

Comment on ‘A critical understanding of the fractal model of metabolic scaling’

Chaui-Berlinck recently published a paper in which he claims that the original West, Brown and Enquist (WBE) model for metabolic scaling (West et al., 1997) is fundamentally flawed (Chaui-Berlinck, 2006). In particular, Chaui-Berlinck asserted that ‘the minimization procedure [of the original WBE model] is mathematically incorrect and ill-posed’ and that the model ‘lacks self-consistency and correct statement’. These are strong accusations and should, therefore, be closely scrutinized. Unfortunately, Chaui-Berlinck’s conclusions are incorrect because of rudimentary mathematical mistakes, and, even worse, these false conclusions are now being perpetuated in the literature. For example, Muller-Landau (Muller-Landau, 2007), in a review for Faculty of 1000, recently drew attention to Chaui-Berlinck’s paper by stating that ‘This article carefully dissects West, Brown and Enquist’s (1997) derivation of allometric scaling of metabolism. It illuminates important logical inconsistencies and mathematical problems with the argument’.

We note that none of the original authors nor the extended scaling community associated with the WBE model were asked to review Chaui-Berlinck’s manuscript. As we show below, the entire basis of Chaui-Berlinck’s paper stems from fundamental mathematical mistakes. In short, the conclusions of Chaui-Berlinck (and, subsequently, Muller-Landau) are completely incorrect. We conclude that Chaui-Berlinck’s paper (Chaui-Berlinck, 2006) should be retracted.

The most egregious errors of Chaui-Berlinck are seen in his equation 5a. Specifically, Chaui-Berlinck makes two mistakes. He first mis-transcribes the original equation from WBE (West et al., 1997) and then makes a fundamental error in his calculus.

In his equation 5a, Chaui-Berlinck insists that he is carefully analyzing the mathematics of the WBE model. He obtains the quotient 0/0 in several equations and then concludes that, because of his analysis, the results of WBE are meaningless. However, Chaui-Berlinck’s results of 0/0 only demonstrate both a misreading of the WBE paper and a basic mathematical error. The first mistake stems from Chaui-Berlinck incorrectly writing equation 9 from WBE as:

$$V_b = \frac{V_c}{(\beta_{>}^2\gamma)^N} \left\{ \left(\frac{\beta_{>}}{\beta_{<}} \right)^{2k} \left[\frac{1-(n\beta_{>}^2\gamma)^k}{1-(n\beta_{>}^2\gamma)} \right] + \left[\frac{1-(n\beta_{>}^2\gamma)^N}{1-(n\beta_{>}^2\gamma)} \right] - \left[\frac{1-(n\beta_{>}^2\gamma)^k}{1-(n\beta_{>}^2\gamma)} \right] \right\}, \quad (1a)$$

but the correct expression, as given in WBE, is:

$$V_b = \frac{V_c}{(\beta_{>}^2\gamma)^N} \left\{ \left(\frac{\beta_{>}}{\beta_{<}} \right)^{2k} \left[\frac{1-(n\beta_{>}^2\gamma)^k}{1-(n\beta_{<}^2\gamma)} \right] + \left[\frac{1-(n\beta_{>}^2\gamma)^N}{1-(n\beta_{>}^2\gamma)} \right] - \left[\frac{1-(n\beta_{>}^2\gamma)^k}{1-(n\beta_{>}^2\gamma)} \right] \right\}. \quad (1b)$$

Notice that he swaps two $\beta_{<}$ for $\beta_{>}$ in the first term inside the parentheses. For the second mistake, he then goes on to evaluate equation 9 from WBE *in a regime where the equation does not hold*. Thus, Eqn 1b (above) contains expressions for geometric sums that hold only for values of $\beta_{<}$, $\beta_{>}$, n and γ such that $n\beta_{<}^2\gamma \neq 1$ and $n\beta_{>}^2\gamma \neq 1$. These expressions are not stated explicitly in WBE because they are apparent from basic rules for sums. The correct result can be obtained directly from equation 9 in the original WBE paper (or Eqn 1b here) by taking the limit $\beta_{>} \rightarrow n^{-1/3}$, corresponding to $n\beta_{>}^2\gamma \rightarrow 1$ (because $\gamma = n^{-1/3}$). Although it is true that the numerator and denominator of the second two terms inside the parentheses both go to zero in this limit, this does *not* equal the limit of the fraction. From introductory calculus, the limit of the fraction as a whole can be obtained using L’hospital’s rule (for example, see <http://mathworld.wolfram.com/LHopitalsRule.html> or even a standard calculus class website such as <http://www.math.tamu.edu/~fulling/coalweb/lhop.htm>). Using L’hospital’s rule simply amounts to taking the derivative of the numerator and denominator separately and *only then* taking the limit of the numerator and denominator in the resultant fraction.

As was done in the original WBE model, a finite geometric sum can be expressed as:

$$\sum_{k=0}^{N-1} x^k = \frac{1-x^N}{1-x}, \quad x \neq 1. \quad (2)$$

The correct result for $x=1$ is found by taking the limit $x \rightarrow 1$ using L’hospital’s rule:

$$\lim_{x \rightarrow 1} \frac{1-x^N}{1-x} = \frac{\lim_{x \rightarrow 1} \left[\frac{d}{dx} (1-x^N) \right]}{\lim_{x \rightarrow 1} \left[\frac{d}{dx} (1-x) \right]} = \frac{\lim_{x \rightarrow 1} (-Nx^{N-1})}{\lim_{x \rightarrow 1} (-1)} = N, \quad (3)$$

or going back to the original sum and recognizing that:

$$\sum_{k=0}^{N-1} 1^k = \sum_{k=0}^{N-1} 1 = N. \quad (4)$$

Unfortunately, Chaui-Berlinck’s criticism did not incorporate these rules.

Now realizing that we can think of x as $n\beta_{>}^2\gamma$, the sum from 0 to $N-1$ as over the N levels of the branching network, and using $\beta_{<} = n^{-1/2}$ along with our previous expressions for the other scaling ratios, equation 9 from WBE (i.e. Eqn 1b here) gives the correct result:

$$V_b = V_c n^{4N/3} \left[\frac{n^{-(N-\bar{k})/3} - n^{-N/3}}{1-n^{-1/3}} + n^{-N/3}(N-\bar{k}) \right] = V_c n^{4N/3} \left(\frac{n^{-\bar{N}/3} - n^{-N/3}}{1-n^{-1/3}} + n^{-N/3} \bar{N} \right). \quad (5)$$

Here, $\bar{N}=N-\bar{k}$, as originally reported in WBE. When $N \gg \bar{N}$ and $\bar{k} \gg 1$, with V_c and \bar{N} constant, we have the original WBE prediction, $M \propto V_b \propto n^{4N/3} \propto N_c^{4/3} \propto B^{4/3}$, where N_c is the number of capillaries in the organism and is directly related to metabolic rate. Consequently, the most critical claim made by Chaui-Berlinck is patently false.

Chaui-Berlinck makes several additional errors. In the equation at the top of the second column on p. 3050, Chaui-Berlinck's treatment of the geometric constants in the Lagrange multiplier calculation is not correct. Specifically, in the original WBE model, $(4/3)\pi(l/2)^3$ is the service volume, and the geometric constant $(4/3)\pi(1/2)^3$ is absorbed into the arbitrary constant λ_k , highlighting the fact that the distinction between a sphere and a cube does not matter for these arguments. Lastly, Chaui-Berlinck rehashes the mistaken ideas of Dodds et al. (Dodds et al., 2001) and Kozlowski and Konarzewski (Kozlowski and Konarzewski, 2004). Interestingly, Chaui-Berlinck perpetuates these flawed arguments once more but does not cite the responses, which does not present a balanced, fair or accurate view of the field (Brown et al., 2005; Savage et al., 2004). In summary, Chaui-Berlinck's paper is riddled with mathematical mistakes that reflect a misreading of the original WBE paper.

10.1242/jeb.006734

References

- Brown, J. H., West, G. B. and Enquist, B. J.** (2005). Yes, West, Brown and Enquist's model of allometric scaling is both mathematically correct and biologically relevant. *Funct. Ecol.* **19**, 735-738.
- Chaui-Berlinck, J. G.** (2006). A critical understanding of the fractal model of metabolic scaling. *J. Exp. Biol.* **209**, 3045-3054.
- Dodds, P. S., Rothman, D. H. and Weitz, J. S.** (2001). Re-examination of the "3/4-law" of metabolism. *J. Theor. Biol.* **209**, 9-27.
- Kozlowski, J. and Konarzewski, M.** (2004). Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? *Funct. Ecol.* **18**, 283-289.
- Muller-Landau, H.** (2007). Evaluation for Chaui-Berlinck J. Exp. Biol. 209:3045. *F1000 Biol.* <http://www.f1000biology.com/article/id/1061698>.
- Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist, B. J. and Brown, J. H.** (2004). The predominance of quarter-power scaling in biology. *Funct. Ecol.* **18**, 257-282.
- West, G. B., Brown, J. H. and Enquist, B. J.** (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122-126.

**Van M. Savage¹, Brian J. Enquist^{2,3,*}
and Geoffrey B. West³**

¹Department of Systems Biology, Harvard Medical School, Boston, MA 02115, USA

²Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

³The Santa Fe Institute, Santa Fe, NM 87501, USA

*e-mail: benquist@email.arizona.edu