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The relation between maternal phenotype and offspring size, explained by overhead material costs of reproduction

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HIGHLIGHTS

- Life history theory predicts a single optimal offspring size.
- Empirical evidence shows great variation in offspring size within populations.
- I solve this incongruity by incorporating overhead costs of reproduction into models.
- Distinction between direct and overhead costs is crucial for this resolution.
- I explore how this can explain why offspring size often varies with maternal size.

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ABSTRACT

Variation in offspring size with female size and other aspects of the maternal phenotype is commonly observed and taxonomically widespread. However, life history theory predicts that optimal offspring size should not depend on maternal size or total reproductive effort. This incongruity persists despite various modifications to theory, that nonetheless, either are limited in their applicability or fail to alter the prediction of fixed offspring size. I demonstrate that the persistence of this theoretical outcome stems from an ideal assumption that reproductive effort relates only to direct material costs, and therefore, equal or proportional to clutch mass or the product of offspring size and number. A major innovation in my study is to explicitly distinguish between direct and overhead components of the costs of reproduction. When overhead energetic costs of reproduction are explicitly incorporated, I readily obtain variation in optimal offspring size with maternal phenotype. This consequence of overhead costs of reproduction has not been demonstrated before. I identify functional forms of such overhead costs that facilitate variation in optimal offspring size. In particular, costs that are more sensitive to offspring size than to offspring number are most effective in causing variation in offspring size. The novelty of the model lies in succeeding to resolve the above incongruity both within the framework of traditional models of optimal offspring size and within more dynamic description of the lifecycle (addressing simultaneously both offspring and maternal performance), including stochastic effects, difference between reserves and structural components of size, and distinction between starvation and extrinsic mortality. My predictions explain several patterns of variation in size and body composition of offspring, with respect to both environmental conditions and maternal phenotype.

1. Introduction

Offspring size is simultaneously a maternal and progeny character (Fox and Czesak, 2000), and is a basic trait involved in continuity of the phenotype (West-Eberhard, 2003), i.e., the bridging of two separate individual lifecycles – that of the mother and that of the offspring. Egg or seed size, hatchling size, and other measures of per offspring maternal investment are life history traits, associated with fundamental tradeoffs, as identified by life history theory (Roff, 2002; e.g., between offspring size and number, Smith and Fretwell, 1974, and between current and future reproduction, Winkler and Wallin, 1987). Moreover, offspring size and maternal provisioning may exert lasting effects on individual performance throughout the entire lifecycle (Marshall and Keough, 2008), for instance, on age-specific survival and growth (Segers and Taborsky, 2011), on expression of alternative phenotypes (Gross, 1991; Moczek, 1998), and on exaggeration of initial phenotypic variation within cohorts (Wall and Begon, 1987; Huss et al., 2007).

Despite 40 years since its publication, the standard point of reference for both empirical and theoretical works on offspring

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size is still the Smith–Fretwell model (Smith and Fretwell, 1974; hereafter SFM). According to this model, maternal fitness is the product of offspring number (e.g., number of eggs) and size-dependent performance of the offspring. The model is summarized by $F(y_p)=nw(y_p)$, where y_p represents the size of offspring (or propagules; e.g., eggs or seeds), F is the maternal fitness, n is the offspring number, and w is the offspring size–performance curve. Within SFM framework, offspring number is taken to be $n(y_p)=E/y_p$, where E denotes total reproductive effort (i.e., the total amount of resources that a mother can divide among many small or few large offspring), leading to an optimality criterion that resembles Charnov's (1976) marginal value theorem:

$$\frac{w'(y_p)}{w(y_p)}-\frac{1}{y_p}=0. \tag{1.1}$$

(Note that this equation is not an ODE, as the performance function, w, is given; it is a non-linear algebraic equation for the optimal offspring size y_p.) Clearly, optimal offspring size depends on the shape of the performance curve, $w(y_p)$, and much subsequent literature explores how this curve changes in different environments or circumstances (Temme, 1986; Lloyd, 1987; McGinley et al., 1987; Morris, 1987; McGinley and Charnov, 1988; Haig, 1990; Schultz, 1991; Morris, 1998; Hendry et al., 2001).

SFM predicts that all offspring should have identical size, given by a single optimal value that does not depend on total reproductive effort (i.e., independent of E or n). However, the assumptions and predictions of SFM have been called into question, in light of observed variation in offspring size within and among females (Kaplan and Cooper, 1984; Reznick and Yang, 1993), correlations between egg size and total reproductive effort (Fox and Czesak, 2000; Caley et al., 2001; Beck and Beck, 2005; Nasution et al., 2010), and trends of increasing or decreasing offspring size with maternal size or age (Landa, 1992; Fox and Czesak, 2000; Kamler, 2005; Marshall and Keough, 2008; Kindsvater et al., 2012). In addition, offspring size and offspring number are two life history traits that must be investigated jointly, as they are tightly linked through the size–number tradeoff (Roff, 2002). However, while Lack's (1954) model of most productive clutch size has been readily corrected to account for effects of parental quality and survival, and thus brought into accord with empirical data (Roff, 2002), the prediction of SFM, that offspring size should be independent of maternal phenotype, has been much more persistent, despite empirical evidence to the contrary and attempts to modify SFM by incorporating effects of maternal survival (Winkler and Wallin, 1987).

This nagging incongruity has led researchers down two paths to its resolution. The first is to consider some constraints on offspring size or number. For example, if offspring number is constrained, increased reproductive effort translates into larger offspring (Begon and Parker, 1986). Similarly, morphological constraint can lead to an increase in offspring size with maternal size (Marshall et al., 2010; Nasution et al., 2010). The second path is based on variation in the offspring size–performance curve (w in Eq. (1.1)) among females. For example, if offspring of larger females experience stronger sib competition (Parker and Begon, 1986), or if larger females secure better oviposition sites (Hendry et al., 2001). This second path also relates to studies that try to explain variation in offspring size within females or clutches (Kaplan and Cooper, 1984; Temme, 1986; McGinley et al., 1987; Kaplan and Cooper, 1988; Haig, 1990; Schultz, 1991) (e.g., due to bet-hedging, when faced with spatio-temporal environmental stochasticity).

However, recent work (Marshall et al., 2010; Kindsvater et al., 2012) casts doubt on morphological constraints, as a general explanation for the relationship between maternal size and offspring size. Similarly, as also pointed out by Jørgensen et al. (2011), explanations based on sib competition and other correlations between maternal phenotype and neonatal environment are taxon-specific (Hendry et al., 2001; Rollinson and Hutchings, 2010; Parker and Begon, 1986), and have proved to be problematic (Hendry and Day, 2003). Given how common and taxonomically widespread the positive correlation between female and offspring sizes is (e.g., insects, Fox and Czesak, 2000; marine invertebrates, Marshall and Keough, 2008; Marshall et al., 2010; Nasution et al., 2010; fish, Reznick and Yang, 1993; Rollinson and Hutchings, 2010; Jørgensen et al., 2011; Kindsvater et al., 2012; plants, Sakai and Harada, 2001; Sakai and Sakai, 2005), it is clear that some fundamental element is still missing from the picture.

Ultimately, offspring provisioning and performance and maternal fitness are cumulative quantities, and their analysis requires a dynamical approach. Many recent studies call for a better incorporation of physiological, developmental and behavioral processes, when addressing the question of size of progeny (Sinervo, 1999; Marshall and Keough, 2008; Uller et al., 2009; Segers and Taborsky, 2011), and the application of dynamical models to the optimal offspring size problem seems to have gained momentum recently (Sakai and Harada, 2001; Kiflawi, 2006; Jørgensen et al., 2011; Marshall et al., 2010; Kindsvater et al., 2010, 2011).

Most recently, two theories have emerged in the context of offspring-size–female-size correlations. First, the model by Jørgensen et al. (2011) suggests that both size-dependent mortality and growth determine the shape of the offspring size–performance curve (see also Sargent et al., 1987; Kiflawi, 2006). They apply their model to live-bearers, and conclude that offspring-size–female-size correlations may arise because prenatal offspring mortality is, in fact, equal to maternal mortality, which may be lower for larger females. This is a very simple, and thus compelling, explanation for the pattern. But, as discussed above for sib competition and similar explanations, it cannot be applied in general.

The second model, by Kindsvater et al. (2011), uses stochastic dynamic programming to describe the maternal energy budget during reproduction, and derive optimal patterns of variation in offspring size and number with maternal age and size. Their model provides a general conclusion that variation in offspring size with maternal size or age depends on survival costs experienced by the mother, which are directly connected with reproduction events. This is indeed a very general explanation that can be applied to many organisms.

In this paper, I complement such recent work, as well as earlier work, and show how the offspring-size–female-size problem is resolved by explicitly accounting for inefficiencies and overhead loss of maternal reserves during reproduction. I first explain the distinction between direct and overhead costs of reproduction. I then demonstrate that by explicitly accounting for such overhead material costs of reproduction, the three-way tradeoff among offspring size, offspring number and maternal survival to future reproduction events can now result in optimal covariation of offspring size with offspring number, total reproductive effort, and maternal phenotype. I also derive a detailed dynamic model of fitness components along the entire lifecycle (i.e., both offspring and maternal performance). In addition to being more biologically realistic, this detailed model allows me to mechanistically obtain predictions of how optimal offspring size and number should vary with the maternal phenotype and with aspects of the physical environment.

2. Generalizing Smith–Fretwell to account for overhead costs of reproduction

Before moving to derive a more detailed dynamic model for optimal offspring size and number (hereafter, OSN), it is worthwhile to examine a simpler model that can nonetheless capture some of the results of the dynamic model that I present further below, while its shortcomings provide the justification for the more detailed model.

Building upon the model of Winkler and Wallin (1987, in itself an extension of SFM to account for maternal survival), fitness is represented by $F(y_p, n) = nw(y_p) + S(Y - ny_p)$, where n and y_p are as in Eq. (1.1), and are the variables to be optimized, while S is the maternal survival that depends on maternal reserves, following the reproduction event. Therefore, Y is a model parameter that represents the amount of maternal reserves prior to reproduction, and the product ny_p represents the total amount of reserves expended in the production of n offspring of size y_p. (Note that I formulate this model in terms of OSN, n and y_p, rather than reproductive effort and offspring size, E and y_p, as Winkler and Wallin did. The two formulations are equivalent, but I find the formulation using n to be more convenient, especially when addressing the question of OSN covariation.)

Solving for the optimal offspring size and number, y_p^* and n^*, by setting $\partial F/\partial y_p$ and $\partial F/\partial n$ to zero, one reproduces the SFM expression for optimal offspring size (Eq. (1.1)). This conclusion was also reached by Winkler and Wallin (1987), i.e., explicitly including maternal survival in the model does not affect the optimal offspring size.

However, there is an implicit assumption in both SFM and Winkler and Wallin (1987), as well as in similar studies (see introduction), that reproductive effort (e.g., amount of maternal reserves expended in reproduction) relates solely to direct costs of producing a clutch of n offspring of size y_p. Therefore, total reproductive effort is given by the product ny_p. However, this is most probably never the case, as reproduction usually involves additional *overhead costs*: reproductive support structures (Kawano and Hara, 1995; e.g., flowers), external structures of eggs or seeds (e.g., egg capsules; Nasution et al., 2010), respiration costs during offspring provisioning (Sakai and Harada, 2001), and others (Harshman and Zera, 2007). As a result, reproductive effort converts to offspring mass with some (often substantial) overhead losses. By introducing such overhead costs on top of the direct costs (ny_p), the fitness function is now $F = nw(y_p) + S(Y - ny_p - y_q)$, where y_q represents such overhead costs, in terms of expended maternal reserves that do not translate into offspring mass. (Below, wherever I use the term 'overhead costs', it stands as a short form for 'overhead costs of reproduction', as explained in this paragraph.)

Given such overhead costs, I obtain the following expression for optimal offspring size:

$$\frac{w'(y_p)}{w(y_p)} - \frac{1 + n^{-1}\partial y_q/\partial y_p}{y_p + \partial y_q/\partial n} = 0. \tag{2.1}$$

As in Eq. (1.1), the first term in Eq. (2.1) relates to offspring performance. The second term arises from the three-way tradeoff between offspring size and number, which determine current reproduction, and future reproduction (maternal survival).

The important difference between the outcome of my model (Eq. (2.1)) and the outcome of SFM (Eq. (1.1)) is that this second term depends not only on offspring size, but also on offspring number (through the explicit appearance of n^{-1} in the numerator, and possible dependence of overhead costs, y_q, on OSN and clutch mass, ny_p). It is easy to verify that if overhead costs are constant (i.e., a fixed parameter) or depend solely on maternal phenotype (i.e., Y in this model), optimal offspring size still obeys Eq. (1.1) (i.e., Eq. (2.1) degenerates to Eq. (1.1)). However, if overhead costs depend also on offspring size and/or number, the resulting optimal offspring size may potentially vary with offspring number, reproductive effort and maternal phenotype, in sharp contrast to the predictions of SFM.

The expression given in Eq. (2.1) is quite general, and manages to demonstrate an effect of the tradeoff between current and future reproduction on optimal offspring size. However, from a biological perspective, this model still suffers from the same weaknesses that were previously mentioned for SFM (e.g., Bernardo, 1996; Marshall and Keough, 2008). Namely that the offspring performance function, w, is phenomenological, and therefore, the model can produce almost any pattern of variation in offspring size; there is no explicit mechanistic modeling of how offspring size translates to performance and fitness components; the model does not explicitly include dynamical aspects of growth and survivorship over the duration of the lifecycle; it does not explicitly address constraints that must operate on life-history traits; and finally, the model does not relate to other influential aspects of the offspring phenotype, such as breakdown of total offspring size into functional components. I now proceed to explore how patterns of variation in offspring size and number emerge within a dynamic model that addresses all of these shortcomings. Although some generality is lost, much biological realism is gained.

3. The dynamic life-history model and its analysis

3.1. Basic definitions

Following much recent modeling of individual growth (Kooijman et al., 1999; Kooijman, 2010; Müller and Nisbet, 2000; Filin, 2009, 2010), I divide the total body mass of an individual into a reversibly changing component (hereafter, reserves; denoted by y) and an irreversibly growing component (hereafter, structure; z). Therefore, organismal size is defined by a pair of values (y,z). Secondly, the dynamics of both size components includes random elements. Consequently, growth paths, $y(t)$ and $z(t)$ (t denotes time), are realizations of stochastic processes. Thirdly, I explicitly model risk of starvation, in addition to extrinsic causes of mortality. Specifically, if reserves, $y(t)$, drop to zero, the individual dies.

The model is size-based, i.e., life-history and developmental transitions are associated with crossing size thresholds. Much like starvation mortality that occurs if some lower boundary of reserves is reached, there is also an upper threshold, above which surplus reserves should be invested into structural growth (i.e., increasing z). This threshold value represents the point where the marginal value of accumulating reserves, thus reducing starvation risk, is equal to the marginal value of increasing structural mass (on the expense of reserves), due to benefits associated with larger structures, such as reduced extrinsic mortality or enhanced foraging ability. This upper threshold depends on the structural size already constructed (i.e., on $z(t)$), therefore, it defines a curve in the z–y coordinate space. Following my previous work (Filin, 2009), I hereafter refer to this curve as the *singular arc*, denoted by $\widehat{y}(z)$. The singular arc represents the optimal strategy for investment in (irreversible) structural growth, or an optimal rule for dividing total body mass between reversible reserves, y, and irreversible structure, z, as the organism grows (Filin, 2009).

Individual growth commences at offspring size, denoted by y_0 and z_0 (the size components of a newborn). Growth proceeds towards the adult phenotype along the singular arc, $\widehat{y}(z)$. Optimally, the offspring phenotype also lies on the singular arc, i.e., $y_0 = \widehat{y}(z_0)$. When producing a clutch of offspring, a gravid female invests all or part of its reserves in n propagules (eggs, seeds, etc.), each containing amount y_p of reserves. Hereafter, I refer to y_p as *propagule size* – it is the amount of reserves (e.g., yolk), required to produce an offspring of size $(y_0,\ z_0)$. Embryonic development transforms propagule reserves, y_p, into offspring phenotype, $(y_0,\ z_0)$. Therefore, the offspring size–number (hereafter, OSN) strategy may be interchangeably represented by either $(y_p,\ n)$ or $(z_0,\ n)$. I can express propagule size, y_p, as a function of offspring structural size, $y_p(z_0) = (1+\alpha)z_0 + \widehat{y}(z_0)$, where α is a fixed parameter that represents energy and material conversion costs while constructing structural mass from reserves (costs that are also involved in derivation of the singular arc; Filin, 2009). (Note that I assume here that costs of converting reserves into structure are similar for both embryonic development and postembryonic growth during the juvenile phase. Relaxing this assumption bears little consequence to the analyses and conclusions of this paper, as I demonstrate in Appendix C.)

Finally, I denote optimal values by z_0^*, y_p^* and n^*.

3.2. Fitness function and optimization objective

Based on optimality consideration (Filin, 2010), the lifecycle is divided into three phases, and the net reproductive rate (i.e., fitness; denoted by F) is the product of three corresponding factors: (i) $\widehat{S}(z_0, z_2)$, survival during the juvenile phase, when simultaneous growth of both structure and reserves occurs, from initial structural size, z_0, to structural size at maturity, z_2, and following the singular arc; (ii) $S(y_1, y_2|z_2)$, survival through a phase of reserves accumulation, in anticipation of reproduction, from $y = y_1 = \widehat{y}(z_2)$, to $y = y_2$ $(y_2 \geq y_1)$, during which only reserves accumulate (keeping z fixed at z_2); (iii) $R(y_p, n|y_2, z_2)$, a *terminal reward*, which relates to reproduction of n offspring with propagule size y_p, obtained once (y_2, z_2) is reached. The parameter y_2 denotes the reserves capacity of a gravid mother.

The optimization objective function is

$$\log\ F(z_0, n|z_2, y_2) = \log\ \widehat{S}(z_0, z_2) + \log\ S(y_1, y_2|z_2) + \log\ R(y_p, n|y_2, z_2)$$

(i.e., z_0 and n, serve as variables, while the maternal size components, z_2 and y_2, are parameters). (Note that fitness, F, is defined in terms of z_0 and n, while the terminal reward, R, is defined in terms of y_p and n; as noted in the previous section, these formulations are interchangeable.)

The optimization problem is then to derive the optimal offspring size (z_0^* or y_p^*) and number (n^*), given maternal structural size (z_2) and size of maternal reserves (y_2).

3.3. Survival components of fitness and the hazard density

The survival components of fitness, $\widehat{S}$ and S, are determined by *hazard density*, denoted by η (Filin, 2009). The hazard density measures mortality per unit of phenotypic change (in this case, unit gain in size), in an analogous fashion to hazard rate, which measures mortality per unit of time.

More formally, the hazard density is the hazard function of the survivorship function S that describes survival through gain in reserves mass, y, while keeping structural mass, z, fixed. Recalling that the dynamics of reserves are stochastic, the hazard density, η, combines in a single quantity both starvation mortality (if reserves become too low) and exposure to extrinsic hazards for variable durations (because growth is stochastic, and therefore, time to reach a given size or developmental milestone is a random variable). Consequently, the hazard density depends on the amount of reserves, y, which provide insurance against starvation, and potentially on other components of the individual phenotype (i.e., structural size, z), $\eta = \eta(y,\ z)$. In previous work (Filin, 2009, 2010), I derived a differential equation for η, from which its size-dependence can be readily obtained, as well as explicit expressions in some special cases (see Appendix B).

It is exactly the separation into reserves and structural size components that brings into light the distinction between starvation risk (dependent on size or state of the organism) and other mortality factors (that may be size-independent). This is one major biological insight that arises from taking a more detailed dynamic approach, compared to the generalized SFM that I explored in the previous section.

In turn, this size-dependence of the hazard density determines the singular arc, $\widehat{y}(z)$, which solves the equation $\partial\eta/\partial z = (1+\alpha)\partial\eta/\partial y$ (Filin, 2009). Given η and $\widehat{y}(z)$, survival through the juvenile phase of simultaneous growth in both reserves and structure, $\widehat{S}$, is determined via a hazard function, provided by the expression $(1+\alpha+\widehat{y}')\eta(y,z)$ (where $\widehat{y}' = d\widehat{y}/dz$; Appendix A; Filin, 2009).

3.4. The form of the terminal reward and overhead costs of reproduction

Propagule size, y_p, represents the direct material cost of providing raw materials for construction of the offspring body through embryonic development. However, as discussed earlier, reproduction involves additional overhead costs. Consequently, the total reproductive effort is given by $ny_p + y_q$, where y_q denotes such additional energetic costs of reproduction and offspring provisioning, on top of the direct material cost, ny_p. After each reproductive bout, maternal reserves are consequently depleted by amount $ny_p + y_q$, and the next reproductive bout occurs once the female has regained these lost reserves (this is similar to the concept of reproduction buffer in Kooijman, 2010).

The survival probability between consecutive reproductive events is given by $s = S(y_2 - ny_p - y_q, y_2|z_2)$. Consequently, the terminal reward is given by $R = n/(1-s)$ (where $(1-s)^{-1}$ is the expected lifetime number of clutches; i.e., a sum of a geometric series). Finally, overhead costs of reproduction, y_q, may depend on many factors, including maternal size, reproductive effort, clutch size, and propagule size, $y_q = y_q(y_p, n|y_2, z_2)$.

3.5. Optimal solution and numerical and graphical examples

A more explicit expression of the optimization objective (or fitness) function can now be written:

$$\log\ F(z_0, n|y_2, z_2) = -\int_{z_0}^{z_2} \eta(\widehat{y}, z)(1+\alpha+\widehat{y}')dz - \int_{y_1}^{y_2} \eta(y, z_2)\ dy + \log\ n - \log(1-s). \tag{3.1}$$

Optimal values, z_0^* and n^*, are provided by setting the partial derivatives of log F (with respect to z_0 and n) to zero. If the optimal solution lies on the boundary of the options set, i.e., on a constraint curve (e.g., $n=1$ for minimum clutch size), the two partial derivatives are combined using the proper Jacobian (Appendix A).

I can, therefore, now obtain the optimal offspring size and number, and observe how they may vary with the maternal phenotype (i.e., with the parameters that represent maternal structural size and amount of reserves: z_2 and y_2, respectively). In addition, through the hazard density, $\eta(y,z)$, I can mechanistically derive environmental effects on optimal OSN. Below, I explore these relationships.

Finally, in order to produce numerical results and graphs for the specific examples below, I followed expressions for calculating the singular arc, as described in Filin (2009, 2010). Numerical work and figure preparation were done in R v. 2.14.1 (R Core Team, 2012, libraries `deSolve`, `nleqslv`, `optimx`).

4. Results

Given the above definitions and expressions for fitness and its components, it is straightforward to derive the following expression for optimal offspring size (or propagule size), after setting the derivatives of log F to zero (Appendix A):

$$\eta(y_0, z_0) - \frac{1+n^{-1}\partial y_q/\partial y_p}{y_p + \partial y_q/\partial n} = 0. \tag{4.1}$$

As seen from this expression, the size-dependence of the hazard density, $\eta(y,z)$, also plays an important role in determining optimal offspring size.

Clearly, Eq. (4.1) is very similar to Eq. (2.1), the only difference being that the ratio w'/w has been replaced by the hazard density evaluated at the offspring phenotype. In both equations, this first term relates to offspring performance. In fact, despite the different fitness measures used in their derivation (finite rate of population increase, in the derivation of Eq. (2.1), following Winkler and Wallin, 1987; net reproductive rate, Eq. (3.1), in the derivation of Eq. (4.1)), it is possible to obtain Eq. (4.1) directly from Eq. (2.1), by substituting $w(y_p)=S(z_0,z_2)S(y_1,y_2|z_2)$ and accounting for the difference in the definition of offspring/propagule size.

In the next section I explore the ideal (SFM) case of no overhead costs of reproduction ($y_q=0$). The following section explores effects of overhead costs and their allometry. The two sections demonstrate how the detailed dynamic model that I developed above, in addition to predicting optimal OSN, also provides predictions regarding optimal offspring composition, and how such optimal values are affected by different environmental circumstances and by constraints that must apply on life-history traits.

4.1. Ideal case

The ideal case, i.e., $y_q=0$, is the scenario in which SFM is formulated. For semelparous lifecycles, all maternal reserves are expended during reproduction, i.e., $ny_p=y_2$. Subsequently, the mother dies of starvation and survival to future reproduction events (s in Eq. (3.1)) is not a consideration (i.e., $s=0$). Iteroparity is achieved by reducing the amount of reserves expended in each reproductive bout. Thus, the mother keeps some reserves that allow her to survive and reproduce another day ($s>0$). The reproductive effort can be reduced by reducing offspring size, offspring number, or both.

As in any optimization problem, the optimal value can lie either within the range of allowed values (options set) or on the boundary of that range. For offspring number, the constraint $\underline{n}\le n\le y_2/y_p$ applies, where $\underline{n}$ represents minimum offspring number. (Typically, $\underline{n}=1$, but other values may be considered; e.g., due to phylogenetic constraints, Itô and Iwasa, 1981). The semelparous case lies on the upper boundary, i.e., $n^*=y_2/y_p$, while the iteroparous case may lie either on the lower boundary, i.e., $n^*=\underline{n}$, or at an intermediate value. As long as it is optimal to reproduce with a clutch size that is larger than the minimal, i.e., $n^*>\underline{n}$, optimal offspring size is obtained by

$$\eta(y_0,z_0)-\frac{1}{y_p}=0 \tag{4.2}$$

(Eq. (4.1) with y_q set to zero). (As I demonstrate in Appendix A, this conclusion is true also for the semelparous case, which lies on the constraint $n=y_2/y_p$.) Although not immediately evident, Eq. (4.2) is basically the SFM expression (Eq. (1.1)), modified to account for additional effects of division into reserves and structure. As in SFM, optimal offspring size, predicted by Eq. (4.2), does not *directly* depend on maternal phenotype. It may still depend *indirectly*, e.g., through phenotype-dependent habitat preference, oviposition site selection, or other ecological alternatives that differ in quality. Such effects enter through the hazard density, $\eta(y,z)$, in a similar fashion to environmental effects on the offspring performance function w (Eq. (1.1)), as explored within the framework of SFM (e.g., McGinley et al., 1987; Hendry et al., 2001).

However, because the size-dependence of η is directly connected to mean growth rate, extrinsic mortality, and level of stochasticity in dynamics of reserves (Appendix B; Filin, 2009), I can mechanistically explore how environmental factors influence offspring size through any of these three pathways.

I demonstrate that in Fig. 1 for a concrete special version of the model (derived in Appendix B). I combine stochastic foraging models from risk-sensitive foraging theory (Stephens and Charnov, 1982) with recent work on allometry (size-dependence) of foraging rates (Brose, 2010; Thierry et al., 2011), and obtain an explicit expression for the hazard density, $\eta(y,z)$ in Eq. (4.2). The general conclusion arising from this analysis is that the two offspring size components (structure, z_0^*, and reserves, $y_0^*=\widehat{y}(z_0^*)$) respond differently to environmental variation. While optimal offspring structural size is more sensitive to how efficiently food intake translates to growth (growth efficiency; Fig. 1a), the reserves component is more sensitive to how stochastic food intake is (intake stochasticity; Fig. 1b). Similarly, Fig. 1c demonstrates that the optimal structural size of the offspring is far less sensitive to changes in food availability, compared to reserves, which decrease steeply as food availability increases.

On the other hand, if it is optimal to reproduce with the minimal clutch size, i.e., $n^*=\underline{n}$, optimal offspring size is obtained

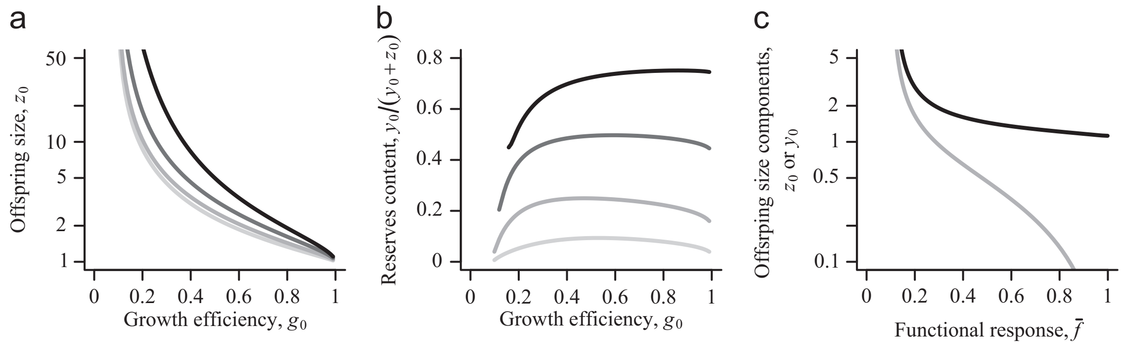

Fig. 1. Optimal size and body composition of offspring, as affected by parameters of the foraging environment. The hazard density and the singular arc depend on three dimensionless parameters that characterize the foraging environment, its interaction with the individual organism, and the scaling of intake rates and mortality risk with individual size, φ_0, which measures the stochasticity in food intake (lower φ_0 means higher intake stochasticity); g_0, which measures the efficiency of transforming food intake into net gain (or loss) of reserves; h_0, which relates to extrinsic hazards during foraging (e.g., predation risk). (a) Structural size of offspring decreases as growth efficiency, g_0, increases, but is also affected by intake stochasticity: $\varphi_0=0.1$ (black), $\varphi_0=1$ (dark gray), $\varphi_0=10$ (gray), $\varphi_0=100$ (light gray). A logarithmic scale is used for offspring size, z_0. The mother compensates for low growth efficiency (which asymptotically increases with body size towards the maximum value of g_0) by raising newborn growth efficiency through increased offspring size. (b) Offspring composition – the fraction of total offspring size that is reserves – varies slightly with growth efficiency, g_0, but is far more sensitive to intake stochasticity, φ_0 (color coding as in panel a). This is understandable given that starvation risk increases as the dynamics of reserves become more stochastic. (c) Variation in food availability, described through the functional response, $\bar{f}$, translates to covariation of g_0 and φ_0, and consequently to variation in both reserves (gray) and structural (black) size components of optimal offspring size. (For all panels, the value of the third parameter h_0 was fixed at 0.1. Size is measured in units of c, the threshold size that an individual must exceed in order to successfully capture and process food items. Values of optimal offspring size were obtained by solving Eq. (4.2) using the expression for η provided in Appendix B. Conversion costs of reserves to structure were set to zero, i.e., $\alpha=0$.)

from

$$\eta(y_0, z_0) - \frac{ns}{1-s}\eta\left(y_2 - \underline{n}y_p,\ z_2\right) = 0, \tag{4.3}$$

Recall that y_2 and z_2 are the maternal size components. Therefore, unlike Eqs. (1.1) and (4.2), Eq. (4.3) predicts that optimal offspring size should depend on maternal phenotype.

Denoting the solution of Eq. (4.2) by y_p^{SF} (i.e., the Smith–Fretwell optimal propagule size), it is fairly straightforward to demonstrate (Appendix A) that in the ideal case, either $y_p^* = y_p^{SF}$ (Eq. (4.2)) and $n^* > \underline{n}$, or $y_p^* < y_p^{SF}$ (Eq. (4.3)) and $n^* = \underline{n}$. As maternal reserves (y_2) decrease, offspring number declines first, and only when it has reached its minimum, reproductive effort is further reduced by lowering offspring size. Joint variation in both offspring size and number, therefore, cannot occur in the ideal case. Either offspring size remains fixed and offspring number increases with maternal size, or vice versa.

4.2. Effects of overhead costs and their allometry

In contrast to the predictions of the ideal case, joint variation in both offspring size and number with maternal phenotype is commonly observed. I, therefore, reintroduce overhead costs and explore Eq. (4.1). First, recall that such costs appear in Eqs. (2.1) and (4.1) through the terms $n^{-1}\partial y_q/\partial y_p$ and $\partial y_q/\partial n$. Consequently, overhead costs can affect optimal offspring size if they depend on propagule size, y_p, or clutch size, n. Fixed overhead costs, or costs that depend solely on maternal phenotype (y_2 and z_2) do not affect optimal offspring size, and the SFM expression (Eq. (4.2)) applies in such cases.

Secondly, given that y_p^{SF} (the SFM value of offspring size) is the solution of Eq. (4.2), and that the left-hand side of Eq. (4.1) represents the expression for $\partial \log F/\partial y_p$ at the optimal point (i.e., after applying the solution of $\partial \log F/\partial n = 0$; Appendix A), it is not difficult to verify that dependence of overhead costs on clutch size ($\partial y_q/\partial n > 0$) tends to increase the optimal offspring size (in comparison to the SFM value, y_p^{SF}), while dependence on propagule size ($\partial y_q/\partial y_p > 0$) tends to decrease the optimal offspring size. The optimal point along the OSN tradeoff shifts towards less and larger offspring, if there are costs associated with offspring number, or towards more and smaller offspring, if there are costs associated with offspring size. Generally, both types of costs operate, and the optimal OSN strategy depends on their relative magnitudes.

Thirdly, in Eq. (4.1), the term $\partial y_q/\partial y_p$ affects offspring size only through its product with n^{-1}. This means that the effect of overhead costs associated with propagule size tends to diminish as clutch size increases. This type of costs is, therefore, likely to cause optimal joint increase in both offspring size and number, as clearly demonstrated in Fig. 2. The biological rationale behind this effect is that as offspring number increases, such costs become less significant on a per-offspring basis, as they are divided among more offspring.

An exhaustive investigation of different allometric relationships of costs, with respect to propagule size and offspring number, is beyond the scope of this paper. I only briefly describe here some additional conclusions that can be easily verified using Eq. (4.1). First, overhead costs that depend solely on clutch mass (i.e., a function of the product ny_p) or are proportional to offspring number (i.e., can be written as $nq(y_p)$, where $q(y_p)$ is some function of propagule size), result in a single fixed optimal offspring size (although not necessarily the value predicted by SFM). This form of cost may occur when some extra material must be expended per propagule that does not directly participate in embryonic development and offspring construction (e.g., dispersal structures of seeds or egg casings).

However, costs that depend nonlinearly on offspring number (but still cannot be written as a function of clutch mass; e.g., of the form $n^a y_p^b$, where a and b are fixed powers and $a \neq 1, b$) may cause variation in optimal offspring size. Most notably, the effect of costs that depend solely on propagule size (a=0, $b > 0$) will decrease as offspring number increases in Eq. (4.1), leading to a strong trend of joint increase in both offspring size and number with maternal size (Fig. 2). Such costs may relate to maternal respiration costs during offspring production and provisioning. If most offspring are produced and provisioned more or less simultaneously, the mother would suffer such metabolic costs of offspring provisioning for a duration that strongly depends on propagule size, but not so much on offspring number (this is similar to the respiration costs considered by Sakai and Harada, 2001).

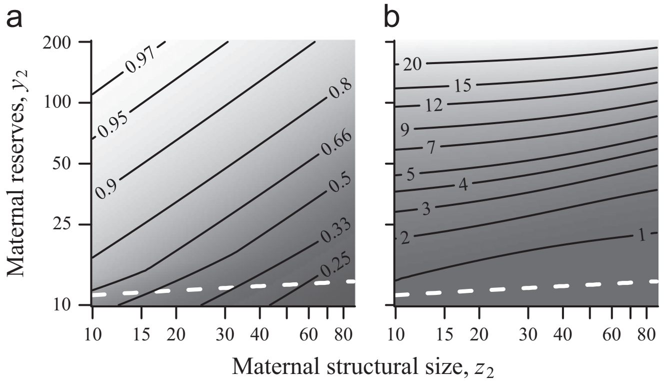

Fig. 2. Variation in optimal propagule size (a) and offspring number (b) with components of the maternal phenotype, z_2 and y_2 (note logarithmic scale of axes), for a case with overhead costs of reproduction that depend on propagule size and maternal structural size. (a) Optimal propagule size, y_p^*, increases with maternal reserves, y_2, and decreases with maternal structural size, z_2, because larger females suffer higher overhead costs of reproduction. However, structurally larger females usually possess higher reserves, possibly leading to an overall positive relationship between maternal and offspring sizes. Contour lines represent selected values of propagule size as fractions of the Smith–Fretwell value, y_p^{SF}. Clearly, propagule size still falls short of y_p^{SF} even for very high maternal reserves. For comparison, a curve for the ideal case is also drawn (white dashed), which separates propagule sizes that are below y_p^{SF} (i.e., given by Eq. (4.3)) from propagule sizes that are equal to y_p^{SF} (Eq. (4.2)) (below and above the curve, respectively). (b) Optimal offspring number, n^*, increases strongly with maternal reserves, and slightly decreases with maternal structural size (and overhead costs associated with it). Again, for comparison, the same ideal case curve is drawn, this time separating cases with $n^* = \underline{n}$ ($\underline{n} = 1$ for this figure) from those with $n^* > \underline{n}$ (below and above the curve, respectively). (The foraging parameters used are $g_0 = 0.35$, $\varphi_0 = 3$ and $h_0 = 0.1$, and overhead costs are given by $y_q = 0.1 z_2 y_p$. As in Fig. 1, size is measured in units of c, and $\alpha = 0$.).

When several kinds of costs occur in combination, variation in offspring size may result, even if not so when each type of cost is considered separately. For example, the sum of a cost that depends nonlinearly on clutch mass (e.g., inefficiency in converting maternal reserves into yolk in eggs) and a cost that is proportional to offspring number (e.g., dispersal structures of seeds). However, a cost that is linearly proportional to clutch mass (ny_p) will interact with other types of cost to reduce the range of variation in optimal offspring size (shifting optimal values towards the SFM value). Finally, such functional forms may include interaction with the maternal phenotype (e.g., if larger females incur higher or lower cost per given offspring and clutch sizes; Fig. 2), thus adding another source of variation in optimal offspring size with maternal phenotype.

5. Discussion

In their review on progeny size in arthropods, Fox and Czesak (2000) apply a domestic metaphor to argue that "…dividing resources among progeny may not be as simple as dividing a pie into pieces …". In this study, I indeed demonstrate that because organisms incur overhead energetic costs during reproduction, optimal offspring size should depend on maternal phenotype. Dividing total reproductive effort or costs of reproduction into direct costs (i.e., provisioning the propagule) and overhead costs (e.g., due to reproductive structures, inefficiencies in provisioning, elevated maternal respiration) is, therefore, crucial. But the consequences of this distinction to the offspring size–number problem have not been systematically explored before. Specifically, overhead costs that depend on propagule size, rather than on offspring number or clutch mass, are most effective in causing gradual increase in both offspring size and number with maternal size (Fig. 2). These conclusions are a main novel result of this work, and I have reached them under fairly general conditions (e.g., general forms of hazard density and overhead costs in Eqs. (4.1)–(4.3)).

In contrast, in the absence of such overhead costs , I obtain the ideal case of the Smith–Fretwell model, where I demonstrate that simultaneous variation in offspring size and number cannot be optimal. For such ideal lifecycles, either offspring size is fixed and offspring number increases with maternal size, which is the case of the Smith–Fretwell model, or offspring size varies with maternal phenotype, but offspring number is fixed at its minimum value, typically reproducing one offspring at a time (as previously found by Kozlowski, 1996). Therefore, it is essential to explicitly consider overhead and indirect costs of reproduction, separating them from the direct costs of providing raw material for embryonic development and offspring construction. Optimal variation in both offspring size and number with total reproductive effort and the maternal phenotype is the result of such inefficiencies in reproduction and offspring provisioning. Demonstrating this requirement, by contrasting with the ideal case, is a second important and novel contribution of this work.

I note that clutch mass is often used in empirical studies as a measure of reproductive effort (Roff, 2002; Caley et al., 2001; Nasution et al., 2010). As this study suggests, this procedure underestimates the full energetic expenditure during reproduction, which may not even exhibit simple proportionality to clutch mass. Allometry of overhead costs of reproduction has important consequences to optimal life-history, and therefore, need to be accounted for.

My model also includes several aspects of phenotypic dynamics that have rarely been considered together for models of optimal offspring size. Most notably, the separation of both offspring and maternal sizes to reserves and structure components. This facilitated a more detailed and realistic description of the phenotypic changes that occur throughout the entire lifecycle, from embryonic development, through juvenile growth, to recovery of maternal reserves between reproduction events. Moreover, this allowed for mechanistic derivation of the fitness components, rather than directly assuming phenomenological expressions for size-dependent survival and fecundity.

The separation into reserves and structure has also allowed me to demonstrate some novel results, with respect to the different paths by which foraging environment affects optimal offspring size, i.e., through mean intake rate, intake stochasticity, or external hazards, and by affecting either reserves or structural components of size (Fig. 1).

5.1. *Offspring size, quality and performance*

Within SFM (e.g., Smith and Fretwell, 1974; McGinley et al., 1987; Hendry et al., 2001), the only source of variability in optimal offspring size is through environmental lability of the offspring size–performance relationship ($w(z_0)$ in Eq. (1.1), or $\eta(y_0, z_0)$ in Eqs. (4.1)–(4.3)). I have similarly found that different environments lead to different optimal offspring sizes, as Fig. 1 demonstrates. In particular, Fig. 1c shows that offspring should get larger as food availability decreases. This prediction is not new (Fox and Czesak, 2000), and it relates to adaptive response to increased starvation risk or higher mortality due to longer development. However, by decomposing body size into its functional components (reserves and structure), I have additionally demonstrated that size components differ in their sensitivity to variation in food availability (Fig. 1). Indeed, it is often the amount of postembryonic yolk or fat reserves of newborns that vary in different environmental circumstances, while lean mass remains relatively unchanged (Goulden et al., 1987; Reznick and Yang, 1993; Rollinson and Hutchings, 2010). Similarly, this finding relates to aspects of offspring quality, other than total body size (i.e., egg or offspring composition; Fig. 1b, c), that also determine offspring performance (Bernardo, 1996).

The results of my model explain why larger offspring or yolk endowment are related to low or unpredictable food conditions (Reznick and Yang, 1993; Guinnee et al., 2004; Kamler, 2005), when the offspring may have to endure relatively long periods of starvation, or to prey, hosts or food items that are tougher or harder to handle (Fox and Czesak, 2000; Messina and Fox, 2001). Low food availability, high stochasticity in food intake, or low conversion efficiency of food intake into reserves, all result in larger progeny (Fig. 1), through which the mother can increase offspring growth efficiency and resistance to starvation, thus excluding too vulnerable stages (body sizes) from the lifecycle (the ‘safe harbor’ hypothesis of Shine, 1989). Moreover, parental care, group living and sociality can similarly reduce the stochasticity in intake rate (Caraco et al., 1995) and boost the growth efficiency experienced by offspring, which then allows to keep the optimal propagule size relatively small (Fig. 1). Therefore, direct material endowment, parental care and sociality act as different paths for improving offspring performance, and may operate in concert (Shine, 1989; Sargent et al., 1987; Jørgensen et al., 2011). Such effects may occur either through reducing external hazards experienced by offspring (Shine, 1989; Bonsall and Klug, 2011; Jørgensen et al., 2011), or through enhancing growth, and thus, reducing risk of starvation, as I described here. Both types of effects can be easily combined and explored mechanistically using the model that I have presented here.

5.2. *Maternal phenotype and offspring size*

Larger females typically produce larger offspring (Fox and Czesak, 2000; Marshall and Keough, 2008; Kamler, 2005; Nasution et al., 2010; Rollinson and Hutchings, 2010; Sargent et al., 1987; Kindsvater et al., 2012), though there are exceptions to this rule and the relationship is sometimes weak (Fox and Czesak, 2000; Rollinson and Hutchings, 2010; Kindsvater et al., 2013). Much of the residual variation may be due to variation in maternal reserves, irrespective of variation in structural size. Indeed, it is generally observed that offspring size is positively correlated with reproductive effort (total maternal expenditure during a reproductive bout, van der Sman et al., 2009; Nasution et al., 2010), is sensitive to maternal diet (Ford and Seigel, 2010), and decreases as maternal reserves are depleted in fish batch spawners and with age or clutch number in some insects (Kamler, 2005; Fox and Czesak, 2000; Jann and Ward, 1999).

These observations are consistent with predicted effects of overhead costs of reproduction and amount of maternal reserves, as I derived in this study (Fig. 2). Moreover, these theoretical findings are further supported by positive correlation between offspring size and clutch size (van der Sman et al., 2009; Jann and Ward, 1999), and by the generally observed concave down (saturating or parabolic) relationship between offspring size and maternal size (Kamler, 2005; Nasution et al., 2010; compare with Fig. 2a).

Empirical work showed that females provision offspring through a single pool of reserves that is accumulated over time (Reznick and Yang, 1993; Kooijman, 2010). This is consistent with the structure of my model. However, females that consistently experience low food rations usually produce relatively small offspring (Reznick and Yang, 1993), apparently inconsistent with the prediction of larger offspring under harsher conditions (discussed above). This incongruity between theory, which predicts larger offspring under food stress, and empirical observations, which consistently demonstrate that unfed or food stressed females lay smaller eggs (Reznick and Yang, 1993; Fox and Czesak, 2000; Ford and Seigel, 2010), is resolved by my theoretical findings. I demonstrate that although external environmental conditions favor larger offspring (Fig. 1), the maternal phenotype, i.e., low maternal reserves, counters this effect, favoring smaller offspring and maternal survival (Fig. 2).

5.3. *Estimation from empirical data*

I developed the general dynamic mode, as well as the specific version used for graphical examples, using biologically meaningful functions, parameters and variables, aiming at increasing realism (e.g., stochasticity and separation of size into structure and reserves). Consequently, components of fitness can be derived from underlying mechanistic processes (e.g., foraging and metabolic expenditure), in a similar fashion to how I applied empirically based parameterization of allometric foraging rates (Brose, 2010; Thierry et al., 2011) in deriving the graphical examples (Appendix B).

In addition, the hazard density (η in Eqs. (4.1)–(4.3)) can be statistically estimated using methods of survival (or failure-time) analysis (Kalbfleisch and Prentice, 2002), given data on growth and mortality of individuals (for examples of such data analyses, see Scharf et al., 2008; Rotkopf and Ovadia, 2014). Alternatively, given empirically derived allometric relationships for metabolic, foraging and mortality rates, the hazard density can be derived, using expressions provided in Appendix B and Filin (2009).

Accurately measuring overhead costs of reproduction (y_q) requires detailed metabolic studies. However, as a first approximation, the mass of reproductive structures that do not directly translate to offspring mass (flowers, egg casings, etc.) can be used. Additionally, maternal metabolic costs during egg provisioning can be estimated using published allometric relationships. For example, length of gestation period in mammals and incubation time in birds increase allometrically with both adult size and egg or offspring size (with an allometric exponent between 0.25 and 0.4; Kooijman, 2010, p. 308). Given that metabolic rate also scales allometrically with body size (exponent typically around 0.75; Reiss, 1989; Calder, 1996), the total maternal metabolic expenditure should increase steeply with both maternal and propagule sizes.

Although one must exercise caution in applying such interspecific (rather than intraspecific) allometric relationships in life-history models, such data is consistent with the form of overhead costs that I found to be most conductive to producing joint variation in offspring size and number (i.e., costs that increase with propagule and maternal sizes, but are less sensitive to offspring number). The significance of my work in this paper is that it provides the quantitative (mathematical) expressions for leveraging such empirically derived patterns and allometries of mechanistic individual-level processes (in many cases already measured or available from the literature), and translating them into quantitative predictions that can then be directly compared to actual patterns of variation in offspring size and number.

5.4. *Comparison with previous theory*

Assuming no variation in reproductive effort or maternal phenotype, the fundamental tradeoff between offspring size and number (Roff, 2002) dictates a negative relationship between these two life history traits. However, this naive prediction rarely fits observations because the tradeoff is usually swamped by other sources of variation (e.g., variation in female body size). In contrast, SFM predicts that offspring size should remain fixed, regardless of any variation in maternal size, offspring number or reproductive effort. This conclusion does not change even when explicitly incorporating the three-way tradeoff between offspring size, offspring number and maternal survival to future reproduction (Winkler and Wallin, 1987). In contrast, Kozlowski (1996) concluded that optimal reproduction of one offspring at a time (i.e., offspring number is fixed) occurs, and that optimal offspring size varies with maternal size.

Given that these models do not account for overhead costs of reproduction, it is now possible to understand, in light of the analyses of this paper, why they do not demonstrate any covariation between offspring size and number. I find in this previous work expressions for optimal offspring size that correspond to degenerate special cases of my expressions (Eqs. (4.2) and (4.3)), obtained by additionally omitting the distinction between reserves and structure, ignoring starvation mortality as a threshold response, and considering deterministic, rather than stochastic, individual growth (e.g., Eq. (6) of Kozlowski, 1996 and Eq. (14) of Sargent et al., 1987).

More recent papers take a more dynamical viewpoint of offspring provisioning and maternal performance, and incorporate an explicit description of size-dependent mortality along the juvenile phase of the lifecycle (Kiflawi, 2006; Jørgensen et al., 2011), risk of starvation under stochastic dynamics of individual state (Kindsvater et al., 2010, 2011), and respiration costs during offspring provisioning (Sakai and Harada, 2001, 2004, 2005). However, such studies do not provide a full dynamical description of the entire lifecycle, either abstracting the adult phase of the lifecycle (e.g, describing reproductive effort using a fixed parameter), or using the non-mechanistic SFM formulation of the size–performance curve to describe the juvenile phase.

Direct survival costs of reproduction that depend on offspring number or reproductive effort may also lead to covariation between offspring size and number (Kindsvater et al., 2011). Such survival costs (e.g., due to increased predation risk during oviposition) may exert a similar effect to overhead material costs of reproduction (ultimately, they both decrease maternal survival between reproduction events). In this paper, however, I derive this survival cost mechanistically, by following the dynamics of maternal reserves. This allows me to identify the sort of cost that is most effective in producing the pattern of increase in offspring size with maternal size – namely overhead energetic cost that depends on offspring or propagule size (rather than on offspring number or clutch mass). Such energetic cost may be interpreted as maternal metabolic expenditure during the period of offspring provisioning, which should last longer for larger offspring. However, in previous work (Sakai and Harada, 2001), inclusion of similar respiration costs does not produce, on its own, variation in optimal offspring size with maternal phenotype.

Perhaps the most important functional aspect of offspring size that is missing from the present work (as well as from all the previous work cited above) is its effect on dispersal ability of offspring. Especially in plants, marine invertebrates and many fish species, where the propagule or the newborn is the dispersal stage, optimal offspring size is bound to be affected and constrained by functional considerations of dispersal ability. In that context, Marshall and Keough (2008) have recently hypothesized that, in marine invertebrates, variation in egg size may translate to variation in offspring dispersal, and therefore, a female may control the dispersal of its offspring by varying egg size (e.g., offspring reserves). This hypothesis bears some resemblance to Carlquist's (1974) concept of ‘precinctiveness’, invoked to explain loss of dispersal ability in island plants, which is associated with evolutionary changes in seed size. Clearly, an incorporation of dispersal with other functional aspects of offspring size and number, as explored in this paper, would be beneficial (e.g., Sakai et al., 1998).

As a final thought, given that the organismal lifecycle must repeatedly pass through the bottleneck of the egg, seed or propagule stage (Bonner, 1974), offspring size is a trait that clearly lies at the interface between evolution and development. Besides lasting influence on survival and performance later in life (Segers and Taborsky, 2011; Marshall and Keough, 2008), offspring size and maternal provisioning may have dramatic effects over subsequent development, such as the expression of alternative morphological and behavioral phenotypes (Gross, 1991; Moczek, 1998). Similarly, population ecologists have studied how initial size differences among individuals may become exaggerated over time (Huss et al., 2007), and explored how such variation influences population dynamics (Grimm and Uchmanski, 2002; Filin and Ovadia, 2007). That offspring size should depend on maternal phenotype, as I demonstrate in this paper, may, therefore, have important consequences to population dynamics and to the expression alternative phenotypes, and consequently their appearance, fixation or loss in different populations (West-Eberhard, 2003).

Acknowledgments

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Appendix A. Derivation of expressions for optimal offspring size

Taking partial derivatives of the objective (fitness) function (Eq. (3.1)) with respect to offspring size and number,

$$\frac{\partial \log\ F}{\partial z_0} = (1+\alpha+\widehat{y}')\left[\eta_0 - \frac{\eta_r s}{1-s}\left(n+\frac{\partial y_q}{\partial y_p}\right)\right], \tag{A.1}$$

$$\frac{\partial \log\ F}{\partial n} = \frac{1}{n} - \frac{\eta_r s}{1-s}\left(y_p + \frac{\partial y_q}{\partial n}\right), \tag{A.2}$$

where $\widehat{y}'$ stands for $d\widehat{y}/dz$, the slope of the singular arc curve, evaluated at $z=z_0$, η_0 is the hazard density of a newborn, i.e., $\eta_0=\eta(y_0,z_0)$ (recall that $y_0=\widehat{y}(z_0)$), s is the maternal survival between consecutive reproduction events, $s=S(y_2-ny_p-y_q,y_2)$, or equivalently, $s=\exp\left(-\int_{y_2-ny_p-y_q}^{y_2}\eta(y,z_2)\,dy\right)$, η_r is the hazard density experienced by the mother immediately following reproduction, when its reserves are depleted, i.e., $\eta_r=\eta(y_2-ny_p-y_q,z_2)$, and finally, recall that y_q (which stands for energetic overhead costs of reproduction) is a function of propagule size and number, $y_q=y_q(y_p,n|z_2,y_2)$. By setting Eqs. (A.1) and (A.2) to zero, the general expression for optimal offspring size, Eq. (4.1), follows straightforwardly.

When the optimal solution lies on the boundaries of the options set, the partial derivatives must be combined, using the appropriate Jacobian, in order to produce an expression for optimal offspring size. When optimal offspring number is at its minimum value, i.e., $n^*=\underline{n}$, it can be treated as just another fixed parameter, and so the optimal offspring size is determined by setting $n=\underline{n}$ in Eq. (A.1), which results in Eq. (4.3) (for the case of $y_q=0$).

For the semelparous case, offspring size is again constrained, this time to follow $n=(y_2-y_q)/y_p$. Substituting x for y_p, $dn/dx=(d/dx)(y_2-y_q)/x=-(y_2-y_q)/x^2-(dy_q/dx)/x=n^{-1}x^{-1}-x^{-1}(\partial y_q/\partial y_p+(dn/dx)\partial y_q/\partial n)$, and so I obtain $dn/dx=-nx^{-1}(1+n^{-1}\partial y_q/\partial y_p)/(1+y_p^{-1}\partial y_q/\partial n)$. The equation for optimal offspring size becomes $d\log\ F/dx=J(\partial/\partial z_0,\ \partial/\partial n)^T\log\ F=0$, where J, the Jacobian, is given by $J=((1+\alpha+\widehat{y}')^{-1}, -nx^{-1}(1+n^{-1}\partial y_q/\partial y_p)/(1+y_p^{-1}\partial y_q/\partial n))$. This last expression expands to

$$\eta_0 - x^{-1}\frac{1+n^{-1}\partial y_q/\partial y_p}{1+y_p^{-1}\partial y_q/\partial n} - \frac{\eta_r s}{1-s} \times\left(n+\partial y_q/\partial y_p - n\frac{1+n^{-1}\partial y_q/\partial y_p}{1+y_p^{-1}\partial y_q/\partial n} - nx^{-1}\partial y_q/\partial n\frac{1+n^{-1}\partial y_q/\partial y_p}{1+y_p^{-1}\partial y_q/\partial n}\right)=0.$$

It is straightforward to verify that the last left-hand side term in the previous expression is identically zero, and so I again obtain Eq. (4.1) for offspring size.

For the case of no overhead costs of reproduction, i.e., $y_q=0$, the above analysis leads to the conclusion that as long as maternal reserves, y_2, are high, such that optimal offspring number is above its lower boundary, i.e. $n^*>\underline{n}$, optimal offspring size is fixed and obeys the SFM expression (Eq. (4.2)). Therefore, only when maternal reserves are low enough, such that $n^*=\underline{n}$, does offspring size decrease below the SFM value. By setting Eq. (A.1) to zero, one obtains $\eta_r s/(1-s)=\eta_0/n$, and substituting in Eq. (A.2), I obtain $\partial\log\ F/\partial n=n^{-1}(1-\eta_0 y_p)$. For the SFM value, $\eta_0 y_p=1$ (Eq. (4.2)), and consequently $\partial\log\ F/\partial n=0$, as indeed should occur for an optimal solution. However, when $n^*=\underline{n}$, the optimal solution lies on a boundary of the options set. Such an optimal solution requires $\partial\log\ F/\partial n<0$, which translates to $\eta_0 y_p>1$, and consequently to an optimal offspring (or propagule) size that is smaller than the corresponding SFM value.

Finally, I note that Eq. (A.1) may admit a second solution (after setting the derivative to zero), given by $(1+\alpha+\widehat{y}')=0$. However, such a solution cannot serve as a local maximum, because the expression $(1+\alpha+\widehat{y}')$ is always nonnegative. This is imposed by the requirement that $(1+\alpha+\widehat{y}')\eta$ is a hazard function (and, therefore, nonnegative; first integrand in Eq. (3.1)). In addition, this nonnegativity arises by the definition of the singular arc, $\widehat{y}(z)$, as an optimal rule for dividing total body mass between reserves and structure. That means that, as z grows (irreversibly), the sum $\widehat{y}+z$ also increases, which leads to the condition $\widehat{y}'>-1$, and consequently, to $(1+\alpha+\widehat{y}')>0$ (i.e., the expression is, in fact, strictly positive). If there was some value of z, for which $(1+\alpha+\widehat{y}')<0$, that would have resulted in two different pairs of values (y_l,z_l) and (y_k,z_k) with identical total body mass $(y_l+z_l=y_k+z_k)$, which both lie on the singular arc, but for which $z_l<z_k$. However, that would contradict the optimality requirement, as one would be able to construct a different and better-performing "singular arc", associated with higher fitness, by eliminating the pair with the lower structural mass (z_l), and directly reaching (y_k,z_k). That is why the original formulation (Filin, 2009) is, in fact, in terms of the singular arc as a function of total body mass. I can finally conclude that the only possible optimal solutions are those described in the main text.

Appendix B. The stochastic foraging submodel

The hazard density, $\eta(y,z)$, encapsulates within it both starvation mortality and extrinsic mortality. Starvation mortality occurs if reserves fall below a certain lower threshold value, the *starvation boundary*, denoted by a. For brevity, I hereafter, assume $a=0$, i.e., starvation mortality occurs when an individual has exhausted all of its reserves (but see Filin, 2009, 2010). Exogenous mortality is determined by the mortality rate, μ. The hazard density, η, is the stochastic-growth equivalent of the ratio μ/g, where g represents individual growth rate, used in deterministic models of optimal life history transitions (Werner and Gilliam, 1984; Ludwig and Rowe, 1990; Rowe and Ludwig, 1991), and also in the context of optimal offspring size (Kiflawi, 2006; Jørgensen et al., 2011).

When individual growth is stochastic, g represents the *mean* growth rate of reserves (Filin, 2009, 2010), i.e., $g\,dt$ is the mean gain in reserves over a short time increment, dt. Similarly, σ^2 represents the level of stochasticity in the growth dynamics of reserves, such that $\sigma^2\,dt$ is the variance of gain in reserves over a short time increment, dt. These definitions allow me to model the dynamics of reserves, $y(t)$, as a diffusion process, or, equivalently, as a solution of a stochastic differential equation (Filin, 2009).

Consequently, the size-dependence (y-dependence) of the hazard density can be obtained from

$$\frac{\partial\eta}{\partial y} = -\eta^2 - 2\frac{g}{\sigma^2}\eta + 2\frac{\mu}{\sigma^2}, \tag{B.1}$$

where g, σ^2, and μ may be functions of both y and z, i.e., growth and mortality may be size-dependent (Filin, 2009). In the simpler case where growth and mortality depend only on size of structures, i.e., depend only on z, a closed-form expression exists given by

$$\eta(y,z) = \chi \coth(\chi y) - \frac{g}{\sigma^2}, \tag{B.2}$$

where $\chi = \sqrt{(g/\sigma^2)^2 + 2\mu/\sigma^2}$ (Filin, 2009; recall that g, σ^2, μ and χ are functions of z). Eq. (B.2) demonstrates that the hazard density is high for low reserves, $\chi y \ll 1$, decreases monotonically as reserves increase, and approaches an asymptotic value, $\eta_\infty = \chi - g/\sigma^2 \geq 0$, when reserves are high, $\chi y \gg 1$. Thus, the hazard density, η, is inherently size-dependent.

Given renewal process formulation of foraging (Stephens and Charnov, 1982), the duration of a foraging cycle, τ, is the sum of searching time, τ_s, and handling time, τ_h. Each consumed food item translates into gain ξ in reserves mass. All food items are identical, therefore, τ_h and ξ do not vary from one foraging cycle to the next. Searching time τ_s is a random variable, varying according to an exponential distribution with mean $\overline{\tau_s}$. The *functional response*, $\overline{f}$, is the mean fraction of time spent handling food items, i.e., $\overline{f} = \tau_h/\overline{\tau}$, where $\overline{\tau} = \overline{\tau_s} + \tau_h$ is the mean duration of a foraging cycle. Using expressions for mean and variance of foraging gain (Stephens and Charnov, 1982), stochastic reserve dynamics can then be described by $g = \overline{f}\xi/\tau_h - b$ and $\sigma^2 = \overline{f}(1-\overline{f})^2\xi^2/\tau_h$. The additional parameter b represents metabolic power, i.e., consumption rate of reserves during foraging.

Metabolic and foraging rates scale with body size. For metabolic costs, $b = b_0 z$, i.e., linearly proportional to structural size (Kooijman, 2010; b_0, a fixed proportionality parameter). Handling and searching times typically decrease with predator:prey size ratio (at least for low and intermediate values of this ratio; Brose, 2010). In particular, there is a threshold size that an individual must exceed in order to successfully capture and process food items (Petchey et al., 2008; Thierry et al., 2011). Denoting this size threshold by c, I use the following allometric expression for handling time:

$$\tau_h(z) = \begin{cases} \dfrac{\tau_0}{(z/c)-1} & \text{for } z > c \\ +\infty & \text{for } z \leq c \end{cases} \tag{B.3}$$

To keep the foraging model relatively simple, I assume size-invariant mortality rate and functional response, i.e., μ and $\overline{f}$ are fixed parameters.

In the model analysis and graphical examples, I follow the dynamics of the nondimensional size variables z/c and y/c along the nondimensional time coordinate t/τ_0. Given these transformations,

$$\frac{g}{\sigma^2} = \varphi_0\left(1 + (g_0 - 1)\frac{(z/c)}{(z/c)-1}\right), \tag{B.4}$$

$$\frac{\mu}{\sigma^2} = h_0(1-g_0)\varphi_0\frac{1}{(z/c)-1}, \tag{B.5}$$

which can then be substituted into Eq. (B.2). These expressions depend on three dimensionless parameters: $\varphi_0 = [\xi(1-\overline{f})^2/c]^{-1}$, $g_0 = 1 - b_0\tau_0 c/\xi\overline{f}$ and $h_0 = \mu/b_0$ as explained in Fig. 1.

Appendix C. Structural growth during embryonic development

The derivations in the main text and Appendices A and B assume that the same overhead costs of structural growth apply both to embryonic development and to postembryonic growth during the juvenile phase of the lifecycle. Such conversion costs of reserves to structure are encapsulated in the fixed parameter α. Relaxing this assumption, I denote such costs during embryonic development by β, while α remains for postembryonic growth. Propagule size is now given by $y_p(z_0) = (1+\beta)z_0 + \widehat{y}(z_0)$, and Eq. (A.1) becomes

$$\frac{\partial \log\, F}{\partial z_0} = (1+\alpha+\widehat{y}')\eta_0 - (1+\beta+\widehat{y}')\frac{\eta_r s}{1-s}\left(n + \frac{\partial y_q}{\partial y_p}\right).$$

The expression for $\partial \log\, F/\partial n$, Eq. (A.2), remains unchanged.

This version of the model yields a solution for optimal offspring size that is only slightly different from the expressions provided in the main text. The general expression becomes

$$\eta(y_0, z_0) - \frac{1 + n^{-1}\partial y_q/\partial y_p}{y_p + \partial y_q/\partial n}\left(\frac{1+\beta+\widehat{y}'}{1+\alpha+\widehat{y}'}\right) = 0,$$

and the comparable expression to the SFM expression (Eq. (4.2)) is

$$\eta(y_0, z_0) - \frac{1}{y_p}\left(\frac{1+\beta+\widehat{y}'}{1+\alpha+\widehat{y}'}\right) = 0.$$

Moreover, because the ratio $((1+\beta+\widehat{y}')/(1+\alpha+\widehat{y}'))$ depends solely on z_0, specific optimal values are different for this version of the model, but the general conclusions of the paper remain unchanged, in particular, the conclusions regarding when offspring size does vary with maternal size, and when it does not.

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