Toward a metabolic theory of life history

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The life histories of animals reflect the allocation of metabolic energy to traits that determine fitness and the pace of living. Here, we extend metabolic theories to address how demography and mass–energy balance constrain allocation of biomass to survival, growth, and reproduction over a life cycle of one generation. We first present data for diverse kinds of animals showing empirical patterns of variation in life-history traits. These patterns are predicted by theory that highlights the effects of 2 fundamental biophysical constraints: demography on number and mortality of offspring; and mass–energy balance on allocation of energy to growth and reproduction. These constraints impose 2 fundamental trade-offs on allocation of assimilated biomass energy to production: between number and size of offspring, and between parental investment and offspring growth. Evolution has generated enormous diversity of body sizes, morphologies, physiologies, ecologies, and life histories across the millions of animal, plant, and microbe species, yet simple rules specified by general equations highlight the underlying unity of life.

biodiversity | unified theories | metabolic ecology | biophysical constraints | demography

> The "struggle for existence" of living beings is not for the fundamental constituents of food . . . but for the possession of the free energy obtained, chiefly by means of the green plant, from the transfer of radiant energy from the hot sun to the cold earth.
>
> Physicist Ludwig Boltzmann (1)
>
> In the struggle for existence, the advantage must go to those organisms whose energy-capturing devices are most efficient in directing available energies into channels favorable to the preservation of the species.
>
> Theoretical biologist Alfred Lotka (2)

Energy is the staff of life. The life history of an organism is the constellation of Lotka's "channels": traits that determine fitness by affecting growth, survival, and reproduction. There is enormous diversity of life histories: from microscopic unicellular microbes with lifespans of minutes to whales and trees with lifespans of centuries; from giant fish, clams, and squids that produce literally millions of miniscule offspring to some birds and bats that fledge a few offspring as large as their parents. Life-history theory has made great progress by analyzing trade-offs between traits, such as number vs. size of offspring, current vs. future reproduction, male vs. female offspring, and sexual vs. asexual reproduction (e.g., refs. 3–9). But life-history theory has been slow to use metabolic energy as the fundamental currency of fitness. Organisms are sustained by metabolism: the uptake, transformation, and expenditure of energy. Fitness depends on how metabolic energy is used for survival, growth, and reproduction.

The millions of species exhibit an enormous variety of anatomical structures, physiological functions, behaviors, and ecologies. Studies of biological scaling and metabolic ecology have revealed unifying patterns and processes, such as effects of body size and temperature on energy use, abundance, and species diversity. We present theory to show how energy metabolism has shaped the evolution of life histories. Underlying the spectacular diversity of living things are universal patterns due to 2 fundamental constraints: 1) a demographic constraint on mortality so that, regardless of the number of offspring produced, only 2 survive to complete a life cycle of one generation; and 2) a mass–energy balance constraint so that over a lifespan in each generation, all of the energy acquired by assimilation from the environment is expended on respiration and production, and energy allocated to production exactly matches energy lost to mortality. Consequently, at steady state, by the time parents have reproduced and died, their energy content has been exactly replaced by the energy content of their surviving offspring. Theory incorporating these constraints accounts for the schedules of survival, growth, and reproduction and predicts the fundamental trade-offs between number and size of offspring and between parental investment and offspring growth.

Theories of Resource Allocation in Life History

Much life-history theory traditionally focused on trade-offs that affect resource allocation to survival, growth, and reproduction—e.g., between number and size of offspring in a clutch or litter or of offspring produced over a lifetime; between semelparous and iteroparous reproduction (i.e., " big bang" or "1 shot" vs. multiple reproductive bouts); between determinate vs. indeterminate growth; and between fast or "r-selected" vs. slow or "K-selected" lifestyles (i.e., rapid maturation and high fecundity vs. slow development and low fecundity). While these theories implicitly recognize that life-history traits are constrained by some "limited resource," they rarely impose mass–energy balance or other biophysical constraints to explicitly identify the resource and quantify its allocation.

Significance

Data and theory reveal how organisms allocate metabolic energy to components of the life history that determine fitness. In each generation, animals take up biomass energy from the environment and expend it on survival, growth, and reproduction. Life histories of animals exhibit enormous diversity—from large fish and invertebrates that produce literally millions of tiny eggs and suffer enormous mortality, to mammals and birds that produce a few large offspring with much lower mortality. Yet, underlying this enormous diversity are general life history rules and trade-offs due to universal biophysical constraints on the channels of selection. These rules are characterized by general equations that underscore the unity of life.

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Consider, for example, the trade-off between number and size of offspring, which is readily apparent across animals with contrasting life histories. At one extreme are large fish and invertebrates, which produce literally millions of tiny, externally fertilized eggs that hatch into independent larvae and feed themselves as they grow to maturity. At the other extreme are bats and altricial birds, which are nourished until they are close to adult size. Clearly, parents which produce tiny offspring must produce many of them to offset the mortality as they grow. In contrast, parents which produce large offspring can produce fewer of them, because they suffer less mortality due to their more developed state and shorter time to maturity.

Most life-history theories assume that a female invests a constant fraction of her energy content or body mass in offspring, and they predict a simple linear trade-off between number and size of offspring. But the various theories and models make somewhat different predictions, depending on whether the trade-off operates within a single clutch or over a lifetime and on how it is affected by schedules of growth and mortality (e.g., refs. 5–14). For example, one theory and some data suggest that "lifetime reproductive effort" is constant: A female invests approximately the same fraction of her body mass in offspring, regardless of her absolute size (4, 5, 13, 14). However, recent empirical studies show that investment in offspring increases with the size of parent in large teleost fish (15) and terrestrial vertebrates (16). Here, we provide a theoretical explanation for these patterns.

Empirical Patterns of Biomass Allocation to Growth, Survival, and Reproduction

To more comprehensively analyze allocation of metabolic energy to offspring, we compiled a database for 36 species of animals, encompassing a wide range of sizes and taxonomic and functional groups. For most species, it is difficult to ensure that these data are collected accurately and consistently, because the majority of animals have indeterminate growth and iteroparous reproduction: They continue to grow and reproduce after reaching maturity. So it is difficult to determine the average number of offspring (N_O) and size of breeding adult (m_A) for a population at steady state. Initially, we avoided this problem by using a subset of the database for 17 semelparous species—i.e., "big bang" or "1-shot" reproducers, which grow to mature size, produce a single clutch or litter, and then die, thereby providing more reliable data on body and clutch sizes (*SI Appendix*, Table S1). We then analyzed an expanded dataset that included an additional 19 iteroparous species. The dataset includes a wide diversity of taxa and environments, from marine, freshwater, and terrestrial invertebrates to fish, lizards, birds, and mammals; they exhibit many orders of magnitude variation in number of offspring, N_O, and body mass of offspring, m_O, and parent, m_A. Figs. 1 and 2 plot number of offspring, N_O, and lifetime reproductive investment, L, as functions of relative size of offspring at independence, $\mu = \frac{m_O}{m_A}$, on logarithmic axes.

Number of Offspring (N_O). We define N_O as the number of independent offspring (i.e., at the end of parental investment) produced by an average female parent in one generation. Across the 36 species, N_O varies negatively with μ (Fig. 1; variables are defined in Table 1). Several aspects of this empirical scaling are especially noteworthy. First, the naïve prediction of a linear trade-off is rejected; there is modest variation around the fitted regression line ($R^2 = 0.91$), and the CIs do not include −1. Second, the relationship is curvilinear when plotted on logarithmic axes, so it is not a power law. Third, N_O depends on the relative size of offspring, μ, but not on the absolute sizes of the offspring, m_O, or the parent, m_A, which vary by more than 10 orders of magnitude, from insects weighing less than 0.01 g to whales weighing more than 100,000,000 g (Figs. 1 and 2 and *SI Appendix*, Table S1). Fourth, semelparous species tend to produce somewhat fewer offspring than iteroparous species.

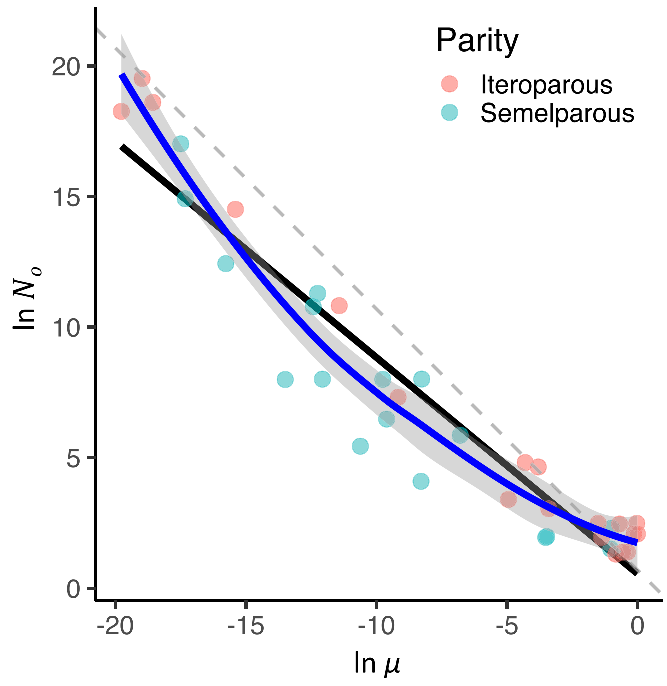

Fig. 1. Plot on logarithmic axes of number of offspring (N_O) as a function of relative offspring size, $\mu = \frac{m_O}{m_A}$, for 36 animal species. The regression fits a power-law scaling relation, $N_O = 0.24\mu^{-0.83}$ (solid black line; $R^2 = 0.91$). The 95% CI (−0.92, −0.74) of the slope does not contain the −1 predicted for a simple linear trade-off (dashed gray line). More importantly, the relation is curvilinear on logarithmic axes, as indicated by statistical LOESS (Locally Estimated Scatterplot Smoothing) fit to the data (solid blue line), indicating a deviation from power-law scaling.

Lifetime Reproductive Effort (L). We define parental investment, I, of energy or biomass in offspring over one generation as

$$I = N_O m_O, \qquad [1]$$

where N_O is the average number of independent offspring produced over an average lifetime and m_O is the average mass of an offspring at independence. So, I is the sum of the biomass in gametes and nutrition invested in offspring by the parent. It can be normalized by adult mass to give the lifetime reproductive investment:

$$L = \frac{I}{m_A} = N_O \frac{m_O}{m_A} = N_O \mu. \qquad [2]$$

This dimensionless parameter is conceptually identical to Charnov's "lifetime reproductive effort" (4, 5, 14). Across the 36 species, L varies widely with μ (Fig. 2). Several aspects are noteworthy. First, L is not constant: It varies about 3,000-fold (from 0.004 to 11.6, or from −6 to 2 on the natural log scale), and CIs for the linear regression do not include 0. Second, the magnitude and pattern of variation are consistent with the curvilinear trade-off shown in Fig. 1. Third, lifetime reproductive investment varies with relative offspring size, μ, but is independent of the absolute size of the parent, m_A (Fig. 2 and *SI Appendix*, Fig. S1).

Our data do not support traditional life-history theories that predict a linear trade-off between number and size of offspring or a constant lifetime reproductive effort—i.e., N_O and L do not vary with relative offspring size, μ, as simple power laws with exponents of −1 and 0, respectively. The U-shaped pattern of L

Table 1. **Model parameters (state variables) appearing in text**

Symbol	Description	Units
E	Energetic definition of fitness ~22.19 kJ·g^{-1} per generation	kJ·g^{-1} per generation
B	Mass-specific rate of biomass production	y^{-1}
Q	Energy density of biomass	kJ·g^{-1}
F	Fraction of production passed to next generation	Dimensionless ratio
G	Generation time $=G_0(m_A^{1/4}-m_O^{1/4})$	y
x	Age (at time, t)	Integer
m_O	Offspring mass at independence	g
m_A	Adult mass	g
μ	Relative offspring mass = M_o/M_A	Dimensionless ratio
N_o	Lifetime # offspring	Integer
I	Parental investment = $N_O m_O$	g
H	*Individual growth* = $(M_A - M_O)/M_A$	Dimensionless (normalized by M_A)
P	Individual biomass production = (I) Investment + growth (H)	Dimensionless (normalized by M_A and generation)
L	Lifetime reproductive investment $=\frac{I}{m_A}=\frac{N_O m_O}{m_A}=N_O\mu$	Dimensionless (normalized by M_A and generation)
D	Mortality rate	y^{-1}
D_A	Adult mortality coefficient	Dimensionless
D_J	Juvenile (initial) mortality coefficient	Dimensionless
b	A constant that quantifies the decrease in mortality rate with age x	Dimensionless constant
N_d	Number of offspring dying at age x	Integer
W	Cohort growth: accumulated mass of all offspring of a parent, $W=\sum_{x=0}^{x=G} N_d m_d$	Dimensionless (normalized by M_A and generation)
C	Cohort production: total production of all offspring of a parent = $I + W$	Dimensionless (normalized by M_A and generation)

as a function of μ is consistent with recent studies of vertebrates: 1) the left-hand side with the increase in L with decreasing offspring size in large teleost fish which produce enormous numbers of miniscule offspring (15); and 2) the right-hand side with increasing L corresponds with increasing offspring size in terrestrial vertebrates that produce fewer larger offspring (16).

A Metabolic Theory of Life History

We now present theory that quantifies how organisms allocate metabolic energy to the components of the life history. Adaptive traits have evolved by natural selection because they promote the components of fitness—survival, growth, and reproduction. On average, however, species have equal fitness because at steady state, parents exactly replace themselves with offspring each generation, birth rates equal death rates, and populations remain constant (17). Our theory is based on this equal-fitness paradigm and its assumption of steady-state nongrowing populations. It is formulated explicitly for sexually reproducing animals, and—like most life-history and demographic theory—it is formulated for the female parent, which usually makes the largest direct resource investment in reproduction, both gametes and any post-fertilization nutrition (e.g., pregnancy and feeding).

Energy and Fitness. Even though the life-history traits that determine fitness, such as fecundity and lifespan, vary by many orders of magnitude, all organisms pass a near-equal quantity of biomass energy (~22.4 kJ/g dry weight) to surviving offspring each generation. This equal-fitness paradigm (17) is defined by the seminal equation $E = BGQF$, where E is energetic fitness, B is the mass-specific rate of biomass production, G is generation time, and Q is the energy density of biomass. Since Q is nearly constant (~22.4 kJ/g dry weight; see also ref. 15), fluxes and stocks can be measured in units of mass, and this equation becomes

$$E = BGF = 1, \qquad [3]$$

where F, the fraction of production that is passed through to surviving offspring, is also relatively constant, varying from ~0.1 to 0.5. So E is lifetime mass-specific biomass production, and at steady state, $E = 1$, because a parent exactly replaces its own biomass with one surviving offspring that successfully breeds in the next generation. The steady-state assumption is robust and realistic. Temporary deviations occur, but species persist because of compensatory ecological and evolutionary processes such as density dependence (e.g., ref. 18) and Red Queen coevolution (e.g., ref. 19).

The equal-fitness paradigm (Eq. **3**) expresses the fundamental trade-off between biomass production, B, and generation time, G: organisms that produce little biomass have short generations and vice versa (17). But it does not indicate how metabolic energy is allocated to the life-history traits of survival, growth, and reproduction to affect fitness. These allocations are subject to 2 powerful constraints: 1) demography and 2) mass–energy balance. They are fundamentally "biophysical" because they can be parameterized in units of mass and energy.

Demographic Constraint: Mortality and Parental Investment.

Mortality as a function of age. Mortality of offspring over ontogeny is necessarily related to ontogenetic growth. The smaller the relative size of offspring at independence and the longer they take to grow to maturity, the greater their mortality. At steady state in generation time, G, the number of offspring remaining alive decreases from $N = N_O$ of body mass m_O at the end of parental nutritional input, to $N = 2$ at maturity with body mass m_A. Empirical evidence clearly shows that mortality rate decreases over ontogeny (e.g., refs. 20–22). In animals, such as large teleost fish and invertebrates, which produce enormous numbers of very small offspring, mortality is very high initially and decreases rapidly with age as the individuals grow to larger, less vulnerable sizes (Fig. 3). Even in birds and mammals, which produce a few relatively large offspring, mortality is higher for the smaller, younger, less-experienced individuals.

We derive the schedule of mortality as a function of offspring age and body mass starting with a very general von Bertalanffy-type model of ontogenetic growth (23, 24). This model, based on the scaling of metabolism as body size increases over ontogeny, also gives an expression for generation time

$$G = G_0\left(m_A^{1/4} - m_O^{1/4}\right), \qquad [4]$$

where G_0 is the normalization coefficient with a unit of [time/mass$^{1/4}$], and the 1/4-power mass-scaling exponents reflect the

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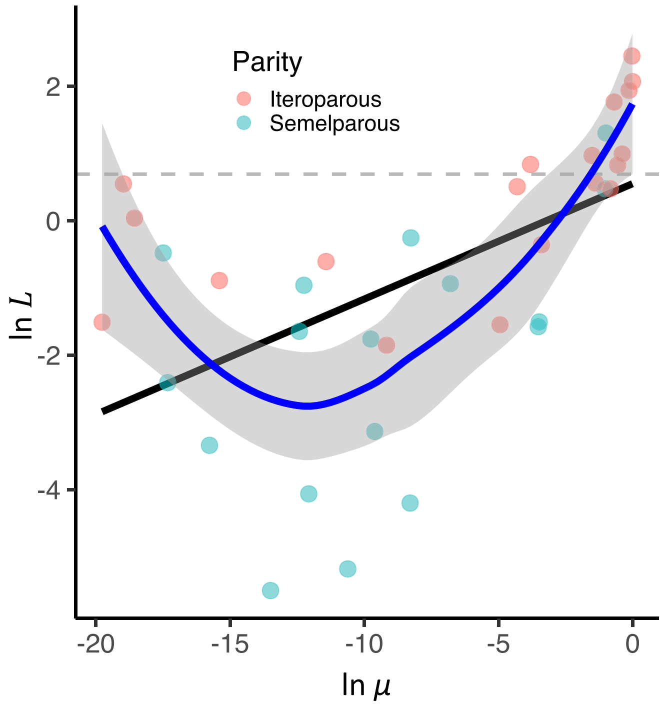

Fig. 2. Plot on logarithmic axes of lifetime reproductive investment ($L = N_O \frac{m_O}{m_A} = N_O \mu$) as a function of relative offspring size, $\mu = \frac{m_O}{m_A}$, for 36 animal species. The fitted regression gives a power-law scaling relation, $L = 0.55\mu^{0.17}$ (solid black line; R^2 = 0.30) with the 95% CIs (0.08, 0.26), so the slope is significantly different from the 0 predicted for a simple linear trade-off (dashed gray line), and lifetime reproductive effort is far from constant (it varies about 3,000-fold: from −6 to 2 on the natural log scale). More importantly, the relationship is curvilinear on logarithmic axes, as indicated by statistical LOESS fit to the data (solid blue line), consistent with Fig. 1 and indicating deviation from power-law scaling.

canonical quarter-power allometries (e.g., refs. 25–30). We assume that over ontogeny, the mortality rate, D, can be expressed as a function of adult mass m_A, offspring mass m_o, and age x:

$$D(x) = D_A m_A^{-1/4} + D_J m_o^{-1/4} \cdot e^{-(b/G)\cdot x}, \qquad [5]$$

where D_J and D_A are coefficients for initial (juvenile) and adult mortality, respectively, and b is a unitless constant such that b/G quantifies how fast the mortality rate decreases exponentially with age x (Fig. 3). We fit the mortality rate of 2 species (Fig. 3) with a general equation $y = \alpha + \beta x e^{-\gamma x}$. This equation has 3 constant parameters, each corresponding to the coefficients in the mortality-rate function (Eq. **5**). i.e., $\alpha = D_A m_A{}^{-1/4}$, $\iota = D_J m_o{}^{-1/4}$, and $\gamma = b/G$. The nonlinear fitting gives the values of α, β, and ι. But the values of D_A, D_J, and b for a given species would require the knowledge of m_i, m_i, and G for that species. Nonetheless, the purpose of Fig. 3 is to show that mortality rate exponentially decays over ontogeny, and Eq. **5** captures the key features of it. Thus, the exact values of D_A and D_J are not necessary.

We address 2 important points about parameter b in Eq. **5**. First, since b is assumed to be a constant, the exponential decay is controlled by generation time, G. Intuitively, if G is large, the mortality rate decreases slowly, because the animals grow slowly and, hence, reach adult size at an older age. For example, painted turtle (Fig. 3*A*) matures at age 6 ∼ 10 y, $b/G \sim 0.48$/y, and $b \sim 5$. The generation time of Humboldt squid is less than a year, and the fitted value of b/G is 13.1; thus, b is larger than 13. Second, b must be >1. Eq. **5** indicates that at maturity when age $x = G$, the exponential decay term, $e^{-b/Gx}$, becomes e^{-b}, and b must be sufficiently large so that e^{-b} is almost 0; then, $D \approx D_A m^{-1/4}$, in agreement with empirically observed scaling of adult mortality rate (e.g., refs. 20 and 30). See *SI Appendix* for derivation.

Number of offspring. Now we use Eq. **5** to derive $N(x)$, the number of offspring surviving to age x, as follows:

By definition: $\frac{dN(x)}{dx} = -N(x)D(x)$, and solving this differential equation gives

$$N(x) = N_o e^{\frac{-D_J m_o^{-1/4}}{(b/G)}\left(1-e^{-(b/G)\cdot x}\right) - D_A M^{-1/4} x}. \qquad [6]$$

Applying the demographic constraint that at steady state, when $x = G$ (generation time), $N(G) = 2$, this equation becomes $N_O = 2e^{D_A m_A^{-1/4} G} e^{D_J(1-e^{-b})/(b/G m_O^{1/4})}$. Since b is relatively large and e^{-b} is almost zero, Eq. **6** reduces to

$$N_o = 2e^{D_A m_A^{-1/4} G} e^{D_J m_o^{-1/4} G/b}. \qquad [7]$$

Substituting Eq. **4**, $G = G_0(m_A^{1/4} - m_O^{1/4})$, and $\mu = m_O/m_A$, $A = D_A G_0$, $J = \frac{D_J G_0}{b}$, we have

$$N_O = 2e^{A\left(1-\mu^{\frac{1}{4}}\right)} e^{J\left(\mu^{-\frac{1}{4}}-1\right)}. \qquad [8]$$

Taking logarithms of both sides gives

$$\ln[N_O] = \ln[2] + (A - J) + \left(J\mu^{-1/4} - A\mu^{1/4}\right). \qquad [9]$$

Fitting Eq. **9** to the data in *SI Appendix*, Table S1 accurately predicts the relationship between the number, N_O, and relative size, $\mu = \frac{m_O}{m_A}$, of offspring, accounting for 92% of the variation

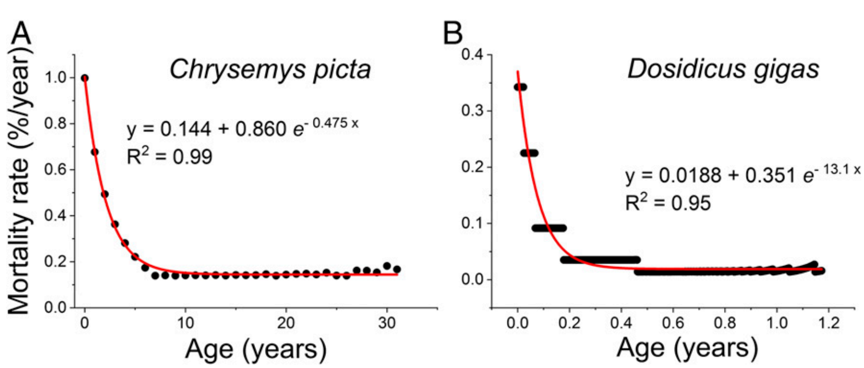

Fig. 3. Exponential decay of mortality rate as a function of age, x, obtained by fitting Eq. **5** to data for painted turtle (*Chrysemys picta*) (*A*) and Humboldt squid (*Dosidicus gigas*) (*B*). Data are from Halley et al. (22).

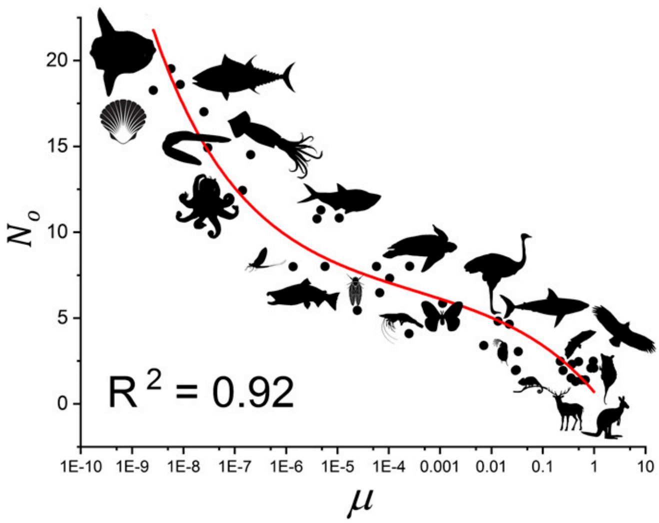

Fig. 4. The model accurately predicts the curvilinear shape of the trade-off between number of offspring, N_o, and relative offspring size, $\mu = \frac{m_O}{m_A}$. The equation $\ln[N_O] = \ln[2] + (A - J) + J\mu^{-1/4} - A\mu^{1/4}$ with the 2 fitted parameters $A = 6.03 \pm 0.5$ and $J = 0.11 \pm 0.01$ (red curve) accounts for 92% of the variation. Icons are not drawn to scale and are not included for all species.

(Fig. 4). The model with the 2 fitted parameters $A = 6.03$ and $J = 0.11$ captures the curvilinear shape of the trade-off between number and size of offspring shown in Fig. 1.

Lifetime reproductive investment. It is now straightforward to predict how lifetime reproductive investment, $L = N_O \frac{m_O}{m_A} = \frac{I}{m_A} = N_O \mu$ (Eq. **2**), varies with μ. Substituting into and following the derivation above gives

$$L = \mu x e^{A-J} e^{J\mu^{-1/4} - A\mu^{1/4}}, \qquad \textbf{[10]}$$

and

$$\ln[L] = \ln[\mu] + (A - J) + \left(J\mu^{-1/4} - A\mu^{1/4}\right). \qquad \textbf{[11]}$$

Fitting the 2 parameters, $A = 6.05$ and $J = 0.01$, gives the predicted relationship shown in Fig. 5 (red curve), which accounts for 36% of the empirical variation. The distinctly curvilinear relationship indicates that lifetime reproductive effort is not constant and independent of offspring size as suggested by Charnov and colleagues (refs. 4, 5, 13, and 14; but see ref. 21). It is consistent with recent findings that larger fish with lower μ and larger terrestrial vertebrates with higher μ invest proportionally more resources and produce a proportionally greater total biomass of offspring (16, 31).

Mass–Energy Balance Constraint. The physical law of mass–energy balance powerfully constrains the uptake of energy from the environment and its allocation to survival, growth, and reproduction. A mass–energy balance diagram for an individual animal over one generation at steady state is depicted in Fig. 6*A*. Biomass is taken up from the environment in the form of food and allocated between respiration, where the majority of the assimilated organic molecules are catabolized to produce ATP and pay the metabolic costs of maintenance and the energy is ultimately dissipated as heat, and production, where a relatively small fraction of assimilated molecules are repackaged into "net new" biomass.

Trade-off between offspring growth and parental investment. The lifetime biomass production of an individual animal, P, is the sum of individual growth plus parental investment, where growth,

$$H = m_A - m_O, \qquad \textbf{[13]}$$

and parental investment, $I = N_O m_O$ (Eq. **1** and Fig. 6*A*). We normalize by dividing by adult mass to obtain an expression for relative or mass-specific lifetime individual production

$$P = \frac{H+I}{m_A} = \frac{m_A - m_O}{m_A} + \frac{N_O m_O}{m_A} = (1-\mu) + L. \qquad \textbf{[14]}$$

It is straightforward to calculate empirical values of $P = \frac{m_A - m_O}{m_A} + \frac{N_O m_O}{m_A} = (1-\mu) + L$ for the 36 animal species in the dataset (*SI Appendix*, Table S1). The result, shown in Fig. 7*A*, is that P shows a U-shaped pattern similar to and reflecting the U-shaped variation in L (Fig. 2). It is also straightforward to substitute the theoretically derived value of L from Eq. **10** and solve Eq. **14** to predict P as a function of μ. Not surprisingly, because the expression for L was obtained by fitting the mortality equation using the observed number of offspring, N_O, the prediction (Fig. 7*A*) closely resembles the empirical pattern. Individual lifetime production, P, varies more than one order of magnitude, from close to one in some insects, aquatic invertebrates, and fish with intermediate values of μ, to >10 in birds and mammals with $\mu \sim 1$. Note, however, the secondary peak >1.5 in some fish and invertebrates with very low values of μ, where parental investment is more than half of maternal body mass.

Allocation of growth and parental investment to cohort production and energetic fitness. The mass–energy balance diagrams show that mass-specific production of an individual, $P = \frac{H+I}{m_A} = (1-\mu) + L$ (Fig. 7*A* and Eq. **14**), is not the same as the mass-specific lifetime biomass production, $\frac{E}{F} = BG = C$, of the equal-fitness paradigm (Fig. 6*B* and Eq. **3**), because P does not include mortality. The parameter $C = E/F$ is the mass-specific production of the entire cohort of offspring produced by a parent, so the sum of the initial parental investment, L, plus the total energy, W, accumulated as

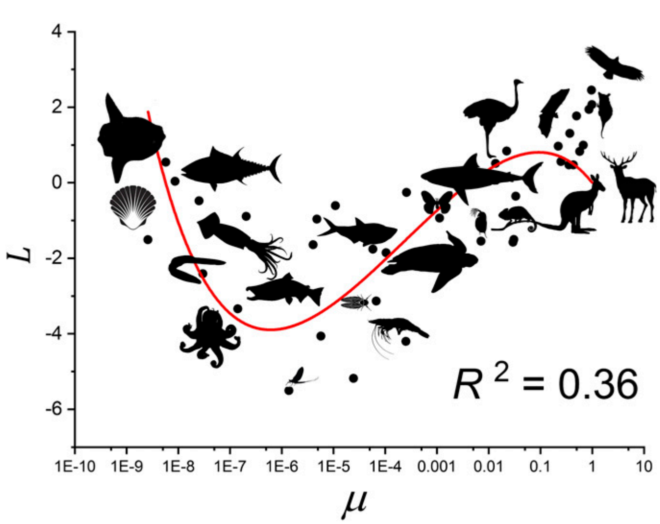

Fig. 5. The model predicts the curvilinear form of the relationship between lifetime reproductive investment, L, and relative offspring size, $\mu = m_O/m_A$. The equation $\ln[L] = \ln[\mu] + (A - J) + (J\mu^{-1/4} - A\mu^{1/4})$ with fitted parameters $A = 6.03 \pm 0.5$ and $J = 0.11 \pm 0.01$ (red curve) accounts for 36% of the empirical variation. This curvilinear relationship is consistent with the relationship between number of offspring and μ shown in Figs. 2 and 4. It is not consistent with previous theory which predicts that lifetime reproductive effort is constant across species. Icons are not drawn to scale and are not included for all species.

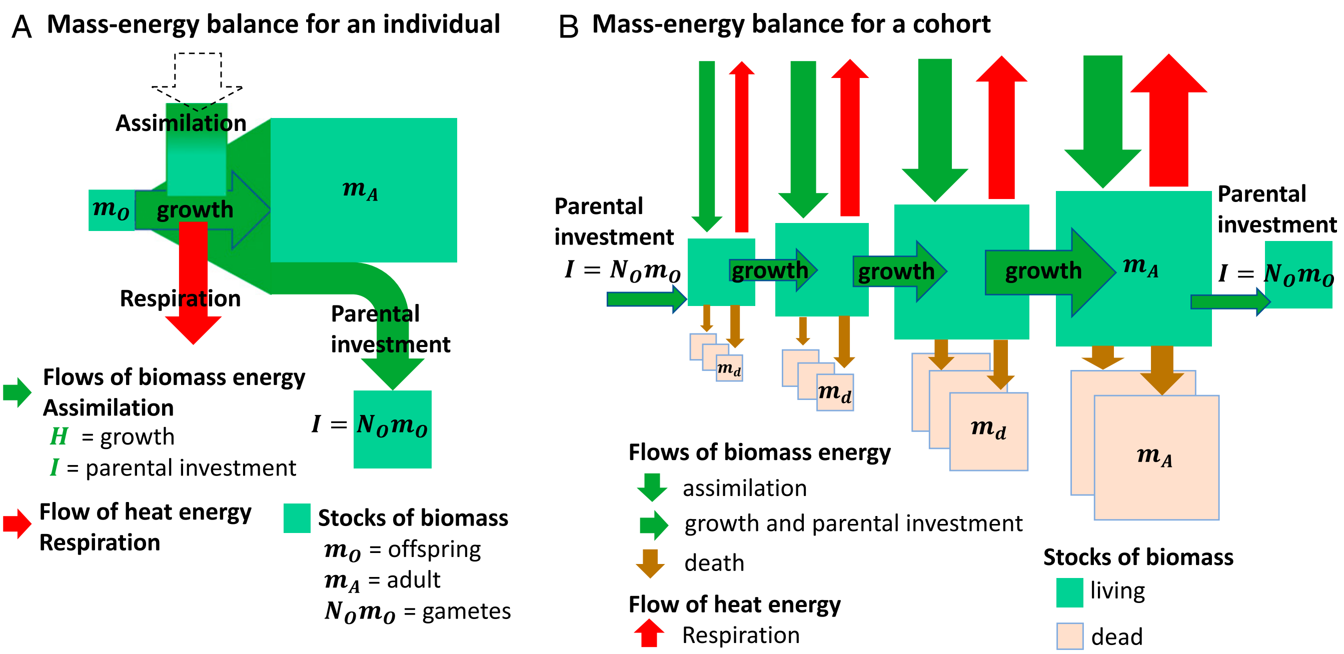

Fig. 6. (*A*) Mass–energy balance for an individual animal over one generation, so lifetime individual production, *P*, is assimilation minus respiration and is divided between growth and parental investment. (*B*) Mass–energy balance for the cohort of offspring produced by a female parent in one generation, so lifetime cohort production, *C*, includes the biomass accumulated by growth of all offspring when they died, including the 2 that replaced their parents.

growth of all offspring up until they died, including the 2 that replaced the parents.

So,

$$C = W + L, \quad [15]$$

where

$$W = \sum_{x=0}^{x=G} N_d m_d, \quad [16]$$

and N_d is the number of offspring dying at age x, and m_d is the mass of those offspring when they died.

Unfortunately, we do not have good data on mortality or growth rates for the species in *SI Appendix*, Table S1, so we cannot evaluate these predictions empirically. We can, however, use our model for mortality to predict W and C as functions of μ. Following Eq. **8**, the number of offspring dying at age x is

$$N_d(x) = N_O S(x) D(x), \quad [17]$$

where $S(x)$ is the survival rate and $D(x)$ is the mortality rate at age x. Converting age to mass, m_x, Eq. **16** becomes

$$W = \int_{x_O}^{x_A} N_d(x) m(x) dx. \quad [18]$$

Solving and normalizing in terms of μ, we obtain W, as a function of μ, as plotted in Fig. 7*B*.

Finally, lifetime cohort production is the sum of cohort growth plus lifetime parental investment, $C = W + L$ (Eq. **15**). These 3 variables are plotted in Fig. 7*B*. Note the linear scale of the x axis. Over most of the range of relative offspring size, cohort growth, W, is constant = 2, but it increases sharply as μ becomes very small ($<10^{-7}$). Cohort lifetime production has a distinctly bimodal distribution, with a modest peak at $\mu \sim 0.1$ and a sharp increase when $\mu < 10^{-7}$. Importantly, C is relatively constant over most of the range, varying by a factor of less than 3-fold. These allocations are consistent with the equal-fitness paradigm, which predicts that lifetime cohort biomass production is relatively constant. The fraction $F = 1/C$, of lifetime cohort production that survives prereproductive mortality and is passed on to the 2 surviving offspring in the next generation, is also relatively constant and within the range, from 0.5 in asexual microbes to perhaps 0.1 in some sexual eukaryotes, as predicted by Brown et al. (17).

The bottom line is that demography and mass–energy balance tightly constrain allocation of metabolic energy to the components of fitness: survival, growth, and reproduction. The near-constant lifetime cohort production reflects a trade-off between growth and parental investment. Most animals are of intermediate body size, produce very small offspring, and allocate much more of their lifetime production to growth than to reproduction. The species that produce a few relatively large offspring allocate most of their production to reproduction (parental investment). The relatively few fish and invertebrate species of very large adult size that start life as microscopic larvae press the limits set by the constraints; they make a sizeable parental investment to produce millions of offspring and offset the very high initial mortality.

Discussion

Applications, Extensions, and Modifications. Living things are amazingly diverse. The species in our analyses (*SI Appendix*, Table S1)—and the millions of animals, plants, and microbes more generally—differ enormously not only in body size, anatomical structure, and physiological function, but also in life-history traits such as generation time, mortality rate, number and size of offspring, and kind and magnitude of parental care. Nevertheless, we show above that single equations predict the schedule of mortality over the life cycle (Eq. **7**); the trade-off between number and relative size of offspring (Eq. **8**); the allocation of biomass to parental investment (Eq. **10**); and the trade-off between growth and parental investment at the level of both an individual (Eq. **14**) and

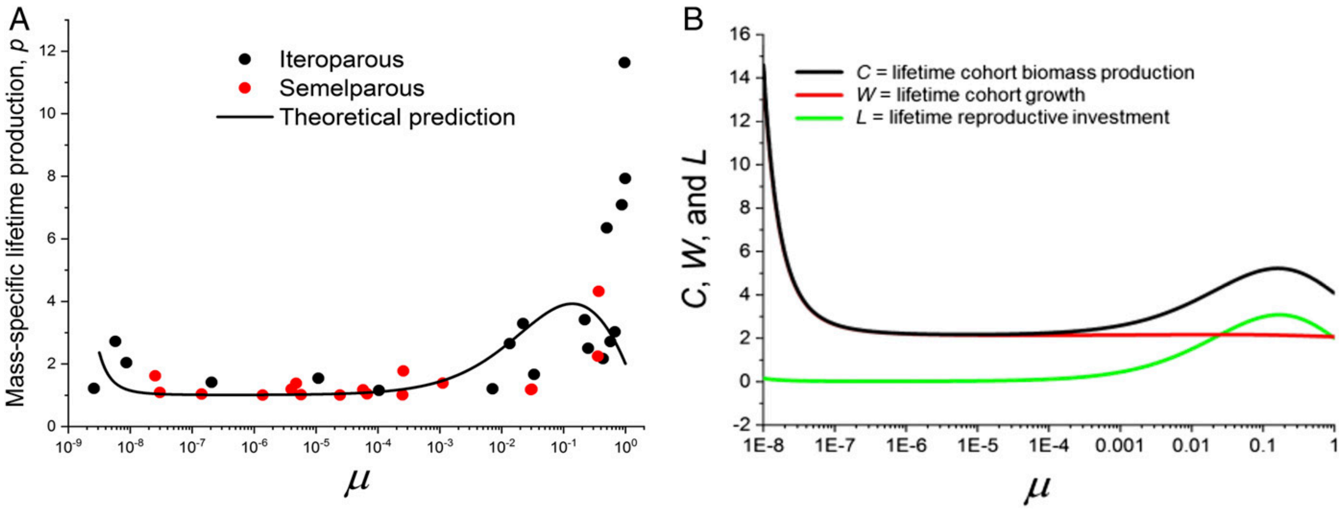

Fig. 7. Mass-specific lifetime production of a single individual and of the cohort of all offspring of a parent, both as a function of relative offspring size, $\mu = m_O/m_A$. (*A*) Empirical and theoretically predicted patterns of mass-specific lifetime production of an individual, $P = (1 - \mu) + L$, which is the sum of individual growth plus parental investment. The data points are the empirical values for the 36 animal species, and the black curve is the theoretically predicted relationship based on the prediction of *L* (Eq. **10** and Fig. 5). (*B*) Lifetime biomass production, *C*, and its 2 components growth, *W*, and parental investment, *L*, for the cohort of all offspring produced by a parent. Note the linear scales of the *y* axes, so the variation in *P* and especially in *C*, *W*, and *L* is only a fewfold.

the entire cohort of offspring produced by a parent (Eq. **18**). The theory predicts and the data in Figs. 1 and 2 show qualitatively similar patterns in both semelparous and iteroparous species. There is, however, a modest quantitative difference, as noted above and addressed below.

Moreover, these interrelationships among dimensionless life-history traits are even more general than the underlying rates and times, which vary with body size, temperature, other intrinsic (biological) traits, and extrinsic (environmental) conditions. For example, there are substantial differences in production and mortality rates and in generation times, even between species with comparable body sizes and temperatures (e.g., in mammals between short-lived rodents and long-lived primates, and in insects between species with multiple generations per year and the accurately named 17-year cicada). Despite such variation, fundamental life-history trade-offs are always preserved because no organisms are exempt from the universal biophysical laws.

Our theory shows that much of this variation is the consequence of 2 biophysical constraints: 1) demography, whereby the number of offspring decreases from $N = N_O$ at independence to $N = 2$ at maturity; and 2) mass–energy balance, whereby relatively constant lifetime mass-specific biomass production is partitioned between growth and parental investment. These 2 constraints are almost tautologies, but together with scaling of metabolic traits with body size and temperature (e.g., refs. 25–27, 29, 32, and 33), they powerfully constrain the life histories of all organisms. So, our theory should apply, with at most minor adjustments, not only to animals as documented here, but also to plants and unicellular microbes (which are not considered explicitly here, but see refs. 31 and 35–37).

Our theory predicts much of the variation in life-history traits across a diverse array of animal species with respect to phylogeny, body size, anatomy, physiology, behavior, and ecology (Figs. 1 and 2 and *SI Appendix*, Table S1). Some of the unexplained variation and deviations from theoretical predictions may be explained by questionable data, but some of this variation is undoubtedly due to characteristics of real species that do not exactly match the simplifying assumptions of the theory. For example, semelparous species tend to produce fewer offspring than iteroparous species of similar body mass and relative offspring size (Fig. 1). More detailed models that incorporate variation with age in fecundity as well as mortality should account for this pattern, because iteroparous species with indeterminate growth have successive bouts of reproduction with increasing numbers of offspring as they grow older and larger. The interesting decrease in parental investment and cohort production as size of offspring approaches size of the parent (i.e., in birds and mammals where $\mu = 0.1$ to 1.0: Figs. 4, 5, and 7) may be due to oversimplification: failure to include nonnutritional parental care that may affect offspring mortality.

Other modifications can address additional complications, such as asexual reproduction, different investments of male and female parents, and effects of parental care on offspring survival. It should be challenging but informative to apply the theory to organisms with complex life cycles, such as parasites in which different ontogenetic stages within a single generation infect different hosts, have different schedules of growth and mortality, and exhibit both sexual and asexual reproduction. In such cases, more detailed analyses will be required to develop and test quantitative predictions.

Ecological and Evolutionary Implications. The theory presented above is one example of how incorporating energetics and metabolism can contribute to a unified conceptual framework for ecology and evolution. The disciplines of demography, behavior, and population and community ecology have traditionally used numbers of individuals as the primary currency for their empirical studies and theoretical models. In contrast, physiology and ecosystem ecology have long used energetic currencies, such as scalings of rates and times with body size and temperature. The result is that these disciplines have remained specialized, with only limited cross-fertilization. But individual organisms are composed of energy and matter, and their structures and dynamics must obey the fundamental biophysical laws. So there is great potential to use metabolism to link patterns and processes across levels of biological organization from individual organisms to ecosystems.

Consider, for example, the paradigmatic "biomass spectrum" and distribution of body sizes in marine ecosystems (e.g., refs. 38–45). In the pelagic zone, solar energy is captured and converted into biomass by tiny unicellular algae; then, it is passed to successively higher size-structured trophic levels as larger predators consume larger prey, culminating in apex fish, bird, and mammal predators. It has long been recognized that the trophic levels comprise a combination of adults of some species and immature stages of species, with larger adults at higher trophic levels (e.g., refs. 40 and 42). For example, newly hatched planktonic larvae of large fish and invertebrates are about the same size as adult zooplankters, whose larvae, in turn, are about the same size as unicellular algae and protists (44, 46). So far, however, life-history theory has rarely been combined with trophic ecology to elucidate how the dynamics of growth, mortality, and reproduction within and across species combine to affect the flows and stocks of energy and biomass in ecosystems (but see refs. 46 and 47).

Another area ripe for unification is the role of key life-history traits in evolutionary diversification of lineages. Biological diversity and ecological dominance of particular taxonomic, functional, and phylogenetic groups often have been attributed to evolutionary innovations in anatomy, physiology, ecology, and behavior—e.g., teleost jaw, amniote egg, endothermy, and primate brain. Life-history traits have received less attention, but have arguably been equally important. For example, special features of the life histories of teleost fish, passerine birds, and placental mammals have undoubtedly played important roles, as these 3 lineages diversified spectacularly after the Cretaceous-Tertiary extinctions. In the pelagic zone, large teleost fish, which produce literally millions of microscopic eggs, largely replaced sharks and rays, which produce a few large eggs or live-born offspring (42, 48). A suite of interrelated traits—endothermy, parental nutrition and care, and production of a few large, independent offspring —are associated with the ecological dominance of birds and mammals in terrestrial environments. The ecological dominance of avian and mammalian predators in cold, high-latitude pelagic marine environments may owe as much to the role of endothermy and large offspring size in reducing mortality and generation time as to the effects of endothermy and associated physiology and behavior in facilitating the capture of slow ectothermic prey (but see refs. 49 and 50). Recently, Morrow et al. (16) have shown that dimensionless life-history variables can be used to define a multidimensional life-history space, within which the different classes of terrestrial vertebrates occupy discrete, largely nonoverlapping subspaces. There is abundant scope to investigate the role of energetics in both constraining and facilitating the filling of life-history spaces, ecological niches, and evolutionary lineages.

Universality Underlying Biodiversity. The most fundamental features of life present a challenging paradox. On the one hand, living things are amazingly diverse. The millions of animal, plant, and microbe species vary enormously in body size, anatomical structure, biochemical, physiological and behavioral function, and ecological relations. On the other hand, underlying all of this variety are universal patterns and processes shared by all species. Many of these reflect the single origin of life and the unique biological network of metabolism that takes physical energy and materials from the environment and converts them into living, self-perpetuating biomass. Shared physical–chemical–biological processes at molecular and cellular levels of organization are reflected in common themes of structure and function at whole-organism, population, and ecosystem levels and common patterns of evolution and biodiversity. So, for example, rates and times of biological processes vary by many orders of magnitude with body size and temperature, but the variation is severely limited by scaling laws (e.g., refs. 25–27, 29, 32, and 33).

The near-tautological equal-fitness paradigm calls attention to an even more universal attribute of living things: All species that persist have nearly equal energetic fitness. At steady state, each parent allocates an identical quantity of energy (~22.4 kJ per g of dry weight per generation) to produce a surviving offspring (17). The present theory shows how this equal-fitness paradigm emerges from 2 universal biophysical constraints: 1) a demographic constraint on mortality, such that no matter the number and size of offspring produced, only one survives to replace each parent; and 2) a mass-balance constraint on metabolism, such that energy acquired by assimilation is allocated between offspring growth and parental investment so as to produce one surviving offspring per parent. Our theory accounts for the classic trade-offs between number and sizes of offspring and between growth and reproduction. Extensions of our theory should account for much of the variation in life history traits across all organisms.

Data availability. All data are available in *SI Appendix*.

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