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The Offspring-Development-Time/Offspring-Number Trade-Off

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ABSTRACT: The metabolic theory of ecology (MTE) states that metabolic rate, ruled mainly by individual mass and temperature, determines many other biological rates. This view of ecology as ruled by the laws of physics and thermodynamics contrasts with life-history-optimization (LHO) theories, where traits are shaped by evolutionary processes. Integrating the MTE and LHO can lead, however, to a synthetic theory of ecology. In this work, we link the two theories to show that offspring development time is the result of both maternal investment in offspring and the metabolic constraints on offspring growth. We formulate a model that captures how offspring development time is the consequence of both offspring growth rate, determined by temperature and allometric scaling in accordance with the MTE, and the size reached by offspring at the end of the developmental period, determined mainly by LHO and reproductive strategies. We first extend the trade-off between offspring size and offspring number to ectotherms, showing that increased body temperatures result in increased resources available for reproduction. We then combine this trade-off with the general ontogenetic growth model to show that there is a trade-off between the number of offspring produced and offspring development time. The model predicts a shorter developmental time in organisms producing larger numbers of offspring.

Keywords: metabolic theory of ecology, life-history optimization, developmental time, clutch size, offspring size, trade-off.

Introduction

Developmental time determines how fast populations grow and reproduce (Savage et al. 2004), so the interest in understanding developmental time transcends the limits of individual energetics and biology. In animal populations, the elapsed time from fertilization of the oocyte to the birth of the new individual is therefore an important life-history trait subject to optimization, depending on reproductive and life-history strategies (Stearns 1992; Roff 2002; Kiørboe and Hirst 2008), but it is also constrained

by physiology, as outlined by the metabolic theory of ecology (MTE; Gillooly et al. 2002).

A difference between the approaches of the MTE and life-history optimization (LHO) is that the MTE seeks to understand the effects of body size on developmental time, whereas LHO examines the evolutionary optimization of body size. Body mass is considered a cause (independent variable) driving developmental time by the MTE but as a consequence (dependent variable) subject to optimization by LHO theories. Ultimately, body mass can affect developmental time in two ways: through allometric effects on metabolic rate controlling how fast an organism grows and through life-history optimizations that set the relative body sizes at which transitions between developmental stages occur and hence the duration of development.

After the development of the MTE, Gillooly et al. (2002) developed a model that predicts a one-quarter-power allometry between embryonic development time and newborn body mass. This general relationship holds for a wide diversity of organisms, regardless of their life histories and taxonomy. The ability of newborn mass to describe developmental time relies on its capacity to capture in a single variable both the effect of the allometric constraints in the allocation of metabolic energy and the length of the trajectories along the ontogenetic growth curve until birth.

Here, we combine this general relationship between offspring size and developmental time with the classical trade-off between number and size of offspring (Smith and Fretwell 1974; Charnov and Ernest 2006) to show that, from an LHO perspective, there is a trade-off between the number of offspring and the duration of development. Conceptually, our model is summarized in figure 1A, with some hypothetical combinations of offspring development time (ODT), offspring size (m_o), mass (M), and the offspring production rate (C) of females. Figure 1B shows the growth curves of these offspring and their size at birth, as well as their expected ODT, while figure 1C shows the resulting relationship between ODT and offspring mass. Females 1 and 2 and females 3 and 4 have the same maternal body size but different reproductive strategies. For

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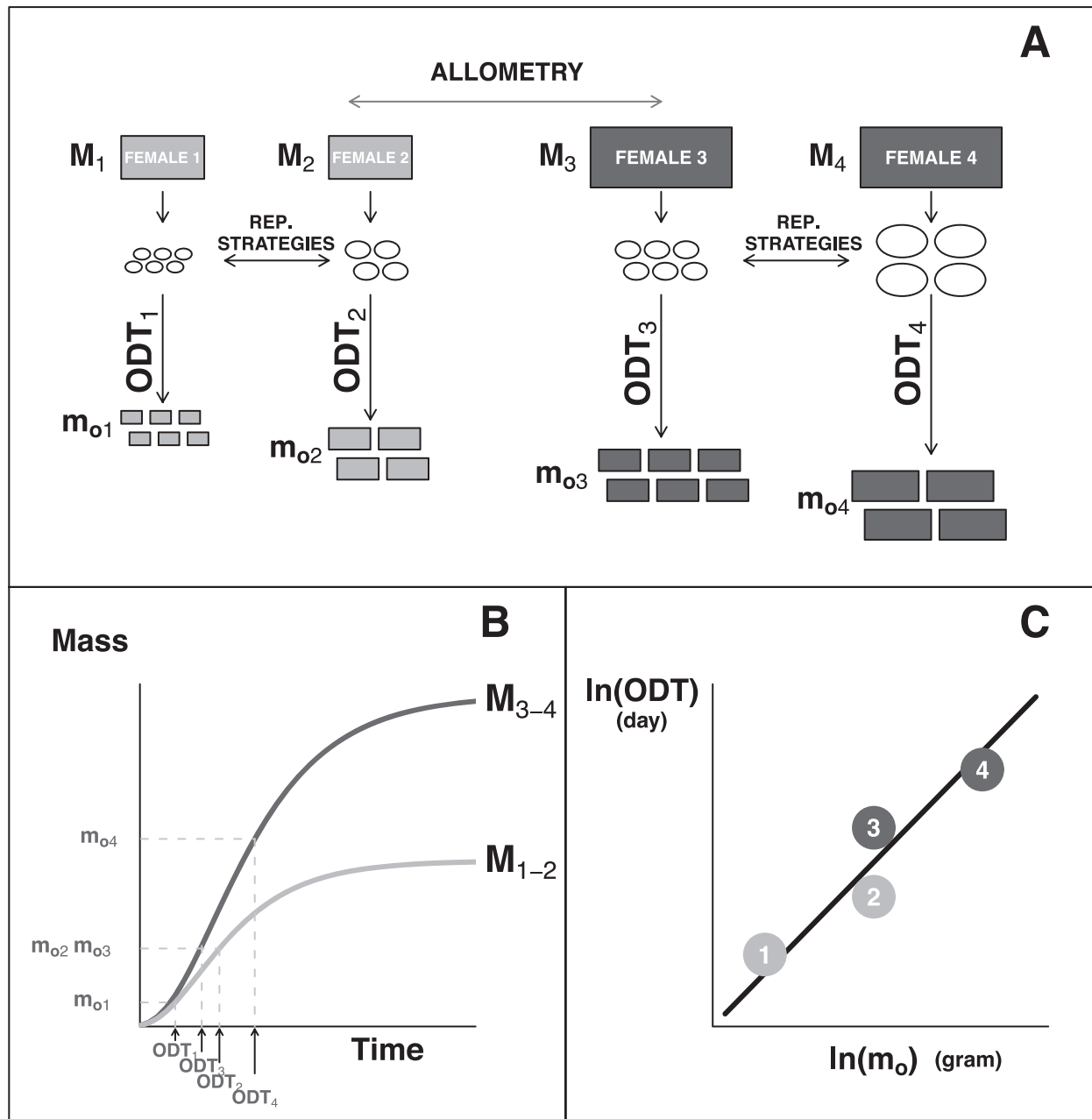


Figure 1: Schematics showing different combinations of adult size, M , offspring size, m_o , and offspring development time, ODT. **A**, Scenarios in which the differences in adult and offspring size between hypothetical species determine the length of their ODT. Pairs of females 1, 2 and 3, 4 have the same adult mass. The size ratio m_o/M is the same for pairs of females 1, 3 and 2, 4. Offspring from examples 2 and 3 have the same size m_o . **B**, Sigmoidal growth curves of these species. Note that the ODT in each case is inferred from the mass of the offspring by projecting the ontogenetic curve to the time axis. **C**, Hypothetical plot of ODT versus offspring size on a log-log scale. The slope of the regression line is 1/4. Each case is plotted according to the expected deviation from the predictions of the metabolic theory of ecology, given the reproductive strategies (rep. strategies) followed.

example, while female 1 invests its reproductive potential in producing many small eggs, female 2 produces a few, larger offspring. The longer developmental time of the offspring of female 2 is mostly due to their longer ontogenetic trajectories, compared to offspring of female 1, with the allometric constraints on metabolic rate having little effect on the difference in ODT. The allometric constraints on metabolism and growth rate play a major role, however, in the different developmental times of the offspring of small females (1, 2) and large females (3, 4). The resulting relationship between ODT and m_o , therefore, captures both reproductive and allometric constraints (fig. 1C).

Our aim is to develop a model for offspring development time that explicitly parameterizes these allometric and reproductive effects. To achieve this, we first extend Charnov and Ernest's (2006) model of the balance between offspring size and number in birds and ectotherms. Those authors suggested that their model for the trade-off between offspring size and number in mammals could be applied more generally if the effects of temperature on maternal metabolic rates were considered. We therefore extend their model to include temperature as a control of reproductive investment, and we test this model with an extensive compilation of empirical data for ectotherms and endotherms, demonstrating the universal generality of Smith and Fretwell's (1974) trade-off. We then put the resulting equation into Gillooly et al.'s (2002) model for embryo developmental time and generate a unifying model that captures the trade-off between offspring number and developmental time.

The Model

We introduce first the trade-off between size and number of offspring, as presented by Charnov and Ernest (2006), and formulate the correction for temperature needed to compare endotherms and ectotherms. We then briefly introduce the general ontogenetic growth model, as developed by West et al. (2001), and the model for developmental time of Gillooly et al. (2002). Finally, we blend the two theories into a unifying model.

LHO Trade-Offs

LHO theories view body mass as a trait that can be optimized and try to understand the trade-offs that lead to different relative body sizes at the transitions between ontogenetic periods. The classic LHO model of Smith and Fretwell (1974) describes how the offspring production rate, C , is directly related to the amount of resources allocated to reproduction in a reproductive event, R , and inversely related to the allocation per offspring, I

($C/R \propto 1/I$). Charnov and Ernest (2006) suggested that in mammals, the investment per offspring is approximated well by the offspring mass (m_o) while the resources diverted to reproduction scale with adult mass (M) raised to the power of $3/4$. They showed that the relationship $C/M^{3/4} \propto m_o^{-1}$ was supported by data for mammals.

For ectotherms, this relationship should be a bit more complex. The amount of resources allocated to reproduction (R) should be proportional to metabolic rate (B) and should depend on body size and temperature, following the general equation $R = C \times m_o \propto B \propto M^{3/4} \times e^{(-E/kT)}$, where $E \approx 0.62$ eV is the average activation energy for metabolic reactions (Gillooly et al. 2001) and k , in eV/K, is Boltzmann's constant. Hence, the Smith and Fretwell (1974) model for optimal offspring size can be expressed as $C \times m_o = \lambda M^{3/4} e^{(-E/kT)}$, where λ is a scaling constant. Rearranging terms, we obtain

$$\frac{C}{\lambda M^{3/4} e^{(-E/kT)}} = \frac{1}{m_o}, \quad (1)$$

which represents the trade-off between offspring number (scaled for the effects of maternal body size and temperature) and offspring size. This model is equivalent to Charnov and Ernest's (2006) model but includes the effects of temperature on reproductive investment and captures the fact that as temperature increases, there is an increase in metabolic rate that leads to faster biomass production and hence a higher daily offspring production rate (C).

The MTE Approach

At the base of the MTE approach to modeling developmental time, and derived from the principles of allocation of metabolic energy at the cellular level, is the general model for ontogenetic growth (West et al. 2001; Hou et al. 2008), where growth rate is described as

$$\frac{\delta m}{\delta t} = am^{3/4} \left[1 - \left(\frac{m}{M} \right)^{1/4} \right], \quad (2)$$

where m is the organism mass at a given time t , M is the asymptotic adult mass, and a is a variable related to fundamental cell properties. The parameter a includes the effect of temperature (T in K) on metabolic rate through the Arrhenius-Boltzmann factor, $a = a_0 e^{(-E/kT)}$, where a_0 is a normalization constant independent of temperature.

This equation parameterizes the classical sigmoidal ontogenetic growth curve present in many organisms (West et al. 2001). The term $1 - (m/M)^{1/4}$ represents the growth efficiency G (the proportion of energy devoted to growth) that is highest at the beginning of development.

Equation (2) is usually simplified, on the assumption

that the growth efficiency during embryo development is maximal ($1 - (m/M)^{1/4} \approx 1$; Gillooly et al. 2002; Moses et al. 2008), leading to

$$\frac{\delta m}{\delta t} = am^{3/4}. \quad (3)$$

Integrating equation (3) from $t = 0$ to the end of offspring development, we obtain Gillooly et al.'s (2002) formulation for offspring development time (ODT),

$$\text{ODT} = \left(\frac{4}{a_0 e^{(-E/kT)}} \right) m_o^{1/4}. \quad (4)$$

The Balance between Offspring Development Time and Offspring Number

The relationship between offspring number and developmental time is obtained first by solving the Charnov-Ernest relationship (Charnov and Ernest 2006), as described in equation (1), for $m_o^{1/4}$,

$$m_o^{1/4} = \lambda^{1/4} \frac{M^{3/16} e^{(-E/4kT)}}{C^{1/4}}, \quad (5)$$

and substituting this expression in equation (4) for offspring development time,

$$\text{ODT} = \lambda^{1/4} \left(\frac{4}{a_0} \right) \frac{M^{3/16} e^{(3E/4kT)}}{C^{1/4}}. \quad (6)$$

This equation expresses offspring development time in maternal terms and shows that developmental time is ruled mainly by temperature, adult mass, and the offspring production rate. It shows that there is a trade-off between the number of offspring that can be produced and the offspring development time.

Material and Methods

We first carried out a bibliographic search in order to test the major prediction of the Charnov and Ernest (2006) model for optimal clutch size (eq. [1]) for endotherms and ectotherms. We compiled data on offspring production rate and the temperature at which this variable was measured for 1,985 species (table S1, available in a zip file online). Next, we also performed a literature search to test the relationships between ODT and mass and temperature, resulting in a database of 2,252 species with a wide diversity of life histories (table S2, available in a zip file online). Finally, we combined the two data sets to study the balance between ODT and offspring production rate predicted by equation (6). Data on ODT and fecundity rarely come from the same reference (tables S1, S2), and usually each

variable was measured at a different temperature. To correct this source of uncertainty, we used the exponential correction of temperature to obtain an estimate of fecundity at the same temperature at which ODT was measured,

$$C' = C \times e^{E/k[(1/T_C) - (1/T_{\text{ODT}})]}, \quad (7)$$

where C' is the estimated fecundity at the temperature at which ODT was measured (T_{ODT}), C is the fecundity for that species, and T_C is the temperature at which C was measured (see tables S1).

Results

The Offspring-Size/Clutch-Size Trade-Off in Endotherms and Ectotherms

Charnov and Ernest (2006) demonstrated an energetic trade-off between the number and size of offspring in mammals. Here, we demonstrate that this balance also holds for a wider diversity of organisms, including both endotherms and ectotherms. A plot of temperature-corrected offspring biomass production versus adult mass in a log-log scale yields a slope of 0.76, not significantly different from 3/4 (t -test of slope different from 0.75: $P = .104$; figure 2; $r^2 = 0.97$), in accordance with the postulates of the MTE. The effect of temperature on offspring production rate also fits the prediction of the MTE. The value of the slope in figure 2B represents the activation energy, E , of the relationship between mass-corrected offspring biomass production and temperature. According to Gillooly et al. (2001), the theoretical value should be 0.62 eV, and our result (0.67 eV) is not significantly different ($P = .201$).

Finally, the universal trade-off between number and size of offspring is corroborated by the inverse isometrical relationship between the mass of the offspring (m_o) and the offspring production rate, as predicted by equation (1) (fig. 2C; $r^2 = 0.98$). The slope of this relationship is -0.986 , only marginally significantly different from -1 ($P = .026$).

The Effects of Offspring Size and Temperature on Offspring Development Time

Following equation (4), once ODT is corrected for the effects of temperature, offspring size explains part of the remaining variability found across taxa (fig. 3A). As predicted by the MTE, the slope of this relationship is not significantly different from 1/4 ($P = .458$). Similarly, a plot of ODT corrected for the effect of mass versus temperature (fig. 3B) has a slope of 0.54, significantly different from but close to the predicted activation energy for the

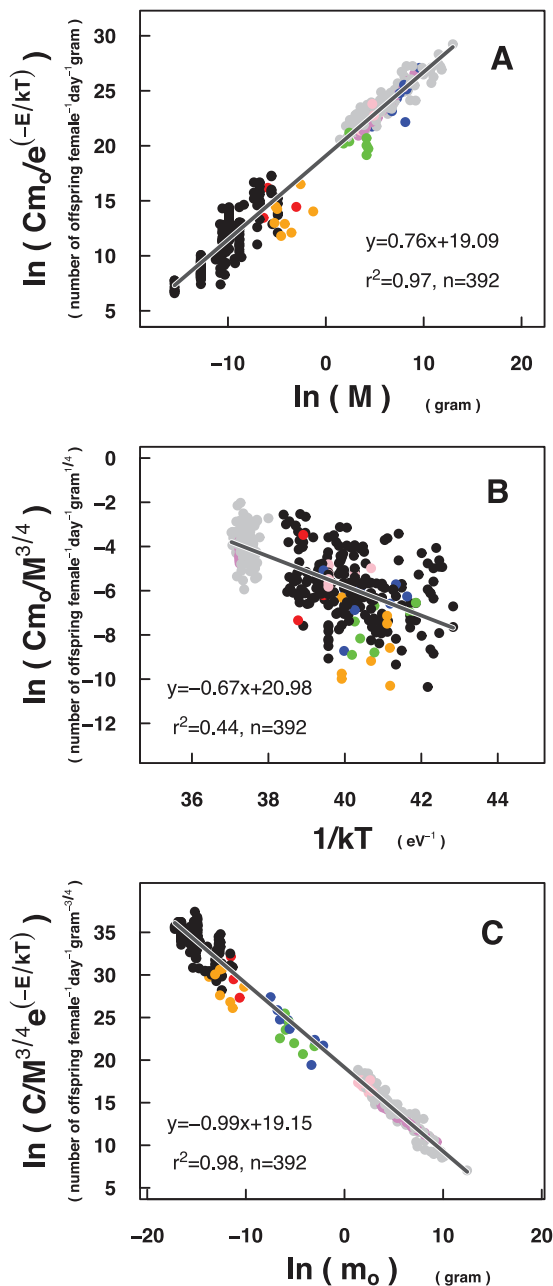


Figure 2: Offspring-size/clutch-size trade-off relating offspring production rate, C , adult mass, M , offspring mass, m_o , and the exponential term including the effect of temperature on offspring production, $e^{-E/kT}$. A, Relationship between the temperature-corrected offspring biomass production and adult mass. B, Effect of temperature on the offspring biomass production once corrected for the effects of female size. C, Inverse isometrical relationship between the offspring production rate corrected for the effects of female mass and temperature and the offspring size. Colors represent groups in the data set: mammals (gray), nonprocellariid birds (pink), procellariids (violet), amphibians (green), fish (blue), univoltine insects (orange), multivoltine insects (red), and zooplankton (black).

metabolic reactions proposed by Gillooly et al. (2001; $P = 1.7 \times 10^{-5}$).

The Trade-Off between Offspring Development Time and Offspring Number

The direct corollary of equation (6) is the existence of a trade-off between offspring development time and offspring production rate. This trade-off is the result of different reproductive strategies of resource allocation between many small and few big offspring. In consequence, once corrected for the effect of temperature and adult body mass, a plot of offspring development time versus offspring production rate shows an inverse relationship (fig. 4; $r^2 = 0.78$). But the estimation of the allometric exponent of offspring production rate on offspring development time using this relationship is not correct because we are already assuming a $3/4$ -scaling allometry when correcting ODT by $M^{3/16}$. In fact, in light of figure 4, the resulting slope, -0.34 , is significantly different from the expected $-1/4$ ($P = 2.2 \times 10^{-16}$). To correctly evaluate the allometric exponent, a nonlinear multiple regression is needed. Taking logarithms in equation (6) and given an allometric exponent α and activation energy E , we obtain the formula

$$\ln(\text{ODT}) = \beta - \alpha \times \ln(C) + (1 - \alpha)\alpha \times \ln(M) + (1 - \alpha)\frac{E}{kT}, \quad (8)$$

where β is a scaling intercept. This equation can be fitted through nonlinear least squares, with α , β , and E as parameters to be estimated. The values obtained by this procedure are close to the predictions of the MTE: $\alpha = 0.269$, with a 95% confidence interval of 0.250–0.288, and $E = 0.480$, with a 95% confidence interval between 0.382 and 0.584.

Discussion

Effects of Body Size and Temperature on Developmental Time

The metabolic theory of ecology (MTE) is grounded on the laws of physics and biochemical kinetics. It states that metabolic rate forms the backbone of ecology, driving many other ecological properties at higher levels of organization (West et al. 2001; Gillooly et al. 2002; Brown et al. 2004; Hou et al. 2008). This view of biology as ruled by the laws of physics and thermodynamics is often seen as too rigid to satisfactorily explain the many evolutionary strategies present among organisms (Harte 2004; O'Connor et al. 2007), and it clashes with the perception

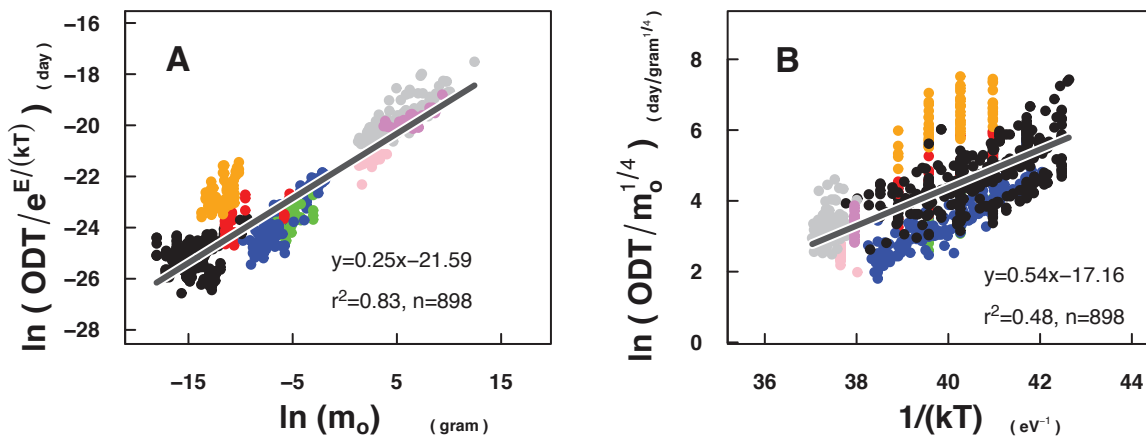


Figure 3: Model for offspring development time from equation (4). A, Relationship between the temperature-corrected offspring development time (ODT) and offspring mass. B, Logarithm of ODT corrected for the effects of offspring mass versus the logarithm of $e^{E/kT}$. Color key as in figure 2.

by life-history theorists that most biological traits are subject to fitness optimization. Combining the MTE with offspring size-number theory, we have shown that it is possible to reconcile these two approaches.

Offspring development comprises the processes of growth and transformation leading from the fertilized zygote to the independence of the offspring. According to the MTE, the time required for offspring development is determined mostly by offspring size and the developmental temperature. These effects are explained as a direct consequence of the faster rates of metabolism of smaller organisms and animals with higher body temperatures (Brown et al. 2004). This explanation, however, downplays the fact that larger newborns usually take longer to develop not only because of their slower metabolism but also because they have to develop to a larger size and hence have a longer ontogenetic trajectory to follow. That is, two species with the same metabolic rate, which hence grow equally fast, can have very disparate developmental times because of optimization of their mass at birth (cases 1 and 2 in fig. 1).

Gillooly et al. (2002) showed that newborn mass explained much of the variability in embryo development time, and we corroborate this result for ODT (fig. 3). In our analysis, we also include an extensive data compilation on marine birds from the order Procellariiformes (such as petrels, albatrosses, and shearwaters) and mammals, which are known to follow very specific reproductive strategies. By doing so and by introducing the notion of ODT, which includes the complete maternal investment per offspring, we extend the universality of the model of Gillooly et al. (2002).

Growth Efficiency and the Simplified Ontogenetic Growth Model

Offspring size captures in a single variable two effects, both of which lead to longer developmental times: slower metabolism with increasing adult asymptotic size (differences between cases 1–2 and 3–4 in fig. 1) and longer ontogenetic growth trajectories with larger mass at birth (differences between cases 1 and 2 and between cases 3 and 4). The only situation not explained by Gillooly et al.'s (2002)

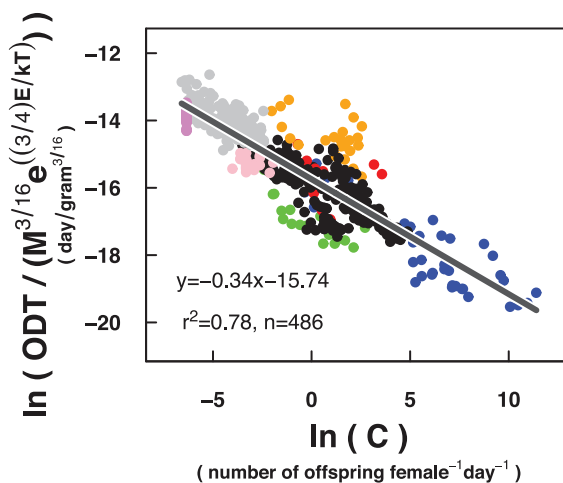


Figure 4: Trade-off between offspring development time (ODT) and offspring number. According to equation (6), there is a balance between ODT and the number of offspring produced by female per unit time. See text for interpretation of the regression slope. Color key as in figure 2.

simplified model and equation (3) is that of differences in developmental time between offspring 2 and 3 in figure 1.

The simplification in equation (4) is usually considered valid (Gillooly et al. 2002; Moses et al. 2008), on the basis that growth efficiency during embryo development is maximal ($1 - (m/M)^{1/4} \approx 1$), that is, on the assumption that mass at birth is minimal compared to adult mass and hence that growth efficiency is well approximated by 1. However, the assumption of $1 - (m/M)^{1/4} \approx 1$ is not always valid, and hence the simplification should be adopted carefully. For instance, using data from our data set, we have found organisms with growth efficiencies close to 0.50 at birth (some species of zooplankton and mammals). Integrating the complete ontogenetic growth model, from equation (2), from $t = 0$ to the end of maternal care and assuming that the mass of the embryo at $t = 0$ is negligible, we obtain the complete model for ODT:

$$\text{ODT} = -\left(\frac{4}{a}\right)M^{1/4}\ln\left(1 - \left(\frac{m_o}{M}\right)^{1/4}\right), \quad (9)$$

where ODT is driven by temperature, adult mass, and the growth efficiency of offspring by means of a size ratio logarithmic term, $\text{SR} = -\ln(1 - (m_o/M)^{1/4})$. Figure A1, available online, shows the ability of this model to describe ODT.

There are, however, some cases where even if mass at birth is not negligible compared to adult mass, the approximation of equation (9) by equation (4) is correct. For example, most mammals in our data set have mass at birth close to 30% of adult mass, and so growth efficiency at birth departs considerably from 1. But the fact that there is a nearly isometrical scaling between adult and offspring mass (fig. 5) implies that the growth efficiency term ($1 - (m/M)^{1/4}$) is invariant across mammalian species and hence that the simplification in equation (3) is still correct, because the term $\ln(1 - (m_o/M)^{1/4})$ is a constant.

On the other hand, other groups do not show invariance in the offspring size : adult size ratio (fig. 5). For example, in fishes, offspring size seems to be very constant across taxa and independent of adult size. So the quotient m_o/M varies with adult mass, and the offspring growth efficiency is different across species. Nevertheless, in this group, the mass of the offspring is very small compared to adult mass, which means that their growth efficiency at birth is close to 1. For this reason, the model in equation (4) is valid to describe their developmental time.

We could not find any cases in our data set to illustrate the situation exemplified by offspring 2 and 3 in figure 1. For these cases, however, a complete model for developmental time derived from equation (2) would be able to

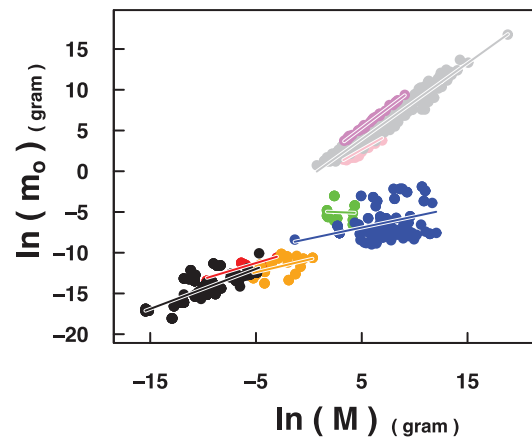


Figure 5: Relationship between offspring and adult size for the groups in our database. This relationship varies strongly, depending on the group considered. The slope of the relationship is 0.93 for mammals, 0.73 for nonprocellarid birds, 0.98 for procellarid birds, 0.27 for fishes, -0.05 for amphibians, 0.30 for univoltine insects, 0.39 for multivoltine insects, and 0.40 for zooplankton. Color key as in figure 2.

account for the differences in offspring development time, and the trade-off between ODT and offspring production rate (C) will still hold (appendix, available online).

The Offspring-Size/Offspring-Number Trade-Off in Endotherms and Ectotherms

Offspring mass is a life-history attribute that can be optimized and can be subject to trade-offs. The balance between the size of newborns and the number of offspring is a central principle of life-history theory (Smith and Fretwell 1974). We have shown that this trade-off can be universally formulated by equation (1), with a striking similarity in how viviparous and oviparous species fall along the same mass- and temperature-corrected trade-off axis (fig. 2C). Interestingly, regardless of the taxonomy, reproductive strategies, or body size, a nearly constant fraction of the assimilated energy is allocated to production of offspring biomass for the wide diversity of organisms considered here. This finding of constant reproductive allocation is in agreement with the results of Meiri et al. (2012) for different species of lizards.

Charnov and Ernest's (2006) model for mammals effectively showed that the resources available for reproduction are not constant across taxa and that the normalization of offspring production rate by the allometric scaling of energy allocation with adult mass is needed. We have shown that maternal body temperatures also affect reproductive potential, with increased reproductive output with increasing temperature. The consideration of the tem-

perature dependence of metabolism has allowed us to successfully apply Charnov and Ernest's (2006) model to birds, fish, amphibians, and invertebrates.

The Trade-Off between Offspring Development Time and Offspring Number

Our analysis should reconcile LHO theorists with the MTE, because it shows that body mass effects include both metabolic scaling and life-history optimizations. By introducing the Smith and Fretwell (1974) trade-off between offspring size and number in the MTE-based model for ontogenetic development of Gillooly et al. (2002), we reach a synthetic approach to modeling developmental time based on a twofold perspective of allometry and life-history optimization. Our model captures both the physiological effects on offspring development time (the effects of temperature and body mass on metabolic rate) and LHO effects through the offspring production rate. There are still differences between groups that might be due to different stoichiometries and the growth rate hypothesis (Gillooly et al. 2002) or to further evolutionary effects not explained by our model.

The interpretation of developmental time as modeled in equation (6) can have important implications for population fitness. This implies that for viviparous species, there could be a trade-off between the number of offspring that can be produced and the duration of parental care. For broadcasting oviparous species, such as many fish, egg development takes place in the water column. This life stage represents an important period for population connectivity while the embryos remain as propagules in the water. The balance between the number of broadcast eggs and the time spent as a propagule links the trade-off described here with the field of population connectivity and genetic flow (Mitarai et al. 2008).

Gillooly et al.'s (2002) model is at the basis of many higher-order predictions of the MTE (Brown et al. 2004; Savage et al. 2004). The integration of metabolic theory and life-history evolution can provide a synthetic theory of population energetics (Economo et al. 2005). Our model is a step in this direction and shows that both theories play a major role in controlling developmental time.

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