Universal Ontogenetic Growth without Fitting Parameters: Implications for Life History Invariants & Population Growth

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ABSTRACT

Since the work of Von Bertalanffy (1957), several models have been proposed that relate the ontogenetic scaling of energy assimilation and metabolism to growth, being able to describe ontogenetic growth trajectories for living organisms and collapse them onto a single universal curve (West et al. 2001; Barnavar et al. 2002). Nevertheless, all these ontogenetic growth models critically depends on fitting parameters and on the allometric scaling of the metabolic rate. Using a new metabolic rate relation (Escala 2019) applied to a Bertalanffy-type ontogenetic growth equation, we find that ontogenetic growth can also be described by an universal growth curve for all studied species, but without the aid of any fitting parameters. We find that the inverse of the heart frequency f_H, rescaled by the ratio of the specific energies for biomass creation and metabolism, defines the characteristic timescale for ontogenetic growth. Moreover, our model also predicts a generation time and lifespan that explains the origin of several 'Life History Invariants' (Charnov 1993) and predicts that the Mathusian Parameter should be inversely proportional to both the generation time and lifespan, in agreement with the data in the literature (Duncan et al. 1997; Dillingham et. al 2016; Hatton et al 2019). In our formalism, several critical timescales and rates (lifespan, generation time & intrinsic population growth rate) are all proportional to the heart frequency f_H, thus their allometric scaling relations comes directly

from the allometry of the heart frequency, which is typically $f_H \propto M^{-0.25}$ under basal conditions.

1. Introduction

Metabolism and growth are two fundamental aspects of living organisms, thus is somewhat natural trying to understand the connections between both processes. Von Bertalanffy (1957) studied ontogenetic growth curves in order to establish connections between metabolism and growth, showing that individual growth curves in living organism can be reproduced from models of metabolic energy allocation. Although several subsequent growth models (Reiss 1989; West et al. 2001; Ricklefs 2003; Hou et al. 2008) differs significantly on the details of their derivation, it shares the same mathematical form of Von Bertalanffy (1957) that basically links patterns of assimilation and growth to the (allometric) scaling of metabolic rate. In particular, West et al. (2001) proposed a general quantitative model based on the allocation of metabolic energy and showed, that individual growth curves can be collapsed onto a single universal curve that describes the growth in all the studied species.

Nevertheless, Banavar et al (2002) illustrated later that the universal growth curve arises from general considerations on energy conservation that are independent of the specific allometric model used by West et al. (2001). In particular, Banavar et al (2002) showed that the data do not distinguish between the exact exponent in the scaling relationship between metabolic rate and mass, with both 2/3 and 3/4 exponents in the metabolic relation fitting equally well. This scaling collapse onto a universal curve that happens when some dimensionless quantities are properly defined, is also equivalent to asseverate that a single self-similar solution is able to successfully fit all the ontogenetic growth curves. Since the universal curve arises from general considerations, it is desirable any independent test on the assumptions behind the models that defines the key dimensionless quantities, which can be discerning between the different models for ontogenetic growth.

In general, all ontogenetic growth models critically depends on the metabolic rate, specifically, on the allometric scaling which exact slope is still matter of debate (White et al. 2007). Recently, the empirical metabolic rate relation was corrected in order to fulfill dimensional homogeneity (Escala 2019), a minimal requirement for any meaningful law of nature (Bridgman 1922), proposing a new metabolic rate (B) formula: $\mathrm{B} = \epsilon(\mathrm{T})\, \eta_{\mathrm{O_2}} \mathrm{f_H}\, \mathrm{M}$, where M is the body mass, $\mathrm{f_H}$ is a (characteristic) heart frequency, $\eta_{\mathrm{O_2}}$ is an specific $\mathrm{O_2}$ absorption factor for different exercising conditions (basal, maximal, etc) and $\epsilon(\mathrm{T}) = \epsilon_0\, \mathrm{e}^{-\mathrm{E_a}/\mathrm{kT}}$ is a temperature correction inspired in the Arrhenius formula (Gillooly et al. 2001), in which $\mathrm{E_a}$ is an activation energy and k is the Boltzmann universal constant. Compared to Kleiber's original formulation (Kleiber 1932), $\mathrm{B} = \mathrm{B_0}(\mathrm{M}/\mathrm{M_0})^{0.75}$, or the Rubner's surface rule proportional to 2/3, this new metabolic rate relation has the heart frequency $\mathrm{f_H}$ as controlling variable (a marker of metabolic rate) and the advantage of being an unique metabolic rate equation for different classes of animals and different exercising conditions, valid for both basal and maximal metabolic rates, in agreement with empirical data in the literature (Escala 2019). In addition, Escala (2020) showed that this new metabolic rate relation can be directly linked to the total energy consumed in a lifespan, being able to explain the origin of variations in the 'rate of living' theory (Speakman 2005; Ramsey et al. 2000).

In this paper, we explore the implications of this new metabolic relation for ontogenetic growth models, with a focus on independently test key quantities in our formulation that can be discerning with the previous models, being organized as follows. We start in §2 applying the results of the new metabolic rate relation (Escala 2019), to an ontogenetic growth equation that shares the same mathematical form of previous models, showing that individual growth curves can also be collapsed onto a single universal curve, but in this case without the aid of any fitting parameter. Section 3 continues with computing the predicted generation time and explaining the origin of several 'Life History Invariants', with satisfactory results. In §4, we study the predicted implications for population growth, showing that agrees with the collected data. Finally in §5, we discuss the results and final implications of this work.

2. Ontogenetic Growth Model

Since different assumptions about the energy allocation get to the same general equation (von Bertalanffy 1957; Reiss 1989; West et al. 2001; Ricklefs 2003; Hou et al. 2008), we will follow the notation in the mass-energy conservation model described in Moses et al. (2008), that revisited the ontogenetic growth model of West et al. (2001), simply because we will compare to their results, using their parameters estimations. The conservation of energy for the allocation of metabolic energy during growth between maintenance of existing tissue and the production of new biomass, can be expressed as $\mathrm{E_m}\,\frac{\mathrm{dm}}{\mathrm{dt}} = \mathrm{B} - \mathrm{B_m}\,\mathrm{m}$ (Moses et al. 2008), where B is the metabolic rate (in J/s or W), $\mathrm{E_m}$ (in J/g) is the energy required to create a unit of biomass and $\mathrm{B_m}$ (in W/g) is the metabolic rate required to maintain an existing unit of biomass.

For the corrected metabolic rate relation, we will restrict to basal (resting) conditions and neglect temperature variations, because ontogenetic growth happens over long periods of time where such variations might tend to cancel (in wild conditions). Under such conditions, is constant the factor $\epsilon(\mathrm{T})\,\eta_{\mathrm{O_2}} \approx 10^{-4.313}\,\mathrm{mlO_2g^{-1}} \approx 10^{-3}\,\mathrm{J/g} \equiv \mathrm{E_{2019}}$ (converting 1 ltr $\mathrm{O_2}$=20.1 kJ; Schmidt-Nielsen 1984), where $\mathrm{E_{2019}}$ is a constant that comes from the best fitted value for the corrected metabolic relation (Eq. 8 of Escala 2019). Therefore, the metabolic rate formula is simply given by $\mathrm{B} = \mathrm{E_{2019}}\,\mathrm{f_H}\,\mathrm{m}$ (Escala 2019) and assuming that the heart frequency scales with body mass m as $\mathrm{f_H} = \mathrm{f_0 m^{-\alpha}}$, (mass-)energy conservation can be expressed as

$$\frac{\mathrm{dm}}{\mathrm{dt}} = \mathrm{am}^{1-\alpha} - \mathrm{bm}\,, \tag{1}$$

where $\mathrm{a} = \mathrm{E_{2019}}\,\mathrm{f_0}/\mathrm{E_m}$ and $\mathrm{b} = \mathrm{B_m}/\mathrm{E_m}$. The general solution of Eq 1 is a classical sigmoidal curve, which general form is given by von Bertalanffy (1957; Eq 6). Noting also that for an initial (birth) mass m_0 and final (asymptotic) mass M, the condition dm/dt = 0 (at m =

M) in Eq 1 is equivalent to $a/b = M^{\alpha}$, the solution to Eq 1 can be written as:

$$\left(\frac{m}{M}\right)^{\alpha} = 1 - \left[1 - \left(\frac{m_0}{M}\right)^{\alpha}\right] \times \exp\left(-\frac{at}{\alpha^{-1}M^{\alpha}}\right). \tag{2}$$

This solution is equivalent to the one found by Banavar et al. (2002) and for the special case of $\alpha = 1/4$, gives the solution given in West et al (2001) (their Eq 5). The solution given by Eq 2 can be rewritten as $r = 1 - e^{-\tau}$, which is the same universal growth curve found in West et al (2001) (and Banavar et al 2002), but using in our case the following variable change:

$$r \equiv \left(\frac{m}{M}\right)^{\alpha} \;\; ; \;\; \tau \equiv \frac{E_{2019}}{E_m}\frac{f_H\, t}{\alpha^{-1}} - \ln\left[1 - \left(\frac{m_0}{M}\right)^{\alpha}\right], \tag{3}$$

where we also replaced $a = E_{2019}\, f_0/E_m$ in Eq 2 (in the definition of τ) and thus, $f_H = f_0 M^{-\alpha}$ is (from now) the heart frequency when the animal reaches the final (asymptotic) mass M. For the particular case of $\alpha = 1/3$, r corresponds also to the fractional size ($r = (m/M)^{1/3} = l/L$), leading to the classical Bertalanffy growth equation, $l(\tau) = L\,(1 - e^{-\tau})$, which has been successfully applied in the fishery industry (Beverton & Holt, 1959; Charnov 2008). In this case, we can explicitly express (in terms of physical quantities) the Bertalanffy growth coeficient as $K \equiv \tau/t = \frac{E_{2019}}{E_m}\frac{f_H}{\alpha^{-1}}$ (from Eq 3 for $m_0 = 0$).

The advantage of this formulation compared to previous ones, is that now the dimensionless time τ is expressed in terms of quantities that are well defined, with clear either physical (E_{2019}, E_m) or biological (f_H, M, etc) meaning, therefore, the dimensionless variables defined in Eq. 3 are now written in a physically transparent form, without the aid of fitting parameters (for example, the parameter a has a fractal dimensionality of [mass$^{\alpha}$]/[time] and is critical in fitting the growth curves in Bertalanffy 1957, West et al 2001, Banavar et al 2002, etc). Noteworthy is that in this formulation for τ, the inverse of the heart frequency f_H^{-1} defines the characteristic timescale for ontogenetic growth, $t_{growth} \equiv f_H^{-1}\frac{E_m}{E_{2019}}$, being rescaled by the ratio of specific energies of biomass creation (E_m) and (basal) metabolism (E_{2019}).

Banavar et al. (2002) showed that the ontogenic growth curves do not distinguish between an exponent of 2/3 or 3/4 ($= 1 - \alpha$) in the mass scaling of the metabolic rate

relation, being both an equally good fit of the current data and consistent with an universal curve $r = 1 - e^{-\tau}$ for ontogenetic growth. Therefore, only for consistency we will assume $\alpha = 1/4$, since we will compare our formulation against data using the fitting parameters from West et al (2001), which assumes such α value.

Since the universal growth curve $r = 1 - e^{-\tau}$, for the τ defined in Eq. 3 (with $\alpha = 1/4$), is mathematically identical to the solution found in West et al (2001) (their Eq 5), when the following condition is fulfilled:

$$t_{\rm growth}^{-1} \equiv \frac{E_{2019}}{E_m} f_H = \frac{a}{M^{1/4}} \ , \tag{4}$$

then it should fit equally well the individual growth curves for the species studied in West et al (2001), if their heart frequencies f_H and specific energies (E_{2019}, E_m) fulfill the condition given by Eq 4, for the parameter a and final mass M found in the fitting procedure of the growth curves in West et al (2001). In order to test if the condition in Eq. 4 is fulfilled in nature, we collected estimations for the energy required to create a unit of biomass E_m (Moses et al. 2008, taking averages when multiple estimations are available) and measurements of heart frequencies f_H for the species studied in West et al (2001), in order to complement them with the parameters a, birth mass m_0 and final mass M that best fit the growth curves studied in West et al (2001). A summary of all the quantities (with the individual references for f_H) are listed in Table 1.

Table 1

Species	a[$g^{1/4}$/day]	m_0[kg]	M[kg]	E_m[J/g]	f_H[#/min]
		West et al 2001		Moses et al. 2008	(Reference)
Cow	0.28	33.3	442	6950	63 (Kovacs et al 2005)
Pig	0.31	0.90	320	6150	70 (Harris 2009)
Rabbit	0.36	0.12	1.35	6100	180 (Detweiler et al. 2004)
Guinea pig	0.21	0.005	0.840	4900	277 (Weibel et al. 2004)
Rat	0.23	0.008	0.280	4350	393 (Weibel et al. 2004)
Shrew	0.83	0.0003	0.0042	1800	835 (Jurgens et al. 1996)
Heron	1.56	0.003	2.7	1400	211 (Machida et al. 2001)
Robin	1.9	0.001	0.022	2000	570 (Welty et al.1988)
Cod	0.017	0.0001	25	13000	32 (Wardle et al. 1973)
Salmon	0.026	0.00001	2.4	7300	30 (Clark et al. 2011)
Guppy	0.10	0.000008	0.00015	1900	120 (Unpublished data)

Figure 1 display the relation given by Eq 4, between the variables a, M, E_m & f_H as a function of the final body mass M. Besides the 7 orders of magnitude in body mass M variations, the relation has a slope consistent with zero ($\propto M^{-0.05}$ and with only 0.22 dex in scatter, comparable to the scatter in metabolic rate relation found in Escala 2019), confirming that the condition in Eq. 4 is fulfilled. This implies that for the specific dimensionless variables defined in Eq. 3, the universal curve ($r = 1 - e^{-\tau}$) will describe the (different) individual growth curves as well as the models in West et al (2001) (and Banavar et al. 2002).

Moreover, the different species displayed in Figure 1 are scattered around the predicted value of E_{2019} ($= 10^{-3}\,Jg^{-1}$; Escala 2019) denoted by the red dashed line, therefore, Fig 1 can be considered the third independent estimation of E_{2019} (in addition of Escala 2019, 2020), supporting the predictability of the formalism presented and showing something characteristic of the exact sciences: fewer (and universal) constants having consistent

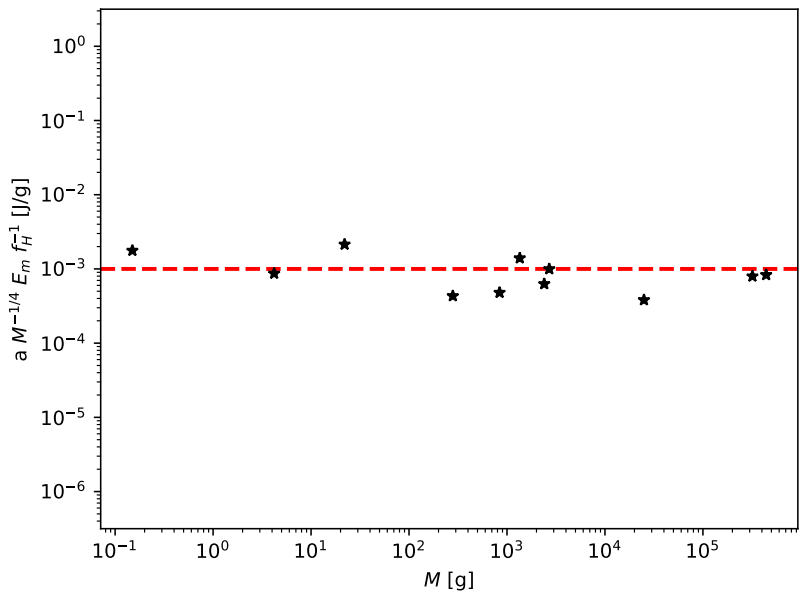

Fig. 1.— The relation between the variables a, M, E_m & f_H, as a function of the final body mass M, showing that does not vary systematically with M, as predicted by Eq 4. The different species displayed in black stars are scattered around the predicted value of E_{2019}, which is denoted by the red dashed line. The best-fitted slope is consistent with zero, $\frac{a}{M^{1/4}} \frac{E_m}{f_H} \propto M^{-0.05}$, with only 0.22 dex in scatter.

measurements in multiple contexts. Finally, Figure 1 strongly supports that the inverse of the heart frequency f_H^{-1}, rescaled by the ratio of the competing specific energies (biomass creation E_m versus metabolism E_{2019}), defines the characteristic timescale for ontogenetic growth $t_{growth} = f_H^{-1} \frac{E_m}{E_{2019}}$.

3. Generation-Time and the origin of some Life History Invariants

The success of the formulation given by Eq. 3, supported by Fig 1, motivates us to study its implications and for that reason, it is interesting to look the predicted generation-time

t_{gen}, which is the time period required for young to grow to its final size and thus mature to reproductive age. The generation time t_{gen} can be straightforwardly determined from the τ defined in Eq. 3, being possible to arrive to the following relation

$$t_{gen} = \left(\tau^* + \ln\left[1 - \left(\frac{m_0}{M}\right)^{\alpha}\right]\right) \frac{E_m}{E_{2019}} \frac{\alpha^{-1}}{f_H} \propto f_H^{-1}\,, \tag{5}$$

where τ^* is the approximate dimensionless time value to reach adult mass (for all species) in the universal growth curve. Eq. 5 gives a generation-time explicitly dependent on the heart frequency f_H, where for the allometric scaling of the heart frequency under basal conditions ($f_H \propto M^{-0.25}$; Brody 1945, Calder 1968) gives the well known mass scaling for the generation-time ($t_{gen} \propto M^{0.25}$; Bonner 1965). Nevertheless, since most biological rates and times scale as $M^{-1/4}$ and $M^{1/4}$ (Savage et al. 2004, Burger et al. 2021), an interesting possible test is to study allometric variations of t_{gen} in big outliers from '1/4 scaling' such as spiders (Anderson 1970, 1974) and other organisms (White et al. 2007), testing if they vary like f_H as predicted by Eq. 5. Another interesting possibility is to directly test the predicted inverse correlation between t_{gen} and f_H.

One of the advantages of having a generation time explicitly dependent on the heart frequency f_H, is that it can be directly linked (Escala 2019, 2020) to the total lifespan t_{life}, using the empirical relation of total number of heartbeats (N_b) in a lifetime $t_{life} = N_b/f_H$ found to be valid in mammals (Levine 1997; Cook et. al 2006). Escala (2020) generalized this relation for all type of living organisms, using the proportionally between heart and respiration frequencies, $f_H = k\, f_{resp}$ (Schmidt-Nielsen 1984), then the empirical relation with lifetime can be rewritten to be valid also for a total number $N_r\,(= N_b/k)$ of 'respiration cycles': $t_{life} = N_b/f_H = N_b/kf_{resp} = N_r/f_{resp}$. Escala (2020) also used this relation to predict the total lifespan energy consumed in living organisms, with satisfactory results if it is required an approximately constant total number $N_r \sim 10^8$ of respiration cycles per lifetime in all living organisms, which further supports the generalization. Combining this relation for a fixed number of respiration cycles per lifetime with Eq 5, we arrive to:

$$G \equiv \frac{t_{gen}}{t_{life}} = \left(\tau^* + \ln\left[1 - \left(\frac{m_0}{M}\right)^{\alpha}\right]\right) \frac{E_m \alpha^{-1}}{E_{2019} N_b} \approx \frac{E_m}{k} \frac{4\,\tau^*}{E_{2019} N_r}\,, \tag{6}$$

where we also approximate for $m_0 << M$ (in agreement with the species listed in Table 1), neglecting minor changes due to the weakly varying logarithm. Eq. 6 directly relates the generation time and lifespan to their respective energies (per unit mass) to create biomass (E_m) and sustain lifespan ($N_b E_{2019}$), only by assuming (mass-)energy conservation (Eq. 1) and with the invariant N_r ($= 1.62\,10^8$ respiration cycles per lifetime; Escala 2020) as critical link between both timescales.

Eq. 6 can be directly compared to the data compiled by Charnov & Berrigan (1990), that summarizes published data for the ratio t_{adult}/t_{gen} in different animal groups, where $t_{adult} = t_{life} - t_{gen}$ is the adult lifespan and noting that such definition is related to the G ratio as $t_{gen}/t_{life} = (1 + t_{adult}/t_{gen})^{-1}$. Also, noting that in Charnov & Berrigan (1990) lifespans are estimated from the inverse of (instantaneous) mortality rates, being effectively fields lifespans and not maximum ones, thus to compare with Eq. 6 a correcting factor 2.5 must be included (McCoy & Gillooly 2008), namely $G^{min} = t_{gen}/t_{life}^{max} = (2.5(1 + t_{adult}/t_{gen}))^{-1}$.

Table 2 summarizes the estimations of G^{min} using the data compiled in Charnov & Berrigan (1990) and compared it with the predicted values from Eq. 6, using estimates of E_m for taxonomic groups (average of juvenile estimates; Moses et al. 2008), k values for such groups (Schmidt-Nielsen 1984; Escala 2020) and a dimensionless time $\tau^* \sim 5$, the approximate value to reach adult mass in universal growth curve (i.e. flat part of the curve in Fig. 2 of West et al 2001). We find that the predicted values are overall consistent with the empirically determined (Table 2), but taking into account that each taxonomic groups of birds, mammals and fishes includes species with up to an order of magnitude different E_m (i.e. cod vs guppy fish in Table 1) and not necessarily the same species studied in Charnov & Berrigan (1990), what is even more relevant is that the relative G^{min} trends (between birds, mammals and fish) observed in Charnov & Berrigan (1990) are successfully predicted by the ratio $\frac{E_m}{k}$.

Table 2

Animal Group	E_m [J/g]	k	Predicted Eq 6	$G^{min} = \frac{t_{gen}}{t_{life}^{max}}$
Birds	4050	9	0.06	0.11
Mammals	5800	4.5	0.16	0.17
Fish	7400	3	0.3	0.28

Eq. 6 shows that the invariant relation between lifespan and age at maturity that is valid within taxonomic groups, as observed by Charnov & Berrigan (1990), might come directly from the existence of another invariant: the approximately constant total number $N_r \sim 10^8$ of respiration cycles per lifetime. This t_{adult}/t_{gen} ratio is indeed one of the studied dimensionless life-history invariants (Calder 1984; Charnov 1993), which sometimes has been criticized to be spurious, just being a form of 'regressing X on X' a random number (Nee et al. 2005). In this work, the generation and lifespan timescales are quantities derived independently, giving a quantitative prediction for being approximately invariant ratio within taxonomic groups, including their inter-specific variations, that comes from the basics energetics of respiration and the creation of new biomass and therefore, having a clear physical interpretation and thus far from being spurious.

Traditionally this relation, expressed in terms of the adult lifespan and age at maturity (which typically marks the stop of animals growth), as in Charnov & Berrigan (1990), has been qualitative explained in terms of life-history evolution theory. Many versions life-history theories predict that the age of maturity should be positively correlated with the lifespan (Charnov 1993), being these patterns a reflection of natural selection (Charnov & Berrigan 1991). In this paper, after rewriting the properties of living organisms in a physical transparent form, we predict the value of this life-history invariant in terms of the relevant energetics (E_m, E_{2019}, k, etc) and find that the constancy mainly comes from the invariant number $N_r \sim 10^8$ of respiration cycles per lifetime, a generalization of the well known relation of constant number of heartbeats in mammal's lifetime (Levine 1997; Cook et. al 2006). Nevertheless, we do not study the origin of how the key parameters (E_m, k, etc) varies across species, animal groups and generations, which should be evolutionary in

origin and thus set by natural selection (Charnov 1993; Gardner et al 2005).

It is direct to realize that some of the other life-history invariants (Charnov 1993), comes directly from the existence of invariant $\mathrm{G} = \mathrm{t_{adult}}/\mathrm{t_{gen}}$ and the universal ontogenetic growth curve. For example, the invariant ratio between the mortality rate (M) and the Bertalanffy growth coefficient (K) (Beverton & Holt 1963, Cushing 1968, Pauly 1980), comes from its the relation with τ in our formulation, $\mathrm{Kt} = \tau$, which at the generation time corresponds to $\mathrm{Kt_{gen}} = \tau^* \sim 5$, according to the universal growth curve (West et al. 2001; Barnavar et al. 2002). Noting also that the mortality rate M is approximately the inverse of the lifespan $1/\mathrm{t_{life}}$ (in the next section we will see a more rigorous definition for M), is straightforward to find that $\mathrm{M/K} = \mathrm{t_{gen}}/(\mathrm{t_{life}}\tau^*) = \mathrm{G}/5$. Another invariant is the ratio between the length at maturity $l(\mathrm{t_{gen}})$ and maximum asymptotic length L (Charnov & Berrigan 1991), which comes also from $\mathrm{Kt_{gen}} = \tau^* \sim 5$, simply recalling the Bertalanffy growth equation (derived in §2): $l(\mathrm{t_{gen}})/\mathrm{L} = 1 - \mathrm{e}^{-\tau^*}$. Finally, the invariant fraction of body mass to reproduction per unit time per life span (Charnov, Turner & Winemiller 2001), comes from the definition of the dimensionless mass r (Eq 3) and the invariant G (Eq 6), being related as $\frac{\mathrm{m(t_{gen})}}{\mathrm{M}}\frac{\mathrm{t_{life}}}{\mathrm{t_{gen}}} = (1 - \mathrm{e}^{-\tau^*})^{1/\alpha}\,\mathrm{G}^{-1}$, noting again that $\tau^* \sim 5$.

4. Implications for Population Growth: Mathusian Parameter and the 'Equally Fitness Paradigm'

Mathus (1798) studied the simplest model of population growth, which can be derived assuming that all individuals are identical and reproduce continuously, therefore, the number of individuals N will change with B births rates and D deaths rate as follows:

$$\frac{\mathrm{dN}}{\mathrm{dt}} = \mathrm{B} - \mathrm{D} = (\mathrm{b_N} - \mathrm{d_N})\mathrm{N} = \mathrm{r_m}\mathrm{N}\,, \tag{7}$$

where $\mathrm{b_N}$ and $\mathrm{d_N}$ are per capita birth and death rates respectively, being $\mathrm{r_m}$ the Malthusian parameter or intrinsic (maximum) population growth rate. The solution of Eq. 7 has an exponential form, given by $\mathrm{N(t)} = \mathrm{N_0}\,\mathrm{e}^{\mathrm{r_m t}}$ and therefore, the Malthusian parameter

$r_m = b_N - d_N$ has units of inverse time and can be rewritten in the following form: $r_m = \bar{b}/t_{adult} - \bar{d}/t_{life}$. The constants $(\bar{b}, \bar{d})$ are now dimensionless, since we have identified t_{life} as the characteristic timescale for death rates and $t_{adult} = t_{life} - t_{gen}$, as the characteristic timescale for the birth rates. The reason for the latter, is that t_{adult} is the reproductive adult lifespan, where it is subtracted from the lifespan the time period required to (grow and) mature to reproductive age, t_{gen}, a time period where is not fulfilled a key assumption in Eq 7, that the individuals are able to reproduce (continuously).

Using the Eq 6 that relates t_{gen} and t_{life}, the Malthusian parameter is then given by:

$$r_m = \left(\frac{\bar{b}}{1-G} - \bar{d}\right) t_{life}^{-1} = \left(\frac{\bar{b}}{1-G} - \bar{d}\right) \frac{f_H}{N_b} \propto f_H \,, \tag{8}$$

which gives a Malthusian parameter r_m again explicitly dependent on the heart frequency f_H. For the allometric scaling of heart frequency under basal conditions ($f_H \propto M^{-0.25}$, Brody 1945, Calder 1968) gives the well known Fenchel (1974) allometry, $r_m \propto M^{-0.25}$, but again as most biological rates and times scale as $M^{-1/4}$ and $M^{1/4}$ (Savage et al. 2004, Burger et al. 2021), a more interesting test will be to study allometric variations of r_m in outliers from '1/4 scaling' in the heart frequency f_H, testing if they vary like f_H as predicted by Eq. 8.

Another prediction of Eq. 8 is an inverse correlation between r_m and t_{life}, which was recently tested by Hatton et al (2019). Fig 2 display the data of Hatton et al (2019) for all types of living organisms, ranging from protists to mammals and birds. Since the present analysis is restricted to organisms with heart, we denoted with the dashed (blue) line the mass scale of 10^{-3} grams, which corresponds to the scale associated to smallest organisms with heart, such as fruit or fairly flies, which coincides in Fig 2 with a transition to a decrease in scatter (for larger masses) and in addition, all individual animal groups (colors in Fig 2) fulfill the relation for masses larger that 10^{-3} grams. The solid black line corresponds to the best fit to the data, consistent with a clear inverse correlation between r_m and t_{life}, with no residual slope with body mass ($r_m t_{life} = 3.35\, M^{0.01}$, scatter of 0.5 dex).

The relative low variation (on average one order of magnitude since the scatter is 0.5

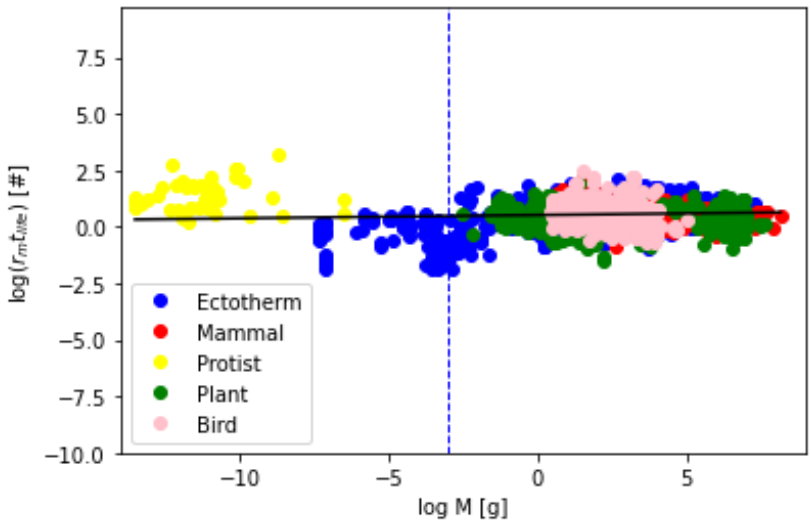

Fig. 2.— Lifetime Growth: Intrinsic (maximum) population growth rates (r_m) multiplied by their lifespans (t_{life}) for all types of living organisms, ranging from protists to mammals and birds, compiled by Hatton et al (2019). The solid black line corresponds to the best fit to the data, with no residual slope with body mass, $r_m t_{life} = 3.35\,M^{0.01}$, with a scatter of 0.5 dex. The dashed blue line the mass scale of 10^{-3} grams, which corresponds to the scale associated to the smallest organisms with heart, where the present analysis is restricted.

dex) and specially, the negligible slope with body mass showed in Fig 2 has been claimed (Hatton et al 2019) to support the so-called 'Equally Fitness Paradigm' (Brown et al 2018; Burger et al. 2020), which states that "most organisms are more or less equally fit, as evidenced by the persistence of millions of plant, animal and microbe species of widely varying size, form and function in the Earth's diverse environments" (Brown et al 2018). In terms of the proposed formalism, Eq. 8 and the low variation of G across animals groups (the factors 2-3 seen in Table 2), implies also a low variation for the parameters $\bar{b}$ and $\bar{d}$ across species. These relatively constant values (implied by Fig 2) for the dimensionless parameters $(\bar{b}, \bar{d})$ associated to the (net) per capita birth and death per characteristic time, besides the spectacular diversity of life histories in terms growth, reproduction and survivorship over the life cycle, which implies very diverse life history strategies in the huge mass range displayed

in Fig 2, supports that selection mechanisms should operate, in terms of equal fit according to Darwinian evolution.

In the fundamental theorem of natural selection, Fisher (1930) states that the rate of increase of mean fitness (caused by natural selection; Price 1972) is equal to the genetic variance of a species, conceptually linking natural selection with genetics. Natural selection can only increase fitness by reducing genetic variance (i.e. selecting away undesirable alleles; Basener & Sanford 2018), thus without mutations and given enough time, selection must reduce genetic variance all the way to zero and fitness must reach a maximum, according to Fisher's theorem and confirmed thru simulations (Basener & Sanford 2018). In general, entropy of a given probability distribution depends on its variance, for example the Gaussian distribution maximizes the entropy for a given variance, thus to reduce genetic variance implies a reduction of genetic entropy, which according to the second law of thermodynamics must be compensated with an increase in entropy in another component of the system (in an isolated system total entropy cannot decrease), which in this case should be an increase in the fitness entropy. The 'Equally Fitness Paradigm' seems to suggest that a constant (maximum) fitness value has been reached by the coexisting species in the current (environment) conditions. Also, according to the second law of thermodynamics maximum entropy happens only in the state of thermodynamic equilibrium, where (the theorem of) equipartition of energy holds. The 'Energetic Equivalence Rule' (Damuth 1981), which has been recently verified for ∼3000 species in Hatton et al. (2019), seem to be a version of such equipartition of energy in live matter and thus, also consistent with being in such state when maximum entropy is reached.

Another relation for $\mathrm{r_m}$ that can be derived using the definition of G (Eq 6), is the one which predicts an inverse correlation with the generation time $\mathrm{t_{gen}}$:

$$\mathrm{r_m} = \left(\frac{\mathrm{G}\bar{\mathrm{b}}}{1-\mathrm{G}} - \mathrm{G}\bar{\mathrm{d}}\right)\frac{1}{\mathrm{t_{gen}}} \propto \mathrm{t_{gen}^{-1}}\,, \tag{9}$$

a relation that again can be tested. For that purpose, we use now the data in Duncan et al.

(1997) that compiles ages at first reproduction ($\sim t_{gen}$) and maximum population growth rates for mammals. Fig 3 displays the data collected in Duncan et al. (1997), which is in overall agreement with Eq 9, with no relevant slope with body mass. The solid line denotes the best-fit to the data ($r_m t_{gen} = 1.38\,M^{-0.067}$), which has an average scatter of 0.2 dex. Dillingham et. al (2016) also found equivalent results on this expected inverse relationship, using more sophisticated bayesian analysis.

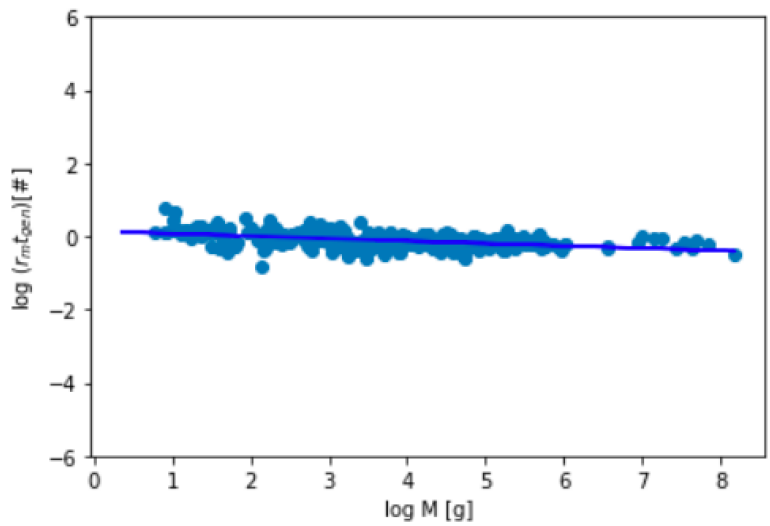

Fig. 3.— Generation times (t_{gen}) times the maximum population growth rates (r_m) for mammals, compiled by Duncan et al. (1997). The solid line denotes $r_m t_{gen} = 1.38\,M^{-0.067}$, which is the best-fit to the data and has an average scatter of 0.2 dex. The best-fitted relation is in overall agreement with the predicted Eq 9, with no relevant slope with body mass.

The normalizations from the best-fit to the data in Figs 2 & 3, gives estimations for $r_m t_{life} \sim 3.35$ (Fig 2) and $r_m t_{gen} \sim 1.38$ (Fig 3), which in principle can be combined with Eq 8 & 9, to determine some of their constants. Unfortunately, it is not possible to determine the constants $(\bar{b}, \bar{d})$ associated to the dimensionless birth and death rates, since Eq 8 & 9 are not (linearly) independent equations, but it is still possible to determine that $\frac{r_m t_{gen}}{r_m t_{life}} = G \sim 0.41$.

This is for average lifespan in the wild because Hatton et al (2019) lifespans were normalized to those, and since maximum lifespans are about 2.5 times average ones in the wild (McCoy & Gillooly 2008), we determine from Figs 2 & 3 that $\frac{t_{gen}}{t_{life}^{max}} = G^{min} \sim 0.16$, which agrees with the value determined from the average of the predicted G values in Table 2 ($G^{min} \sim 0.17$).

5. Summary

In this paper, we explore the implications of the new metabolic relation (Escala 2019) for ontogenetic growth and found that it can be described by an universal ontogenetic growth curve for all studied species, without the aid of ad-hock fitting parameters. The same universal growth curve in West et al (2001) and Banavar et al (2002) is found when some dimensionless quantities are properly defined, but in our case the characteristic growth timescale (t_{growth}) is set by the inverse of the heart frequency f_H^{-1}, rescaled by the ratio between the specific energies (per unit of mass) required for metabolism and to create new biomass, all quantities with clear physical or biological meaning and not obscure fitting parameters. The result of universal growth have the same interpretation as before in terms of conservation of energy, since it comes from the same Bertalanffy-type equation, but in our case the result do not rely on a specific model. Instead, this illustrates the advantages when empirical data is properly described and quantified, arising to this simple description without extra assumptions.

We also explore the implications of the discussed ontogenetic growth model for the generation time, finding that predicted t_{gen} can explain the origin of several 'Life History Invariants', when is it combined with the invariant number of respiration cycles per lifetime, a relation that comes from the generalization of the well known relation of constant number of heartbeats in mammal's lifetime (Levine 1997; Cook et al. 2006). In particular, the invariant ratio between lifespan and the age at maturity ($G = \frac{t_{gen}}{t_{life}}$), which has been traditionally explained in terms of life-history evolution theory, in our formalism the value of this life-

history invariant it is predicted in terms of the relevant energetics and the invariant number of respiration cycles per lifetime. The predicted G and its variation between taxonomic groups, shows both consistency with the empirically determined value (Table 2). We also showed that other life-history invariants (Charnov 1993), comes directly from the existence of the universal the ontogenetic growth curve and the invariant G.

We finally studied the predictions for population growth, finding that the invariant G implies a Mathusian Parameter r_m, or intrinsic population growth rate, inversely proportional to both t_{gen} and t_{life}. We find that these inverse relations are indeed observed in nature, with no relevant slope with body mass and relatively low scatter (0.5 dex for $r_m t_{life}$ in Fig 2 & 0.2 dex for $r_m t_{gen}$ in Fig 3). The ratio $G^{min} = \frac{t_{gen}}{t_{life}^{max}}$ that can be estimated from the two best fitted relations ($\frac{r_m t_{gen}}{r_m t_{life}^{max}} = G^{min} \sim 0.16$), which is also consistent with our predicted G^{min} (~ 0.17; Table 2). Also, we find relatively constant values for the total birth and deaths per capita per characteristic time ($\bar{b}$ and $\bar{d}$ in Eq. 8), besides the Earth's diversity of life histories in living organisms, supporting the so-called 'Equally Fitness Paradigm'.

In our formalism, the allometric scaling relations for several critical timescales and rates (t_{life}, t_{gen} & r_m) are all coming from being proportional to f_H, therefore, the $f_H \propto M^{-1/4}$ mass scaling directly explains other well known allometries (for lifespan, generation-time and the Fenchel allometry), naturally explaining why most biological times and rates scale as $M^{-1/4}$ and $M^{1/4}$ (Savage et al. 2004, Burger et al. 2021). Also, the variations from 1/4 scaling should be explained in terms of the variation in the f_H mass scaling, since such quantities (t_{life}, t_{gen} and r_m) should have the same mass scaling as f_H, regardless if is 1/4 or not, as it was the case for the metabolic rate relation (Escala 2019).

Nevertheless, our formalism is empirically motivated and do not explain why f_H should scale as $M^{-1/4}$ or with another exponent, thus it is compatible with previous/other attempts that explains the exponent for the allometric scaling of metabolism and related quantities (West et al 1997, 1999; Banavar et al 1999, 2010; Darveau et al 2002), as far as the mechanism is based on the anatomy and physiology of the circulatory system. The difference between

both approaches, it is similar to the difference in physics between the (empirically-based and axiomatic) laws of thermodynamics and the statistical mechanics that explain them, being in this case the new metabolic rate and the invariant number of respiration cycles per lifetime the analogous to the thermodynamical laws, a synthesis that is also required towards the formulation of a general theory of biodiversity (Marquet 2017).

Finally, it is important to emphasize that our predictions were successfully tested without the aid of any free (fitting) parameters at all. The fitting procedures were done in Figs 1, 2 & 3 only to compare with our predictions, but not to determine any free parameter for our formalism. Moreover, the constants that defines the critical relations for metabolism (E_{2019}) and lifespan (N_r), are successfully tested further in Fig 1 (E_{2019}) and in the G value determine by Figs 2 & 3 (E_{2019} and N_r; Eq. 6), showing that the two simple relations for metabolism and lifespan used in this paper can successfully explain a variety of complex phenomena. This resembles the reductionism seen in physics since (at least) Galileo and Newton, where simple laws accounts for multitudes of complex phenomena.

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