Optimal Semelparity

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Abstract

Semelparous organisms have a simple life-cycle characterized by death after reproduction. We assume that semelparous life histories can be separated into a juvenile non-reproductive period followed by an adult period during which reproduction is possible. We derive formulas for the optimal age and size at reproduction and for the optimal size of offspring (e.g., seeds) and formally prove for the first time when the optimal size of the offspring does not depend on the optimal size at reproduction and when the optimal size at reproduction does not depend on the optimal size of the offspring.

Keywords: semelparous, monocarpic, optimal life histories, optimal size, seed size

Introduction, Assumptions and Notation

"Plants of any size have seeds that vary approximately 400-650-fold between species", as Venable and Rees (2009) point out; they note that "*Sequoia sempervirens* has a seed mass of 0.0037 gram." Species of animals also vary widely in the size of offspring. What evolutionary factors determine the size

of mature adults vs. the size of progeny? This question is the subject of a large body of literature. Moles et al. (2005), Rees and Venable (2007), Falster et al. (2008) and Venable and Rees (2009) provide useful overviews of the literature on plants. An early framework was proposed by Smith and Fretwell (1974) and expanded by Geritz et al. (1999). Charnov (1993) developed a different perspective with a focus on mammals. Our contribution is to build a biodemographic framework that unifies predictions about adult size and offspring size in simple, precisely-defined optimization models and to rigorously prove key implications of these models. We achieve simplicity by focusing on semelparous species, which reproduce once and die.

Evolutionary biologists have taken advantage of the simplicity of the semelparous life history. For example, demographic models have been developed to explore how stochasticity affects reproductive delays (Tuljapurkar 1990), how variation in growth shapes plasticity in timing of reproduction (Burd et al. 2006), and how the evolution of reproductive delays interacts with pre-reproductive delays such as seed-banks (Rees et al. 2006). However, to date, no single analytical framework providing dynamic insights into optimal life-histories of semelparous species has been developed. There is a need for such theory to separate the effects of complexities such as changing predation regimes and resource limitation (Abrams and Rowe 1996) and stochastic environments (Tuljapurkar 1990) from patterns driven by the general principles underlying demographic trajectories. Here we make a start at filling this gap by providing an analytical framework that unifies treatment of the two main axes of life-history variation in such species: the optimal timing of reproduction and the optimal offspring size. We focus on the simplest case of constant environments and constant population size.

The life cycle of semelparous species can be viewed as a two-phase process driven by different mechanisms. Stage 1 is a juvenile non-reproductive period, in which some individuals survive to become adults. Adults can reproduce and when they do, they die. Hence stage 2 is the period of life in which individuals seek to maximize their reproduction by weighing at each instant the benefits of delaying reproduction further with the risk of death associated with this delay. Mortality in stage 1 is assumed to be independent of mortality in stage 2. We assume size 1 is the milestone between the two stages. Without loss of generality, we can further assume that size 1 corresponds to adult age 0. In an analysis of the optimal timing of reproduction, it is not necessary to consider stage 1: knowledge of how long it took the organism to reach size 1 is irrelevant. Table 1 summarizes the basic

characteristics of stage 1 vs. stage 2.

Stage	Growth	Mortality	Reproduction
Stage 1	Yes	Yes	No
Stage 2	Yes	Yes	Yes

Table 1: Basic characteristics of two life-history stages for semelparous species

Let a be the age of the organism, age 0 being the age when size 1 is reached; in stage 1 ages are negative. Let $\xi(a)$, $m(a)$, and $\mu(a)$ denote the organism's size, its reproduction capacity, and the force of mortality, respectively, at age a. By assumption, $\xi(0) = 1$. Let α denote the age at which reproduction occurs. Let $n(\alpha, \iota)$ be the number of offspring produced, with each offspring (e.g., seed) being the same size ι. Note that $0 < \iota \leq 1$. Finally, let $p(\iota)$, $0 \leq p(\iota) < 1$, be the probability that an organism born at size ι survives to size 1.

In this article we address three questions about semelparous organisms. First, what is the optimal age at reproduction and what is the organism's size at this age? Second, what is the optimal number of offspring and what is the optimal size of each offspring? Third and most importantly, does the optimal size of an organism at reproduction $\hat{\xi}_0$ affect the optimal size of its offspring $\hat{\iota}_1$? Figure 1 summarizes the framework we will use to answer these questions by distinguishing between the life history of parents vs. offspring. Our first question is what determines $\hat{\xi}_0$, which is assumed to be equal to $\hat{\xi}_1$. Our second question is what determines $\hat{\iota}_0$, which is assumed to be equal to $\hat{\iota}_1$. Our third and most important question concerns the relationship between $\hat{\xi}_0$ and $\hat{\iota}_1$. The assumptions we made about the separation of the two stages imply that $\hat{\xi}_0$ and $\hat{\iota}_0$ are independent and, similarly, $\hat{\xi}_1$ and $\hat{\iota}_1$ are independent. The key question is whether $\hat{\iota}_1$ and $\hat{\xi}_0$ are independent. This formulation has not been clearly developed in previous studies (e.g., Kiflawi 2006) and is a key contribution.

For simplicity of exposition, we will henceforth consider semelparous species that are plants with offspring that are seeds.
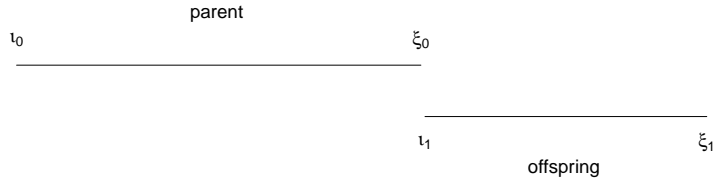
Figure 1: Life-histories of sizes of parents and offspring

Optimal age and size at reproduction

Stage 2, which starts once seed size no longer affects the risk of dying, is the stage of adult growth during which reproduction is possible. If reproduction occurs only at age α and if the chance $\ell(\alpha)$ of surviving to α is constant over time and across environments, then the net reproduction rate R for such semelparous species can be expressed as

$$R = e^{r\alpha} = \ell(\alpha)\, m(\alpha), \tag{1}$$

where r is the rate of population growth, and $m(\alpha)$ measures reproduction at age α; $m(a)$ at any age a other than α is zero. This implies that

$$e^{-r\alpha}\, \ell(\alpha)\, m(\alpha) = 1 \tag{2}$$

(Roff 2002,p189), an expression that resembles the more complicated Lotka equation,

$$\int_0^\infty e^{-ra}\, \ell(a)\, m(a)\, da = 1. \tag{3}$$

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Proof that r represents the growth rate in the Lotka equation is not straight-forward and depends on the assumption of stable populations (Arthur and Vaupel 1984), but (2) for semelparous species is true by definition. The simplicity of (2) facilitates analytical insights into optimal age at reproduction and optimal offspring size.

Solving (2) for r yields

$$r = \frac{ln\left[\ell(\alpha)\,m(\alpha)\right]}{\alpha} \tag{4}$$

(Roff 2002,p189). The value of α that maximizes r is the optimal age at reproduction, $\hat{\alpha}$. It satisfies the condition

$$\left.\frac{dr}{d\alpha}\right|_{\alpha=\hat{\alpha}} = 0, \tag{5}$$

Inserting the expression for r from (4) into (5), solving for α the equation for the derivative, and rearranging terms yields the requirement that the optimal age at reproduction, denoted by $\hat{\alpha}$, must satisfy:

$$\acute{m}(\hat{\alpha}) - \mu(\hat{\alpha}) = \frac{ln\left[\ell(\hat{\alpha})\,m(\hat{\alpha})\right]}{\hat{\alpha}}, \tag{6}$$

where $\acute{m}(\alpha) = \left[dm(\alpha)\,/\,d\alpha\right]/\,m(\alpha)$ and $\mu(\alpha) = \left[-d\ell(\alpha)\,/\,d\alpha\right]/\,\ell(\alpha)$. Note that $\acute{m}(\alpha)$ is the relative rate of improvement in reproductive capacity at age α, and $\mu(\alpha)$ is the hazard of death (force of mortality) at age α. Substituting (4) into (6) shows that

$$\acute{m}(\hat{\alpha}) - \mu(\hat{\alpha}) = r(\hat{\alpha}). \tag{7}$$

In equilibrium, $r = 0$ and the optimal age at reproduction is defined by a balance between the rate of growth in reproductive capacity and the force of mortality,

$$\acute{m}(\hat{\alpha}) = \mu(\hat{\alpha}). \tag{8}$$

Eq. (8) implies that reproduction should be delayed as long as the reproductive benefits of further growth outweigh the risk of mortality occasioned by delaying. The optimal age at reproduction is the age at which the benefits of further growth are exactly offset by the risk of dying.

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The optimal size at reproduction $\hat{\xi} = \xi(\hat{\alpha})$ is the size of the semelparous organism at the optimal age at reproduction. As a result, this optimal size can be determined by

$$\acute{m}_\xi(\hat{\xi}) \frac{d\hat{\xi}}{da} = \mu(\hat{\xi}), \tag{9}$$

which results directly from (8) by viewing it as a necessary condition for the optimal size rather than the optimal age. That is, at the optimal size, the increase in reproduction with an increase in size multiplied by the change in size in an additional unit of time (or age) must be counterbalanced by the risk of death during that unit of time.

If environmental conditions worsen such that the rate of growth in reproductive capacity at all ages decreases, when population equilibrium is reached the new optimal $\hat{\alpha}_1$ is younger than $\hat{\alpha}$. If mortality increases, the optimal age is also younger, $\hat{\alpha}_2$. If both occur simultaneously, the optimal age is even younger $\hat{\alpha}_3$.

Both (7) and (9) are true by definition, whatever functional forms are used for $m(\alpha)$ and $\ell(\alpha)$. Specific functional forms can be used to make more specific predictions. Mortality can be a declining function of size in many species and is known to be so in semelparous plants (Metcalf et al. 2003). An appropriate model could therefore be

$$\mu(a) = \frac{b}{\xi(a)} + c, \tag{10}$$

where b and c are constants, and $\xi(a)$ denotes size at age a. The parameter b captures the causes of death that decline with size, $b = 0$ captures no size dependence, and c captures ubiquitous causes of death that are independent of size. Reproductive output is generally an increasing function of size and can be modelled as

$$m(a) = \phi\xi(a)^\eta, \tag{11}$$

where ϕ is a scaling parameter and η determines whether there are economies ($\eta > 1$) or dis-economies ($\eta < 1$) of scale in transforming size into reproductive output. Growth can be described using

$$\frac{d\xi}{da} = k\xi^{0.75} - \kappa\xi, \tag{12}$$

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where the parameter k captures how the growth rate increases with size, and κ modulates the increase so that eventually size reaches an asymptote. For illustration, we use the exponent 0.75, following predictions from the fractal model of scaling (West et al. 2001). However, using a different exponent would not alter the main conclusions of the article. This equation provides a fairly general description of asymptotic growth. If size at age 0 is 1, we have

$$\xi(a) = \left(\frac{k}{\kappa} - \left(\frac{k}{\kappa} - 1 \right) e^{\frac{-\kappa}{4} a} \right)^4, \tag{13}$$

where the asymptotic size is defined by $(\frac{k}{\kappa})^4$.

The optimal age of reproduction varies with respect to five of the six model parameters: b and c, determining general and size-dependent levels of mortality, k and κ, accounting for the speed and asymptotic form of plant growth, as well as fertility's scaling parameter η. Moreover, the substitution of (10), (11), and (12) in (9) results in an expression for the optimal $\hat{\xi}$ that is explicitly independent of the scaling parameter ϕ.

$$\frac{\eta}{\xi} \left(k\xi^{0.75} - \kappa\xi \right) = \frac{b}{\xi} + c, \tag{14}$$

which reduces to

$$(\eta\kappa + c)\xi - \eta k \xi^{0.75} + b = 0 \tag{15}$$

The latter is a quartic equation for $\xi^{0.25}$ and its analytic solution is given by Ferrari's formula. Letting

$$A = \frac{\eta k}{\eta\kappa + c}, \qquad B = \frac{b}{\eta\kappa + c}, \qquad C = \sqrt[3]{\frac{1}{16} A^2 B + \sqrt{\frac{1}{256} A^4 B^2 - \frac{1}{27} B^3}},$$

we can express the positive root of the quartic equation (14) as follows

$$\xi = -\frac{A}{4} + \frac{1}{2} \sqrt{\frac{A^2}{4} + 2C + \frac{2B}{3C}} + \frac{1}{2} \sqrt{\frac{7A^2}{4} + 2C + \frac{2B}{3C} + \frac{A^3}{4\sqrt{\frac{A^2}{4} + 2C + \frac{2B}{3C}}}} \tag{16}$$

Eq. (16) implies that ξ increases with A and decreases with B. Therefore, the optimal size at reproduction $\hat{\xi}$ will increase with positive changes in the

reproduction scale parameter η or the determinant of asymptotic size $\frac{k}{\kappa}$, as well as negative changes in mortality parameters b or c.

These mathematical results aid biological insight. Because optimal size does not depend on the parameter ϕ, species suffering proportional reduction in offspring production will, certibus paribus, not vary in flowering size (Mylius and Diekmann 1995). An example of such proportional reduction in offspring production might be density dependence of seed establishment (Metcalf et al. 2003). Furthermore, if species' relative ranking with respect to asymptotic size k/κ, scaling of reproductive output with size η, and mortality parameters, b and c, are known, relative ranking in terms of flowering size could be predicted.

Optimal seed size and number

Let $p(\iota)$ be the probability that a seed germinates and grows to $\alpha = 0$ and size $\xi = 1$ when the plant can reproduce and initial size ι no longer influences mortality. Generally $p(\iota)$ increases with seed size ι Venable and Rees (2009). Let reproductive output, i.e., number of seeds produced, be denoted by $n(\alpha, \iota)$ which is an increasing function of plant age (and size), and a decreasing function of seed size. The net reproductive rate is then

$$R(\alpha, \iota) \,=\, e^{r(\alpha,\iota)\alpha} \,=\, p(\iota)\,\ell(\alpha)\,n(\alpha,\iota). \tag{17}$$

Following the same logic as in eq. (1), (2), (4)–(8), this implies that optimal age at reproduction satisfies

$$\acute{n}_\alpha(\hat{\alpha}, \iota) \,-\, \mu(\hat{\alpha}) \,=\, r(\hat{\alpha}, \iota) \tag{18}$$

and the optimal offspring size is specified by

$$\acute{n}_\iota(\alpha, \hat{\imath}) \,+\, \acute{p}(\hat{\imath}) \,=\, r(\alpha, \hat{\imath}) \tag{19}$$

where $\acute{n}_\alpha(\alpha, \iota) \,=\, (dn(\alpha, \iota)/d\alpha)\,/\,n(\alpha, \iota)$ and $\acute{n}_\iota(\alpha, \iota) \,=\, (dn(\alpha, \iota)/d\iota)\,/\,n(\alpha, \iota)$ are the relative derivatives of the number of offspring with respect to age at reproduction and seed size, respectively, $\acute{p}(\iota) \,=\, (dp(\iota)/d\iota)\,/\,p(\iota)$ is the relative derivative with respect to seed size of the probability that a seed of size ι will reach size $\xi = 1$. Because of the definition of stage 1 and stage 2, optimal time at reproduction depends only on α in stage 2 and does not depend on time taken by a seed to grow to $\xi = 1$ (Kiflawi 2006).

If the population is in equilibrium, with $r = 0$, then

$$\acute{n}_\alpha(\hat{\alpha}, \iota) = \mu(\hat{\alpha}) \qquad (20)$$

and

$$\acute{n}_\iota(\alpha, \hat{\iota}) = -\acute{p}(\hat{\iota}) \qquad (21)$$

Eq. (20) is similar to (8) and provides the same insight into the timing of reproduction. Eq. (21), on the other, hand implies that optimal offspring size is the size at which the benefits accrued through investing less in each offspring and thereby producing more offspring are offset by the risk of mortality for an offspring of that size.

Specific functional forms can be used to deepen understanding. The number of seeds n of size ι produced at age α can be determined by

$$n(\alpha, \iota) = \frac{\phi \xi(\alpha)^\eta}{\iota^\beta}, \qquad (22)$$

where β is a parameter that captures economies of scale in producing larger offspring. The probability of reaching size $\xi = 1$ can be specified by a function

$$p(\iota) = \left(\frac{\iota - \iota_0}{1 - \iota_0} \right)^\gamma, \qquad 0 < \gamma < 1, \qquad (23)$$

where ι_0 is the minimal possible seed size and γ accounts for the speed of reaching reference size $\xi = 1$. As a result, the optimal offspring size $\hat{\iota}$ will be the solution of (19) i.e.

$$\hat{\iota} = \frac{\beta \iota_0}{\beta - \gamma} \qquad (24)$$

When is Optimal Seed Size Independent of Optimal Adult Size at Reproduction

Eq. (24) implies that the optimal seed size $\hat{\iota}$ does not depend on the optimal plant size at reproduction $\hat{\xi}$. Using (21) it similarly can be shown that optimal plant size at reproduction does not depend on the optimal size of the seeds produced. This mutual independence holds in general if the number of seeds of size ι produced at age α is proportional to the product of a function of adult size and a function of seed size, i.e.

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$$n(\alpha, \iota) = C\,F(\iota)G(\alpha), \qquad C \equiv const \qquad (25)$$

In this case

$$\acute{n}_\iota = \acute{F}_\iota \qquad (26)$$

does not depend on $\hat{\xi}$ and neither does $\acute{p}(\iota)$. Similarly,

$$\acute{n}_\alpha = \acute{G}_\alpha \qquad (27)$$

Eq. (25) is the condition, in our framework, for the independence of the parent's optimal size at reproduction and the optimal seed size of its offspring. Eq. (22) provides an example. The condition is not implausible but it also is not trivial. For instance, in (22) β might be a function of ξ: bigger plants might be more efficient at producing large seeds than smaller plants are. Also in (22), η might be a function of ι: the relationship between plant size and reproductive capacity may be modulated by seed size.

Note that the assumptions about a juvenile vs. an adult stage imply that $\hat{\xi}_0$ is independent of $\hat{\iota}_0$ and $\hat{\xi}_1$ is independent of $\hat{\iota}_1$ (see Figure 1). To prove independence of optimal seed size and optimal size at maturity, it is also necessary to show that $\hat{\xi}_0$ and $\hat{\iota}_1$ are independent. Eq. (25) gives the condition for this.

The independence of two characteristics means that the optimal value of either of them does not depend on the value of the other characteristic. This causal independence is different from lack of empirical correlation. For instance, suppose a species grows in two environments, one unfavorable (perhaps because of poor soil or lack of sunlight) and the other favorable. Then the time it takes a plant to grow from seed to adult size and the time it takes for the plant to grow from adult size to maturity might be correlated across the two environments: e.g., both times might be long in the unfavorable environment and short in the favorable one. The long time to develop, however, does not cause the long time to mature: the unfavorable environment causes both and the correlation is merely a statistical association.

Conclusion

The simplicity of the semelparous life cycle permits formulation of general mathematical models that predict key features of life histories. The analytical framework presented here unifies predictions of timing of reproduction

and offspring size. This framework provides insights into how basic demographic features shape the diversity of age trajectories across species, and proving in particular when dependence between optimal offspring size and optimal size at maturity will occur and when it will not. These results permit separation of these patterns from complications such as variation in growth, across environments, individuals (Metcalf et al. 2003) and through time (Rees et al. 2000). Variants of the models may also be relevant for other life-history switches such as metamorphosis (Wilbur and Collins 1973).

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