

Title: Life history, death and taxes

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Abstract

The life histories of organisms and the trophic dynamics of ecosystems are shaped by taxes paid in the form of dead offspring. No organism is exempt from the tax because mortality is ubiquitous in the struggle of life. New theory and data highlight how the tax: i) reflects the proportion of the biomass produced over a life cycle that is lost to mortality and consumed in the ecosystem, ii) is predicted by the number and relative size of offspring, iii) varies widely across species from <50% to >99.9%, depending on fecundity and parental care, and iv) supplies energy and nutrition to other organisms in the ecosystem. Taxes levied on individuals and populations support the maintenance, infrastructure and functioning of ecosystems and human economies, alike.

Introduction

“Nothing is certain except death and taxes” Benjamin Franklin, 1879.

All organisms die and pay taxes. At the end of a life cycle at steady state, parents have replaced themselves and the bodies of their offspring have been recycled in the ecosystem. Across the diversity of life, Darwinian fitness is equal across species despite enormous variation in offspring mortality. At one extreme are miniscule protists and algae and also large sharks, reptiles, birds and mammals, which produce a few relatively large offspring that experience low mortality. At the other extreme are parasitic worms, giant clams, teleost fish and trees which produce literally billions of tiny offspring that experience high mortality. The dead bodies of offspring are a mortality tax paid to the ecosystem. This tax is a cost that individuals and populations must pay in order to leave surviving offspring and stay in the evolutionary game. The tax is an essential but inadvertent contribution to the structure, function and energy flow in ecosystems and the maintenance of biodiversity.

The recently formulated equal fitness paradigm (EFP): (1–4) is a new theory, based on fundamental laws of physics and demography. The EFP has implications for the structure and function of ecosystems and the origin and persistence of biodiversity. Darwinian evolution by natural selection is the outcome of the universal struggle of individuals and populations to acquire a share of the solar energy captured by green plants to use for survival and reproduction. Fitness can be measured in units of biomass energy per generation as

$$M = P_{coh}GF = 1 \quad 1$$

where P_{coh} is the mass-specific rate of biomass production allocated to growth and reproduction in watts or j/g/sec, G is generation time in sec, and F is the dimensionless fraction of production passed on to **surviving** offspring.

This seminal equation implies that at steady state all organisms are equally fit, because parents replace themselves with an equal number, biomass and energy content of surviving offspring in the next generation. The tradeoff between production rate, P_{coh} , and generation time, G , has profound implications for how the acquisition and allocation of energy affects the evolution of life histories, the structure and function of ecosystems, and the origin and maintenance of biodiversity. Receiving less attention and the focus of this paper is the parameter F , the fraction of biomass produced in a generation that is passed on to surviving offspring.

The mortality tax

Here we designate the complementary fraction, $C = 1 - F$, as a mortality tax: the biomass energy cost to leave surviving descendants and maintain populations. The mortality tax

is paid in the bodies of offspring left in the ecosystem and consumed by other organisms: herbivores, carnivores and detritivores.

Theoretical prediction of C : It is intuitively obvious that the value of C reflects the magnitude of mortality. At steady state in sexual organisms only two offspring survive to replace their male and female parents. Highly fecund organisms that produce enormous numbers of offspring leave most of them as dead bodies in the ecosystem. By contrast organisms that produce only a few offspring pay a much smaller tax of dead offspring. Here we extend the EFP and present new theory to predict that the energy value of the mortality tax is a function of the number and relative size of offspring.

The energy used by organisms for the biological work of growth, survival and reproduction is ultimately derived from solar energy through photosynthesis of green plants (5–8). Animals, plants and microbes achieve fitness by consuming and assimilating energy and allocating some fraction of biomass to growth and reproduction in order to leave surviving offspring in the next generation (e.g., 1; 1–4). In sexual organisms, the efficiency of reproduction, F , the fraction of parental biomass production passed on to surviving offspring is

$$F = \frac{2m_A}{m_{tot}} = \frac{2m_A}{2m_A + m_{pre}} \quad 2$$

where $2m_A$ is the body mass of the two offspring that survive to replace the parents, m_{tot} is the total biomass produced by the entire cohort, and m_{pre} is the total biomass of the cohort lost to pre-reproductive mortality (i.e., that dies without reproducing ($m_{pre} = \sum_{x=0}^{x=G} m_x d_x$, where m_x is the body mass and d_x is the number of offspring dying at age x). Assuming a life history with a constant mortality rate (8), the survival curve decays exponentially until only two parents remain alive, $N(t) = 2$ at age $t = G$ [See supplemental]. When body mass at generation time, $t = G$, is close to the adult mass the derivation can be approximated and simplified to predict

$$C \approx 1 - \left(\frac{2}{N_0}\right) \quad 3.$$

Surprisingly, despite its important applications and implications, the ecosystem tax, C , seems to have gone unnoticed, or at least unappreciated in the evolution, ecology and biodiversity literature.

Evaluating the theory: Values of C vary by more than two orders of magnitude from <50% to >99.9% across the diversity of life histories (Fig. 1). Interestingly, C does not scale with adult body mass (Fig. 2). This is in contrast to P_{coh} and G , which generally decrease and increase with adult body mass, respectively, by ~20 orders of magnitude from 10^{-11} g microbes to 10^9 g whales and trees (10).

The new theory predicts the empirical patterns of variation ($R^2 = 0.81$). C is correlated positively with fecundity (number of offspring produced per lifetime) and negatively with relative size of offspring and parental investment in offspring nutrition and care (Fig. 2). C is low in asexual unicellular prokaryotes and eukaryotes which reproduce by mitotic fission. Over a life cycle of one generation at steady state, a parent cell divides to produce two offspring; one dies and leaves its biomass in the ecosystem and the other doubles in mass and volume to replace the parent, so $C = m_A / 2m_A = 1/2$ or a tax of 50%. Other tiny animals and plants that produce a few relatively large offspring also experience low mortality and pay low taxes ($C < 90\%$).

By contrast, larger animals and plants exhibit wide variation in C . At one extreme are giant clams, tunas and other teleost fishes, trees, and parasites with complex life cycles that

produce enormous numbers (sometimes billions) of miniscule offspring that suffer very high mortality. Although most of the offspring die while still small and young, they pay the highest mortality taxes: $C > 99.9\%$; At the other extreme are vertebrates, such as sharks and rays, reptiles, birds, and mammals, that invest a large fraction of assimilated energy in nutrition and care of a few relatively large offspring, experience low mortality, and pay correspondingly low taxes: $C \approx 50\text{-}90\%$. Overall, the data support the rough approximation that $C \approx 1 - \frac{2}{N_o}$ (eq 3).

The deviations from the theoretical prediction in Fig 1 appear to be due largely to special adaptive features of life histories that violate the simplifying assumptions of the generalized model (above and in supplemental). In particular, growth and survival rates often fluctuate with age or environmental conditions rather than being constant over the life cycle from birth to maturity. For example, many species have adaptively modified phenology to fit the biological time of the life cycle into the diel, seasonal and annual rhythms of geochronological time in the extrinsic environment; salmon, univoltine insects and temperate mammals are emblematic examples (4). Other organisms have evolved combinations of fecundity and survival – and hence values of P_{coh} , G and C – by expanding on traditional life history tradeoffs, such as between the number and size of offspring (e.g., 2). For example, some internal parasites with complex life cycles and alternating episodes of sexual and asexual reproduction have evolved extremely high $P_{coh}G$, correspondingly low F , and high C to achieve enormous fecundity of which few offspring ultimately infect hosts.

Broader implications

I. Parental investment—The forgoing theoretical and empirical presentation indicates how the mortality tax C , has played a major role in the evolution of life histories by affecting how parents allocate biomass to rear their offspring (Fig. 3). An underlying constraint is that across eukaryotes there is little variation in zygote size: ~ 0.1 mg of protoplasm, not counting energy stored in yolk of eggs or endosperm of seeds. The smallest species, with little growth and limited mortality of offspring between independence and maturity, pay a relatively small tax. The lineages that have evolved larger body sizes have adopted a range of parental investment strategies: i) at one extreme are organisms that produce enormous numbers of miniscule offspring (e.g., naked zygotes) that develop without additional parental inputs, experience high mortality and pay a high tax; and ii) at the other extreme are organisms that invest a large fraction of production in parental nutrition and care to reduce mortality, produce a few large offspring, and pay a low tax. The first group includes teleost fish and several lineages of mollusks, arthropods, parasitic “worms” and tree-sized plants. The second group includes sharks and rays, reptiles, birds and mammals.

These diverse life histories appear to represent evolutionary stable strategies. The tuna-shark dichotomy in marine fish is an emblematic example (11). Interestingly, the tendency to produce enormous numbers of tiny offspring and pay a high tax, as seen in large invertebrates and teleost fish is a secondary, derived strategy, and not an inherently adaptive, universal trend. Ancient lineages of fish that once dominated marine ecosystems, including extinct placoderms and coelacanths and extant sharks and rays, had evolved internal fertilization to produce a few relatively large offspring. Yet over the last 65 million years, these lineages have been largely displaced by the explosive adaptive radiation of teleost fishes – including cods, mackerels, tunas, billfishes and molas – which produce enormous numbers of minute larvae and pay some of the highest mortality taxes of any organisms.

The evolutionary trend of terrestrial and some aquatic vertebrates to reduce the tax by investing in offspring nutrition and care is also a derived adaptive trait. Birds and mammals diverged from ancestral fish, amphibians and reptiles in making the tradeoff to produce fewer, larger offspring and leave fewer dead offspring in the ecosystem. The epitome of the few-large offspring strategy is represented by bats, primates and altricial birds, in which parents make large investments to rear offspring to nearly adult size. In many cases, they reduce the tax not only by supplying nutrition, but also by using specialized individual, family or social group behaviors to protect offspring from predators and other sources of mortality. Death and taxes are certain in the evolution of life histories, but the former can be postponed and the latter reduced while maintaining equal fitness across species.

II. Ecosystem energetics—The mortality tax and its variation across different kinds of organisms has profound implications for the organization and trophic dynamics of ecosystems. Energy flows through ecosystems as organisms at lower (producer) trophic levels die and are consumed by organisms at the next higher (consumer) trophic levels; plants acquire solar energy from the sun and produce biomass via photosynthesis, herbivores (primary consumers) assimilate energy by consuming plants, carnivores (higher-level consumers) feed on herbivores, and detritivores – mostly bacteria and fungi – assimilate dead biomass from multiple trophic levels.

In accordance with the Second Law of Thermodynamics, the capacity to do useful work decreases each time energy is converted from one trophic level to the next. The efficiency of this conversion is

$$L_{l_2/l_1} = \frac{P_{l_{n+1}}}{P_n} = \frac{P_{l_{n+1}}}{A_{n+1}} = \frac{P_{l_{n+1}}}{P_{n+1} + R_{n+1}} \quad 5$$

where L_{l_2/l_1} is the trophic or “Lindeman efficiency” (12) of an individual organism, population or entire trophic level, expressed as the ratio of the biomass production rate, $P_{l_{n+1}}$, of a higher (consumer) trophic level over the biomass production rate of the lower (producer) trophic level, P_n , from which it obtains its assimilated energy (or alternatively measured as ratios of rates of assimilation, A_{n+1} , or respiration, R_{n+1}). There is a large literature on the trophic efficiencies of different kinds of organisms and ecosystems, with wide variation in reported values of L : from $<<1\%$ to $\approx 50\%$ (13). There is no universal theoretical value, in part because L depends on C which varies from ~ 50 to $>99.9\%$. Note that calculation of L and C requires a metabolic life table (e.g., (14–17) to include all biomass and mortality produced by juvenile stages as well as adults of the relevant trophic level. With this caveat, the ecosystem mortality tax accounts for much of the variation in trophic organization of ecosystems. For example, terrestrial forests and kelp stands have large standing stocks of biomass largely because trees and macro-algae pay such high mortality taxes (e.g., (14).

III. Red Queen interactions and biodiversity—The mortality tax plays an important role in the origin and maintenance of biodiversity. As Boltzmann (5) and Lotka (8) have emphasized, in the Darwinian struggle for existence all organisms compete for a share of the solar energy converted to biomass by photosynthesis in green plants. In most ecosystems, the nearly all net primary production is consumed as the species at different trophic levels interact to assimilate energy and synthesize ATP to fuel the biological work of maintenance, growth and reproduction. Van Valen (7, 18) used the terms “zero sum game” and “Red Queen” to encompass the diverse competitive,

predator-prey and mutualistic ecological interactions and co-evolutionary adaptations among coexisting species. In the zero sum struggle for usable energy, any species that obtains a temporary advantage is soon checked by paying more tax as it interacts with and becomes a resource for another species. The overall effect is resource limitation, density dependence, and steady-state populations: the 2-for-2 replacement of parents by offspring that results in equal fitness across species and the persistence of biodiversity.

Conclusion

Death is a part of life. All living things are mortal. When organisms die, their biomass is consumed by other organisms and recycled in the ecosystem. The energy content of bodies can be viewed as a necessary tax paid to leave surviving offspring in the next generation. The relative magnitude of the tax varies with the number and relative size of offspring, reflecting the proportion of the biomass produced over a life cycle that is lost to mortality. The Red Queen and the mortality tax are both causes and consequences of the EFP. To paraphrase Benjamin Franklin, death and taxes are certain in the economies of both nature and humans. They are simultaneously costs paid by individuals and populations, and investments in the ecosystems that sustain life.

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Competing interests: Authors declare that they have no competing interests.

Data and materials availability: Original data sources are referenced and calculations provided in the supplementary materials.

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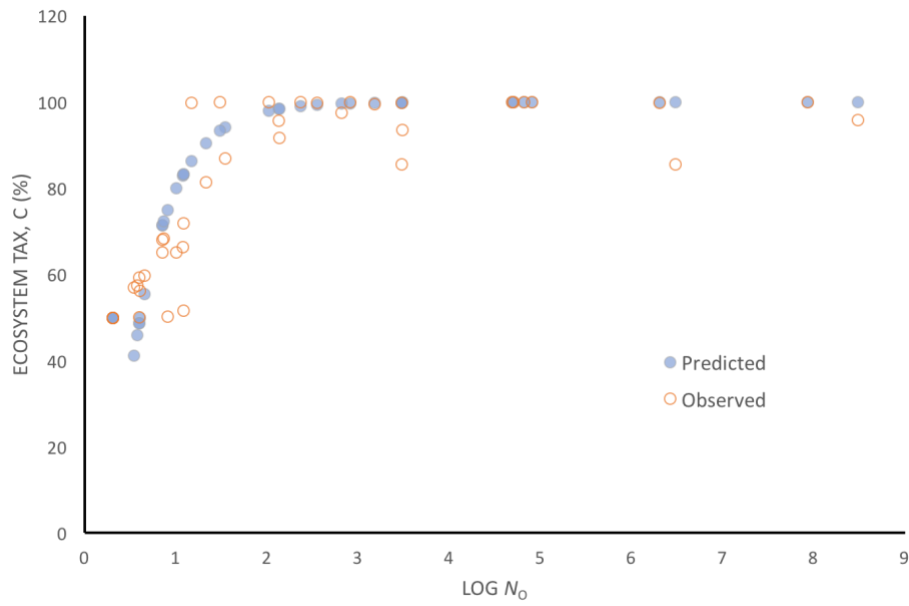


Fig. 1. Theoretically predicted and empirically estimated ecosystem tax, C , as a function of number of offspring (N_0). Both theory and data estimate the tax to be very high ($C > 0.99$) for species producing > 100 offspring.

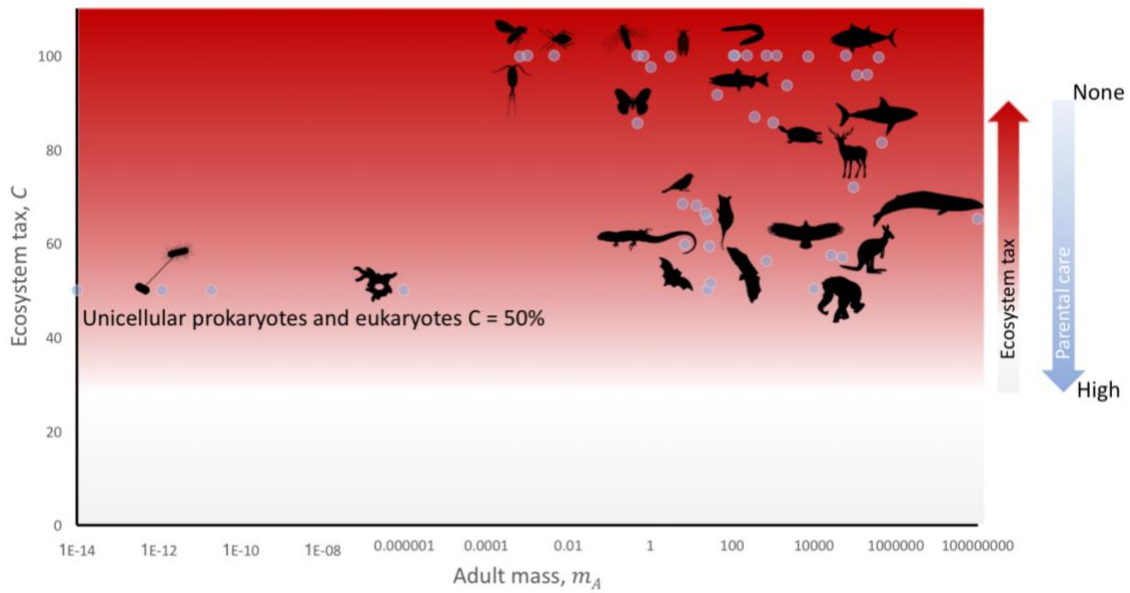
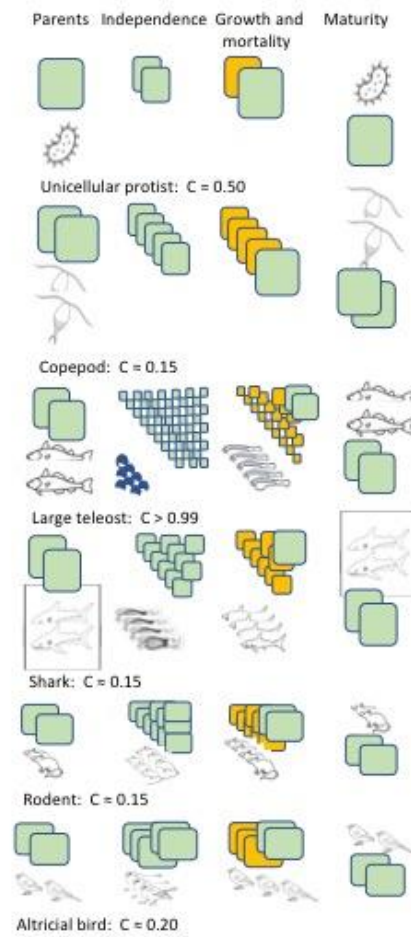


Fig. 2. Number of offspring as a function of adult body mass and parental care. Small species have only a few offspring, whereas large organisms produce from few to many offspring depending on parental care strategy.



300 **Fig. 3.** Graphical depictions (not to scale) of the variation in the tax (sum of orange squares) paid by model organisms with diverse life histories.

Supporting information:

Life history, death and taxes

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This file includes:

Supporting Text

Figs. S1, S2, S3

References

Data S1

Supporting Text:

In sexual organisms, the efficiency of reproduction, F , the fraction of parental biomass production that is passed on to surviving offspring is

$$F = \frac{2m_A}{2m_A + W} = \frac{2m_A}{\sum_{m=m_O}^{m=m_A} N_d m_d} \quad 1$$

where m_A is the mass of a parent that dies after reproducing and m_d is mass of an offspring at death. Assuming a

generalized life history with a constant mortality rate (I) of $D(T) = d = \frac{\text{Log}(\frac{N_0}{2})}{G}$ where N_0 is the initial number of

offspring, and G is the generation time, the survival curve decays exponentially, $N(t) = N_0 e^{-\frac{\text{Log}(\frac{N_0}{2})}{G} \times t}$, until only two parents remain alive, $N(t) = 2$ at age $t = G$. So, the number of offspring dying $N_d = N(t)D(t)$.

The complementary fraction of production lost in dead bodies is the mortality tax C :

$$C = 1 - F = 1 - \frac{2m_A}{\sum_{m=m_O}^{m=m_A} N_d m_d} = \frac{2m_A}{\int_0^G N(t) \times D(t) \times m(t) dt} \quad 2$$

where the summation is over age, t , from independence, $t = 0$ to the average generation, $t = G$. We apply the

general ontogenetic growth model (2, 3): $m(t) = m_A \left(1 - \frac{m_A - m_O}{m_A} e^{-k(a,G)t}\right)$, where the growth rate, $k(a, G) =$

$\frac{\text{Ln}\left[\frac{a(m_A - m_O)}{m_A}\right]}{G}$ is assumed to be a constant from independence, m_O , at $t = 0$, to maturity, m_A , at $t = G$. Since the curve is sigmoidal, mathematically it takes forever to reach adult mass M_A , the assumption of the constant is necessary to determine the simple growth rate in a way such that a certain fraction of the adult mass is reach at the age, $t=G$, and the constant a specifies the fraction of adult mass the curve reaches at generation time G , e.g., If the fraction is 90%, $a=1/(1-0.9)=10$; If the fraction is 99%, $a=1/(1-0.99)=100$; if the fraction is 99.9%, $a=1/(1-0.999)=1000$, etc.

$$\text{Rearranging equation 2 gives } C = 1 - \frac{2}{N_0} \frac{\text{Log}\left[\frac{aN_0}{2}\right]}{\text{Log}\left[a\left(\frac{N_0}{2}\right)^\mu\right]} \quad 3$$

where $\mu = \frac{m_O}{m_A}$ is the relative size of offspring at independence from parental inputs.

When body mass at generation time, $t = G$, is very close to the asymptotic mass (i.e., the constant a is much larger than $\frac{N_o}{2}$), then Eqn. 3 can be approximated and simplified as

$$C = 1 - \left(\frac{2}{N_o}\right) \quad 4.$$

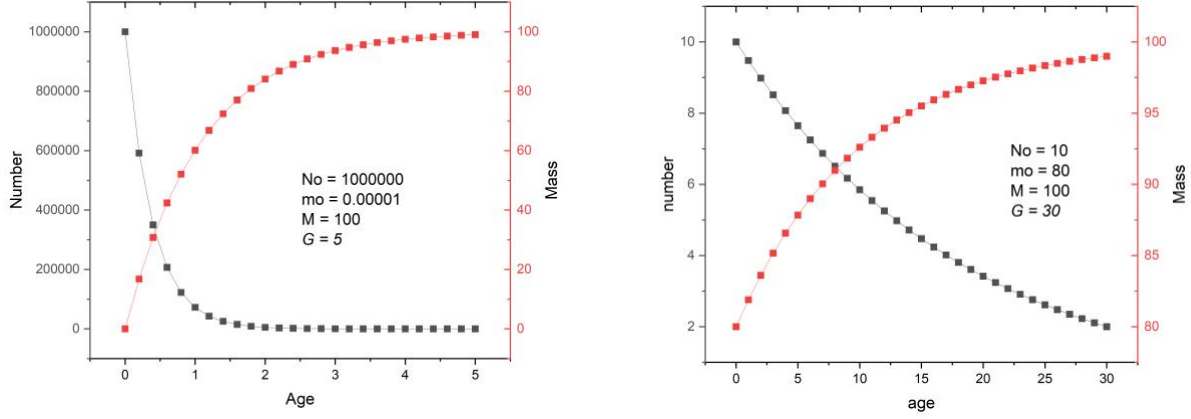


Fig. S1. Two hypothetical species with different generation times, G numbers of offspring, N_o , masses of offspring at birth, m_o but similar adult body masses, m_A .

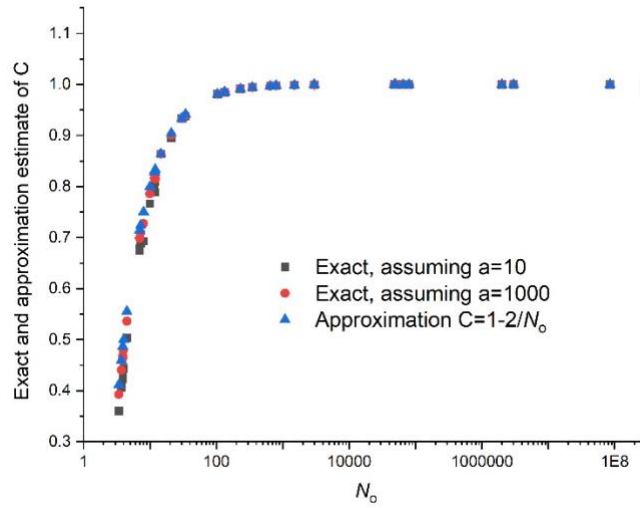


Fig. S2. Shows three curves, estimated by the exact solution Eqn.2, when $a=1000$ (99.9% of adult mass) and $a=10$ (90% of adult mass), and the approximation Eqn. 3, respectively. Sigmoidal growth takes forever to reach asymptotic adult mass, $m = m_A$, so we assume $a = 0.99$ in Figure 1 main text.

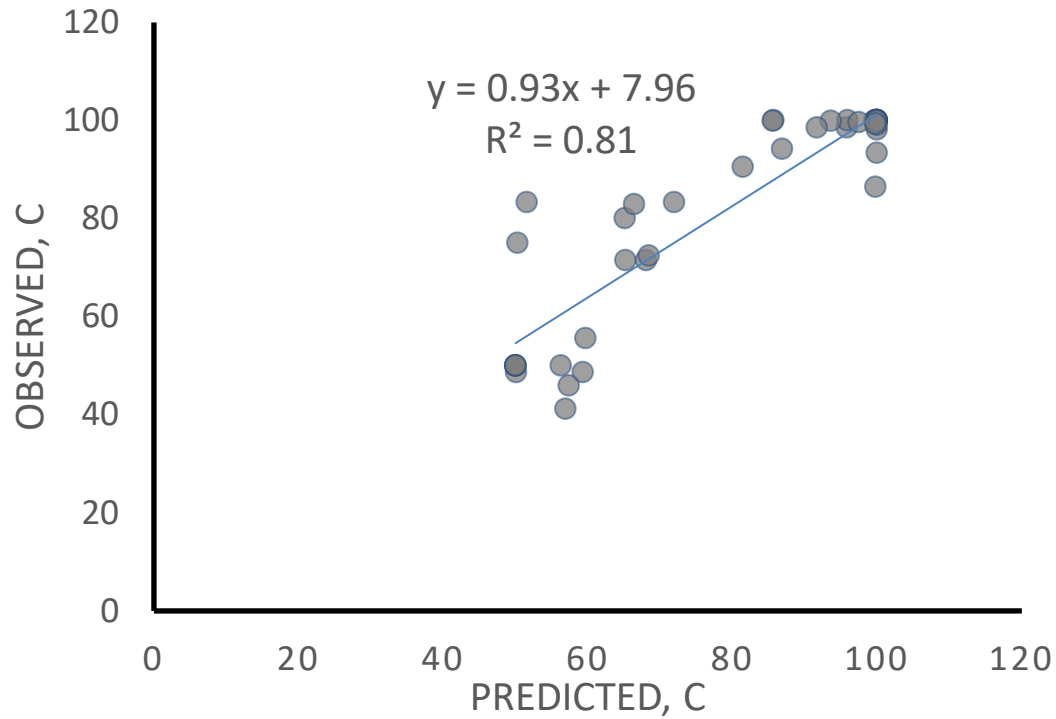


Fig. S3. Shows the correlation between predicted and observed values of C from Figure 1 main text.

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Calculations and graphs using just the reduced "high quality" datasets from refs

Common Name	Refs	mA = adult mass (g)	mO = offspring mass (g)	NO = Number of offspring	log NO	G = generation time (Y)	F Calculated	C = 1 - F	F assuming $\alpha = 90\%$	F assuming $\alpha = 99\%$	F assuming $\alpha = 99.90\%$	F = No. Parents/NO	C=1-(No. Parents/NO)*100
Ningauai	Burger et al. 2019 PNAS	7.00	2.5	4.50	0.65	1.000	0.40	59.71	0.53	0.49	0.48	0.44	55.56
Brazilian gracile opossum	Burger et al. 2019 PNAS	25.00	12	10	1.00	1.000	0.35	65.12	0.25	0.23	0.22	0.20	80.00
Brown antechinus	Burger et al. 2019 PNAS	27.50	8	3.9	0.59	1.000	0.41	59.36	0.61	0.56	0.55	0.51	48.72
Red kangaroo	Burger et al. 2019 PNAS	2650.00	11500	3.7	0.57	3.000	0.43	57.43	0.61	0.58	0.57	0.54	45.95
Blue whale	Burger et al. 2019 PNAS	1000000.00	25000000	7	0.85	5.000	0.35	65.22	0.39	0.34	0.32	0.29	71.43
Deermouse	Burger et al. 2019 PNAS	22.00	11	11.7	1.07	1.000	0.34	66.39	0.22	0.20	0.19	0.17	82.91
Deer	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	9100.00	20000	12	1.08	3.000	0.28	71.91	0.25	0.21	0.20	0.17	83.33
Pan troglodytes	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	4900.00	21000	3.4	0.53	20.000	0.43	56.97	0.66	0.63	0.61	0.59	41.18
Flying fox	Burger et al. 2019 PNAS	700.00	400	4	0.60	3.000	0.44	56.25	0.56	0.53	0.52	0.50	50.00
Eptesicus fuscus	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	25.00	24.9	3.9	0.59	2.000	0.50	50.06	0.51	0.51	0.51	0.51	48.72
Andean condor	Burger et al. 2019 PNAS	1010.00	10000	8.00	0.90	5.000	0.50	50.33	0.25	0.25	0.25	0.25	75.00
House sparrow	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	30.00	29	12.00	1.08	2.000	0.48	51.61	0.17	0.17	0.17	0.17	83.33
Ostrich	Burger et al. 2019 PNAS	11100.00	1500	132	2.12	5.000	0.04	95.78	0.04	0.03	0.02	0.02	98.48
Labord's chameleon	Burger et al. 2019 PNAS	13.53	0.4	7.00	0.85	1.000	0.32	68.07	0.43	0.36	0.34	0.29	71.43

Trans Volcanic Bunchgrass Lizard	Burger et al. 2019 PNAS	6.19	0.19	7.24	0.86	1.000	0.32	68.46	0.42	0.35	0.33	0.28	72.39
Chrysemys picta	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	350.00	4.14	34.3	1.54	5.000	0.13	86.93	0.13	0.09	0.08	0.06	94.17
Leatherback turtle (Costa Rica)	Burger et al. 2019 PNAS	384000.00	40.1	1500.00	3.18	9.000	0.00	99.60	0.01	0.00	0.00	0.00	99.87
Great white shark	Burger et al. 2019 PNAS	450000.00	15000	21.00	1.32	20.000	0.19	81.42	0.19	0.14	0.13	0.10	90.48
Gadus chalcogrammus	Burger et al. 2019 PNAS	119.50	0.00028	64762	4.81	5.000	0.00	99.99	0.00	0.00	0.00	0.00	100.00
Herring	Burger et al. 2019 PNAS	110.00	0.0012	50000.00	4.70	1.000	0.00	99.99	0.00	0.00	0.00	0.00	100.00
kokanee salmon	Burger et al. 2019 PNAS	700	0.13	800	2.90	3.000	0.00	99.99	0.01	0.01	0.00	0.00	99.75
Alewife	Burger et al. 2019 PNAS	230	0.0011	80000	4.90	1.000	0.00	100.00	0.00	0.00	0.00	0.00	100.00
American shad (Southern US pops)	Burger et al. 2019 PNAS	1241	0.005	48000	4.68	1.000	0.00	100.00	0.00	0.00	0.00	0.00	100.00
Atlantic cod	Burger et al. 2019 PNAS	7300	0.0015	2000000	6.30	8.000	0.00	99.80	0.00	0.00	0.00	0.00	100.00
Tuna	Burger et al. 2019 PNAS	60000.00	0.00052	85000000	7.93	17.000	0.00	100.00	0.00	0.00	0.00	0.00	100.00
Ocean sunfish	Burger et al. 2019 PNAS	200000.00	0.00115	300000000	8.48	3.000	0.04	95.91	0.00	0.00	0.00	0.00	100.00
Oncorhynchus nerka	Burger et al. 2021 Ecol Lett; Burger et al. 2020	2200.00	0.13	3000	3.48	4.000	0.06	93.60	0.00	0.00	0.00	0.00	99.93
Eel	Burger et al. 2019 PNAS	1000.00	0.00003	3000000	6.48	11.000	0.14	85.64	0.00	0.00	0.00	0.00	100.00
Salmo trutta	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	43.55	0.09	135	2.13	2.500	0.08	91.66	0.04	0.03	0.02	0.01	98.52

Pseudocalanus minutus (copepod)	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	0.0007	0.000002	14.7	1.17	0.500	0.00	99.80	0.25	0.19	0.18	0.14	86.39
Drosophila pseudoobscura	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	0.0010	0.00001	30	1.48	0.250	0.00	100.00	0.14	0.11	0.09	0.07	93.33
Pea aphid	Burger et al. 2019 PNAS; Burger et al. 2021 Ecol Lett	0.0045	0.009	104.00	2.02	0.250	0.00	100.00	0.01	0.01	0.01	0.02	98.08
Caddisfly	Burger et al. 2019 PNAS	0.49024	0.000012	230	2.36	1.000	0.00	100.00	0.03	0.02	0.01	0.01	99.13
Mayfly	Burger et al. 2019 PNAS	0.48601747	0.00000067	2959	3.47	1.000	0.14	85.61	0.00	0.00	0.00	0.00	99.93
Dobsonfly	Burger et al. 2019 PNAS	0.692	0.00004	2976	3.47	1.000	0.00	99.90	0.00	0.00	0.00	0.00	99.93
Seventeen-year cicada	Brown et al. 2022 ICB	1.0455	0.00007	650	2.81	17.000	0.02	97.52	0.01	0.01	0.01	0.00	99.69
Cecropia moth	Burger et al. 2019 PNAS	3.071791045	0.003	350	2.54	1.000	0.00	99.80	0.02	0.01	0.01	0.01	99.43
Single-celled protist (E coli)	DeLong et al. 2010 PNAS	1.20E-12	6E-13	2.00	0.30	0.003	0.50	50.00	0.50	0.50	0.50	0.50	50.00
Prokaryote (small) Francisella tularensis	DeLong et al. 2010 PNAS	1.00E-14	5E-15	2.00	0.30	0.003	0.50	50.00	0.50	0.50	0.50	0.50	50.00
Amoeba (protist)	DeLong et al. 2010 PNAS	9.55E-07	4.775E-07	2.00	0.30	0.003	0.50	50.00	0.50	0.50	0.50	0.50	50.00
Prokaryote (large) Azotobacter agilis	DeLong et al. 2010 PNAS	1.90E-11	9.5E-12	2.00	0.30	0.003	0.50	50.00	0.50	0.50	0.50	0.50	50.00