

## DARWINIAN DYNAMICS OF A JUVENILE-ADULT MODEL

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**ABSTRACT.** The bifurcation that occurs from the extinction equilibrium in a basic discrete time, nonlinear juvenile-adult model for semelparous populations, as the inherent net reproductive number  $R_0$  increases through 1, exhibits a dynamic dichotomy with two alternatives: an equilibrium with overlapping generations and a synchronous 2-cycle with non-overlapping generations. Which of the two alternatives is stable depends on the intensity of competition between juveniles and adults and on the direction of bifurcation. We study this dynamic dichotomy in an evolutionary setting by assuming adult fertility and juvenile survival are functions of a phenotypic trait  $u$  subject to Darwinian evolution. Extinction equilibria for the Darwinian model exist only at traits  $u^*$  that are critical points of  $R_0(u)$ . We establish the simultaneous bifurcation of positive equilibria and synchronous 2-cycles as the value of  $R_0(u^*)$  increases through 1 and describe how the stability of these dynamics depend on the direction of bifurcation, the intensity of between-class competition, and the extremal properties of  $R_0(u)$  at  $u^*$ . These results can be equivalently stated in terms of the inherent population growth rate  $r(u)$ .

**1. Introduction.** A model for the dynamics of a population structured by juvenile (immature) and adult (mature) classes is described by the equations

$$J' = f\varphi(J, A)A \quad (1a)$$

$$A' = s\sigma(J, A)J \quad (1b)$$

where  $J$  and  $A$  denote juvenile and adult densities, respectively, and  $J'$  and  $A'$  denote these densities after one unit of time. Here  $\varphi$  and  $\sigma$  model density-dependent effects on these rates and  $\varphi(0, 0) = \sigma(0, 0) = 1$  so that  $f$  and  $s$  are inherent (low

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density) fertility and survivorship rates. The unit of time is taken as the maturation period, and it is assumed that no adult survives longer than one time unit. As a result, these model equations are applicable to a *semelparous* or *monocarpic* life history. Studies of this model, sometimes referred to Ebenman's model, and its extension to include more than one juvenile class, include [1], [2], [4], [5], [6], [8], [9], [10], [11], [13], [14], [15], [16], [17], [19], [20], [21], [22], [24], [25], [26], [27], [28], [30], [32], [33].

The dynamics implied by (1) can be varied and complex. They depend crucially on specific properties of the nonlinear density terms  $\varphi$  and  $\sigma$ . However, one general dynamic feature of (1) is the nature of the bifurcation that occurs as  $R_0 = fs$  (the inherent net reproductive number) increases through 1 and the extinction equilibrium  $(J, A) = (0, 0)$  loses stability [2], [5], [9]. Two entities simultaneously bifurcate from  $(0, 0)$  at  $R_0 = 1$  that offer two radically different dynamic alternatives, namely, a branch of positive equilibria and a branch of synchronous 2-cycles. The former represent equilibrium states with overlapping generations and the latter represent periodic oscillations with non-overlapping generations. In this dynamic dichotomy, which of the two dynamics is stable and which is unstable depends on the direction of bifurcation and on the intensity of competition between the two classes, as determined by  $\varphi$  and  $\sigma$ . See Theorem 2.2 in Section 2.

In the model (1) fertility and survivorship rates  $f\varphi$  and  $s\sigma$  change in time only in that they depend on the time varying densities  $J$  and  $A$ . There are, however, numerous other reasons why these vital rates can change in time, one important reason being that they are subject to natural selection. Our goal in this paper is to investigate the juvenile-adult model (1) in an evolutionary setting in which adult fertility and juvenile survival also depend on mean phenotypic trait  $u$  whose dynamics are subject to Darwinian evolution. We are interested in the role, if any, that the dynamic dichotomy described above plays in this evolutionary setting. Does the dichotomy always occur and, if so, what form does it take? Under what circumstances will natural selection favor stabilized populations with overlapping generations or oscillations with non-overlapping generations?

Following the methodology of evolutionary game theory (EGT), we model the dynamics of the mean phenotypic  $u$  by assuming that its change in time is proportional to the change in fitness as a function of  $u$ , which is taken to be the population growth rate  $\ln r$  where  $r = r(J, A, u)$  is the spectral radius of the projection matrix

$$\begin{pmatrix} 0 & f(u)\varphi(J, A, u) \\ s(u)\sigma(J, A, u) & 0 \end{pmatrix}$$

associated with the planar map (1) (see [31]). Specifically,

$$r(J, A, u) = \sqrt{R_0(J, A, u)} \tag{2}$$

where

$$R_0(J, A, u) \doteq f(u)s(u)\varphi(J, A, u)\sigma(J, A, u)$$

is the **net reproductive number** (expected offspring produce per individual per lifetime when population densities are held at  $J$  and  $A$  and the mean trait is fixed at  $u$ ). Thus, the Darwinian equations associated with the semelparous juvenile-adult

model (1) are

$$J' = f(u) \varphi(J, A, u) A \tag{3a}$$

$$A' = s(u) \varphi(J, A, u) J \tag{3b}$$

$$u' = u + v \partial_u \ln r(J, A, u) \tag{3c}$$

where  $v$  is the (assumed constant) variance in the phenotypic trait at any given time. Here we use the notation  $\partial_u$  for partial differentiation with respect to  $u$ .

We refer to (3) as the *EGT-JA model* (evolutionary game theoretic, juvenile-adult model). Notice that we can re-write the trait equation (3c) as

$$u' = u + \frac{1}{2} v \partial_u \ln R_0(J, A, u)$$

in which case the model uses  $R_0(J, A, u)$  as a measure of fitness in place of  $r$  [29].

When  $v = 0$ , i.e. in the absence of evolution, the equations (3) reduces to (1) with a fixed mean trait  $u$ . As the value of the  $R_0(0, 0, u) = f(u) s(u)$  increases through 1, the extinction equilibrium  $(J, A) = (0, 0)$  loses stability. The quantity  $R_0(0, 0, u)$  is the *inherent net reproductive number*, i.e., the net reproductive number in the absence of density effects. The dynamic bifurcation that occurs as a result of this destabilization is well understood [2], [5], [9]. A branch of positive equilibria and a branch of synchronous 2-cycles (periodic cycles of period 2 in which only one class is present at each time step) bifurcate from the extinction equilibrium as  $R_0(0, 0, u)$  increases through 1. A branch *bifurcates to the right (forward)* if, near the bifurcation point, the equilibria or 2-cycles exist for  $R_0(0, 0, u) \gtrsim 1$ . If both branches bifurcate to the right (which occurs, for example, if density dependent effects are all negative, i.e. there are no Allee effects), then one branch is stable and the other is unstable. The positive equilibria are stable if the between-class density effects (competition) are weak and the synchronous 2-cycles are stable if they are strong. These two alternatives, as determined by the relative intensities of between-class and within-class competition, represent a *dynamic dichotomy* at the bifurcation point  $R_0(0, 0, u) = 1$ . It is also possible that a branch *bifurcates to the left (backward)*, i.e. the equilibria or 2-cycles exist for  $R_0(0, 0, u) \lesssim 1$ . See Theorem 2.2. For a recent account of these phenomena, for this and higher dimensional models, see [9].

Our main goal in this paper is to establish the occurrence of such a dynamic alternative for the EGT-JA model (3) when  $v > 0$  and evolution occurs. In Sections 2 and 3 we investigate the existence and stability of extinction equilibria for the evolutionary model (3). In Sections 4 and 5 we prove the occurrence of a dynamic dichotomy at the point where an extinction equilibrium loses stability. Our results provide criteria for the evolutionary stability of either equilibria with overlapping generations or oscillations with non-overlapping generations. These criteria will show how the trait dependence of adult fertility and juvenile survival rates, in addition to density effects on these rates, determine which of these two alternatives occurs in an evolutionary setting, at least as implied by the EGT-JA model (3).

**2. Preliminaries.** Let  $U$  denote an open interval in  $R^1$  and let  $\Omega$  denote an open set in  $R^2$  that contains the origin. Let  $R_+^1$  and  $R_+^2$  denote the open positive cones in  $R^1$  and  $R^2$  respectively. Let  $\partial_J$ ,  $\partial_A$ , and  $\partial_u$  denote partial derivatives with respect to  $J$ ,  $A$ , and  $u$  respectively. We find it convenient to introduce a parameter  $b > 0$

into the EGT-JA model (3) by setting

$$f(u) = b\beta(u)$$

where  $\beta(u)$  is normalized as in the following assumption.

A1:  $\beta, s \in C^2(U, (0, 1])$  and  $\sigma \in C^2(\Omega \times U, [0, 1])$  where  $\sigma(0, 0, u) \equiv 1$  and  $\varphi(0, 0, u) \equiv 1$  for all  $u \in U$  and  $\max_U \beta(u) = 1$ .

The normalizing assumption  $\max_U \beta(u) = 1$  in A1 implies that  $b$  is the **maximum inherent adult fertility rate**  $f(u) = b\beta(u)$  obtainable on the trait interval  $U$ . The quantity  $b$  will be a convenient bifurcation parameter. The EGT-JA model equations (3) become

$$J' = b\beta(u)\varphi(J, A, u)A \quad (4a)$$

$$A' = s(u)\sigma(J, A, u)J \quad (4b)$$

$$u' = u + vd(J, A, u) \quad (4c)$$

where

$$d(J, A, u) \doteq \frac{1}{2} \frac{\partial_u [\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)]}{\beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)}.$$

Note that the trait equation (4c) does not contain  $b$ . Because of this, we find it convenient to introduce

$$\bar{R}_0(J, A, u) \doteq \beta(u)s(u)\sigma(J, A, u)\varphi(J, A, u)$$

so that we can write

$$d(J, A, u) \doteq \frac{1}{2} \frac{\partial_u \bar{R}_0(J, A, u)}{\bar{R}_0(J, A, u)} \quad (5)$$

in the trait equation (4c). Note that

$$R_0(J, A, u) = b\bar{R}_0(J, A, u).$$

**Definition 1.** (a) An extinction equilibrium  $(J, A, u)$  is an equilibrium of (4) in which  $J = A = 0$ . A positive equilibrium  $(J, A, u)$  is an equilibrium of (4) in which  $J > 0, A > 0$ , i.e., an equilibrium that lies in  $R_+^2 \times U$ .

(b) A critical trait  $u = u^*$  satisfies the equation  $d(0, 0, u^*) = 0$ , i.e., satisfies  $\partial_u r(0, 0, u) = \partial_u R_0(0, 0, u) = 0$ .

The following Lemma is obvious.

**Lemma 2.1.** *A point  $(J, A, u) = (0, 0, u)$  is an extinction equilibrium if and only if  $u = u^*$  is a critical trait. If  $u^*$  is a critical trait, then  $(0, 0, u^*)$  is an extinction equilibrium for all values of  $b \in R_+^1$ .*

Under assumption A1, the defining equation for a critical trait reduces to

$$\beta(u)\partial_u s(u) + s(u)\partial_u \beta(u) = 0. \quad (6)$$

Thus, at a critical trait  $u^*$  either both derivatives  $\partial_u s(u^*) = \partial_u \beta(u^*) = 0$  or they are both nonzero and of opposite signs. The latter case expresses a trade-off between juvenile survivorship and adult fertility with increasing mean trait value  $u$ . For more on the biological implications of these alternatives see the examples in Section 6.

Without loss in generality, by a change of trait reference point, we can assume that a critical trait of interest is placed at 0:

A2.  $u^* = 0 \in U$  is a critical trait.

Under this assumption,  $(J, A, u) = (0, 0, 0)$  is an extinction equilibrium for all values of  $b$ . If this extinction equilibrium is stable, then orbits can “evolve to extinction”. We study the stability and instability properties of this extinction equilibrium in the Section 3.

In the absence of evolution ( $v = 0$ ) the trait  $u$  remains constant and the population dynamics are governed by the equations

$$J' = b\beta(u)\varphi(J, A, u)A \tag{7a}$$

$$A' = s(u)\sigma(J, A, u)J \tag{7b}$$

in which  $u$  is simply a fixed parameter. A positive equilibrium  $(J, A)$  of this non-evolutionary model is one that lies in  $R_+^2$ . A synchronous 2-cycles is a periodic orbit that lies on  $\partial R_+^2 \setminus \{(0, 0)\}$ . A synchronous 2-cycle clearly consists of two alternating points  $(J, 0)$  and  $(0, A)$  of non-overlapping classes. Theorem describes the bifurcation of positive equilibria and, simultaneously, of synchronous 2-cycles, using  $b$  as a bifurcation parameter.

We need the following definitions.

**Definition 2.** Define the quantities

$$\begin{aligned} c_w(u) &\doteq \partial_J \sigma(0, 0, u) + s(u)\partial_A \varphi(0, 0, u) \\ c_b(u) &\doteq \partial_J \varphi(0, 0, u) + s(u)\partial_A \sigma(0, 0, u) \\ a_{\pm}(u) &\doteq c_w(u) \pm c_b(u). \end{aligned}$$

The quantities  $c_w(u)$  and  $c_b(u)$  are measures of, respectively, the within-class and between class competition intensity, at low population densities and at mean trait  $u$ . The quantity  $a_+(u)$  is a (weighted) sum of all competitive effects and  $a_-(u)$  is a measure of the difference between within-class and between-class competition (at low densities and mean trait  $u$ ).

For a fixed value of  $u$ , by a *branch of equilibria of (7) that bifurcates from the extinction equilibrium* we mean a continuum of equilibria  $(J(b), A(b))$  that are functions of  $b$  such that  $(J(0), A(0)) = (0, 0)$ . A similar definition holds for a bifurcating branch of 2-cycles.

**Theorem 2.2.** [5], [9] *Assume A1 and  $v = 0$ . For any fixed value of  $u \in U$ , the extinction equilibrium  $(J, A) = (0, 0)$  is stable for  $b < 1/s(u)\beta(u)$  and unstable for  $b > 1/s(u)\beta(u)$ .*

(a) *If  $a_+(u) \neq 0$  then there exists a branch of positive equilibria that bifurcates from the extinction equilibrium at  $b = 1/s(u)\beta(u)$ . If  $a_+(u) < 0$  then the bifurcation is to the right and, for  $b \gtrsim 1/s(u)\beta(u)$ , the bifurcating positive equilibria are*

- (i) *(locally asymptotically) stable if  $a_-(u) < 0$*
- (ii) *unstable if  $a_-(u) > 0$ .*

*If  $a_+(u) > 0$  then the bifurcation is to the left and the bifurcating positive equilibria are unstable.*

(b) *If  $c_w(u) \neq 0$  then there exists a branch of synchronous 2-cycles  $a$  that bifurcates from the extinction equilibrium at  $b = 1/s(u)\beta(u)$ . If  $c_w(u) < 0$  then the bifurcation is to the right and, for  $b \gtrsim 1/s(u)\beta(u)$ , the bifurcating 2-cycles are*

- (i) *(locally asymptotically) stable if  $a_-(u) > 0$*
- (ii) *unstable if  $a_-(u) < 0$ .*

*If  $c_w(u) > 0$  then the bifurcation is to the left and the bifurcating 2-cycles are unstable.*

It is this theorem, for the non-evolutionary case  $v = 0$  in EGT-JA model (4), that we want to extend to the evolutionary case when  $v > 0$ . To accomplish this we will utilize the following ingredients of its proof that can be found in [5] and [9]. Near the bifurcation point, the bifurcating positive equilibria in Theorem 2.2(a) have, for  $\varepsilon \approx 0$ , the parametric representations

$$J(\varepsilon) = -\frac{1}{a_+(u)}\varepsilon + O(\varepsilon^2), \quad A(\varepsilon) = -\frac{s(u)}{a_+(u)}\varepsilon + O(\varepsilon^2)$$

$$b(\varepsilon) = \frac{1}{s(u)\beta(u)} + \frac{1}{s(u)\beta(u)}\varepsilon$$

and the eigenvalues of the Jacobian of the map (7) evaluated at these equilibria have the expansions

$$\lambda_1(\varepsilon) = 1 - \frac{1}{2}\varepsilon + O(\varepsilon^2) \tag{8a}$$

$$\lambda_2(\varepsilon) = -1 + \frac{1}{2}\frac{a_-(u)}{a_+(u)}\varepsilon + O(\varepsilon^2). \tag{8b}$$

These eigenvalues determine the stability of the equilibria and the assertions of the Theorem 2.2(a). Near the bifurcation point, the two points that make up the bifurcating synchronous 2-cycles in Theorem 2.2(b) have the form  $(J(\varepsilon), 0)$  and  $(0, A(\varepsilon))$  with parametric representations given by

$$J(\varepsilon) = -\frac{1}{c_w(u)}\varepsilon + O(\varepsilon^2), \quad A(\varepsilon) = -\frac{s(u)}{c_w(u)}\varepsilon + O(\varepsilon^2)$$

for  $\varepsilon \approx 0$ . The eigenvalues of the Jacobian of the composite map of (7) associated with these cycles have the expansions

$$\lambda_1(\varepsilon) = 1 - \varepsilon + O(\varepsilon^2) \tag{9a}$$

$$\lambda_2(\varepsilon) = 1 + \frac{a_-(u)}{a_+(u)}\varepsilon + O(\varepsilon^2). \tag{9b}$$

These eigenvalues determine the stability of the synchronous 2-cycles and the assertions of the Theorem 2.2(b).

**Remark 1.** If only negative feedback density terms are present, i.e. all derivatives  $\partial_J\sigma$ ,  $\partial_A\sigma$ ,  $\partial_J\varphi$  and  $\partial_A\varphi$  at  $J = A = 0$  are negative or zero, then  $c_w(u)$ ,  $c_b(u)$  and  $a_+(u)$  are negative. By Theorem 2.2 both branches of positive equilibria and synchronous 2-cycles bifurcate to the right and one branch is stable and the other is unstable. In this dynamic dichotomy, the positive equilibria are stable if  $|c_w(u)| > |c_b(u)|$ , i.e. the magnitude of within-class competition intensity is larger than that of between-class competition. In the opposite case, when  $|c_w(u)| < |c_b(u)|$ , the synchronous 2-cycles are stable.

**Remark 2.** Note that in Theorem 2.2 left bifurcations, which can only occur if positive feedback terms (positive derivatives  $\partial_J\sigma$ ,  $\partial_J\varphi$ ,  $\partial_A\sigma$  or  $\partial_A\varphi$ ) are present and of sufficient magnitude, are unstable. It is also possible that the two branches bifurcate in opposite directions. In this case, a little reflection on the stability-instability criteria in the theorem shows that the right bifurcating branch is stable.

**Remark 3.** Theorem 2.2 is a more concise (and slightly corrected) statement of Theorem 4.1 in [5]. (Assertions about possible stable bifurcations to that theorem are incorrect.)

**3. Stability of extinction equilibria.** To study local stability by linearization we need the Jacobian associated with the Darwinian equations (4). First, we define

$$P = \left( \begin{array}{c|c} b\beta(u) [\partial_J \varphi(J, A, u)] A & b\beta(u) \varphi(J, A, u) + b\beta(u) [\partial_A \varphi(J, A, u)] A \\ \hline s(u) \sigma(J, A, u) + s(u) [\partial_J \sigma(J, A, u)] J & s(u) [\partial_A \sigma(J, A, u)] J \end{array} \right),$$

which is the Jacobian of the population dynamic equations (4) in the absence of evolution ( $v = 0$  and  $u$  remains constant). Define the vector quantities

$$\hat{\psi} = \begin{pmatrix} b\partial_u [\beta(u) \varphi(J, A, u)] A \\ \partial_u [s(u) \sigma(J, A, u)] J \end{pmatrix}, \quad \hat{\rho} = \begin{pmatrix} \partial_J d(J, A, u) & \partial_A d(J, A, u) \end{pmatrix}.$$

Then the Jacobian associated with the EGT-JA model (4) is

$$\mathfrak{J} = \begin{pmatrix} P & \hat{\psi} \\ v\hat{\rho} & 1 + v\partial_u d \end{pmatrix}.$$

The Linearization Principle requires an evaluation of  $\mathfrak{J}$  at the equilibrium of interest and a study of the eigenvalues for the resulting  $3 \times 3$  matrix. In this section we are interested in extinction equilibria; specifically, under A2 we are interested in the equilibrium  $(J, A, u) = (0, 0, 0)$ .

**Definition 3.** A superscript “0” denotes evaluation at the extinction equilibrium  $(J, A, u) = (0, 0, 0)$ .

For example,  $s^0 = s(0)$ ,  $a_+^0 = a_+(0)$ , and so on.  $\partial_J^0 \varphi$  denotes partial differentiation of  $\varphi(J, A, u)$  with respect to  $J$  followed by an evaluation at  $(J, A, u) = (0, 0, 0)$ .

Evaluated at the extinction equilibrium  $(0, 0, 0)$  the Jacobian becomes

$$\mathfrak{J}^0 = \begin{pmatrix} P^0 & \text{col}(0, 0) \\ \hat{\rho}^0 & 1 + v\partial_u^0 d \end{pmatrix}, \quad P^0 \doteq \begin{pmatrix} 0 & b\beta^0 \\ s^0 & 0 \end{pmatrix}.$$

The eigenvalues of  $\mathfrak{J}^0$  are

$$\lambda_{\pm} = \pm \sqrt{b\beta^0 s^0}, \quad \lambda_3 = 1 + v\partial_u^0 d.$$

A calculation shows, in lieu of A1, (5), and (6), that

$$\partial_u^0 d = \frac{1}{2\beta^0 s^0} \partial_{uu}^0 \bar{R}_0. \tag{10}$$

We make the assumption

$$\text{A3: } \partial_{uu}^0 \bar{R}_0 \neq 0$$

and define

$$b^0 \doteq \frac{1}{\beta^0 s^0}. \tag{11}$$

We summarize these results in the following theorem.

**Theorem 3.1.** Assume A1, A2 and A3.

- (a) If  $-4\beta^0 s^0 < v\partial_{uu}^0 \bar{R}_0 < 0$  then the extinction equilibrium  $(0, 0, 0)$  is
  - (i) unstable for  $b > b^0$  and
  - (ii) (locally asymptotically) stable for  $b < b^0$ .
- (b) If  $\partial_{uu}^0 \bar{R}_0 > 0$  or  $v\partial_{uu}^0 \bar{R}_0 < -4\beta^0 s^0$ , then the extinction equilibrium  $(0, 0, 0)$  of (4) is unstable for all  $b$ .

A calculation shows that

$$\partial_{uu}^0 \bar{R}_0 = \partial_{uu}^0 (\beta s) = s^0 \partial_{uu}^0 \beta + 2\partial_u^0 \beta \partial_u^0 s + \beta^0 \partial_{uu}^0 s$$

(cf. A1 and (6)).

**Remark 4.** If  $\partial_{uu}^0 \bar{R}_0 = 0$  then  $\lambda_3 = 1$  and the extinction equilibrium is non-hyperbolic. Nonetheless it is unstable if  $b > b^0$  since  $P^0$  has a positive eigenvalue  $\lambda_+ > 1$ . If, on the other hand,  $b < b^0$  then  $|\lambda_{\pm}| < 1$  the linearization principle fails to hold.

**Remark 5.** In lieu of the relationship (2) between  $r$  and  $R_0$ , Theorem 3.1 remains valid with  $\partial_{uu}^0 \bar{R}_0$  replaced by  $\partial_{uu}^0 \bar{r}$  where the normalized inherent net reproductive number  $\bar{R}_0(J, A, u)$  is replaced by the normalized inherent population growth rate

$$\bar{r}(J, A, u) = \sqrt{\bar{R}_0(J, A, u)}.$$

**Remark 6.** If  $\bar{R}_0(0, 0, u)$  has a local minimum ( $\partial_{uu}^0 \bar{R}_0 > 0$ ) at  $u = 0$  as a function of  $u$ , then the extinction equilibrium is unstable. If  $\bar{R}_0(0, 0, u)$  has a local maximum at  $u = 0$  ( $\partial_{uu}^0 \bar{R}_0 < 0$ ), then the extinction equilibrium loses stability as  $b$  increases through  $b^0$ .

**Remark 7.** Since  $R_0(0, 0, u) = b\beta(u)s(u)$  one could, if desired, use  $R_0^0 = b\beta^0 s^0$  (or  $r^0 = \sqrt{b\beta^0 s^0}$ ) as the bifurcation parameter in Theorems 2.2 and 3.1 instead of  $b$ . In this case, the bifurcation occurs at the critical value  $R_0^0 = 1$  (or  $r^0 = 1$ ).

In case (a) of Theorem 3.1 we expect a bifurcation will occur that creates non-extinction equilibria. This is the subject of the Section 4.

**4. Bifurcation of positive equilibria and their stability.** Our goal in this section is to prove the bifurcation of positive equilibria at the critical value  $b = b^0$  defined by (11) and to give criteria for their stability. The equilibrium equations for (4) are

$$J = b\beta(u)\varphi(J, A, u)A \tag{12a}$$

$$A = s(u)\sigma(J, A, u)J \tag{12b}$$

$$0 = d(J, A, u) \tag{12c}$$

which we note have the solution  $(J, A, u) = (0, 0, 0)$  for all values of  $b$ . We will establish the existence of positive equilibria by use of the Implicit Function Theorem. For this purpose, we will make the additional assumption

$$\text{A4: } a_+^0 \neq 0$$

This assumption implies that some density effects are in effect near  $(0, 0, 0)$ .

By a **branch of equilibria that bifurcates from the extinction equilibrium** we mean a continuum of equilibria  $(J(b), A(b), u(b))$  of the EGT-JA model (4) that are functions of  $b$  such that  $(J(0), A(0), 0) = (0, 0, 0)$ . Algebraically,  $b$  appears in equation (12a) and therefore the solutions  $(J(b), A(b), u(b))$  of those equations depend on  $b$ . The bifurcation is **to the right (or forward)** if the equilibria are positive for  $b \gtrsim b_0$  and **to the left (backward)** if the equilibria are positive for  $b \lesssim b_0$ .

**Theorem 4.1.** *Assume A1-A4. There exists a branch of positive equilibria  $(J, A, u)$  of the EGT-JA model (4) that bifurcates from the extinction equilibrium  $(0, 0, 0)$  at  $b = b^0$ . The bifurcation is to the right if  $a_+^0 < 0$  and to the left if  $a_+^0 > 0$ . Near the bifurcation point, the branch of positive equilibria has a parameterization in terms of  $\varepsilon \doteq (b - b^0) / b^0 \approx 0$  of the form*

$$\begin{aligned} J(\varepsilon) &= -\frac{1}{a_+^0} \varepsilon + O(\varepsilon^2) \\ A(\varepsilon) &= -\frac{s^0}{a_+^0} \varepsilon + O(\varepsilon^2) \\ u(\varepsilon) &= \frac{\partial_J^0 d + s^0 \partial_A^0 d}{a_+^0 \partial_u^0 d} \varepsilon + O(\varepsilon^2) \end{aligned} \tag{13}$$

Before giving a proof, we point out some observations about the bifurcation described in this theorem.

**Remark 8.** Theorem 4.1 also implies the existence of negative equilibria for values of  $b$  on the opposite side of  $b^0$  from those values that give positive equilibria. Thus, the bifurcation in this theorem is a transcritical bifurcation. The negative equilibria are not, of course, of any biological interest.

**Remark 9.** If all density effects are of negative feedback type, that is to say, if

$$A5: \partial_J^0 \varphi \leq 0, \partial_J^0 \sigma \leq 0, \partial_A^0 \varphi \leq 0, \partial_A^0 \sigma \leq 0, \text{ but not all equal to } 0$$

then clearly  $c_w^0$  and  $c_b^0$  are nonnegative and one is nonzero. As a result  $a_+^0 < 0$  and the bifurcation is to the right. A bifurcation to the left requires at least one density dependent effect to be a **positive feedback or an Allee effect** (i.e., at least one of these partial derivatives is positive) and that the positive feedback effects be of sufficient magnitude so that  $a_+^0 > 0$ . In particular, if only Allee effects occur (i.e.,  $\partial_J^0 \varphi, \partial_J^0 \sigma, \partial_A^0 \varphi$  and  $\partial_A^0 \sigma$  are all non-negative and not all are equal to 0), then the bifurcation is to the left.

**Remark 10.** Since the variance  $v$  does not appear in the equilibrium equations, it follows that the bifurcating branch of positive equilibria in Theorem 4.1 do not depend on  $v$  (the speed of evolution).

*Proof.* By the definition of critical trait  $u^* = 0$  we have  $d(0, 0, 0) = 0$ . Moreover, assumption A3 implies  $\partial_u^0 d \neq 0$  and, as a result, we can apply the Implicit Function Theorem to solve the equilibrium equation (12c) for

$$u = \eta(J, A), \quad \eta(0, 0) = 0. \tag{14}$$

By the smoothness assumptions in A1, this solution is twice continuously differential in  $J$  and  $A$ . A substitution of this solution into the two remaining equilibrium equations (12a)-(12b) reduces the equilibrium equations to the two algebraic equations

$$J = b\beta(\eta(J, A)) \varphi(J, A, \eta(J, A)) A \tag{15a}$$

$$A = s(\eta(J, A)) \sigma(J, A, \eta(J, A)) J \tag{15b}$$

for  $(J, A) \in \mathbb{R}_+^2$ . Our goal now is to solve these equations for  $(J, A) = (J(b), A(b)) \neq (0, 0)$  by using the Implicit Function Theorem. We cannot do this using equations

(15) as they stand because they possess the trivial solution  $(J, A) = (0, 0)$  for all  $b$  (and the fact that the Implicit Function Theorem yields unique solutions). We can overcome this difficulty by deriving a system of equations equivalent to (15), in so far as nontrivial are concerned, for which  $(J, A) = (0, 0)$  is no longer a solution for all  $b$ . To do this we substitute the right side of equation (15b) for the factor  $A$  on right side of equation (15a). As far as positive solutions are concerned, we can cancel  $J$  from the resulting equation and obtain the equivalent system

$$\begin{aligned} 1 &= b\beta(\eta(J, A))s(\eta(J, A))\sigma(J, A, \eta(J, A))\varphi(J, A, \eta(J, A)) \\ A &= s(\eta(J, A))\sigma(J, A, \eta(J, A))J. \end{aligned} \quad (16)$$

We apply the Implicit Function Theorem to these equations, which we write this as  $f_1(J, A, b) = 0$  and  $f_2(J, A, b) = 0$  where

$$\begin{aligned} f_1(J, A, b) &\doteq b\beta(\eta(J, A))s(\eta(J, A))\varphi(J, A, \eta(J, A))\sigma(J, A, \eta(J, A)) - 1 \\ f_2(J, A, b) &\doteq s(\eta(J, A))\sigma(J, A, \eta(J, A))J - A. \end{aligned}$$

Since these equations are satisfied by  $J = A = 0$  and  $b = b^0$ , the Implicit Function theorem applies at this point provided the determinant

$$\Delta(J, A, b) \doteq \det \begin{pmatrix} \partial_J f_1(J, A, b) & \partial_A f_1(J, A, b) \\ \partial_J f_2(J, A, b) & \partial_A f_2(J, A, b) \end{pmatrix}$$

is nonzero at this point. In that event, the Implicit Function Theorem guarantees the existence of a (twice continuously differentiable) solution

$$J = J(b), \quad A = A(b) \quad \text{with } J(b^0) = 0, \quad A(b^0) = 0 \quad (17)$$

of (16) for  $b$  near  $b^0$ . To calculate the entries in the determinant  $\Delta(0, 0, b^0)$  we first make some preliminary observations. By the chain rule

$$\partial_J \beta(\eta(J, A))|_{J=A=0} = \partial_u^0 \beta \partial_J^0 \eta \quad \text{and} \quad \partial_A \beta(\eta(J, A))|_{J=A=0} = \partial_u^0 \beta \partial_A^0 \eta$$

and therefore, by (6), we have

$$\begin{aligned} \partial_J [\beta(\eta(J, A))s(\eta(J, A))]|_{J=A=0} &= [\beta^0 \partial_u^0 s + s^0 \partial_u^0 \beta] \partial_J^0 \eta = 0 \\ \partial_A [\beta(\eta(J, A))s(\eta(J, A))]|_{J=A=0} &= [\beta^0 \partial_u^0 s + s^0 \partial_u^0 \beta] \partial_A^0 \eta = 0. \end{aligned}$$

Using these facts and the normalization of  $\sigma$  and  $\varphi$  in A1, we obtain

$$\begin{aligned} \partial_J f_1(0, 0, b^0) &= \partial_J^0 \varphi + \partial_J^0 \sigma \\ \partial_A f_1(0, 0, b^0) &= \partial_A^0 \varphi + \partial_A^0 \sigma. \end{aligned}$$

Simpler calculations show  $\partial_J f_2(0, 0, b^0) = s^0$  and  $\partial_A f_2(0, 0, b^0) = -1$  and we arrive at

$$\Delta(0, 0, b^0) = \det \begin{pmatrix} \partial_J^0 \varphi + \partial_J^0 \sigma & \partial_A^0 \varphi + \partial_A^0 \sigma \\ s^0 & -1 \end{pmatrix} = -a_+^0$$

which is nonzero by assumption A3. The resulting solutions (17) of equations (16), together with (14), yield a branch of equilibria of the form

$$(J(b), A(b), u(b)) = (J(b), A(b), \eta(J(b), A(b)))$$

that are continuously differentiable for  $b \approx b^0$  and satisfy  $(J(b^0), A(b^0), u(b^0)) = (0, 0, 0)$ .

What remains is to determine when these equilibria are positive. One way to do this is from the signs of the derivatives  $\partial_b^0 J$  and  $\partial_b^0 A$ , which can be calculated

from the equations (16) by implicit differentiation with respect to  $b$  followed by an evaluation at  $b = b^0$ . These straightforward calculations yield the equations

$$0 = \beta^0 s^0 + (\partial_J^0 \sigma \partial_b^0 J + \partial_A^0 \sigma \partial_b^0 A) + (\partial_J^0 \varphi \partial_b^0 J + \partial_A^0 \varphi \partial_b^0 A) \quad \text{and} \quad \partial_b^0 A = s^0 \partial_b^0 J$$

which imply  $\partial_b^0 J = -1/a_+^0 b^0$  and  $\partial_b^0 A = -s^0/a_+^0 b^0$ . Thus, we have the Taylor expansions

$$J(b) = -\frac{1}{a_+^0 b^0} (b - b^0) + O\left((b - b^0)^2\right), \quad A(b) = -\frac{s^0}{a_+^0 b^0} (b - b^0) + O\left((b - b^0)^2\right)$$

which give the parameterization (13). The assertions in Theorem 4.1 about the direction of bifurcation follow directly from these parametric formulas.  $\square$

The intersecting branches of equilibria involved in a transcritical bifurcation typically exhibit the Exchange of Stability Principle. As a result, the direction of bifurcation typically determines which branches are stable and which are unstable [18]. Here by “typical” is meant that at the bifurcation point the projection matrix has a strictly dominant eigenvalue (i.e., the matrix is primitive). The bifurcation in Theorem 4.1, however, is not generic in this sense because at bifurcation *both* eigenvalues of the Jacobian leave the unit circle. As a result we cannot invoke the Exchange of Stability Principle to determine the stability properties of the bifurcating branch of equilibria. Indeed, as seen in the following theorem, the Exchange of Stability Principle does not hold for this problem (as it does not for the non-evolutionary model in Theorem 2.2).

**Theorem 4.2.** *Assume A1-A3 hold and that  $v > 0$ .*

(a) *If  $\partial_{uu}^0 \bar{R}_0 < 0$  and  $v \approx 0$ , then the extinction equilibrium  $(0, 0, 0)$  of (4) is (locally asymptotically) stable for  $b < b^0$  and unstable for  $b > b^0$ . With regard to the bifurcating positive equilibria, we have the following two alternatives.*

*If  $a_+^0 < 0$  then near the bifurcation point, i.e. for  $b \gtrsim b^0$ , the (right bifurcating) positive equilibria in Theorem 4.1 are*

- (i) *(locally asymptotically) stable if  $a_-^0 < 0$*
- (ii) *unstable if  $a_-^0 > 0$ .*

*If  $a_+^0 > 0$  then near the bifurcation point, i.e. for  $b \lesssim b^0$ , the (left bifurcating) positive equilibria in Theorem 4.1 are unstable.*

(b) *If  $\partial_{uu}^0 \bar{R}_0 > 0$  then the extinction equilibrium  $(0, 0, 0)$  of (4) is unstable for all  $b$  and the bifurcating positive equilibria in Theorem 4.1 are unstable near the bifurcation point (i.e., for  $b \approx b^0$ ).*

A proof of this Theorem appears in Appendix A.

If the assumption is made that only negative feedback density effects are present (assumption A5), then the bifurcation at  $b = b^0$  will be to the right and the stability/instability criteria in Theorem 4.2(i) and (ii) can be re-written as  $c < 1$  and  $1 < c$ , respectively, where

$$c \doteq \frac{c_b^0}{c_w^0} = \frac{\partial_J^0 \varphi + s^0 \partial_A^0 \sigma}{\partial_J^0 \sigma + s^0 \partial_A^0 \varphi} \geq 0 \tag{18}$$

is the ratio of within-class to between-class competitive intensity.

**Corollary 1.** *Assume A1-A5 hold and that  $\partial_{uu}^0 R_0 < 0$ . For small  $v \approx 0$  the (right bifurcating) positive equilibria in Theorem 4.1 are, at least for  $b \gtrsim b^0$ , (locally asymptotically) stable if  $c < 1$  and unstable if  $c > 1$ .*

The stability criterion  $c < 1$  in this corollary means between-class competition is weak (relative to within-class competition). The result is an evolution towards an equilibration dynamic with overlapping generations. On the other hand, the instability criterion  $c > 1$  means between-class competition is strong (relative to within-class competition). In this case a question arises about the asymptotic dynamics, which we address in Section 5.

**Remark 11.** The destabilization of the extinction equilibrium in Theorem 3.1(a) and the bifurcations in Theorem 4.1 occur as  $b$  increases through  $b^0$ . These theorems can also be stated using  $R_0^0 = b\beta^0 s^0$  (or  $r = \sqrt{b\beta^0 s^0}$ ) as the bifurcation parameter, in which case the bifurcation occurs at critical value 1.

**5. Bifurcation of synchronous 2-cycles and their stability.** The map defined by (4) holds the boundary set  $\partial R_+^2 \times U$  invariant in a special way. A point  $(J, 0, u) \in \partial R_+^2 \setminus \{(0, 0)\} \times U$  (with only juveniles present) is mapped to a point of the form  $(0, A, u) \in \partial R_+^2 \setminus \{(0, 0)\} \times U$  (with only adults present) and vice versa. We refer to orbits on  $\partial R_+^2 \setminus \{(0, 0)\} \times U$  as *(positive) synchronous orbits* since the generations are temporally synchronized so as never to overlap. A *synchronous cycle* is a periodic synchronous orbit. A synchronous 2-cycle arises from a fixed point  $(J, 0, u) \in \partial R_+^2 \setminus \{(0, 0)\} \times U$  of the composite map arising from (1). In other words, synchronous 2-cycles arises from solutions of the two equations

$$\begin{aligned} J &= b\beta(u + vd(J, 0, u))\varphi(0, s(u))\sigma(J, 0, u)J, u + vd(J, 0, u)s(u)\sigma(J, 0, u)J \\ 0 &= d(J, 0, u) + d(0, s(u))\sigma(J, 0, u)J, u + vd(J, 0, u) \end{aligned}$$

for  $J > 0$  and  $u \in U$ . Note that  $J = 0, u = u^*$  solve these equations for all values of  $b$ , provided  $u^*$  is a critical point. Without loss in generality, we assume  $u^* = 0$  is a critical trait (i.e. A2 holds). Since we seek solutions with  $J > 0$ , we can cancel  $J$  from both sides of the first equation. This results in the following equations

$$1 = b\beta(u + vd(J, 0, u))s(u)\varphi(0, s(u))\sigma(J, 0, u)J, u + vd(J, 0, u)\sigma(J, 0, u) \quad (19a)$$

$$0 = d(J, 0, u) + d(0, s(u))\sigma(J, 0, u)J, u + vd(J, 0, u) \quad (19b)$$

whose solutions with  $J > 0$  yield the first point  $(J, 0, 0)$  of a synchronous 2-cycle. Using these equations, we prove the following theorem in Appendix B.

**Theorem 5.1.** *Assume A1-A3 hold and that  $c_w^0 \neq 0$ . For small  $v \approx 0$  there exists a branch of synchronous 2-cycles of the EGT-JA model (4) that bifurcates from the extinction equilibrium  $(0, 0, 0)$  at  $b = b^0$ . The bifurcation is to the right if  $c_w^0 < 0$  and to the left if  $c_w^0 > 0$ .*

This theorem shows that a bifurcation of synchronous 2-cycles accompanies the bifurcation of positive equilibria at  $b = b^0$  in Theorem 4.1.

**Remark 12.** If density dependence entails only negative feedback effects, i.e. if A5 holds, then the dual bifurcations of positive equilibria and synchronous 2-cycles are both to the right.

**Remark 13.** A parameterization of the bifurcating branch of synchronous 2-cycles in terms of  $\varepsilon$ , analogous to that of the bifurcating equilibria in Theorem 4.1, is given by (29) in the proof of Theorem 5.1 in Appendix B.

Theorem 4.2 provides criteria for the stability of the bifurcating positive equilibria. The following companion theorem gives stability criteria for the bifurcating synchronous 2-cycles. A proof appears in Appendix C.

**Theorem 5.2.** *Assume A1-A3 hold,  $c_w^0 \neq 0$  and that  $v > 0$ .*

(a) *Suppose  $\partial_{uu}^0 \bar{R}_0 < 0$  and  $v \approx 0$ .*

*If  $c_w^0 < 0$  then near the bifurcation point, i.e. for  $b \gtrsim b^0$ , the (right bifurcating) synchronous 2-cycles in Theorem 5.1 are*

(i) *(locally asymptotically) stable if  $a_-^0 > 0$*

(ii) *unstable if  $a_-^0 < 0$ .*

*If  $c_w^0 > 0$  then near the bifurcation point, i.e. for  $b \lesssim b^0$ , the (left bifurcating) synchronous 2-cycles in Theorem 5.1 are unstable.*

(b) *If  $\partial_{uu}^0 \bar{R}_0 > 0$  then the bifurcating 2-cycles in Theorem 5.1 are unstable near the bifurcation point (i.e., for  $b \approx b^0$ ), regardless of the direction of bifurcation.*

In the case of no Allee effects, we have the following companion (concerning the bifurcating synchronous 2-cycles) to Corollary 1 (concerning the bifurcating positive equilibria).

**Corollary 2.** *Assume A1-A5 hold and that  $\partial_{uu}^0 \bar{R}_0 < 0$ . For small  $v \approx 0$  the (right bifurcating) synchronous 2-cycles in Theorem 5.2 are, for  $b \gtrsim b^0$ , (locally asymptotically) stable if  $c > 1$  and unstable if  $c < 1$ .*

## 6. Discussion.

**6.1. Conclusions.** The main goal in this paper is to investigate attracting evolutionary states for a semelparous population by means of an evolutionary game theory version (4) of the basic juvenile-adult matrix model (3) (known as Ebenman’s model). Extinction and persistence are, of course, two fundamental concerns in population dynamics and the approach taken here is begin by considering the existence and stability of evolutionary extinction states (Theorem 3.1). Extinction states can only occur at mean trait values  $u^*$  that are critical points of the inherent (low density) net reproductive number

$$R_0(0, 0, u) = b\beta(u) s(u)$$

(or equivalently the inherent population growth rate  $r(0, 0, u) = \sqrt{R_0(0, 0, u)}$ ) as a function of  $u$ .

Our approach uses bifurcation theory and utilizes a fertility modulus  $b$  (the maximal trait dependent adult fertility rate) as a bifurcation parameter, although one can equivalently use the value of the inherent net reproductive number  $R_0^0 = b\beta(u^*)\varphi(u^*)$  at the critical trait (or the inherent population growth rate  $r_0^0 = \sqrt{R_0^0}$ ). As  $b$  increases through a critical value, or equivalently as  $R_0^0$  increases through 1, we found that two possible persistent states arise: positive equilibria with overlapping generations and synchronous 2-cycles with non-overlapping generations. A number of bifurcation scenarios are possible (Theorems 4.1, 4.2, 5.1, and 5.2).

The possible bifurcation scenarios are schematically summarized in Figure 1 for the case when the inherent net reproductive number  $R_0(0, 0, u)$  has a local maximum at the critical trait  $u = u^*$ . (If  $R_0(0, 0, u)$  has a local minimum, both bifurcating branches are unstable, as is the extinction equilibrium.) In this case, the extinction equilibrium at  $u = u^*$  loses stability as  $R_0^0$  increases through 1, and the directions of bifurcation and the stability properties of the bifurcating branches of equilibria

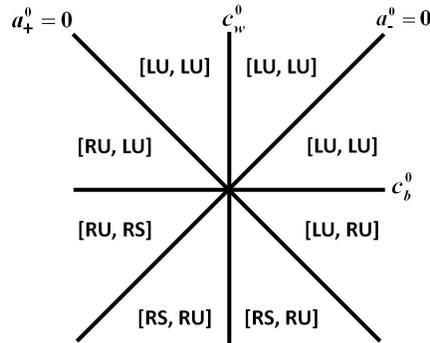


FIGURE 1. As a function of  $R_0^0 = 1$  a bifurcation of positive equilibria and synchronous 2-cycles occurs at  $R_0^0 = 1$  in the model (4). Under the assumptions that  $\partial_{uu}^0 R_0 < 0$  and  $v \approx 0$ , the direction of bifurcation and stability properties of the two bifurcating branches are determined by the relative sizes of the class competition measures  $c_b^0$  and  $c_w^0$  as given in Theorems 4.1, 5.1, 4.2 and 5.2. The  $(c_b^0, c_w^0)$ -plane is divided into eight sectors inside each of which the bifurcation scenarios are described by a bracketed pair. The first and second entries in these pairs give both the direction of bifurcation and the stability property of the positive equilibria and synchronous 2-cycles respectively. L and R denote left and right bifurcation and S and U denote a stable and an unstable bifurcation. For example, [RU, RS] means that the branch of positive equilibria bifurcates to the right and is unstable and the branch of synchronous 2-cycles bifurcates to the right and is stable.

and 2-cycles are determined by the relative sizes of the quantities

$$\begin{aligned} c_w^0 &\doteq \partial_J \sigma(0, 0, u^*) + s(u^*) \partial_A \varphi(0, 0, u^*) \\ c_b^0 &\doteq \partial_J \varphi(0, 0, u^*) + s(u^*) \partial_A \sigma(0, 0, u^*). \end{aligned}$$

$c_w^0$  and  $c_b^0$  which respectively measure the intensities of within-class and between-class competition (at low densities and at the critical trait  $u^*$ ). We point out some notable conclusions seen in Figure 1.

Recall that Allee effects of sufficient magnitude are required for  $c_w^0$  or  $c_b^0$  to be positive. If (as in A5) Allee effects not present (or are weak), then  $c_w^0 < 0$  and  $c_b^0 < 0$  and (the third or southwest quadrant in) Figure 1 shows that a dynamic dichotomy occurs in the bifurcation at  $R_0^0 = 1$ . That is to say, either the branch of positive equilibria or the branch of synchronous two cycles is stable (but not both). Moreover, which branch is stable is determined by the sign of  $a_-^0 \doteq c_w^0 - c_b^0$ . Specifically, strong within-class competition intensity ( $a_+^0 \doteq c_w^0 + c_b^0 < 0$ ) results in stable positive equilibria while strong between-class competition intensity ( $a_-^0 > 0$ ) results in stable synchronous 2-cycles. This dynamic dichotomy is a kind of generational competitive exclusion phenomenon analogous to the competitive exclusion principle for different species. This result can be conveniently expressed in terms of the competition ratio  $c$  defined by (18), which is a measure of the relative

strength of between-class competition:

$$c > 1 \implies \begin{array}{l} \text{bifurcating positive equilibria are unstable} \\ \text{bifurcating synchronous 2-cycles are stable} \end{array} \tag{20a}$$

$$c < 1 \implies \begin{array}{l} \text{bifurcating positive equilibria are stable} \\ \text{bifurcating synchronous 2-cycles are unstable.} \end{array} \tag{20b}$$

We also see from Figure 1 that a sufficiently strong Allee effect (i.e., when  $c_w^0$  or  $c_b^0$  is positive) results in the instability of both bifurcating branches with one sole exception. That exception occurs in the lower sector of the fourth (southeast) quadrant in Figure 1 where it is seen that the bifurcating positive equilibria are stable. This sector in Figure 1 describes the case of between-class Allee effects only between-class ( $c_b > 0$  and  $c_w < 0$ ) but not of sufficient strength so that  $a_+^0$  is positive. It also exhibits the dynamic dichotomy described above that occurs in the third (southwest) quadrant.

Some other observations from Figure 1 are:

- (1) If a left bifurcation occurs, then both branches are unstable.
- (2) A stable bifurcation occurs only if there are negative density effects of sufficient magnitude in within-class competition ( $c_w^0 < 0$ ).
- (3) Between-class Allee effects of sufficient magnitude ( $c_b^0 > 0$ ) imply the branch of synchronous 2-cycles is unstable

**6.2. Examples.** The location of critical traits  $u^*$  is dependent only on the inherent vital rates  $s(u)$  and  $b\beta(u)$ , as the defining equation (6) shows. Density effects, i.e. the coefficients  $\sigma(J, A, u)$  and  $\varphi(J, A, u)$ , play no role in determining the critical traits. Their role is to determine the direction of bifurcation and the stability properties of the bifurcating equilibria and synchronous 2-cycles. Since both  $s^0$  and  $\beta^0$  are positive it follows from (6) that  $\partial_u^0 s$  and  $\partial_u^0 \beta$  satisfy one of two cases:

$$\begin{array}{l} \text{(a) } \partial_u^0 s \partial_u^0 \beta < 0 \\ \text{(b) } \partial_u^0 s = \partial_u^0 \beta = 0. \end{array} \tag{21}$$

To obtain a stable bifurcation we need in addition that  $\partial_{uu}^0 R_0 < 0$  or equivalently that

$$\beta^0 \partial_{uu}^0 s + 2\partial_u^0 s \partial_u^0 \beta + s^0 \partial_{uu}^0 \beta < 0. \tag{22}$$

Case (21a) describes a trade-off between the inherent juvenile survivorship  $s(u)$  and adult fertility  $\beta(u)$  in the sense that they have opposite monotonicities as a function of the mean trait  $u$ . In Case (21b), inequality (22) implies that at least one second derivative  $\partial_{uu}^0 s$  and  $\partial_{uu}^0 \beta$  must be negative. That is to say, one of the vital rates  $s$  or  $\beta$  must attain a (local) maximum at  $u^*$ .

In the examples below, we use the Leslie-Gower functionals [23]

$$\sigma(J, A) = \frac{1}{1 + c_{11}J + c_{12}A}, \quad \varphi(J, A) = \frac{1}{1 + c_{21}J + c_{22}A} \tag{23a}$$

$$c_{ij} \geq 0 \text{ and at least one } c_{ii} > 0. \tag{23b}$$

for which the negative density conditions in A5 hold, Inequality (22) implies the dynamic dichotomy (20) occurs at the bifurcation point, with stability determined by the competition ratio

$$c = \frac{c_{21} + s^0 c_{12}}{c_{11} + s^0 c_{22}}.$$

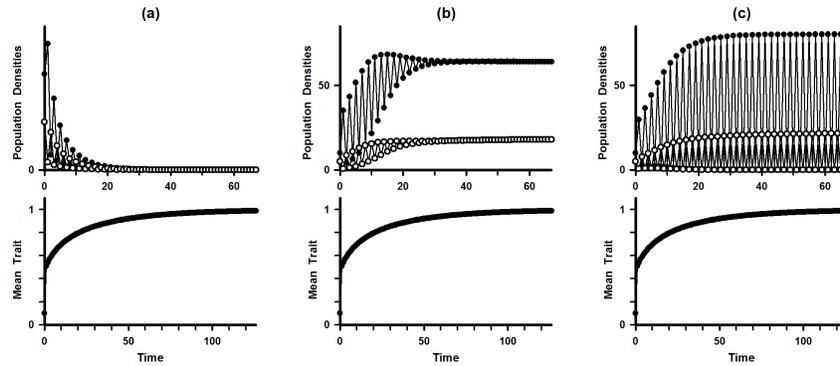


FIGURE 2. Graphs show sample times series of all three state variables  $J$ ,  $A$  and  $u$  for the EGT-JA model (4) with inherent survival and fertility parameters (24) and density factors (23). Parameter values are  $c_{11} = 0.01$ ,  $c_{12} = 0.005$ ,  $c_{21} = 0.001$ ,  $c_{22} = 0.005$  and  $v = 0.03$ . Initial conditions are  $(J, A, u) = (10, 5, 0.1)$ . Solid circles are juveniles and open circles are adults.

(a) For  $R_0^0 = 0.75 < 1$  (i.e.  $b = 3 < 4$ ) the population evolves to extinction with asymptotic mean trait  $u = 1$ .

(b) For  $R_0^0 = 2 > 1$  (i.e.  $b = 8 > 8$ ) the competition ratio is  $c = 0.28 < 1$  and the population evolves to stable positive equilibrium with overlapping generations.

(c) With parameter values as in case (b), except with the between-class competition coefficient  $c_{21}$  increased from 0.001 to 0.02, the competition ratio becomes  $c = 1.8 > 1$ . The result is that the population now evolves to a stable, synchronous 2-cycles with non-overlapping generations.

**Example 1.** The parameter specifications

$$s(u) = \frac{u}{1+u}, \quad \beta(u) = \frac{1}{1+u} \quad (24)$$

defined on the trait interval  $U = R_+^1$  provide an example of (21a). Adult fertility  $b\beta(u)$  is a decreasing function of  $u$ , attaining its maximum  $b$  at  $u = 0$  and decreasing to 0 as  $u \rightarrow +\infty$ . Juvenile survival  $s(u)$  is an increasing function of  $u$ , starting from 0 at  $u = 0$  and increasing to 1 as  $u \rightarrow +\infty$ . From

$$R_0(0, 0, u) = b \frac{u}{(1+u)^2}, \quad \partial_u R_0(0, 0, u) = b \frac{1-u}{(1+u)^3}$$

we find that the only critical trait is  $u^* = 1$ . It follows that the only extinction equilibrium is  $(J, A, u) = (0, 0, 1)$  and the bifurcation value of  $b$  is  $b^0 = 4$ . Moreover  $\partial_{uu}^0 R_0 = -b/8 < 0$  and the dynamic dichotomy (20) occurs as  $b$  increases through 4 or, equivalently, as  $R_0^0 = b/4$  increases through 1. Figure 2 illustrates the evolution to extinction prior to the bifurcation and the two dynamic alternatives (according to whether  $c$  is greater or less than 1) that occur after bifurcation.  $\square$

Case (21b) means each individual inherent vital rate  $s(u)$  and  $\beta(u)$  has a critical point at  $u = u^*$ . Suppose we assume both second derivatives  $\partial_{uu}^0 s$  and  $\partial_{uu}^0 \beta$  are

nonzero. Then the condition  $\partial_{uu}^0 \bar{R}_0 = \beta^0 \partial_{uu}^0 s + s^0 \partial_{uu}^0 \beta < 0$  required for a stable bifurcation implies two possibilities: either  $\partial_{uu}^0 s$  and  $\partial_{uu}^0 \beta$  are both negative or they have opposite signs. In the first case,  $s(u)$  and  $\beta(u)$  have (local) maxima at  $u = u^*$ . The second case represents, as in Case (21A), a trade-off between these vital rates, at least in a (deleted) neighborhood of the critical trait  $u^*$  where they have opposite monotonicities. Furthermore,  $\beta^0 \partial_{uu}^0 s + s^0 \partial_{uu}^0 \beta < 0$  requires that the rate maximized must have a (negative) concavity sufficiently large in magnitude, relative to the (positive) concavity of the rate that is minimized. In other words, the distribution of the maximized vital rate for  $u$  near  $u^*$  must be sufficiently narrow if we are to have the possibility of a stable bifurcation. Under this condition, the dynamic dichotomy (20) occurs. The next example illustrates this trade-off scenario.

**Example 2.** The parameter specifications

$$s(u) = \frac{2m}{2 + \alpha u^2}, \quad \beta(u) = \frac{2\theta + u^2}{2 + u^2} \tag{25a}$$

$$\alpha > 0, \quad 0 < m, \theta < 1 \tag{25b}$$

defined on the trait interval  $U = R^1$ , describe a situation in which juvenile survival and adult fertility have opposite monotonicities (representing a trade-off between these two inherent vital rates) at all trait values except  $u = 0$  where juvenile survival is maximized (at  $m$ ) and adult fertility is minimized (at  $b\theta$ ). Over the trait interval  $U$ , adult fertility  $b\beta(u)$  ranges from its maximum  $b$  to a minimum  $b\theta$ , and juvenile survival  $s(u)$  ranges from a minimum of 0 to a maximum of  $m < 1$ . This case therefore provides an example of case (21b) at critical trait  $u^* = 0$  where a calculation using

$$R_0(0, 0, u) = b \frac{2\theta + u^2}{2 + u^2} \frac{2m}{2 + \alpha u^2}$$

shows  $\partial_{uu}^0 R_0 = b(1 - \theta - \alpha\theta)$ . Consequently, at critical trait  $u^* = 0$

$$\begin{aligned} \partial_{uu}^0 R_0 < 0 \text{ if } \alpha > \alpha_0 &\doteq \frac{1 - \theta}{\theta} \\ \partial_{uu}^0 R_0 > 0 \text{ if } \alpha < \alpha_0. \end{aligned}$$

Thus, the dynamic dichotomy (20) occurs if  $\alpha > \alpha_0$  and does not occur if  $\alpha < \alpha_0$  (when all bifurcating branches are unstable). Note that  $\alpha = -\partial_{uu}^0 s$  measures concavity of  $s(u)$  at 0 where it attains its maximum value. It is a measure of how broadly or tightly distributed juvenile survival is around 0 has a function of the mean trait  $u$ . If this distribution is sufficiently narrow, i.e., if  $\alpha > \alpha_0$ , then the dynamic dichotomy (20) at extinction equilibria  $(J, A, u) = (0, 0, 0)$  occurs as  $R_0^0 = bm\theta$  increases through 1. If this distribution is sufficiently broad, i.e., if  $\alpha < \alpha_0$ , then all bifurcating branches are unstable. In the latter case, however, there exist other critical traits at which the dynamic dichotomy does occur. Specifically, a calculation shows that  $\partial_u R_0(0, 0, u) = 0$  has two other roots when  $\alpha < \alpha_0$ , namely

$$u_{\pm} = \pm u_0 \text{ where } u_0 = \left( -2\theta + 2 \left[ (1 - \theta) \left( \frac{1}{\alpha} - \theta \right) \right]^{1/2} \right)^{1/2}$$

Therefore, bifurcations also occur in the neighborhood of the extinction equilibria  $(J, A, u) = (0, 0, u_{\pm})$ . A straightforward, but tedious calculation shows  $\partial_{uu}^0 R_0 < 0$  at both of these critical traits  $u_{\pm}$ . It follows that at both of these critical traits, the

dynamic dichotomy (20) occurs, with the bifurcations occurring at the extinction equilibria  $(J, A, u) = (0, 0, u_{\pm})$  as the inherent net reproductive number

$$R_0(0, 0, u_{\pm}) = b \frac{2\theta + u_0^2}{2 + u_0^2} \frac{2m}{2 + \alpha u_0^2}$$

increases through 1. A consequence of this result is the occurrence of multiple attractors. See Figure 3 for examples of both cases  $\alpha < \alpha_0$  and  $\alpha > \alpha_0$ .  $\square$

The Leslie-Gower functions (23) used in Examples 1 and 2 are trait  $u$  independent. In general, when  $\sigma = \sigma(J, A)$  and  $\varphi = \varphi(J, A)$  are trait independent, then the trait equation (4c)

$$u' = u + v \frac{1}{2} \frac{\partial_u [\beta(u) s(u)]}{\beta(u) s(u)}$$

in the EGT-JA model (a one dimensional map) is uncoupled from the population dynamics equations (4a)-(4b). This provides an analytic approach to this special case that treats the population dynamic equations (4a)-(4b) as a nonautonomous system of difference equations. For example, if orbits of the trait equation are known to equilibrate, then the population dynamic equations become asymptotically autonomous, for which there are means of analyses based on the limiting equation (obtained by replacing  $u$  in the  $J$  and  $A$  equations by its equilibria value). We do not pursue this approach here for these models.

We point out, however, that one consequence of the trait independence of the density terms  $\sigma$  and  $\varphi$  (as in Examples 1 and 2) is that the component  $u$  remains fixed at  $u^*$  along the bifurcating branch of positive equilibria. This is not generally the case, as is shown in Theorem 4.1 by (13). We conclude with an example in which density dependence is trait dependent.

**Example 3.** In this example we again use the inherent rates (24), for which as we saw in Example 1, there is a unique critical trait  $u^* = 1$  and the dynamic dichotomy (20) occurs as  $b$  increases through  $b^0 = 4$ . However, we now assume that the density effects on juvenile survival are also trait dependent. Specifically, we assume the competitive coefficients in the Leslie-Gower functional (23) for juvenile survival  $\sigma$  are decreasing functions of  $u$ . In this way, an increased mean trait  $u$  implies juveniles are less affected by competition as well as enjoying an increased inherent survival rates. Specifically, for this example we use

$$\sigma(J, A, u) = \frac{1}{1 + c_{11} \frac{1}{1+u} J + c_{12} \frac{1}{1+u} A}, \quad \varphi(J, A) = \frac{1}{1 + c_{21} J + c_{22} A} \tag{26}$$

in place of the trait independent functions (23). In the dynamic dichotomy (20), stability is determined by the competition ratio (18), which is now

$$c = \frac{4c_{21} + c_{12}}{2c_{11} + 2c_{22}}.$$

Figure 4 illustrates the occurrence of the dynamic dichotomy as it depends on this value of  $c$ . In Figure 4(a) the positive equilibria are stable, since  $c < 1$ . In this example, unlike in Example 1, the trait component of the positive equilibria is not fixed at the critical trait  $u^* = 1$ , but varies along the bifurcating branch. This is clearly seen in Figure 4(a) where the equilibrium value of  $u$  is approximately 2.1967. The trait component  $u$  of the orbit appears to equilibrate in Figure 4(b) also, although this is not the case. The trait component  $u$  is 2-periodic with a small amplitude not visible in this graph.  $\square$

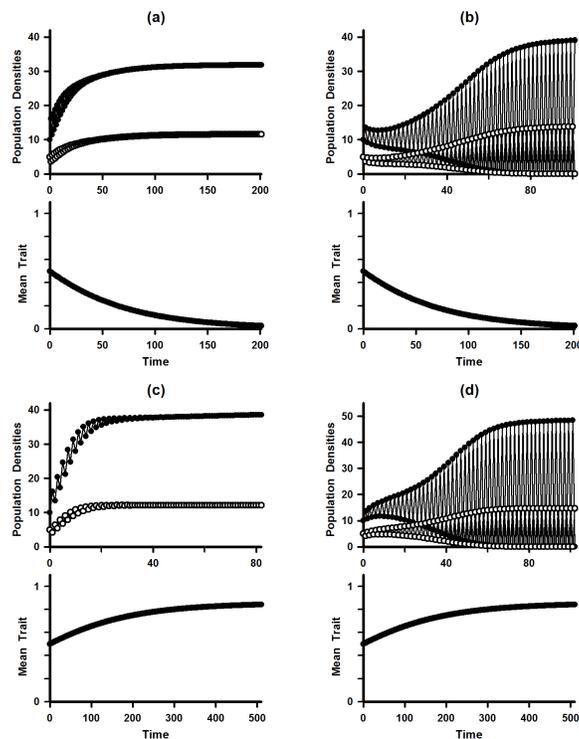


FIGURE 3. Graphs show sample times series of all three state variables  $J, A$  and  $u$  for the EGT-JA model (4) with inherent survival and fertility parameters (25) and density factors (23). The parameter values  $c_{11} = 0.01, c_{12} = 0.005, c_{22} = 0.005$  and  $v = 0.03$  are the same as in Figure 2, as are the initial conditions  $(J, A, u) = (10, 5, 0.5)$ . We take  $b = 6, m = 0.5$  and  $\theta = 0.5$ , which implies  $\alpha_0 = 1$ .

For  $\alpha = 2 > \alpha_0$  the only extinction equilibrium occurs for  $u^* = 0$ . For these parameter values  $R_0^0 = 1.5 > 1$  and the attractor in the dynamic dichotomy depends on the competition ratio  $c$ . In (a)  $c_{21} = 0.001$  implies  $c = 0.28 < 1$  and we see equilibration with overlapping generations. In (b)  $c_{21} = 0.02$  implies  $c = 1.8 > 1$  and we see a synchronous 2-cycle with non-overlapping generations. Note  $u$  tends to  $u^* = 0$  in both cases.

For  $\alpha = 0.5 < \alpha_0$  the bifurcations at the extinction equilibrium  $(0, 0, 0)$  are unstable. Bifurcations occur, however, at two other extinction equilibria  $(0, 0, u_{\pm})$  associated with two nonzero critical traits  $u_{\pm} \approx \pm 0.8556$ . For these parameter values  $R_0^0 \approx 2.7846 > 1$  and the attractor in the dynamic dichotomy depends on the competition ratio  $c$ . In (c)  $c_{21} = 0.001$  implies  $c = 0.28 < 1$  and we see an equilibration with overlapping generations. In (d)  $c_{21} = 0.02$  implies  $c = 1.8 > 1$ , and we see a synchronous 2-cycle with non-overlapping generations. Note  $u$  tends to critical trait  $u_+ \approx 0.8556$  in both cases. A dynamic dichotomy similar to that shown in (c) and (d) also occurs in the bifurcation at extinction equilibrium  $(0, 0, u_-)$  (not shown).

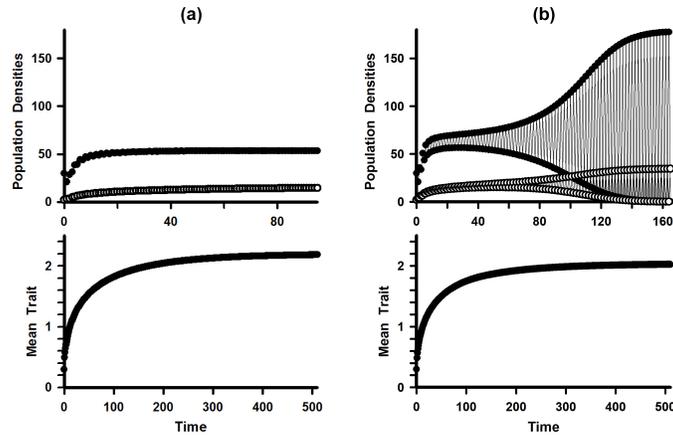


FIGURE 4. Graphs show sample times series of all three state variables  $J, A$  and  $u$  for the EGT-JA model (4) with inherent survival and fertility parameters (24) and density factors (26). As in Example 1, the unique critical trait is  $u^* = 1$  and a dynamic bifurcation occurs as  $b$  increases through  $b^0 = 4$ . Parameter values are  $b = 20$  and  $v = 0.17$ . The initial conditions are  $(J, A, u) = (30, 2, 0.3)$ .

(a) The competition coefficients (26) are  $c_{11} = 0.06$ ,  $c_{12} = 0.04$ ,  $c_{21} = 0.015$  and  $c_{22} = 0.01$  which yield a competition coefficient  $c = 0.71429 < 1$ . As a result the orbit equilibrates with overlapping generations. The trait  $u$  equilibrates at approximately 2.1967.

(b) All parameters remain unchanged in (a) except  $c_{11}$  is decreased to 0.04 with the result that  $c = 1.0417 > 1$ . As a result the orbit approaches a synchronous 2-cycle. Although the trait  $u$  appears to equilibrate, it is 2-periodic of a small amplitude. ( $u$  oscillates between approximately 2.032 and 2.037.)

**6.3. Final remarks.** Theorems 3.1-5.2 provide a general account of the bifurcation possibilities for the evolutionary game theoretic version (4) of the (semelparous) juvenile-adult matrix model (1). This analysis is made possible by the known bifurcation possibilities of the non-evolutionary model (1) (Theorem 2.2). The two dimensional population model (1) is basic in the sense that it is the lowest dimensional model for a semelparous juvenile-adult population. For higher dimensional models (i.e., for models with longer juvenile maturation periods) the bifurcation possibilities are not completely known, even for non-evolutionary models. For three dimensional models (two juvenile stages and one adult stage) the nature of the dynamic dichotomy is known under certain monotonicity assumptions (A5 extended to three dimensions) [6]. In this case, the dichotomy is no longer between positive equilibria and synchronous cycles (in this case, 3-cycles), but is between positive equilibria and the boundary of the positive cone (as an attractor or repeller). Whether this extended dichotomy holds in higher dimensional models remains an open question (in both the evolutionary and non-evolutionary case), although it is known to hold for some special types of non-evolutionary models [8], [9].

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**Appendix A. Proof of Theorem 4.2.** To determine stability and instability criteria of the positive equilibria (13) by linearization, we evaluate the Jacobian  $\mathfrak{J}$  of (4) at the equilibrium and study the eigenvalues of the resulting matrix. Since the equilibria (13) are functions of  $\varepsilon \approx 0$ , so is the Jacobian and its eigenvalues. We study these eigenvalues for small  $\varepsilon$  and also for small  $v$ . We denote the dependencies on  $\varepsilon$  and  $v$  by writing

$$\mathfrak{J}(\varepsilon, v) = \begin{pmatrix} P(\varepsilon) & \hat{\psi}(\varepsilon) \\ v\hat{\rho}(\varepsilon) & 1 + v\partial_u d(\varepsilon) \end{pmatrix}$$

where  $P(\varepsilon)$  is the  $2 \times 2$  matrix whose first and second columns are

$$\begin{pmatrix} b(\varepsilon)\beta(u(\varepsilon))[\partial_J\varphi(J(\varepsilon), A(\varepsilon), u(\varepsilon))]A(\varepsilon) \\ s(u(\varepsilon))\sigma(J(\varepsilon), A(\varepsilon), u(\varepsilon)) + s(u(\varepsilon))[\partial_J\sigma(J(\varepsilon), A(\varepsilon), u(\varepsilon))]J(\varepsilon) \end{pmatrix}$$

$$\begin{pmatrix} b(\varepsilon)\beta(u(\varepsilon))\varphi(J(\varepsilon), A(\varepsilon), u(\varepsilon)) + b(\varepsilon)\beta(u(\varepsilon))[\partial_A\varphi(J(\varepsilon), A(\varepsilon), u(\varepsilon))]A(\varepsilon) \\ s(u(\varepsilon))[\partial_A\sigma(J(\varepsilon), A(\varepsilon), u(\varepsilon))]J(\varepsilon) \end{pmatrix}$$

respectively and where

$$\hat{\rho}(\varepsilon) = \begin{pmatrix} \partial_J d(J(\varepsilon), A(\varepsilon), u(\varepsilon)) & \partial_A d(J(\varepsilon), A(\varepsilon), u(\varepsilon)) \end{pmatrix}$$

$$\hat{\psi}(\varepsilon) = \begin{pmatrix} b\partial_u[\beta(u(\varepsilon))\varphi(J(\varepsilon), A(\varepsilon), u(\varepsilon))]A(\varepsilon) \\ \partial_u[s(u(\varepsilon))\sigma(J(\varepsilon), A(\varepsilon), u(\varepsilon))]J(\varepsilon) \end{pmatrix}$$

are row and column vectors respectively. Let  $\lambda_i = \lambda_i(\varepsilon, v)$ ,  $i = 1, 2, 3$ , denote the eigenvalues  $\mathfrak{J}(\varepsilon, v)$ . Since the positive equilibrium is independent of  $v$  and since  $v$  appears in only the trait equation, it follows that the only appearance of  $v$  in the Jacobian  $\mathfrak{J}(\varepsilon, v)$  is in its third row only.

(a) If we set  $\varepsilon = 0$ , we find from  $\hat{\psi}(0) = \text{col}(0, 0)$  and

$$P(0) = \begin{pmatrix} 0 & \frac{1}{s^0} \\ s^0 & 0 \end{pmatrix}$$

that the eigenvalues of

$$\mathfrak{J}(0, v) = \begin{pmatrix} P(0) & \text{col}(0, 0) \\ v\hat{\rho}(0) & 1 + v\partial_u^0 d(0) \end{pmatrix}$$

satisfy, for all  $v \geq 0$ ,

$$\begin{aligned} \lambda_1(0, v) &= 1, & \lambda_2(0, v) &= -1 \\ \lambda_3(0, v) &= 1 + v \frac{1}{2} \frac{1}{\beta^0 s^0} \partial_{uu}^0 \bar{R}_0. \end{aligned}$$

Suppose  $\partial_{uu}^0 \bar{R}_0 < 0$ . Then  $\partial_v \lambda_3(0, v) < 0$  for all  $v \geq 0$ . By uniform continuity, given any  $c_1 > 0$  there exists a  $c_2 > 0$  such that  $\partial_v \lambda_3(\varepsilon, v) < 0$  for  $v$  and  $\varepsilon$  in the square  $\Sigma = \{0 \leq v \leq c_1, -c_2 \leq \varepsilon \leq c_2\}$ . By continuity it follows from  $\lambda_3(\varepsilon, 0) = 1$  that  $\lambda_3(\varepsilon, v) < 1$  on  $\Sigma$ , and by taking  $c_1$  smaller if necessary that  $-1 < \lambda_3(\varepsilon, v) < 1$  on  $\Sigma$ . As a result, the stability of the bifurcating positive equilibria (for small  $\varepsilon$  and  $v$ ) depends on the eigenvalues  $\lambda_1(\varepsilon, v)$  and  $\lambda_2(\varepsilon, v)$ .

If we set  $v = 0$  then we see from

$$\mathfrak{J}(\varepsilon, 0) = \begin{pmatrix} P(\varepsilon) & \hat{\psi}(\varepsilon) \\ \text{row}(0, 0) & 1 \end{pmatrix}$$

that  $\lambda_3(\varepsilon, 0) = 1$  and that  $\lambda_1(\varepsilon, 0)$  and  $\lambda_2(\varepsilon, 0)$  are the eigenvalues of  $P(\varepsilon)$ , the Jacobian of the model in the absence of evolution. Lower order expansions for the latter two eigenvalues have been calculated in [5] (also see [2] and [9]) and are given by (8):

$$\lambda_1(\varepsilon, 0) = 1 - \frac{1}{2}\varepsilon + O(\varepsilon^2), \quad \lambda_2(\varepsilon, 0) = -1 + \frac{1}{2} \frac{a_+^0}{a_+^0} \varepsilon + O(\varepsilon^2).$$

If  $a_+^0 > 0$  then the bifurcation in Theorem 4.1 is to the left and the positive equilibria (13) correspond to  $\varepsilon \lesssim 0$ . Since

$$\partial_\varepsilon \lambda_1(\varepsilon, 0) = -\frac{1}{2} + O(\varepsilon)$$

is negative for  $\varepsilon \approx 0$ , we conclude (by continuity) that  $\partial_\varepsilon \lambda_1(\varepsilon, v) < 0$  on a square  $\Sigma = \{0 \leq v \leq c_1, -c_2 \leq \varepsilon \leq c_2\}$  for some  $c_1, c_2 > 0$ . This, together with  $\lambda_1(0, v) = 1$ , implies  $\lambda_1(\varepsilon, v) > 1$  on  $\Sigma$  with  $\varepsilon < 0$  and the instability of the bifurcating positive equilibria follows.

On the other hand, if  $a_+^0 < 0$  then the bifurcation in Theorem 4.1 is to the right and the positive equilibria correspond to  $\varepsilon \gtrsim 0$ . Then  $\lambda_1(\varepsilon, v) < 1$  on  $\Sigma$  with  $\varepsilon \gtrsim 0$  and  $\lambda_1(\varepsilon, v) \gtrsim 1$  on  $\Sigma$  with both  $\varepsilon \gtrsim 0$  and  $v \approx 0$  small. In this case, stability is consequently determined by the remaining eigenvalue  $\lambda_2(\varepsilon, v)$ . Note that

$$\partial_\varepsilon \lambda_2(\varepsilon, 0) = \frac{1}{2} \frac{a_-^0}{a_+^0} + O(\varepsilon).$$

If the leading coefficient is negative, then an argument like that applied to  $\lambda_1$  implies  $\lambda_2(\varepsilon, v) < -1$  on  $\Sigma$  with  $\varepsilon \gtrsim 0$  and the instability of the bifurcating positive equilibria follows. On the other hand, if the leading coefficient is positive, then a similar argument implies  $\lambda_2(\varepsilon, v) \gtrsim 1$  on  $\Sigma$  with  $\varepsilon \gtrsim 0$  and  $v \approx 0$  small. The stability of the bifurcating positive equilibria follows.

(b) We know from Theorem 3.1(b) that in this case the extinction equilibrium is unstable for all  $b > 0$ . What we need to show is that the bifurcating positive equilibria are also unstable. We do this by showing that  $\lambda_3(\varepsilon, v) > 1$  for  $\varepsilon \approx 0$ , which shows (by linearization) the instability of the positive equilibrium near the bifurcation point. Since  $\partial_{uu}^0 \bar{R}_0 > 0$  it follows that  $\partial_v \lambda_3(0, v) > 0$  for all  $v \geq 0$ . We conclude (by uniform continuity) that given any  $c_1 > 0$  there exists a  $c_2 > 0$  such

that  $\partial_v \lambda_3(\varepsilon, v) > 0$  for  $v$  and  $\varepsilon$  in the square  $\Sigma = \{0 \leq v \leq c_1, -c_2 \leq \varepsilon \leq c_2\}$ . This fact, together with  $\lambda_3(\varepsilon, 0) = 1$  implies  $\lambda_3(\varepsilon, v) > 1$  on  $\Sigma$ .

**Appendix B. Proof of Theorem 5.1.** Write the 2-cycle equations (19) as

$$g_1(J, u, b) = 0 \tag{27a}$$

$$g_2(J, u) = 0 \tag{27b}$$

where

$$g_1(J, u, b) \doteq b\beta(u + vd(J, 0, u))s(u)\varphi(0, s(u)\sigma(J, 0, u)J, u + vd(J, 0, u))\sigma(J, 0, u) - 1$$

$$g_2(J, u) \doteq d(J, 0, u) + d(0, s(u)\sigma(J, 0, u)J, u + vd(J, 0, u)).$$

Our goal is to solve equations (27) for  $J$  and  $u$ , at least when  $b \approx b^0$ , by use of the Implicit Function Theorem. We begin by noting that  $J = 0, u = 0$  satisfies both equations (27) when  $b = b^0$ .

A calculation shows

$$\partial_u^0 g_2 = (2 + v\partial_u^0 d)\partial_u^0 d$$

which is nonzero for  $v \approx 0$ , since  $\partial_{uu}^0 \bar{R}_0 \neq 0$  implies  $\partial_u^0 d \neq 0$ . The Implicit Function Theorem implies the existence of a (twice continuously differentiable) solution of equation (27b), which we denote by

$$u = \eta(J), \quad \eta(0) = 0 \text{ for } J \approx 0.$$

We substitute this solution into the first equation (27a) to obtain an equation  $g(J, b) = 0$  for  $J$ , where

$$g(J, b) \doteq b[\beta(\eta(J) + vd(J, 0, \eta(J)))]s(\eta(J)) \tag{28}$$

$$\times [\varphi(0, s(\eta(J))\sigma(J, 0, \eta(J))J, \eta(J) + vd(J, 0, \eta(J)))]\sigma(J, 0, \eta(J)) - 1$$

We will use the Implicit Function Theorem to solve this equation for  $J = J(b)$  by first noting, by the definition of  $b^0$ , that

$$g(0, b^0) = b^0 \beta^0 s^0 - 1 = 0.$$

If  $\partial_J^0 g \neq 0$  then the Implicit Function Theorem implies the existence of a (twice continuously differentiable) solution

$$J = J(b), \quad J(b^0) = 0 \text{ for } b \approx b^0.$$

This solution yields (twice continuously differentiable) solutions of equations (27)

$$J = J(b), \quad u = \eta(J(b)) \text{ for } b \approx b^0.$$

$$\text{satisfying } J(b^0) = 0, \quad u(b^0) = 0$$

These solutions correspond to 2-cycles whose first point is  $(J(b), 0, \eta(J(b)))$ . The proof of Theorem 5.1 will be complete when we show two things:  $\partial_J^0 g \neq 0$  and that  $J(b)$  is positive for  $b \approx b^0$ .

The calculation of the derivative  $\partial_J^0 g$  from (28) is tedious but straightforward. Remembering that  $\partial_u^0 \sigma = 0$  and  $\partial_u^0 \varphi = 0$  follow from A1 and  $\beta^0 \partial_u^0 s + s^0 \partial_u^0 \beta = 0$  follows from the definition of a critical trait (see (6)), we find that

$$\partial_J^0 g = \partial_J^0 \sigma + s^0 \partial_A^0 \varphi + vb^0(1 + \partial_u^0 d)s_0 \partial_u^0 \beta \partial_J^0 \eta$$

$$= c_w^0 + vb^0(1 + b^0 \partial_{uu}^0 \bar{R}_0/2)s_0 \partial_u^0 \beta \partial_J^0 \eta$$

(see (10)). The assumption that  $c_w^0 \neq 0$  implies that  $\partial_J^0 g \neq 0$  for  $v \approx 0$ .

Finally, to determine the sign of  $J(b)$  for  $b$  near  $b^0$  we can implicitly differentiate  $g(J(b), b) = 0$  with respect to  $b$  and obtain

$$\partial_b^0 J = -\frac{\partial_b^0 g}{\partial_J^0 g} = \frac{-\beta^0 s^0}{c_w^0 + vb^0 (1 + b^0 \partial_{uu}^0 \bar{R}_0/2) s_0 \partial_u^0 \beta \partial_J^0 \eta}.$$

Defining  $\varepsilon \doteq (b - b^0) / b^0$  we have

$$J(\varepsilon) = \frac{-1}{c_w^0 + vb^0 (1 + b^0 \partial_{uu}^0 \bar{R}_0/2) s_0 \partial_u^0 \beta \partial_J^0 \eta} \varepsilon + O(\varepsilon^2).$$

This gives us a parameterization of the branch of bifurcating synchronous 2-cycles

$$\begin{aligned} \begin{pmatrix} J(\varepsilon) \\ 0 \\ u_1(\varepsilon) \end{pmatrix} &= \begin{pmatrix} \frac{-1}{c_w^0 + vb^0 (1 + b^0 \partial_{uu}^0 \bar{R}_0/2) s_0 \partial_u^0 \beta \partial_J^0 \eta} \\ 0 \\ u_1 \end{pmatrix} \varepsilon + O(\varepsilon^2) \\ \begin{pmatrix} 0 \\ A(\varepsilon) \\ u_2(\varepsilon) \end{pmatrix} &= \begin{pmatrix} 0 \\ \frac{-s^0}{c_w^0 + vb^0 (1 + b^0 \partial_{uu}^0 \bar{R}_0/2) s_0 \partial_u^0 \beta \partial_J^0 \eta} \\ u_2 \end{pmatrix} \varepsilon + O(\varepsilon^2). \quad (29) \\ b(\varepsilon) &= b^0 + b^0 \varepsilon \end{aligned}$$

Formulas for the first order coefficients  $u_1$  and  $u_2$  could be derived by implicit differentiation of equation (27b), but we have no need for these formulas here.

Note: In the absence of evolution ( $v = 0$ ), this parameterization is the same as (9).

**Appendix C. Proof of Theorem 5.2.** To study the stability of the 2-cycles by linearization we investigate the eigenvalues of the Jacobian of the composite map. This Jacobian equals the product of the model Jacobian  $\mathfrak{J}$  (see proof of Theorem 4.2 in Appendix A) evaluated at the two points of the 2-cycle parameterized by (29). Thus, we are interested in the product  $\mathfrak{J}_2(\varepsilon, v) \mathfrak{J}_1(\varepsilon, v)$  where

$$\mathfrak{J}_1(\varepsilon, v) = \begin{pmatrix} P_1(\varepsilon) & \hat{\psi}_1(\varepsilon) \\ v\hat{\rho}_1(\varepsilon) & 1 + v\partial_u d_1(\varepsilon) \end{pmatrix}$$

in which the  $2 \times 2$  matrix  $P_1(\varepsilon)$  is

$$\left( \begin{array}{c|c} 0 & b(\varepsilon) \beta(u_1(\varepsilon)) \varphi(J(\varepsilon), 0, u_1(\varepsilon)) \\ \hline \frac{s(u_1(\varepsilon)) \sigma(J(\varepsilon), 0, u_1(\varepsilon)) +}{s(u_1(\varepsilon)) [\partial_J \sigma(J(\varepsilon), 0, u_1(\varepsilon))] J(\varepsilon)} & \frac{s(u_1(\varepsilon))}{\times [\partial_A \sigma(J(\varepsilon), 0, u_1(\varepsilon))] J(\varepsilon)} \end{array} \right)$$

with

$$\begin{aligned} \hat{\rho}_1(\varepsilon) &= \begin{pmatrix} \partial_J d(J(\varepsilon), 0, u_1(\varepsilon)) & \partial_A d(J(\varepsilon), 0, u_1(\varepsilon)) \end{pmatrix} \\ \hat{\psi}_1(\varepsilon) &= \begin{pmatrix} 0 \\ \partial_u [s(u_1(\varepsilon)) \sigma(J(\varepsilon), 0, u_1(\varepsilon))] J(\varepsilon) \end{pmatrix} \\ \partial_u d_1(\varepsilon) &= \partial_u [d(J(\varepsilon), 0, u_1(\varepsilon))] \end{aligned}$$

and

$$\mathfrak{J}_2(\varepsilon, v) = \begin{pmatrix} P_2(\varepsilon) & \hat{\psi}_2(\varepsilon) \\ v\hat{\rho}_2(\varepsilon) & 1 + v\partial_u d_2(\varepsilon) \end{pmatrix}$$

in which the  $2 \times 2$  matrix  $P_2(\varepsilon)$  is

$$\left( \begin{array}{c|c} \frac{b(\varepsilon)\beta(u(\varepsilon))}{s(u_2(\varepsilon))\sigma(0,A(\varepsilon),u_2(\varepsilon))} & \frac{b(\varepsilon)\beta(u_2(\varepsilon))\varphi(0,A(\varepsilon),u_2(\varepsilon)) + \times [\partial_J\varphi(0,A(\varepsilon),u_2(\varepsilon))]A(\varepsilon)}{0} \\ \hline & \frac{b(\varepsilon)\beta(u_2(\varepsilon))[\partial_A\varphi(0,A(\varepsilon),u_2(\varepsilon))]A(\varepsilon)}{0} \end{array} \right)$$

with

$$\begin{aligned} \hat{\rho}_2(\varepsilon) &= \begin{pmatrix} \partial_J d(0,A(\varepsilon),u_2(\varepsilon)) & \partial_A d(0,A(\varepsilon),u_2(\varepsilon)) \end{pmatrix} \\ \hat{\psi}_2(\varepsilon) &= \begin{pmatrix} b\partial_u[\beta(u_2(\varepsilon))\varphi(0,A(\varepsilon),u_2(\varepsilon))]A(\varepsilon) \\ 0 \end{pmatrix} \\ \partial_u d_2(\varepsilon) &= \partial_u d(0,A(\varepsilon),u_2(\varepsilon)). \end{aligned}$$

We are interested in the three eigenvalues  $\lambda_i(\varepsilon, v)$  of the product  $\mathfrak{J}_2(\varepsilon, v)\mathfrak{J}_1(\varepsilon, v)$ , which is

$$\left( \begin{array}{c|c} \frac{P_2(\varepsilon)P_1(\varepsilon)}{v\hat{\rho}_2(\varepsilon)P_1(\varepsilon) + v(1+v\partial_u d_2(\varepsilon))\hat{\rho}_1(\varepsilon)} & \frac{P_2(\varepsilon)\hat{\psi}_1(\varepsilon)}{v\hat{\rho}_2(\varepsilon)\hat{\psi}_1(\varepsilon) + (1+v\partial_u d_2(\varepsilon))\hat{\psi}_2(\varepsilon)} \\ \hline & \frac{P_2(\varepsilon)\hat{\psi}_1(\varepsilon) + (1+v\partial_u d_2(\varepsilon))\hat{\psi}_2(\varepsilon)}{\times (1+v\partial_u d_1(\varepsilon))} \end{array} \right).$$

When  $\varepsilon = 0$  (recall  $\hat{\psi}_1(0) = \hat{\psi}_2(0) = \text{col}(0, 0)$ ) this product becomes the block diagonal matrix

$$\mathfrak{J}_2(0, v)\mathfrak{J}_1(0, v) = \begin{pmatrix} P_2(0)P_1(0) & \text{col}(0, 0) \\ v\hat{\rho}_2^0 P_1(0) + v(1+v\partial_u d_2^0)\hat{\rho}_1^0 & (1+v\partial_u d_2^0)(1+v\partial_u d_1^0) \end{pmatrix}$$

where

$$P_2(0)P_1(0) = \begin{pmatrix} 0 & \frac{1}{s^0} \\ s^0 & 0 \end{pmatrix}^2 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}.$$

Since

$$\begin{aligned} \partial_u^0 d_1 &= \partial_u d(J(\varepsilon), 0, u_1(\varepsilon))|_{\varepsilon=0} = \partial_u^0 d = \frac{1}{2\beta^0 s^0} \partial_{uu}^0 \bar{R}_0 \\ \partial_u^0 d_2 &= \partial_u d(0, A(\varepsilon), u_2(\varepsilon))|_{\varepsilon=0} = \partial_u^0 d = \frac{1}{2\beta^0 s^0} \partial_{uu}^0 \bar{R}_0. \end{aligned}$$

Thus, we have

$$\begin{aligned} \lambda_1(0, v) &\equiv 1, \quad \lambda_2(0, v) \equiv 1 \text{ for all } v \\ \lambda_3(0, v) &= \left(1 + v \frac{1}{2\beta^0 s^0} \partial_{uu}^0 \bar{R}_0\right)^2. \end{aligned}$$

(a) Assume that  $\partial_{uu}^0 \bar{R}_0 < 0$ . Then  $\lambda_3(0, v) < 1$  for all  $v \approx 0$  and by continuity  $\lambda_3(\varepsilon, v) < 1$  for all  $v \approx 0$  and  $\varepsilon \approx 0$ . Stability of the 2-cycles in this case depends on the two eigenvalues  $\lambda_1(\varepsilon, v)$  and  $\lambda_2(\varepsilon, v)$ , which we now study in more detail. As seen above, these eigenvalues satisfy  $\lambda_1(0, v) \equiv 1$  and  $\lambda_2(0, v) \equiv 1$  for all  $v \geq 0$ . From

$$\mathfrak{J}_2(\varepsilon, 0)\mathfrak{J}_1(\varepsilon, 0) = \begin{pmatrix} P_2(\varepsilon)P_1(\varepsilon) & P_2(\varepsilon)\hat{\psi}_1(\varepsilon) + \hat{\psi}_2(\varepsilon) \\ \text{row}(0, 0) & 1 \end{pmatrix}.$$

we see that

$$\lambda_1(\varepsilon, 0) = \eta_1(\varepsilon), \quad \lambda_2(\varepsilon, 0) = \eta_2(\varepsilon)$$

where  $\eta_i(\varepsilon)$  are the eigenvalues of the product  $P_2(\varepsilon)P_1(\varepsilon)$ . This product of the  $2 \times 2$  matrices

$$P_1(\varepsilon) = \left( \begin{array}{c|c} 0 & \frac{b(\varepsilon)\beta(u_1(\varepsilon))\varphi(J(\varepsilon), 0, u_1(\varepsilon))}{s(u_1(\varepsilon))} \\ \hline \frac{s(u_1(\varepsilon))\sigma(J(\varepsilon), 0, u_1(\varepsilon)) + s(u_1(\varepsilon))[\partial_J\sigma(J(\varepsilon), 0, u_1(\varepsilon))]J(\varepsilon)}{s(u_1(\varepsilon))} & \frac{[\partial_A\sigma(J(\varepsilon), 0, u_1(\varepsilon))]J(\varepsilon)}{s(u_1(\varepsilon))} \end{array} \right)$$

$$P_2(\varepsilon) = \left( \begin{array}{c|c} \frac{b(\varepsilon)\beta(u_2(\varepsilon))\varphi(0, A(\varepsilon), u_2(\varepsilon)) + b(\varepsilon)\beta(u_2(\varepsilon))[\partial_A\varphi(0, A(\varepsilon), u_2(\varepsilon))]A(\varepsilon)}{s(u_2(\varepsilon))\sigma(0, A(\varepsilon), u_2(\varepsilon))} & \frac{b(\varepsilon)\beta(u_2(\varepsilon))\varphi(0, A(\varepsilon), u_2(\varepsilon)) + b(\varepsilon)\beta(u_2(\varepsilon))[\partial_A\varphi(0, A(\varepsilon), u_2(\varepsilon))]A(\varepsilon)}{0} \\ \hline \frac{s(u_2(\varepsilon))\sigma(0, A(\varepsilon), u_2(\varepsilon))}{s(u_2(\varepsilon))\sigma(0, A(\varepsilon), u_2(\varepsilon))} & 0 \end{array} \right)$$

is triangular and, as a result, its eigenvalues  $\eta_1(\varepsilon)$  and  $\eta_2(\varepsilon)$  are the diagonal entries:

$$\eta_1(\varepsilon) = \frac{b(\varepsilon)\beta(u_2(\varepsilon))\varphi(0, A(\varepsilon), u_2(\varepsilon)) + b(\varepsilon)\beta(u_2(\varepsilon))[\partial_A\varphi(0, A(\varepsilon), u_2(\varepsilon))]A(\varepsilon)}{s(u_1(\varepsilon))\sigma(J(\varepsilon), 0, u_1(\varepsilon)) + s(u_1(\varepsilon))[\partial_J\sigma(J(\varepsilon), 0, u_1(\varepsilon))]J(\varepsilon)}$$

$$\eta_2(\varepsilon) = \frac{s(u_2(\varepsilon))\sigma(0, A(\varepsilon), u_2(\varepsilon))}{[b(\varepsilon)\beta(u_1(\varepsilon))\varphi(J(\varepsilon), 0, u_1(\varepsilon))]}.$$

Now both eigenvalues satisfy  $\eta_i(0) = 1$ . In order to determine whether the eigenvalues are less than or greater than 1 for  $\varepsilon \approx 0$  we calculate the first order terms in their  $\varepsilon$ -expansions, namely, we calculate the derivatives  $\partial_\varepsilon^0\eta_i$  from the formulas for  $\eta_i(\varepsilon)$ . The derivatives of  $\eta_i$  with respect to  $\varepsilon$  are straightforward, although tedious, applications of the product and chain rules. When they are evaluated at  $\varepsilon = 0$  one needs to use the first order coefficients in the  $\varepsilon$ -expansions (29) of the 2-cycle, from which it follows for example that  $\partial_\varepsilon^0 A = s^0\partial_\varepsilon^0 J$  and, for  $v = 0$ ,

$$\partial_\varepsilon^0 J = \frac{-1}{\partial_J^0\sigma + s^0\partial_A^0\varphi} = \frac{-1}{c_w^0}.$$

We also recall the following facts:  $\partial_u^0\sigma_i = 0$  and  $\partial_\varepsilon^0 b = b^0$ ,  $\beta^0\partial_u^0 s + s^0\partial_u^0\beta = 0$  (see 6) and  $u_2 = u_1 + v[\partial_J^0 d\partial_\varepsilon^0 J + \partial_u^0 du_1] = u_1$  when  $v = 0$ . The result of these calculations is (also see [5], p. 26)

$$\partial_\varepsilon^0\eta_1 = -1, \quad \partial_\varepsilon^0\eta_2 = \frac{a_-^0}{c_w^0}.$$

In summary, we have that

$$\lambda_1(\varepsilon, 0) = 1 - \varepsilon + O(\varepsilon^2), \quad \lambda_2(\varepsilon, 0) = 1 + \frac{a_-^0}{c_w^0}\varepsilon + O(\varepsilon^2) \text{ for } \varepsilon \approx 0$$

$$\lambda_1(0, v) \equiv 1, \quad \lambda_2(0, v) \equiv 1 \text{ for all } v \geq 0.$$

From these expansions we can deduce the following. For a right bifurcation, i.e. when  $c_w^0 < 0$  and hence positive 2-cycles exist for  $\varepsilon \gtrsim 0$ , the eigenvalue  $\lambda_1(\varepsilon, v) \lesssim 1$  for  $\varepsilon \gtrsim 0$  and  $v \approx 0$ . This means stability is determined by the eigenvalue  $\lambda_2$ .

(i) Arguing as with  $\lambda_1$  in (i), we find that  $\lambda_2(\varepsilon, v) > 1$  for  $\varepsilon \gtrsim 0$  and  $v \approx 0$  if its  $\varepsilon$  coefficient is positive, i.e.,  $a_-^0 < 0$ .

(ii) Similarly  $\lambda_2(\varepsilon, v) \lesssim 1$  for  $\varepsilon \gtrsim 0$  and  $v \approx 0$  if its  $\varepsilon$  coefficient is negative, i.e.,  $a_-^0 > 0$ .

For a left bifurcation  $\partial_\varepsilon \lambda_1(\varepsilon, 0) < 0$ , i.e., when  $c_w^0 > 0$ , we have (by continuity) that  $\partial_\varepsilon \lambda_1(\varepsilon, v) < 0$  for  $\varepsilon \approx 0$  and  $v \approx 0$ . Thus, the eigenvalue  $\lambda_1(\varepsilon, v) > 1$  and 2-cycles are unstable.

(b) If  $\partial_{uu}^0 \bar{R}_0 > 0$  then  $\lambda_3(0, v) > 1$  for all  $v$  and by continuity  $\lambda_3(\varepsilon, v) > 1$  for all  $v$  and all  $\varepsilon \approx 0$ .

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