The evolution of intermittent breeding

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Abstract A central issue in life history theory is how organisms trade off current and future reproduction. A variety of organisms exhibit intermittent breeding, meaning sexually mature adults will skip breeding opportunities between reproduction attempts. It's thought that intermittent breeding occurs when reproduction incurs an extra cost in terms of survival, energy, or recovery time. We have developed a matrix population model for intermittent breeding, and use adaptive dynamics to determine under what conditions individuals should breed at every opportunity, and under what conditions they should skip some breeding opportunities (and if so, how many). We also examine the effect of environmental stochasticity on breeding behavior. We find that the evolutionarily stable strategy (ESS) for breeding behavior depends on an individual's expected growth and mortality, and that the conditions for skipped breeding depend on the type of reproductive cost incurred (survival, energy, recovery time). In constant environments there is always a pure ESS, however environmental stochasticity and deterministic population fluctuations can both select for a mixed ESS. Finally, we compare our model results to patterns of intermittent breeding in species from a range of taxonomic groups.

Keywords evolutionarily stable strategy, intermittent breeding, low frequency reproduction, skipped spawning

1 Introduction

One of the central issues of life history theory concerns the timing of reproduction. Past theoretical work has addressed the problem of whether to reproduce once or multiple times (Cole, 1954; Charnov and Schaffer, 1973), at what age to start reproducing (Wittenberger, 1979; De Roos and Persson, 2001; Gårdmark et al, 2003), as well as to what extent multiple semelparous strategies can coexist within a population (Mylius and Diekmann, 2001; Davydova et al, 2003; Diekmann et al, 2005). However in many iteroparous species, sexually mature adults will skip breeding opportunities in between reproduction events, a behavior known as 'intermittent breeding' (e.g., Calladine and Harris, 1997) or 'low-frequency reproduction' (e.g., Bull and Shine, 1979).

This is thought to occur for two main reasons – either due to a physiological or physical constraint, or due to an adaptive response to a life-history tradeoff. Individuals can be constrained by a reproductive cycle that lasts for more than 12 months (e.g., blue king crabs – Jensen and Armstrong 1989; king penguins – Le Bohec et al 2007; blacktip sharks – Castro 1996; snow skinks – Olsson and Shine 1999) or constrained by limited access to breeding sites due to either environmental conditions (e.g., inclement weather in snow petrels – Chastel et al 1993) or social factors (e.g., competition in Eurasian oystercatcher – Bruinzeel 2007). Tradeoffs can be among a number of factors relating to survival, growth and fecundity, but all stem from the general tradeoff that parents face between current reproductive success and future potential reproduction (the prudent parent hypothesis; Drent and Daan 1980). Within the bird literature the individual heterogeneity in quality hypothesis is often invoked to explain the coexistence of breeding and non-breeding individuals within a single population where non-breeding individuals are often of 'poorer quality' (e.g., Bradley et al, 2000; Cam and Monnat, 2000). However this hypothesis addresses the existence of variance in strategies across a population, and not the motivation for non-breeding individuals to skip reproduction.

In this paper, we present a model for the evolution of intermittent breeding. We determine under what conditions individuals should breed at every opportunity, and under what conditions they should skip some breeding opportunities (and if so, how many). We also examine the effect of environmental stochasticity and deterministic population fluctuations on breeding behavior. In a previous paper, we studied intermittent breeding in the context of breeding migrations and limited our analysis to the situation where individuals could either reproduce annually or skip at most one year before reproducing (Shaw and Levin, 2011). Here we extend both the biological context as well as the mathematical analysis, allowing individuals to skip any number of years between reproduction attempts.

2 Intermittent breeding

Intermittent breeding is most commonly exhibited by long-lived species that have a costly 'accessory' activity associated with reproduction (e.g., breeding migration, live bearing, egg brooding – Bull and Shine 1979). The accessory cost can be in terms of survival (e.g., higher mortality during reproduction), time (e.g., recovery period post-breeding), or energy (e.g., energy cost of incubating eggs). We allow for these different types of costs in our model and discuss our results in terms of each cost type below. To account for the case where reproduction incurs a survival cost, we assume that the annual survival of an individual that chooses

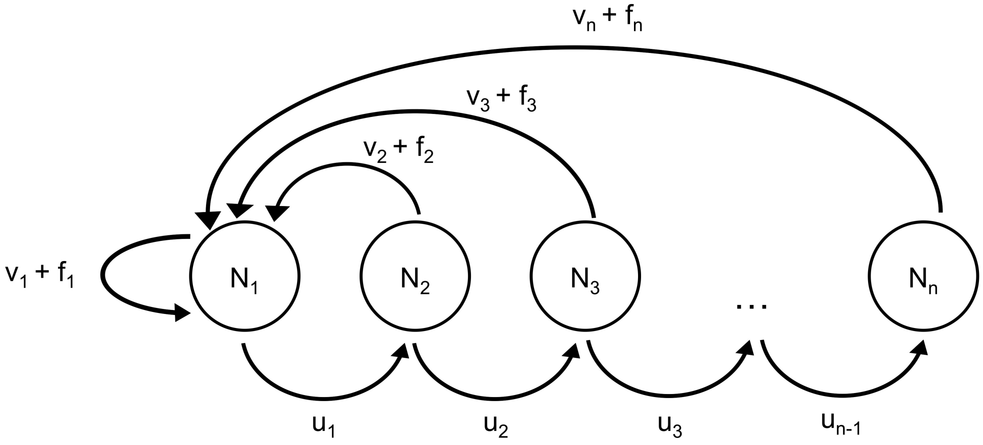

Figure 1: Life cycle graph of our n-stage matrix model (equation 1) where N_i is the number of individuals who have gone i years since last reproducing, u_i is the probability that an individual in class i chooses to skip an additional year before reproducing and survives, v_i is the probability that an individual in class i chooses to reproduce and survives, and f_i is number of juveniles born to a reproducing individual in class i.

to reproduce, σ_r, is less than or equal to that of an individual that chooses to skip reproduction, σ_s ($\sigma_r \leq \sigma_s$). Although reproducing individuals may have a lower survival, they gain the benefit of immediate reproduction (with fecundity ϕ), whereas individuals that skip must wait until a future opportunity to reproduce. In ‘capital breeding’ species, individuals can store energy across seasons to use in future breeding attempts (Bonnet et al, 1998; Stephens et al, 2009). Here we assume that the fecundity of an individual that skips an extra year is potentially higher than if it had reproduced the previous year ($\phi_i \leq \phi_{i+1}$, where ϕ_i is the fecundity of an individual that has gone i years since last reproducing). We explore several variants of the exact fecundity function Φ (the vector of ϕ_i), but generally assume that it is monotonically increasing. The question we seek to answer is, given these tradeoffs, how many breeding opportunities should an individual skip between reproduction attempts?

For an individual that has currently waited i years since it last reproduced, we denote the probability that it will now reproduce as θ_i. Alternatively it skips this breeding opportunity with probability $1 - \theta_i$. The strategy of an individual is then defined by its vector of θ_i values ($i = 1, 2, 3, \ldots$), which we denote Θ. The best strategy, if it exists, is the Evolutionarily Stable Strategy (ESS), which we denote Θ^* – the vector Θ that, when adopted by a population of individuals, cannot be invaded by a mutant with any other Θ (Maynard Smith and Price, 1973).

The model (Figure 1), is given by

$$\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t) \tag{1a}$$

where

$$\mathbf{A} = \begin{bmatrix} v_1 + f_1 & v_2 + f_2 & v_3 + f_3 & \dots & v_n + f_n \\ u_1 & 0 & 0 & \dots & 0 \\ 0 & u_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & u_{n-1} & 0 \end{bmatrix} \tag{1b}$$

and $\mathbf{N} = [N_1, N_2, \dots, N_n]$ is a vector of the number of individuals that have gone i years since reproducing. This is a discrete-time matrix population model, where time (t) corresponds to sequential potential breeding opportunities (e.g., years) and each class (N_i) corresponds to an individual's 'condition,' the number of years since it last reproduced. Here, $u_i = (1 - \theta_i)\ \sigma_s$ is the probability an individual moves up a class (skips reproduction and survives), $v_i = \theta_i\ \sigma_r$ is the probability an individual reproduces and survives, and $f_i = \theta_i\ \phi_i\ DD$ is the fecundity of a reproducing individual. We assume that the density-dependence (DD) is continuously differentiable in $\mathbf{N}$, and otherwise it can be of any form as long as

$$DD(0, \dots, 0) = 1\ , \tag{2a}$$

$$\text{and} \qquad \frac{\partial DD}{\partial N_i} < 0 \quad \forall\ N_i\ . \tag{2b}$$

This form of density-dependence can be viewed as representing either competition among adults (adults compete for a limited number of breeding sites and only those that are successful can reproduce) or as competition among eggs (all reproducing adults produce eggs, only a fraction of which survive).

In our model the only differences among individuals are the number of years since they last reproduced; we do not track individual age or size separately from this. Individuals that skip a breeding opportunity move up a condition class. All individuals that have reproduced move back into the N_1 class, having exhausted their energy stores, and all newborn individuals start in this class (see Figure 1). For species with a juvenile phase where individuals go through one or more seasons before they become sexually mature, the juvenile survival rate is included in the f_i term. For now, we assume that annual survival when skipping a breeding opportunity (σ_s) is the same, no matter how many breeding opportunities have been skipped previously, and similarly that annual survival when reproducing (σ_r) is the same, no matter how many breeding opportunities have been skipped.

3 Model Equilibria and Stability

Before we can determine the best breeding behavior strategy (the Evolutionarily Stable Strategy vector Θ^*), we first need to find the equilibria of the model (1) and their stability. In addition to the trivial equilibrium, there is a single possible non-trivial equilibrium, which is given by

$$\overline{DD} = \frac{L}{K} \tag{3a}$$

$$\text{where} \qquad L = 1 - \sum_{i=1}^{n} l_i v_i \ , \tag{3b}$$

$$K = \sum_{i=1}^{n} \theta_i \phi_i l_i \tag{3c}$$

and $l_i = \prod_{j=1}^{i-1} u_j$ is the probability that an individual skips breeding and survives to class i (with $l_1 = 1$). In this model the lifetime reproductive success, R_0, of an individual can be calculated iteratively from

$$R_0 = f_1 + v_1 R_0 + u_1 f_2 + u_1 v_2 R_0 + u_1 u_2 f_3 + u_1 u_2 v_3 R_0 + \ldots \tag{4}$$

as $R_0 = (DD)(K/L)$. At equilibrium, $R_0 = (\overline{DD})(K/L)$, which is equal to one as expected.

We can determine under what conditions this equilibrium is stable, by considering the Jacobian,

$$\mathbf{J} = \begin{bmatrix} H_1 & H_2 & H_3 & \ldots & H_n \\ u_1 & 0 & 0 & \ldots & 0 \\ 0 & u_2 & 0 & \ldots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & u_{n-1} & 0 \end{bmatrix} \tag{5a}$$

where

$$H_i = v_i + \theta_i \phi_i \overline{DD} + \left(\sum_{j=1}^{n} \theta_j \phi_j \overline{N}_j \right) \left(\left. \frac{\partial DD}{\partial N_i} \right|_{eq} \right) \ . \tag{5b}$$

At equilibrium $\overline{N}_i = l_i \overline{N}_1$, which allows us to rewrite this as

$$H_i = v_i + \theta_i \phi_i \overline{DD} + K \overline{N}_1 \left(\left. \frac{\partial DD}{\partial N_i} \right|_{eq} \right) \ . \tag{5c}$$

Note that except for the v_i term, this is structurally the same as the model considered by Levin and Goodyear (1980). We can show, using logic similar to that in Levin and Goodyear (1980), that this equilibrium exists biologically (equilibrium population size is non-negative) as long as

$$1 < \frac{K}{L} \tag{6}$$

(see Electronic Supplementary Material), or equivalently, if $R_{0V} > 1$, where R_{0V} is the lifetime reproductive success in a 'virgin' environment (one without competition, which occurs when $DD = 1$ in our model; Metz et al 2008).

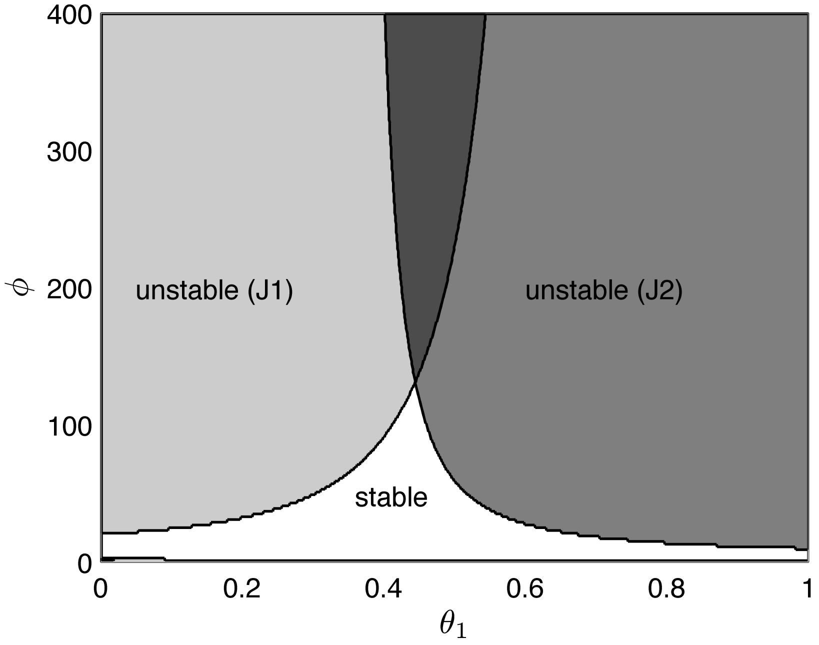

Figure 2: Stability diagram for a simple case of the model, with Ricker density-dependence, $n = 2$, $\phi_1 = \phi_2 = \phi$, $\sigma_s = 0.5$, and $\sigma_r = 0.1$. With no loss of generality, we set $\theta_2 = 1$ and only consider different values of θ_1. The boundaries of the stable region are given by the three Jury criteria: J1 ($1 + u_1\ H_2 > 0$), J2 ($1 + H_1 - u_1\ H_2 > 0$), and J3 ($1 - H_1 - u_1\ H_2 > 0$) where u_i and H_i are defined earlier in the paper. See Figure 2 in Goodyear (1980) and Figure 10 in Levin and Goodyear (1980) for similar results.

This equilibrium is stable as long as the value of K/L falls below an upper bound which, unfortunately, cannot be written down analytically, but which can be computed numerically. Above this bound, the fixed-point equilibrium will become unstable and the system goes through a series of bifurcations. In the case where $n = 2$ (and therefore $\mathbf{A}$ becomes a 2-by-2 matrix), the region of stability is delineated by three curves in $\theta_1 - \phi$ space (Figure 2), which correspond to the three Jury criteria for a 2-by-2 matrix (see Lewis 1977). Crossing the right (J2) stability curve in Figure 2 leads to a series of period-doubling bifurcations (2-cycle, 4-cycle, 8-cycle, etc), whereas crossing the left (J1) stability curve leads to more complex dynamics with higher order n-cycles or quasi-periodic solutions possible, and possibly chaotic behavior deeper into the region of instability. Simulations show that in the 'peak' of the equilibrium stable region (in Figure 2) there is also a stable 3-cycle. The stability region is largest for intermediate values of θ_1, since this is when reproduction is spread across the greatest number of classes. When all individuals reproduce immediately, θ_1 will be high, and the model is easily destabilized by high fecundity (ϕ) values. When all individuals skip many opportunities between breeding attempts, θ_1 will be low, and this time lag between reproduction events is destabilizing. For the analysis that follows, we assume this non-trivial equilibrium is stable.

4 Evolutionarily Stable Strategies

To determine the number of opportunities an individual should skip between reproduction attempts, we calculate Θ^* (the vector of ESS values of θ_i). As long as the population size is constant, we can calculate Θ^* analytically as follows (Metz et al, 1992; Ferriere and Gatto, 1995; Caswell, 2001; McGill and Brown, 2007). The growth rate of a mutant type (with $\Theta = \Theta_M$) in a resident population (with $\Theta = \Theta_R$) is governed by the matrix, $\mathbf{J}$, given by

$$\mathbf{J} = \begin{bmatrix} v_1 + \overline{f}_1 & v_2 + \overline{f}_2 & v_3 + \overline{f}_3 & \dots & v_n + \overline{f}_n \\ u_1 & 0 & 0 & \dots & 0 \\ 0 & u_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & u_{n-1} & 0 \end{bmatrix} \tag{7a}$$

where

$$u_i = (1 - \theta_{i,M})\sigma_s \tag{7b}$$
$$v_i = \theta_{i,M}\ \sigma_r \tag{7c}$$
$$\overline{f}_i = \theta_{i,M}\ \phi_i\ \overline{DD}(\Theta_R) \tag{7d}$$

and the density-dependence is a function of the resident equilibrium population size ($\overline{N}_{i,R}$) given by equation (3). Since this is a non-negative irreducible matrix, by the Perron-Frobenius theorem we know that it has a positive real dominant eigenvalue, which is the growth rate $G(\Theta_M, \Theta_R)$. The ESS is the vector Θ^* such that

$$G(\Theta^*, \Theta^*) > G(\Theta_M, \Theta^*)$$
$$\text{or}$$
$$G(\Theta^*, \Theta^*) = G(\Theta_M, \Theta^*) \qquad \text{and} \qquad G(\Theta^*, \Theta_M) > G(\Theta_M, \Theta_M) \tag{8}$$

for all values of $\Theta_M \neq \Theta_R$. To find the ESS, we consider the eigenvalues, λ, for the mutant type in an environment dominated by the resident type, which are the roots of the characteristic equation of the Jacobian

$$\lambda^n \left[1 - \sum_{i=1}^{n} \lambda^{-i}(v_i + \overline{f}_i) l_i\right] = 0\ .$$

The nontrivial eigenvalues can be found by solving the simplified equation

$$\sum_{i=1}^{n} \lambda^{-i}(v_i + \overline{f}_i) l_i = 1\ . \tag{9}$$

Since the left hand side of (9) is monotonically decreasing in λ for real λ, the value of λ that solves this equation (the dominant eigenvalue) is greater than 1 if and only if

$$\sum_{i=1}^{n} (v_i + \overline{f}_i) l_i > 1$$

or equivalently, using (3b), (3c) and (7d),

$$1 - L(\Theta_M) + K(\Theta_M)\overline{DD}(\Theta_R) > 1 \; .$$

Using equation (3a) for the density-dependence imposed by the resident type, this means that if

$$\frac{K(\Theta^*)}{L(\Theta^*)} > \frac{K(\Theta_M)}{L(\Theta_M)} \tag{10}$$

for all $\Theta_M \neq \Theta^*$, then nothing can invade and Θ^* is an ESS. Here, the ESS is the strategy that maximizes R_{0V} and hence minimizes the contribution of the density-dependence term. Therefore, our model exhibits optimization and pessimization principles, and it follows that the ESS is also continuously stable (Diekmann, 2004; Metz et al, 2008).

Considering the value of each θ_i one at a time, we can write L and K, separating out the components that depend on θ_1 from the rest, as

$$\begin{aligned} L &= 1 - \sum_{i=1}^{n} \theta_i \; \sigma_r(i) \; \sigma_s^{i-1} \left[\prod_{j=1}^{i-1} (1-\theta_j) \right] \\ &= 1 - \theta_1 \; \sigma_r(1) - (1-\theta_1) \; \alpha_1(\Theta) \end{aligned}$$

and

$$\begin{aligned} K &= \sum_{i=1}^{n} \theta_i \; \phi_i \; \sigma_s^{i-1} \left[\prod_{j=1}^{i-1} (1-\theta_j) \right] \\ &= \theta_1 \; \phi_1 + (1-\theta_1) \; \gamma_1(\Theta) \end{aligned}$$

where $\alpha_1(\Theta)$ and $\gamma_1(\Theta)$ include all the terms that depend on $\theta_2, \theta_3, \ldots, \theta_n$. Plugging these values into inequality (10), we find that the ESS value of θ_1 is

$$\theta_1^* = \begin{cases} 1 & \text{if } \phi_1 \Big(1 - \alpha_1(\Theta)\Big) > \gamma_1(\Theta) \Big(1 - \sigma_r(1)\Big) \\ 0 & \text{if } \phi_1 \Big(1 - \alpha_1(\Theta)\Big) < \gamma_1(\Theta) \Big(1 - \sigma_r(1)\Big) \; . \end{cases} \tag{11}$$

If $\theta_1^* = 1$, the value of θ_2 is irrelevant. However, if $\theta_1^* = 0$, then we can calculate θ_2^* as above. Generally, if $\theta_a^* = 0$ for all $a < b$, then θ_b^* can be calculated by rewriting L and K, separating out the components that depend on θ_b, as

$$\begin{aligned} L &= 1 - \theta_b \; \sigma_r(b) \; \sigma_s^{b-1} - (1-\theta_b) \; \alpha_b(\Theta) \\ \text{and } K &= \theta_b \; \phi_b \; \sigma_s^{b-1} + (1-\theta_b) \; \gamma_b(\Theta) \end{aligned}$$

where $\alpha_b(\Theta)$ and $\gamma_b(\Theta)$ include all the terms that depend on $\theta_{b+1}, \ldots, \theta_n$. Then θ_b^* is given by

$$\theta_b^* = \begin{cases} 1 & \text{if } \phi_b \; \sigma_s^{b-1} \Big(1 - \alpha_b(\Theta)\Big) > \gamma_b(\Theta) \Big(1 - \sigma_r(b) \; \sigma_s^{b-1}\Big) \\ 0 & \text{if } \phi_b \; \sigma_s^{b-1} \Big(1 - \alpha_b(\Theta)\Big) < \gamma_b(\Theta) \Big(1 - \sigma_r(b) \; \sigma_s^{b-1}\Big) \; . \end{cases} \tag{12}$$

By induction we can see that all θ_i^* values will be equal to either 0 or 1 and we are only concerned with the value of a θ_j^* if $\theta_{j-1}^* = 0$ (since otherwise if $\theta_{j-1}^* = 1$, the value of θ_j^* is irrelevant). Therefore the ESS strategy is $\theta_i^* = 0$ for all i except $i = j$ (all individuals reproduce after exactly j years) where j is the first value where

$$\frac{\sigma_s^{j-1}\ \phi_j}{1-\sigma_r\sigma_s^{j-1}} > \frac{\sigma_s^{j}\ \phi_{j+1}}{1-\sigma_r\sigma_s^{j}}\ . \tag{13}$$

Note that there is a limited region of parameter space in which there is no well defined ESS.

The left hand side of the inequality (13) is ratio of the growth rate to mortality rate of an individual that reproduces every j years and the right hand side is the same ratio for an individual that reproduces every $j+1$ years, so the ESS is essentially the strategy that maximizes the ratio between growth and mortality. For a given set of model parameters, there is always one best behavior – individuals should always reproduce after j years, no more no less, meaning the ESS is always a pure strategy (each θ_i^* is equal to 0 or 1).

The fundamental condition that determines whether intermittent breeding will be favored over annual reproduction (and if so how many years should be skipped between breeding attempts) is due to a tradeoff of current versus future reproduction. For a particular species, the details of this tradeoff will depend on the relative magnitude and shapes of the parameter (survival, fecundity) functions. The possibilities of interest are that: 1) fecundity may increase as a function of years skipped (if individuals can store energy across years), or it may be constant, 2) annual survival in breeding years may be the same as non-breeding survival, or it may be less (if reproduction has a mortality cost), and 3) annual survival in breeding years may increase as a function of years skipped (if individuals recover body condition), or it may be constant. Below we discuss the three scenarios under which these variants can combine to select for intermittent breeding, which correspond to the three types of accessory cost to reproduction mentioned above: time, energy, and survival.

4.1 Scenario 1: Reproduction has accessory time cost

If there is no fecundity benefit to postponing reproduction (i.e. $\phi_i = \phi_{i+1}$) then intermittent breeding will not be favored, even if there is a survival cost to reproduction ($\sigma_r < \sigma_s$). However, if we let survival during reproduction (σ_r) be a function of the number of years skipped, i.e. $\sigma_r = \sigma_r(i)$, then intermittent breeding will be favored in the absence of a fecundity benefit as long as

$$\sigma_r(j+1) - \sigma_r(j) > \frac{1-\sigma_s}{\sigma_s^j}\ . \tag{14}$$

Note that intermittent breeding will only be favored here if annual survival is sufficiently high ($\sigma_s > 0.5$). This scenario is likely to be true for species that require a lengthy recovery period following reproduction, where individuals would potentially have lower survival if they tried to reproduce in two sequential years, than if they skipped a year between reproduction attempts. This scenario also applies to species where individuals must complete a time-consuming maintenance activity, like moult in birds. Birds moult in order to replace deteriorating feathers, which impact flight ability, and consequently the enegetic costs of flight as well as the ability to escape predators (Barta et al, 2006). This time tradeoff leads to some

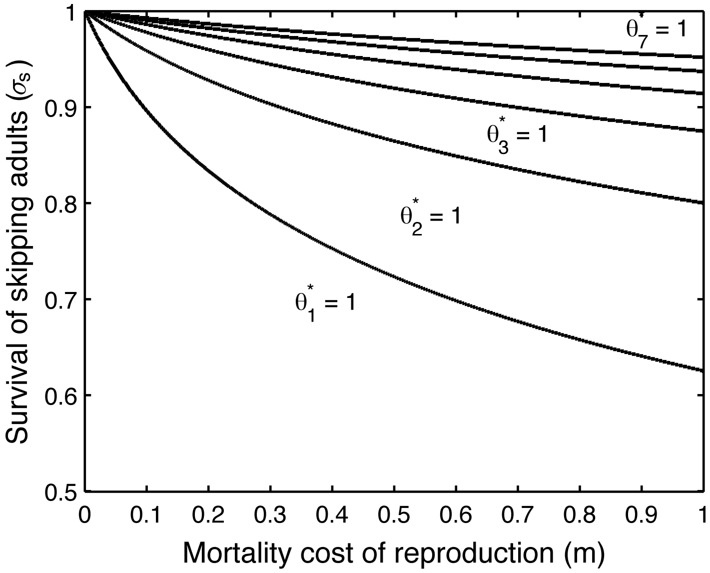

Figure 3: Contour plot showing analytically calculated ESS values as a function of the mortality cost of reproduction (m) and annual survival of a non-reproducing individual (σ_s). Lines indicate boundaries between j values where $\theta^*_j = 1$ and $\theta^*_i = 0 \; \forall \; i \neq j$. For these simulations the fecundity function was given by $\phi_i = 2i/(3+i)$.

annual breeding species where individuals occasionally forgo breeding in a give year in order to moult (Langston and Rohwer, 1996).

4.2 Scenario 2: Reproduction has accessory energy cost

If there is no survival cost to reproduction and no post-reproduction recovery time needed ($\sigma_s = \sigma_r = \sigma$), intermittent breeding is only favored when the fecundity benefit to skipping is quite high, i.e.

$$\frac{\phi_{j+1}}{\phi_j} > \frac{1-\sigma^{j+1}}{\sigma(1-\sigma^j)} \; . \tag{15}$$

In order to skip even one year, the fecundity (ϕ_2) must be more than double the individual's fecundity if it were to breed annually (ϕ_1). This occurs when reproduction has an accessory energy cost that is independent of the number of offspring produced. For example, as described in Bull and Shine (1979), if an individual can accumulate enough energy to produce 20 eggs each year but must pay an energetic cost equivalent to 10 eggs per reproduction event. An individual reproducing annually will be able to produce 10 each year, but an individual reproducing biennially will be able to produce 30 eggs every other year (assuming it has the capacity to store the extra energy).

4.3 Scenario 3: Reproduction has accessory survival cost

Finally, if no recovery time is needed, $\sigma_r(i) = \sigma_r(i+1)$, but there is a survival cost to reproduction (in terms of increased mortality m), such that $\sigma_r = (1-m)\sigma_s$, where $0 \leq m \leq 1$, then only a slight fecundity benefit is required to select for intermittent breeding. This is the scenario we will consider for the remainder of the paper. In this case, the ESS behavior is for an individual to postpone reproduction until the benefits of waiting one more year (in terms of fecundity) no longer outweigh the costs (in terms of survival). In general, an individual should increase the number of years between reproduction attempts as the cost of skipping reproduction decreases (σ_s increases) and the cost of reproducing (m) increases (Figure 3). The exact form and values of the fecundity function Φ will affect if and where the transitions in the ESS strategy occur. A clear tradeoff between reproduction and survival has rarely been demonstrated empirically (Reznick, 1985). However, in species where reproduction involves an 'accessory' activity, this activity can incur a survival cost. For example, in species that must migrate to reproduce, migrating individuals often incur an extra mortality cost (e.g., Atlantic salmon; Jonsson et al, 1991).

5 Empirical Comparisons

Although our model makes quantitative predictions about expected breeding behavior, comparing these predictions to empirical observations requires having estimates of survival and fecundity life history parameters (σ_s, $\sigma_r(i)$ and ϕ_i), which is often quite difficult. An alternative approach is to compare model predictions and empirical observations qualitatively by looking at trends in behavior with respect to a parameter. This approach is often easier and has the potential to give more insight.

For example, in Atlantic salmon (*Salmo salar*), reproducing individuals have a higher mortality (due to migration) than non-reproducing individuals. Our results predict that as the mortality cost of reproduction increases, individuals should increase the number of years they skip between breeding attempts. Jonsson et al (1991) compared salmon from two populations, one with lower mortality during migration (those that migrated up smaller rivers) and one with higher mortality (larger rivers). Individuals in the first population reproduced (migrated) annually whereas those in the second population reproduced biennially. A second example comes from Northwestern salamanders (*Ambystoma gracile*), where individuals living at high altitudes experience a shorter summer and require a longer period of recovery following reproduction than salamanders at lower altitude. From our model, we would expect females at lower altitude to reproduce more frequently than those at high altitude, which matches observed behavior (Eagleson, 1976).

In our model we assume that fecundity rates are fixed across all individuals and years, such that if any individual reproduces after i years its fecundity will be exactly ϕ_i. In reality there is variation in how individuals experience their environment. Although it is outside the scope of the model presented here, an equivalent strategy in this case would be to reproduce after a certain state threshold (body condition, level of energy stores, etc.) has been reached instead of waiting a fixed number of years. This appears to be the strategy that many species with intermittent breeding use, including birds (e.g., blue petrels, *Halobaena caerulea*; Chastel et al 1995), snakes (e.g., diamond-backed rattlesnakes, *Crotalus atrox* and asp vipers, *Vipera* *aspis*; Tinkle 1962; Naulleau and Bonnet 1996), sea turtles (e.g., green, *Chelonia mydas* and leatherback, *Dermochelys coriacea*; Solow et al 2002; Caut et al 2008), and fish (e.g., Atlantic salmon, *Salmo salar*; Thorpe 1994). This type of threshold approach is also used in energy budget models to determine age of first reproduction (e.g. De Roos and Persson, 2001).

6 Fluctuating Population Size

For very high fecundity (ϕ_i values), the non-trivial equilibrium given by (3) becomes unstable and the system goes through a series of bifurcations. With these fluctuations, the population size is no longer constant and the vector Θ^* must be calculated in terms of the average growth rate, where the average is taken across all the population sizes that the system visits (see Appendix in Shaw and Levin 2011 for detailed methods). Since the distribution of population sizes cannot be expressed analytically, it must be simulated. For simulations we must specify the exact form of density-dependence; here we used Ricker-type density-dependence of the form

$$DD = \exp\left[-\beta \sum_{i=1}^{n} \theta_i \phi_i N_i\right] \tag{16}$$

where β is a constant (Ricker, 1954, 1975). We also had to specify the value of n, the maximum number of years an individual could wait before reproducing.

To determine the ESS values of the vector Θ, we evolved the set of θ_i^* values simultaneously as follows. We initiated a resident population with $\theta_i = 1 \; \forall \; i$, then attempted to invade it with 10 different mutant types (separately) that had both slightly higher and slightly lower values for each θ_i (except for θ_n, which was fixed at 1). If a mutant was able to invade the resident population, we set it as the new resident type, and if multiple mutants could invade, we chose the type with the highest growth rate. We denote the ESS vector Θ^* to be given by the vector of the values of θ_i that when adopted by all individuals in the resident population, was able to resident invasion by mutants for 5 sequential invasion attempts (of 10 mutants each). In most cases, no single vector Θ met this criterion – usually the resident value of each θ_i in the population oscillated among several very similar values of θ_i. If an ESS was not found within 200 sequential attempts, the ESS was recorded as the average values of the residential type for each θ_i over the last 100 invasion attempts. In the following figures the ESS values of θ_i are shown with one standard deviation bars.

This fluctuation in population size leads to a fluctuation in the strength of density dependence, which in turn causes variable offspring survival. This selects for intermittent breeding even in cases where we might otherwise expect annual breeding – e.g., when there is no fecundity benefit ($\phi_i = \phi_{i+1}$) nor survival benefit ($\sigma_r(i) = \sigma_r(i+1)$) for postponing reproduction, as in Figure 4. A similar result was discussed by Ellner (1987) in the context of population fluctuations selecting for dormancy.

7 Stochastic Environments

To determine how environmental stochasticity influences the evolved reproductive behavior in our model, we allowed fecundity to vary randomly across years. We assumed that at each

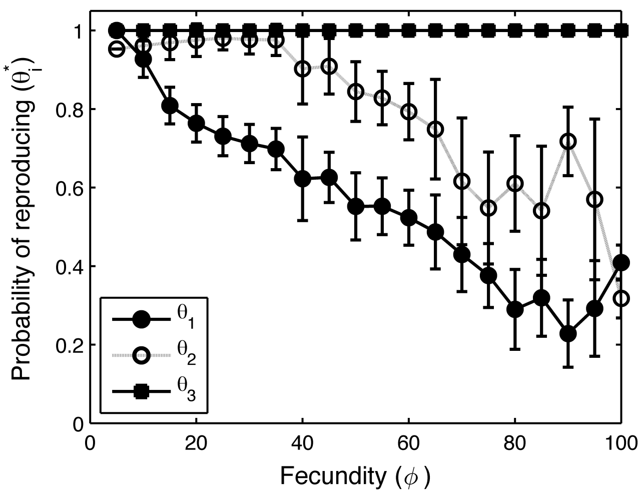

Figure 4: The ESS reproductive behavior, θ_i^*, as a function of fecundity ϕ. For large values of ϕ the fixed point equilibrium becomes unstable and the population bifurcates to a two-cycle, which selects for intermediate values of θ_i. Simulations were run with $n = 3$, $\sigma_s = 0.9$, $m = 0.9$, $\phi_i = \phi$ for all i.

time t the environment was randomly in one of two possible states with probability p and $1 - p$ respectively. One state represents a 'bad' year where $\Phi = \Phi_{lo}$ (Φ being the vector of fecundities of all n classes) and the other state represents a 'good' year where $\Phi = \Phi_{hi}$. We considered two different forms of what constitutes a 'bad' year:
Form 1) $\Phi_{lo} = a$ (fecundities of all reproducing individuals are low but non-zero), and
Form 2) $\Phi_{lo} = 0$ (all reproduction fails or all newborns die).
With a stochastic environment, the population size is no longer constant and we use the methods described above for the fluctuating population size to calculate the ESS.

In the stochastic version of the model we found the same basic patterns as in the deterministic version under equilibrium conditions: namely that an increasing cost of reproduction (m) and a decreasing cost of skipping reproduction (increased σ_s), both select for individuals to skip more years between reproduction attempts. However, unlike in Section 4, there were often conditions under which the ESS behavior was a probabilistic strategy (where $0 < \theta_i^* < 1$). This can also be interpreted as a situation where individuals with different strategies (in terms of the number of skipped years between reproduction events) coexisting within a population. These intermediate values of θ_i^* are due to two mechanisms that act in the stochastic version of the model, described below.

7.1 Mixed strategies in response to mixed conditions

The first mechanism occurs when an environment dominated by good years selects for a different evolved Θ^* than an environment dominated by bad years. For example, consider the case where good years (with Φ_{hi}) select for individuals to wait 4 years between reproduction attempts ($\theta_4^* = 1$ and $\theta_i^* = 0 \; \forall \; i \neq 4$), whereas bad years (with Φ_{lo}) select for individuals to

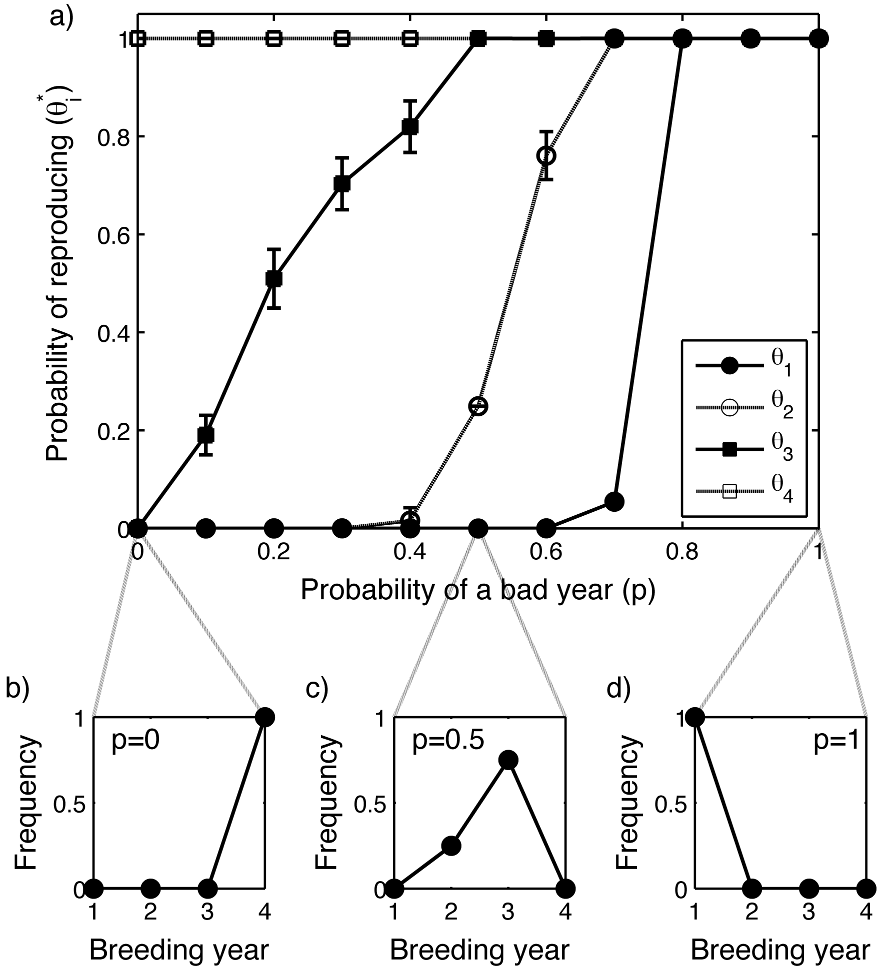

Figure 5: The ESS reproductive behavior in the stochastic model under different probabilities of a bad year (p). Panel a) shows the evolved individual strategy in terms of θ_i^* (probability that an individual who has skipped i years will now reproduce) as a function of p. Panels b-d) show the evolved individual strategy as the frequency of years between reproduction attempts, $\psi(i)$, for a given value of p (each ones represents a vertical 'slice' of panel a). Simulations were run with $n = 4$, $\sigma_s = 0.9$, $m = 0.9$, $\Phi_{hi} = 4i/(3+i)$ and $\Phi_{lo} = 1$.

reproduce annually ($\theta_1^* = 1$ and $\theta_i^* = 0 \; \forall \; i \neq 1$, e.g., if in bad years everyone has reduced but equal fecundity then there is no benefit to postponing reproduction, Form 1 above). In this case, the evolved Θ^* depends on the relative frequency of good and bad years (Figure 5). Figure 5a shows the evolved θ_i^* values as a function of the probability of a bad year – an environment with only bad years ($p = 1$) selects for $\theta_1^* = 1$, an environment with only good years ($p = 0$) selects for $\theta_4^* = 1$, and an environment with both good and bad years ($0 < p < 1$) selects for intermediate θ values. A perhaps more intuitive way of viewing this result is by looking at an individual's strategy as a frequency distribution of years between reproduction attempts, which can be expressed as

$$\psi(i) = \theta_i \prod_{j=1}^{i-1} (1 - \theta_j) \; . \tag{17}$$

Each panel in figure 5b-d shows the evolved $\psi(i)$ values for a different probability of a bad year.

7.2 Mixed strategies to spread the risk

The second mechanism that selects for intermediate values of θ_i^* occurs when the fecundity in bad years is so low that the population is at risk of extinction, Form 2 of stochasticity above (Φ_{lo} is so low that it violate inequality (6), the lower stability condition of the non-trivial equilibrium). In this case, there is selection for individuals to 'spread the risk' of extinction by skipping a variable number of years between reproduction events, resulting in intermediate values of θ_i^* (Figure 6). This occurred even if the fecundity of all individuals was the same ($\phi_i = \phi_{i+1}$), which has the counterintuitive effect of selecting for individuals to postpone reproduction when there is no fecundity benefit for doing so. Figure 6a shows the evolved θ_i^* values as a function of the fecundity of a bad year and each panel 6b-d shows the $\psi(i)$ values (frequency of years between reproduction attempts) for a different fecundity in a bad year. Here, as the severity of a bad year increases (Φ_{lo} decreases), the variance in $\psi(i)$ increases. When there is no risk of extinction $\Phi_{lo} = 1$, there is no selection to spread the risk and the ESS is just $\theta_1^* = 1$.

Although we can make specific predictions about the expected breeding behavior in stochastic environments, being able to compare these predictions to empirical data requires a system where the variation in environmental conditions is well-characterized, which is rare to find. Nevoux et al (2010) compared reproduction strategies in two populations of Black-browed albatross (*Thalassarche melanophrys*) one where some individuals breed in a more variable environment (South Georgia, Atlantic Ocean) and others breed at a less variable site (Kerguelen, Indian Ocean). The authors found that individuals in the more variable environment skipped breeding more often.

8 Discussion

Intermittent breeding, also referred to as low frequency reproduction, is a behavior where a sexually mature adult skips one or more breeding opportunities between reproduction attempts. This behavior is commonly exhibited by long-lived species where reproduction comes

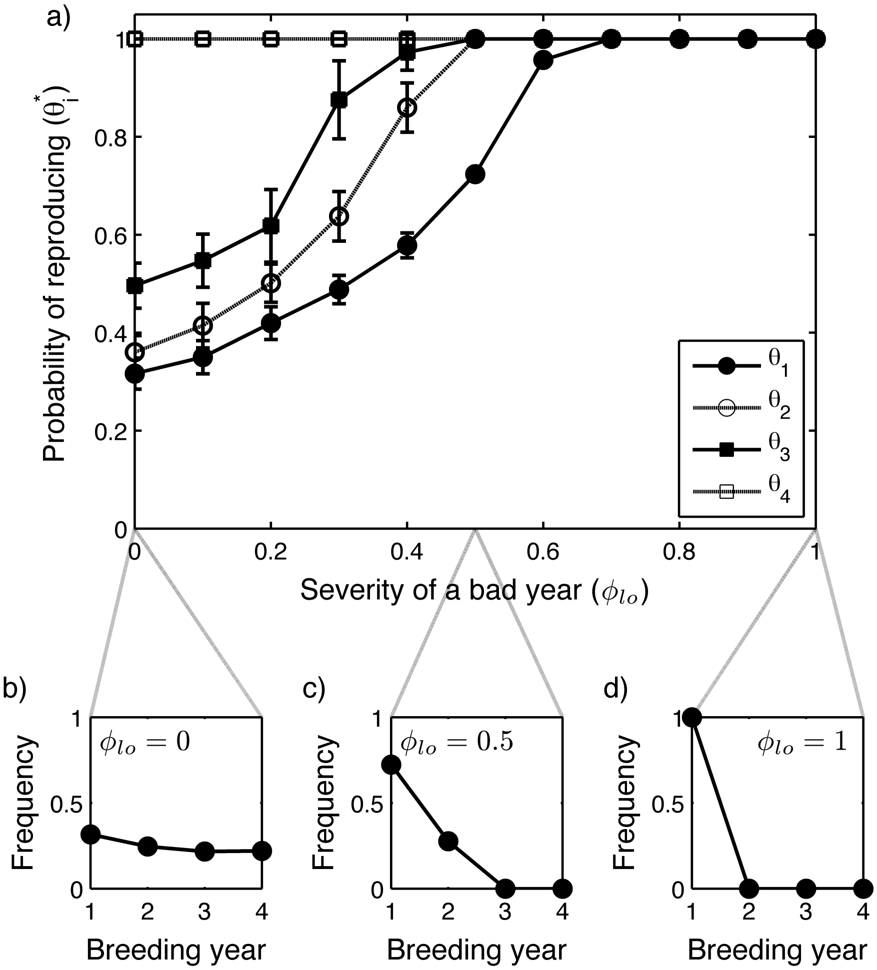

Figure 6: ESS reproductive behavior in the stochastic model under different fecundities in bad year (Φ_{lo}): panel a) shows the evolved values of θ_i^* (probability that an individual who has skipped i years will now reproduce) as a function of Φ_{lo} and panels b-d) show the frequency of years between reproduction attempts, $\psi(i)$, for a given value of Φ_{lo} (each ones represents a vertical 'slice' of panel a). Simulations were run with $n = 4$, $\sigma_s = 0.9$, $m = 0.9$, $\Phi_{hi} = 3$ for all ϕ_i, and $p = 0.4$.

with a high accessory cost in terms of time, energy, or survival. Here, we present a model to understand how life-history tradeoffs can favor intermittent breeding, and we determine how many breeding opportunities an individual should skip. We find that generally the best (ESS) reproductive strategy is the one that maximizes the ratio between growth and mortality. The conditions under which the ESS strategy involved skipping breeding attempts (intermittent breeding) depend on the type of accessory cost (time, energy or survival) associated with reproduction.

In constant environments, our model predicts that there should be a pure ESS in behavior (all individuals in a population skip exactly the same number of years between reproduction attempts; $\theta_i = 0$ or $1 \; \forall \; i$). While this may be true in some biological populations, in most cases there is at least some variation in individual strategies, both across individuals and across years for a single individual. We have shown that including uncertainty in environmental conditions or fluctuations in population size both select for strategy variation within a population (mixed ESS; $0 < \theta_i^* < 1$). Additionally, a number of other factors that we did not include in our model also could potentially select for individual variation – for example variation in individual condition or experience.

As with all models, we have made a number of simplifying assumptions that could be relaxed to include more biological realism (at the cost of added complexity). Here we assume that in stochastic environments individuals cannot anticipate whether a particular year will be good or bad. It may be the case that individuals can determine from conditions prior to the breeding season whether it is likely to be a good or bad year and adjust their decision to reproduce accordingly. In the case where individuals can guess the environmental conditions perfectly each year, we expect that individuals would no longer act to 'spread the risk' but instead would only postpone reproduction if the benefits outweigh the costs, as in the deterministic model. We also assume that that non-reproducing individuals only gain a benefit as a function of the years since they last bred. However, in species where non-reproducing individuals grow in body size, the benefit of skipping is cumulative across reproduction attempts. Accounting for this extra benefit in our model would involve adding age or stage structure on top of the condition structure, making the model quite unwieldy. However, this relationship could be explored in a model of a different form.

There are a number of parallels between the work presented here and the broader literature on life history tradeoffs. Tradeoffs between survival and current reproduction (e.g., when juvenile survival is higher than adult survival or when reproductive success increases with age, size, or status) select for postponing the age of first reproduction (see Stearns 1976 for a review, also Wittenberger 1979; De Roos and Persson 2001; Gårdmark et al 2003). Tradeoffs between the short-term and long-term survival of a lineage can select for "intergenerational discounting" where individuals invest more in themselves and less in their offspring (Livnat et al, 2005), an effect that can be amplified with increased uncertainty in offspring number (although this depends on shape of utility curve; Arrow and Levin 2009). Nonlinear life history tradeoffs, size-dependent vital rates, and uncertainty in season length all favor indeterminate growth (a period of simultaneous growth and reproduction) over determinate growth (a single switch from 100% growth to 100% reproduction; bang-bang strategy – see Perrin and Sibly 1993 for a review). In a series of models of plant growth and seed production, Cohen (1971; 1976) found that the optimal strategy was determinate growth, except when either a plant's lifespan is uncertain, or when somatic growth comes with an additional reproduction or survival advantage (e.g., increased survival or attractiveness with size). If we consider intermittent breeding to be equivalent to indeterminate growth, this suggests that the approaches that have been previously used to understand when organisms should have determinate or indeterminate growth can also be used to understand how indeterminate the growth should be (i.e. how many opportunities to skip between reproduction attempts, as we do here). There are also parallels between our results and other areas of research such as seed dormancy (see Discussion in Shaw and Levin 2011).

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Electronic Supplementary Material

Using logic similar to Levin and Goodyear (1980), we can determine the stability of the equilibria of model (1), which is governed by the Jacobian

$$\mathbf{J} = \begin{bmatrix} H_1 & H_2 & H_3 & \dots & H_n \\ u_1 & 0 & 0 & \dots & 0 \\ 0 & u_2 & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & u_{n-1} & 0 \end{bmatrix}$$

where

$$H_i = v_i + \theta_i \ \phi_i \ \overline{DD} + K \ \overline{N}_1 \left(\frac{\partial DD}{\partial N_i}\bigg|_{eq} \right) \ .$$

The eigenvalues, λ, of $\mathbf{J}$ are the roots of the characteristic equation, given by

$$\lambda^n - H_1 \ \lambda^{n-1} - H_2 \ u_1 \ \lambda^{n-2} - H_3 \ u_1 \ u_2 \ \lambda^{n-3} - \dots - \ H_n \ u_1 \ u_2 \dots u_{n-1} = 0 \ . \tag{S.1}$$

Since $l_i = \prod_{j=1}^{i-1} u_j$, this can be rewritten as

$$\lambda^n \left[1 - \sum_{i=1}^{n} \lambda^{-i} l_i H_i \right] = 0 \ . \tag{S.2}$$

At the trivial equilibrium, $H_i = v_i + \theta_i \ \phi_i$, which is positive for all i. In this case, $\mathbf{J}$ is a non-negative irreducible matrix, so by the Perron-Frobenius theorem we know that it has a positive real dominant eigenvalue, and to find it we solve

$$1 = \sum_{i=1}^{n} \lambda^{-i} \ l_i \ H_i \ . \tag{S.3}$$

The right hand side (RHS) of (S.3) is a monotonically decreasing function of λ. If $\lambda = 0$, the RHS is infinite, and if $\lambda = 1$, the RHS becomes

$$= \sum_{i=1}^{n} l_i \ v_i \ + \ \sum_{i=1}^{n} l_i \ \theta_i \ \phi_i \tag{S.4}$$

$$= 1 - L + K \ . \tag{S.5}$$

Therefore the dominant eigenvalue of $\mathbf{J}$, the value of λ that satisfies (S.3), will be less than 1 as long as $1 - L + K < 1$ or equivalently $K < L$. This is the stability condition for the trivial equilibrium.

At the non-trivial eqiulibrium, $\overline{DD} = L/K$. Since $DD(0) = 1$ and $\partial DD/\partial N_i \leq 0$, we require that $L < K$ in order for the non-trivial equilibrium to exist biologically ($\overline{N}_i \geq 0$). This is one of the stability conditions for the non-trivial equilibrium. There is an additional set of stability requirements, which are harder to derive analytically since for the non-trivial equilibrium,

$$H_i = v_i + \theta_i \phi_i \overline{DD} + K\overline{N}_1 \left(\frac{\partial DD}{\partial N_i}\bigg|_{eq} \right) \ , \tag{S.6}$$

which is no longer always positive and therefore we cannot use the Perron-Frobenius theorem. When these stability conditions are violated (e.g., the lines in Figure 2 are crossed), the fixed-point equilibrium becomes unstable and the system goes through a series of bifurcations.