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FORUM

Demystifying the West, Brown & Enquist model of the allometry of metabolism

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Summary

1. The allometry of metabolic rate has long been one of the key relationships in ecology. While its existence is generally agreed on, the exact value of the scaling exponent, and the key mechanisms that determine its value, are still hotly debated.
2. The network model of West, Brown & Enquist (*Science* **276**, 122–126, 1997) predicts a value of $^3/_4$ but, although appealing, this model has not been generally accepted.
3. Here we reconstruct the model and derive the exponent in a clearer and much more straightforward way that requires weaker assumptions than the original model. Specifically, self-similarity of the network is not required. Our formulation can even be used if one or several assumptions of West *et al*. (1997) are considered invalid.
4. Moreover, we provide a formula for the proportionality constant (i.e. the intercept of the allometric scaling relation) that shows explicitly where factors as temperature and stoichiometry affect metabolism.

Key-words: Allometric scaling, metabolic theory, organismal transport network, fractal topology

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Introduction

It has been long recognized that for many taxa (e.g. mammals) allometric relations of the form $Y = Y_0 M^x$ exist, where Y is an organismal property (e.g. growth rate, metabolic rate or life span), M is the body mass, Y_0 is a taxonomic-group specific constant, and x is a characteristic exponent (Calder 1984; Peters 1983). Probably the most important of these allometric relations is the relation for the basal metabolic rate, because many other allometric relations depend on it, and particularly on the value of x. Both empirical and theoretical studies have been carried out to study this exponent. Empirical studies report values ranging from $^2/_3$ to $^3/_4$ (e.g. Dodds, Rothman & Weitz 2001; Savage *et al*. 2004) and both extremes of this range have gained theoretical support. An old and simple argument for the value $^2/_3$ (Rubner 1883) is the following. In an organism at steady state (i.e. constant temperature), the heat produced by metabolism must equal the heat dissipated to the environment via the organism's body surface. Thus the metabolic rate is proportional to the body surface area, which scales with the $^2/_3$ power of body size. This very simple model ignores the fact that metabolic processes require resources (e.g. oxygen) and does not seem to do justice to the complex structures that have evolved to transport resources to the cells.

Almost a decade ago, West, Brown & Enquist (1997) used the fact that many taxa have fractal-like networks for resource transport to predict a value of $^3/_4$ for the allometric exponent x. This model, although appealing and a stimulus for follow-up studies (see reviews by Brown *et al*. 2004; Marquet *et al*. 2005), has still not been generally accepted, as evidenced by a vigorous recent debate in *Functional Ecology* between the original authors on the one hand (hereafter called WBE) and Kozlowski & Konarzewski (hereafter called K&K) on the other (Kozlowski & Konarzewski 2004, 2005; Brown, West & Enquist 2005). Other authors have also heavily criticized the assumptions and derivation of this model (e.g. Banavar, Maritan & Rinaldo 1999; Dodds *et al*. 2001). The main message emerging from this debate is that the model as formulated by WBE is not at all clear. It sorely needs a thorough reconstruction for a correct understanding and subsequent empirical testing of (elements of) the model and further theoretical development. In this paper we aim to provide such a thorough reconstruction. We describe the structure of the transport network, WBE's assumptions (regardless of whether they are plausible or not) and their mathematical translations. For optimal transparency, we sometimes deviate from the notation

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Table 1. Conversion of notation used in this article to those in West *et al.* (1997). Symbols that are not listed either have the same meaning in both papers, or appear only in this article

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}	$\dot{Q}_k$
Velocity at level $k + 1$ averaged over the cross-sectional area	u_{k+1}	$\bar{u}_k$

of WBE. See Table 1 for conversion of our notation to that of West, Brown & Enquist (1997). Furthermore, we generalize the model in three ways. First, we formulate the model in such a way that the derivation of the allometric exponent of $x = {}^3/_4$ does not require the branching network distributing resources to the cells to be self-similar. Second, where the proportionality constant Y_0 is usually ignored, we present a formula for this constant. Third, our formulation can be used as a basis for models that make different assumptions from those of WBE, making the theory amenable to rigorous testing. We discuss how the disagreement between WBE and K&K can be understood in the light of the reconstructed, generalized model.

Model

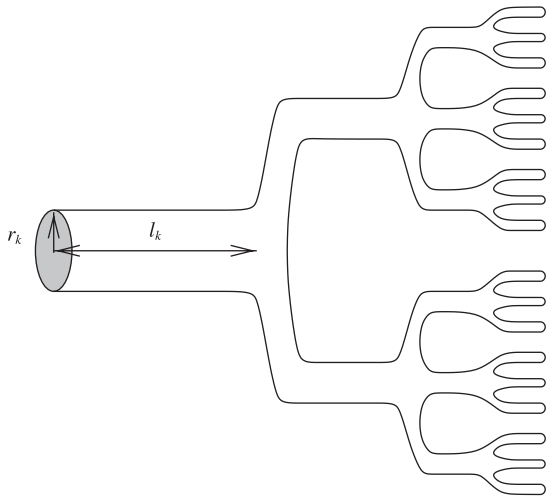
TOPOLOGY OF THE TRANSPORT SYSTEM

Assumption 1: The transport system of oxygen has a fractal-like branching topology as shown in Fig. 1

West *et al.* (1997) make a somewhat stronger assumption than assumption 1, by requiring the network to be a self-similar fractal, but self-similarity is not necessary, as will become clear below. For illustrative purposes we take the blood transport system as an example, but the topology also applies to other hierarchical transport systems found in organisms. The first level in the branching system (aorta) has value $k = 1$ and the last level (capillaries) has value $k = C$. Each level consists of N_k identical pipes (vessels) of radius r_k, length l_k, cross-sectional area $A_k = \pi r_k^2$ and volume $V_k = \pi r_k^2 l_k$. Each vessel at level k splits at a node into ν_k vessels at level $k + 1$. Hence, N_k is a product of all ν_i at levels up to (but not including) level k, that is $N_k = \prod_{i=1}^{k-1} \nu_i$ and generally $N_1 = 1$. Conversely, the number of branches originating from each vessel at level k is the quotient of the number of vessels at levels $k + 1$ and k:

$$\nu_k = \frac{N_{k+1}}{N_k} \qquad \text{(eqn 1)}$$

For the vessel radius r_k and the vessel length l_k we can define the quantities ρ_k and λ_k analogously:



k	1	2	3	4
ν_k	2	3	3	
N_k	1	2	6	18

Fig. 1. Topology of the transport network. In this example the total number of levels is $C = 4$, going from 1 (aorta) to 4 (capillaries). The number of branches originating from each vessel at level k is ν_k.

$$\rho_k = \frac{r_{k+1}}{r_k} \qquad \text{(eqn 2)}$$

$$\lambda_k = \frac{l_{k+1}}{l_k} \qquad \text{(eqn 3)}$$

We use Greek symbols to indicate that these quantities are quotients. These quantities are convenient because they allow us to express the radius, length and number of vessels at level k in terms of the radius, length and number of vessels at the last level, the capillary level (which has a special status in the model):

$$r_k = \frac{r_C}{\prod_{i=k}^{C-1} \rho_i} \qquad \text{(eqn 4)}$$

$$l_k = \frac{l_C}{\prod_{i=k}^{C-1} \lambda_i} \qquad \text{(eqn 5)}$$

$$N_k = \frac{N_C}{\prod_{i=k}^{C-1} \nu_i} \qquad \text{(eqn 6)}$$

We also define the following quantities:

$$\alpha_k = \frac{N_{k+1}A_{k+1}}{N_k A_k} = \frac{N_{k+1}\pi r_{k+1}^2}{N_k \pi r_k^2} = \frac{N_{k+1} r_{k+1}^2}{N_k r_k^2} = \nu_k \rho_k^2 \qquad \text{(eqn 7)}$$

$$\varphi_k = \frac{N_{k+1}V_{k+1}}{N_k V_k} = \frac{\frac{4}{3}\pi N_{k+1}\left(\frac{l_{k+1}}{2}\right)^3}{\frac{4}{3}\pi N_k \left(\frac{l_k}{2}\right)^3} = \frac{N_{k+1} l_{k+1}^3}{N_k l_k^3} = \nu_k \lambda_k^3 \qquad \text{(eqn 8)}$$

Thus, the quantity α_k represents the ratio of the total cross-sectional areas of levels $k + 1$ and k, and φ_k represents the ratio of the total of volumes around the vessels at levels $k + 1$ and k, the interpretation of which will be discussed below. These quantities will be shown to be useful in translating assumptions made by West *et al.* (1997) into mathematical terms.

Finally, we define the three basic topological quantities S_1, S_2 and S_3 which will be helpful in our derivation below:

$$S_1 = \sum_{k=1}^{C} \frac{1}{\prod_{i=k}^{C-1} \nu_i \rho_i^2 \lambda_i} \qquad \text{(eqn 9)}$$

$$S_2 = \sum_{k=1}^{C} \frac{1}{(N_k)^{\frac{1}{3}} \prod_{i=k}^{C-1} \alpha_i (\varphi_i)^{\frac{1}{3}}} \qquad \text{(eqn 10)}$$

$$S_3 = \sum_{k=1}^{C} \frac{1}{(N_k)^{\frac{1}{3}}} \qquad \text{(eqn 11)}$$

S_1 and S_2 are related as:

$$\begin{aligned} S_1 &= \sum_{k=1}^{C} \frac{1}{\prod_{i=k}^{C-1} \alpha_i \left(\frac{\varphi_i}{\nu_i}\right)^{\frac{1}{3}}} \\ &= \sum_{k=1}^{C} \frac{\prod_{i=k}^{C-1} (\nu_i)^{\frac{1}{3}}}{\prod_{i=k}^{C-1} \alpha_i^{\frac{1}{3}} (\varphi_i)^{\frac{1}{3}}} \\ &= \sum_{k=1}^{C} \frac{\left(\frac{N_C}{N_k}\right)^{\frac{1}{3}}}{\prod_{i=k}^{C-1} \alpha_i (\varphi_i)^{\frac{1}{3}}} \\ &= (N_C)^{\frac{1}{3}} \sum_{k=1}^{C} \frac{1}{(N_k)^{\frac{1}{3}} \prod_{i=k}^{C-1} \alpha_i (\varphi_i)^{\frac{1}{3}}} \\ &= (N_C)^{\frac{1}{3}} S_2 \end{aligned} \qquad \text{(eqn 12)}$$

where we have used equations (7) and (8) to derive the first line from equation (9) and equation (6) to obtain the third line from the second. If $\alpha_i = 1$ and $\varphi_i = 1$ for all i we observe that $S_2 = S_3$.

So far we have only used definitions and the assumption that the network has the topology of Fig. 1. We are now ready to take the first step towards the allometry of metabolism.

The total volume of the transport fluid, blood, contained at branching level k of the network, is given by:

$$\begin{aligned} V_{b,k} &= N_k \pi r_k^2 l_k \\ &= \pi \left(\frac{N_C}{\prod_{i=k}^{C-1} \nu_i}\right)\left(\frac{r_C}{\prod_{i=k}^{C-1} \rho_i}\right)^2 \left(\frac{l_C}{\prod_{i=k}^{C-1} \lambda_i}\right) \\ &= \frac{\pi N_C r_C^2 l_C}{\prod_{i=k}^{C-1} \nu_i \rho_i^2 \lambda_i} \end{aligned} \qquad \text{(eqn 13)}$$

and hence the total blood volume is the sum over all levels:

$$\begin{aligned} V_b &= \pi N_C r_C^2 l_C \sum_{k=1}^{C} \frac{1}{\prod_{i=k}^{C-1} \nu_i \rho_i^2 \lambda_i} \\ &= \pi N_C r_C^2 l_C S_1 = \pi (N_C)^{\frac{4}{3}} r_C^2 l_C S_2 \end{aligned} \qquad \text{(eqn 14)}$$

This leads to the following expression for the total number of capillaries:

$$N_C = \left[\frac{V_b}{\pi r_C^2 l_C S_2}\right]^{\frac{3}{4}} \qquad \text{(eqn 15)}$$

This equation will be inserted in the expression for the metabolic rate below. Note the $^3/_4$ exponent that appears in this expression, as it will finally determine the allometric exponent of $x = {}^3/_4$ under the assumptions of the model.

FLOW THROUGH THE TRANSPORT SYSTEM

Let us denote by Q_k the blood flow at level k, i.e. the total volume flowing through the vessel cross-sectional area A_k per unit of time. Let us further denote by u_k the velocity of the fluid at level k, averaged over the cross-sectional area. We have:

$$Q_k = A_k u_k \qquad \text{(eqn 16)}$$

and the total flow through all the vessels at level k is then $N_k Q_k = N_k A_k u_k$.

Assumption 2: The proportionality between organismal metabolic rate and blood volume flow is independent of body size

The basal metabolic rate B is usually calculated from the rate of oxygen consumption by the organism. This rate is proportional to the total volume flow in the aorta, $N_1 Q_1$, and is thus given by:

$$B = f_0 N_1 Q_1 \qquad \text{(eqn 17)}$$

where f_0 is the change in oxygen concentration due to metabolic processes in the cells. Assumption 2, also made by West *et al.* (1997), states that f_0 is independent of body size.

Assumption 3: The transport fluid (blood) is incompressible

Water and blood are virtually incompressible, and also gases (e.g. in insect tracheae) can be treated this way provided that the transport velocity u is smaller than the speed of sound (Tritton 1988). For an incompressible fluid, conservation of mass throughout the network implies that (Berne & Levy 1986):

$$N_k Q_k = N_{k+1} Q_{k+1} \quad \text{(eqn 18)}$$

for all k. West *et al.* (1997) directly assume that equation (18) holds. Now, instead of equation (17) we can write:

$$B = f_0 N_C Q_C = f_0 N_C A_C u_C \quad \text{(eqn 19)}$$

Inserting equation (15) we have:

$$B = f_0 A_C u_C \left[\frac{V_b}{\pi r_C^2 l_C S_2}\right]^{\frac{3}{4}} = f_0 \pi r_C^2 u_C \left[\frac{V_b}{\pi r_C^2 l_C \sum_{k=1}^{C} \frac{1}{(N_k)^{\frac{1}{3}} \prod_{i=k}^{C} \alpha_i (\varphi_i)^{\frac{1}{3}}}}\right]^{\frac{3}{4}} \quad \text{(eqn 20)}$$

FURTHER ASSUMPTIONS

Three further assumptions are now sufficient to lead to a prediction of $x = 3/4$.

Assumption 4: The blood volume is proportional to body size

This assumption, adopted by West *et al.* (1997), states that the total volume of blood in the transport system, V_b, scales allometrically with exponent 1:

$$V_b = V_{b0} M^b \quad \text{(eqn 21)}$$

$$b = 1 \quad \text{(eqn 22)}$$

Empirical evidence for mammals and birds indeed show allometric scaling with b very close to 1 (Peters 1983; Calder 1984; Schmidt-Nielsen 1984).

Assumption 5: Terminal units are size-invariant

The terminal units, i.e. the capillaries, have properties that do not depend on body mass M. Thus r_C, l_C and u_C do not depend on M. This is a crucial assumption of West *et al.* (1997), because the only remaining way the metabolic rate in equation (20) can depend on body size, apart from the dependence of V_b on body size, expressed by equation (21), is by its dependence on S_2. This is however, prevented by assumption 6.

Assumption 6: The quantity S_2 defined in equation (10) does not depend on body size, M

West *et al.* (1997) made three separate assumptions to support this assumption. First they assumed that the network is area-preserving. This means that the total area of all vessels at level k equals the total cross-sectional area of all vessels at any other level. As this also applies to level $k + 1$, this entails $\alpha_k = 1$ for all k (see the definition of α_k in equation (7)). Second, West *et al.* (1997) assumed that the network is 'space-filling'. The interpretation of this assumption is the main cause of the disagreement between WBE and K&K, as we will discuss below. West *et al.* (1997) interpret it as preservation of the quantity $4/3\ \pi N_k (l_k/2)^3$ across all levels k (which is mathematically equivalent to preservation of $N_k l_k^3$). This then leads to $\varphi_k = 1$ for all k (see the definition of φ_k in equation (8)). Third, they made an assumption that can be translated in our new framework as the assumption that the quantity S_3 (see equation (11)) does not depend on body size M. The only way that S_3 can depend on body size is through the number of levels C. In Fig. 2 we have plotted S_3 *vs* the total number of levels C and we observe that S_3 quickly converges to a constant value. Moreover, this value is less than an order of magnitude larger than the value for $C = 1$. This strongly supports the assumption that S_3 does not depend on M. The three assumptions together imply that S_2 does not depend on body size M. Assumption 6 may, however, also be supported by other sets of assumptions.

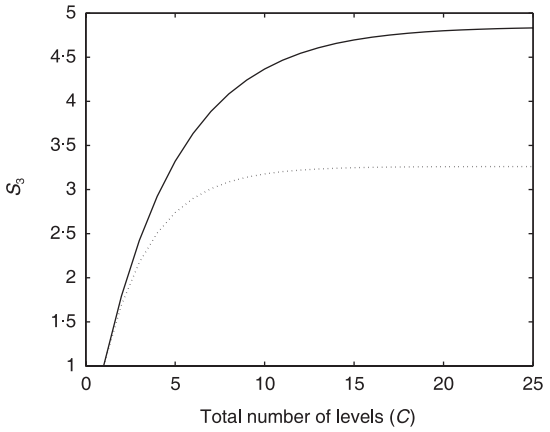


Fig. 2. Dependence of the quantity $S_3 = \sum_{k=1}^{C} [1/(N_k)^{\frac{1}{3}}]$ on the total number of levels, C, for two networks. Solid curve: a network where at each node the number of vessels doubles ($\nu_k = 2$ for all k). Dotted curve: a network where at each node the number of vessels triples ($\nu_k = 3$ for all k). Note the small linear scale at the y-axis which implies that even for small C the dependence of S_3 on C and hence on M is negligible.

Inserting equation (21) in equation (20) gives:

$$B = B_0 M^{\frac{3}{4}b} \quad \text{(eqn 23)}$$

with $b = 1$ under assumption 4, see equation (22). The proportionality factor B_0 is given by:

$$B_0 = f_0 \pi r_C^2 u_C \left[\frac{V_{b0}}{\pi r_C^2 l_C \sum_{k=1}^{C} \frac{1}{(N_k)^{\frac{1}{3}} \prod_{i=k}^{C-1} \alpha_i (\varphi_i)^{\frac{1}{3}}}}\right]^{\frac{3}{4}} \quad \text{(eqn 24)}$$

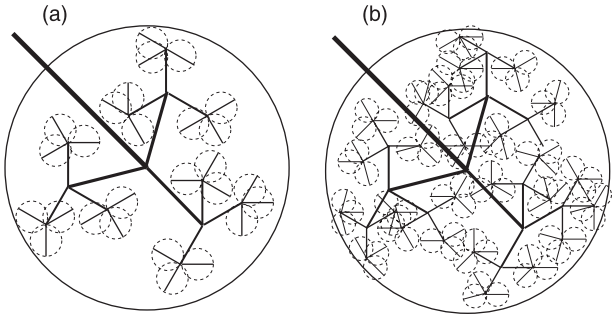


Fig. 3. Illustration of the quantity $N_k l_k^3$ at level k (a) and level $k + 1$ (b). Here $k = 4$. The quantity $N_k l_k^3$ is the sum of volumes of all circles (spheres in three dimensions) at level k.

which does not depend on body size if the assumptions of the model hold. This formula is a new result, not given by West *et al.* (1997), which may have far-reaching consequences, as we discuss below.

Discussion

We have given a new presentation of the WBE network model, and derived a value of $x = {}^3/_4$ for the allometric scaling exponent of metabolism, with more explicit statement of the assumptions. Of all assumptions, assumption 6 requires the most scrutiny. In turn, of the three supporting assumptions that can be used to justify assumption 6, the preservation of the quantity $N_k l_k^3$ across the hierarchical levels of the network, is the most questionable, and has been the topic of vigorous debate. The misunderstanding about this supporting assumption is caused by the fact that West *et al.* (1997) state that the network is 'space-filling' and that $N_k l_k^3$ is proportional to the 'service volume' of all vessels at level k. This terminology suggests an erroneous biological interpretation of $N_k l_k^3$. 'Service volume' seems to correspond to a part of the body to which the network delivers oxygen, and 'space-filling' gives the impression that the whole body of the organism should be filled with such service volumes. Such interpretations indeed lead to a contradiction. If the volume to which oxygen is delivered is assumed to be proportional to $N_C l_C^3$ and this volume fills all space (i.e. the whole body), it should naturally scale with body size M_1. However, assumption 5 implies that l_C^3 is independent of body size, and the total model shows that N_C scales with $M^{3/4}$ (if $b = 1$), leading to an overall scaling of $N_C l_C^3$ with $M^{3/4}$. The only way to solve this contradiction is to drop the biological interpretation of $N_C l_C^3$ as the total body volume and to reconsider the assumption that the quantity $N_k l_k^3$ is preserved across the hierarchical levels of the network. Figure 3 shows how this supporting assumption that the quantity $N_k l_k^3$ is the same for all levels k can be envisaged. The sum of volumes of all circles (spheres in three dimensions) at level k is, apart from a proportionality constant, given by $N_k l_k^3$. Preservation of $N_k l_k^3$ thus means that it is a geometrical property of the network that the sum of the volumes around vessels remains constant rather than a biological property. This seems a plausible assumption, but theoretical support is scarce. Preservation of $N_k l_k^3$ is a stronger assumption than actually needed. All we need, is that the quantity S_2 is roughly independent of body size M. This can be true, even if $N_k l_k^3$ decreases with k and thus $\varphi_k < 1$, because this can be countered by $\alpha_k > 1$. Particularly note that φ_k is raised to the power ${}^1/_3$ in S_2 which implies that any deviations of φ_k from unity will be reduced. Hence, quite a strong deviation from 1 is needed to make S_2 strongly dependent on C and thus on body size.

Our reformulation of WBE's model deviates from their formulation in two important ways. West *et al.* (1997) suggest that cross-sectional area preservation combined with preservation of $N_k l_k^3$ optimizes the efficiency of the network (i.e. minimizes the hydrological resistance). This leads West (1999) to argue that the allometric scaling with exponent $x = {}^3/_4$ ultimately reflects that 'organisms have evolved so that the energy required to sustain them is minimized'. Dodds *et al.* (2001) show that this suggestion is unsubstantiated. In fact, assuming preservation of $N_k l_k^3$, maximal efficiency corresponds to preservation of $N_k r_k^3$ instead of $N_k r_k^3$. We therefore do not use an energy minimization principle to support assumption 6, but stick to area-preservation itself (a geometric principle). Furthermore, in contrast to what West *et al.* (1997) state, we do not require the network to be a self-similar fractal in order to obtain a scaling of $x = {}^3/_4$. Self-similarity (i.e. $\nu_k = \nu$, $\rho_k = \rho$, $\lambda_k = \lambda$ for all k) simplifies the product

$$\prod_{i=k}^{C-1} \alpha_i (\varphi_i)^{\frac{1}{3}}$$

to

$$\alpha^{C-1} (\varphi)^{\frac{C-1}{3}}$$

but this is not necessary to make S_2 independent of body size.

Under different assumptions from those of assumption 6, equation (14) will still hold, but the body size independence of S_2 is then no longer valid. To obtain the allometric scaling exponent under these different assumptions, S_1 must be expressed as a product of an N_C^p (p being some exponent) and an S_2' such that S_2' is largely body size independent. (In the case of WBE's assumptions, we had $p = {}^1/_3$ and $S_2' = S_2$). The consequences of these assumptions and their implications need to be explored further.

We have provided a new formula for the proportionality factor of metabolic scaling, B_0. If measurements can be carried out to estimate the quantities that make up this proportionality factor, we have an alternative test of the network model. The results could even indicate a (slight) body size dependence of this proportionality factor. It has already been suggested that B_0 may depend on body size, e.g. through f_0 (K & K 2004), or through l_C and r_C (Dawson 2001, 2003), which, respectively,

violate assumptions 2 and 5. Our formulation of the model allows for easy incorporation of such deviations by way of equation (24). The quantity B_0 is a crucial factor in themetabolic theory of ecology (Brown *et al*. 2004), in which B_0 shows explicitly where factors as temperature and stoichiometry affect metabolism. Our formula shows that these factors should affect metabolism via f_0, the proportionality constant that relates metabolic rate to the total blood flow through the aorta.

In sum, our reformulation of the network model and our new derivation indeed entails the exponent $x = {}^3/4$, and the assumptions under which this result is obtained are weaker than stated by West *et al.* (1997). Furthermore, if any of these assumptions is violated (and there is some evidence for this), our formulation provides a basis for incorporating such assumptions and finding the corresponding allometric scaling exponent, which then might differ from ${}^3/4$. Our reformulation opens up the theory to rigorous experimental testing. Finally, we have provided a mechanistic formula for the proportionality factor, B_0, which plays a central role in the metabolic theory of ecology, and we have argued that, under alternative model assumptions, B_0 might depend on body size.

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References

Banavar, J.R., Maritan, A. & Rinaldo, A. (1999) Size and form in efficient transportation networks. *Nature* **399**, 130–132.

Berne, R.M. & Levy, M.N. (1986) *Cardiovascular Physiology*, 5th edn. Mosby, St. Louis, MO.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789.

Brown, J.H., West, G.B. & Enquist, B.J. (2005) Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant. *Functional Ecology* **19**, 735–738.

Calder,W.A. III (1984) *Size, Function, and Life History*. Dover, Mineola, NY.

Dawson, T.H. (2001) Similitude in the cardiovascular system of mammals. *Journal of Experimental Biology* **204**, 395–407.

Dawson, T.H. (2003) Scaling laws for capillary vessels of mammals at rest and in exercise. *Proceedings of the Royal Society of London B* **270**, 755–763.

Dodds, P.S., Rothman, D.H. & Weitz, J.S. (2001) Re-examination of the '3/4-law' of metabolism. *Journal of Theoretical Biology* **209**, 9–27.

Kozłowski, J. & Konarzewski, M. (2004) Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? *Functional Ecology* **18**, 283–289.

Kozłowski, J. & Konarzewski, M. (2005) West, Brown and Enquist's model of allometric scaling again: the same questions remain. *Functional Ecology* **19**, 739–743.

Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. & Rivadeneira, M. (2005) Scaling and power-laws in ecological systems. *Journal of Experimental Biology* **208**, 1749–1769.

Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.

Rubner, M. (1883) Ueber den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Zeitschrift für Biologie* **19**, 535–562.

Savage, V.M., Gillooly, J.F., Woodruff, W.H., West, G.B., Allen, A.P., Enquist, B.J. & Brown, J.H. (2004) The predominance of quaternary-power scaling in biology. *Functional Ecology* **18**, 257–282.

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

Tritton, D.J. (1988) *Physical Fluid Dynamics*, 2nd edn. Clarendon Press, Oxford.

West, G.B. (1999) The origin of universal scaling laws in biology. *Physica A* **263**, 104–113.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.

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