Energy Uptake and Allocation during Ontogeny

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Abstract

All organisms face the problem of how to fuel ontogenetic growth. We present a model, empirically grounded on data from birds and mammals, that correctly predicts how growing animals allocate food energy between synthesis of new biomass and maintenance of existing biomass. Previous energy budget models have typically been based on rates of either food consumption or metabolic energy expenditure. Our model provides a framework that reconciles these two approaches and highlights the fundamental principles that determine rates of food assimilation and rates of energy allocation to maintenance, biosynthesis, activity, and storage. The model predicts that growth and assimilation rates for all animals should cluster closely around two universal curves. Data for mammals and birds of diverse body sizes and taxa support these predictions.

The "food of life" and the "fire of life"—the combustion of food to supply the energy that fuels growth, maintenance and activity—is fundamental to animal survival (1). A large body of previous work has used energy budget models to understand ontogenetic growth (1–7). These have contributed importantly to many conceptual and applied problems, including life history theory, animal husbandry, and biomedicine. Still largely missing, however, is a complete quantitative framework that specifies how food is transformed into metabolic energy and stored biomass. Here, we present such a framework, which quantifies explicitly how assimilated food is transformed into biomass and metabolic energy during ontogeny.

When an animal is growing, some fraction of the assimilated food is oxidized to fuel the total metabolic rate, B_{tot}, while the remaining fraction is synthesized and stored as biomass, S (Fig. 1). Thus, the energy flux of assimilated food, A, sometimes called the rate of intake of metabolizable energy (1,2), is expressed as

$$A = B_{tot} + S = B_{tot} + E_c \, dm/dt \qquad (1)$$

where A is defined as the combustion energy content of ingested food per unit time minus the combustion energy content of excreta per unit time, E_c is the combustion energy content of a unit biomass, and dm/dt is the rate of change in biomass, m, at time, t.

We build on an ontogenetic growth model (OGM), which specifies the allocation of metabolic energy between growth and maintenance and views the scaling of metabolic rate with body size as the primary constraint on growth (7). It partitions the basal metabolic rate, B_{basal}, between the rate of energy expenditure to maintain the existing biomass, B_{maint}, and

the rate to synthesize the new biomass, B_{syn} (Fig. 1): so, $B_{basal} = B_{maint} + B_{syn} = B_m m + E_m dm/dt$, where $B_m \sim M^{-1/4}$ is the mass-specific maintenance metabolic rate, M is the adult body mass, and E_m is the energy required to synthesize a unit of biomass.

It is difficult to measure B_{basal} over ontogeny, because animals grow even while resting. Therefore for growing animals a more operational and realistic parameter is resting metabolic rate, B_{rest}, which is the sum of B_{basal} and Specific Dynamic Action (SDA), the increment due to digestion. SDA is the energy expended for intestinal absorption, nutrient transport, amino acid oxidation, and protein synthesis (8,9). Since some fraction of metabolic rate is allocated to SDA during growth (8–11), we modify the OGM to obtain

$$B_{rest} = B_{maint} + B_{syn} = B_m m + E_m dm/dt \tag{2}$$

where B_m is larger here than in the OGM, which ignored SDA.

It is important to recognize the difference between the terms $S = E_c dm/dt$ in Eq. 1 and $B_{syn} = E_m dm/dt$ in Eq. 2, and, consequently, the difference between E_m and E_c. Energy expended during growth is partitioned between the energy content stored in the newly synthesized biomass, and the energy expended in synthesizing this biomass from the constituent materials. So, S is the rate of accumulated energy content of new biomass, and E_c is its combustion energy content. On the other hand, B_{syn} is the metabolic power expended on biosynthesis, and E_m is the energy expended to synthesize a unit of biomass. The term B_{syn} corresponds to the organizational work of growth (2) and is completely dissipated as heat, not conserved in stored biomass. In the OGM the energy expended on biosynthesis was incorrectly estimated using the empirical combustion energy (7).

For adult mammals and birds, the total metabolic rate is typically referred to as field metabolic rate, and the relationship between total and resting metabolic rates is expressed as $B_{tot}(M) = B_{act}(M) + B_{rest}(M) = f B_{rest}(M)$, where B_{act} is the rate of energy expenditure for locomotion, feeding, and other activities, and f, the activity scope, is a dimensionless parameter (12–14). In adult endotherms f is approximately 2–3 and independent of body mass (12-14). Assuming a similar relationship holds during growth we can write, using Eq. 2, $B_{tot}(m) = f B_{maint}(m) + f B_{syn}(m)$. We define the dimensionless storage coefficient, $\gamma = S/B_{syn} = E_c/E_m$, as the ratio of the energy stored in a unit of biomass to the energy expended to synthesize this biomass. Substituting γ and B_{tot} into Eqs. 1 and 2 gives

$$\begin{aligned} A(m) &= B_{maint}(m) + B_{act}(m) + B_{syn}(m) + S(m) \\ &= [f + \gamma] B_{rest}(m) - \gamma B_{maint}(m) \end{aligned} \tag{3}$$

Equation 3 is quite general, independent of how B_{rest}, B_{maint} or f scale with m. Empirical measurements of metabolic rate over ontogeny and theoretical evidence linking growth and metabolism show that resting metabolic rate $B_{rest}(m) \approx B_0 m^{3/4}$ over ontogeny, where B_0 is constant for a given taxon (14, 15). The mass-specific maintenance rate, taking into account SDA, is $B_m \approx B_0 M^{-1/4}$ (7). Using these scaling relations in Eq. 3 yields

$$\begin{aligned} A(m) &= [f + \gamma] B_0 m^{3/4} - \gamma B_0 M^{-1/4} m \\ &= B_{rest,adult} [(f + \gamma)\mu^{3/4} - \gamma\mu] \end{aligned} \tag{4}$$

where μ ($\equiv m/M$) is relative mass, and $B_{rest,\,adult} \approx B_0 M^{3/4}$ is the resting metabolic rate at the adult size.

Note that equation 4 predicts that during ontogeny the food assimilation rate, A, unlike metabolic rate, does not obey a simple power law as a function of body mass, m. This prediction is well supported (14). In Fig. 2, we plot some examples of the normalized assimilation rate, ($A/B_{rest,\,adult}$), versus μ for six different animals and fit the data with equation 4. Values of f, γ and R^2 for these and several other bird and mammal species are in table S1 (14). The storage coefficient, $\gamma = E_c/E_m$, can in principle be determined independently from the energetics of biosynthesis. The energy content of biomass, E_c, averages about 24000 J/g for dry mass(16), with four-fold variation across vertebrates of different taxa and ontogenetic stages(17). In contrast to E_c, E_m, the energy expended to synthesize a unit of biomass, is difficult to determine empirically (but see 14). Theoretical considerations suggest that the average energy required for biosynthesis of macromolecules from monomers is about 2400 J/g (14). This theoretical value of E_m gives an upper bound of $\gamma \sim 10$, the precise value depending on the additional energy expended on biosynthesis, metabolism, and excretion (3). For mammals and birds, γ averages about 3 and ranges from 1 to 9 depending on species, diet, and age (3, 14, 18). This is consistent with values ranging from 0.8 to 7 for fish, birds and mammals estimated from the OGM (14, 15). We estimated from food assimilation that γ ranges from 0.6 to 5.3 with an average of 2.71 ± 1.18 (table S1), showing that despite some variation, the empirical measurements are in agreement with the theoretical prediction. Values of f vary somewhat, depending on activity levels and behavior. The mean value of f estimated from food assimilation is 2.67 ± 0.61 (table S1), also in agreement with data for adult mammal and bird species (14).

When growth ceases, i.e., $\mu = 1$ ($m = M$), equation 4 predicts that the food assimilation rate equals the total metabolic rate, which scales with mass, M. So, $A = fB_0 M^{3/4}$ across adults of different species. Data for ad libitum energy intake from food of 120 species of zoo mammals with body masses ranging from 0.025kg to 3000kg show $A = 7.07 M^{0.75}$, clearly supporting the prediction (14, 19, see also 20). Taking the average value of B_0 for resting metabolic rates of mammals, 3.92 W/kg$^{3/4}$ (14), gives $f \approx 1.8$. This is somewhat less than that expected for wild animals, which may reflect lower activity levels in captivity.

Our model predicts that growth rates of diverse animals should exhibit universal properties. The fraction of energy assimilation rate allocated to growth is the sum of S and B_{syn}. With Eq. 2 and the definition of γ, this fraction, $S + B_{syn} = (1 + \gamma)B_{rest,\,adult}(\mu^{3/4} - \mu)$. If we normalize this quantity with respect to $(1 + \gamma)B_{rest,\,adult}$, then all animal species, regardless of taxon or adult mass, should fall on the same parameterless universal curve, $\mu^{3/4} - \mu$. This further predicts that the maximum energy utilization rate for growth occurs when $d(\mu^{3/4} - \mu)/d\mu|_{\mu=\mu_0} = 0$, which gives $\mu_0 = (3/4)^4 = 0.316$. Equation 3 suggests a way to test these predictions. If we subtract the rate of metabolism for activity, B_{act}, and maintenance, B_{maint}, from the assimilation rate, A, the difference gives the rate of energy assimilation allocated to growth, $S + B_{syn}$. This quantity, normalized as above, is plotted as a function of the relative mass μ in Fig. 3A. The normalized assimilation rates for mammals and birds of widely varying body sizes and taxa clearly show such universal properties, clustering closely around the predicted parameterless curve with a peak at ~ 0.316.

Additionally, the rate of energy allocation to growth must be proportional to the growth rate, dm/dt, so the universal curve and the value of $\mu_0 = (3/4)^4 = 0.316$ can be derived independently from the growth rate equation, Eq. 2, $dm/dt = (B_0/E_m)m^{3/4}[1 - (m/M)^{1/4}]$. This can be re-expressed as $(E_m M^{1/4}/B_0)d\mu/dt = \mu^{3/4} - \mu$. Data for normalized growth rates, $(E_m M^{1/4}/B_0)d\mu/dt$, for diverse mammals and birds, measured independently from the above measurements of assimilation rate, support this prediction (Fig. 3B). So, estimations from

the rate of food assimilation and the rate of change in body mass independently predicted analogous universal curves with a maximum at a normalized body mass of ~ 0.316.

The predicted allometric scalings of metabolic energy allocation are summarized in Fig. 4A, which shows the rates of food assimilation, and total, resting, and maintenance metabolism for two individuals of different adult size depicted by different colors. The figure illustrates the complete energy budget during growth, $A = B_{maint} + B_{act} + B_{syn} + S$, and allocation of energy at any given size is shown by the colored vertical lines. The assimilation rate, A, of a growing individual does not scale as a power law with mass, whereas its rates of total and resting metabolism, B_{tot} and B_{rest}, both scale as $m^{3/4}$, and its maintenance rate, $B_{maint} = B_m m$ scales linearly. In contrast, for adults of different sizes, rates of assimilation and total (dashed black line) and resting (maintenance, solid black line) metabolism all scale as $M^{3/4}$. Across species of different adult masses, growth ceases when all resting metabolism is allocated to maintenance (7) so that $B_{rest} = B_{maint}$, as indicated in Fig. 4A (colored circles) representing two different adult masses, M_1 and M_2. Finally, if otherwise identical individuals vary in energy allocated to activity, thereby having different values of B_{act} and B_{tot}, they must compensate by adjusting their assimilation rates, A, if they are to mature at the same adult mass, M.

One implication of the model is that when two individuals with the same B_0, f, and γ, but different adult body masses, M_1 and M_2 ($M_1 > M_2$), have the same body mass, m, during growth, the assimilation rate of the one with the greater adult mass, M_1, must be larger than the one with the smaller adult mass M_2, i.e., $A(m,M_1) - A(m, M_2) \propto (M_2^{-1/4} - M_1^{-1/4})m > 0$. To test this prediction, we plotted the assimilation rates of three pairs of closely related animals, assumed to have the same B_0, f, and γ, as a function of body mass m during growth. As illustrated in Fig. 4B, when members of each pair had the same body mass, m, during growth, the one with larger adult size (M) had a higher assimilation rate.

Our quantitative, predictive model for the energy budget of an individual during growth differs from phenomenological models that fit curves to data. It also differs from dynamic energy budget theory (DEB), which assumes a 2/3 power scaling of food assimilation rate during ontogeny, based on the idea that energy uptake is limited by absorptive surface area, which scales like any simple geometric surface (4). By contrast, our model predicts that food assimilation rate cannot have a simple power-law scaling relation with body mass during ontogeny. Furthermore, DEB assumes that food assimilation rate is supply-limited, whereas our model views assimilation rate as arising from the developing organism matching food supply to metabolic energy demand. Our model provides a point of departure for addressing pathological cases of imbalance between supply and demand such as starvation or overeating. It captures the salient features of energy acquisition and allocation during ontogenetic development, and quantitatively predicts universal assimilation and growth rate curves in agreement with data for mammals and birds. How well it captures the fundamental features of growth in other organisms, such as ectothermic vertebrates, insects, aquatic invertebrates, plants, and unicellular algae and protists, remains to be seen.

Acknowledgments

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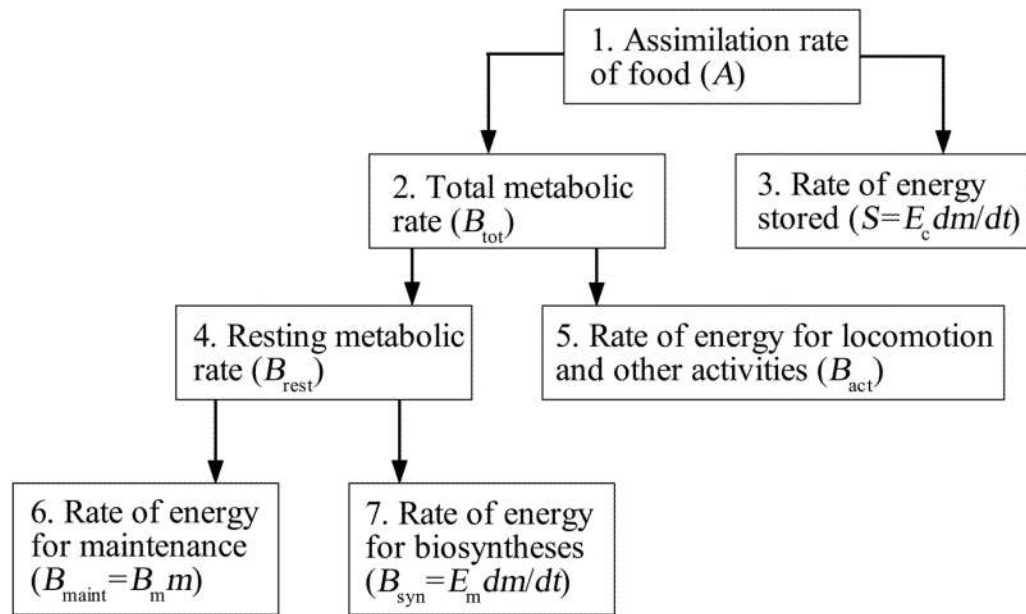20. Kirkwood JK. J Nutrition 1991;121(Supp 11):29.

Fig. 1.
Partitioning of assimilated energy during ontogeny. Partitioning between Boxes 2 and 3 represents Eq. 1, and partitioning between Boxes 6 and 7 represents Eq. 2.
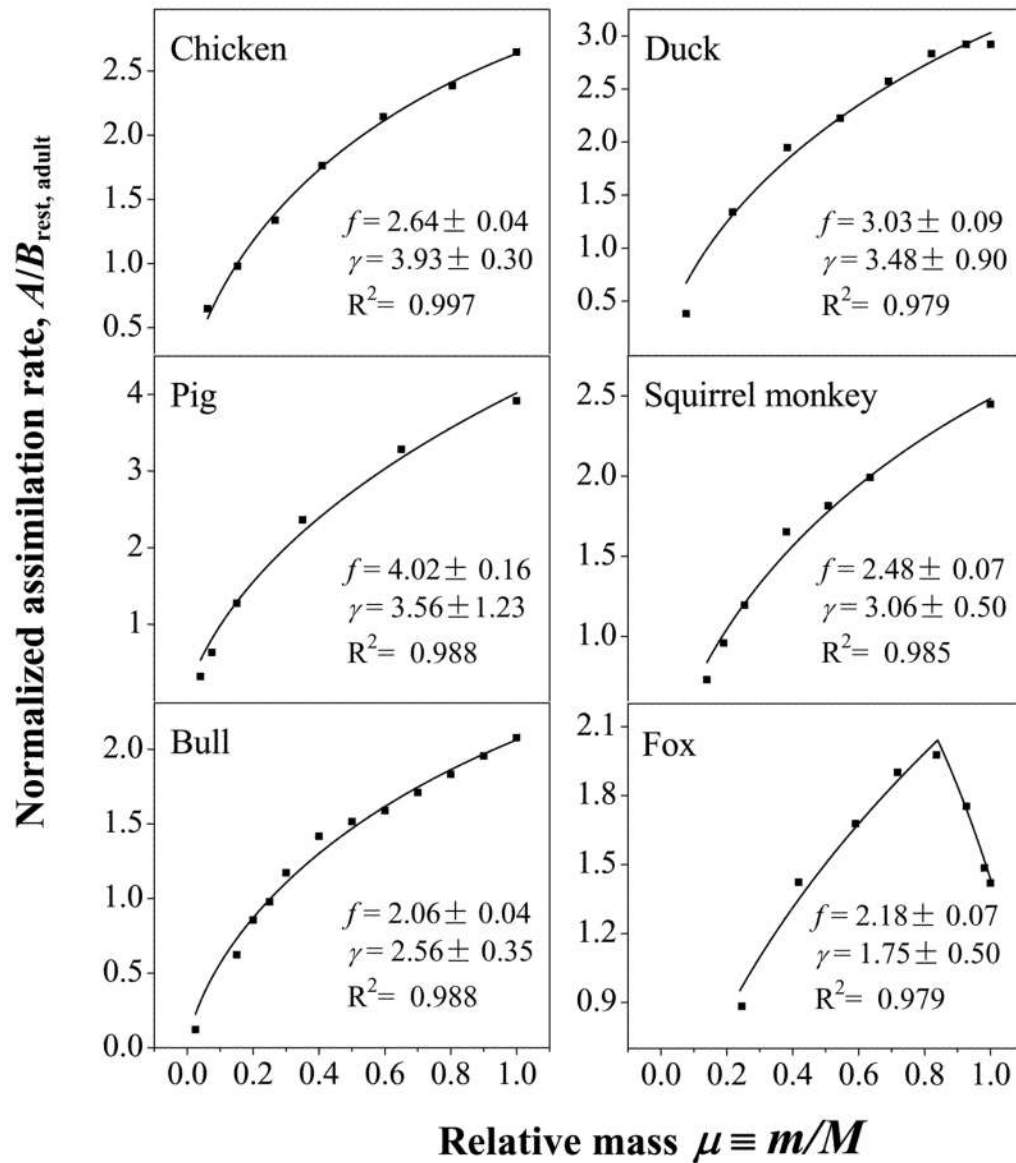
Fig. 2.
Examples of normalized assimilation rate as a function of relative body mass for six mammals and birds (squares). The solid lines are fits of our model to these data using Eq. 4. (Parameters, f and γ, are estimated using nonlinear least squares regression method based on the Levenberg-Marquardt algorithm.)The majority of assimilation rate curves reported in the literature are monotonic, but a few, including curves for furbearers such as fox, are peaked relationships (14).
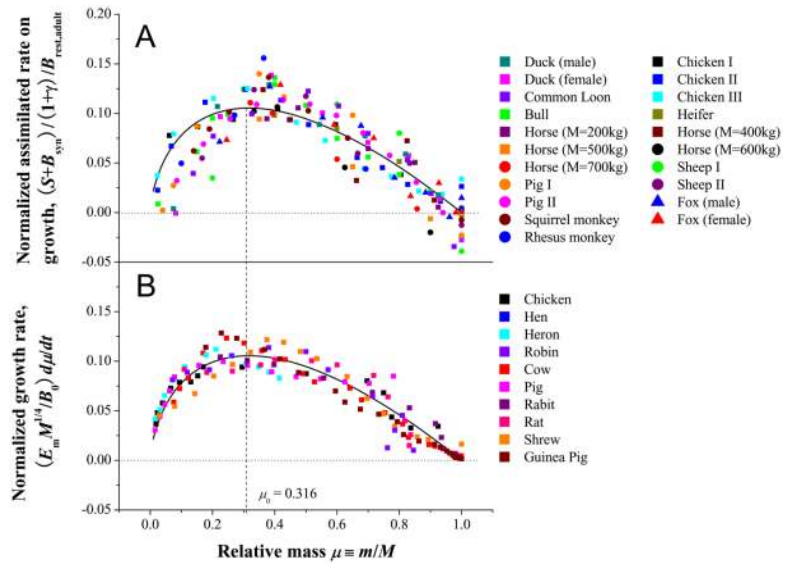
Fig. 3.
Two growth curves that are 'universal' in the sense that they are based on principles of energy allocation and predicted to be independent of taxon and body size: (**A**) universal rate of assimilation of food for growth, and (**B**) universal rate of change in body mass. The empirical estimates (14, colored symbols for different organisms, with assimilation and growth rates measured independently in different studies) closely match the theoretical predictions (continuous curves which peak at 0.316).
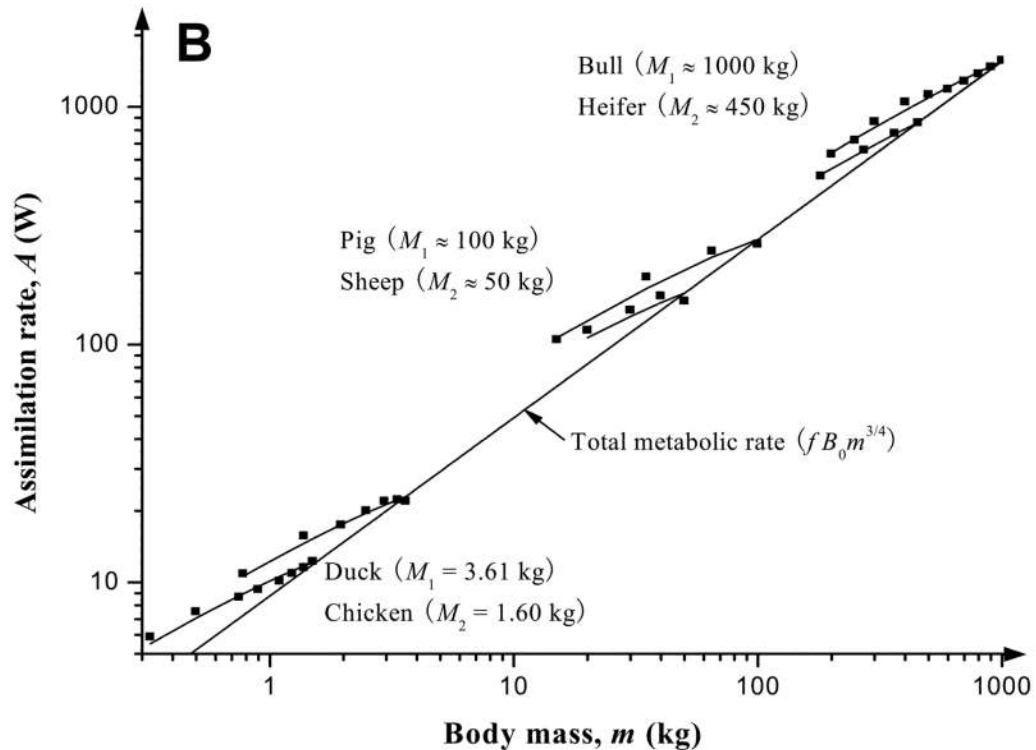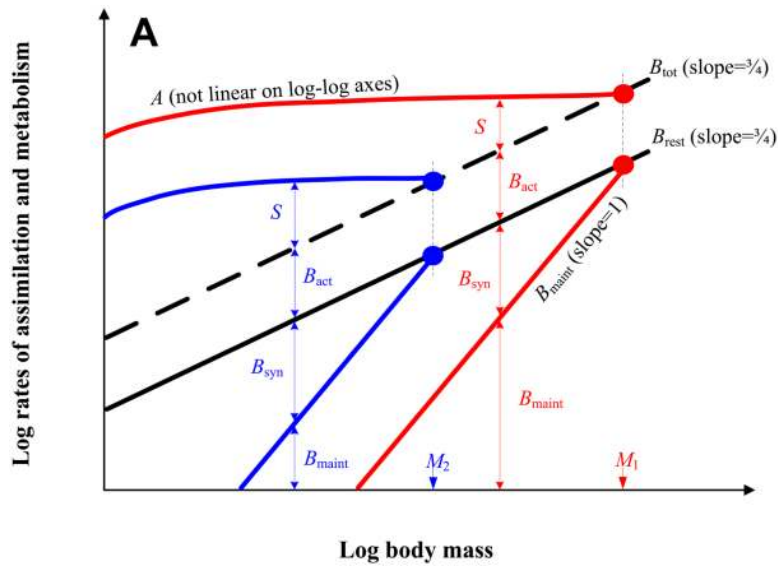
Fig. 4.
(**A**) Schematic illustrating the allometric scalings of energy allocation during growth for two individual organisms (shown with different colors) of different adult sizes, M_1 and M_2. For each individual, the colored vertical lines illustrate how at any given body mass during ontogeny, the rates of energy allocated to maintenance (B_{maint}), biosynthesis (B_{syn}), activity (B_{act}), and storage (S) sum to equal the rate of assimilation, A. The scalings across individuals of two different body sizes are shown as dashed and solid black lines for total and resting metabolic rates respectively, with the colored dots corresponding to these rates at the adult sizes, M_1 and M_2. (**B**) Assimilation rate as function of body mass for 3 pairs of mammals or birds. To facilitate comparison, we assume that $f = 2.67$ for all animals.