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The Evolution of Offspring Size across Life-History Stages

Holly K. Kindsvater[1,*] **and Sarah P. Otto**[2]

1. Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada;   2. Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

ABSTRACT: Females vary in the size of offspring that they produce, often in a manner that depends on maternal age or stage. This is puzzling, given that offspring size is predicted to evolve to a single optimal value where the gain in fitness from being larger exactly offsets the fitness lost to the mother by producing fewer offspring. We used a stage-structured life-history model to determine the optimal offspring size for females in different stages. We found that optimal offspring size does not vary with maternal stage when offspring fitness depends only on its size and not on the stage of the mother. This negative result holds even with density dependence, when larger offspring compete better. However, a trade-off between offspring size and maternal survival affects the optimal offspring size. The future reproductive value of the female, coupled with the costs and benefits of offspring investment, drives the evolution of stage-dependent offspring size. If producing larger offspring is riskier for mothers, females produce smaller offspring when their reproductive value in the next time step is large relative to current reproductive prospects. These analyses provide a novel framework for understanding why offspring size varies in age- and stage-structured populations.

Keywords: egg size, seed size, fecundity, costs of reproduction, maternal effect, matrix model, age-structured populations.

Introduction

Variation in offspring size among mothers at different life-history stages has been widely documented in plants and animals (Clutton-Brock 1991; Venable 1992; Bernardo 1996; Fox and Czesak 2000; Leishman et al. 2000; Guinnee et al. 2007; Marshall and Uller 2007; Räsänen and Kruuk 2007; Benton et al. 2008; Marshall et al. 2010; Kindsvater et al. 2012). Yet why some mothers within a population make smaller offspring and others larger remains unclear. Indeed, classic life-history theory predicts that selection will minimize variation in offspring size, with evolution proceeding toward an optimal offspring size where the number of surviving offspring is maximized (Smith and Fretwell 1974; Lloyd 1987). This optimal size can differ among environments. As a consequence, several studies have focused on how maternal investment per offspring, including egg size, seed size, and parental care, varies with ecological factors, such as predation (Reznick and Endler 1982; Walsh and Reznick 2009), competition (Leishman et al. 2000; Allen et al. 2008; Lieps et al. 2013), mating system (Sargent et al. 1987; Petersson and Jarvi 2007; Harris and Uller 2009; Llorens et al. 2013; Kindsvater and Alonzo 2014), and dispersal status (Rees and Westoby 1997; Burgess et al. 2013). Offspring size or quality has been observed to vary with maternal age or size, however, even within an environment (Einum and Fleming 2000; Sakai and Harada 2001; Giron and Casas 2003; Berkeley et al. 2004; Guinnee et al. 2007; Rollinson and Hutchings 2011; Kindsvater et al. 2012; Zas et al. 2013). These stage-dependent differences can be quite dramatic. For example, 17-year-old black rockfish (*Sebastes melanops*) have a six-fold higher larval provisioning (oil glob size) than 5–6-year-old females (Berkeley et al. 2004).

Despite these empirical patterns, there are few theoretical explanations for stage- or age-dependent offspring size in the same environment. Most of these theories focus on the size of the mother. Parker and Begon (1986) investigated sibling competition and predicted that mothers of larger size, with more total resources to invest in reproduction, tend to invest in larger offspring rather than more offspring, to reduce density-dependent competition among siblings. Similarly, if there is a fixed clutch size, females with more resources will invest in larger offspring (Begon and Parker 1986). Jørgensen et al. (2011) noted that larger mothers may also be at lower risk of dying while rearing offspring; thus, the optimal rearing time and offspring size should scale with maternal size. Focusing instead on resource provisioning while rearing offspring, Sakai and Harada (2001) demonstrated that larger mothers produce larger (and fitter) offspring if they can provision at a faster rate than smaller mothers. Effectively, these models alter the offspring survival function in a manner that depends on maternal resource investment, shifting the optimal off-
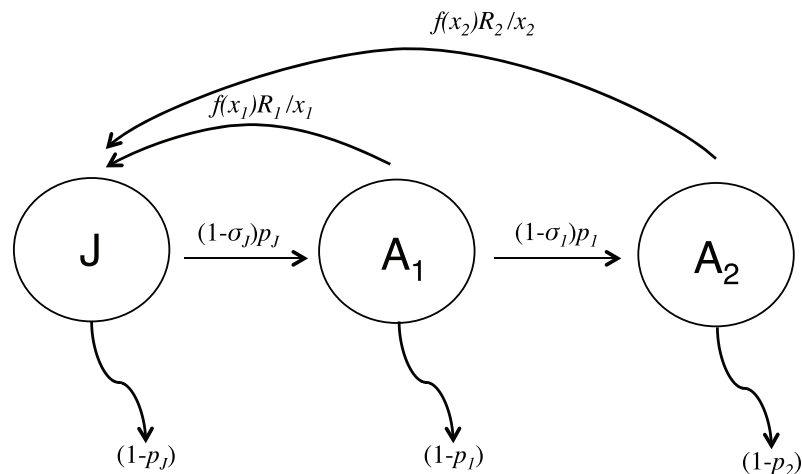
Figure 1: Diagram of the baseline stage-structured model. The proportion of individuals in each stage at equilibrium is determined by the fertility of females in each stage ($R_i f_i(x_i)/x_i$), stage-specific survival (p_i), and the probability of remaining in a given stage (σ_i). Individuals that reach stage A_2 remain in that stage until death. We assume that A_2 females are older and/or larger than A_1 females.

spring size predicted by Smith and Fretwell (1974; hereafter, the Smith-Fretwell optimum).

An alternative possibility is that the size or number of offspring may negatively impact maternal survival. These costs of reproduction will change the relative fitness benefits of current reproduction and future reproductive value (Williams 1966). These costs to maternal survival could arise through several mechanisms. For example, in both plants and animals, larger seeds or eggs are known to develop more slowly (Thorpe et al. 1984; Sargent et al. 1987; Shine 1989; Leishman et al. 2000; Zas et al. 2013). These larger progeny may reduce maternal fitness if females are more attractive to herbivores when bearing large progeny (Miles et al. 2000). Larger offspring could also reduce her ability to evade predators (Ghalambor et al. 2004), demand more resources than a mother would otherwise give during gestation (Haig 1993; Schrader and Travis 2009), or require extended postnatal care (Shine 1989; Kolm and Ahnesjo 2005; Klug et al. 2013). In addition, larger offspring could increase perinatal mortality of the mother (Wells et al. 2012).

The trade-off between offspring size and maternal survival was investigated in a previous numerical study using specific functional relationships between offspring number, size, and maternal survival (Kindsvater et al. 2011). This study found that with a fixed life span, younger females alter their reproductive strategies to increase survival more than older females, even when reproductive effort was held constant across ages. For example, if having a larger brood reduces female survival, younger mothers evolved to produce fewer offspring than older females. This result suggests that a female should alter the number

and/or size of her offspring in a manner that depends on her future reproductive value, but it was difficult to determine the exact nature of the relationship because the predictions were sensitive to the model parameters. Here, we build on this previous result by building a stage-structured model that allows us to make explicit the link between the reproductive value of mothers at different life-history stages (or ages) and optimal offspring size/number. We distinguish between changes in reproductive value that arise from increased reproductive effort with age (as in fish or trees) and those that arise from increased mortality with age (as in senescent organisms).

Our objective in this article is to clarify the conditions under which females at different life-history stages will produce different-sized offspring, incorporating both the possibility of a trade-off between offspring size and number and between offspring size and female survival. Throughout, we refer to per-offspring investment as offspring size, but we note that our models apply equally to other metrics of maternal investment in offspring (e.g., duration of parental care). We build an explicitly stage-dependent life-history model, using general functions to describe the trade-off between offspring size, x, and offspring fitness, $f_i(x)$, as well as between offspring size and maternal survival, $p_i(x)$, for females in stage i. We determine when these trade-offs cause mothers in different stages to have different optimal offspring sizes.

We also explore the effect of juvenile competition (among nonsiblings) on stage-dependent variation in offspring size. Comparing species or populations experiencing different levels of competition indicates that more severe competition among juveniles favors larger offspring,

both empirically (based on evidence from plants and animals: Marshall et al. 2006; Allen et al. 2008; Bashey et al. 2008; Leips et al. 2009, 2013; Llorens et al. 2013) and theoretically (Rees and Westoby 1997; Geritz et al. 1999). Whether such competition will also drive females of the same species but at different stages to produce offspring of different sizes is unclear.

We first present a baseline version of our model using a life-history model with three stages (juvenile and two adult stages) to understand the evolution of offspring size in the case where only offspring size and number trade off and when competition is absent. We then investigate how offspring size changes relative to this baseline when offspring size affects female survival. In an appendix, we show that equivalent results apply regardless of the number of life stages. Last, we ask how density-dependent competition affects the optimal offspring size for females in each stage.

Model

Baseline Case

We begin with a simple stage-structured model, where we track the number of females in each of three life-history stages: a juvenile stage, J; a first adult stage, A_1; and a second adult stage, A_2 (fig. 1). The two adult stages may represent female size, age, or reproductive stages. The life cycle consists of reproduction, followed by adult mortality, and finally transitions among life stages. A female adult in stage i produces a number of offspring, n_i, a proportion, $f_i(x_i)$, of which survive the mortality phase, where $f_i(x_i)$ is any positive function of offspring size, x_i, assuming a minimum viable investment ($x_i > 0$). We assume that the total amount of resources available to a female for reproduction in stage i is fixed at R_i and that offspring number trades off with offspring size, such that $n_i = R_i/x_i$. The females present in the previous time step survive the mortality phase with probability p_J for juveniles, p_1 for females in the first reproductive stage, and p_2 for females in the second reproductive stage (surviving females return to the second stage in the latter case). We initially assume that these survival probabilities are independent of the size of offspring produced. (Survival may depend on the total reproductive effort R_i expended in stage i, but this is held fixed and described by p_i.) Finally, surviving individuals remain in the same stage with probability σ_i, otherwise moving to the next stage (all newly produced young enter the juvenile stage).

This life-history model can be represented by a system of linear equations describing the number of females at each stage:

$$J(t + 1) = \sigma_J p_J J(t) + A_1(t)\frac{R_1 f_1(x_1)}{x_1}$$
$$+ A_2(t)\frac{R_2 f_2(x_2)}{x_2}, \tag{1a}$$

$$A_1(t + 1) = (1 - \sigma_J)p_J J(t) + \sigma_1 p_1 A_1(t), \tag{1b}$$

$$A_2(t + 1) = (1 - \sigma_1)p_1 A_1(t) + p_2 A_2(t). \tag{1c}$$

Over the long-term, the population will either grow or shrink, depending on the magnitude of the leading eigenvalue, λ, of equations (1) written in matrix form. We thereby determine the offspring size of mothers in stage i that will maximize this leading eigenvalue. Specifically, the leading eigenvalue is the largest root of the characteristic polynomial:

$$\lambda^3 - (\sigma_J p_J + \sigma_1 p_1 + p_2)\lambda^2$$

$$+ \lambda\left(\sigma_J p_J(\sigma_1 p_1 + p_2) + \sigma_1 p_1 p_2 - (1 - \sigma_J)p_J\frac{R_1 f_1(x_1)}{x_1}\right)$$

$$- \sigma_J p_J \sigma_1 p_1 p_2 + (1 - \sigma_J)p_J$$

$$\times \left(p_2\frac{R_1 f_1(x_1)}{x_1} - (1 - \sigma_1)p_1\frac{R_2 f_2(x_2)}{x_2}\right) = 0. \tag{2}$$

If second-stage females can reproduce, the population growth rate will be larger than that of an equivalent population that cannot reproduce in the second stage, so $\lambda > \lambda_{R_2=0}$. This expression can be rearranged to show that $\chi = \lambda^2 - (\sigma_J p_J + \sigma_1 p_1)\lambda - \sigma_J p_J \sigma_1 p_1 - (1 - \sigma_J)p_J R_1 f_1(x_1)/x_1$ must be positive, a convenient fact that we use below. All derivations are detailed in a supplementary Mathematica (ver. 8) package (supplementary material, available online as a zip file).[1] Parameters are summarized in table 1.

Differentiating equation (2) implicitly with respect to x_1, we find that

$$\frac{\partial\lambda}{\partial x_1} = \frac{(1 - \sigma_J)p_J(\lambda - p_2)}{\chi + (2\lambda - \sigma_J p_J - \sigma_1 p_1)(\lambda - p_2)}T_1^{SF}, \tag{3a}$$

where

$$T_i^{SF} = \frac{R_i}{x_i}\left(f_i'(x_i) - \frac{f_i(x_i)}{x_i}\right). \tag{3b}$$

The fraction in equation (3a) is positive within growing populations (because σ_i and p_i both lie between 0 and 1,

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[1] Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

Table 1: Summary of parameters

Parameter	Description
J	Number of individuals in the juvenile stage
A_1	Number of individuals in the first reproductive stage (small or young females)
A_2	Number of individuals in the second reproductive stage (large or old females)
i	Index referencing either first or second reproductive stage
R_i	Total reproductive effort in stage i
x_i	Size of offspring produced in stage i; could be egg size, seed size, parental care duration, or some other metric of maternal investment
n_i	Number of offspring produced in stage i; $n_i = R_i/x_i$
p_i	Proportion of females surviving from one stage to the next; can be p_J, p_1, or p_2; where offspring size trades off with maternal survival, p_i is the function $p_i(x_i)$
σ	Proportion of females remaining in a given stage; can be σ_J or σ_1
λ	The dominant eigenvalue of the linear system; represents the growth rate of a population or genotype
χ	A compound term in the denominator of the characteristic polynomial that is always positive
ψ_i	The average reproductive value in the next time step expected for a female currently in stage i
T_i^{SF}	Smith-Fretwell optimum; if T_i^{SFX}, it is the optimum incorporating the reproductive value in the next time step
v_i	The reproductive value of females in stage i (see the appendix)
M	Subscript denoting a mutant strategy
O_i	The offspring produced by females in stage i before competition among juveniles occurs
$h(a, b)$	Function describing the interaction between a pair of competitors, a and b
α	Determines the strength of density-dependent competition among offspring
κ_{ji}	Positive constant representing the benefits of reducing competition for a larger mutant offspring produced by females in stage i when competing with offspring from mothers in stage j
ρ	Shape parameter determining the shape of the offspring fitness curve $f(x)$ in the examples presented in figures 2–4

χ is positive, and $\lambda > 1$). Therefore, the sign of equation (3a) depends on T_1^{SF} (denoting the Smith-Fretwell term), which equals the derivative with respect to x_1 of the number of surviving offspring $n_1(x_1)f_1(x_1) = (R_1/x_1)f_1(x_1)$. It follows that first-stage females are selected to increase offspring size, x_1, as long as the fitness costs of fewer offspring, $n_1'(x_1)f_1(x_1)$ are weaker than the fitness benefits of larger offspring, $n_1(x_1)f_1'(x_1)$. This process will continue until the point $f_1'(x_1) = f_1(x_1)/x_1$, where the product $n_1(x_1)f_1(x_1)$ is maximized, or the point where the best strategy is to make a single large offspring, whichever occurs first. The analogous result holds for $d\lambda/dx_2$. Therefore, the baseline version of our model extends Smith and Fretwell (1974) and Lloyd (1987, eq. [4]) to stage-structured populations. This classic result is shown in figure 2, using the function

$$f(x) = \left[1 - \left(\frac{x_{max} - x}{x_{max} - x_{min}} \right)^{1/\rho} \right]^{\rho},$$

which varies in shape according to the parameter ρ. We use this function and parameters to illustrate the major findings of our model, but our analytical results do not rely on this specific function (see the supplementary material for other example relationships between offspring size and survival).

This baseline model clarifies that if the survival of off-spring depends only on the size of the offspring and not on the stage of the mother ($f(x)$ is the same for all females), then females will evolve to produce the same optimal-sized offspring (which occurs where $T_i^{SF} = 0$). That is, it is immaterial whether a mother's reproductive effort (R_i) or survival rate (p_i) rises or declines with age; her optimal offspring size will be the same. This model predicts stage-dependent variation in offspring size only when the fitness of the offspring of a given size depends on the mother's stage (i.e., $f_i(x_i)$ varies with female stage i). For example, if offspring of first-stage (say, small) females have very low fitness unless the offspring are large (as in the solid black curve in fig. 2A) while almost all offspring of large mothers survive (upper pale short-dashed curve), then small mothers will evolve to produce a single large offspring while large mothers will produce many smaller offspring (fig. 2B). See "Discussion" for examples where maternal stage may influence the fitness of offspring as a function of offspring size.

Trade-Offs between Female Survival and Per-Offspring Investment

We next investigate an additional trade-off affecting the evolution of offspring size, namely, when the survival rate of a mother depends on the size of offspring she produces.
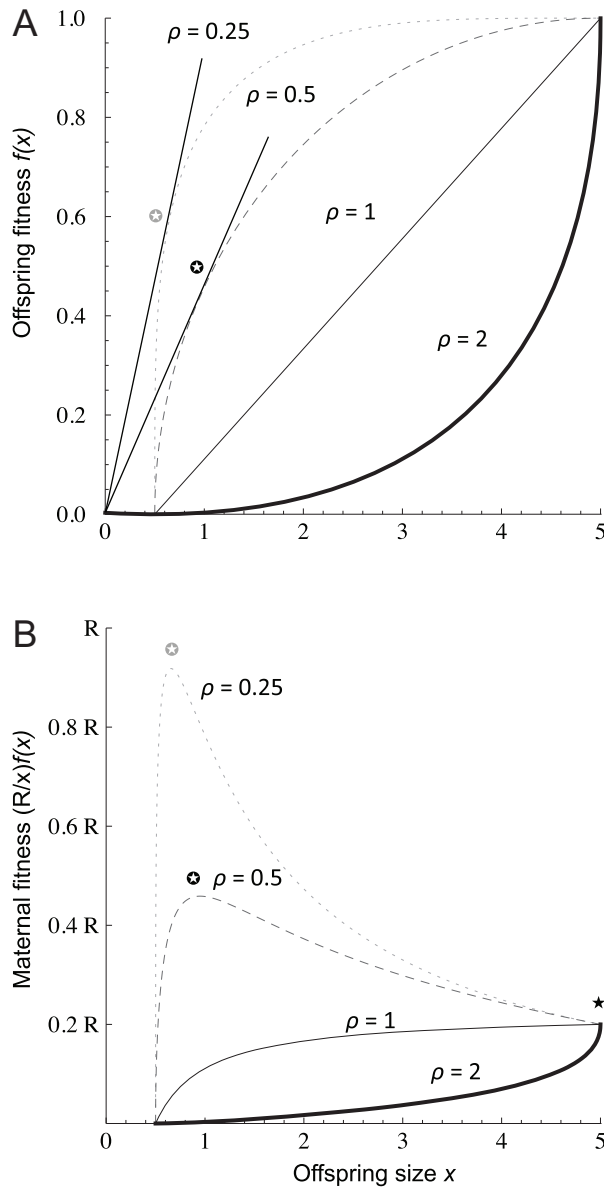
Figure 2: Possible relationships between survival and maternal investment per offspring (size). In *A*, example offspring fitness functions, $f_i(x_i)$, vary from convex (solid black curve) or linear (straight line) to concave (short- and long-dashed gray lines) according to a shape parameter ρ. Fitness is a positive function of investment between a minimum and maximum level, $x_{min} = 0.5$ and $x_{max} = 5$. In *B*, we show how the product of offspring number and offspring survival (maternal fitness) varies as a function of offspring size for the survival functions illustrated in *A*. Because of the trade-off between offspring size and number, maternal fitness is maximized at intermediate offspring sizes (stars in circles for short- and long-dashed gray lines) or at the maximum possible size (stars for solid black curves). For the concave cases, *A* also shows the optimal points (stars in circles) as those where the tangent (thin line, $f_i'(x_1)$) equals the rise over run, $f_i(x_1)/x_1$, a geometric interpretation of the Smith-Fretwell condition (eq. [3b]).

Alternatively, it might be the number of offspring produced, not their size, that impacts a mother's survival (e.g., if having more offspring is more likely to attract predators); this is, however, mathematically equivalent to having offspring size affect survival because we assume a fixed reproductive budget with $(n_i = R_i/x_i)$. To allow for any possible trade-off, we let the adult survival probability depend on the size of offspring produced and on the stage of the mother $p_i(x_i)$.

Equations (1b) and (1c) then become

$$A_1(t + 1) = (1 - \sigma_J)p_J J(t) + \sigma_1 p_1(x_1)A_1(t), \quad (4a)$$

$$A_2(t + 1) = (1 - \sigma_1)p_1(x_1)A_1(t) + A_2(t)p_2(x_2). \quad (4b)$$

To determine the optimal offspring size, we again solve for the characteristic polynomial and use implicit differentiation of the leading eigenvalue to determine how the growth rate of a population changes with x_i. For females in stage 1, we find that

$$\frac{d\lambda}{dx_1} = \frac{(1 - \sigma_J)p_J(\lambda - p_2(x_2))}{\chi + (2\lambda - \sigma_J p_J - \sigma_1 p_1(x_1))(\lambda - p_2(x_2))} T_1^{SFX},$$

$$(5a)$$

whose sign is determined by

$$T_i^{SFX} = \frac{R_i}{x_i}\left(f_i'(x_i) - \frac{f_i(x_i)}{x_1}\right) + \psi_i p_i'(x_i). \quad (5b)$$

The effect of changing the size of offspring produced by second-stage females yields a similar equation (supplementary material), whose sign depends on T_2^{SFX}. (T_i^{SFX} represents the Smith-Fretwell term, extended to include trade-offs between offspring size and maternal survival.)

According to equation (5b), the importance of the trade-off with maternal survival on the evolution of offspring size depends on the impact of producing larger offspring on maternal survival, $p_i'(x_i)$, multiplied by ψ_i. The term ψ_i can be shown to equal the average reproductive value of a surviving mother in the next time step:

$$\psi_1 = \sigma_1 v_1 + (1 - \sigma_1)v_2, \quad (6a)$$

$$\psi_2 = v_2, \quad (6b)$$

where

$$v_1 = \frac{\lambda - p_J \sigma_J}{p_J(1 - \sigma_J)}, \quad (7a)$$

$$v_2 = \frac{(R_2/x_2)f_2(x_2)}{\lambda - p_2(x_2)} \quad (7b)$$

are the reproductive values of adult females currently in adult stage 1 and 2, respectively. (Reproductive values are given by the left eigenvector associated with the leading

eigenvalue of the transition matrix. They describe the contribution of individuals in each stage to the long-term population growth, measured here relative to the juvenile class, and are never negative.)

Importantly, while equation (5a) was based on a three-stage model, the form of T_i^{SFX} remains the same regardless of the number of stages (see the appendix for equivalent results in a model with an arbitrary number of stages). Thus, the optimal offspring size for females in stage i is where $T_i^{\mathrm{SFX}} = 0$ is satisfied, even with an arbitrary number of stages. This result raises several important points. We expect the classic Smith-Fretwell optimum to be reached for any stage in which the female's survival does not depend on offspring size ($p_i'(x_i) = 0$) or if the female has no expected future reproductive success ($\psi_i = 0$). If the survival of a female can be increased substantially by making smaller offspring ($p_i'(x_i) < 0$), then the optimal offspring size will be shifted down from the Smith-Fretwell optimum (given by setting eqq. [3] to 0). However, even if females in all stages face the same survival trade-off (identical $p(x)$ functions) and offspring fitness depends only on offspring size and not maternal stage (identical $f(x)$ functions), the optimal offspring size will still vary among females of different stages as long as their expected reproductive values in the next time step differ, contrary to the baseline model (eq. [3b]). This is a novel result that we investigate next.

Assuming that maternal survival declines with offspring size ($p_i'(x_i) < 0$; opposite predictions hold if $p_i'(x_i) > 0$), females who are likely to have high reproductive value in the next time step relative to their current reproductive resources (high ψ_i relative to R_i) should evolve smaller and less costly offspring than females with a low reproductive potential (low ψ_i relative to R_i). This means that when reproductive effort (R_i) increases with age or stage (e.g., because of indeterminate growth), females will tend to have increasingly large offspring as they age, assuming female survival does not depend on her age. To unpack this further, in figure 3 we consider the effects of female survival and reproductive effort on reproductive value separately in the multistage version of our model (see the appendix).

First, all else being equal, if female survival $p_i(x_i)$ declines with stage (dark triangles, short- or long-dashed curves), causing her reproductive value to also decline with stage ("senescence," fig. 3A), younger females should produce smaller offspring to maximize their chances of surviving to reproduce again while young, when they will still have high reproductive value. By contrast, if female survival increases with stage, younger females should produce larger offspring, to maximize their current fitness, because young females are more likely to face low survival than older females in the subsequent time step. In the three-

stage model, this requires that stage 1 females can return to the first stage (otherwise, all females have identical future reproductive values). This is not necessary in the multistage model (fig. 3).

Second, predictions are more subtle when reproductive effort (R_i) varies with female stage (holding survival rates, $p_i(x_i)$, constant with i) because both future reproductive value ψ_i and current effort R_i will change, and it is their relative value that determines how much offspring size should depart from the Smith-Fretwell optimum (eqq. [5]). For example, in figure 3, when reproductive resources rise with age and survival does not depend on maternal age (gray short-dashed curves), young females have lower reproductive values than older females (fig. 3A). Nevertheless, young females still invest in smaller offspring than older females because it matters more to them that they survive to reproduce in the future, when their reproductive value will be higher (fig. 3C). More complex results are possible, however, when reproductive effort rises nonlinearly with age or when maternal survival and reproductive effort both vary with age (e.g., gray squares with dashed line in fig. 3). In particular, the optimal offspring size can decline and then rise with age if reproductive reserves R_i rise with age and $p_i(x_i)$ (survival after reproduction) does not depend on age. For example, if R_i rises slightly with age early in life and then increases rapidly later, females of intermediate age produce the smallest offspring because they are close (in age) to having massive reproductive potential. In other words, it behooves them most to survive (see the example in the supplementary material).

Finally, the shape of the offspring fitness function will affect the extent to which optimal offspring size in each stage differs from the Smith-Fretwell optimum even if we assume that the function $f(x)$ does not vary with maternal stage. If the fitness function rises rapidly and then flattens out (fig. 2, upper pale short-dashed curve), we expect only modest differences in optimal offspring size with maternal age because of the rapid decline in number of surviving offspring away from the optimum. Conversely, if the function is concave up (fig. 2, solid black curve), the largest possible offspring (a clutch size of 1) will evolve unless the survival costs to the female's survival are sufficiently strong. When $f(x_i)$ is linear or nearly so, we expect the largest deviations from the Smith and Fretwell (1974) predictions.

Density-Dependent Interactions among Juvenile Nonrelatives

The demographic model explored above is predicated on a growing population and ignores density-dependent processes that regulate population size. Here, we expand on
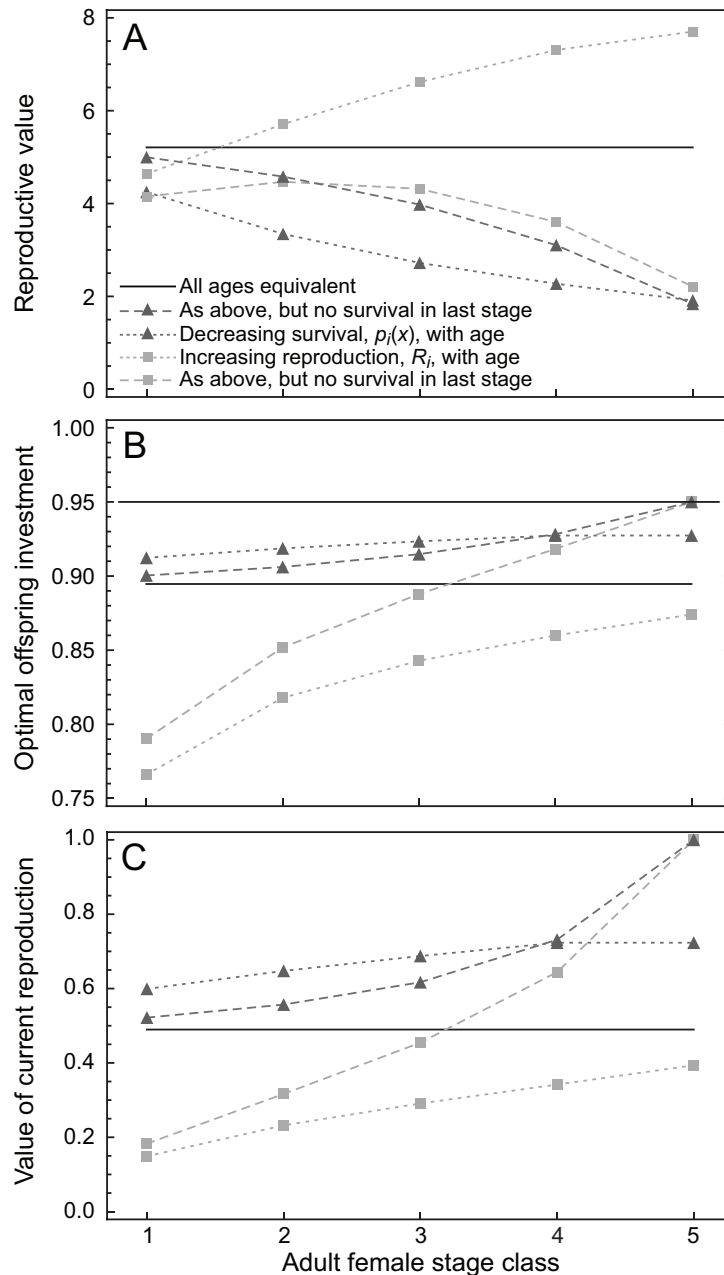
Figure 3: The evolution of offspring size in a multistage life cycle. We used the multistage demographic model (eq. [A1]) to determine the optimal investment in offspring for several mortality and reproduction schedules. Female survival in stage i declined with offspring investment (x_i) and with female stage (short-dashed triangle curves: $z = 0.2i$; all other curves: $z = 0$), according to the function $p_i = 0.9 - 0.04x_i - z_i$ (except black lines with $p_i = 0.9$). Female reproductive investment in class i was set to $R_i = 5$ except for the light gray curves (short and long dashed) where investment rose with age, for which $R_i = i$. Surviving females progressed to the next stage ($\sigma_i = 0$); females in the last stage were assumed to return to this class ($\sigma_5 = 1$) except for the long-dashed curves (dark triangles and light squares), where this stage was assumed to be terminal ($\sigma_5 = 0$). Consequently, reproductive values varied among female stages (A). For the cases explored, younger females always invested less in each offspring than older females (B), except when all females had equal reproductive resources and survival probabilities (black line at 0.89); offspring sizes are always less than or equal to the Smith-Fretwell optimum at 0.95 (longer black line), because of the trade-off between offspring size and female survival. The optimal size of offspring depends on a female's current reproductive resources relative to her reproductive value in the next time step, $R_i/(R_i + \psi_i)$ (see eq. [A4]), as in C; this fraction ranges from 0 (when females do not reproduce in the current stage) to 1 (when females have no future reproductive success). Other parameters are as follows: $p_1 = 0.25$; offspring fitness function $f(x)$ from figure 2 with $\rho = 0.5$; no competition.

the previous case to consider how adding density-dependent interactions among nonsiblings affects the optimal offspring size. Empirically, the strength of density-dependent competition experienced by juveniles is known to affect maternal allocation tactics (Allen et al. 2008; Lieps et al. 2013; Llorens et al. 2013), but there are few models predicting how density dependence affects the evolution of offspring size. For simplicity, we assume that density dependence acts only on the juvenile stage and that juveniles do not return to the juvenile stage ($\sigma_J = 0$, no seed bank); this latter assumption is relaxed in the supplementary material. Allowing the survival of newly produced offspring to depend on the total number of offspring in the population, equation (1a) then becomes

$$J(t + 1) = O_1[1 - \alpha (O_1 + O_2)]$$
$$+ O_2[1 - \alpha (O_1 + O_2)], \qquad (8)$$

where $O_i = A_i(t)(R_i/x_i)f_i(x_i)$ is the total number of surviving offspring produced by females in stage i before competition and α determines the strength of competition. We assume that this system reaches a stable equilibrium and then consider the dynamics of a rare mutant strategy, M, that alters the size of offspring produced:

$$J_M(t + 1) = O_{1M}[1 - \alpha (O_1 + O_2)]$$
$$+ O_{2M}[1 - \alpha (O_1 + O_2)], \qquad (9a)$$

$$A_{1M}(t + 1) = J_M(t)p_J + \sigma_1 A_{1M}(t)p_1, \qquad (9b)$$

$$A_{2M}(t + 1) = (1 - \sigma_1)A_{1M}(t)p_1 + A_{2M}(t)p_2. \qquad (9c)$$

While the density-dependent term $(1 - \alpha (O_1 + O_2))$ ought to include mutant offspring as well, their impact on competition has no qualitative effect while the mutant is rare. To facilitate the analysis, we further assume that the mutant propagule size is only slightly different from the resident ($x_{iM} = x_i + \delta x_i$, where δ is small). Performing a local stability analysis, we find that a mutant that increases offspring size can again invade only if T_i^{SFX} is positive (eq. [5b]), where the ψ_i functions equal the average reproductive values of surviving first- and second-stage females (eqq. [6]) for a population that is nearly constant in size (as when λ is near 1 in the previous density-independent model). Conveniently, this demonstrates that our previous results are not sensitive to the assumption of density independence.

Large offspring may, however, have greater competitive success, which is not included in equations (8) and (9). We next allow competition to depend on juvenile size via pairwise interactions between a competitor, a, and a focal individual, b, according to the competitive function $h(a, b)$. This function, which is analogous to the competition coefficient in the Lotka-Volterra model, allows for asymmetries

in the effect of one type on another (e.g., larger offspring may compete strongly for the resources of small offspring, but smaller individuals may exert little effect on large ones; see also Geritz et al. [1999] for a similar approach to modeling competition). Equation (8) then becomes

$$J(t + 1) = O_1[1 - \alpha (h(x_1, x_1)O_1 + h(x_2, x_1)O_2)]$$
$$+ O_2[1 - \alpha (h(x_1, x_2)O_1 + h(x_2, x_2)O_2)]$$
$$(10)$$

(previously, $h(a, b) = 1$). Equations (9) are similarly revised to account for size-dependent competition (details are provided in the supplementary material).

Again, we assume mutant propagule size is only slightly different from the resident ($x_{iM} = x_i + \delta x_i$) and perform a Taylor series of the leading eigenvalue resulting from a local stability analysis of the system. Mutant strategies that cause females in stage i to produce larger offspring spread when the following is positive:

$$\frac{R_i}{x_i}\left(f_i'(x_i) - \frac{f_i(x_i)}{x_1} - \kappa_{1i}\frac{\partial h(x_1, x_i)}{\partial x_i} - \kappa_{2i}\frac{\partial h(x_2, x_i)}{\partial x_i}\right) + \psi_i p_i'(x_i),$$
$$(11)$$

where ψ_i is similar to the reproductive value of surviving mothers in stage i but with additional density-dependent terms, $\partial h(x_j, x_i)/\partial x_i$ is the change in the competition function experienced by slightly larger mutant offspring produced by stage i mothers interacting with offspring produced by females in stage $j = 1$ or 2 ($\partial h(x_j, x_i)/\partial x_i$ is assumed to be negative to reflect the release from competition experienced by larger offspring), and κ_{ji} are positive constants that measure the benefits to a mother in stage i of reducing the competition experienced by her offspring:

$$\kappa_{ji} = f_i(x_i)\frac{\alpha O_j}{1 - \alpha (h(x_1, x_i)O_1 + h(x_2, x_i)O_2)}. \qquad (12)$$

See details in the supplementary material.

Competition among offspring essentially shifts the Smith-Fretwell optimum (term in parentheses in eq. [11]). That the κ_{ji} are positive (eq. [12]) implies that the contribution of competition to equation (11) will be positive when larger offspring compete better against smaller competitors ($\partial h(x_j, x_i)/\partial x_i > 0$). This is the mathematical manifestation of the idea that selection should favor increased offspring size in more competitive environments regardless of maternal stage, as found in many species (Hutchings 1991; Bashey 2008; Lieps et al. 2013).

While competition can drive differences in the optimal size of offspring for all females, it does not, by itself, drive differences in offspring size between female life stages (fig.
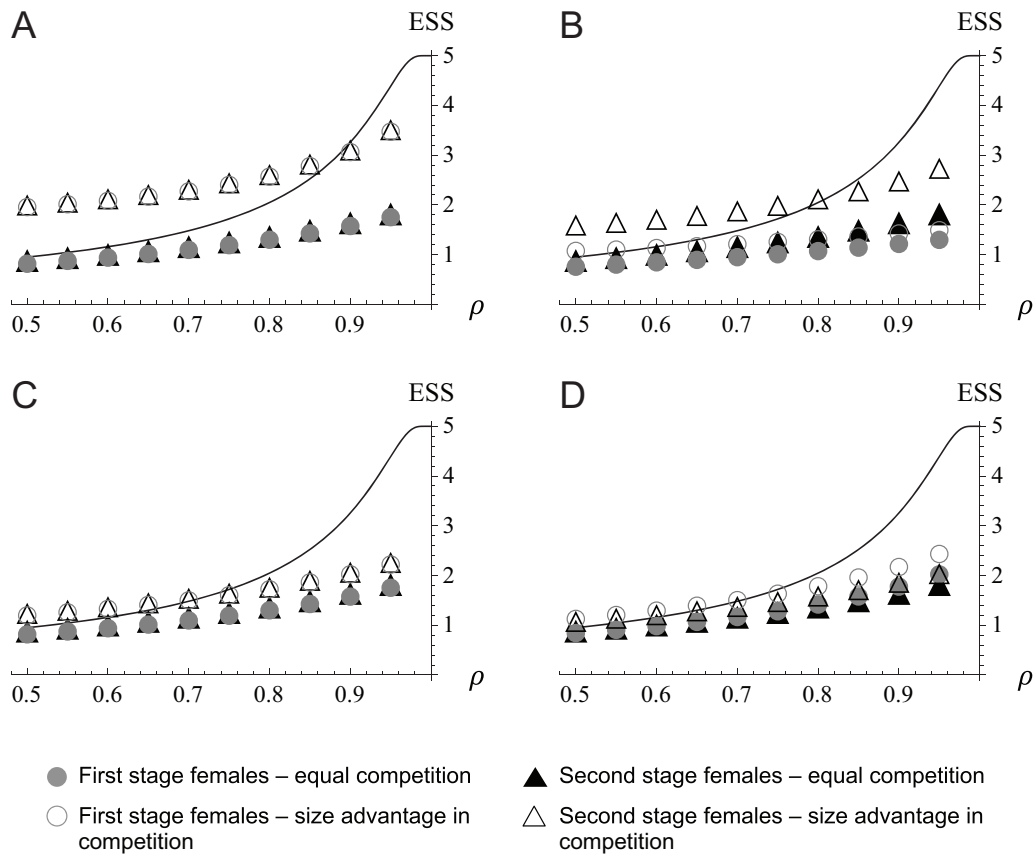
Figure 4: Interacting effects of the offspring fitness function, reproductive value, and density-dependent competition on the optimal offspring size. *A*, First consider the case where all individuals are equally competitive (filled symbols, $\alpha = 0.001$, $\kappa_{i,j} = 0$), with two adult stages (gray symbols are first-stage females; black symbols are second-stage females). Reproductive effort and survival are equal ($R_1 = R_2 = 5$ and $p_J = p_{0,1} = p_{0,2} = 0.8$, with $p_i(x) = p_{0,i} - 0.05x$), and all females move from one stage to the next ($\sigma_1 = \sigma_1 = 0$) so that future reproductive value (ψ_i) is equal for all females. Consequently, offspring size does not depend on maternal stage. The *X*-axis ρ impacts the shape of the offspring fitness function, as shown in figure 2. The solid black line is the evolutionarily stable strategy (ESS) given by the Smith-Fretwell optimum. *B*, Older females have greater reproductive effort ($R_1 = 2.5$ and $R_2 = 5$). In this case, future reproductive value relative to current reproductive resources (ψ_i/R_i) is highest for first-stage females (see fig. 3), so first-stage females (circles) have a smaller optimal offspring size than second-stage females (triangles). *C*, As in *A*, but first-stage females have lower survival ($p_{0,1} = 0.5$ and $p_{0,2} = 0.8$); nevertheless, the optimal offspring size does not differ among females because all surviving females enter the second stage (and have equal future reproductive value). *D*, Scenario identical to *C* except that some females remain in the first stage ($\sigma_1 = 0.7$), which increases the relative reproductive value of this stage so that first-stage females produce larger offspring. In all cases, when bigger offspring are more competitive (open symbols, $\alpha = 0.001$ and $\kappa_{i,j} = 0.1$), larger offspring are always optimal (open symbols are always above filled symbols). Size-dependent competition does not by itself cause offspring size to vary among females in different stages (*A*, *C*), although it can interact with differences in future reproductive value (*B*, *D*).

4*A*, 4*C*). To see this, consider equation (11) in the case where offspring fitness depends only on offspring size and not maternal stage ($f_i(x) = f(x)$ for all *i*) and where there is no offspring size/maternal survival trade-off ($p_i'(x_i) = 0$). In this case, in the absence of competition, all females would have the same optimal offspring size where $T_i^{SF} = 0$. If we then introduce competition into a population with no stage-dependent variation in offspring size ($x_1 = x_2 = x$), equation (11) becomes

$$\frac{R_i}{x_i}\left\{f'(x) - \frac{f(x)}{x} - f(x)\frac{\alpha(O_1 + O_2)}{1 - \alpha h(x,x)(O_1 + O_2)}\frac{\partial h(x,x_i)}{\partial x_i}\bigg|_{x_i = x}\right\}.$$

(13)

Competition therefore selects for smaller or larger offspring, depending on the sign of the term in braces. It will do so for all sizes equally, however, given that this term does not depend on maternal stage *i*.

The effects of size-dependent competition are more intricate when other factors cause optimal offspring sizes to differ among female stages, such as a trade-off with maternal survival (fig. 4; supplementary material). In this case, the extent and even the sign of departures from the Smith-Fretwell optimum size depend on the specific functional forms that underlie reproductive value (ψ_i) and competition ($h(a, b)$), as density dependence affects both of these terms (through ψ_i and κ_{ji}). Negative departures (smaller offspring) are expected when producing smaller offspring increases maternal survival ($p_i'(x_i) < 0$), but positive departures (larger offspring) are expected because of their competitive advantage. The magnitude of the departure also depends on the shape of the fitness function; for example, when ρ is very small, the Smith-Fretwell optimum is strongly constrained (fig. 2B), and the optimal offspring size approaches the Smith-Fretwell prediction (fig. 4; note that solid symbols lie nearer the black curve for small ρ).

Our results indicate that competition alone cannot explain stage-dependent offspring size, although it can modulate the impact of other factors, supporting the conclusion that "the importance of density-dependent selection as a major force [driving] the evolution of offspring size in natural populations remains arguable" (Schrader and Travis 2012, p. 1481).

Discussion

Our approach combines elements of existing theories of offspring size to examine these processes in a single model (Williams 1966; Smith and Fretwell 1974; Sargent et al. 1987; Sakai and Harada 2001; Charnov 2002; Jørgensen et al. 2011; Kindsvater et al. 2011). In doing so, we are able to gain insights into the evolution of offspring size that apply to plant and animal taxa with stage- or age-structured life histories. We show that stage-dependent variation in offspring size and number is predicted to arise primarily when the fitness of offspring depends on the maternal stage (i.e., females have different Smith-Fretwell optima) or when females pay survival costs that depend on offspring size. In the absence of these factors, neither differences in reproductive value, survival probability, nor competition will drive stage-dependent differences in offspring size.

The offspring fitness function $f(x)$ has been argued to be essential to understanding variability in offspring size x (Jørgensen et al. 2011; Rollinson and Hutchings 2013). Indeed, among-female differences in the offspring fitness function can explain stage-dependent variation in maternal investment per offspring. Whether such differences are likely to exist depends on the species in question and whether the stage of the mother matters to offspring survival above and beyond the offspring's own size, for example, because experience raising offspring or habitat quality depends on maternal stage. Even when offspring fitness depends only on offspring size ($f(x)$ the same for all females), the extent to which trade-offs between offspring size and maternal survival drive departures from the Smith-Fretwell optimum depends on the shape of $f(x)$. When the survival of offspring exhibits strong diminishing returns (as in the upper pale short-dashed curve in fig. 2A), the Smith-Fretwell optimum sits atop a very steep peak (fig. 2B), preventing much stage-dependent variation in offspring size.

While the focus of our analyses was a life-history model with three life stages, our main results apply to life histories with any number of stages or ages (appendix). In particular, if the fitness of offspring does not depend on maternal stage and if mothers survive at equal rates, regardless of the size of offspring they produce, then we expect all females to evolve to produce the same optimal-sized offspring, regardless of how reproductive effort and survival change with age. We identified two main explanations for why offspring size would depend on maternal stage.

The first explanation is that the fitness of an offspring of a given size depends on the stage of its mother ($f_i(x)$ varies among females). As mentioned in the introduction, a variety of mechanisms may underlie maternal stage–dependent differences in the expected fitness of offspring. Some of these mechanisms depend on differences among stages in the amount of resources available for reproduction, with females with more resources tending to produce larger broods that may be subject to more sibling competition (Parker and Begon 1986). Others may depend on the physiological capacity or experience of the mother. For example, larger females may be able to provision offspring more efficiently and thus make offspring of larger size and fitness for a given per-offspring investment (Sakai and Harada 2001, with x now representing the per-offspring investment). Alternatively, experienced females may be better able to nest in higher-quality territories and protect their brood (Einum and Fleming 2002), leading to higher fitness for offspring of all sizes. Larger or more experienced mothers might also be able to choose mates that better provision their young, which again leads to higher survival for a given maternal investment in each offspring, favoring smaller offspring (Kindsvater and Alonzo 2014).

The second explanation is that, if offspring investment is costly to maternal survival, selection will favor stage-dependent differences in offspring size because these costs will have different effects on younger versus older females, depending on their current versus future reproductive prospects. That producing eggs is costly to female survival is widely known, but whether it is more costly to produce larger eggs than to produce another offspring will vary

among species. For example, in some species larger seeds or eggs develop more slowly (Thorpe et al. 1984; Shine 1989; Llorens et al. 2013; Zas et al. 2013). These larger progeny may reduce maternal fitness if there are risks associated with larger seeds (e.g., increased attractiveness to herbivores) or with bearing offspring (e.g., reduced ability to evade predators).

When offspring size is linked to maternal survival, stage-dependent variation in offspring size arises naturally, even when this link is the same for all mothers ($p(x)$ is the same for all females). This is a subtle but important point. When the only trade-off involves offspring size and number, stage-dependent variation is not expected (unless this trade-off varies among females) because the product of this trade-off is always in the same stage: a surviving offspring. By contrast, when offspring size trades off with maternal survival, the product differs: a surviving female in a particular stage. Thus, as long as females have different reproductive values at different stages, the optimal offspring size will vary among females. Several biological mechanisms could lead to differences in reproductive value at different life stages (and therefore to differences in offspring sizes). First, in species with indeterminate growth, older females are expected to have higher reproductive effort because they are larger and can acquire more resources. This mechanism could potentially explain the increase in larval provisioning found in black rockfish (Berkeley et al. 2004) and swordtails (Kindsvater et al. 2012), as these fish species both have indeterminate growth and increasing reproductive effort with age. Second, older females might devote more resources to reproduction in species where older females are more experienced or able to secure a better mate, although paternal effects on offspring fitness might also affect the optimal offspring size in that case (Harris and Uller 2009; Kindsvater and Alonzo 2014). Finally, if older females have lower reproductive effort as a result of senescence, we predict that younger females will produce larger offspring than other females, as is seen in some insects (e.g., Giron and Casas 2003).

Our result that females can alleviate the effects of density-dependent competition by producing larger offspring is both intuitive and consistent with empirical work relating density to maternal investment (e.g., Bashey 2008; Leips et al. 2009). Females respond to density by adjusting maternal investment only if increasing investment improves offspring performance in competition. Furthermore, while density-dependent competition can select for larger offspring that are more competitive, it will tend to do so equally for all females, unless one of the factors discussed above already causes offspring size to depend on maternal age.

While our results are fairly general and are derived for the variety of functional relationships that might describe how offspring survival, maternal survival, and competition depend on offspring size, several caveats must be borne in mind. The first is that we have treated the evolution of offspring size as a continuous variable, when in fact the number of offspring has to be discrete. Holding the total reproductive resource budget (R_i) constant for each life stage, offspring size should then take on discrete values. This effect has been treated in previous models (e.g., Lloyd 1987; Kindsvater et al. 2010). Alternatively, the resource budget, offspring size, and offspring number may be considered as expectations of an underlying distribution, in which case having a noninteger expected number of offspring gains meaning. A second caveat is that we held the reproductive effort for a female in stage i constant, but R_i will itself evolve as offspring size evolves because of the attendant changes to offspring and maternal survival, which are known to affect the evolution of reproductive effort (Williams 1966; Stearns 1992). The net result of selection on offspring size and reproductive budget for females in different life-history stages has been investigated previously (Kindsvater et al. 2011) but deserves further attention.

An important implication of our study is that if offspring size (or number) does impact female survival, life-table data providing the specific mortality rates and reproductive effort of females at different life stages could be used to predict intrapopulation variation in offspring size. In particular, if having smaller offspring enhances maternal survival, a female is predicted to produce smaller offspring when her expected reproductive value in the next time step is large relative to her current reproductive resource allocation. It also suggests that offspring size and number will be most variable in species where mortality rates and reproductive effort differ across a female's life span. In particular, we expect variable offspring sizes to be most common in species where large individuals have disproportionately high fertility (such as many fish and trees) or in species that senesce. Future empirical studies that consider differences in female reproductive value and potential costs to females of producing larger offspring hold much promise for predicting when and why offspring size depends on a mother's life stage.

APPENDIX

Scaling Up to Multiple Stages or Ages

Here we generalize the stage-structured model to an arbitrary number of stages. Denoting stage-specific fecundity by $m_i = (R_i/x_i)f_i(x_i)$ and stage-specific survival by $p_i = p_i(x_i)$, equations (1) and (4) can be generalized to an arbitrary number of stages. In matrix form,

$$\mathbf{M} = \begin{pmatrix} \sigma_J p_J + m_J & m_1 & m_2 & \dots & m_\omega \\ (1-\sigma_J)p_J & \sigma_1 p_1 & 0 & \dots & 0 \\ 0 & (1-\sigma_1)p_1 & \sigma_2 p_2 & \dots & 0 \\ \dots & \dots & \dots & \dots & 0 \\ 0 & 0 & 0 & \dots & \sigma_\omega p_\omega \end{pmatrix}. \quad (A1)$$

Using classic results of matrix algebra (see Otto and Day 2007, box 10.2), the effect of a change in offspring size, x_i, on the growth rate of the population is given by

$$\frac{\partial \lambda}{\partial x_i} = \frac{\vec{v}(d\mathbf{M}/dx_i)\vec{u}}{\vec{v}\vec{u}}, \quad (A2)$$

where element u_i of the column vector $\vec{u}$ represents the fraction of the population at stage i at the stable age distribution, v_i of the row vector $\vec{v}$ represents the reproductive value of females of stage i, and $\vec{v}\vec{u}$ is the average reproductive value of the population. Taking the derivative of $\mathbf{M}$ and carrying out the matrix multiplication gives

$$\frac{\partial \lambda}{\partial x_i} = \frac{u_i}{\vec{v}\vec{u}}\left(v_J\frac{dm_i}{dx_i} + \sigma_i v_i \frac{dp_i}{dx_i} + (1-\sigma_i)v_{i+1}\frac{dp_i}{dx_i}\right). \quad (A3)$$

Dividing by v_J and carrying out the derivative of the fecundity term, we regain equations (5), generalized to an arbitrary number of stages, the sign of which depends on

$$T_i^{\text{SFX}} = \frac{R_i}{x_i}\left(f_i'(x_i) - \frac{f_i(x_i)}{x_i}\right) + \psi_i p_i'(x_i), \quad (A4)$$

where

$$\psi_i = \sigma_i \frac{v_i}{v_J} + (1-\sigma_i)\frac{v_{i+1}}{v_J}. \quad (A5)$$

The term ψ_i represents the expected reproductive value of a surviving female in the next time step relative to the reproductive value of a juvenile. The evolutionarily stable strategy (ESS) offspring size, x_i, is that which causes equation (A4) to equal 0.

Begon and Parker (1986) also examined a demographic model with multiple age classes, but their question differed in assuming a fixed total reproductive budget summed across the life span. Then, by assuming that an equal number of offspring is produced in each time step, they were able to determine the optimum offspring size at each age.

Thus, the inherent trade-off was very different (larger offspring now trading off with smaller offspring in the future). They also assumed that strategies that maximize lifetime reproductive success (the sum of m_i multiplied by the probability of surviving to stage i) would evolve, an assumption that holds true only for populations of constant size (Metz et al. 2008).

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