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MPIDR WORKING PAPER WP 2008-012
MARCH 2008 (REVISED MARCH 2010)

Optimal semelparity

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Abstract

Semelparous organisms have a simple life-cycle characterized by immediate death after reproduction. We introduce a new analytical framework for semelparous life histories based on separating their reproductive and non-reproductive period. Under this assumption we prove that the optimal size at reproduction does not depend on the optimal size of the seeds produced.

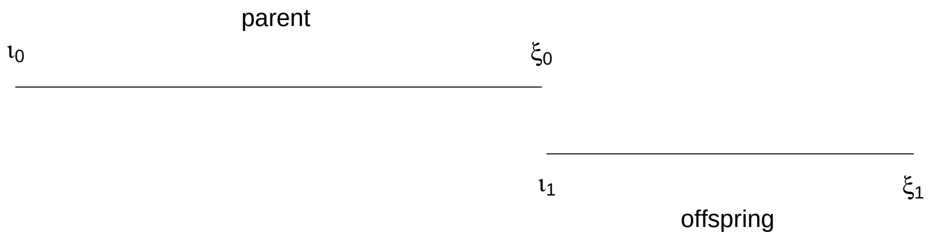
keywords: semelparous, optimal life histories, optimal size

Introduction, Assumptions and Notation

The life cycle of semelparous species can be viewed as a two-phase process, driven at each step by different mechanisms. Stage 1 is a non-reproductive period, in which a certain part of the offspring *survives to maturity.* Stage 2, on the other hand, represents the adult phase, in which individuals *maximize their net reproductive rate*, comparing at each instant the benefits of delaying reproduction further with the risk of death associated with this delay. We will assume size 1 is the milestone between the two phases. Without loss of generality, we can further assume that size 1 corresponds to (adult) age 0. Indeed, if we are interested in the optimal timing of reproduction, then we do not take into account Stage 1, i.e. we do not need to know how long it took the organism to reach size 1. All the assumptions above imply that we treat mortality in Stage 1 as independent of mortality in Stage 2.

In our model for semelparous species we will designate by a the age of the organism, age 0 being the age when size 1 is reached. We will denote by $\xi(a)$, $m(a)$, and $\mu(a)$ the organism's size, its reproduction capacity, and the force of mortality, respectively, at age a. By assumption, we have $\xi(0) = 1$. Let us further denote the age at which reproduction actually takes place by α. The number of offspring produced will be designated by $n(\alpha, \iota)$, where we assume each offspring has one and the same size ι. Note that $0 < \iota < 1$. Finally, we will assume that the probability of surviving to size 1 for each organism born with size ι is $p(\iota)$, $0 \le p(\iota) < 1$.

In this paper we would like to address three questions regarding semelparous organisms. First of all, what is the optimal age at reproduction and what is the organism's size it corresponds to? Secondly, what is the optimal number of descendants and what is their optimal size? The most important question we would like to address is whether the optimal size of an organism at reproduction $\hat{\xi}_0$ affects the optimal size of its offspring $\hat{\iota}_1$ and under what conditions?



Stage	Growth	Mortality	Reproduction
Stage 1	Yes (from ι to 1)	Yes	No
Stage 2	Yes (from 1 onwards)	Yes	Yes

Table 1: Life-Cycle Phases for Semelparous Species

Model for Stage 2

Stage 2 is the "stage" at which the trade-off between growth and reproduction, controlled by the risk of dying, takes place. It is instrumental for understanding the optimal life-cycle strategies of semelparous species and, therefore, deserves special attention.

The trade-off between offspring size and offspring number has long been the focus of interest by evolutionary biologists. The model we would like to propose adds an explicit demographic framework to formulations first introduced in Smith and Fretwell (1974), but remains simpler than Geritz et al. (1999) where larger offspring have both higher survival and higher competitive ability.

Stage 2, which starts once seed size no longer affects the risk of dying, is a stage of adult growth, during which reproduction is possible. We allow α to denote age in the second stage, so that $\alpha = 0$ is the start of stage 2 and end of stage 1. Let ι denote seed size. Let $p(\iota)$ be the probability that a seed germinates and grows until initial size no longer influences mortality, i.e. to $\alpha = 0$ and size taken as $\xi = 1$. Generally $p(\iota)$ increases with seed size ι. Let reproductive output i.e., number of seeds produced, be denoted by $n(\alpha, \iota)$ which is an increasing function of plant size (and age), and a decreasing function of seed size. The net reproductive rate is then

$$R \,=\, p(\iota)\, l(\alpha)\, n(\alpha, \iota). \tag{1}$$

If the population is in equilibrium, maximizing r is generally equivalent to maximizing R (Taylor et al., 1974). Further, Mylius and Diekmann (1995) showed that maximizing R provides the evolutionary stable strategy if population regulation operates on offspring establishment. Such density dependence characterizes many semelparous species (Metcalf et al., 2003). The optimal life history is therefore defined by the derivative or relative derivative of R being equal to zero. Hence, the optimal age at reproduction can be specified by

$$\frac{\frac{dR}{d\alpha}}{R} \,=\, 0 \,=\, \acute{n}_{\alpha}(\hat{\alpha}, \iota) \,-\, \mu(\hat{\alpha}) \tag{2}$$

where $\acute{n}_{\alpha}(\alpha, \iota) \;=\; (dn(\alpha, \iota)/d\alpha) \,/\, n(\alpha, \iota)$ defines the rate of change in the number of offspring produced at age α. Equation (2) implies $\acute{n}_{\alpha}(\hat{\alpha}, \iota) \;=\; \mu(\hat{\alpha})$, which is similar to the result obtained in (17). Note that 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). The optimal offspring size is specified by

$$\frac{\frac{dR}{d\iota}}{R} = 0 = \acute{n}_{\iota}(\alpha, \hat{\iota}) + \acute{p}(\hat{\iota}) \tag{3}$$

where $\acute{p}(\iota) = (dp(\iota)/d\iota) \, / \, p(\iota)$ and $\acute{n}_{\iota}(\alpha, \iota) = (dn(\alpha, \iota)/d\iota) \, / \, n(\alpha, \iota)$. This implies $\acute{p}(\hat{\iota}) = -\acute{n}_{\iota}(\alpha, \hat{\iota})$. At equilibrium, 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 (Fig. 3).

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

$$n(\alpha, \iota) = \phi \xi^{\eta}(\alpha) \left(1 - \iota^{\beta}\right), \qquad \beta > 1 \tag{4}$$

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

$$p(\iota) = \left(\frac{\iota - \iota_0}{1 - \iota_0}\right)^{\gamma}, \qquad 0 < \gamma < 1, \tag{5}$$

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 (3) i.e.

$$\frac{\beta\hat{\iota}^{\beta-1}}{1-\hat{\iota}^{\beta}} = \frac{\gamma}{\hat{\iota}-\iota_0} \tag{6}$$

The latter implies that the optimal seed size $\hat{\iota}$ does not depend on the optimal plant size at reproduction $\hat{\xi}$.

This result holds in general if the number of seeds of size ι produced at age α has the following functional form

$$n(\alpha,\iota) = C\,F(\iota)G(\alpha), \qquad C \equiv const \tag{7}$$

That is, $n(\alpha,\iota)$ is a product of two functions depending separately on seed size ι and age at reproduction α. In this case

$$\acute{n}_{\iota} = \acute{F}_{\iota} \tag{8}$$

does not depend on $\hat{\xi}$ and neither does $\acute{p}(\iota)$. As a result, (8) is a necessary condition for the independence of the parent's optimal size at reproduction from the optimal seed size of its offspring.

Optimal age and size at reproduction

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 fill 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 will concentrate on the simplest case of constant environments.

If reproduction occurs only at age α and if the chance $l(\alpha)$ 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

$$R = e^{r\alpha} = l(\alpha)\, m(\alpha), \tag{9}$$

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

$$e^{-r\alpha}\, l(\alpha)\, m(\alpha) \;=\; 1 \tag{10}$$

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

$$\int_0^\infty e^{-ra}\, l(a)\, m(a)\; da \;=\; 1. \tag{11}$$

Proof that r represents the growth rate in the Lotka equation is not straightforward and depends on the assumption of stable populations (Arthur and Vaupel, 1984), but (10) for semelparous species is true by definition. The simplicity of (10) facilitates analytical insights into optimal age at reproduction and optimal offspring size.

Solving (10) for r yields

$$r \;=\; \frac{ln\,[l(\alpha)\, m(\alpha)]}{\alpha} \tag{12}$$

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

$$\left.\frac{dr}{d\alpha}\right|_{\alpha=\hat{\alpha}} \;=\; 0, \tag{13}$$

Inserting the expression for r from (12) into (13), 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:

$$\acute{m}(\hat{\alpha}) \;-\; \mu(\hat{\alpha}) \;=\; \frac{ln\,[l(\hat{\alpha})\,m(\hat{\alpha})]}{\hat{\alpha}}, \tag{14}$$

where $\acute{m}(\alpha) \;=\; [dm(\alpha)\,/\,d\alpha]\,/\,m(\alpha)$ and $\mu(\alpha) \;=\; [-dl(\alpha)\,/\,d\alpha]\,/\,l(\alpha)$. 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 (12) into (14) shows that

$$\acute{m}(\hat{\alpha}) \;-\; \mu(\hat{\alpha}) \;=\; r(\hat{\alpha}). \tag{15}$$

Fig. 1 illustrates how (15) determines the optimal age at reproduction $\hat{\alpha}$.

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,

$$\acute{m}(\hat{\alpha}) \;=\; \mu(\hat{\alpha}). \tag{16}$$

From (16), 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.

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

$$\acute{m}_{\xi}(\hat{\xi})\,\frac{d\hat{\xi}}{da} = \mu(\hat{\xi}), \tag{17}$$

which results directly from (16) 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 $\hat{\alpha}$ (Fig. 2). If mortality increases, the optimal age is also younger, $\hat{\alpha}_2$. If both occur simultaneously, the optimal age is even younger $\hat{\alpha}_3$.

The optimal age at reproduction will shift when population growth rates or growing condition change. If the effects of neutral genetic drift, varying environments, or feedback loops through density dependence are negligible, we can predict changes in genotype prevalence associated with our optimality condition (16). If either population growth (Fig. 1) or environmental deterioration (Fig. 2) are maintained over several generations, genotypes in the population that reproduce younger will spread. If the deterioration occurs within a generation, and individuals can detect environmental cues indicating population growth (Fig. 1) or increased mortality or decreased rate of growth in reproductive capacity (Fig. 2), selection will favor individuals that can plastically alter α towards younger ages. The model species *Arabidopsis thaliana* is known to show plasticity in flowering time and is a good candidate for testing this prediction. Both within species and cross-species comparisons will shed further light on these patterns; e.g. semelparous plant species with slower rates of growth in size have been shown to flower at smaller sizes (Metcalf et al., 2006), an expected outcome from Fig. 2 if mortality patterns are similar.

Both (15) and (17) are true by definition, whatever functional forms are used for $m(\alpha)$ and $l(\alpha)$. 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

$$\mu(a) = \frac{b}{\xi(a)} + c, \tag{18}$$

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

$$m(a) = \phi \xi(a)^{\eta}, \tag{19}$$

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

$$\frac{d\xi}{da} = k\xi^{0.75} - \kappa\xi, \tag{20}$$

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

$$\xi(a) = \left(\frac{k}{\kappa} - \left(\frac{k}{\kappa} - 1 \right) e^{\frac{-\kappa}{4} a} \right)^4 , \tag{21}$$

where the asymptotic size is defined by $(\frac{k}{\kappa})^4$. Fig. 1 and Fig. 2 were graphed using these functional forms.

Effect of Model Parameters on Optimal Age at Reproduction

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 (18), (19), and (20) in (17) results in an expression for the optimal $\hat{\xi}$ that is explicitly independent of the scaling parameter ϕ.

$$\frac{\eta}{\xi} \left(k\xi^{0.75} - \kappa\xi \right) = \frac{b}{\xi} + c \, , \tag{22}$$

which reduces to

$$(\eta\kappa + c)\xi - \eta k \xi^{0.75} + b = 0 \tag{23}$$

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

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

we can express the positive root of the quartic equation (22) as it follows

$$\xi = -\frac{A}{4} + \frac{1}{2}\sqrt{\frac{A^2}{4} + 2C + \frac{2B}{3C}} + \frac{1}{2}\sqrt{\frac{7A^2}{4} + 2C + \frac{2B}{3C} + \frac{A^3}{4\sqrt{\frac{A^2}{4} + 2C + \frac{2B}{3C}}}} \tag{24}$$

As a result, ξ increases with A and decreases with B. Therefore, the optimal size of 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 this 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.

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 plasticity within species in response to environmental cues. This permits separation of these patterns from complications such as variation in growth, both across 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).

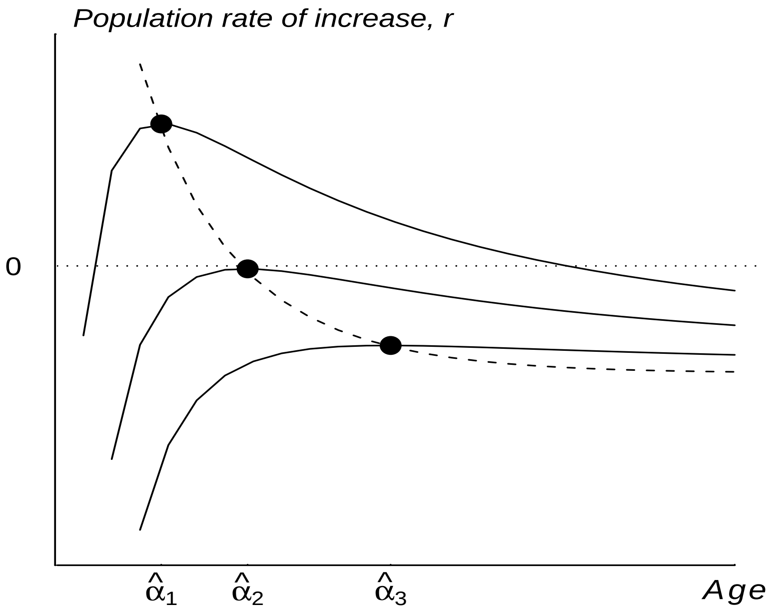


Figure 1: The optimal age at reproduction $\hat{\alpha}$ is defined when $r(\alpha)$ (three solid curves) is maximal and equal to $\acute{m}(a) - \mu(a)$ the difference between the rate of growth of reproductive capacity and the force of mortality (dashed line). Note that $\hat{\alpha}$ increases as $r(\hat{\alpha})$ decreases. Where the solid curve and dashed curve intersect at the horizontal dotted line, the population is at equilibrium, $r(\hat{\alpha}) = 0$ and $\acute{m}(\alpha) = \mu(\alpha)$. We produced the graph using (18)-(20), with $k = 3$, $\kappa = 1$, $\eta = 1$, $b = 0.6$, and $c = 0.1$. We used $\phi = 0.100$, $\phi = 0.042$, and $\phi = 0.020$ respectively, for the three solid curves.

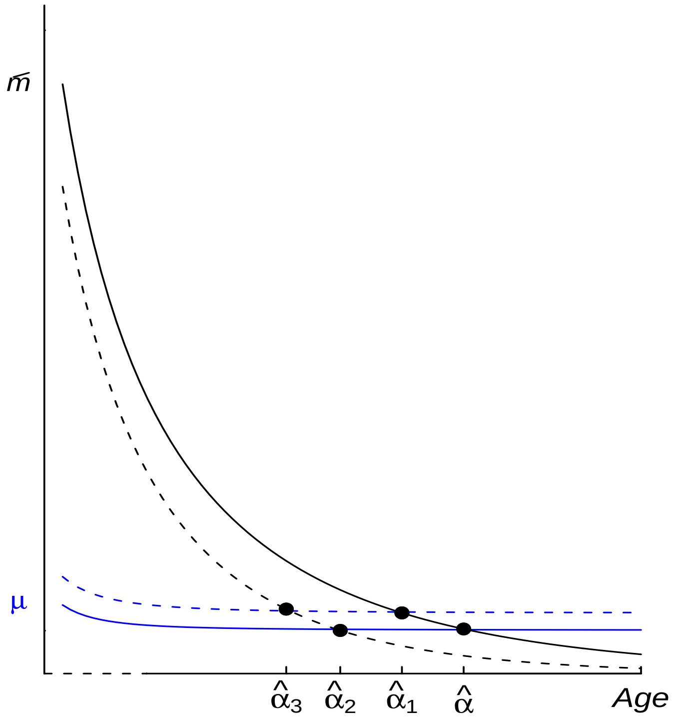


Figure 2: If $r = 0$, then at the optimal age at reproduction, the force of mortality $\mu(a)$ (blue line) is equal to the rate of growth of reproductive capacity $\acute{m}(a)$, (black line). The equilibrial optimum decreases if conditions worsen as a result of increased mortality ($\hat{\alpha}_1$) or a decreased rate of growth in reproductive potential ($\hat{\alpha}_2$) or both ($\hat{\alpha}_3$). We produced the graph by using (18)-(20), with $k = 5$, $\kappa = 0.9$, $\eta = 3$, $b = 4.2$, $c = 0.3$ and $\phi = 1$ for the best environment. We set $\kappa = 1.4$ to slow growth and $c = 0.4$ to increase mortality.

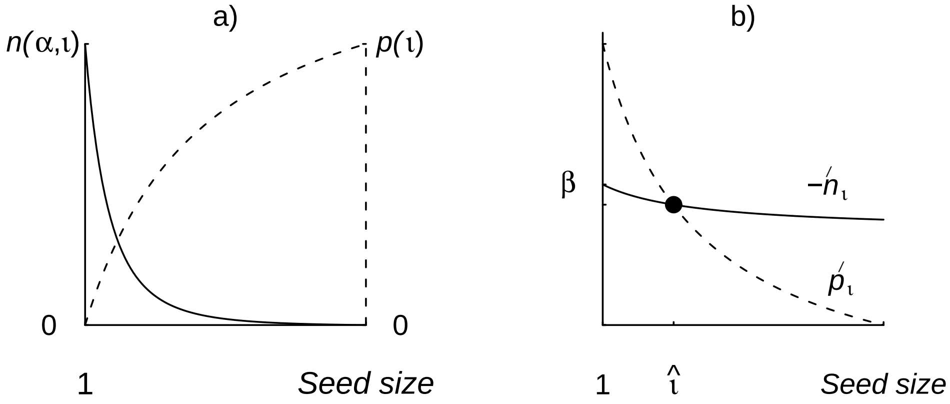


Figure 3: a) $n(\alpha,\iota)$ is the number of offspring of size ι produced by individuals reproducing at age α (solid line) and $p(\iota)$ is the probability of surviving until recruitment (dashed line). b) If the population growth rate $r = 0$, then at the optimal offspring size $\hat{\iota}$, the force of offspring mortality $\acute{p}(\iota)$ (dashed line) is equal to the rate of decrease with seed size of offspring number $-\acute{n}_\iota(\alpha,\iota)$ (full line). To produce the graph it was assumed that $n(\alpha,\iota) = m(\alpha)/(\iota^\beta)$, $m(\alpha)$ as in (19) and β is an elasticity parameter capturing economies or diseconomies of scale in producing more offspring. In this case $\acute{n}_\iota(\alpha,\iota) = -\beta/\iota$ and at equilibrium, the optimal offspring size is defined by $\acute{p}(\hat{\iota}) = \beta/\hat{\iota}$.

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Acknowledgements:

The authors thank David Thomson and Kenneth Wachter for their helpful comments and suggestions.