Revisiting a Model of Ontogenetic Growth: Estimating Model Parameters from Theory and Data

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abstract: The ontogenetic growth model (OGM) of West et al. provides a general description of how metabolic energy is allocated between production of new biomass and maintenance of existing biomass during ontogeny. Here, we reexamine the OGM, make some minor modifications and corrections, and further evaluate its ability to account for empirical variation on rates of metabolism and biomass in vertebrates both during ontogeny and across species of varying adult body size. We show that the updated version of the model is internally consistent and is consistent with other predictions of metabolic scaling theory and empirical data. The OGM predicts not only the near universal sigmoidal form of growth curves but also the $M^{1/4}$ scaling of the characteristic times of ontogenetic stages in addition to the curvilinear decline in growth efficiency described by Brody. Additionally, the OGM relates the $M^{3/4}$ scaling across adults of different species to the scaling of metabolic rate across ontogeny within species. In providing a simple, quantitative description of how energy is allocated to growth, the OGM calls attention to unexplained variation, unanswered questions, and opportunities for future research.

Keywords: metabolism, allometry, scaling, bioenergetics, ontogeny.

Nearly all characteristics of organisms vary with body size. It has long been recognized that most of this variation can be described by allometric equations or power laws of the form $Y = Y_0 M^{\gamma}$, where Y is some variable, such as metabolic rate or life span; Y_0 is a normalization constant that typically varies with trait, taxon, and other factors; M is a measure of body size, typically mass; and γ is another constant, the allometric or scaling exponent. Ever since Kleiber (1932) showed that whole-organism metabolic rate, B, scales as $B = B_0 M^{3/4}$, it has been recognized that γ often takes on values that are close to simple multiples of 1/4 (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown et al. 2004; Savage et al. 2004; West and Brown 2005). Both historically and recently, skeptics have claimed that at least some exponents are closer to thirds than quarters (e.g., Heusner 1982; White and Seymour 2003; Glazier 2005), but this debate does not negate the importance of understanding biological scaling laws and the processes that generate them. In particular, it does not negate the importance of understanding theoretically and empirically how resources are allocated to growth and maintenance as body size increases during ontogeny.

Biologists have devoted considerable attention to patterns of ontogenetic growth and development. Numerous mathematical models have been proposed to describe growth (e.g., see references in Ricklefs 2003), but most of these are justified simply because they give good statistical fits to empirical data. West et al. (2001) developed an ontogenetic growth model (OGM) that was intended to provide a general mechanistic model of organism growth. In contrast to most previous models (but see von Bertalanffy 1957; Koojiman 2000), the OGM related parameters to other fundamental biological properties and predicted sigmoidal growth curves that appear to match empirically measured curves for a variety of animal taxa. In particular,

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the OGM characterized the bioenergetics of growth: the rates at which energy is assimilated and then allocated between production of new biomass and maintenance of existing biomass. Additionally, the OGM assumed that whole-organism metabolic rate scales as $M^{3/4}$, and it predicted other quarter-power scaling relationships that are consistent with empirical observations.

Since the OGM was published, it has received considerable attention, including both support (e.g., Gillooly et al. 2001, 2002; Guiot et al. 2003, 2006) and criticism (e.g., Banavar et al. 2002; Ricklefs 2003; Makarieva et al. 2004; van der Meer 2006). Some of the criticisms have been addressed previously (West et al. 2002, 2004), and we plan to respond to additional criticisms in articles by Makarieva et al. (2004) and van der Meer (2006) in a separate article of our own. In this article, we reconsider the OGM, revaluate its assumptions and predictions, provide additional conceptual and empirical clarification of the parameters, and discuss more general biological implications.

Overview of the OGM

The OGM was based on conservation of energy. The rate at which energy is devoted to growth or production of new biomass is equal to the rate at which metabolic energy is assimilated minus the rate at which energy is allocated to maintenance of existing biomass, which can be expressed as

$$E_{\mathrm{m}}\frac{dm}{dt} = B - B_{\mathrm{m}}m, \tag{1}$$

where E_{m} is the quantity of metabolic energy required to create a unit of biomass (which we express in J/g), m is mass at time t, B is the rate of metabolic energy assimilation (in J/s or W), and B_{m} is the metabolic rate required to maintain an existing unit of biomass (in W/g).

The OGM assumed that the scaling of metabolism during ontogeny parallels interspecific scaling, so $B \approx B_0 m^{3/4}$. The model also assumed that B_{m} is constant during ontogeny, reflecting a constant mass-specific cost during ontogeny for maintaining existing biomass. Thus, B_{m} was assumed to be independent of m but (as we show in "Ontogenetic and Interspecific Scaling Are Equivalent") dependent on adult mass, M. Thus, in the OGM, equation (1) was written as

$$\frac{dm}{dt} = am^{\alpha} - bm^{\beta}. \tag{2}$$

The original OGM assumed that $a = B_0/E_{\mathrm{m}}$, $\alpha = 3/4$, $b = B_{\mathrm{m}}/E_{\mathrm{m}}$, and $\beta = 1$. We again use $\alpha = 3/4$ in the development of this article, largely to simplify our presentation. In appendix A in the online edition of the *American Naturalist*, we show how the framework can be generalized to other values of α.

Equations (1) and (2) are simply statements of conservation of energy, and so they must be valid, although the actual values of the parameters remain to be tested. Here, we parameterize the model in units of biomass rather than in units of cells, as was done in the original OGM. We make this change for practical reasons rather than because of any logical or conceptual problem with the model of West et al. (2001), which parameterized growth in terms of the number of cells (N_{c}) and the rate of energy expenditure to create (E_{c}) and maintain (B_{c}) a cell. It is more straightforward to estimate parameters from empirical data in terms of biomass.

Ontogenetic and Interspecific Scaling Are Equivalent

Here, we show that the OGM predicts that the ontogenetic and interspecific scaling exponents are equivalent. Following equation (2), growth ceases, and maximum size (M) is reached when all metabolic intake is required for maintenance, so that $aM^{\alpha} = bM^{\beta}$, which can be rearranged as $B_{\mathrm{m}} = B_0 M^{-1/4}$ under the assumptions $\alpha = 3/4$ and $\beta = 1$. When growth stops at asymptotic size M, total metabolism is equal to maintenance metabolism ($B = B_{\mathrm{m}}M$), and substituting $B_{\mathrm{m}} = B_0 M^{-1/4}$, then $B = B_0 M^{3/4}$. So, the interspecific scaling of adult mass-specific and whole-organism metabolic rates, $B_{\mathrm{m}} \propto M^{-1/4}$ and $B \propto M^{3/4}$, respectively, are necessary consequences of the ontogenetic scaling exponent ($\alpha = 3/4$). In appendix A, we show that assuming $\alpha = 3/4$ requires $B_{\mathrm{m}} \propto M^{-1/4}$ and $B \propto M^{3/4}$ between species even if we relax the assumption that $\beta = 1$. More generally, the theory predicts the same scaling exponent for ontogenetic and interspecific scaling independent of the values of α, β, or a in equation (2).

Empirical Estimates of α, the Ontogenetic Metabolic Scaling Exponent

Numerous studies provide data on how metabolic rate scales with mass for adult animals of different species. The preponderance of evidence supports an interspecific scaling exponent of 3/4 (Hemmingsen 1960; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Brown et al. 2004; Savage et al. 2004), although there has been continued debate over whether it is closer to 3/4 or 2/3 (e.g., Heusner 1982; White and Seymour 2003).

There are fewer studies that examine how metabolic rate scales with mass during ontogeny. Glazier (2005) reviewed allometric scaling of metabolic rate within species, including both cases where body size changes during ontogeny and cases where body size varies among adult in-

dividuals. He found that there is a wide range of observed scaling exponents and concluded that α is significantly different from 3/4 more often than it is significantly different from 2/3. However, relatively few studies in Glazier's review measured metabolic rate over a sufficient mass range to obtain a meaningful estimate of α. Glazier listed 497 studies for which a mass range (R_M = maximum mass/minimum mass) is reported. We plot α versus R_M in figure 1. In the 417 studies in which R_M is less than two orders of magnitude, the mean value of α is 0.70 with a mean 95% confidence interval (CI) of ± 0.22. In the 79 studies in which R_M is greater than two orders of magnitude, the mean exponent is 0.79 with a mean 95% CI of ± 0.07. Thus, in 84% of the studies, R_M is less than two orders of magnitude, and there is enormous variation in α between studies and wide CIs within studies; these studies do not provide a meaningful estimate of α, and they do not distinguish between $\alpha = 2/3$ and $\alpha = 3/4$. In the studies with $R_M \geq 100$, the mean value of α (0.79) is substantially closer to 3/4 than to 2/3, and there is much less variation within and between studies. The same trend is evident when α is analyzed within taxonomic or functional groups (e.g., within vertebrates, and within invertebrates, further divided into terrestrial, benthic, and pelagic species; table 1). Glazier's conclusion that α is more often different from 3/4 than from 2/3 is largely the result of including a large number of studies with small R_M in the analysis. There is certainly variation in empirical estimates of α, but in studies with sufficient mass range, α is consistently much closer to 3/4 than to 2/3.

We compile and analyze data on metabolic rate during ontogeny from FishBase (Froese and Pauly 2006) and find a similar trend in α: it is close to 3/4, and it is less variable when calculated for species with larger mass range. We considered only the 19 fish species for which there were at least 20 data points for "standard" or "routine" metabolism measured under unstressed conditions and for which mass varied by at least one order of magnitude. The data were adjusted for temperature variation by normalizing all metabolic rates to 20°C (following Gillooly et al. 2002). Figure 2 shows a histogram of the regression slopes; the mean and median exponent is 0.80. The standard error (SE) of the mean is 0.04, but the mean SE over all slopes is 0.07. The 95% CI includes 0.75, and the distribution is similar to the distributions of interspecific scaling exponents for a variety of taxa in Peters (1983, fig. 4.1; mean = 0.74, median = 0.74, SE = 0.01). Withers (1992, fig. 4.7) also showed a similar distribution for in-

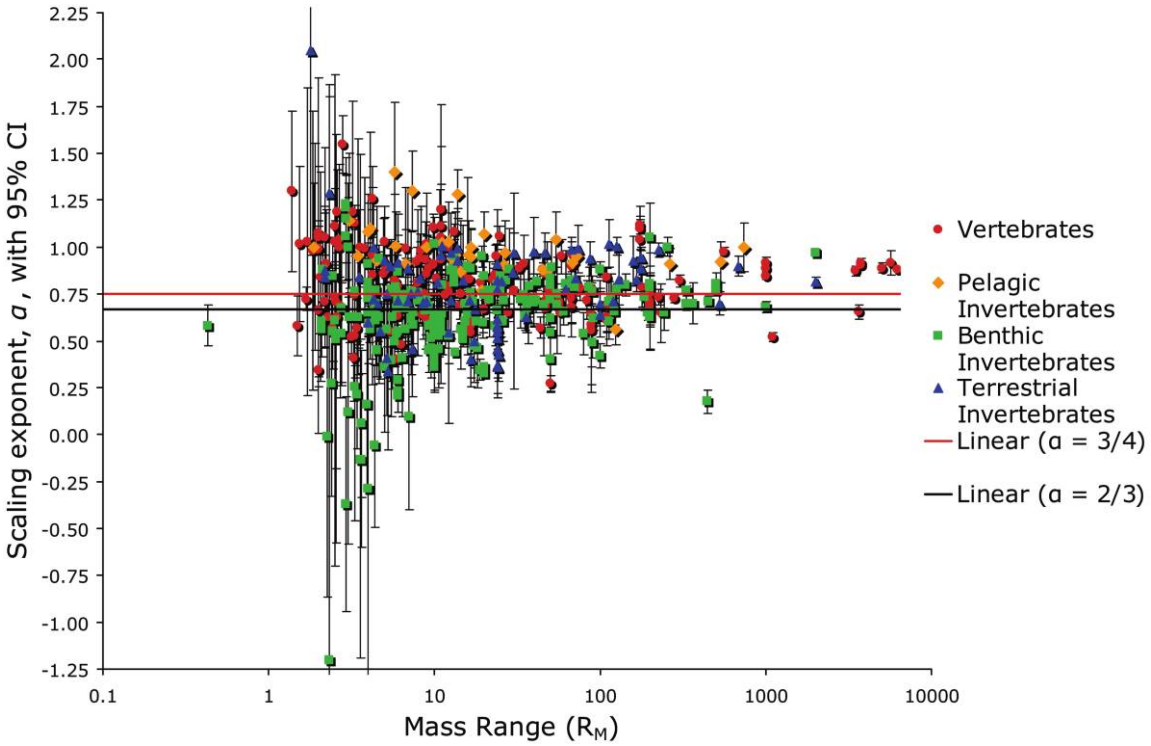

Figure 1: Metabolic scaling exponent α as a function of the range of masses (R_M = maximum mass/minimum mass) from each study reported by Glazier (2005). Lines indicating $\alpha = 3/4$ and $\alpha = 2/3$ are shown for reference.

Table 1: Mean slopes and 95% confidence intervals (CIs) of the ontogenetic scaling exponent (α) in different taxonomic groups

Group and R_M	Mean α	Mean CI	N
All:			
>100	.79	.07	79
<100	.70	.22	417
All	.74	.18	496
Vertebrates:			
>100	.82	.07	34
<100	.82	.20	138
All	.82	.18	172
All invertebrates:			
>100	.77	.07	47
<100	.69	.21	278
All	.70	.19	325
Pelagic invertebrates:			
>100	.85	.10	4
<100	1.00	.21	29
All	.98	.20	33
Benthic invertebrates:			
>100	.73	.06	28
<100	.61	.20	187
All	.63	.18	215
Terrestrial invertebrates:			
>100	.84	.08	15
<100	.77	.22	60
All	.78	.19	75

Note: The data are analyzed separately for mass ranges (R_M) <100, >100, and all together. When $R_M > 100$, the CI is much smaller, and α is closer to 3/4. Data from Glazier (2005).

traspecific and interspecific scaling exponents (mean intraspecific = 0.72, interspecific = 0.76). Clarke and Johnston (1999) found a similar ontogenetic scaling exponent in teleost fish but with more variation (mean = 0.79, SE = 0.11; they analyzed temperature separately, so the mass-scaling analysis includes variation due to temperature).

In figure 3 we plot the allometric regression lines for whole-organism metabolic rate during ontogeny for seven of the above 19 species of fish that span at least three orders of magnitude in body mass. An ANCOVA indicates a significant interaction between species identity and slope of the regression line ($F = 161.5$, $P < .001$). Although slopes vary between species, the slopes cluster around 0.75. The mean is 0.78, and the SE of the mean = 0.02. The mean SE averaged over the seven individual slopes is also 0.02, much smaller than the mean SE of 0.09 for the 12 species for which $10 < R_M < 1{,}000$. In figure 3 we show the close agreement between the interspecific and ontogenetic scaling of metabolism by superimposing the interspecific regression obtained by Peters (1983). For the regression $B = B_0 m^{\alpha}$ in fishes at 20°C, Peters gives $\alpha = 0.8$ and $B_0 = 0.4$ W/kg$^{0.8}$, which is equivalent to $B_0 = 0.002$ W/g$^{0.8}$.

Brody (1945) compared the scaling of metabolism during ontogeny to the interspecific scaling (Brody 1945, fig. 13.9). Although the ontogenetic curves lie close to the interspecific curves, Brody noted that ontogenetic trajectories frequently appear to have varying slopes and breaks in the scaling relations such that earlier in the juvenile period, metabolic scaling is nearly linear, and later it is more shallow (see also Post and Lee 1996 for fish). A number of subsequent analyses support the 3/4 power scaling of metabolism during ontogeny in domesticated animals (Webster et al. 1976; Agricultural Research Council 1980; Garret and Johnson 1983; National Research Council 2000). Additional studies compare both ontogenetic scaling exponents and coefficients for domestic animals, and again they find that they are close to the interspecific values: exponents of 0.74 for rams and 0.76 for wethers with a scaling coefficient of 3.7 W/kg$^{3/4}$ (Blaxter et al. 1982) and exponent of 0.75 with a scaling coefficient of 3.7 W/kg$^{3/4}$ for beef cattle (Lofgreen and Garrett 1968).

We do not claim that the ontogenetic metabolic exponent, α, is precisely 3/4 for all stages of ontogeny for all species. Rather, all of these analyses (Brody 1945; Peters 1983; Withers 1992; Post and Lee 1996; Clarke and Johnston 1999; Glazier 2005; and our analysis of data from Froese and Pauly 2006) give a consistent picture of α: (1) the average value of α is approximately 3/4, the same as the interspecific metabolic scaling exponent; (2) α is closer to 3/4 and is estimated with much greater precision when there is a larger range in body mass in the study; and (3)

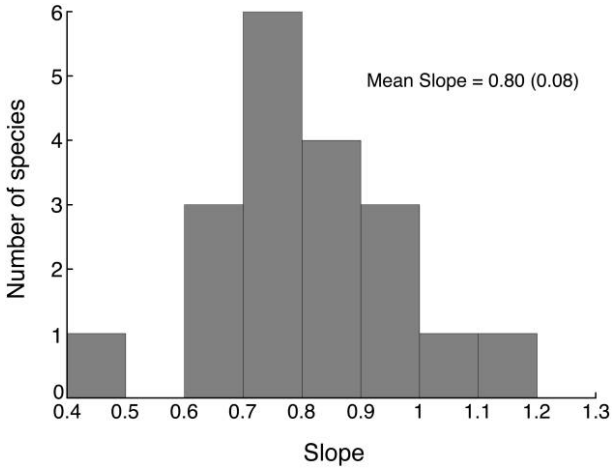

Figure 2: Frequency histogram of the scaling exponent for metabolic rate and mass during ontogeny for 19 species of fish (data from Froese and Pauly 2006). The mean slope is 0.80 ± 0.08 (95% confidence interval). Metabolic rate is corrected to 20°C following Gillooly et al. (2002).

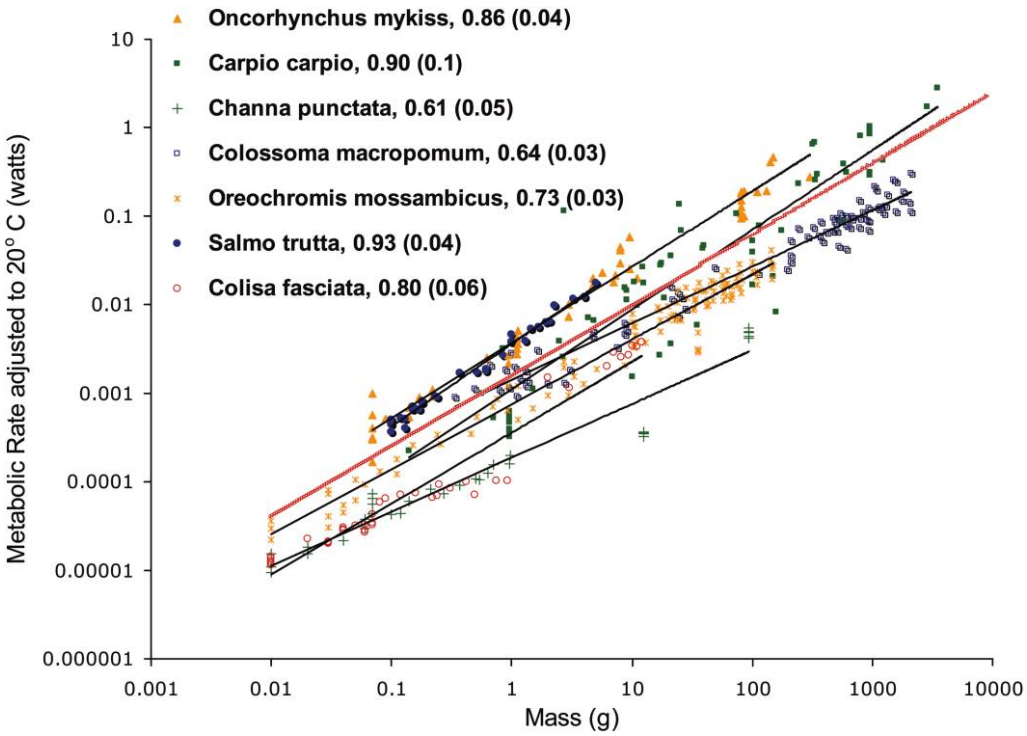

Figure 3: Scaling of metabolic rate with body mass during ontogeny for seven fish species, each of which spans greater than three orders of magnitude in mass. Metabolic rate is corrected to 20°C following Gillooly et al. (2002). Separate regression lines are shown for each of the seven species that have a mean slope of 0.78. The slope, α (with 95% confidence interval), is reported for each species. The thick red line gives the interspecific scaling of metabolism at 20°C with $B = B_0 = 0.002$ W/g$^{0.8}$ reported by Peters (1983).

there is meaningful variation in α, both between species (as is evident in fig. 1, even for large R_M) and over the ontogeny of individual species (as has been shown previously by Brody [1945], Post and Lee [1996], and Glazier [2005]). We emphasize that the existence of variation in α in no way invalidates the study of the central tendency in α.

These results all suggest that despite some variation, the canonical value of the scaling exponent for whole-organism metabolic rate is 3/4, both during ontogeny and among adults of many different vertebrate species. Thus, we set the parameter $\alpha = 3/4$ in equation (2) because it is both theoretically supported (West et al. 1997, 1999; West and Brown 2005) and the best approximation of metabolic scaling over a variety of species. Since there may be meaningful biological variation in α for some species or during some periods of ontogeny, we also give general forms for all of our numbered equations valid for any α (table A1 in the online edition of the *American Naturalist*). We also discuss how variation in α affects our parameter estimates from empirical data. We encourage further investigations into the causes of variation in α.

Estimating the Metabolic Scaling Exponent, α, from Growth Times

The OGM predictions closely fit growth curves by assuming that $\alpha = 3/4$. However, others have pointed out that plots of mass as a function of time or of growth rate as a function of mass provide insufficient resolution to distinguish whether α is closer to 3/4 or 2/3 (Banavar et al. 2002; Makarieva et al. 2004). For example, Banavar et al. (2002) showed that both $\alpha = 3/4$ and $\alpha = 2/3$ closely fit the same data (however, that analysis is not dimensionally consistent [West et al. 2002], and it fails to adjust the B_0 parameter to reflect alternative scaling exponents). The von Bertalanffy growth equation (with $\alpha = 2/3$, $\beta = 1$) has provided reasonable fits to large quantities of fishery data for decades (von Bertalanffy 1957; Beverton and Holt 1959; Charnov 1993). So, fitting models to curves of mass versus time (or renormalized mass vs. renormalized time) often cannot distinguish between $\alpha = 3/4$ and $\alpha = 2/3$.

Here, we show that it is possible to estimate α more precisely by analyzing growth times. This is a particularly powerful method for determining α empirically, because

time to some benchmark stage or size can be measured more easily and reliably than metabolic rate. First, we consider growth to some size m, where m/M is small. For embryos in which $m \ll M$, we simplify equation (2) to $dm/dt \approx am^{3/4}$. Integrating to solve for time (t) to grow to mass (m) gives

$$t \approx \frac{4}{a} m^{1/4}. \tag{3}$$

So we predict that early in ontogeny, the time to reach a given mass will follow $t \propto m^{\delta}$, where $\delta = 1/4$. More generally, $\delta = 1 - \alpha$, so the exponent relating growth times to mass can be used to determine the ontogenetic metabolic exponent. In a wide variety of vertebrate taxa (reviewed in Peters 1983; Calder 1984) including amphibians, birds, and fish, time to hatching scales with mass at hatching with an exponent very close to $\delta = 1/4$ (Rahn and Ar 1974; Linstedt and Calder 1981; Peters 1983; Vleck and Vleck 1987, 1996; Charnov 1993; Purvis and Harvey 1995; Gillooly et al. 2001, 2002). For example, in the most comprehensive study relating incubation time to egg mass, $\delta = 0.217$ and $r^2 = 0.74$ for 475 birds (Rahn and Ar 1974). Ricklefs and Starck (1998) reports that several earlier studies find $0.21 < \delta < 0.24$, but he found that within particular orders, the exponent is much lower. Significant phylogenetic effects are also found by Ricklefs and Nealen (1998). Vleck and Vleck (1996) suggest that the most meaningful regression is between incubation time and dry mass of the embryo at hatching; they found $\delta = 0.251 \pm 0.05$ and $r^2 = 0.66$ for 52 species. All of these early studies are consistent with $\delta = 1/4$, except Ricklefs's analyses within smaller taxonomic groups, where δ is much lower. None of these studies are consistent with $\delta = 1/3$.

Next, we consider the more general case in which m may be a larger fraction of M. The OGM predicts the time, t, to grow to any size m, given by integrating equation (2) (West et al. 2001; Gillooly et al. 2002):

$$t = -\frac{4}{a} M^{1/4} \ln\left[1 - \left(\frac{m}{M}\right)^{1/4}\right]. \tag{4}$$

If (m/M) is a fixed fraction of adult mass (M), then equation (4) predicts $t_m \propto M^{\delta}$, where $\delta = 1/4$. More generally, appendix A shows that $\delta = 1 - \alpha$, even if β deviates from 1. For 60 mammal species with reliable life tables, Purvis and Harvey (1995) report scaling exponents for $t_m \propto M^{\delta}$, where (i) t_m is age at weaning ($\delta = 0.215$, SE = 0.026) and (ii) t_m is age at maturity ($\delta = 0.219$, SE = 0.023). Both exponents are indistinguishable from 1/4 but significantly different from 1/3. However, using phylogenetic contrasts, Purvis and Harvey find that the ratio m/M decreases slightly as M increases, potentially altering the interpretation of δ.

To address variation in m/M, we analyze a more extensive data set (Ernest 2003) with 630 terrestrial mammals for which adult mass (M), gestation time (t_g), and mass at birth (m_g) are all reported. We analyze primates separately because they are known to exhibit different scaling relationships (Charnov and Berrigan 1993). We first report two simple analyses similar to those reported above. Using ordinary least squares (OLS or Type 1) regression, t_g scales with m_g by $t \propto m^{0.28 \pm 0.01}$ (95% CI, $r^2 = 0.82$) and with adult mass by $t \propto M^{0.26 \pm 0.01}$ (95% CI, $r^2 = 0.81$). These exponents are slightly larger than those reported above, and the first is significantly greater than 1/4.

Now we explicitly include m/M as a variable in our analysis by rearranging terms in equation (4). We calculate the regression of $t_g / \ln[1 - (m_g/M)^{1/4}]$ versus M using two statistical methods. The OLS regression is traditionally used, but it assumes that all measurement error is in the dependent variable and none is in the independent variable; reduced major axis (RMA or Type 2) regression assumes that measurement error is equally distributed between the dependent and the independent variables (Warton et al. 2006; O'Connor et al. 2007). In this case we suggest that gestation times are measured with as much accuracy as body mass; however, the dependent variable contains equation error and measurement error in three variables (gestation time, adult body mass, and newborn body mass), so there may be somewhat more error in the dependent variable. We suggest that the best estimate for the exponent lies somewhere between the RMA and the OLS estimates.

In the regression equation $t_g / \ln[1 - (m_g/M)^{1/4}] \propto M^{\delta}$, the RMA estimate for δ is 0.29 and the OLS is 0.28 ($r^2 = 0.89$, 95% CI is ± 0.01; data shown in fig. 4). Both estimates are between 1/4 and 1/3, and both estimates are distinguishable from both 1/3 and 1/4. We also analyzed the six orders with at least 20 species represented in the data. Using OLS, exponents range from 0.17 for primates to 0.29 for rodents, with a mean exponent of 0.23; with RMA the range is 0.22–0.34, with a mean of 0.27. We also find similar exponents for time from conception to weaning (0.28 and 0.29, ± 0.01, through all data points for OLS and RMA, respectively). These estimates do not clearly distinguish a single exponent that is either 1/4 or 1/3.

The exponents in earlier studies are much more clearly 1/4; however, more thorough analysis of statistical methods and variation in the ratio m/M is warranted. We suggest that further careful reporting and analysis of biological times may provide more precise estimates of the scaling exponent. We continue to use 1/4 powers in our model and refer interested readers to appendix A for a more

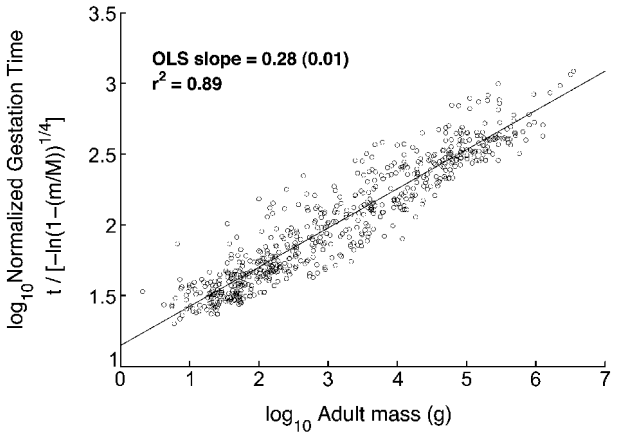

Figure 4: Gestation time (t_g) normalized by relative mass at birth versus adult body mass (M) for 630 species of terrestrial mammals (data from Ernest 2003). Time t_w is the sum of the gestation period and the time between birth and weaning. The slope of the regression is 0.28 ± 0.01 (95% confidence interval), and the reduced major axis exponent is 0.29. Both values are distinguishable from 1/4 and 1/3.

general model in which α (and therefore δ) can take different values.

Estimating the Energy to Create Biomass (E_m)

We define E_m as the quantity of metabolic energy required to create a given quantity of biomass. The E_m does not include the energy content of biomass, only the total metabolic work the organism expends to create biomass from preformed organic molecules. The E_m is conceptually important because it links the fundamental biological currencies of energy and biomass; however, E_m is difficult to characterize theoretically and very difficult to measure empirically. Empirical measures of E_m require separating the energy used for growth from that used for maintenance. Since growing organisms also expend energy on maintenance, these allocations of energy are difficult to disentangle. This explains why there is so little literature discussing this fundamental quantity.

In the original OGM, West et al. (2001) used the energy content of vertebrate tissue (~7,000 J/g; Cummins and Wuycheck 1971; Peters 1983) to estimate E_m, but Makarieva et al. (2004) point out that these are not the same. The energy content of biomass is not necessarily equivalent to the metabolic energy required to produce that biomass. Equating these two quantities fails to account for the preformed, energy-rich organic molecules present in yolk or food. It also fails to account for the metabolic work performed by the organism in order to process energy and materials to produce new biomass.

Even though E_m may be difficult to measure empirically, its theoretical importance dictates that methods be devised to estimate it. Here, we use two methods to estimate E_m from empirical growth curves. First, we calculate an upper bound for E_m in embryos, based on the assumption that the maintenance metabolic rate is negligibly low. Second, we estimate E_m for embryos and juveniles by applying the OGM to estimate the fraction of the metabolic rate that is used to fuel production of new biomass.

An Empirical Upper Bound on E_m

First, we calculate an upper bound on E_m from the growth and metabolism early in ontogeny by assuming that the energy devoted to maintenance is sufficiently small that it can be ignored. Thus, E_m can be calculated by multiplying the metabolic rate that is allocated to growth (B_g) by the time taken to add new biomass: $E_m = B_g(dt/dm)$. Determining B_g precisely is difficult, but total metabolic rate (B) is obviously an upper bound on B_g. Early in ontogeny, where mass is <5% of adult mass, B is a reasonable approximation of B_g. This gives

$$E_m \approx B\frac{dt}{dm}. \tag{5}$$

Table 2 gives the mean value of E_m calculated from equation (5) for nine embryos: six mammals (3,500–9,200 J/g), chicken (1,600 J/g), quail (3,500 J/g), and trout (2,700 J/g). Here, B is estimated from $B_0 m^{3/4}$, where B_0 is the interspecific scaling exponent for the appropriate taxonomic group (Peters 1983) and dt/dm is measured empirically (a series of discrete measures of dt/dm is given in growth curves from sources listed in table 2; E_m is calculated as an average over these intervals for each species). We note that scaling of metabolic rate of bird embryos is approximated by $B = 650m^{3/4}$ J/g$^{3/4}$/day, but in adult birds, $B = 2{,}000m^{3/4}$ J/g$^{3/4}$/day (Peters 1983). We use the appropriate B_0 for embryos to calculate E_m for the chicken and quail embryos. If instead, we use empirical measurements of B (Needham 1931; Williams and Swift 1988), then we obtain a mean $E_m = 1{,}040$ J/g for the chicken and $E_m = 2{,}859$ J/g for the quail, both close to the estimate of E_m obtained using the scaling equation for B. These relatively low values for E_m in chick eggs are close to the estimated value of $E_m = 1{,}230$ J/g by Vleck et al. (1980). In "A More Detailed Analysis of E_m Based on Dry Biomass in Embryos," we discuss how changing water content of embryos during development may alter these estimates.

We can also estimate E_m in embryos from growth times and equation (3). The scaling between time and size at hatching or birth has been determined empirically for birds, fish, and mammals (table 3). By setting the scaling constant in these equations equal to $4/a$ and remembering

Table 2: Estimates of E_m from individual growth curves

Taxonomic group and species	Data source	Upper bound on E_m (J/g)	OGM estimate of E_m (J/g)
Bird embryos:			
Quail	Williams and Swift 1988	2,900	2,800
Chicken	Brody 1945	1,000[a]	800[a]
Fish embryo:			
Trout	Needham 1931	3,200	1,100
Mammal embryos:			
Rat	Needham 1931	4,000	3,100
Guinea pig	Needham 1931	7,600	4,900
Rabbit	Needham 1931	3,500	2,700
Sheep	Needham 1931	5,800	5,700
Pig	Needham 1931	8,200	7,100
Cow	Needham 1931	9,200	6,900
Juvenile birds:			
Heron	West et al. 2001		1,400
Robin	West et al. 2001		2,000
Chicken 1	West et al. 2001		5,300
Chicken 2	Brody 1945		7,500
Juvenile fish:			
Guppy	West et al. 2001		1,900
Salmon	West et al. 2001		7,300
Cod	West et al. 2001		13,000
Juvenile mammals:			
Shrew	West et al. 2001		1,800
Rat 1	West et al. 2001		6,600
Rat 2	Needham 1931		4,600
Rabbit	West et al. 2001		9,500
Pig	West et al. 2001		5,200
Cow	West et al. 2001		7,000
Mean E_m		5,000	4,800

Note: The energy an organism requires to create biomass (E_m) in joules per gram estimated from individual growth curves. The upper bound is calculated from equation (5), and the ontogenetic growth model (OGM) estimate is calculated from equation (7). The referenced growth curves list mass m at time t, and from these we estimate dm/dt at a given mass m. The values reported in table 2 are the mean of E_m over all intervals (dt) of the growth curve. For the OGM estimate of E_m, the average 95% confidence interval is $\pm 30\%$ both during ontogeny (calculated from the variation in E_m from individual intervals in the growth curve) and between species. Growth curves were obtained from the data sources.

[a] E_m for the chicken embryo is based on wet biomass. Adjusting the estimate to account for the low percentage dry biomass in chicken embryos raises the comparable estimate of E_m several-fold (see text).

that $a = B_0/E_m$, we obtain estimates of E_m for mammal embryos (8,000 J/g), bird embryos (1,530 J/g), and fish embryos (3,030 J/g; table 3). As in the previous section, this estimate is an upper bound, since it assumes that all metabolic energy is used for growth. These estimates give an average value of E_m for each taxonomic group that is consistent with the estimates calculated from growth curves of individual species in those taxa (table 3).

Incorporating Growth Efficiency into Estimates of E_m

The OGM makes a testable prediction for growth efficiency and describes its nonlinear dependence on relative mass. The growth efficiency (R) is defined as the proportion of metabolic power devoted to growth: $R = B_g/B = (am^{3/4} - bm)/(am^{3/4})$. Since $b = aM^{-1/4}$, then

$$R = 1 - \left(\frac{m}{M}\right)^{1/4}. \tag{6}$$

During ontogeny, R decreases as the proportion of metabolic rate allocated to maintenance increases. Since $B_g = RB$, then equation (5) can be rewritten to calculate E_m at any stage of ontogeny:

$$E_m = \left[1 - \left(\frac{m}{M}\right)^{1/4}\right] B_0 m^{3/4} \frac{dt}{dm}. \tag{7}$$

Table 3: Estimates of E_m for birds, fish, and mammals

	Upper bound from growth curves (eq. [5]; table 2)	Upper bound from growth times (eq. [4])	OGM estimate from growth curves (eq. [7]; table 2)	OGM estimate from growth times (eq. [8])
Bird embryos ($N = 2$)	1,900	1,500[a]	1,800	…
Fish embryos ($N = 1$)	3,200	3,000[b]	1,100	…
Mammal embryos[d]	6,100	9,800[c]	4,800	7,500
Juvenile birds ($N = 4$)	…	…	4,000	…
Juvenile fish ($N = 3$)	…	…	7,400	…
Juvenile mammals[e]	…	…	5,800	5,800

Note: Upper bound and ontogenetic growth model (OGM) estimates for the energy to create biomass (E_m in J/g) averaged for each developmental stage and taxonomic group. Upper bounds on E_m are estimated for embryos under the assumption that maintenance energy is small enough to ignore. Upper bounds and OGM estimates from growth curves are the means of values reported in table 2. The OGM estimate from growth times uses equation (8) and data from Ernest (2003), shown in figures 4 and 5. Upper bounds from growth times are calculated using equation (3) and empirical regression equations for time t to a developmental stage as a function of mass m at that stage for each taxonomic group.

[a] Calculated from bird embryo time to hatching: $t = 52m^{0.24}$, with t in days and m in kilograms, and $B_0 = 650$ J/day/g$^{3/4}$ (Peters 1983).

[b] Calculated from fish embryo time to hatching and metabolism normalized to 0°C: $E_m = B_0 e^{5.74}/4$/day/g$^{1/4}$ and $B_0 = 40$ J/day/g$^{3/4}$ (Gillooly et al. 2002).

[c] Calculated from mammal gestation time: $t = 20.5m^{0.27}$, with t in days and m in grams (Ernest 2003) and $B_0 = 1{,}600$ J/day/g$^{3/4}$ (Peters 1983).

[d] $N = 7$ growth curves, $N = 630$ growth times.

[e] $N = 6$ growth curves, $N = 310$ growth times.

We use growth curves (that provide M and dt/dm) and B_0 (Peters 1983) to estimate mean values of E_m for each time step in the growth curve for each species listed in table 2. There is nearly an order of magnitude variation within and across species, with the most clear systematic variation existing between embryos and juveniles. Although significant, this variation is small relative to the many orders of magnitude of differences in body size between small embryos and large mammals. Causes of this variation are discussed in "A More Detailed Analysis of E_m Based on Dry Biomass in Embryos" and "Conclusions about Estimates of E_m." For embryos, the estimates from equation (7) are close to, but slightly less than, the estimates from equation (5), which assumes negligible maintenance metabolism. This is expected because inclusion of the maintenance term reduces the estimate of energy used for growth.

We can use the OGM to estimate E_m from growth times by rearranging equation (4) to

$$E_m = -\frac{B_0 t M^{-1/4}}{4 \ln [1 - (m/M)^{1/4}]}. \quad (8)$$

Equation (8) implicitly incorporates the OGM definition of the growth efficiency, R, in equation (6). We use equation (8) to estimate E_m during the embryonic and juvenile (postembryonic) periods for mammals; B_0 is taken from Peters (1983), and t, m, and M are reported by Ernest (2003; gestation data are also shown in fig. 4). Histograms of E_m values estimated using equation (8) are given in figure 5*A* for 310 juvenile mammals (mean = 5,774 J/g, SD = 1,709, 95% CI = 5,584–5,966) and in figure 5*B* for 630 mammal embryos (mean = 7,532 J/g, SD = 2,854, 95% CI = 7,308–7,754). A more accurate estimate of E_m during the juvenile period is obtained by the more complicated equation that accounts for mass at birth $\gg 0$, derived by Gillooly et al. (2002, box 2), which gives a value of E_m that is approximately 10% lower.

A More Detailed Analysis of E_m *Based on Dry Biomass in Embryos*

The amount of energy required to create an average unit of biomass is E_m. We hypothesize that E_m is approximately constant when the composition of resources and biomass is essentially the same. However, there may be considerable variation in E_m over different tissue types and conditions.

The growth of bird embryos is a paradigm for ontogeny because the resources for growth are fixed and well defined (the yolk) and because the embryo uses minimal energy for nongrowth-related purposes until it begins to breathe on its own at pipping. However, in developing embryos, there may be considerable variation in water content. For example, the dry mass of a chick embryo is only 5% of wet mass at day 6, but it increases to 18% by day 19 (Murray 1926*a*) and averages 30% in adults (Peters 1983). Our analysis until now has implicitly assumed constant water content; thus, our estimates of E_m in embryos are low in part because of low dry-biomass content.

Using data from Murray (1926*a*, 1926*b*), we calculate the regressions between metabolism and wet and dry biomass in the chick embryo. For wet biomass, the scaling relationship is $B = 800m^{0.84}$, with B measured in joules per day and m measured in grams ($r^2 = 0.99$). For dry biomass, $B = 4{,}800m^{0.62}$ ($r^2 = 0.99$). We use two methods to estimate E_m. First, we follow the methods we applied

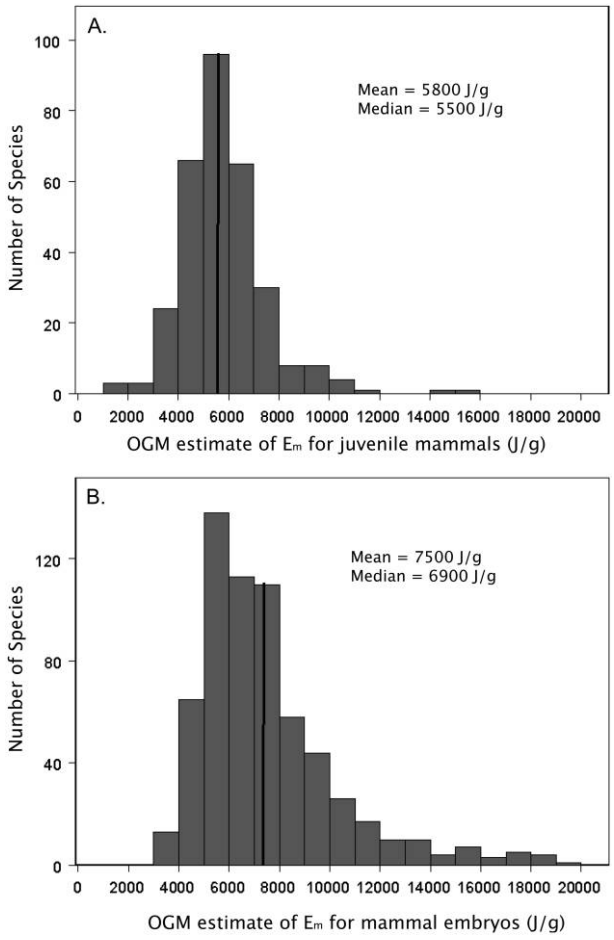

Figure 5: Frequency histograms of E_m from (*A*) the time to birth and (*B*) the time to weaning in mammals. The E_m is calculated from the ontogenetic growth model using equation (8). For 630 embryos, E_m = 7,531 ± 114, and for 310 juvenile mammals, E_m = 5,774 ± 97 (SE). Data from Ernest (2003).

above: we use the regression equations for B to calculate an average value of E_m over all time steps using the general form of equation (7) in appendix A. Averaging E_m for each day for which we have data for wet biomass (days 6–18), we obtain $E_{m_{wet}}$ = 1,270 ± 26 J/g (95% CI), similar to the estimate in table 2 from data in Needham (1931). Using the same method for dry biomass, we obtain $E_{m_{dry}}$ = 17,300 ± 8,000 J/g (95% CI). In order to compare $E_{m_{dry}}$ with the value estimated for juveniles that are approximately 30% water, we multiply $E_{m_{dry}}$ by 0.3 and obtain 5,200 ± 2,400 J/g, a value very close to the value for most juvenile birds and mammals in table 2. Thus, if we adjust estimates of E_m to the same water content, E_m for the chick is four times our initial estimate and very close to that estimated for juveniles.

We note substantial variation in $E_{m_{dry}}$ (reflected in the wide CIs) that declines from about 30,000 J/g in days 6 and 7 to 10,000 J/g in days 14–19. In order to further analyze variation in $E_{m_{dry}}$ during ontogeny, we calculated $E_{m_{dry}}$ as the slope of the regression between integrated power consumption and dry embryo mass.

From this we obtain an estimate of $E_{m_{dry}}$ = 21,300 ± 633 (SD) J/g for days 6–12 of incubation (in which 10% of the embryo's mass is accumulated) and $E_{m_{dry}}$ = 11,600 ± 118 J/g in days 13–18 (for 90% of embryo mass accumulation). These numbers correspond to an $E_{m_{wet}}$ in a juvenile that is 30% dry biomass of 7,200 J/g in days 6–12 and 3,500 J/g in days 13–18. The values of E_m estimated from the data in Altman and Dittmer (1968) and Romijn and Lokhorst (1960) are consistent with these values. All of these estimates indicate (i) when percentage of dry biomass is considered, E_m in chick embryos is much closer to our estimates of E_m in juveniles, but (ii) $E_{m_{dry}}$ is about twice as high early in ontogeny versus late in ontogeny, which is where the majority of biomass increase occurs.

Data from Murray (1926*a*, 1926*b*) indicate that it is important to consider the changing ratio of wet to dry biomass when estimating the scaling of metabolic rate during ontogeny. Bell et al. (1987) measured dry and wet biomass of sheep embryos and found that the dry biomass nearly doubles, from 10.8% of wet biomass in an early period (days 73–79) to 20.8% in a later period (days 128–140) of embryonic development. Further, Bell et al. calculated the metabolic exponents α = 0.89 (r^2 = 0.99) for wet biomass and α = 0.73 for dry biomass (r^2 = 0.99). We can also compare their value of B_0 for dry biomass in embryos with the value of B_0 for the interspecific regression for adults in Peters (1983). Assuming 30% dry biomass for adults, then the adult B_0 for dry biomass is 9 J/s/kg$^{-3/4}$. Converting Bell's intercept (-0.65 on a $\log_{10}$ scale, measured for milliliters of oxygen per minute, with mass in grams) to the same units gives a very similar dry biomass B_0 of 11 J/s/kg$^{-3/4}$. Thus, both the slope and intercept are very similar in embryos and adults when wet biomass is converted to dry.

Conclusions about Estimates of E_m

We used several different data sources and methods to estimate E_m (the quantity of energy required to produce 1 g of biomass) in different vertebrates at different stages of ontogeny: (i) growth curves and growth times were used to obtain an upper bound on E_m for embryos, based on the assumption that maintenance metabolism is small during embryonic development; (ii) the OGM and allometric estimates of metabolism were used to estimate E_m for embryos and juveniles; and (iii) E_m was estimated from directly measured metabolism and growth of dry biomass in chick embryos. In the chick embryos, where we had empirical data

for metabolic rate measured during growth, allometric equations and empirical data gave similar estimates of E_m as long as we accounted for variation in water content.

The results, summarized in table 3, span nearly an order of magnitude, from about 1,100–1,800 J/g for embryos developing in bird and fish eggs to 4,000–7,500 J/g for mammal embryos and juvenile (posthatching or postbirth) fish, birds, and mammals. The estimates from the OGM explicitly assume that some fraction of energy is allocated to maintenance rather than growth, so it is expected that the OGM-based estimates for embryos were somewhat lower than the upper-bound estimates obtained by assuming that maintenance energy is negligible. Variation in water content between taxa and during ontogeny may explain much of the variation in our estimates. Other sources of variation probably include (i) differences among taxa in the energy required to create biomass, (ii) measurement error in growth rates and times, and (iii) variation in the scaling exponent, α. In appendix B in the online edition of the *American Naturalist*, we show that varying α between 0.65 and 0.85 generates approximately 50% variation in E_m from our estimates using growth curves. Clearly, there are further sources of variation; even in the ideal case, chick embyros with dry biomass and metabolism directly measured, E_m varies twofold from days 6–10 to days 13–18.

In mammals, where we assumed that metabolic rates of embryos have the same scaling as adults (consistent with the results of Bell et al. [1987]), estimates of E_m were similar for embryos and adults. In birds, however, E_m appears to be systematically lower for embryos than for posthatching chicks and adults. This parallels the systematically lower metabolic rate of bird embryos. Both of these low values are due, in part, to low dry-biomass content in embryos. Additionally, these low values may reflect other biologically important differences: bird embryos are supplied with yolk, an ideal food source that does not have to be processed as much as food obtained outside of the egg. Additionally, bird eggs are incubated, so embryos grow under near-optimal temperatures and do not expend energy to thermoregulate.

It is important to note that relatively constant values of E_m are obtained from the empirical growth curves only when $\beta = 1$. The assumption that $\beta = 1$ can be interpreted as an assumption that mass-specific maintenance metabolism does not vary systematically during ontogeny. This assumption is consistent with the analysis of Brody (1945), Vleck et al. (1980), and Ricklefs (2003) for precocial birds.[1] If instead we assume $\beta < 1$, for example, $\beta = 0.8$, then E_m is much larger and highly variable (ranging from nearly 0 to 106 J/g) during ontogeny and between species. These values seem unrealistic given the estimates of E_m in embryos (~103 J/g), where maintenance metabolism should be small. The OGM (with $\beta = 1$) provides an average estimate of E_m that varies by only 30% (95% CIs of the species' means), with total variation of approximately one order of magnitude. We find this to be a surprisingly consistent estimate across multiple species of fish, birds, and mammals in different life stages and with body sizes that vary by many orders of magnitude. By assuming that mass-specific maintenance metabolism does not vary systematically during ontogeny, the empirical estimates of E_m also do not vary systematically during ontogeny.

To put variation of E_m in context, we note that the average energy content of biomass in different vertebrate species (estimated by Cummins and Wuycheck [1971]) varies by a similar amount (greater than fourfold), and their estimate is for dry biomass, which is free of the substantial variation that can be introduced by water content. Thus, it is not surprising to see fivefold variation in E_m when it is based on wet biomass.

Discussion

The OGM is based on the premise that metabolic rate, which is the overall rate of energy use, fuels growth and development and that allocation of this metabolic energy between production of new biomass and maintenance of existing biomass is the dominant process controlling growth. Of course there is variation in growth rate that is not explained by our model. Although there is some variation in the allometric exponents, much of the variation in growth rate is probably due to differences in normalization constants between species and between individuals within species that differ in genetic factors, nutrition, and environmental conditions. Variation in water content may be particularly important. Investigating the causes of variation should be facilitated by comparison of data with predictions of models, such as the OGM, that deliberately leave out such complexities and provide first-order predictions based on a few first principles and measurable quantities.

We parameterize the OGM with an ontogenetic metabolic scaling exponent, $\alpha = 3/4$. This canonical value is used here because it is predicted theoretically and frequently observed empirically. Glazier's (2005) compilation of scaling data suggests that there is considerable variation in α, but in figure 1, we show that much of that variation comes from attempting to estimate α from studies with very little mass range; such studies result in a highly variable but on average lower estimate of α with wide CIs. The generally lower value of α is expected because vari-

[1] Ricklefs (2003) estimates $\beta > 1$ for altricial birds; however, this estimate is misleading because it does not take into account the decrease in water content during ontogeny, as discussed by West et al. (2004).

ation around a scaling line tends to lower the statistical estimate when mass range is small; the paucity of data sets with sufficient ontogenetic mass range may create the illusion that α is lower in ontogenetic versus interspecific studies. Some of the variation may also reflect periods during ontogeny in which scaling shifts and causes scale breaks in some analyses (Brody 1945; Post and Lee 1996; Glazier 2005).

Consistent with estimates of α, the scaling exponent δ, relating growth times to body mass ($\delta = 1 - \alpha$), is consistent with 1/4 in most cases, again, with some variation. Analysis of gestation times in mammals indicates a slightly higher exponent that is between 1/4 and 1/3. We highlight that estimates of scaling exponents are sensitive to a number of factors: having sufficient variation in body size, use of RMA or OLS regression, variation in water content, and relative mass at which biological times are measured. In addition to making predictions based on $\alpha = 3/4$, we give a more general set of equations that relate growth times, metabolic rate, and the energetic cost of producing biomass for any α (app. A). These equations are independent of the actual value of α so that the model can be applied to specific instances where α deviates from 3/4.

One fundamental quantity in the OGM is E_m, the quantity of metabolic energy required to create a unit of biomass. There are measurements of metabolic rate at different stages of growth and development, but these offer little information on how the energy is allocated between production and maintenance. Above, we have used two methods to estimate E_m. The first method gives an upper bound by assuming that maintenance is negligible very early in development, so all metabolic energy is expended on growth. The second method uses the OGM to estimate the proportion of energy that is expended on growth. Both methods give generally similar values of E_m for embryos, on the order of 6,000 J/g for mammal embryos and 2,000 J/g for embryos of birds and fish developing in eggs. Only the second method can be used to estimate E_m in juveniles after hatching or birth, and it gives estimates of E_m on the order of 6,000 J/g for all three taxa. The low values of E_m for embryos may be due largely to low dry-biomass percentages in embryos.

These estimates are based on using the mean value of $\alpha = 3/4$. In appendix B we show that our estimates of E_m for a particular species are sensitive to α for that species. For example, if $\alpha = 0.65$, our E_m estimate from growth curves would be about 50% too low. Despite our uncertainty about the precise value of E_m, it is noteworthy that our estimate is similar across broad taxonomic groups that vary widely in production rates and body mass. This is consistent with the finding of Ernest et al. (2003) that temperature-corrected population biomass production scales with a similar exponent and normalization constant across taxonomic groups.

Addressing the problem of estimating E_m led us to think carefully about theoretical and empirical issues underlying the metabolic cost of growth and development. There is some evidence (e.g., for juvenile mammals and for fish and chick embryos) that α is close to 1 during early development. Much of the variation in E_m and some of the variation in α may be due to variation in water content; high water content may contribute to the low estimates of E_m, particularly in embryos and in juvenile altricial birds (the effect of water content in juvenile birds is discussed in West et al. 2004 in response to Ricklefs 2003). The E_m may also vary during ontogeny as the growing organism uses different food resources, produces increasingly differentiated and specialized cell and tissue types, and relies on an increasingly large and costly infrastructure of circulatory, respiratory, digestive, excretory, and integrative systems to maintain existing tissue and produce new biomass. We encourage further empirical studies to better estimate the parameters of the OGM in a variety of taxa over various stages of ontogeny. Studies that report wet and dry biomass and metabolic rate through ontogeny and that carefully consider appropriate statistical methods are needed to give more precise estimates of the parameters.

Analytical models, such as the OGM, are deliberate oversimplifications of a more complex reality. Their utility depends on the extent to which they capture some fundamental essence of how nature works, the extent to which their assumptions are reasonable and their logic is sound, and their simplicity, explanatory power, internal consistency, and consistency with observations. The OGM is based on simple, robust assumptions about growth and metabolism. It is internally consistent and predicts several observable quantities and scaling relationships: growth curves, growth times, the curvilinear decline in growth efficiency, and the close linkage between the allometric scalings of metabolic rate as body mass varies both within species during ontogeny and between related species of different adult size. Furthermore, unlike models that provide only statistical descriptions of growth curves based on goodness of fit, the OGM is a mechanistic model. Like von Bertalanffy's (1957) earlier model (which assumed $\alpha = 2/3$ and $\beta = 1$ based on the presumed allometric scaling of "anabolism" and "catabolism"), the OGM provides a first-order quantitative characterization of how energy is allocated between growth and maintenance during ontogeny. Because the model is deliberately simplified, it is inevitable that measurements of real organisms will deviate somewhat from model predictions. The ultimate utility and durability of the OGM will depend on the extent to which it captures the fundamental process of energy allocation during ontogeny, incorporates meaningful pa-

rameters, and contributes to understanding the real differences in growth trajectories among diverse kinds of organisms.

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