathematical fronts, their paper formed the basis for a potentially more useful model created by Etienne, Apol and Olff (EAO) in 2006. The beginning of the WBE model will be discussed, up to an irrecoverable step, at which point the discussion will move on to the EAO model.

The notation here is that used in the EAO paper, as follows:

Quantity	This paper	West et al. (1997)
Level number	$k+1$	k
Range of level numbers	$k = 1 \ldots C$	$k = 0 \ldots N$
Level number of last level (capillaries)	C	N
Quotient of number of vessels at levels $k+1$ and k	ν_{k+1}	n_k
Quotient of vessel radius at levels $k+1$ and k	ρ_{k+1}	β_k
Quotient of vessel length at levels $k+1$ and k	λ_{k+1}	γ_k
Metabolic scaling parameter	x	a
Blood flow at level $k+1$	Q_{k+1}	Q_k
Velocity at level $k+1$ averaged over the cross-sectional area	u_{k+1}	$\ddot{}_k$

Figure 1: Table 1 from Etienne et. al.

The WBE Model

We are considering "circulation system" – that is, a system whereby the nutrients necessary for metabolism are transported to the cells. This system has a discrete number, C, of vessel sizes ranging from the largest (the "aorta") to the smallest ("capillaries"). At a node, the k-level vessel branches into v_k of the $k+1$ vessels. Each of these vessels has a characteristic length, radius, pressure drop, velocity and rate of flow. *The amount of fluid is conserved*, so

$$\dot{Q}_0 = N_{k+1}\dot{Q}_{k+1} = N_{k+1}\pi r_{k+1}^2 \bar{u}_{k+1} = N_c \pi r_c^2 \bar{u}_c. \tag{1}$$

Assumption: The smallest units have invariant size. Thus, the properties of vessels listed above, at the capillary size, are independent of animal size.

This fluid flow, $\dot{Q}$, is linked directly to the rate nutrients are delivered to cells, so $\dot{Q} \propto B \propto M^a$. Then, by equation 1, $N_c \propto M^a$.

Putting aside the question of why these networks are self-similar and fractal, if we assume they are, then the following occurs. At each node, a vessel branches into n smaller vessels, whose radii decrease in a constant proportion $\rho = \frac{r_{k+1}}{r_k}$ (which maintains area) and whose lengths decrease at a constant rate $\lambda = \frac{l_{k+1}}{l_k}$ (which reflects the space-filling property). Now $N_c = n^N$ and we can rewrite the allometric equation $N_c = (M/M_0)^a$ as

$$N = \frac{a \cdot ln(M/M_0)}{ln(n)} \tag{2}$$

Now, *the total amount of blood must fill all these blood vessels*, resulting in the geometric sum

$$V_b = \sum_{k=0}^{C} N_{k+1} V_{k+1} = \sum_{k=0}^{C} \pi r_{k+1}^2 l_{k+1} n^k \approx \frac{V_c(\lambda\rho^2)^{-C}}{1 - n\lambda\rho^2}. \tag{3}$$

If one accepts this fractal nature and further *assumes that the volume of the blood (and volume of the capillaries) scales directly with mass*, or equivalently, $(\lambda\rho^2)^{-C} \propto M$ (contradicting(?) assumption of $N_c \propto (M/M_0)^a$ leading to equation 2, from Kozlowski and Konarzewski), then by rearranging equation 2 the scaling exponent becomes

$$a = -\frac{ln\ n}{ln(\lambda\rho^2)}. \tag{4}$$

If we *assume the system is space filling*, that is, $4/3\pi(l_k/2)^3 N_k \approx 4/3(l_{k+1}/2)^3 N_{k+1}$, then $\lambda = n^{-1/3}$. Similarly, the *assumption that the cross-sectional area is preserved at each junction*, $\pi r_k^2 N_k \approx \pi r_{k+1}^2 N_{k+1}$, implies $\rho = n^{-1/2}$. With equation 4, we find $a = 3/4$.

To achieve this result, WBE invoke an energy-minimization principle along with a pipe-branching model. These assumptions are fraught with errors, not the least that their choices of ρ_k, λ_k *and* n_k do not necessarily lead to the Lagrange multiplier absolute minimum (Dodds, Rothman and Weitz). Additionally, many of the assumptions, such as the branching structure, are not necessarily biological.

WBE Revised: The Etienne, Apol and Olff Model.

The goal is to create a more flexible and general theory which proscribes a formula for the constant B_0 in the allometric equation $B = B_0 M^a$.

Assumption 1. Substitute the fact that vascular systems are fractal-like for the strict self-similarity property in WBE. This makes the quantities v_k, ρ_k *and* λ_k functions of k. We also define total cross-sectional area and volume ratios as

$$\alpha_k = v_k \rho_k^2 \tag{5}$$
$$\phi_k = v_k \lambda_k^3 \tag{6}$$

and other useful quantities

$$r_k = \frac{r_c}{\Pi_{i=k}^{C-1} \rho_i} \qquad S_1 = \sum_{k=1}^{C} \frac{1}{\Pi_{i=k}^{C-1} v_i \rho_i^2 \lambda_i}$$
$$l_k = \frac{l_c}{\Pi_{i=k}^{C-1} \lambda_i} \qquad S_2 = \sum_{k=1}^{C} \frac{1}{\Pi_{i=k}^{C-1} \alpha_i (\phi_i)^{1/3}}$$
$$N_k = \frac{N_c}{\Pi_{i=k}^{C-1} v_i} \qquad S_3 = \sum_{k=1}^{C} \frac{1}{N_k^{1/3}}.$$

The total volume of transport fluid (blood) at level k is

$$V_{b,k} = N_k \pi r_k^2 l_k = \frac{\pi N_c r_c^2 l_c}{\Pi_{i=k}^{C-1} v_i \rho_i^2 \lambda_i}. \tag{7}$$

So the total blood volume is the sum over k

$$V_b = \pi N_c r_c^2 l_c S_1 = \pi (N_c)^{4/3} r_c^2 l_c S_2. \tag{8}$$

Thus we can solve for the number of capillaries

$$N_C = \left(\frac{V_b}{\pi r_c^2 l_c S_2} \right)^{3/4} \tag{9}$$

Assumption 2. The proportion of blood flow to metabolic rate is independent of body size. In other words, $B = f_0 N_1 Q_1$, where f_0 is the change in O_2 levels by metabolic action. The value of f_0 is assumed/shown to be independent of M.

Assumption 3. Water is incompressible. This physical fact is equivalent to $N_k Q_k = N_{k+1} Q_{k+1}$ and rules out such systems as lungs. Thus we find

$$B = f_0 N_c Q_c = f_0 N_c A_c u_c \tag{10}$$

and so with equation 9 we relate the metabolic rate to the total blood volume. Three additional assumptions are needed to achieve the 3/4 scaling.

$$B = f_0 A_c u_c \left(\frac{V_b}{\pi r_c^2 l_c S_2} \right)^{3/4} = f_0 \pi r_c^2 u_c \left(\frac{V_b}{\pi r_c^2 l_c \sum_{k=1}^{C} \frac{1}{(N_k)^{1/3} \Pi_{i=k}^{C} \alpha_i (\phi_i)^{1/3}}} \right)^{3/4} \tag{11}$$

Assumption 4. Blood volume is proportional to body size. The allometric equation $V_b = V_{b0} M^b$ with $b = 1$ has been demonstrated empirically.

Assumption 5. The capillaries are size independent. Then the quantities r_c, l_c *and* u_c do not depend on M.

Assumption 6. The quantity S_2 does not depend on M. This was justified by West with the following assumtions:

1. The network is area preserving or $\alpha_k = 1 \ \ \forall k$.
2. The network is space filling or $\phi_k = 1 \ \ \forall k$.
3. S_3 does not depend on body mass.

Under all these assumptions, the metabolic rate is

$$B = B_0 M^{3/4b} \quad with \tag{12}$$

$$B_0 = f_0 \pi r_c^2 u_c \left(\frac{V_{b0}}{\pi r_c^2 l_c \sum_{k=1}^{C} \frac{1}{N_k^{1/3} \Pi_{i=k}^{C-1} \alpha_i (\phi_i)^{1/3}}} \right)^{3/4} . \tag{13}$$

We see all the values in equation 13 must not vary (too much) with M. If plotted, S_3 clearly converges to an asymptotic value quickly, within about 10 levels.

On the other hand, if any of these values did vary, we could accommodate those fluctuations into our model by including some extra scaling into equation 12. The space filling requirement is the most controversial and mysterious and least well grounded in a biological principle. On the other hand, even if ϕ_k does vary some with k or with M, since the coefficient formula uses its 3rd root, its influence should be minimal.