DR. MICHAEL R. KEARNEY (Orcid ID : 0000-0002-3349-8744)

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Corresponding author email id: m. Kearney@unimelb.edu.au

A comment on the growth model of Sibly and Brown

Michael R. Kearney and Sebastian A. L. M. Kooijman

Sibly and Brown (2020) proposed a new equation and conceptual theory for asymptotic animal growth that we found to have mathematical and conceptual problems. We show that, mathematically, their model simply becomes a case of the generalised von Bertalanffy model (von Bertalanffy, 1951) and that their conceptual interpretation produces a mathematical contradiction that would violate mass conservation.

Formal theories for animal growth have been sought for 100 years, since Pütter (1920) derived what has become known as the von Bertalanffy growth curve. Pütter thought of growth as proportional to the difference between the anabolic and catabolic biomass flow rates, where

$$\frac{dm}{dt} \approx am^{\frac{2}{3}} - bm$$

and the anabolic and catabolic coefficients, a and b , have dimensions of mass time⁻¹ mass^{-2/3} and mass time⁻¹ mass⁻¹, respectively. von Bertalanffy (1951) later generalised this model as a purely allometric one with variable exponents for anabolic and catabolic fluxes, i.e.

$$\frac{dm}{dt} \approx am^c - bm^d.$$

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West, Brown and colleagues (West, Brown & Enquist, 2001; Hou *et al.*, 2008) later developed an equation for growth in mass that equates to the generalised von Bertalanffy model and argued for exponent c as $3/4$ on the basis of optimality arguments about resource delivery through fractally branching networks. Kooijman (1986, 2010) expanded upon Pütter's original model to incorporate embryonic development, maturation and reproduction, and to include a metabolic smoother (reserve), separate to the structure, which acts to buffer resource delivery constraints to cells. In Kooijman's model, with constant food and shape, the structure (not the total biomass) grows according to an equation of Pütter's form with the same exponents. However, conceptually, growth relates to the difference between assimilation and maintenance, not anabolism and catabolism.

Sibly and Brown's (2020) recent contribution makes a case for c to take a value of $2/3$ and for d to take a value of $3/4$ on an appeal to the empirical scaling of food assimilation rate and respiration at rest, respectively. Thus

$$\frac{dm}{dt} \approx am^{2/3} - bm^{3/4}$$

and, at ultimate mass m_∞ , $b = am^{-1/12}$ (note that they erroneously had $b = am^{1/12}$ and this error propagated through the rest of their reasoning, and their a later became α in the discussion).

The rate of growth is the flow of materials available for growth divided by the cost of growth, thus one needs a parameter for this cost, say g , that includes both materials and labour and is in units of mass required per mass built. Thus

$$\frac{dm}{dt} = \frac{am^{\frac{2}{3}} - bm^{\frac{3}{4}}}{g}$$

which is a case of the generalised von Bertalanffy equation mentioned above. Then, by inserting the notion of scaled mass into this equation, $x = m/m_\infty$ so $m = xm_\infty$ and $b = am^{-1/12}$ from above, and writing the differential equation in relation to scaled mass by dividing by m_∞ , one obtains

$$\frac{dx}{dt} = \frac{am_\infty^{\frac{2}{3}}(x^{\frac{2}{3}} - x^{\frac{3}{4}})}{m_\infty g}$$

which simplifies to

$$\frac{dx}{dt} = \frac{a(x^{\frac{2}{3}} - x^{\frac{3}{4}})}{m_{\infty}^{\frac{1}{3}}g}$$

Sibly and Brown, if they corrected their definition of b as $b = am^{-1/12}$, would have instead obtained the mathematically equivalent formula

$$\frac{dx}{dt} = \frac{am_{\infty}^{\frac{2}{3}}(x^{\frac{2}{3}} - x^{\frac{3}{4}})}{qr}$$

where q is the total number of cells in the body and r is the number of macromolecules needed to make a cell (which must include overhead costs, g so $\frac{qr}{g} = m_{\infty}$).

Sibly and Brown's equation is therefore not new in structure, but they focused on growth in respect to scaled mass x because they interpreted it mechanistically as the fraction of developed cells to the total number of cells (growing and developed). Their key idea is that of a direct competition between these two types of cells in relation to supply from capillaries. Leaving aside the fact that many organisms without capillaries follow the same pattern of growth, Sibly and Brown's conceptual argument, specifically their Assumption 1, is inconsistent with the mathematical formulation because they state that $am^{2/3}$ is "the rate at which animals acquire macromolecules" and $bm^{3/4}$ is "the number supplied to developed cells". To avoid a dimensional error (and the implication that growing cells have no maintenance costs), they need to say that $bm^{3/4}$ is the rate that macromolecules are used by the entire biomass for maintenance, i.e. not just the developed cells. Thus, Sibly and Brown's mathematical model does not follow from their conceptual reasoning; it simply follows from their empirically justified assumptions of the exponents for the generalised von Bertalanffy curve.

More problematically, Sibly and Brown's conceptual reasoning leads to an implication that capillaries have zero mass and that growing cells have the same mass as developed cells, even though they are growing. They state:

- 1) The body consists of capillaries (C), growing (G) and developed (D) cells.
- 2) The number of capillaries (n_C) at age t behaves as $n_C(t) = c_1 m(t)^{2/3}$ for m is mass of the individual and c_1 is a constant.
- 3) The delivery of macromolecules per capillary remains constant.

4) If fully grown, the individual consists of q developed cells, which do not grow, but require all transported macromolecules as maintenance.

5) The fraction of developed cells equals $x = \frac{m}{m_\infty}$.

6) Macromolecules are either delivered to developed cells or to growing cells.

7) The number of macromolecules needed to produce a developed cell is a constant, r .

From 1) follows that in terms of masses, we have $m = m_C + m_G + m_D$. From 4) follows that capillaries do not need maintenance, and from 6) that they have no mass, so $m_C = 0$. It will not be easy to give capillaries mass within the present reasoning given their supposed scaling in 2) and the growing vs. developed cells rule in 5). Assumption 2) is surprising given Sibly and Brown's previous position that respiration scales with mass to the power $3/4$ because of the scaling of capillaries with body weight (Banavar *et al.*, 2010).

From 5) follows $\frac{n_D(t)}{n_D(t) + n_G(t)} = \frac{m_G(t) + m_D(t)}{m_\infty}$. This clearly cannot work at the point of the first embryonic cell division. Moreover, the only situation consistent with 7) and 5) is that the average mass of a developed cell M_D is equal to that of a growing cell M_G . Otherwise, while the organism is growing, $\frac{n_D(t)}{n_G(t) + n_D(t)} > \frac{m}{m_\infty}$ when $M_G > M_D$, and vice versa. A cell obviously cannot grow and have constant mass at the same time. Yet this is where we are led under the assumption of constant cell production costs combined with an interpretation of $\frac{m}{m_\infty}$ as the proportion of fully developed cells.

Sibly and Brown are clearly aiming for a physiologically plausible formulation for growth that would lead to testable observations at the tissue and cellular level. This is an important aspiration, but it first requires a physically plausible theoretical framework of metabolism capturing embryo, juvenile and adult stages. Such theory already exists, as mentioned above. We strongly agree with Sibly and Brown that the development of new research programs into the physiological implications of metabolic theory, using some of the ideas mentioned in their discussion, would be highly worthwhile.

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Author/s:

Kearney, MR;Kooijman, SALM

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