Evolutionary Ecology Research, 2010, **12**: 327–346

Effects of age- and state-dependent allocation on offspring size and number

Holly K. Kindsvater[1], Suzanne H. Alonzo[1], Marc Mangel[2]
and Michael B. Bonsall[3]

[1]Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut, USA,
[2]Center for Stock Assessment Research and Department of Applied Mathematics and Statistics,
University of California, Santa Cruz, California, USA and
[3]Department of Zoology, University of Oxford, Oxford, UK

ABSTRACT

Background: Empirical evidence from a range of taxa suggest age and condition can affect offspring size and number, but supporting theory is limited.

Question: How do age and condition influence offspring size and number?

Method: Dynamic state-dependent optimization.

Key assumptions: We model a capital-breeding life history where an individual matures with all reserves available for reproduction.

Results: We find that mortality risk and density-dependent offspring survival favour variation in allocation patterns. We predict that in species with sibling competition, females will reduce clutch size, but can compensate for fewer numbers of offspring with plasticity in offspring size and by reproducing several times over their life. In habitats with low mortality risk and some sibling competition, we predict an increased optimal offspring size in larger and older females.

Keywords: density dependence, inter-generational transfers, life-history plasticity, maternal age, maternal effect, state dependence.

INTRODUCTION

Theory aimed at predicting maternal allocation of resources to clutch size and offspring size has historically considered these traits independently. As a result, life-history predictions generally follow from two well-developed lines of thinking about allocation to reproductive traits. The first, the dynamics of offspring number, is the study of how limited resources of fixed size (eggs or larvae) are predicted to be distributed over time in response to ecological and physiological conditions. The formal study of the dynamics of offspring number

---

Correspondence: H.K. Kindsvater, Department of Ecology and Evolutionary Biology, Yale University, PO Box 208106, New Haven, CT 06520, USA. e-mail: holly.kindsvater@yale.edu

was initiated by David Lack in his classic work on birds (e.g. Lack, 1966; Klomp, 1970). The second line of thinking, the statics of offspring size, is the study of how limited resources (gonadal reserves) are distributed among offspring during a single reproductive event in a constant environment. A study by Smith and Fretwell (1974) predicted a single optimum for offspring size in a given environment for all females. These seminal papers provide the foundation for much of the subsequent work on offspring size and number (Begon and Parker, 1986; Parker and Begon, 1986; Stearns, 1992; Fox *et al.*, 2001). Parker and Begon (1986) and Begon and Parker (1986) take the first steps towards addressing clutch size and offspring size simultaneously. They show that variation in offspring size can be optimal when one considers density dependence among siblings in a clutch. With an age-dependent model, Begon and Parker (1986) show that if resources are depleted as females age, they should produce smaller eggs or smaller clutches.

While these theories explain some of the variation in reproductive behaviour across populations, we still do not have a theory that can explain the full complexity of observed female allocation strategies, especially across multiple habitats. In particular, increased offspring size in older females has been documented in insects (Fischer *et al.*, 2006; Plaistow *et al.*, 2007), fish (Reznick *et al.*, 1996; Berkeley *et al.*, 2004; Gagliano and McCormick, 2007; Donelson *et al.*, 2009), reptiles (Eitam *et al.*, 2005), birds (Vieyra *et al.*, 2009), and mammals (Broussard *et al.*, 2006), but cannot be explained by current theory. Several models have been proposed to explain this variation, including parent–offspring conflict or sibling competition (Parker and Begon, 1986; Roitberg and Mangel, 1993), and the non-independence of reproductive effort and offspring size (Winkler and Wallin, 1987; Caley *et al.*, 2001; Uller *et al.*, 2009). The latter idea suggests that considering the trade-off between current and future reproduction may be important for understanding empirical allocation patterns. Allocation to reproductive traits generally is considered as a series of independent events, in which a female allocates to reproductive effort and then partitions those resources among offspring size and number. However, in species in which these traits are related, understanding allocation patterns will be more complex. For example, if the quality of reproductive habitat affects current reproductive effort (e.g. Lalonde and Roitberg, 1994; Reiskind and Wilson, 2004), each female may allocate to size and number differently, depending on her expectation of future reproductive success. Thus habitat quality can affect size and number indirectly even if an analysis based on environmental factors [i.e. the graphical analysis of Smith and Fretwell (1974)] predicts a single offspring size.

We seek to integrate the classic models of clutch size and offspring size in a state- and age-dependent framework to address unexplained empirical complexity in female allocation patterns. To do so, we use stochastic dynamic programming (Houston *et al.*, 1988; Mangel and Clark, 1988; Mangel and Ludwig, 1992; Houston and McNamara, 1999; Clark and Mangel, 2000).

To some degree, our model confirms the general predictions of Parker and Begon (1986) and Begon and Parker (1986). However, their method uses Lagrange multipliers, and therefore is a constrained optimization. Our approach is more direct, and provides a more complete picture of how density-dependent offspring survival and adult mortality change allocation patterns when age and state vary. We show that by explicitly considering age- and state-dependent interactions, we can predict that females can compensate for density dependence if they have plasticity in offspring size, or if they can spread their reproduction over multiple events. Furthermore, we can extend our approach to address when complexity in reproductive habitat can lead to increased variability in both offspring size and number. Most significantly, our approach can predict increased offspring size and clutch size among older females.

CLASSIC ALLOCATION MODELS

To clarify our approach, we revisit the classic models of optimal allocation to clutch size and offspring size, which we will later integrate into our dynamic state-dependent modelling framework. The theory of the dynamics of offspring number (reviewed in Clark and Mangel, 2000, Ch. 4) assumes that a mother has a fixed number of reproductive propagules (e.g. eggs), all of the same initial size (though not necessarily final size) that can be distributed across time and space. In the simplest case, no new propagules are produced within a season and thus one denotes by $F(e, t)$ the accumulated reproductive success (fitness) from time t until the end of the reproductive season, given that the available number of propagules is e. We can assume the female experiences a variety of reproductive opportunities i (e.g. mates of differing quality or hosts of different types), characterized by an increment in accumulated fitness $f_i(c)$ when opportunity i is encountered and c propagules are used. The key assumption is that $f_i(c)$ is a hump-shaped function in c, so that there is an optimum number of propagules per reproductive event [this is Lack's original insight, which led to the 'Lack clutch size' (Lack, 1966)]. Imagine, for example, that a female can encounter at most one kind of opportunity i in each time period, and her probability of encountering opportunity i is given by λ_i. Thus $\Sigma_i \lambda_i$ is the chance of encountering *any* reproductive opportunity in a single period of time and $1 - \Sigma_i \lambda_i$ is the probability of no reproductive opportunity in a single period $(0 \le \Sigma_i \lambda_i \le 1)$. If μ is the per period rate of mortality, then the probability of surviving a single period is $\exp(-\mu)$ (Mangel, 2006) and $F(e, t)$ satisfies the canonical equation for allocation processes:

$$F(e, t) = \sum_i \lambda_i \max_c [f_i(c) + \exp^{-\mu} F(e - c, t + 1)] \tag{1}$$

with the condition in the final time step T, $F(e, t) = 0$. Equation (1) can be solved through backward iteration, and the process of solving it generates the optimal number, $c^*(i, e, t)$, of propagules (e.g. eggs) to invest in a reproductive opportunity when current reserves are e and opportunity i presents itself. This approach predicts shifts in clutch size as an individual ages. In general, clutch size is predicted to increase in older females as their opportunity for future fitness diminishes.

The classic theory explaining variation in offspring size (taken as a proxy for the level of investment) predicts a single optimum for a given environment (Smith and Fretwell, 1974; Parker and Begon, 1986; Roff, 1992; Stearns, 1992; Roff *et al.*, 2002). The predicted optimum applies to all females, regardless of their age or state. If offspring size (a proxy for maternal investment) is denoted by s, each female's fitness in each reproductive event is the product of the number of offspring produced, n, and the fitness from investment in each offspring, $f(s)$. Smith and Fretwell (1974) proposed $f(s)$ is a sigmoid function of maternal investment s, where $f(0) = 0$, and $f(s)$ saturates and has a point of inflection (Fig. 1 here). Thus, if at a certain moment a female has g reserves to invest in reproduction and produces offspring of size s, so that the number of offspring is $n = g/s$, the fitness associated with this reproductive event is

$$W(g, s) = \frac{g}{s} f(s). \tag{2}$$

Differentiating with respect to s and setting the derivative equal to 0 gives the condition for optimal investment (Smith and Fretwell, 1974),

$$f'(s) = \frac{f(s)}{s} \tag{3}$$

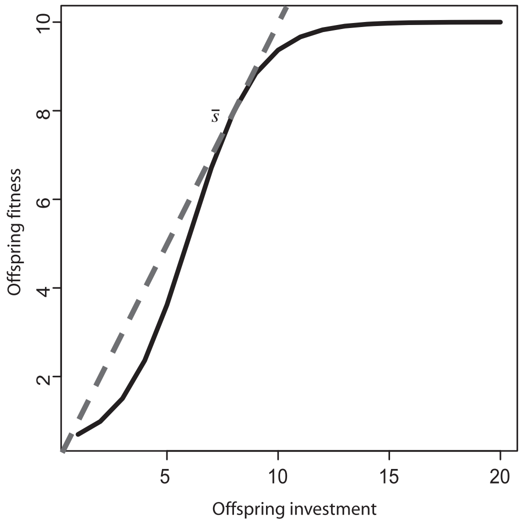


Fig. 1. The offspring fitness function. The dashed line is the tangent passing through the origin, which tells us the optimum in a Smith-Fretwell analysis, $\bar{s}$ (here, $\bar{s} = 8$). Parameters are summarized in Table 1. The fitness function is $f(s) = \phi\left(\frac{1 + m\exp(-s/v)}{1 + p\exp(-s/v)}\right)$, where ϕ, m, p, and v determine the shape of the saturating curve. For this function, $f'(s) = \frac{\phi\exp(s/v)(-m+p)}{(\exp(s/v)+p)^2 v}$ and $f''(s) = \frac{\phi\exp(s/v)(\exp(s/v)-p)(-m+p)}{(\exp(s/v)+p)^3 v^2}$. Following Smith and Fretwell (1974), we assume this function is determined by environmental factors and is independent of maternal state, G.

and by writing $f(s)/s = [f(s) - f(0)/s - 0]$ we see that the optimum number of offspring can be computed by a marginal value argument similar to the marginal value theorem for patch residence time (Smith and Fretwell, 1974; Mangel, 2006). Note that, as with the Lack clutch, maternal investment is predicted to be independent of reproductive reserves g.

In their work on variable reproductive effort, Begon and Parker (1986) take the first step towards integrating the theories of optimal offspring size and clutch size, and consider dynamic allocation to both traits. They address the impacts of plasticity in egg size *or* clutch size on lifetime maternal fitness. The authors predict that both egg and clutch size will decline as females age and reserves are depleted; survival probability from one reproductive event to the next determines the magnitude of the decrease in egg size. They also conclude that females with more energy available upon maturity will initially produce larger eggs; however, egg size is predicted to decrease with age.

In a complementary paper, Parker and Begon (1986) develop a model where clutch size and egg size are allowed to vary simultaneously. They examine the optimal allocation patterns for females with varying amounts of resource. They also address how density-dependent offspring survival (due to sibling competition) affects allocation. With no density dependence, their model supports the classic prediction of one optimal egg size (Smith and Fretwell, 1974). With density dependence, they conclude there will be no variation in clutch size, but offspring size will increase, especially in mothers with large amounts of resource.

Parker and Begon (1986) conclude that females with sequential reproductive events may have variable allocation to clutch size and egg size, depending on the survival probability between reproductive events and female resource status. Although this body of work is a strong approach for understanding why females may show state- and age-dependent maternal effects on allocation to clutch size and egg size, it does not include an age-dependent (dynamic) model of allocation with full plasticity in both offspring size and number. Furthermore, it does not provide an explanation for the empirical pattern of older females producing more, larger eggs than young females.

Motivated by this problem, we develop a fully plastic model of dynamic allocation of gonadal energy reserves (which we distinguish from somatic energy requirements) to offspring size and number over the reproductive life of a female. We assume that the female matures and has a series of opportunities to reproduce until a fixed endpoint, when there is no opportunity for future fitness (this is the maximum lifespan, although a female may die from external mortality before this point). At every reproductive event, we allow simultaneous allocation to offspring number and offspring size. Our framework predicts how a female allocates resources to current reproduction in each of the reproductive events in the female's life. We compare allocation patterns of females that mature with a range of initial energetic states. We then evaluate how female mortality risk, which determines her expectation of future reproductive opportunities, influences allocation patterns (cf. Williams, 1966). We then address how density-dependent effects on offspring fitness affect allocation. We can use this framework to determine the offspring phenotypes produced by females of varying age and condition, first in a single environment and then when the female can choose between two habitats. With this approach, we can address the hypothesis that interactions between female mortality, density-dependent offspring fitness, and heterogeneity in reproductive habitat can lead to increased allocation to offspring size and number.

THE FULL STATE- AND AGE-DEPENDENT FRAMEWORK

To address the effects of female age and state on the classic predictions for offspring size and number, we consider a female that matures with all energy reserves available for reproduction [i.e. a capital breeder (Stearns, 1992)]. We assume that she has the opportunity to reproduce multiple times until the end of the reproductive period, at which point there is no opportunity for further fitness. This assumption allows us to assess how allocation decisions affect the lifetime fitness of the female. We use a dynamic state-dependent life-history model to find the optimal allocation to offspring size and number for females in a range of states at every age. We assume that a female matures with a given set of resources g that must be used by age A. At every reproductive event, she can allocate resources to offspring size s, number n, or save them for future reproduction if age $a < A$. For simplicity, we assume that a female's risk of mortality is constant for all ages and is independent of her reproductive state. We explicitly model $f(s)$, the fitness a female gains from offspring investment (conditional on offspring survival) as a saturating function [Fig. 1, following Smith and Fretwell (1974)].

To link the theories of offspring number and investment, we next introduce within-clutch density dependence into the fitness a mother accrues from a reproductive event. Negative density dependence could arise due to increased competition for food (Lalonde and Roitberg, 1994; Eitam *et al.*, 2005) or reduced offspring survival with increased numbers (Klug *et al.*, 2006). In particular, we assume effects of density on offspring survival when n offspring are produced and captured by the per-capita survival $\exp(-\beta n)$, so that the increment in lifetime fitness from producing n offspring and investing s in each of them is $w(n, s) = n\exp(-\beta n)f(s)$. We assume that density dependence is unrelated to the size of offspring produced, leaving the mechanism for density dependence open.

Consider a female whose reproductive state at age a is $G(a)$. If in the current period she produces n offspring and invests s resource into each of them and she survives to the next reproductive opportunity, her reserves will be $G(a + 1) = G(a) - ns$. We define $W(g, a)$ as the maximum expected accumulated reproductive success between a and age A for a female with $G(a) = g$ resources, where the maximum is taken over offspring number and maternal investment. We assume no reproduction occurs at the maximum age, and thus $W(g, A) = 0$. If the female survives from one age to the next with probability $\exp(-\mu)$, then for previous ages

$$W(g, a) = \max_{n, s} [n\exp(-\beta n)\, f(s) + \exp(-\mu) W(g - ns, a + 1)]. \tag{4}$$

Note that if we define $V(n, s, g, a)$ as the maximum accumulated fitness from reproduction for a female whose reserves are $G(a) = g$ and who makes n offspring of size s, equation (4) becomes

$$W(g, a) = \max_{n, s}\ V(n, s, g, a). \tag{5}$$

We solve equation (4) backwards in time and use linear interpolation to minimize the effects of any discontinuities in the future fitness calculation (Clark and Mangel, 2000) that could arise in the numerical solutions. The solution of equation (4) generates optimal offspring number $n^*(g, a)$ and optimal offspring size $s^*(g, a)$ as a function of age and reproductive reserves.

We next address the case in which a female can choose to reproduce in a number of different habitats (e.g. Binckley and Resetarits, 2003) by generalizing equation (4). In such a case, the strength of density-dependent effects on offspring fitness and female mortality risk are both indexed by habitat (β_h and μ_h respectively). This generalization of equation (4) leads to

$$W(g, a) = \max_{n, s, h} [n\exp(-\beta_h n)\, f(s) + \exp(-\mu_h) W(g - na, a + 1)] \tag{6}$$

and we now compute $h^*(g, a)$ – the optimal habitat for reproduction when reproductive reserves at age a are g – in addition to solving for $n^*(g, a)$ and $s^*(g, a)$. Note that whether we use equation (4) or equation (6), the prediction of optimal number and investment depends on the strength of density dependence, the mortality rate, maximum age, and the parameters that characterize offspring fitness $f(s)$.

Once we have computed the optimal offspring number $n^*(g, a)$ and investment $s^*(g, a)$ as a function of reserves and age, we compare the realized life-history patterns of females that reach sexual maturity in a range of states. Each female allocates according to the optimal behaviour matrix generated by equation (4). This will allow us to compare the allocation to offspring size and number for females at each age, assuming that the female's assessment of the strength of density dependence and mortality risk does not change over her life.

These analyses show us when the classic models for clutch size and offspring size will hold, and when we expect to see variation as a result of female age, state, and their interaction with density-dependent offspring fitness and adult mortality risk. We conduct sensitivity analyses in which we vary the maximum age A and the ranges of energetic reserves, maximum offspring number, and maximum offspring size. For simplicity, we use only one offspring fitness function (Fig. 1) for all results and analyses. Altering the offspring fitness curve by changing the parameter values did not qualitatively change our predictions.

Table 1. Summary of the model parameters

Parameter	Value	Description
ϕ	10	Shape parameters in the offspring fitness function in Fig. 1. Together they determine the steepness of the curve, the inflection point, and the asymptote
M	1.5	
P	55	
v	2	
s	8	Optimal offspring size predicted by a Smith-Fretwell analysis
β	0–1	Shape parameter in the density-dependent term of the offspring fitness function
μ	0–1	Shape parameter determining mortality risk in each time period
G, g	1–300	Energetic reserves, equivalent to the female's state at age
A, a	1–20	Female age; A is the maximum length of the reproductive period, after which there is no opportunity for reproduction
n	1–40	The number of progeny the females can make in each reproductive bout; the optimum number is n^*
s	1–50	Offspring size or per-offspring effort; the optimum size is s^*
h	—	Habitat type: when a female is given a choice of reproducing in two habitats of varying density dependence and mortality risk; the optimum habitat is h^*
W	—	Fitness associated with a reproductive event at a given age and state
V	—	Maximum accumulated fitness

Based on the parameters in Table 1, a Smith-Fretwell analysis of Fig. 1 predicts an optimal offspring size $\bar{s} = 8$ units of resource. This value provides a baseline expectation for offspring size. Given our aim is to explore potential mechanisms explaining empirical patterns of variable offspring size and number, comparing this prediction with the outcome of the dynamic model is a clear way to understand when we expect to see state- and age-dependent variation in these traits.

RESULTS

The static effects of density dependence: end-of-life or high-mortality situations

To confirm how density dependence affects allocation within a single reproductive event, it is useful to consider the heuristic case of equation (4) when $a = A - 1$ or μ is large, such that future fitness is essentially 0. In this limiting case, the reproducing female with reproductive reserves g obtains fitness $w(g, s) = (g/s)f(s)\exp(-\beta g/s)$ by producing g/s offspring and investing s units of resource in each one. The optimality condition for offspring investment is then

$$f'(s) = \frac{f(s)}{s}\left[1 - \frac{\beta g}{s}\right]. \tag{7}$$

When $\beta = 0$, we recover the Smith-Fretwell condition (the solution to equation 3). If $\beta > 0$ (introducing density dependence), the optimal investment in offspring increases. The magnitude of the increase depends upon the female's reproductive reserves. To approximate this effect, we use $\bar{s}$ to denote the solution of the Smith-Fretwell condition (equation 3), so that $f'(\bar{s}) = f(\bar{s})/\bar{s}$. We then assume that β is small, such that the s^* predicted by equation (4) can be approximated as $s \approx \bar{s} + k\beta + o(\beta)$ where k is a constant (to be determined) and $o(\beta)$ denotes terms that are higher order in β (Mangel, 2006). If we then multiply both sides of equation (4) by s^2, substitute the approximation for s into the result, and collect terms according to the power of β, we find that, $k = gf(\bar{s})/\,|f''(\bar{s})|$, where $f''(\bar{s})$ is the curvature of the investment–offspring fitness curve at the Smith-Fretwell optimum. We are thus able to assess how female allocation to offspring size is affected by within-clutch density dependence when the female uses all her energetic reserves for current reproduction and does not save anything for future reproductive events.

Dynamic allocation to offspring size and number increases maternal fitness

We model the fitness from putting n offspring into a single reproductive event as $n\exp(-\beta n)$; the maximization of this function gives us the Lack clutch for that single event. By setting the derivative of this function to 0 and solving for n we find that the Lack clutch for a given value of β is $1/\beta$. As above, the classic prediction for optimal offspring size without density dependence is $\bar{s}$. Our dynamic state-dependent framework thus allows us to compute the fitness of life-history strategies with varying plasticity in offspring size and number. In Fig. 2, we calculate the lifetime expected fitness upon maturity for females with a range of initial energetic reserves G. As a baseline, we find the fitness for females with no opportunity for plastic allocation: they must make $1/\beta$ offspring of size $\bar{s}$. For these females, no fitness is

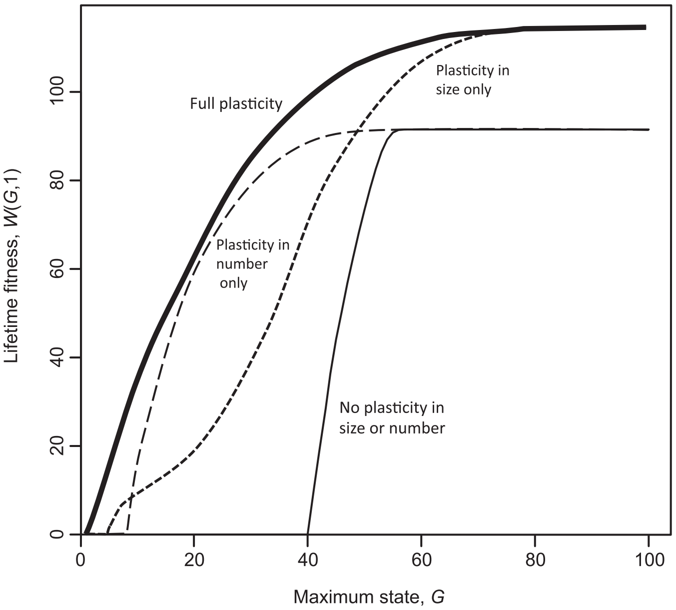


Fig. 2. The fitness profiles for females with different types of plasticity in offspring size and number, where $\mu = 0.1$ and $\beta = 0.2$. We compare the fitness of a female that makes the Lack clutch of offspring size, $\bar{s}$ (no plasticity in size or number), with the fitness of females that can make variable clutch sizes but of fixed offspring size, females that can make the Lack clutch but vary offspring size, and females that are fully plastic at every age. We evaluate the lifetime fitness of females with a range of initial energetic reserves, G. This shows the potential fitness advantage of plasticity in each trait.

possible unless they have enough state to invest at least $\bar{s}(1/\beta)$ in current reproduction. We then compare this baseline fitness with the fitness of three plastic strategies. We find the lifetime fitness for females that can only make a fixed size of offspring, but can vary the number in a clutch; females that make a fixed number of offspring but can vary their size; and females that can vary both size and number of offspring at each reproductive event. Due to negative density dependence in offspring fitness, females that can only vary offspring number (but must make $\bar{s}$ sized offspring) have a lower asymptotic fitness than females with a fully-plastic strategy, indicating that a fixed offspring size is costly for this level of density dependence, β. In contrast, for this scenario females that can increase offspring size (but not number) can approach the fitness of the fully-plastic strategy if they have sufficient state to make large offspring.

The differences in fitness for the three plastic life histories in Fig. 2 depend on the strength of density dependence. As density dependence weakens (i.e. β gets smaller), the fitness of females with the fully-plastic and fixed-offspring-size (plasticity in number only) strategies are closer together, although the fully-plastic strategy is always better. The female with the fixed-clutch-size strategy (plasticity in size only) cannot achieve comparable fitness in a scenario with low density dependence, so in a scenario with smaller β the fitness lines of the fixed-clutch size and fixed-offspring-size strategies no longer intersect. The effect of mortality rate on the fitness of each strategy is much less important. Increasing μ reduces the maximum fitness possible for each strategy, so it lowers the asymptote of each curve. This moves the upper intersection of the fixed-offspring-size and fixed-clutch-size strategies slightly to the left, meaning that females with these strategies reach equivalent fitness at a lower G. Therefore, we predict selection will favour the evolution of plasticity in offspring size in species where density-dependent interactions within a clutch are present.

Density dependence and mortality risk shape offspring size and number

In a homogenous environment, without density-dependent offspring survival, and when female mortality risk is low, we predict that female fitness is maximized at an offspring size $\bar{s}$ and that offspring number will be adjusted according to the level of total reproductive effort (Fig. 3). Indeed, we find that when we solve for the optimal allocation pattern for females in the range of possible states, without density dependence and with low mortality risk, we find no age-dependent variation in offspring size. Our model predicts females with varying amounts of state will vary mostly in clutch size; however, weak integer effects stemming from variation in state will also lead to variation in offspring size. In Fig. 3A, we present the mean increase in offspring size for all females and do not represent this state-dependent variation. With weak density dependence among siblings, the mean offspring size in a population of females of varying initial states is predicted to be above $\bar{s}$. This increase in the mean offspring size results from larger offspring produced by high-state females in the population. As β increases (to 0.6), the optimal offspring size s^* increases substantially, and the optimal offspring number n^* decreases. The best allocation pattern with strong density dependence is to make a clutch size of one very large offspring (Fig. 3B); when mortality is very high the optimal offspring size increases further, demonstrating a synergistic effect of adult mortality and density dependence.

Optimal offspring number changes only with the strength of density dependence, and is independent of mortality risk (Fig. 3B). We therefore predict that the greatest departures from the Smith-Fretwell optimum will be in those populations or species with strong

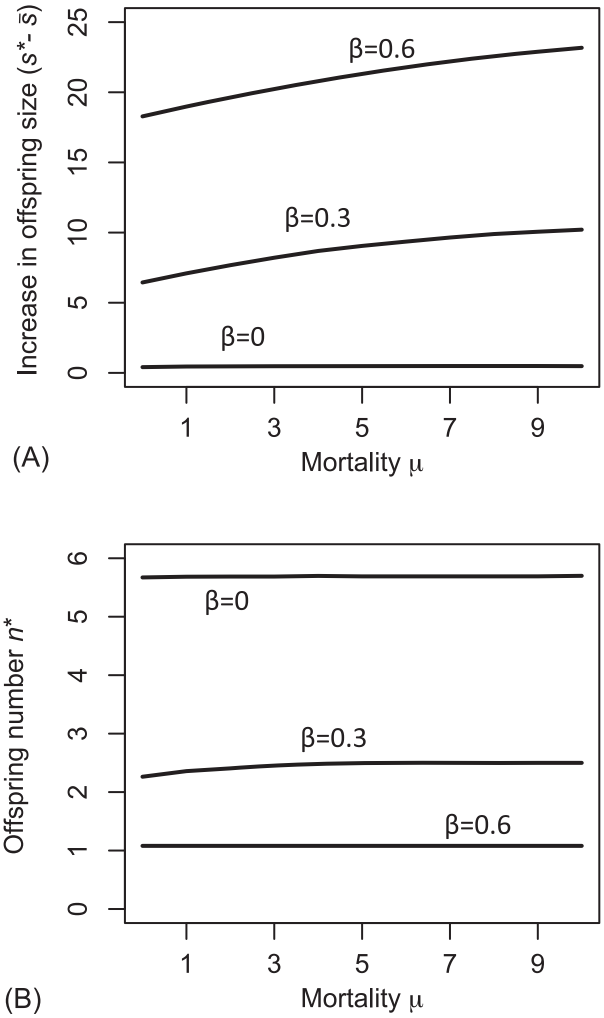


Fig. 3. (A) The shift in offspring size s^* from $\bar{s}$ for a population of females with the range of states $G(a) = g$. We examine changes in the average $s^*(g, a)$ over a range of values for μ (female mortality risk) and for three values of β (translating to no, weak, and strong density dependence in offspring survival). Each line denotes the shift in the mean investment in offspring size for the population evolving under that parameter scenario; this value represents the state- and age-dependent variation among females in each parameter scenario. For this analysis, $\bar{s} = 8$; we see that only populations with no density dependence are predicted to have an optimal offspring size near this value. (B) The average number of offspring $n^*(g, a)$ for a population of females over the range of states $G(a) = g$, calculated for a range of values for μ (mortality risk of a female) and for the same three values of β. As in panel (A), each line denotes the mean number of offspring produced by the population in that parameter scenario; this value represents state- and age-dependent variation among females. Note that there is little variation in offspring number as μ changes.

density-dependent competition or survival in a sibling group. Optimal offspring size (Fig. 3A) is also affected by adult mortality risk. With high mortality risk, females have little to gain by saving for future reproduction. When mortality risk is low, a female is more likely to respond to density-dependent offspring fitness by lowering reproductive effort in each reproductive event, and instead reproducing more times during her life.

Effects of age on offspring size and number

We predict age-dependent variation in allocation strategy when mortality risk is low, and females are likely to survive for multiple reproductive events, because females save less for future reproduction as they age. This pattern is amplified when density dependence in offspring fitness also favours smaller clutches and repeated reproductive events. With density dependence, females reduce clutch size, and thus have extra energy. Young females in high state save this extra energy for future reproduction, but older females in high state invest it in current reproduction, making larger offspring. In Fig. 4, we present the case when density dependence is relatively weak, and show the optimal allocation for females in a range of states at every age. Even with weak density dependence, the optimal allocation strategy is for females with sufficient state to increase both offspring size *and* clutch size as they age. However, the most extreme age dependence in offspring size will be for individuals whose state and age place them in the top right corner of the matrix. When we simulate a cohort of individuals starting from a range of initial states and behaving optimally, we find it is unlikely any individuals will reach old age in high state. Our model approximates a life history where females do not replenish their state as they age; therefore, females only move down in state as they deplete their resources. Thus, offspring size and number may indeed be predicted to generally increase as females age, but the pattern is confounded in the simulation by the females' change in state. Once in lower state, females are predicted to produce smaller offspring [similar to the results of Begon and Parker (1986)]. However, females in low state still produce offspring of variable sizes, because integer effects intensify for older females in low state (Fig. 4). If we focus on individuals with the same state but of varying ages, we can control for the confounding effects of state. For females that evolve under the conditions presented in Fig. 4 ($\mu = 0.05$, $\beta = 0.1$), we can ask if accounting for female age explains any of the variance in offspring size and number among females in the same state. All comparisons are among females in low to intermediate state, since females are rarely in high state after the initial reproductive event. We find that for 13% of cases, older females produce larger offspring; for 10% of cases, older females produce larger clutches. When we do the same analysis for an environment with slightly stronger density dependence ($\beta = 0.2$) and the same mortality, we find that for 31% of cases, older females produce larger offspring, and for 10% of individuals older females produce larger clutches. These age-dependent shifts in offspring size are relatively small (usually only one unit of resource). This pattern suggests that while age-dependent variation may be subtle, including age can be important in explaining the variance in life-history patterns measured in species with capital breeding and some density-dependent offspring fitness.

A two-habitat case

In the simplest multi-habitat version of the model, a female can move among habitats that vary in the strength of density dependence and mortality risk. This is akin to the situation where the female can reproduce in a spatially structured environment, with distinct habitat types. We assume that there is no cost of dispersal between habitats. In Fig. 5, we summarize two cases of the two-habitat analysis. In each case, we compare two habitats (H1 and H2)

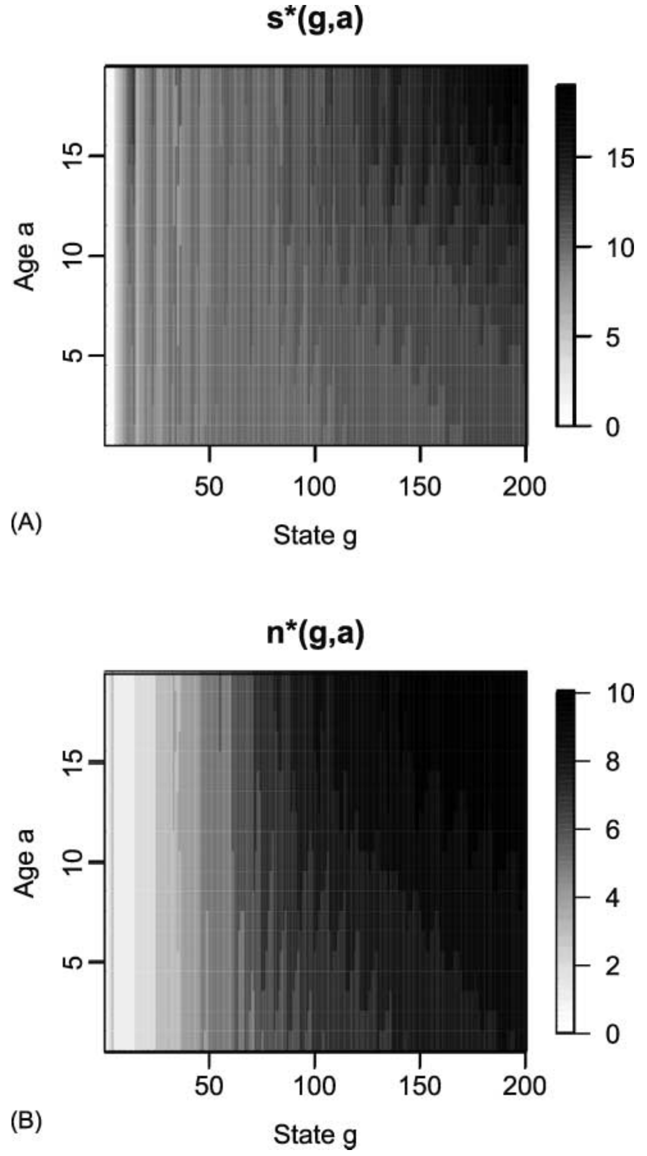


Fig. 4. Reproductive allocation in an environment where $\mu = 0.05$ and $\beta = 0.1$. We solve for the optimum at every combination of the full range of states and ages: (A) allocation to offspring size and (B) allocation to offspring number. Darker shading corresponds to increased allocation. Note that for females in low state, variation in s^* due to integer effects increases with female age (upper right corner of panel (A)).

that vary in adult mortality rate and strength of density-dependent offspring fitness. In the first case (Fig. 5, left column of panels), both habitats have a relatively high mortality risk and relatively strong density dependence. In the second case (Fig. 5, right column of panels), we compare two high-quality habitats: the relative differences between H1 and H2 are the same but the absolute degree of riskiness and strength of density dependence is much less. The three rows of Fig. 5 summarize h^*, s^*, and n^* respectively, for every combination of energetic state g and age a. Regardless of habitat, total reproductive effort (the product of s^* and n^*) increases with age and state, although the details of how reserves are distributed between offspring size and number depend on the details of each case.

In case 1, if a young female has low energetic reserves, she can only produce a few offspring (so she makes offspring of near-optimal size), and chooses the habitat with low mortality risk to maximize her own survival (H1). An old female with low reserves, however, is predicted to reproduce in H2. Since she has little opportunity for future fitness, she chooses the habitat that maximizes current reproductive success. In contrast, females with high reserves can make more, larger offspring each time. They reproduce in H2 at all ages to minimize density dependence. As H2 is risky, and females have low expected future fitness, the optimal strategy is to invest all energy available in reproduction during each reproductive event.

In case 2, because mortality risk is so much lower in both environments, all females expect fairly high future fitness, despite differences in state. Young females and females in low state all reproduce in H1, and make small clutch sizes. In contrast to case 1, the cost of saving some reproductive reserves in each event is very low in H1. Females make small clutches to minimize density dependence. As the females age, and the expectation of future fitness diminishes (e.g. as the end of life approaches), it becomes profitable for a female to make larger clutches, and therefore to reproduce in H2, where density dependence is much weaker. We observe this shift at an earlier age for females in high state, because they have enough reserves to make larger clutches. As young females in low state are limited to small clutch sizes, they are better off maximizing survival by remaining in H1 until later in life. When mortality is generally low, as it is in this case, we see age-dependent shifts in reproductive strategy accompanied by changes in reproductive habitat.

This analysis reveals how mortality and density dependence interact to influence the optimal allocation pattern. Including the effect of heterogeneity in reproductive habitat in our model led to a greater range of predicted offspring sizes. The range of offspring sizes produced by females in the second case is much smaller than the first, because in the second case females have a good chance of surviving to reproduce more than once, and saving some available energy is less costly. Females in low-risk environments with density dependence are therefore predicted to spread their energy resources over several reproductive events, and produce less variable offspring sizes.

DISCUSSION

We address female allocation by bringing the theories of optimal offspring number and optimal offspring investment together in a dynamic state-dependent framework (equation 7). This framework allows us to consider how female age and state interact with the effects of density-dependent offspring fitness and female mortality risk. Our model shows that different combinations of adult mortality risk and density dependence predict a range of life-history patterns that deviate from classical predictions. We confirm the result of Parker and Begon (1986), and show that even very weak density dependence can be important in driving variation in allocation to offspring size and number (Fig. 3). In addition, we show that including state- and age-dependence can predict increased offspring size as well as clutch size if females do not have an incentive to save the extra energy for future

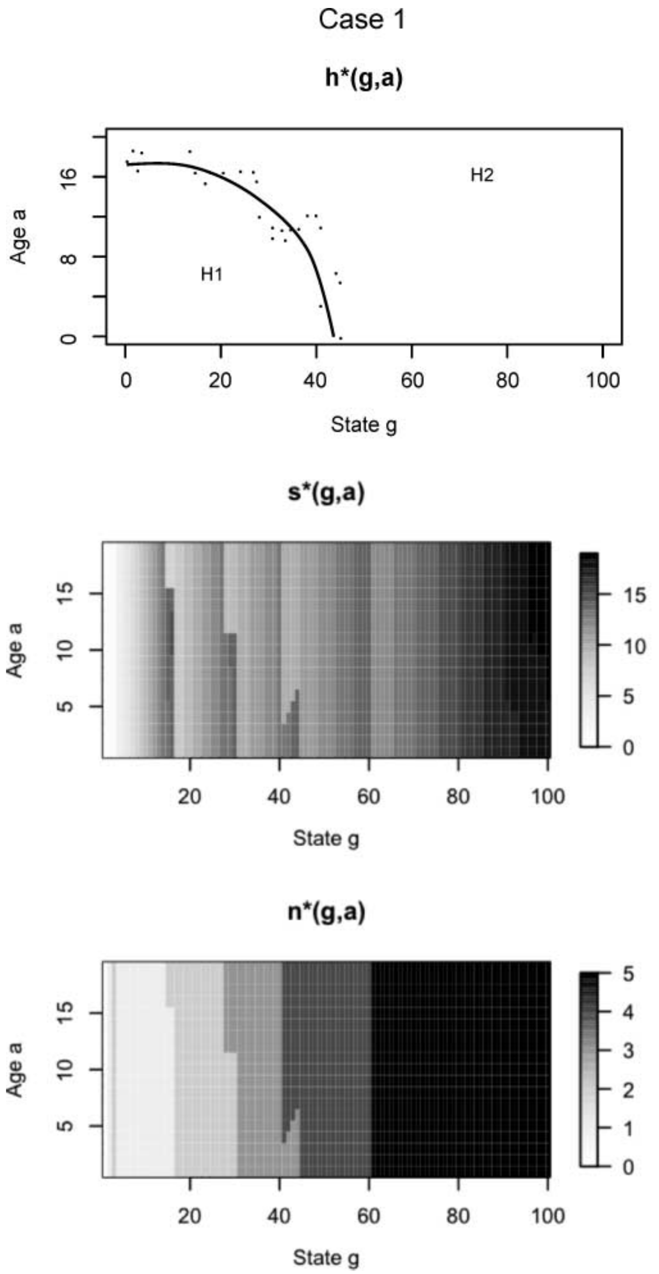
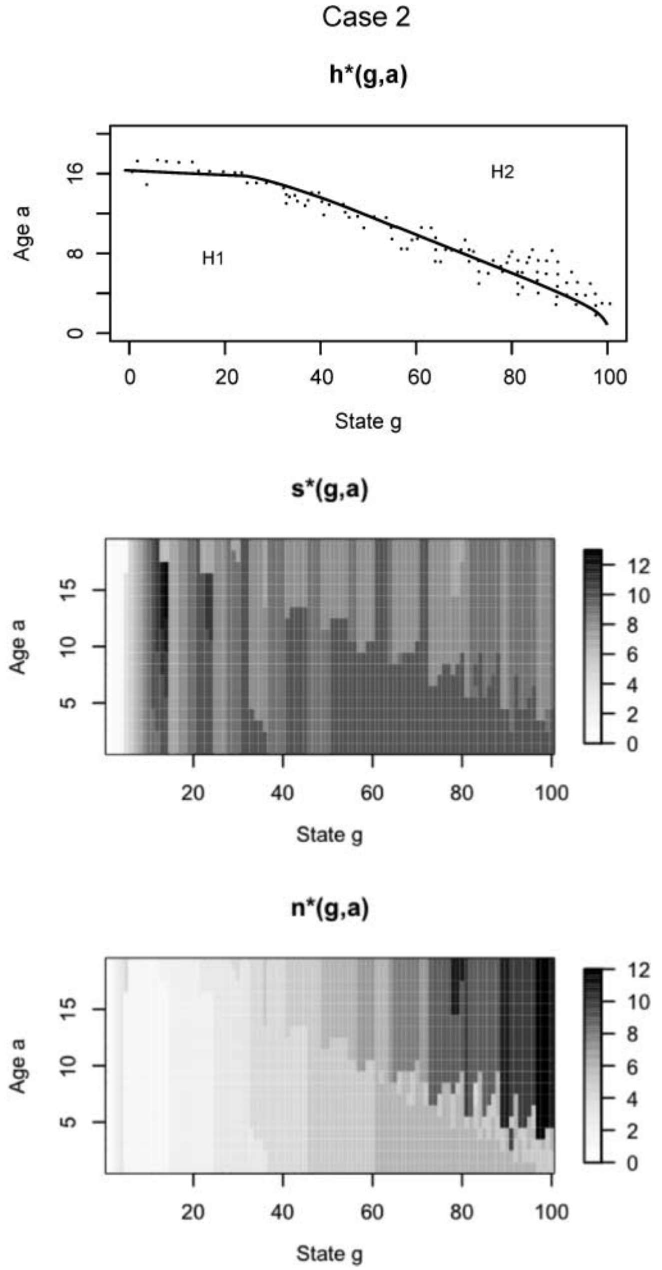


Fig. 5. Two cases of reproduction in two habitats. For case 1 (left-hand column), in H1 $\mu = 0.2$ and $\beta = 0.3$; in H2 $\mu = 0.3$ and $\beta = 0.2$. For case 2 (right-hand column), in H1 $\mu = 0.01$ and $\beta = 0.1$; in H2 $\mu = 0.1$ and $\beta = 0.01$. In both cases, H1 is less risky than H2, but density dependence is stronger. Top row: optimal habitat for reproduction. Dots reflect variation due to integer effects; lines are drawn by eye to represent the general boundary where habitat preference shifts. Middle row: optimal offspring size for every combination of state and age. Bottom row: optimal offspring



number for every combination of state and age. In both cases, low-energy females are better off reproducing in H1, to maximize survival. As age (*a*) and state (*g*) increase, females are better off reproducing in H2, where their allocation pattern may also change. We see the habitat shift accompanies age-dependent shifts in allocation to offspring size and number in case 2, where mortality is generally low, but not in case 1. This is due to the reduced expectation of future fitness for all females in case 1.

reproduction. Our model also predicts that heterogeneity in habitat quality can lead to variation in female reproductive patterns, depending on her age and condition. This integrative approach moves beyond previous studies predicting optimal allocation to offspring size, because it addresses interactions between an individual's age and state that arise as the trade-off between current and future reproduction changes over the lifetime of a female. To our knowledge, this is the first time that theory has predicted age-dependent increases in optimal offspring size.

In general, we find that considering future fitness when predicting allocation to offspring size and number can be important for understanding life-history patterns in species that have high survival. This is especially true for species with density dependence in offspring fitness. Finally, we find that integer effects can interact with variation in individual state, and can explain variation in offspring size *and* number.

We address the effect of density-dependent offspring survival because it is a clear mechanism linking total reproductive effort and individual offspring fitness. We model density-dependent offspring fitness as a declining function of the number of offspring produced, but assume that differences in offspring size do not affect density-dependent interactions. Furthermore, we consider the effects of density-dependent offspring fitness alone; we do not address effects of density on maternal resources because we consider a population with non-overlapping generations. To be as general as possible, we have not specified whether the mechanism of density dependence is due to increased competition for limited food [e.g. among insect larvae that are laid on the same host plant (Lalonde and Roitberg, 1994)] or due to decreased survival through early life [e.g. sand goby eggs with paternal care have reduced survivorship at higher densities (Klug *et al.*, 2006)]. Although addressing density dependence in this way overlooks the possibility of indirect effects of offspring size on competition for resources, we suspect that indirect effects of size competition among siblings are most important when there are variable offspring sizes within a clutch. Our model precludes this scenario, since it assumes that maternal allocation is equal within a clutch. Instead, our model focuses on general effects of clutch size, so it also applies to the empirical pattern of reduced survival among larger clutches (Klug *et al.*, 2006), which does not have a size-dependent mechanism. It also includes the possibility that increased maternal allocation to larval energy stores could reduce competition for resources among siblings in early life.

When clutch sizes are low, as they are in our model results, it is possible for variation in offspring size to arise due to *integer effects*, which occur as offspring number must be an integer (Ricklefs, 1968; Charnov and Downhower, 1995). When the best offspring size does not divide evenly into total reproductive effort (i.e. $g/s^* = n$ is a non-integer), and it is not advantageous to save that energy for future reproduction, the female can either make another offspring but decrease individual offspring size, or she can increase offspring size until n is an integer. Female state also contributes to the integer effects (Fig. 5; middle and bottom row): as female state increases, so does g, incrementally. Therefore, integer effects explain some degree of the predicted variation from $\bar{s}$ in our results. While this sort of variation is not widely studied, we suspect it is common in nature (Charnov and Downhower, 1995).

Our model predicts mothers in high state will increase total reproductive effort and offspring size when density dependence is strong (Fig. 3A), as they age [i.e. they are near the end of their reproductive period (Fig. 4)], or a combination of the two (Fig. 5). With some density dependence, a female will reduce clutch size, leaving her with some extra energy, which she can either save or put into offspring size. With some chance of mortality, the incentive to save energy is small. In this scenario, if females do not simultaneously increase offspring size, and they do not reproduce again, they are effectively squandering their remaining reproductive reserves. Therefore, we predict both females in high-mortality environments and old females should make larger offspring than young females in low-mortality environments. The results of our simulation suggest that old females rarely have enough state to make large offspring. This is because females will not reach old age in high state, since in our model females do not replenish their gonadal energy reserves once they begin reproduction. Despite this pattern, our simulation shows that even though females make smaller clutches as they age, they may still make larger offspring, depending on their state. This is because older females in low state still produce variable offspring sizes due to integer effects. Based on our analysis, we can speculate that the empirical pattern of increased reproductive effort in old females (e.g. Berkeley *et al.*, 2004) is most likely to occur in species where state can be replenished over the course of the breeding period, and/or where state and age are correlated. These species are likely income breeders, and so the mechanisms generating state- and age-dependent variation in these cases are outside the scope of our current predictions. However, our results demonstrate that variable allocation patterns in older females can be explained by state-dependent integer effects.

We address the question of reproductive habitat choice in our analysis because there is a rich literature documenting female preference for higher-quality reproductive habitats in some taxa, including insects (Reiskind and Wilson, 2004), anurans (Binckley and Resetarits, 2003), and fish (Hendry *et al.*, 2001). A female's perception of habitat quality can affect her clutch size (Lalonde and Roitberg, 1994; Reiskind and Wilson, 2004). If it is available, a female will always choose the habitat where the strength of density dependence is weakest, and her own risk of mortality is lowest. The interesting case is when she must trade-off her own survival and the fitness of her offspring; the best habitat choice depends on a female's expectation of the future. Furthermore, the cases compared in Fig. 5 show that the effect of habitat choice on allocation strategy depends on the overall quality of both habitats as well as the relative strengths of density dependence and mortality risk. In case 1, both habitats are risky enough that there is little age-dependent variation in allocation to offspring size *or* number. In contrast, age-dependent variation in number is present in case 2. In this case, we also see age-dependent variation in offspring size due to integer effects (which arise as a consequence of the variation in offspring number), not density dependence.

One could extend this approach to habitat heterogeneity to include travel costs among habitat. In such a case, habitat would be another state variable. This is an example of how our approach can be relevant to the interpretation of differences in individual reproductive rates and population age structure when habitats are heterogeneous.

We show that variation in offspring size and number depends upon two factors: the rate of mortality that the female experiences and the strength of density dependence, which females may perceive imprecisely. Indeed, it is likely that individuals in the same population but at different locations would have different estimates of both of these factors. All else being equal, it is evolutionarily advantageous for individuals to be pessimistic about (over-estimate) predation risk (Bouskila and Blumstein, 1992) and to be optimistic about (also over-estimate) opportunities for reproduction (Roitberg, 1990). Similar work on variance in the estimates of the strength of density dependence does not exist, but we can speculate that modest variation in experiences up to the time of reproduction may lead to great variation in reproductive behaviour.

In the model presented here, we explicitly separate maximum age A and mean age (roughly $1/\mu$). This could allow one to explore how these two different metrics of lifespan affect the pattern of optimal reproductive effort, thus complementing work in which their effects on diversity have been explored (Bonsall and Mangel, 2004; Mangel *et al.*, 2007).

Although our model is of an organism with continuous reproduction, some species have an annual cycle of changes in energetic reserves. Our model could be extended to address this scenario with the introduction of a within-year time variable t and the sequential coupling of reserves across years (*sensu* Mangel and Clark, 1988; Clark and Mangel, 2000). This is just one of the ways in which our framework can be extended to address a broader range of life histories.

Until now, empirical variation in offspring size could not be explained fully by classic life-history models. Our approach is the first to demonstrate how within-clutch density dependence and female mortality risk can interact to shape total reproductive effort, as well as the trade-off between offspring size and number. Such an integrative approach is necessary if we are to understand the evolution of female allocation strategies.

ACKNOWLEDGEMENTS

This work has been supported by the US EPA Science to Achieve Results Fellowship (H.K.K.), Yale University (S.H.A. and H.K.K.), NSF (S.H.A. and M.M.), the Center for Stock Assessment Research and the Lenfest Ocean Program (M.M.), and the Royal Society (M.B.B. and S.H.A.).

REFERENCES

Begon, M. and Parker, G. 1986. Should egg size and clutch size decrease with age? *Oikos*, **47**: 293–302.

Berkeley, S.A., Chapman, C. and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, **85**: 1258–1264.

Binckley, C.A. and Resetarits, W.J. 2003. Functional equivalence of non-lethal effects: generalized fish avoidance determines distribution of gray treefrog, *Hyla chrysoscelis*, larvae. *Oikos*, **102**: 623–629.

Bonsall, M.B. and Mangel, M. 2004. Life-history trade-offs and ecological dynamics in the evolution of longevity. *Proc. R. Soc. Lond. B*, **271**: 1143–1150.

Bouskila, A. and Blumstein, D.T. 1992. Rules of thumb for predation hazard assessment – predictions from a dynamic model. *Am. Nat.*, **139**: 161–176.

Broussard, D.R., Michener, G.R. and Dobson, F.S. 2006. Age-specific resource investment strategies: evidence from female Richardson's ground squirrels (*Spermophilus richardsonii*). *J. Zool.*, **268**: 389–394.

Caley, M.J., Schwarzkopf, L. and Shine, R. 2001. Does total reproductive effort evolve independently of offspring size? *Evolution*, **55**: 1245–1248.

Charnov, E.L. and Downhower, J.F. 1995. A trade-off-invariant life-history rule for optimal offspring size. *Nature*, **376**: 418–419.

Clark, C.W. and Mangel, M. 2000. *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford: Oxford University Press.

Donelson, J.M., Munday, P.L. and McCormick, M.I. 2009. Parental effects on offspring life histories: when are they important? *Biol. Lett.*, **5**: 262–265.

Eitam, A., Blaustein, L. and Mangel, M. 2005. Density and intercohort priority effects on larval *Salamandra salamandra* in temporary pools. *Oecologia*, **146**: 36–42.

Fischer, K., Bot, A.N.M., Brakefield, P.M. and Zwaan, B.J. 2006. Do mothers producing large offspring have to sacrifice fecundity? *J. Evol. Biol.*, **19**: 380–391.

Fox, C.W., Roff, D.A. and Fairbairn, D.J. 2001. *Evolutionary Ecology: Concepts and Case Studies*. Oxford: Oxford University Press.

Gagliano, M. and McCormick, M.I. 2007. Maternal condition influences phenotypic selection on offspring. *J. Anim. Ecol.*, **76**: 174–182.

Hendry, A.P., Day, T. and Cooper, A.B. 2001. Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.*, **157**: 387–407.

Houston, A., Clark, C., McNamara, J. and Mangel, M. 1988. Dynamic models in behavioral and evolutionary ecology. *Nature*, **332**: 29–34.

Houston, A.I. and McNamara, J.M. 1999. *Models of Adaptive Behaviour*. Cambridge: Cambridge University Press.

Klomp, H. 1970. Determination of clutch-size in birds: a review. *Ardea*, **58:** 1–124

Klug, H., Lindstrom, K. and Mary, C.M.S. 2006. Parents benefit from eating offspring: density-dependent egg survivorship compensates for fillial cannibalism. *Evolution*, **60**: 2087–2095.

Lack, D. 1966. *Population Studies of Birds*. Oxford: Clarendon Press.

Lalonde, R.G. and Roitberg, B.D. 1994. Pollen availability, seed production, and seed predator clutch size in a tephritid thistle system. *Evol. Ecol.*, **8**: 188–195.

Mangel, M. 2006. *The Theoretical Biologist's Toolbox: Quantitative Methods for Ecology and Evolutionary Biology*. Cambridge: Cambridge University Press.

Mangel, M. and Clark, C.W. 1988. *Dynamic Modeling in Behavioral Ecology*. Princeton, NJ: Princeton University Press.

Mangel, M. and Ludwig, D. 1992. Definition and evaluation of the fitness of behavioral and developmental programs. *Annu. Rev. Ecol. Syst.*, **23**: 507–536.

Mangel, M., Kindsvater, H.K. and Bonsall, M.B. 2007. Evolutionary analysis of life span, competition, and adaptive radiation, motivated by the Pacific rockfishes (*Sebastes*). *Evolution*, **61**: 1208–1224.

Parker, G.A. and Begon, M. 1986. Optimal egg size and clutch size – effects of environment and maternal phenotype. *Am. Nat.*, **128**: 573–592.

Plaistow, S., St. Clair, J., Grant, J. and Benton, T. 2007. How to put all your eggs in one basket: empirical patterns of offspring provisioning throughout a mother's lifetime. *Am. Nat.*, **170**: 520–529.

Reiskind, M.H. and Wilson, M.L. 2004. *Culex restuans* (Diptera: Culicidae) oviposition behavior determined by larval habitat quality and quantity in southeastern Michigan. *J. Med. Entomol.*, **41**: 179–186.

Reznick, D.N., Butler, M.J., Rodd, F.H. and Ross, P. 1996. Life-history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution*, **50**: 1651–1660.

Ricklefs, R. 1968. On the limitation of brood size in passerine birds by the ability of adults to nourish their young. *Proc. Natl. Acad. Sci. USA*, **61**: 847–861.

Roff, D. 1992. *The Evolution of Life Histories: Theory and Analysis*. London: Chapman & Hall.

Roff, D.A., Mostowy, S. and Fairbairn, D.J. 2002. The evolution of trade-offs: testing predictions on response to selection and environmental variation. *Evolution*, **56**: 84–95.

Roitberg, B.D. 1990. Optimistic and pessimistic fruit flies: measuring the costs of estimation errors. *Behaviour*, **114**: 65–82.

Roitberg, B.D. and Mangel, M. 1993. Parent–offspring conflict and life history consequences in herbivorous insects. *Am. Nat.*, **142**: 443–456.

Smith, C.C. and Fretwell, S.D. 1974. Optimal balance between size and number of offspring. *Am. Nat.*, **108**: 499–506.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Uller, T., While, G.M., Wapstra, E., Warner, D.A., Goodman, B.A., Schwarzkopf, L. 2009. Evaluation of offspring size–number invariants in 12 species of lizard. *J. Evol. Biol.*, **22**: 143–151.

Vieyra, L., Velarde, E. and Ezcurra, E. 2009. Effects of parental age and food availability on the reproductive success of Heermann's gulls in the Gulf of California. *Ecology*, **90**: 1084–1094.

Williams, G.C. 1966. Natural selection costs of reproduction and a refinement of Lack's principle. *Am. Nat.*, **100**: 687–690.

Winkler, D.W. and Wallin, K. 1987. Offspring size and number – a life-history model linking effort per offspring and total effort. *Am. Nat.*, **129**: 708–720.