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A DARWINIAN DYNAMIC MODEL FOR THE EVOLUTION OF POST-REPRODUCTION SURVIVAL

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We derive and study a Darwinian dynamic model based on a low dimensional discrete time population model focussed on two features: density dependent fertility and a trade-off between inherent (density free) fertility and post-reproduction survival. Both features are assumed to be dependent on a phenotypic trait subject to natural selection. The model tracks the dynamics of the population coupled with that of the population mean trait. We study the stability properties of equilibria by means of bifurcation theory. Whether post-reproduction survival at equilibrium is low or high is shown, in this model, to depend significantly on the nature of the trait dependence of the density effects. An Allee effect can also play a significant role.

Keywords: Evolutionary population dynamcs; life history strategy; semelparity; Allee effect.

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1. Introduction

Of fundamental interest in population dynamics are the life history strategies of individuals (i.e. the ways in which they allocate resources and behavioral activities toward reproduction, survival, growth, etc.) and the trade-offs that are involved in these efforts.[1,2] One basic question of long standing historical interest concerns the trade-off between reproductive effort and post-reproduction survival. This question has often focussed narrowly on semelparity (no post reproduction survival) versus iteroparity. In response to arguments that evolution should favor semelparity,[3] investigators pursued circumstances and mechanisms that would support post-reproduction survival and its selection by evolution.[4] These include trade-offs between reproductive effort and post-reproduction survival, nonlinear density effects, spatial effects, variable environments, and combinations of these. In this paper we will investigate the first two of these by means of an evolutionary version of a low dimensional, discrete time population dynamic equation as derived by the methodology of evolutionary game theory.[5] The model tracks coupled dynamics of the population and of the population mean of a phenotypic trait that is subject to natural selection. The trait of an individual is assumed to determine individual's inherent fertility, but in trade-off with the probability that the individual survives the

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reproduction event so as to reproduce again. The individual's trait, together with the population mean trait, is also assumed to influence the effect that population density has on the individual's fertility.

The underlying population dynamic equation that we use is a basic, one dimensional discrete time model for an unstructured population in which an allocation fraction describes the fertility versus survival trade-off. The Darwinian dynamic model includes a coupled equation for the dynamics of the mean trait.[6] The model studied here differs from the one studied in Ref. 7 in several ways, the most important ones being that it includes a simplified fertility distribution with respect to the trait and the inclusion of an Allee effects on fertility. The main goal is to determine circumstances when post-reproduction survival is low and circumstances when it is high.

The underlying population model and its asymptotic dynamics are presented in Section 2. The evolutionary extension of the model is derived in Section 3. A local bifurcation result, which follows from known general theorems, establishes the basic dynamic feature of the model, namely, the bifurcation of positive equilibria as the extinction state destabilizes and that forward bifurcations are stable and backward bifurcations are unstable. The stability properties of positive equilibria outside a neighborhood of this bifurcation point are studied for two special cases that differ in the way density effects depend on the evolving trait. These two cases highlight how density effects can play a crucial role in whether evolution selects for low or high post-reproduction survival probability: the first case, which involves a certain symmetry in the trait influence on the density effect (which is a common assumption in Darwinian dynamic models[5]), leads only to zero post-reproduction survival probability (semelparity) while the second case, which is built on a hierarchical (or asymmetric[13]) trait dependence, can lead to equilibrium states with high post-reproduction survival probability (iteroparity).

2. Difference equation models for population dynamics with a fertility-survival trade-off

Difference equations have a long history of use in population dynamics and in studies of asymptotic dynamics, with a focus on basic questions of extinction versus survival and equilibration, but also on more complicated dynamics such as periodic cycles and chaos. A scalar difference equation for the dynamics of an unstructured population, in the absence of immigration or emigration, predicts the population density at a sequence of census times based on the assumption that at time $t+1$ the population will consist only of survivors from the previous census at time t plus newborns. While different sequencing scenarios can be modeled, we will assume a short reproductive season, just prior to which the population census is taken, is followed by a maturation period at the end of which another reproductive episode occurs, a total of one time unit later.

By the fertility of an individual we mean the number newborns produced that survive to the next census. By post-reproduction survival we mean the probability an individual survives so as to reproduce again. To account for a trade-off between fertility and survival, we assume these are negatively correlated; that is, a resource allocation that increases one will decrease the other. As a basic model for this relationship we denote fertility by bf and post-reproduction survival by $s(1-f)$ where b and s are the maximal possible fertility rate and survival probability and f is an "allocation" fraction. Then we have

$$x_{t+1} = r x_t$$

where

$$r = bf + s(1-f)$$

$$b > 0, \quad 0 \leq s < 1, \quad 0 < f \leq 1$$

is the per capita population growth rate.

Note that if $b \leq s$ then $x_{t+1} \leq s x_t$ which implies $\lim_{t \to +\infty} x_t = 0$, for any initial population density $x_0 \geq 0$. Therefore we assume

$$s < b.$$

Then fitness, which we take to be[2, 8, 9]

$$\ln r = \ln\left((b-s) f + s\right),$$

is maximized when $f = 1$, that is to say when post-reproduction survival is 0 and the population is semelparous.[3]

We can model the effects on population density on fertility (and newborn survival) by including a multiplicative factor $\beta(x)$ to the fertility term in bf, i.e. by writing $bf\beta(x)$. We require that $\beta(x)$ is positive for nonnegative x and that $\beta(0) = 1$ so that bf retains the interpretation of inherent or intrinsic (i.e. density free) fertility. We could do the same for post-reproduction survival by including a factor on $s(1-f)$, but in this paper we only consider density effects on fertility (and newborn survival). This results in a nonlinear difference equation

$$x_{t+1} = r(x_t)\, x_t \tag{2.6}$$

$$r(x) = bf\beta(x) + s(1-f) \tag{2.7}$$

for the population dynamics.

The equilibrium equation $x = r(x)\, x$ shows that $x = 0$ is an (extinction) equilibrium for all parameter values and that positive equilibria are positive roots of the equation $r(x) = 1$ or

$$bf\beta(x) + s(1-f) = 1.$$

With f and s fixed, positive equilibria depend on b. A solution pair $[b, x]$ of this equation is called a *positive equilibrium.* Note that $[b, 0]$ is an extinction equilibrium for all b. If the x component of an equilibrium pair $[b, x]$ is a (locally asymptotically) stable equilibrium pair of (2.6)-(2.7), then we simply say it is a *stable equilibrium pair*. A considerable amount can be said about this model with regard to equilibria and their stability properties under the following conditions.

A1: *Assume in the population growth rate (2.7) that*
(a) $0 \leq s < 1$ *and* $b > s$;
(b) $0 \leq f \leq 1$;
(c) $\beta(x)$ *is a positive valued, twice continuously differentiable function on open interval* I_x *containing the half line* $x \geq 0$.

A straightforward application of the linearization principle shows that the extinction equilibrium $x = 0$ loses (local asymptotic) stability as b increases through the critical value

$$b_0 := \frac{1 - s + fs}{f}.$$

Note that $b_0 > s$. There exists a continuum C of positive equilibria

$$[b, x] = \left[\frac{1 - s(1 - f)}{f\beta(x)}, x\right] \tag{2.10}$$

for all $x > 0$. The graph of this continuum in the (b, x)-plane meets the extinction equilibrium $[b_0, 0]$ and the branch is said to (transcritically) bifurcate from $x = 0$ at $b = b_0$. Positive equilibria located on decreasing segments of the graph are unstable and those locally on increasing segments are (locally asymptotically) stable at least near bifurcation points.[6,10] In particular the positive equilibria near the bifurcation point $[b_0, 0]$ are stable if the bifurcation is forward (i.e. $\beta'(0) < 0$) and unstable if it is backward (i.e. $\beta'(0) > 0$). A backward bifurcation in a population model typically gives rise to a strong Allee effect,[11] by which is meant a scenario with (at least) two attractors, one of which is the extinction equilibrium.

In the next section we let natural selection determine model parameters in equations (2.6)-(2.7). We have a particular interest in Allee effects and towards that end will utilize the factor

$$\beta(x) = \frac{1 + ax}{1 + cx + ax^2}, \quad a, c > 0. \tag{2.11}$$

This factor with $a = 0$ in (2.6)-(2.7) gives the well known discrete logistic (or Beverton-Holt) equation. The coefficient c describes the intensity of the negative effects due to intraspecific competition. If $a > c$ then $\beta'(0) = a - c > 0$ and an increase in low level density x will increase fertility. Such a positive effect of density is called an Allee component[12] and we will call a the Allee coefficient. (Many other mathematical expressions for the density factor β have been used to incorporate Allee components into models.[12])

Some straightforward analytic geometry shows that the graph of continuum C of positive equilibrium pairs (2.10)-(2.11) that lie in the first quadrant of the (b, x)-plane has the two possible configurations shown in Fig.1. When $a < c$ there is a positive equilibrium of (2.6)-(2.7) for and only for $b > b_0$. When $a > c$ a positive equilibrium exists if and only if $b > b^*$ where

$$b^* := \frac{1-s}{af}\left(2\sqrt{1+a-c}+c-2\right) > 0 \tag{2.12}$$

in which case there are two positive equilibria for $b^* < b < b_0$ and one positive equilibrium for $b \geq b_0$. Stability (or instability) of an equilibrium x_e by means of linearization can be studied by determining when

$$\lambda\left(x_e\right) := \left.\frac{dr\left(x\right)x}{dx}\right|_{x=x_e}$$

satisfies $\left|\lambda\left(x_e\right)\right| < 1$ (or $\left|\lambda\left(x_e\right)\right| > 1$). The result is that when $c < a$ the unique positive equilibrium is (locally asymptotically) stable for all $b > b_0$. On the other hand, when $c > a$ the larger of the two positive equilibria is stable when $b^* < b < b_0$ and the smaller is unstable, while the unique positive equilibrium is stable when $b \geq b_0$. For details see the Appendix.

Note that when $a > c$ there is a strong Allee effect, which has two major implications: initial condition dependent survival or extinction for b on the interval $b^* < b < b_0$ and a tipping point b^* (called a tangent or blue-sky bifurcation point) for which survival becomes impossible for $b < b^*$.

3. A Darwinian model

In this section we formulate a Darwinian dynamic version of the population model (2.6)-(2.7) by means of evolutionary game theory methodology.[5,14] The parameter f determines a life history strategy in that it determines probability of post-reproduction survival and repeated reproduction. Strict semelparity occurs if $f = 1$, but in keeping with the critique of the binary distinction between semelparity versus iteroparity,[4] we will simply refer to low and high post-reproduction survival. Our goal is to investigate the life history strategy that evolution favors, specifically, whether at equilibrium the level of post-reproduction survival is low or high.

We assume that model parameters are dependent on a phenotypic trait which is subject to natural selection by Darwinian principles. The trait of an individual, denoted by v, determines its allocation fraction $f = f\left(v\right)$ between fertility and post-reproduction survival. We also assume that the individual's trait also determines the intensity of the effect that population density has on the individual's fertility. This intensity is in relation to the traits of other individuals with whom it is competing or cooperating, who will be represented in the model by the population's mean trait u. More specifically we assume, as is often done,[5] the effects of density on an individual with trait v depend on the difference $z = v - u$, i.e. $\beta\left(x, z\right)$ is a function of $z = v - u$. These assumptions imply that the per capita growth rate has the form

$$r\left(x, u, v\right) = bf\left(v\right)\beta\left(x, v-u\right) + s\left(1 - f\left(v\right)\right). \tag{3.1}$$

Under certain assumptions (including that the trait v is at all times normally distributed with a constant variance), the evolutionary game theory methodology provides the equations

$$x_{t+1} = r\left(x_t, u_t, v\right)\big|_{v=u_t} x_t \tag{3.2}$$

$$u_{t+1} = u_t + \sigma^2\, \partial_v \ln r\left(x_t, u_t, v\right)\big|_{v=u_t} \tag{3.3}$$

for the discrete time dynamics of the population x_t and the population mean trait u_t. Here the notation ∂_v stands for the partial derivative $\partial/\partial v$. The constant σ^2 (which is related to the assumed constant variance in the trait) is called the *speed of evolution.* If $\sigma^2 = 0$ then $u_t = u_0$ remains fixed (evolution does not occur) and the model reduces to the first equation for x_t with the resulting dynamics as described in Section 2.

With r defined by (3.1) the model equations (3.2)-(3.3) become

$$x_{t+1} = \left[bf\left(u_t\right)\beta\left(x_t, 0\right) + s\left(1 - f\left(u_t\right)\right)\right] x_t \tag{3.4}$$

$$u_{t+1} = u_t + \sigma^2 \frac{bf'\left(u_t\right)\beta\left(x_t, 0\right) + bf\left(u_t\right)\partial_z\beta\left(x_t, 0\right) - sf'\left(u_t\right)}{bf\left(u_t\right)\beta\left(x_t, 0\right) + s\left(1 - f\left(u_t\right)\right)}. \tag{3.5}$$

The assumptions under which we consider these equations are the following.

A2: *Assume in the population growth rate (3.1) that*

(a) $0 < s < 1$ *and* $b > s$;

(b) $f(v)$ *is a twice continuously differentiable function on an open interval* I_v *of* 0 *that satisfies* $0 \leq f(v) \leq 1$ *and* $f(0) = 1,\ f''(0) < 0$;

(c) $\beta(x, z)$ *is a positive valued, twice continuously differentiable function on* $I_x \times I_z$*, where* I_z *is an open interval of* 0*, that satisfies* $\beta(0, z) \equiv 1$ *for* $z \in I_z$.

A2(b) is based on the assumption that there exists a trait at which an individual's fertility attains its maximum b and that. without loss in mathematical generality, it is attained at trait $v = 0$. Note that inherent survival $s\left(1 - f(v)\right)$ equals 0 at $v = 0$ and hence an individual with trait $v = 0$ is semelparous. In A2(c) the assumption $\beta(0, z) \equiv 1$ implies $bf(v)$ is the distribution of inherent or intrinsic (i.e. density free) fertility rates as a function of v.

If, as an example, the density factor is (2.11), then we have

$$\beta(x, z) = \frac{1 + a(z)\,x}{1 + c(z)\,x + a(z)\,x^2}$$

where to complete a model formulation one needs to specify how the competition coefficient $c(z)$ and the Allee coefficient $a(z)$ depend on the difference $z = v - u$ between the individual's trait v and the trait u of the typical individual in the population. Frequently used for this purpose are Gaussian-like distributions $c_0 \exp\left(-wz^2\right)$, $w > 0$. This describes the situation in which the individual experiences the maximum density effect when it has the mean trait $v = u$ and in which lower density effects occur symmetrically in v around u. In contrast to this *symmetric* sub-model is the expression $c_0 \exp(-wz)$, $w > 0$, in which larger values of v decrease the density effect, a situation we will refer to as *hierarchical competition* (or asymmetric competition[13]).

The first step in analyzing equations (3.4)-(3.5) is to consider the existence and stability of equilibria. If evolution occurs (i.e. $\sigma^2 > 0$), then (x, u) is an *equilibrium* if and only if x and u satisfy the two equilibrium equations

$$x = [bf(u)\,\beta(x,0) + s(1 - f(u))]\,x \tag{3.7}$$

$$0 = bf'(u)\,\beta(x,0) + bf(u)\,\partial_z\beta(x,0) - sf'(u)\,. \tag{3.8}$$

An equilibrium $(x, u) = (0, u)$ is an *extinction equilibrium*. An equilibrium (x, u) with $x > 0$ is a *positive equilibrium*. We consider these two types of equilibrium pairs in the following two sections.

3.1. *Existence and stability of extinction equilibria*

The first equilibrium equation (3.7) is clearly satisfied by $x = 0$ for all values of b and s, in which case the second equilibrium equation (3.8) reduces to $f'(u) = 0$. (Note by A2 that $b > s$ and $\partial_z\beta(0,0) = 0$.) In other words, $(x, u) = (0, u)$ is an extinction equilibrium if and only if u is a critical point of $f(u)$, in which case it exists for all values of b and s. By assumption A2, $(x, u) = (0, 0)$ is an extinction equilibrium whose trait component $u = 0$ gives maximum inherent fertility.

To perform a stability analysis by linearization, we calculate the Jacobian matrix associated with the Darwinian equations (3.4)-(3.5) and evaluate it $(x, u) = (0, 0)$. The result is the matrix

$$\begin{pmatrix} b & 0 \\ \square & 1 + \sigma^2 \frac{b-s}{b} f''(0) \end{pmatrix}$$

whose eigenvalues are

$$\lambda_1(b) = b > s, \quad \lambda_2(b) = 1 + \sigma^2 \frac{b-s}{b} f''(0) < 1.$$

($\square$ denotes an unneeded term.) Stability by linearization occurs if and only if both eigenvalues satisfy $|\lambda_i(b)| < 1$. A study of these two inequalities yields the Lemma 3.1, in which we need the two quantities

$$\sigma_0^2 := -\frac{1}{1-s}\frac{2}{f''(0)} > 0$$

$$b^{**} := s\frac{\sigma^2 f''(0)}{\sigma^2 f''(0) + 2}.$$

Note that b^{**} satisfies $s < b^{**} < 1$ when $\sigma^2 > \sigma_0^2$

Lemma 3.1 *Assume A2.*

(a) If $\sigma^2 < \sigma_0^2$ then the extinction equilibrium $(0, 0)$ of (3.4)-(3.5) is (locally asymptotically) stable for $b < 1$ and unstable for $b > 1$. At $b = 1$ the Jacobian eigenvalues satisfy $\lambda_1(1) = 1$ and $|\lambda_2(1)| < 1$.

(b) If $\sigma^2 > \sigma_0^2$ *then the extinction equilibrium* $(0,0)$ *is (locally asymptotically) stable for* $b < b^{**}$ *and unstable for* $b > b^{**}$*. At* $b = b^{**}$ *the Jacobian eigenvalues satisfy* $|\lambda_1(b^{**})| < 1$ *and* $\lambda_2(b^{**}) = -1$*.*

Lemma 3.1 implies a destabilization of the extinction equilibrium $(0,0)$ as b increases through $b = 1$ if the speed is not too fast, i.e. $\sigma^2 < \sigma_0^2$. Because this destabilization occurs as an eigenvalue increases through 1, we anticipate it will result in a transcritical bifurcation of positive equilibria. This bifurcation is described in Theorem 3.1.

On the other hand, Lemma 3.1 implies that if the speed of evolution is fast enough, i.e. if $\sigma^2 > \sigma_0^2$, then $(0,0)$ destabilizes at a lower value of b, namely as b increases through $b^{**} < 1$. This destabilization occurs because eigenvalue decreases through -1. We therefore anticipate it will result in a period doubling bifurcation and the creation of 2-cycle oscillations. We leave this conjecture for future study and assume $\sigma^2 < \sigma_0^2$.

3.2. *Bifurcation of positive equilibria and their stability*

The destabilization of the extinction equilibrium at $b = 1$ in Lemma 3.1(a) suggests a bifurcation of positive equilibria as b increases through b_0. With all other parameters held fixed, we consider the existence of positive equilibri pairs (x,u) as a function of b and define $[b,(x,u)]$ as an *equilibrium pair*, which we call a *positive equilibrium pair* if $x > 0$. Conditions under which a bifurcation of positive equilibrium pairs from the extinction equilibrium pair $[1,(0,0)]$ are provided by general bifurcation theorems for evolutionary difference equation models that can be found in Refs. 15–17. Specifically, from Theorems 1 and 2 in Ref. 17 we have the following theorem.

Theorem 3.1 *Assume A2 holds. If* $\sigma^2 < \sigma_0^2$ *and* $\partial_x\beta(0,0) \neq 0$*, then in an open neighborhood of* $[1,(0,0)]$ *there exists a continuum of positive equilibrium pairs* $[b,(x,u)]$ *of (3.4)-(3.5) whose closure contains* $[1,(0,0)]$*.*

(a) If $\partial_x\beta(0,0) < 0$ *then the bifurcation is forward and stable, i.e. the positive equilibria* (x,u) *exist for* $b > 1$ *(but near 1) and are (locally asymptotically) stable.*

(b) If $\partial_x\beta(0,0) > 0$ *then the bifurcation is backward and unstable, i.e. the positive equilibria* (x,u) *exist for* $b < 1$ *(but near 1) and are unstable.*

This theorem extends the bifurcation alternatives in Fig. 1 for the non-evolutionary population model to the Darwinian model (3.4)-(3.5), at least in a neighborhood of the bifurcation point $[1,(0,0)]$. However, it does not address the existence or the stability properties of positive equilibrium pairs outside a neighborhood of the bifurcation point. The global existence of the bifurcation continuum of positive equilibrium pairs follows from general theorems in Ref. 15, but whether the two global bifurcation alternatives, and their stability properties, shown in Fig. 1 hold for the evolutionary model (3.4)-(3.5) remains an open question.

The positive equilibria in Theorem 3.1 have trait components that lie near $u = 0$ and therefore imply a life history strategy of low post-reproduction survival (as predicted in Ref. 4). On the other hand, model equations studied in Ref. 7 show that equilibria lying outside a neighborhood of the bifurcation point can, under certain circumstances, have trait components u that yield high post reproductive survival. The models studied in Ref. 7 assume negative density effects only (hence they exhibit only a forward stable bifurcation) and assume the fertility distribution $bf\left(v\right)$ has, in addition to the global maximum at the semelparous trait $v = 0$, a local maximum at a positive trait significantly different from 0. The latter critical trait yields a high post-reproduction survival and accounts for this possibility in positive equilibria far from the bifurcation point. A drawback of that example of evolutionarily selected post-reproduction survival is that it occurs for large inherent fertility rates, whereas in natural populations it is generally the opposite: semelparous populations tend to have the higher inherent fertility rates. In the next section we consider a different scenario which will produce high reproductive survival at lower inherent fertility rates, a scenario in which Allee effects play a key role.

3.3. *A application*

Consider the Darwinian equations (3.4)-(3.5) with fertility distribution $bf\left(v\right)$ given by

$$f\left(v\right) = \exp\left(-w_1 v^2\right) \tag{3.11}$$

and trait dependent density factor (2.11)

$$\beta\left(x, z\right) = \frac{1 + a\left(z\right)x}{1 + c\left(z\right)x + a\left(z\right)x^2} \tag{3.12}$$

where $z = v - u$. We consider the two cases: the case when the competition coefficient $c\left(z\right)$ is symmetric

$$c\left(z\right) = c_0 \exp\left(-w_2 z^2\right), \quad w > 0 \tag{3.13}$$

and the case when it is hierarchical

$$c\left(z\right) = c_0 \exp\left(-w_2 z\right), \quad w > 0. \tag{3.14}$$

In both cases $c_0 > 0$ measures the negative effects on fertility experienced by an individual with mean trait $v = u$. In both cases we take the Allee coefficient to be

$$a\left(z\right) = a_0 \exp\left(-w_3 z^2\right), \quad w_3 > 0 \tag{3.15}$$

so that the maximum benefit due to the positive effect of increased density $a_0 > 0$ (say, due to protection of newborns by the population) accrues to newborns inheriting the mean trait $v = u$.

We assume

$$\sigma^2 < \sigma_0^2 = 1/w_1\left(1 - s\right)$$

so that Theorem 3.1 applies. A calculation shows $\partial_x \beta(0,0) = a_0 - c_0$. By Theorem 3.1 the bifurcation at $b_0 = 1$ is forward if $c_0 > a_0$ and backward if $a_0 < c_0$.

The equations for positive equilibria are

$$\begin{aligned} 1 &= bf(u)\,\beta(x,0) + s(1 - f(u)) \\ 0 &= bf'(u)\,\beta(x,0) + bf(u)\,\partial_z\beta(x,0) - sf'(u)\,. \end{aligned}$$

Since $f'(u) = -2w_1 u f(u)$, we can re-write these equations as

$$\begin{aligned} 1 - s &= (b\beta(x,0) - s)\,f(u) \\ 0 &= -2w_1 u\,(b\beta(x,0) - s)\,f(u) + bf(u)\,\partial_z\beta(x,0)\,. \end{aligned}$$

Use of the first equation in the second equation yields, after some algebra, the equation

$$u = bf(u)\,\partial_z\beta(x,0)\,\frac{1}{2w_1(1-s)}.$$

Finally, after a calculation of $\partial_z\beta(x,0)$ we obtain

$$u = -c'(0)\,x\frac{1 + a(z)\,x}{\left(1 + c(z)\,x + a(z)\,x^2\right)^2}\frac{bf(u)}{2w_1(1-s)}. \tag{3.18}$$

which is an equation satisfied by all positive equilibrium pairs $[b,(x,u)]$.

Near the bifurcation point the population density x is low and the trait component u of a positive equilibrium is close to 0 and, as a result, there is low post-reproduction survival. From (3.18) we see (since the right side tends to 0 as $x \to +\infty$) that any equilibrium (x,u) with a high density x component also has a low trait component u and therefore low post-reproduction survival. In the two cases considered below, we see that whether or not there exist equilibria with trait components that are sufficiently greater than 0 (so as to result in a significant post-reproduction survival probability) depends on trait dependency properties of the density term β.

3.3.1. *Symmetric competition coefficient* $c(z)$

In this case $c'(0) = 0$ and (3.18) implies $u = 0$ for all equilibria (x,u). The x component therefore satisfies the equation $1 = b\beta(x,0)$ which is the equilibrium equation of the non-evolutionary equation (2.6)-(2.7) studied in Section 2, but with $s = 0$ and β given by (2.11). It follows that all positive equilibrium pairs are $[b,(x,0)]$ where (b,x) lies on one of the two bifurcation diagrams in Fig. 1. Specifically, there exists a unique positive equilibrium pair $[b,(x_1,0)]$ for each $b > 1$ and when $c > a$ these are the only positive equilibrium pairs. When $c < a$ there exist two additional positive equilibrium pairs $[b,(x_1,0)]$ and $[b,(x_2,0)]$ when $b^* < b < b_0$. (This is true for all $\sigma^2 > 0$.)

Thus, in this case of a symmetric competition coefficient, all positive equilibria (regardless of the direction of bifurcation or stability properties) have trait component $u = 0$. This means that the post-reproduction survival probability of a "typical" individual (i.e. one that inherits the mean trait) is 0 and, in this sense, the population is a semelparous.[3]

3.3.2. *Hierarchical competition coefficient* $c(z)$

When the trait dependent competition coefficient has the hierarchical form (3.14) the trait components u of the positive equilibria $[b,(x,u)]$ near the bifurcation point $[1,(0,0)]$ are necessarily near 0, but they not equal to 0 as is the case when the coefficient has the symmetric form (3.13). This can be seen from (3.18) and $c'(0) = -2w_2c_0 < 0$, which implies u is positive for any positive equilibrium pair $[b,(x,u)]$ with u near 0.

Although we have no rigorous proof, numerical simulations show that it is possible for positive equilibrium pairs to exist, outside of a close neighborhood of the bifurcation point, for which the trait component u is sufficiently positive so as to yield a high post-reproduction survival probability $s(1-f(u))$. This is illustrated by the numerically simulated examples in Fig. 2 where (for a selection of parameter values) we see a sample orbit that approaches a positive equilibrium for each value of b in an increasing sequence. As b increases, the equilibrium population density x increases (not unexpectedly) while the equilibrium trait u decreases. The post-reproduction survival probability at equilibrium $s(1-f(u))$ is, for the lowest values of b in Fig. 2, over 0.5 (per unit time); for larger values of b, however, it is less than 0.005 (per unit time). The explanation for this is that in this particular example $a_0 > c_0$ and a backward bifurcation induced strong Allee effect occurs (as in Fig. 1 for the non-evolutionary model). It remains an open problem for this evolutionary model to establish rigorously the existence of stable, positive equilibria with large trait components and determine whether or not a backward bifurcation induces a strong Allee effect (as is suggested by the case $b = 0.9 < 1$ in Fig. 2).

4. Concluding remarks

The basic population dynamic difference equation (2.6)-(2.7) was formulated so as to describe a trade-off between fertility and post-reproduction survival and to allow for density dependence in fertility. We formulated an evolutionary version of the model using evolutionary game theoretic methodology[5,6] so as to allow inherent fertility and post-reproduction survival of an individual, as well as the effects of density on fertility on these vital rates, to depend on a phenotypic trait v of the individual that is subject to natural selection. The resulting Darwinian equations (3.4)-(3.5) describe the dynamics of the population density x and the mean population trait u. Our goal was to investigate, via this model, what life history strategy evolution will favor; specifically, to determine conditions under which evolution will favor low post-reproduction survival (what can be called a semelparous life history strategy) and conditions under which it will favor high post-reproduction survival (an iteroparous life history strategy). We assume there exists a trait at which fertility is maximized (namely, without loss in mathematically generality, $v = 0$).

General theorems imply the creation of positive equilibria (via a transcritical bifurcation) as the maximal fertility rate b increases and the extinction equation $x = 0$ destabilizes. The usual alternates hold with regard to their stability, namely, forward bifurcating equilibria are stable and backward bifurcating equilibria are unstable. This local bifurcation theorem concerns only positive equilibria near the bifurcation point, which necessarily have mean trait components near $u = 0$. This means they are equilibrium states with low post-reproduction probabilities.

Any equilibria with trait components far from $u = 0$ that yield equilibrium states with high post-reproduction survival must therefore occur outside the neighborhood of the bifurcation point. Their existence and stability are very model dependent. We illustrated this by a specific model with components components (3.11), (3.12), (3.14), (3.15), and either (3.13) or (3.14). This example shows the key role that the trait dependence of the density effects have on fertility. In the case of a symmetric dependence (3.13) of the competition coefficient on the trait difference $v - u$ we proved that only equilibria with zero post-reproduction survival exist. This case supports Cole's assertion that evolution favors semelparity.[3] We also showed, however, that a hierarchical dependence of the competition coefficient on $v-u$ can yield equilibrium traits with high post-reproduction probabilities. This is illustrated by the numerical examples in Fig. 2. In that specific example the Allee component plays a key role by providing a backward bifurcation induced strong Allee effect. A rigorous proof of this, and of the existence and stability of equilibria with high reproduction survival probability, remain open mathematical problems.

We conclude with another comment concerning the question of what life history strategy is favored by evolution. In evolutionary theory of life history strategies there is the concept of an evolutionary stable strategy or trait (ESS). For the trait component of an equilibrium to be an ESS trait, not only must the equilibrium be stable as an equilibrium of the Darwinian equations, but (in order to resist invasion by similar mutant species) the trait must lie on a global maximum of the adaptive landscape at equilibrium. That is to say, if (x_e, u_e) is a stable positive equilibrium, then it is an ESS if (only if) the *adaptive landscape* $\ln r\,(x_e, v, u_e)$ attains a global maximum at $v = u_e$.[5]

The adaptive landscapes at equilibrium for the simulated examples in Fig. 2 are shown in Fig. 3. The equilibrium mean trait component does indeed lie on at a global maximum of the fitness landscape for all but the two larger b values shown. This example exhibits the following interesting scenario as inherent fertility increases.

1. At low fertility rates evolution selects an ESS trait that yields a high post-reproduction survival probability (iteroparity).
2. At higher fertility rates evolution selects a ESS trait that yields a low post-reproduction survival probability.
3. At the highest fertility rates evolution selects a trait that yields an even lower post-reproduction survival probability, but the trait is no longer an ESS.

Thus, as inherent fertility increases, evolution selects more and more in favor of a semelparous-like life history strategy, but one which eventually loses its ESS status.

This is but one scenario possible for this specific example. Further analysis of this example for other parameter values and, more widely, of other Darwinian model components (3.4)-(3.5) will no doubt reveal other, even contrasting, scenarios. The model, as simple as the population and trait dynamics are assumed to be, offers a fruitful starting point for the investigation of these evolutionary questions concerning life history strategies and provides interesting challenges for rigorous mathematical analysis.

5. Appendix

The goal is to establish the two bifurcation diagram possibilities for the non-evolutionary model equations (2.6)-(2.7) with $\beta(x)$ is given by (2.11) that are shown in Fig.1. For notational simplicity, let $\bar{b} = bf$ and $\bar{s} = s(1-f)$ and re-write the positive equilibrium equation $r(x) = 1$

$$\bar{b}\frac{1+ax}{1+cx+ax^2} + \bar{s} = 1.$$

Treating $\bar{b} = \bar{b}(x)$ as a function of $x > 0$, we have

$$\bar{b}(x) = (1-\bar{s})\,\frac{1+cx+ax^2}{1+ax} \tag{5.2}$$

and

$$\bar{b}'(x) = \frac{1-\bar{s}}{(1+ax)^2}q(x)$$

where

$$q(x) := c - a + 2ax + a^2x^2.$$

The quadratic $q(x) > 0$ for all $x > 0$ if $c > a$. If $c < a$, then $q(x)$ has unique positive root (which is then a critical point of $\bar{b}(x)$)

$$x^* = \frac{1}{a}\left(\sqrt{1+a-c} - 1\right)$$

and $q(x) < 0$ for $0 < x < x^*$ and $q(x) > 0$ for $x > x^*$. These properties of $q(x)$ give the following facts about $\bar{b}(x)$: (a) $c > a$ implies $\bar{b}(x)$ is monotone increasing (from $1-\bar{s}$ to $+\infty$) for $x \geq 0$ and (b) $c < a$ implies $\bar{b}(x)$ is monotone decreasing for $0 < x < x^*$ and monotone increasing for $x > x^*$, reaching a global minimum of $\bar{b}^* = \bar{b}(x^*)$, i.e.

$$\bar{b}^* = \frac{1-s}{a}\left(2\sqrt{1+a-c} + c - 2\right).$$

It follows that when $c > a$ there exists a positive equilibrium $x_1 > 0$ if and only if $\bar{b} > 1-\bar{s}$, in which case it is unique. It also follows that when $c < a$ there exist exactly two positive equilibria $x_1 > x_2 > 0$ for b on the interval $\bar{b}^* < \bar{b} < 1-\bar{s}$

and exactly one positive equilibrium $x_1 > 0$ when $\bar{b} \geq 1 - \bar{s}$. Note that $q\left(x_2\right) < 0$ and $q\left(x_1\right)$ since the roots lie on opposite sides of x^*. Reverting back to $b = \bar{b}/f$ and $s = \bar{s}/\left(1 - f\right)$, obtain two bifurcation diagrams in Fig. 1 where the bifurcation point $1 - \bar{s}$ for $\bar{b}$ becomes the bifurcation point $b_0 = \left(1 - s\left(1 - f\right)\right)/f$ for b.

To study the stability of a positive equilibrium $x = x_e > 0$ by means of the linearization principle, we consider

$$\lambda\left(x\right) = \left(r\left(x\right)x\right)' = \bar{b}\frac{a\left(c-1\right)x^2 + 2ax + 1}{\left(ax^2 + cx + 1\right)^2} + \bar{s}.$$

Evaluating this at a positive equilibrium $x_e > 0$ and using (5.2), we obtain

$$\lambda\left(x_e\right) = \left(1 - \bar{s}\right)\frac{a\left(c-1\right)x_e^2 + 2ax_e + 1}{\left(1 + ax_e\right)\left(ax_e^2 + cx_e + 1\right)} + \bar{s}. \tag{5.8}$$

By linearization x_e is (locally asymptotically) stable if $\left|\lambda\left(x_e\right)\right| < 1$.

First we see that

$$\frac{a\left(c-1\right)x_e^2 + 2ax_e + 1}{\left(1 + ax_e\right)\left(ax_e^2 + cx_e + 1\right)} > -1$$

since this inequality is equivalent to

$$a\left(c-1\right)x_e^2 + 2ax_e + 1 > -\left(1 + ax_e\right)\left(ax_e^2 + cx_e + 1\right)$$

or

$$a^2x_e^3 + 2cax_e^2 + 3ax_e + cx_e + 2 > 0$$

which is true. From (5.8) follows

$$\lambda\left(x_e\right) > \left(1 - \bar{s}\right)\left(-1\right) + \bar{s} = 2\bar{s} - 1 > -1.$$

We are left to consider $\lambda\left(x_e\right) < 1$. First notice that this inequality is equivalent to the inequality

$$\frac{a\left(c-1\right)x_e^2 + 2ax_e + 1}{\left(1 + ax_e\right)\left(ax_e^2 + cx_e + 1\right)} < 1.$$

Multiply this inequality by the denominator and bring the left side of the result to the right side. The result, after a cancellation of a factor x_e, is the equivalent inequality

$$0 < q\left(x_e\right).$$

We conclude that $\lambda\left(x_e\right) < 1$ and x_e is stable if $q\left(x_e\right) > 0$. Reversing the inequality in these manipulations shows that $\lambda\left(x_e\right) > 1$ and hence x_e is unstable if $q\left(x_e\right) < 0$.

We showed above that when $c > a$, the unique positive equilibrium x_1 that exists if (and only if) $\bar{b} > 1 - \bar{s}$ (equivalently $b > b_0$) satisfies $q\left(x_1\right) > 0$ and is therefore (locally asymptotically) stable.

In the case $c < a$ we showed above that $q\left(x_1\right) > 0$ and $q\left(x_2\right) < 0$. Thus, the smaller equilibrium $x_2 > 0$ that exists when $\bar{b}^* < \bar{b} < 1 - \bar{s}$ (equivalently $b^* < b < b_0$ where $b^* = \bar{b}^*/f$) is unstable, and the larger equilibrium x_1 that exists for all $\bar{b} > \bar{b}^*$ (equivalently $b > b^*$) is (locally asymptotically) stable.

Acknowledgments

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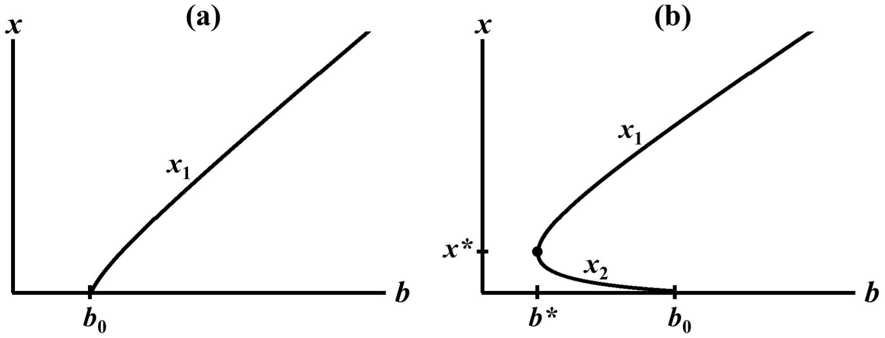

Fig. 1. shown are the two possible graphs of the positive equilibrium pairs $[b, x]$ of (2.6)-(2.7) with $\beta(x)$ given by (2.11). The equilibrium $x_1 > 0$ is (locally asymptotically) stable and $x_2 > 0$ is unstable. The extinction equilibrium $x = 0$ is stable for $b < b_0$ and unstable for $b > b_0$. (a) $a < c$ implies a forward bifurcation and the existence of a unique, stable positive equilibrium x_1 for and only for $b > b_0$. (b) $a > c$ implies a backward bifurcation which creates a strong Allee effect with a unstable equilibrium $x_2 > 0$ and a stable equilibrium $x_1 > 0$ for $b^* < b < b_0$ and a unique stable positive equilibrium x_1 for $b \geq b_0$.

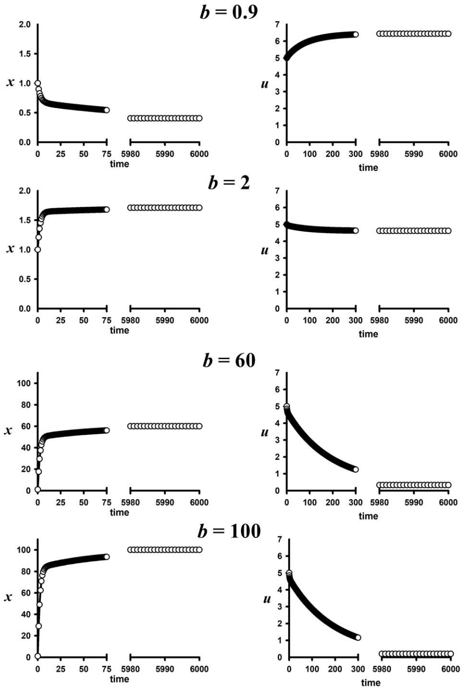

Fig. 2. A sample solution (x_t, u_t), for each value of b_0 in the shown sequence of selected values, is seen converging to a positive equilibrium for the Darwinian equations (3.4)-(3.5) with model components (3.11), (3.12), (3.14), and (3.15). The remaining parameter values are $s = 0.9$, $c_0 = 0.1$, $a = 10$, $w_1 = 0.05$, $w_2 = 20$, $w_3 = 0.1$, and $\sigma^2 = 0.5$. In order of increasing b values, the post-reproduction survival probabilities at equilibrium $s\,(1 - f\,(u_e))$ are respectively 0.79, 0.59, 0.13, 0.040, 0.0049, and 0.0018 (to 2 significant digits).

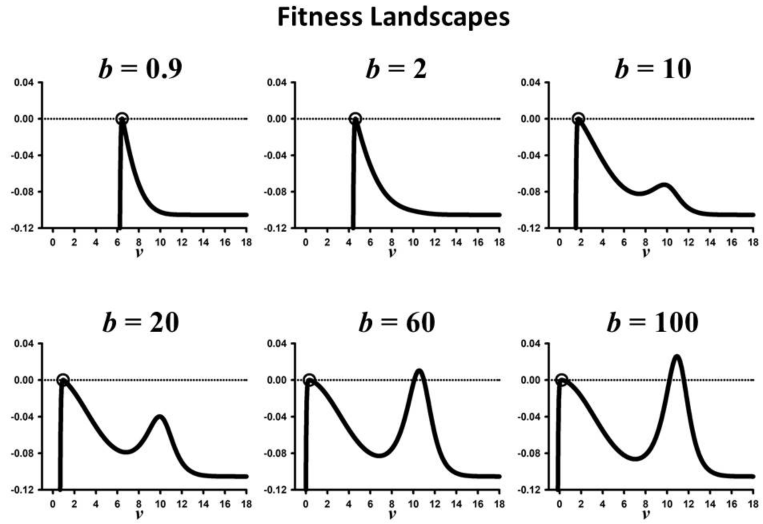

Fig. 3. Shown are the adaptive landscapes for the equilibria in Fig. 2. The open circles indicate that $v = u_e$ lies on a maximum where $r(x_e, u_e, u_e) = 1$ (since x_e is a positive equilibrium). Note that as b increases (to $b = 60$ and 100) a second (local) maximum appears that eventually becomes the global maximum at which point u_e is no longer an ESS.