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Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant

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Introduction

In a recent paper Kozłowski & Konarzewski (2004; K & K hereafter) criticized the model of allometric scaling proposed by West, Brown & Enquist (1997; WBE hereafter) as being 'mathematically incorrect' and 'biologically unjustified.' In so doing, they misread our paper, misrepresented our model, and made serious mistakes.

The WBE theory shows how the quarter-power scalings of metabolic rate and many other biological attributes have their origin in the fractal-like designs of resource distribution networks. These designs are based on three simple principles: (1) a space-filling network that branches hierarchically to supply all parts of the three-dimensional body; (2) body-size invariant terminal units, such as capillaries or leaf petioles; and (3) minimization of the energy and time required to distribute resources. The WBE model of the mammalian cardiovascular systems additionally shows quantitatively and realistically how the scalings of the structure and hydrodynamics solve the problem of distributing blood from a beating heart through elastic hierarchically branching arteries to body-size invariant capillaries. The model correctly predicts not only the scaling parameters and absolute values of many characteristics of mammalian cardiovascular systems that have been measured by biomedical researchers (see Table 1 in WBE), but also the values in the hypothetical numerical example proposed by K & K (see Table 1, below). By applying the fundamental principles listed above to other resource supply networks in different taxa of organisms, the WBE model explains the origin of the ubiquitous quarter-power scaling exponents that have puzzled biologists since the 1930s (e.g. Kleiber 1932; Peters 1983; McMahon & Bonner 1983; Calder 1984: Schmidt-Nielsen 1984).

K & K's fundamental error

K & K's statement that 'WBE's model is mathematically incorrect' is itself incorrect. K & K erred because they misinterpreted the second of WBE's 'three unifying principles or assumptions': '(2) the final branch of the network (such as the capillary in the circulatory system) is a size-invariant unit.' As pointed out in the quotations below, WBE clearly state that only the characteristics of the capillaries themselves are assumed to be invariant. Nevertheless, K & K incorrectly interpreted this size-invariance to mean that each capillary must supply a constant volume of tissue. Having got this critical part wrong, they went on to make incorrect calculations and to draw erroneous conclusions about the scaling of total number of capillaries, total blood volume, and whole-organism metabolic rate. Predicting the scaling of the 'service volume' of tissue supplied by a capillary is an integral part of the WBE theory. WBE prove that the service volume increases with body size, as $M^{1/4}$, and this is integral to proving that both total number of capillaries and-whole organism metabolic rate scale as $M^{3/4}$. The essence of the WBE theory is that geometric constraints and optimization criteria for the vascular network require that as body size increases, each invariant capillary supplies resources at a constant rate to a larger volume of tissue, causing whole-organism metabolic rate to increase non-linearly or allometrically rather than linearly or isometrically with body mass.

It is obvious that K & K did not understand the distinction, clearly made by WBE, that even though capillaries are assumed to be invariant terminal units of the network, the service volumes of tissue supplied by each capillary are free to vary and subsequently proven to scale allometrically as $M^{1/4}$. Thus, WBE write 'the important assumption (*is*) . . . that the terminal units (capillaries) are invariant, so r_c, l_c, $\tilde{u}$, and consequently Δp_c, are independent of body size' (where r_c, l_c, $\tilde{u}_c$, Δp_c, are, respectively, the radius and length and the average velocity and change in pressure of blood for a capillary). WBE continue 'the invariance of capillary parameters implies (*that the total number of capillaries*) $N_c \propto M^{3/4}$ rather than the naïve expectation that $N_c \propto M$, so the volume serviced by each capillary must scale as $M^{1/4}$, and capillary density per cross-sectional area of tissue as $M^{-1/12}$.' WEB also state 'one can also prove from the energy minimization principle that $V_b \propto M$.' In contrast, K & K incorrectly state that 'size-invariance here means that capillary number scales isometrically

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Table 1. Numerical example comparing the scaling of hypothetical mammalian cardiovascular systems according to K & K's calculations (in their Table 1) and to our calculations based on the WBE model. Like K & K, we assume that each larger vessel branches into $n = 5$ smaller vessels, and for consecutive levels the radius ratio $\beta = n^{-1/2}$ equals 0·4472 (we have corrected what appears to be a typographical decimal point error in the legend of K & K's Table 1), and the length ratio $\gamma = n^{-1/3}$ equals 0·5848. The values in bold-faced type highlight the differences between K & K's calculations and our own. These differences are due entirely to the values of body mass, which K & K assumed to scale linearly with the number of capillaries. K & K erred by assuming that the service volume of tissue supplied by each capillary was invariant; this caused them to calculate body mass, M, incorrectly and to obtain an unrealistic exponent = 4/3 for the scaling of total blood volume. The WBE model by contrast requires that blood volume, V_b, scales linearly with body mass, and this forces the number of capillaries, N_c, and hence metabolic rate to scale allometrically as $M^{3/4}$. When the calculations are performed as specified by the WBE model, they give the predicted values for the scaling exponents: 3/4 for number of capillaries, total volume of blood in capillaries, and whole-organism metabolic rate; 1/4 for service volume of tissue supplied by each capillary, and –1/4 for the number of capillaries per unit body mass and mass-specific metabolic rate

				Scaling exponent (b)	
Number of generations of branches	$N = 7$	$N = 9$	$N = 11$	K & K	WBE
Radius of capillary (r_c)	0·0003	0·0003	0·0003	0	0
Length of capillary (l_c)	0·03	0·03	0·03	0	0
Number of capillaries (N_c)	78 125	1 953 125	48 828 125	**1·00**	**0·75**
Volume of blood in capillaries ($N_c\ V_c$)	0·0007	0·0166	0·4140	**1·00**	**0·75**
Volume of blood in body (V_b)	0·0673	4·9644	364·0	**1·33**	**1·000**
K & K body mass ($M_{K\&K}$)	**1·10**	**27·61**	**690·29**		
WBE body mass (M_{WBE})	**1·10**	**81·49**	**5410·5**		

(with exponent 1) with size.' But in our model the size invariance of the properties of individual capillaries in no way implies that the total number of capillaries must scale isometrically. The invariance of capillaries and the scaling of their total number (or of the service volume) are independent variables. Having made the unwarranted assumption that $N_c \propto M$, K & K then draw the incorrect conclusion that 'the amount of blood in the capillaries, $N_c V_c$ is proportional to body mass M, and total blood volume increases with body mass (body volume) much faster.' Conspicuously, K & K offered neither an alternative analytical model nor an arithmetic example to show how the straw-man paradox they have created is resolved or how whole-organism metabolic rate might realistically scale with body mass.

In their critique K & K rediscovered a fundamental problem in the scaling of mammalian vascular systems and other distribution networks that supply resources to fuel the metabolism of three-dimensional organisms. If the whole organism metabolic rate, B, and/or number of capillaries, N_c, scale linearly with body mass, M (i.e. isometrically or as M), then the total volume of blood, V_b, must increase allometrically, as M^{σ}, where $\sigma > 1$. Conversely, if V_b scales linearly with M, then B and N_c must decrease allometrically as M^{α}, where $\alpha = 1/\sigma < 1$. This is precisely the problem that organisms have solved by the evolution of fractal-like resource distribution networks. The WBE theory shows explicitly how this is realized in a pulsatile circulatory system and why the solution takes the empirically observed form: $\alpha = 3/4$, so $B \propto N_c \propto M^{3/4}$ and $V_b \propto M$. The theory also shows how the analogous scaling behaviour of nonpulsatile vascular plant systems follows from the same set of principles.

It is a trivial exercise to check the mathematical correctness and consistency of the model using a simple representative numerical example, as suggested by K & K and presented in their Table 1. However, their results, reproduced in part in our Table 1, were based on the erroneous assumption that $N_c \propto M$, so it led to incorrect calculations. Although K & K's calculation in which each branching of a parent vessel gives rise to five daughter vessels is not biologically realistic, it is mathematically sufficient and we have retained it as well as most of their parameterisations. K & K's error can readily be exposed by simply ensuring that blood volume scales linearly with body mass as required by the WBE theory. This automatically corrects K & K's additional error that had the number of capillaries scaling linearly with body mass.

This critical difference is all that is required to obtain the correct scalings for all parameters in K & K's example: volume of blood, $V_b \propto M$; number of capillaries, N_c, and whole organism metabolic rate, $B \propto M^{3/4}$; volume serviced by each capillary $\propto M^{1/4}$; capillary density per cross-sectional area of tissue $\propto M^{-1/12}$; and capillary density per volume of tissue and mass-specific metabolic rate $\propto M^{-1/4}$. Like the WBE model that generated them, these numerical calculations show how mammals (and other organisms with tubular vascular networks) avoid the problem of total blood volume increasing faster than linearly with body mass. As body size increases, mammals increase the service volume of tissue supplied by each capillary, thereby decreasing the density of capillaries and mass-specific metabolic rate.

K & K make other incorrect or misleading statements

Like most other published criticisms of WBE, K & K devoted the majority of their paper to the scaling of

metabolic rates and a few attributes of the vascular systems of mammals. They largely ignored the fact that our model correctly predicts the quarter-power allometries observed empirically in other systems and organisms. K & K also made additional comments that were either incorrect or misleading. We briefly highlight some of the most important ones.

Oxygen or nutrients? With respect to mammalian vascular systems, K & K stated 'It is not clear … whether the amount of oxygen or nutrients (*in the blood*) is proportional to the fluid volume.' Indeed, WBE make no distinction between oxygen and nutrients, because they assume that both resources are delivered to the tissues via the blood. Since the blood is assumed to remain in the arterial vessels while flowing from the heart to the arterioles, WEB logically assume that oxygen and nutrients are transported at rates set by cardiac output and ultimately by whole-organism metabolic rate. This is consistent with the fact that the biochemical reactions of metabolism impose precise stoichiometric requirements for oxygen and nutrients. Did K & K mean to imply that the same arterial vessels could supply oxygen and nutrients to tissues with different allometric scalings?

Plant vascular system. K & K's stated that 'vessels do not really branch; they diverge at "branching" points. In the (*WBE*) model, a vessel of higher order splits to *n* vessels of lower order and disappears.' Fig. 1b in WBE clearly diagrams the 'plant vessel-bundle system composed of diverging vessel elements.' Furthermore, we have published a detailed model for the dynamics and allometric scaling of whole-plant resource supply networks and metabolism (West, Brown & Enquist 1999; hereafter WEB; see also Enquist, West & Brown 2000). The model explicitly incorporates not only the vessel-bundle structure but also the 'mechanical role' of plant vascular systems. WEB also answer K & K's question 'what is the final unit and service volume in this case?' WEB write 'we have modelled the transport of fluid from the trunk to the petioles through the xylem vessels of angiosperms.' So, the invariant terminal unit is the leaf petiole, thereby avoiding the complications of within-leaf network structure and dynamics raised by K & K. In the plant model there is no precise analog to service volume, but the number of leaves (petioles) is shown to scale as $M^{3/4}$ as observed empirically. So leaves are separated by greater distances on larger plants, similarly to the capillaries of mammals.

Insect tracheal system. WBE do not present a model for insect tracheal systems. They do imply, however, that if whole-organism metabolic rates of insects scale as $M^{3/4}$, as a recent analysis suggests (Addo-Bediako, Chown & Gaston 2002), then similar principles of fractal-like design should apply to the structure and function of the tracheal system. This remains a testable hypothesis, and one which the comments of K & K certainly have not falsified.

Lungs. K & K admitted that 'the lungs of mammals probably most resemble a self-similar space-filling fractal.' They went on to note 'that reptiles and amphibians, however, have spongy lungs' as if this necessarily excludes the possibility of some hierarchical fractal-like system for gas exchange. This is premature, since neither WBE nor K & K have attempted to model explicitly the design of such 'spongy lungs' in relation to the allometric scaling of reptilian and amphibian metabolic rates.

Vertebrate vascular system and *resting* vs. *active metabolic rate*. K & K and others (e.g. Darveau *et al*. 2002) have implied that WBE is unrealistic for mammals, because it does not capture the changes in blood flow that accompany variation in activity and metabolic rates within organisms. Neither WBE nor anyone else to our knowledge has modelled in detail how mammals shift blood flow and change metabolic rate in response to the varying metabolic demands of different tissues during different kinds and levels of activity (see West *et al*. 2003; Savage *et al*. 2004; Weibel *et al*. 2004). Nevertheless, the fundamental principles of the WBE model can be generalized to a much wider range of cardiovascular designs than a simple system of fixed branching tubes. WBE enumerate the 'features of the simple pipe model (*that*) remain valid for all networks.' They illustrate by developing a more detailed analysis for pulsatile flow through elastic vessels. This basic framework should still be applicable to vascular networks supplying resources during various levels of activity. It will likely need to be modified, however, because it is well known that heart rate increases and blood flow is shunted to skeletal muscles during aerobic activity.

Additionally, Savage *et al*. (2004) suggested that natural selection has acted to maximize fitness by applying the WBE optimization criteria to the scaling of metabolic rates of free-living, reproducing organisms in the wild. Such field metabolic rates have been measured for mammals and shown to scale as $M^{3/4}$ (Nagy 2001; Savage *et al*. 2004). Physiologists have frequently measured basal metabolic rates (BMR), which are standardized to ensure resting, fasting, post-absorbtive states, but are of questionable relevance to free-living animals. Nevertheless, BMR does appear to scale very close to $M^{3/4}$, with some deviations in the very smallest mammals as predicted by WBE (Savage *et al*. 2004). Physiologists have also measured maximal sustained aerobic metabolic rates ($\dot{V}O_2\ max$) of mammals. It is likely that in maximal activity animals maximize physiological performance and metabolic output rather than minimizing energy required to distribute resources. It remains an open question whether natural selection has incorporated the optimization principles of WBE into the scaling of $\dot{V}O_2\ max$, but recent analyses suggest that the scaling exponent for such rates is greater than 3/4 (Weibel *et al*. 2004).

Does 3/4 scaling really exist? K & K cited several studies to argue that 'the ubiquity of 3/4 scaling claimed by WBE must be rejected.' In the same issue of *Functional Ecology* as K & K, Savage *et al*. (2004) critically reviewed the literature, compiled the most

extensive data yet on the scaling of basal, field, and maximal metabolic rates of mammals, and performed meta-analyses of the allometric scaling exponents for whole-organism metabolic rate, mass-specific rates, and biological times in a wide variety of organisms. As concluded by several influential reviews of allometry in the early 1980s (Peters 1983; McMahon & Bonner 1983; Calder 1984: Schmidt-Nielsen 1984), the preponderance of evidence does indeed support the pervasiveness of quarter-power allometries for biological rates and times (Savage *et al*. 2004; Brown *et al*. 2004a,b).

Conclusions

Kozłowski & Konarzewski (2004) made serious errors in their criticism of West, Brown & Enquist (1997). Most importantly, by incorrectly assuming that the service volume supplied by each capillary remains invariant with body mass, K & K created and were unable to resolve a paradox: that number of capillaries and total blood volume cannot realistically both scale linearly (isometrically) with body mass. K & K illustrated their critique by presenting a numerical example that had blood volume scaling as $M^{4/3}$, which was obviously unrealistic. Here, we have corrected their numerical example to conform with the theoretical requirements of WBE by having blood volume scaling linearly with M. The corrected example correctly predicts that the service volume scales allometrically as $M^{1/4}$, and the number of capillaries and whole organism metabolic rate scale as $M^{3/4}$. The WBE model shows from basic principles why it is both mathematically possible and biologically realistic for resource supply networks to have the empirically observed quarter-power scalings.

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