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A comment on the growth model of Sibly and Brown

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

37

38 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
39 value of $3/4$ on an appeal to the empirical scaling of food assimilation rate and respiration at rest,
40 respectively. Thus

$$41 \quad \frac{dm}{dt} \approx am^{2/3} - bm^{3/4}$$

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

44

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

$$48 \quad \frac{dm}{dt} = \frac{am^{2/3} - bm^{3/4}}{g}$$

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

$$52 \quad \frac{dx}{dt} = \frac{am_\infty^{2/3}(x^{2/3} - x^{3/4})}{m_\infty g}$$

53 which simplifies to

54

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

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

57

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

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

60

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

73

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

77

1) The body consists of capillaries (C), growing (G) and developed (D) cells.

78

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
79 and c_1 is a constant.

80

3) The delivery of macromolecules per capillary remains constant.

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

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

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

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

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

92

93 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

94 cell division. Moreover, the only situation consistent with 7) and 5) is that the average mass of a
95 developed cell M_D is equal to that of a growing cell M_G . Otherwise, while the organism is growing,

96 $\frac{n_D(t)}{n_G(t) + n_D(t)} > \frac{m}{m_\infty}$ when $M_G > M_D$, and vice versa. A cell obviously cannot grow and have constant mass

97 at the same time. Yet this is where we are led under the assumption of constant cell production costs

98 combined with an interpretation of $\frac{m}{m_\infty}$ as the proportion of fully developed cells.

99

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

106

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109

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