

Evolution of Delayed Reproduction in Uncertain Environments: A Life-History Perspective

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ABSTRACT: Environmental uncertainty alone can select for delayed reproduction; however, its relative role in the evolution of delayed reproduction across life histories is not known. Along a life-history spectrum from low-survival/high-fertility species to high-survival/low-fertility species, we show that the latter are more likely to evolve delayed reproduction if fertility varies over time. By contrast, if survival varies over time, low-survival life histories are more likely to evolve delays. If there is variation in both survival and fertility, and if this variation is positively associated, the evolutionarily stable reproductive delay is decreased (relative to independent variation in survival and fertility). Conversely, if variation in survival and fertility is negatively associated, the evolutionarily stable reproductive delay is increased. We further show that environmental uncertainty can drive the evolution of delayed reproduction in an iteroparous organism but only in the special case where juvenile survival is greater than adult survival. For common iteroparous life histories (adult survival > juvenile survival), environmental uncertainty does not select for delayed reproduction. Thus, any benefits that delayed reproduction might have on reproduction or survival could be especially important in explaining the common observation of delayed reproduction in many vertebrates and perennial plants.

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A broad range of species delay the onset of first reproduction. In many plant species, seed dormancy considerably extends the period before reproduction, and in invertebrates, juvenile diapause and dauer states play similar roles. In most plant and animal species, gradual forms of developmental delay (e.g., growth and behavioral acquisition) can also lead to delayed reproduction (Stearns 1992). In a seminal article, Cole (1954) proposed that delayed reproduction has a more influential effect on fitness than other demographic traits, thus spurring interest in the study of its evolution (e.g., Lewontin 1965; Cohen 1966; McLaren 1966; Gadgil and Bossert 1970; Oli and Dobson 2003; Rees et al. 2006). Delayed reproduction also affects the evolution of other life-history traits, such as age-specific survival and fertility (Hamilton 1966), and is thus of central interest in the field of life-history evolution.

Early fascination with reproductive delay stemmed from the fact that, even in the absence of mortality, delayed onset of reproduction is never adaptive in a constant environment. Early investment in the next generation produces a greater future return on rate-sensitive currencies of fitness (e.g., λ , r) than postponed investment does (Cole 1954; Tuljapurkar 1990). Thus, delayed reproduction can evolve in a constant environment only if it confers a benefit to reproduction or survival that is sufficient to counter the inherent cost of delayed reproduction (i.e., a life-history trade-off). For example, delayed reproduction is advantageous in many plants and animals when it results in growth to a larger size at maturity and, subsequently, a greater reproductive output (e.g., Schaffer and Rosenzweig 1977; Bell 1980; Roff 1981, 1984, 1986; Stearns and Crandall 1981, 1984).

Evolution, however, takes place in changing environments, and the effects of environmental uncertainty (i.e., stochastic variation over time in climate, predators, food resources, etc.) can drastically alter life-history evolution in quantitative and qualitative ways (e.g., Orzack 1993).

Most often, delayed onset of reproduction is polyphenic (i.e., variable across individuals; akin to being a probabilistic process), and in such cases Tuljapurkar (1990) demonstrated that environmental uncertainty alone can drive the evolution of delayed reproduction in structured populations. In essence, polyphenic delay in a life cycle creates a form of bet hedging whereby a female's offspring are spread across future stage classes. This reduces variance in expected fitness, which in turn maximizes mean fitness in an uncertain environment (Gillespie 1974; Tuljapurkar 1982).

Tuljapurkar and colleagues demonstrated that environmental uncertainty can drive differences in delayed reproduction among populations that experience different levels of environmental stochasticity, and it can maintain polymorphisms in genes coding for delayed reproduction whenever heterozygotes have intermediate phenotypes and higher fitness than homozygotes (Tuljapurkar 1990; Tuljapurkar and Istock 1993; Tuljapurkar and Wiener 2000). Extending this area of research, Wilbur and Rudolf (2006) recently showed that selection should favor the evolution of delayed reproduction in uncertain environments even (1) when mortality occurs among individuals that delay reproduction, (2) when population density affects components of fertility, and (3) among iteroparous as well as semelparous organisms.

Nonetheless, fluctuations in resources, competition, and predation can produce temporal variation and density dependence in any vital rate (sensu Nicholson 1933), not just in fertility, which has typically been the focus (e.g., Tuljapurkar 1990; Wilbur and Rudolf 2006). Fertility and survival can also negatively covary over time when resources are limited and must be allocated among the vital rates (i.e., a trade-off), or they can positively covary when variance in resource abundance—and hence in acquisition—swamps patterns of resource allocation (van Noordwijk and de Jong 1986). A further consideration is that an organism's background of life-history characteristics (e.g., parity, fertility, juvenile survival, and adult survival) moderate the net cost of delayed reproduction and should thus have a strong effect on its evolution. Greater attention needs to be paid to these ecological and life-history realities in order to provide empirical researchers with more specific predictions of how environmental uncertainty should affect the evolution of delayed reproduction.

To address these research needs, we developed stage-based matrix models that explicitly separate the effects of environmental uncertainty and density dependence. Using these models, we conducted sequential invasibility analyses to examine how all of the life-history and environmental features mentioned above affect evolutionarily stable (ES) probabilities of delayed reproduction in uncertain environments. Our findings clarify how environmental un-

certainty can drive the evolution of delayed reproduction across a continuum of life histories in the presence of density dependence, iteroparity, and covariation between fertility and survival, or lack thereof.

Methods

Demographic Models

To model the evolutionary dynamics of organisms that can delay reproduction and to address each of our objectives, we began with a simple density-independent two-stage matrix projection model (Neubert and Caswell 2000):

$$\begin{bmatrix} J(t+1) \\ A(t+1) \end{bmatrix} = \begin{bmatrix} S_J p & F \\ S_J(1-p) & S_A \end{bmatrix} \begin{bmatrix} J(t) \\ A(t) \end{bmatrix}. \quad (1a)$$

Its corresponding difference equations are

$$J(t+1) = S_J p J(t) + F A(t), \quad (1b)$$

$$A(t+1) = S_J(1-p) J(t) + S_A A(t). \quad (1c)$$

In these equations, J and A represent the respective abundances of juveniles and adults, S_J and S_A are the corresponding probabilities of surviving from time step t to $t+1$, p is the probability that a juvenile will delay transition to adulthood (i.e., delay of first reproduction), and F denotes adult fertility (i.e., the number of newly produced juveniles per adult). Generations overlap when either $p > 0$ or when $S_A > 0$. To keep the model as general as possible, we made no assumptions about the lower-level vital rates constituting F , as these differ among species. Similar to Wilbur and Rudolf (2006), we assumed the same S_J value for individuals that delay reproduction and those that do not. When $S_J < 1$, delayed reproduction has two costs: the cost of delayed investment in the next generation and the risk of mortality during this period of delay. Because we were interested in the effects of environmental uncertainty and the background of life-history characteristics on the evolution of delayed reproduction, we did not include any direct benefits for delayed reproduction in our model.

To include the density-regulating forces of competition and predation, we used the Ricker function to separately model density regulation of fertility:

$$\begin{bmatrix} J(t+1) \\ A(t+1) \end{bmatrix} = \begin{bmatrix} S_J p & F e^{-aN(t)} \\ S_J(1-p) & S_A \end{bmatrix} \begin{bmatrix} J(t) \\ A(t) \end{bmatrix}, \quad (2a)$$

juvenile survival:

$$\begin{bmatrix} J(t+1) \\ A(t+1) \end{bmatrix} = \begin{bmatrix} S_J e^{-aN(t)} p & F \\ S_J e^{-aN(t)} (1-p) & S_A \end{bmatrix} \begin{bmatrix} J(t) \\ A(t) \end{bmatrix}, \quad (2b)$$

and adult survival:

$$\begin{bmatrix} J(t+1) \\ A(t+1) \end{bmatrix} = \begin{bmatrix} S_J p & F \\ S_J (1-p) & S_A e^{-aN(t)} \end{bmatrix} \begin{bmatrix} J(t) \\ A(t) \end{bmatrix}. \quad (2c)$$

This allowed us to compare the fitness consequences of density dependence in each vital rate and also to compare density-dependent dynamics with density-independent dynamics. In these equations, the exponential function is denoted by e , a determines the strength of density dependence (a always = 0.001), and, for simplicity, we assumed that vital rates were regulated by total abundance, $N(t) = J(t) + A(t)$, rather than by abundance of specific life-cycle stages.

Modeling Environmental Uncertainty

To examine the effects of environmental uncertainty on evolutionary dynamics, we first modeled temporal variation in each vital rate separately. Because fertility is always ≥ 0 , we simulated random temporal sequences of $F(t)$ using a gamma distribution. Survival probabilities, on the other hand, are bounded between 0 and 1. Therefore, we simulated random sequences of $S_J(t)$ and $S_A(t)$ using beta distributions. The maximum variance (and coefficient of variation [CV]) of a probability is also constricted and is directly related to the expected value. For example, the maximum CV for an expected value of 0.50 is 1, whereas the maximum CV for an expected value of 0.05 is 4.36. For this reason, we measured the level of uncertainty in survival relative to its maximum CV (see Morris and Doak 2004). To keep our simulations within biologically plausible levels of temporal variation in vital rates, we focused on fertility CVs between 0 and 1 and variation in survival probabilities ranging between 0% and 50% of the maximum CV. For simulations in which we considered more extreme levels of temporal variation in vital rates, see appendix B in the online edition of the *American Naturalist*.

When temporal variation in more than one of the vital rates had an effect on ES probabilities of delayed reproduction, we further examined the effects of negative and positive covariation in vital rates by creating bivariate probability distributions. This was done by (1) defining a correlation structure between two of the vital rates mentioned above and (2) using a copula (sensu Sklar 1959) to link the univariate marginal distributions of relevant vital rates (e.g., to link the gamma distribution of $F(t)$ with the beta distribution of $S_J(t)$). All correlation coefficients between -1 and 1 were considered, and stochastic se-

quences of correlated vital rates were generated from the bivariate distributions (see app. A in the online edition of the *American Naturalist* for annotated Matlab code that steps through the general procedure of using a copula).

We then substituted temporal sequences of vital rates for each of the above-mentioned scenarios (univariate and bivariate cases) into our density-independent matrix models, making them temporally stochastic:

$$\mathbf{N}(t+1) = \mathbf{A}(t)\mathbf{N}(t), \quad (3)$$

or into the density-dependent matrix models (e.g., substituting $F e^{-aN(t)}$ with $F(t)e^{-aN(t)}$), making them nonlinear and temporally stochastic:

$$\mathbf{N}(t+1) = \mathbf{A}(t, N(t))\mathbf{N}(t). \quad (4)$$

In the former, the vital rates in \mathbf{A} depend on the environment at time t ; in the latter, they depend on the environment at time t and total abundance $N(t)$. The effects of density ($e^{-aN(t)}$) were modeled separately from density-independent sources of temporal variation in each vital rate (e.g., $F(t)$). This allowed us to examine density dependence and density-independent temporal variability in the same vital rate (e.g., $F(t)e^{-aN(t)}$) or in separate vital rates (e.g., density dependence in juvenile survival and density-independent temporal variation in fertility). Beverton-Holt functions for density dependence ($x(t)/(1 + aN(t))$, where x denotes any vital rate) were also considered for each scenario; however, ES probabilities of delayed reproduction arising from Beverton-Holt simulations were nearly identical to those from Ricker simulations. Thus, we focused primarily on Ricker functions for modeling density dependence.

Life Histories

Our demographic models (eqq. [1]–[4]) encompass both semelparous and iteroparous life histories. When $\bar{S}_A = 0$ (where \bar{x} denotes expected value), adults are truly semelparous and equation (1c) reduces to $A(t+1) = S_J(1-p)J(t)$. Conversely, increasing \bar{S}_A increases a life history's level of iteroparity.

Capitalizing on this flexibility of the models, we considered a continuum of semelparous and iteroparous life histories. We simulated semelparous life histories ranging from low chances of survival ($\bar{S}_J = 0.05$) and high reproductive output to high chances of survival (\bar{S}_J as high as 0.95) and low reproductive output. Two contrasting sets of iteroparous life histories were considered. In one, juvenile survival was less than adult survival and imposed a “high cost” on delayed reproduction, which is typical of vertebrates and many perennial plants. Life histories of

adults ranged from low survival ($\bar{S}_A = 0.05$) and high reproductive output to high survival (\bar{S}_A as high as 0.95) and low reproductive output. In the other set, juvenile survival was greater than adult survival, thus imposing a “low cost” on delayed reproduction, which might be representative of terrestrial invertebrates in which larval stages are more protected from predation than adults. Cavi-morph rodents may also follow this life-history pattern (Kraus et al. 2005). Across iteroparous life histories with a low cost of delayed reproduction, \bar{S}_j ranged between 0.05 and 0.95. A value of \bar{F} was always chosen such that each life history had an equivalent and positive fitness (0.02) when $p = 0$ in a constant environment with negligible effects of density. The same \bar{F} value was used in all stochastic and density-dependent environments. For simulations in which a value of \bar{F} was instead chosen such that life histories always had fitnesses of 0.02 when $p = 0$, regardless of the level of environmental uncertainty, see appendix C in the online edition of the *American Naturalist*.

Invasion Analysis

For each life-history and environmental scenario described above, we were interested in finding the stochastic ES level of p , denoted by p^* . To find p^* , an appropriate measure of fitness in an uncertain environment must be assigned to each competing phenotype (i.e., each p in the set $0 \leq p \leq 1$).

For density-independent populations in uncertain environments, we projected abundance over time using equation (3) and estimated fitness for each level of p with the stochastic population growth rate:

$$\ln \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} \ln(N(t)), \quad (5)$$

which was estimated using $\ln \lambda_s = (1/T) \sum_{t=0}^{T-1} g(t)$ (Heyde and Cohen 1985; $g(t) = \ln(N(t+1)/N(t))$, where $T = 100,000$ refers to the time horizon and $t = 0$ refers to a time after which transient dynamics were discarded). In our use, the stochastic population growth rate measures the rate of invasion of a new phenotype p_i into the resident population p_r . At the genetic level, $\ln \lambda_s$ represents the invasion rate of a new allelic mutation that alters the phenotype of p_i into the resident genotype. The level of p conveying maximal $\ln \lambda_s$ is therefore defined as p^* , which was found by performing a numerical search.

For novel invading phenotypes that face uncertain environments and competition or predation, the eventual success or failure of invasion depends on population density. To find p^* in density-dependent uncertain environments, we first chose a starting value for the resident phe-

notype p_r . We then defined the resident’s dynamics by iterating its demography through equation (4) such that it could reach its equilibrium and then continued the iteration for T time steps to obtain a sequential series of the resident’s dynamics. Next, we projected the evolutionary dynamics for a range of invaders ($0 \leq p_i \leq 1$) using a modification of equation (4):

$$N_i(t+1) = A_i(t, N_r(t))N_i(t), \quad (6)$$

in which an invader’s vital rates A_i depend on the environment at time t and total density of the resident $N_r(t)$ (we assume that effects of the invader’s density on itself and the resident are negligible because it invades from very low density; Metz et al. 1992). Each invader’s fitness was then measured with the invasion exponent:

$$\vartheta = \lim_{t \rightarrow \infty} \frac{1}{t} \ln(N_i(t)). \quad (7)$$

The only difference between equation (5) and equation (7) is that, in the calculation of ϑ , the invader’s vital rates depend on total density of the resident at each time step, $N_r(t)$ (eq. [7] was estimated in like manner as eq. [5]). Mathematically, ϑ is the dominant Lyapunov exponent of equation (7) and is on the same numeric scale as $\ln \lambda_s$. Invasion will succeed if $\vartheta > 0$ and will fail if $\vartheta \leq 0$ (Metz et al. 1992). Among invading phenotypes that could successfully invade the resident, the one with the greatest ϑ value was set as the new resident and the steps described above were repeated (always using the same set of uncertain environmental conditions) until we identified a phenotype that could not be invaded by any other (i.e., a “while” statement was run until the difference between p_i and the most fit p_i was less than 1×10^{-5}), which by definition is p^* (Metz et al. 1992; Metcalf and Pavard 2007).

Results

Density-Independent Dynamics

Semelparous Life Histories. Among semelparous life histories with density-independent dynamics, the evolutionary advantage of delayed reproduction generally increased with environmental uncertainty in fertility (e.g., see symbols in fig. 1, which denote p^* in different environments). Fitness landscapes were broader in highly variable environments, leading to a variety of phenotypes in the neighborhood of p^* with similar fitness. In addition, the temporal dynamics of stage structure for phenotypes with p values slightly greater than 0 often resulted in those phe-

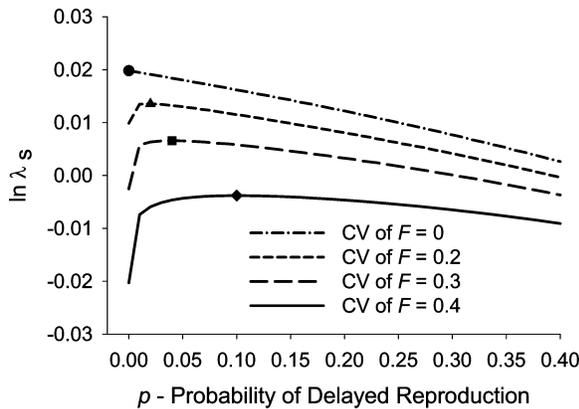


Figure 1: An example depicting fitness ($\ln \lambda_s$) of competing p phenotypes in four populations of semelparous organisms ($\bar{S}_j = 0.95$ and $\bar{F} \approx 1.10$ in each scenario) that experience different levels of temporal variation in fertility (F ; coefficient of variation [CV] of F). Symbols denote the evolutionarily stable probability of delay p^* in each environment.

notypes having much greater fitness than phenotypes with $p = 0$ (e.g., fig. 1).

Adding to these basic results, we found that interspecific patterns of p^* across life histories changed according to the vital rate(s) that varied with environmental uncertainty. Increased temporal variation in fertility increased p^* much more rapidly for semelparous life histories with a low cost of delayed reproduction (i.e., high \bar{S}_j) than for those with a high cost (i.e., low \bar{S}_j ; fig. 2). Contrary to these findings, increased temporal variation in juvenile survival increased p^* much more rapidly in semelparous life histories with a high average cost of delayed reproduction (i.e., low \bar{S}_j) compared with those with a low average cost (i.e., high \bar{S}_j ; fig. 3). In both cases, each life history's p^* eventually reached an asymptote as environmental uncertainty approached extreme levels (figs. B1, B2).

When $F(t)$ and $S_j(t)$ varied together in an independent fashion, the evolved pattern of p^* across life histories exhibited a combination of the aforementioned results (e.g., fig. 4, *black line*). Relative to this scenario, positive temporal covariation between $F(t)$ and $S_j(t)$ resulted in the evolution of lower p^* values across life histories, whereas negative covariation led to the evolution of higher p^* values (e.g., fig. 4).

Iteroparous Life Histories. Contrary to the results for semelparous life histories, delayed reproduction never evolved in any of the iteroparous life histories with a high cost of delayed reproduction (i.e., $p^* = 0$ for all life histories with $\bar{S}_j < \bar{S}_A$ at all levels of temporal variation in $F(t)$, $S_j(t)$, or $S_A(t)$), nor did it evolve in any of the life histories with a

low cost of delayed reproduction (i.e., $\bar{S}_j > \bar{S}_A$) when $S_j(t)$ or $S_A(t)$ varied over time. Only large amounts of temporal uncertainty in $F(t)$ could overcome the existing environmental buffer of iteroparity to drive the evolution of delayed reproduction in life histories with a low cost of delayed reproduction (figs. 5, B3).

Density-Dependent Dynamics

Semelparous Life Histories. Among semelparous life histories, density dependence in fertility or juvenile survival introduced novel sources of temporal variation in life history (in addition to the density-independent sources of variation in $F(t)$, $S_j(t)$, or covariation in both) that had a slight effect on quantitative levels of p^* across life histories. Nevertheless, relationships between life history, temporal (co)variation in vital rates, and p^* (not shown) were very similar to the corresponding density-independent results described above (figs. 2–4).

Iteroparous Life Histories. In the presence of density dependence in fertility, juvenile survival, or adult survival, delayed reproduction never evolved in iteroparous life histories with a high cost of delay (i.e., $p^* = 0$ at all levels of temporal variation in $F(t)$, $S_j(t)$, or $S_A(t)$). Furthermore, delayed reproduction did not evolve in any iteroparous life history with a low cost of delay when $S_j(t)$ or $S_A(t)$ varied over time in the presence of density dependence in $F(t)$, $S_j(t)$, or $S_A(t)$. Delayed reproduction, however, did evolve in the low-cost life histories when $F(t)$ was highly variable over time and $F(t)$, $S_j(t)$, or $S_A(t)$ was density dependent. Furthermore, all interspecific patterns (not

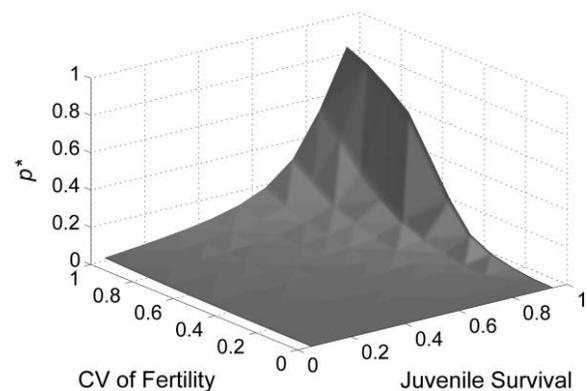


Figure 2: Evolutionarily stable probabilities of delayed reproduction (p^*) across semelparous life histories and increasing levels of temporal uncertainty in fertility (F ; depicted by the coefficient of variation [CV]). Note that this is not a fitness surface; rather, the Z-axis represents p^* for a wide variety of life histories and temporal variation in fertility.

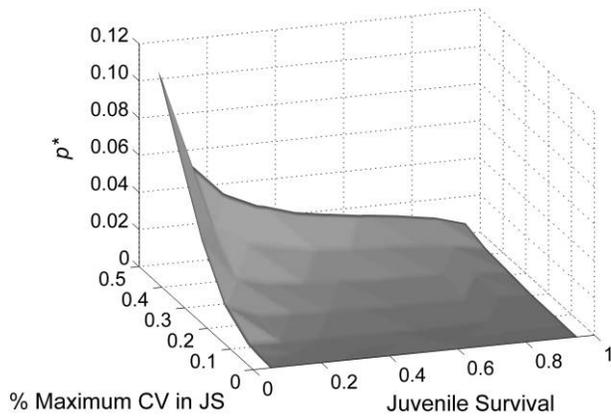


Figure 3: Evolutionarily stable probabilities of delayed reproduction (p^*) across semelparous life histories and increasing levels of temporal uncertainty in juvenile survival (JS; depicted by percentage of the maximum coefficient of variation [CV] in JS that is possible for each life history).

shown) were similar to the density-independent results (figs. 5, B3).

Discussion

It has long been known that delayed reproduction can evolve if the cost of waiting is repaid with a benefit of increased fecundity (McLaren 1966). If no direct payoff occurs, the advantage of delaying is less transparent, but is still amenable to evolutionary analysis. In the same year as McLaren's (1966) article, Cohen (1966) showed that, in the absence of any benefit to reproduction or survival, temporal uncertainty in fecundity (a component of fertility in our model) can drive the evolution of delayed reproduction. These two seminal papers led the way for modern evolutionary studies of delayed reproduction. However, because past studies have focused on just a handful of life histories, it has been impossible to determine whether environmental uncertainty can drive the evolution of delayed reproduction in all types of organisms. Here, by examining a continuum of life histories in different types of uncertain environments, we have shown that environmental uncertainty can drive the evolution of delayed reproduction in all semelparous organisms and in a special case of iteroparity in which juveniles have a higher probability of survival than adults (which occurs in some terrestrial invertebrates). Interestingly though, environmental uncertainty cannot drive the evolution of delayed reproduction in common types of iteroparous organisms whose adults have a greater probability of survival than juveniles (e.g., most vertebrates and perennial plants) and do not have a fixed limit to life span.

Past work suggests that delayed reproduction evolves in

semelparous organisms facing environmental uncertainty in fertility (i.e., reproductive output) because delay creates a stage structure that would not otherwise exist in a semelparous life history. The addition of a population structure ensures that the offspring of a given cohort are spread across future generations, which can enhance fitness in a stochastic environment by creating a buffer against the effects of poor reproductive conditions (fig. 1; Tuljapurkar 1990; Tuljapurkar and Istock 1993; Tuljapurkar and Wiener 2000; Wilbur and Rudolf 2006). Adding to past work, we have shown that the expected value of juvenile survival has a strong influence on ES probabilities of delayed reproduction (p^*) because it affects the cost of delay. Across populations inhabiting a spectrum of increasingly stochastic environments, semelparous organisms with a low cost of delay (i.e., high \bar{S}_j) should exhibit rapidly increasing p^* until an upper asymptote is reached in extremely stochastic environments (figs. 2, B1). Climate change is expected to lead to increasingly variable environments (Karl and Trenberth 2003; Jain et al. 2005; Salinger 2005), and thus, given adequate genetic variation, we might expect a single population's optimal delay p^* to increase in the future. Organisms with a high cost of delay (low \bar{S}_j), on the other hand, should not exhibit delayed reproduction unless they inhabit environments where fertility is highly stochastic; even still, p^* is not expected to be as great as it would be for low-cost life histories in a comparable environment (fig. 2).

Temporal uncertainty in survival, however, can lead to the evolution of a different form of bet hedging in semelparous organisms. Across environments of increasing

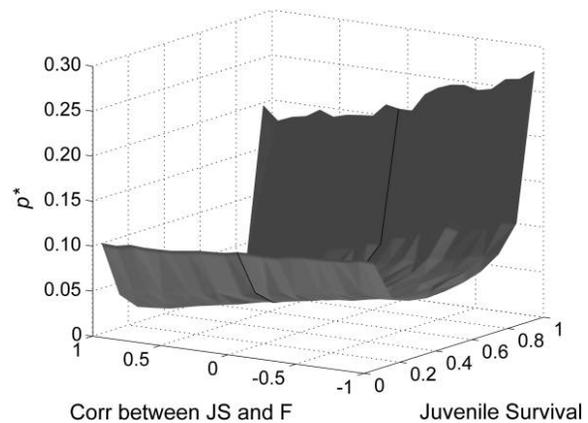


Figure 4: An example of evolutionarily stable probabilities of delayed reproduction (p^*) across semelparous life histories and different levels of correlation (Corr) between juvenile survival (JS; percent of maximum coefficient of variation [CV] = 0.50) and fertility (F ; CV = 0.50) over time. The black line indicates independent temporal variation in JS and F .

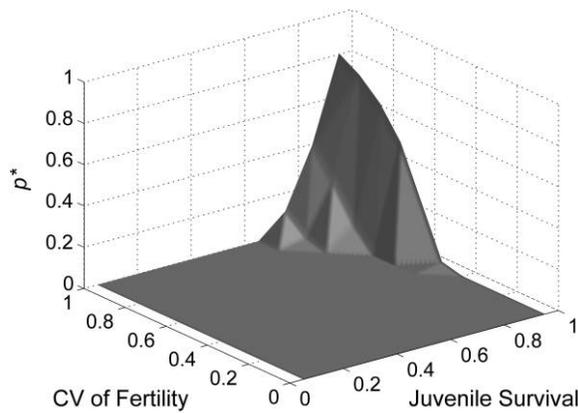


Figure 5: Evolutionarily stable probabilities of delayed reproduction (p^*) across the “low-cost” iteroparous life histories (see “Methods” for description of life histories) and increasing levels of temporal uncertainty in fertility.

uncertainty in the probability of survival, we found that p^* actually increased more rapidly in semelparous organisms with a high average cost of delayed reproduction, relative to those with a low average cost (fig. 3). In organisms with low \bar{S}_j , temporal variability in survival can lead to situations where $S_j(t)$ sometimes approaches 0. In such instances, a phenotypic strategy without polyphenic delay in reproduction rapidly becomes extinct because all juveniles attempt to recruit at the same time, but few successfully make it, resulting in catastrophically low recruitment to the adult reproductive stage. A strategy with polyphenic delay in reproduction, however, spreads the risk of offspring attempting recruitment in dangerous times (e.g., years of high predation). Polyphenic delay can therefore result in a reserve of individuals surviving a bad time step that can take advantage of potentially very good survival conditions in future time steps as they attempt recruitment, thereby enhancing the long-term recruitment rate and fitness of the strategy. Consequently, life histories with low \bar{S}_j values more readily evolved delayed reproduction when faced with uncertainty in survival (fig. 3) because they had so much more to gain from delayed reproduction relative to life histories with high \bar{S}_j values and not because they experienced a lesser cost of delay (quite the contrary; they experienced a higher cost).

Simultaneous variation in fertility and survival over time should thus lead to both low-cost and high-cost life histories evolving greater p^* values relative to semelparous life histories with moderate costs (i.e., \bar{S}_j near 0.5; fig. 4, *black line*). Temporal covariation between survival and fertility did not alter this life-history pattern in our simulations; however, it did alter the quantitative values of p^* . One might intuitively expect positive covariation between

survival and fertility to have the same variance-magnifying effect as positive autocorrelation in environmental conditions. For example, Tuljapurkar (1990) found that the temporal variance of fertility in iteroparous organisms was augmented by positive autocorrelation in a stochastic environment, which consequently led to the evolution of greater p^* values. However, we found just the opposite: positive covariation between $F(t)$ and $S_j(t)$ had an uncertainty-dampening effect and led to the evolution of smaller p^* values. On the other hand, negative covariation (representative of the classical fertility-survival trade-off) led to the evolution of greater p^* values (fig. 4). Interestingly, density dependence in either $F(t)$ or $S_j(t)$ never affected the qualitative pattern of our results and had little effect, if any, on quantitative values of p^* in each life-history and environmental scenario. Thus, the effects of population density on the evolution of delayed reproduction may have a lesser importance than some have suggested (e.g., Ellner 1985; Wilbur and Rudolf 2006; Ratikainen et al. 2008).

Iteroparity can also buffer a life history against environmental uncertainty (Orzack and Tuljapurkar 1989), and previous research suggests that natural selection should opt for either delayed reproduction or iteroparity, but not both, in an uncertain environment (Tuljapurkar and Wiener 2000). However, using a model similar to ours, Wilbur and Rudolf (2006) recently challenged this idea and demonstrated simultaneous selection for increased delay in the onset of both reproduction and iteroparity. Our results, however, show that this can occur only in special circumstances. Wilbur and Rudolf (2006) considered a handful of iteroparous life histories where juveniles had a greater probability of survival than adults (i.e., $\bar{S}_j > \bar{S}_A$, which occurs in some terrestrial invertebrates), as well as situations where environmental variability affected fertility but not juvenile or adult survival. As juvenile survival becomes greater than adult survival, an iteroparous life history nears the realm of semelparity (Neubert and Caswell 2000), and thus, temporal uncertainty in fertility affects the evolution of p^* in much the same way it does across semelparous life histories (figs. 2 and 5). It just takes greater stochasticity in the environment for delayed reproduction to overcome the existing buffer of iteroparity and become adaptive. Similarly, the degree of iteroparity can be decreased by placing a short, finite limit to adult life span in a model, which also allows for an iteroparous life history to evolve delayed reproduction in an uncertain environment (Tuljapurkar 1990, p. 1,141; D. N. Koons, unpublished data). However, life expectancies of iteroparous organisms seem to be quite plastic (e.g., Oeppen and Vaupel 2002), and thus, it may not be realistic to fix life span in evolutionary models (e.g., our model does not). Furthermore, fertility conditions, not survival probabilities, must be uncertain for delayed reproduction to evolve

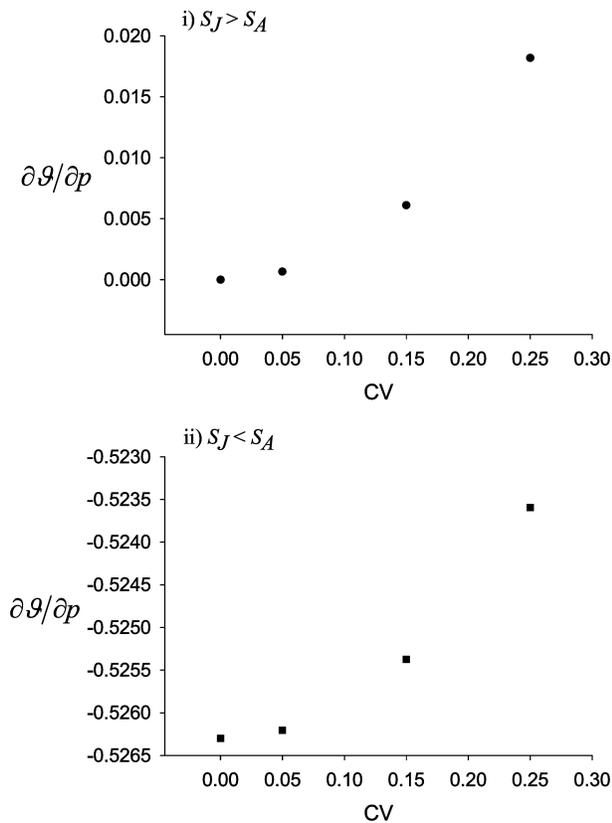


Figure 6: Sensitivity of the invasion exponent ϑ with respect to changes in delayed reproduction p (i.e., directional selection gradients on p) for (i) a set of “low-cost” iteroparous parameters $S_J > S_A$ in Wilbur and Rudolf’s (2006) model (clutch size $C = 12$, $a = 0.001$, survival from metamorphosis to age 1 $S_M = 0.3$, $S_J = 1$, $S_A = p = 0.7$) relative to (ii) a set of “high-cost” iteroparous parameters where $S_J < S_A$ ($C = 12$, $a = 0.001$, $S_M = 0.3$, $S_J = 0.5$, and $S_A = p = 0.7$). Wilbur and Rudolf (2006) always considered $S_J > S_A$ and focused mainly on modeling environmental uncertainty by changing the coefficient of variation (CV) in a , which controls the strength of density dependence according to a normal distribution (also done in i and ii). Note that our parameter p is equivalent to Wilbur and Rudolf’s (2006) parameter b .

in an iteroparous organism with $\bar{S}_J > \bar{S}_A$. We found that the very existence of iteroparity conveys buffering capabilities that delayed reproduction cannot overcome in an environment where survival chances (juvenile or adult) are uncertain (i.e., $p^* = 0$ in stochastic survival simulations).

Moreover, no matter the level of temporal stochasticity in $F(t)$, $S_J(t)$, or $S_A(t)$ we simulated, and no matter which vital parameter was affected by population density, delayed reproduction never evolved (i.e., $p^* = 0$) in an iteroparous organism with $\bar{S}_J < \bar{S}_A$, a life-history pattern that is representative of vertebrates and perennial plants. In fact, we even recreated Wilbur and Rudolf’s model with $\bar{S}_J < \bar{S}_A$

and found that, although the strength of selection for delayed reproduction increases with the level of temporal variation in the environment, the direction of selection always remained quite negative (fig. 6), indicating that delayed reproduction is selected against when $\bar{S}_J < \bar{S}_A$. Thus, it is important to consider a large life-history parameter space when attempting to explain the mechanisms responsible for delayed reproduction.

Delayed reproduction is common in iteroparous organisms with $\bar{S}_J < \bar{S}_A$ (Shine and Charnov 1992; Franco and Silvertown 1996, 2004; Heppell 1998; Heppell et al. 2000; Sæther and Bakke 2000), but we have shown that environmental uncertainty alone cannot drive its evolution. Thus, any benefits that delayed reproduction might have on survival or reproduction might be especially important in explaining common empirical observations of delayed reproduction among vertebrates and perennial plants (e.g., late age or stage at maturity). That said, uncertainty is ubiquitous in the real world, and in order to better understand the benefits delayed reproduction might have on other vital rates, biologists should consider cost-benefit functions that change with fluctuating environmental conditions. Fluctuating trade-offs have been shown to have important consequences on the evolution of clutch size (Orzack and Tuljapurkar 2001) and survival (Metcalf and Koons 2007). Delayed reproduction should be no exception, and future studies should examine how environmental variability in the costs and benefits of delayed reproduction influence its evolution, especially in vertebrates and perennial plants.

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