

Comment on “Energy Uptake and Allocation During Ontogeny”

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We demonstrate that the model of energy allocation during ontogeny of Hou *et al.* (Reports, 31 October 2008, p. 736) fails to account for the observed elevation of metabolic rate in growing organisms compared with similarly sized adults of different species. The basic model assumptions of the three-quarter power scaling for resting metabolism and constancy of the mass-specific maintenance metabolism need to be reassessed.

Growth curves $m(t)$ (where m is body mass and t is time) of different biological species are often similar in shape and can be described by several mathematical functions—logistic, Gompertz, or von Bertalanffy curves (I)—each showing satisfactory agreement with the data. Rather than improving the goodness of fit of various mathematical models, a conspicuous challenge for theoretical biology has recently been to understand the biological mechanisms underlying ontogenetic growth and to link them quantitatively to the organismal energy budget (2, 3). We do not agree with the claim of Hou *et al.* (4) that the proposed model of energy allocation during ontogeny correctly captures the essentials of growth energetics.

In the Hou *et al.* model (4), resting metabolic rate $B_g(m)$ of the growing organism is postulated to be partitioned between the rate of energy for maintenance $B_{\text{maint}} = B_m m$ and the rate of energy for biosynthesis $B_{\text{syn}} = E_m dm/dt$, $B_g(m) = B_m m + E_m dm/dt$, where B_m and E_m are mass-independent parameters. Mathematically, the model is a variant

of Bertalanffy growth curve $dm/dt = am^\alpha - bm$, with constant $a > 0$ and $b > 0$ and $\alpha = 3/4$. The model assumes that the scaling of $B_g(m)$ parallels the interspecific scaling of resting metabolic rate $B_i(M) = B_0 M^{3/4}$ (B_0 in $\text{W kg}^{-0.75}$) of adult organisms with species-specific adult body mass M , where B_0 is taxon-specific. As the organism approaches adulthood, $m \rightarrow M$ and $B_g(m) \rightarrow B_i(M)$. Parallel scaling and coincidence of the two functions at $m = M$ means that the two functions are identical, $B_g(m) = B_0 m^{3/4} = B_i(m)$. To put it vividly, the model presumes that a tiger cub and an adult cat of equal body mass should have one and the same metabolic rate.

However, it has repeatedly been observed that young animals have elevated metabolic rates compared with what is predicted for their body mass from interspecific scaling (5–8). For eight species of mammals, in Fig. 1A we plotted resting metabolic rate during ontogeny normalized by the interspecific scaling of resting metabolic rate, $K \equiv B_g(m)/B_0 m^{0.75}$, taking $B_0 = 4 \text{ W kg}^{-0.75}$ as the mean established for mammals and birds in table S7 of Hou *et al.* (4). Recent large-scale analyses of metabolic scaling across life’s major domains (9–11) have emphasized the importance of a rigorous control for biological activity for the resulting metabolic allometries. All measured at rest in

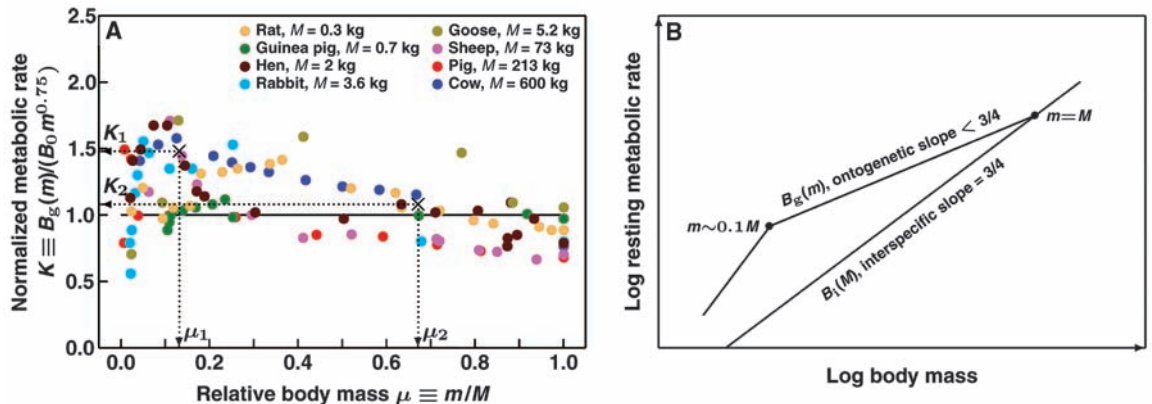
the postabsorptive state, the eight largest values of metabolic rates in early ontogeny (at $\mu < 0.5$) of the eight studied species (one value for each species) correspond to mean relative body mass $\mu_1 = 0.13 \pm 0.04$ ($\pm 1 \text{ SE}$) and average $K_1 = (1.48 \pm 0.08)$ times the interspecific scaling function for the corresponding body masses m (Fig. 1A). For comparison, the eight largest values of metabolic rates measured later in ontogeny (at $\mu \geq 0.5$) correspond to $K_2 = 1.08 \pm 0.08 < K_1$ and $\mu_2 = 0.67 \pm 0.06$, indicating the expected convergence between the ontogenetic and interspecific scaling at $\mu \rightarrow 1$ (Fig. 1A). The observed one-and-a-half time change from K_1 to K_2 is numerically substantial in the model’s framework. This is clear because, assuming the 3/4 scaling for resting metabolic rate, the decrease of the mass-specific metabolic rate with μ growing from 0.13 to 1 constitutes $0.13^{-1/4} = 1.7$ times. The model thus takes into account the 1.7-fold drop in mass-specific metabolic rate but neglects the additional 1.5-fold change that occurs as a result of the peculiarities of ontogenetic metabolic scaling shown in Fig. 1A. Another conspicuous feature of the ontogenetic metabolism is the sharp rise of K observed very early in ontogeny in many species (3). In summary, in line with the available large-scale review of ontogenetic scaling exponents across diverse taxa (12), the available evidence for mammals and birds testifies against a simple power law for metabolic rate $B_g(m)$ during ontogeny and against its 3/4 scaling with body mass (Fig. 1B).

Second, in the framework of Hou *et al.* (4) the parameter $B_m = B_0 M^{1/4}$ (W kg^{-1}) is interpreted as maintenance metabolic rate, which is independent of body mass during ontogeny but is different in species with different adult body mass M . This quantity is not defined in measurable terms (3), and the biological appropriateness of such a parameterization is not justified. It presumes that, irrespective of how metabolically active the tissues of the growing organism are, the energy expenditures on their maintenance are the same. From daily life one knows that an intensely working mechanism (e.g., a car) needs repair and regular

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Fig. 1. Resting metabolic rate of a growing organism does not coincide with resting metabolic rate of a similarly-sized adult organism from a different species and scale as body mass in the 3/4th power. (A) Horizontal line shows the 3/4 scaling postulated for metabolic rate during ontogeny in the model of Hou *et al.* (4). Points indicate the observed metabolic rate during ontogeny for different species [data from (7)] versus relative body mass $\mu = m/M$, where M is adult body mass. Crosses indicate means of the largest K values at $\mu < 0.5$ and $\mu \geq 0.5$. (B) Schematic diagram illustrating the absence of a simple power law for resting metabolic rate during ontogeny. At approximately one-tenth of adult body



mass, $m \sim 0.1 M$, metabolic rate $B_g(m)$ is considerably greater than predicted from the interspecific scaling. To coincide with the latter at $m = M$, $B_g(m)$ must change with body mass with a log-log slope shallower than the assumed 3/4 of the interspecific scaling.

maintenance more often than a rarely exploited one. In logical contrast, in the model of Hou *et al.* (4), a slowly metabolizing adult organism spends more on the maintenance of a gram of its tissues per unit time than an equally sized actively metabolizing youngster of a different species. There are no grounds for postulating constant mass-specific maintenance expenditures. Moreover, in the Hou *et al.* model, $B_m = [B_g(m) - E_m dm/dt]/m$ is constant if only $B_g(m) = B_0 m^{3/4}$. Since, according to the data of Fig. 1A, $B_g(m) \neq B_0 m^{3/4}$, this means that B_m is not independent of body mass.

Generally, until empirical methods are elaborated to define and independently measure the different biochemical components of metabolic

rate (if this is at all possible, e.g., using isotope analysis), mathematical partitioning of metabolic rate during ontogeny into several terms that scale differently with body mass will remain purely formal and thus unable to shed new light on the fundamentals of ontogenetic growth. Additionally, from the available analyses, a demand clearly emerges for new empirical studies with simultaneous measurements of growth, metabolic, and food assimilation rates from early ontogeny to adulthood in a larger number of species.

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