

The Global Dynamics of a Discrete Juvenile-Adult Model with Continuous and Seasonal Reproduction

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In honor of the 65th birthday of Professor J.M. Cushing

Abstract

A general discrete juvenile-adult population model with time-dependent birth rate and nonlinear survivorship rates is studied. When breeding is continuous, it is shown that the model has a unique globally asymptotically stable positive equilibrium provided the net reproductive number is larger than one. If it is smaller than one, then the extinction equilibrium is globally asymptotically stable. When breeding is seasonal, it is shown that there exists a unique globally asymptotically stable periodic solution provided the net reproductive number is larger than one. When this value is less than one, the population goes to extinction. Conditions on the birth rate where the population with seasonal breeding survives while the population with continuous breeding becomes extinct are provided.

1 Introduction

Although most of the current literature on discrete-time population dynamics concentrates on autonomous models, in recent years several researchers have devoted considerable attention to studying non-autonomous discrete-time population models with focus on parameters that vary periodically [2], [3], [5], [7]-[9], [12]-[18], [20]-[29]. The main question addressed in many of these papers is whether cycles generated by time-dependent parameters due to a fluctuating or seasonal environment are attenuant (deleterious) or resonant (advantageous). In [9] the authors conjectured that

cycles in a population governed by a scalar Beverton-Holt nonlinear difference equation with periodic carrying capacity are attenuant for all periods. This conjecture was confirmed in many papers including [12, 13, 14, 24, 25, 26].

Such investigations were recently extended to age and stage structured models. For instance, in [5], the author studied the following model:

$$\begin{cases} J(t+1) = b(t)\phi(c_1J(t), c_2A(t))A(t) \\ A(t+1) = s_1(t)\sigma_1(c_{11}J(t), c_{12}A(t))J(t) + s_2(t)\sigma_2(c_{12}J(t), c_{22}A(t))A(t). \end{cases}$$

where $b(t)$ and $s_i(t)$ are the (periodic) inherent fertility and survival rates, and ϕ and σ_i account for the effects of stage specific population densities on these rates. The c_i and c_{ii} are constant competition coefficients. The author showed that a global branch of positive cycles exists. Furthermore, he showed that periodic oscillations can be either advantageous or deleterious with the phase relationship among the oscillations in the inherent fertility and survival rate being a determining factor.

In [15], the authors studied the following age-structure Leslie model

$$\begin{cases} x_1(t+1) = \sum_{i=1}^N x_i(t)g_i(t, x_i(t)) \\ x_2(t+1) = x_1(t) \\ \vdots \\ x_N(t+1) = x_{N-1}(t), \end{cases}$$

where $x_i(t)$ is the population size of the i th age class at time t and $g_i(t, x_i)$ is the periodic fecundity of the i th age class. They showed that a periodic environment is disadvantageous for a population whenever there is no synchrony between the number of age classes and the period of the environment.

Motivated by a population of green tree frogs, *Hyla cinerea*, the authors in [3] fully analyzed the two-stage discrete model with stage specific competition,

$$\begin{cases} x(t+1) = b(t)y(t) \\ y(t+1) = \frac{x(t)}{\alpha_1 + k_1x(t)} + \frac{y(t)}{\alpha_2 + k_2y(t)} \end{cases}$$

where $x(t)$ and $y(t)$ are the number of juveniles and adults, respectively, at time t , and $b(t)$ is the time-dependent birth rate. The authors showed that the globally attracting cycles generated by period-2 birth rates of the form $b(2t) = 0$ and $b(2t+1) = \hat{b}$ are advantageous for low birth rates and are deleterious for high birth rates.

In [2], the global asymptotic stability results were extended to the three-stage model given by

$$\begin{cases} x(t+1) = b(t)z(t) \\ y(t+1) = s_1(x(t))x(t) \\ z(t+1) = s_2(y(t))y(t) + s_3(z(t))z(t), \end{cases}$$

where $x(t)$, $y(t)$, and $z(t)$ represent the number of juveniles, nonbreeding adults and breeding adults, respectively, at time t . The function $b(t)$ is the time-dependent birth

rate, and s_i is the nonlinear survivorship rate for stage i . Here, it was demonstrated that unlike the two stage model, period-2 birth rates are not advantageous for low birth rates. The arguments in [2, 3] rely on reducing the model to a higher order scalar difference equation and applying a result on monotone scalar difference equations from [19].

In general, the juvenile stage for some species is longer than the breeding season (e.g., the *Bafo Boreas* frog [29]). Thus, when the time unit is assumed to be the length of the breeding season, only a fraction of the juvenile population will transition to the adult stage in one-time unit and the rest remain juveniles. This assumption leads to a model which cannot be reduced to a single equation. Thus, we provide different arguments than those in [2, 3] to study global stability. Furthermore, the Jacobian in this case is a full matrix. Therefore, the local stability analysis involves much more complicated calculations.

The paper is organized as follows: In Section 2, we develop the model and analyze two cases: continuous breeding and seasonal breeding with period-2 birth rate. In both cases, we show that if the inherent net reproductive number is less than one, the population will become extinct. If it is greater than one, then in the continuous case, the unique interior equilibrium is globally asymptotically stable, and in the case of seasonal breeding, we have a globally asymptotically stable unique 2-cycle. In Section 3, we provide conditions under which the population with seasonal breeding survives while the population with continuous breeding goes to extinction. In Section 4 we summarize our results and give concluding remarks. Finally, in the Appendix we provide the calculations for the local asymptotic stability of the periodic solution for the seasonal birth rate.

2 Two-stage discrete model

The model developed here is a juvenile-adult discrete model where it is assumed that the juveniles and adults only compete with themselves and not with each other. Let $J(t)$ and $A(t)$ denote the number of juveniles and adults, respectively, at time t . Let $S_1(J)$ represent the survivorship of the juveniles and $S_2(A)$ represent the survivorship of the adults at time t . We will denote the time-dependent birth rate as $b(t)$. Thus, we obtain the following model:

$$\begin{cases} J(t+1) = (1-\gamma)S_1(J(t))J(t) + b(t)A(t) \\ A(t+1) = \gamma S_1(J(t))J(t) + S_2(A(t))A(t) \\ (J(0), A(0)) \in \mathbb{R}_+^2 \setminus (0, 0), \end{cases} \quad (2.1)$$

where γ is the fraction of the juveniles that become adults in one time unit. Hence, we assume $0 < \gamma \leq 1$. Also, we assume for the remainder of this paper that S_1 and S_2 have the following properties:

- (H1) For $i = 1, 2$, $S_i(x) \in C^1[0, \infty)$, $S'_i(x) < 0$, $(S_i(x)x)' > 0$, $\lim_{x \rightarrow \infty} S_i(x) = 0$, $\lim_{x \rightarrow \infty} S_i(x)x = \hat{a}_i < \infty$, and $S_i(0) = a_i$ ($0 < a_i < 1$).

Clearly, (H1) is satisfied by the Beverton-Holt dynamics given by $S_i(x) = \frac{a_i}{1+k_ix}$ for $i = 1, 2$.

A model similar to (2.1) has been used in [29] to assess the contribution of egg mortality to amphibian declines. Specifically the authors focused on two species (*Bufo boreas* and *Ambystoma macrodactylum*) with contrasting life-history strategies (one has a birth rate more than one hundred times larger than the other). Their elasticity analysis showed that for a range of density dependence scenarios both species were more sensitive to changes in post-embryonic survival parameters, particularly juvenile survival.

We will analyze the model (2.1) for two cases. In the first case, we assume $b(t) = b$, a positive constant, and in the second case, we assume $b(t)$ is periodic with period 2. The following result follows from [1]. Here, $P : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ is said to be monotone if $x \leq y$ implies $P(x) \leq P(y)$, where vector inequalities hold componentwise.

Lemma 1. *Let $P : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ be a continuous, monotone map and $c \leq d$ be points in \mathbb{R}_+^2 . If $c \leq P(c)$ and $P(d) \leq d$, and if P has a unique fixed point x^* in the order interval $[c, d] \equiv \{x \in \mathbb{R}_+^2 | c \leq x \leq d\}$, then every solution sequence of the discrete system $x(t+1) = P(x(t))$, starting in $[c, d]$, converges to x^* .*

2.1 Continuous breeding

We now consider (2.1) with continuous breeding. For the remainder of the section, we assume $b(t) = b$, a positive constant, in (2.1). The model (2.1) can be written as

$$x(t+1) = B(x(t))x(t), \quad (2.2)$$

where $x(t) = (J(t), A(t))^T$ and B has the form

$$B(x) = \begin{pmatrix} (1-\gamma)S_1(J) & b \\ \gamma S_1(J) & S_2(A) \end{pmatrix}.$$

First, we will use the techniques in [10] to find the net reproductive number \mathcal{R}_0 , which is the expected number of offspring per juvenile over the course of its lifetime. Define the fertility matrix as

$$G = \begin{pmatrix} 0 & b \\ 0 & 0 \end{pmatrix}$$

and the transition matrix as

$$T = \begin{pmatrix} (1-\gamma)a_1 & 0 \\ \gamma a_1 & a_2 \end{pmatrix}. \quad (2.3)$$

Note that the inherent projection matrix $B(0) = G + T$. Thus, the net reproductive number is the positive strictly dominant eigenvalue of the matrix $G(I - T)^{-1}$. Therefore, we get

$$\mathcal{R}_0 \equiv \frac{\gamma b a_1}{(1 - a_2)(1 - (1 - \gamma)a_1)}.$$

Now, the system (2.1) always has the trivial steady state $E_0 = (0, 0)$. If (2.1) has a nontrivial interior steady state $E_1 = (\bar{J}, \bar{A})$, then E_1 must satisfy

$$1 = (1 - \gamma)S_1(J) + \gamma bS_1(J) + (1 - (1 - \gamma)S_1(J))S_2(A(J)) \equiv F(J), \quad (2.4)$$

where

$$A(J) = \frac{1}{b}J(1 - (1 - \gamma)S_1(J)).$$

Note that

$$A'(J) = \frac{1}{b}(1 - (1 - \gamma)(S_1(J)J)') > 0,$$

since $0 < (S_1(J)J)' = S_1'(J)J + S_1(J) \leq S_1(J) < 1$ by (H1). Therefore,

$$F'(J) = (1 - \gamma)S_1'(J)(1 - S_2(A)) + \gamma bS_1'(J) + (1 - (1 - \gamma)S_1(J))S_2'(A)A' < 0.$$

Since $F'(J) < 0$ and $\lim_{J \rightarrow \infty} F(J) = 0$, we see that if $F(0) = (1 - \gamma)a_1 + \gamma b a_1 + a_2 - (1 - \gamma)a_1 a_2 > 1$, which is equivalent to $\mathcal{R}_0 > 1$, then (2.1) has a nontrivial unique interior steady state $E_1 = (\bar{J}, \bar{A})$. Furthermore, it can be shown that (2.1) is point dissipative. In fact, it is clear that \mathbb{R}_+^2 is positively invariant and from (H1), it follows that

$$A(t+1) = \gamma S_1(J)J(t) + S_2(A)A(t) \leq \gamma \hat{a}_1 + \hat{a}_2 \leq \hat{a}_1 + \hat{a}_2$$

$\forall t = 0, 1, \dots$. Therefore, we have

$$A(t) \leq \hat{a}_1 + \hat{a}_2 \quad \forall t = 1, 2, \dots$$

Using this we get

$$J(t+1) \leq (1 - \gamma)\hat{a}_1 + b(\hat{a}_1 + \hat{a}_2) \quad \forall t = 1, 2, \dots,$$

hence

$$J(t) \leq (b+1)\hat{a}_1 + b\hat{a}_2 \quad \forall t = 2, 3, \dots$$

Thus, every forward solution enters the following compact set in at most two time steps and remain there forever:

$$K = \{(J, A) \in \mathbb{R}_+^2 \mid J \in [0, (b+1)\hat{a}_1 + b\hat{a}_2], A \in [0, \hat{a}_1 + \hat{a}_2]\}. \quad (2.5)$$

Now, we prove the following stability result for system (2.1).

Theorem 2.1. *Let $b(t) = b$, a positive constant, for $t = 0, 1, \dots$*

- (a) *If $\mathcal{R}_0 < 1$, then the system (2.1) has only the trivial steady state $E_0 = (0, 0)$, and E_0 is globally asymptotically stable.*
- (b) *If $\mathcal{R}_0 > 1$, then there exists a (unique) nontrivial interior steady state $E_1 = (\bar{J}, \bar{A})$ in addition to E_0 , and E_1 is globally asymptotically stable.*

Proof: (a) Assume $\mathcal{R}_0 < 1$. The system (2.1) only has the trivial steady state $E_0 = (0, 0)$ since $F(0) < 1$. Define the map $P : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ to be the right side of (2.1). Linearizing the system (2.1) and evaluating the resulting Jacobian matrix at E_0 gives us

$$DP(E_0) = \begin{pmatrix} (1 - \gamma)a_1 & b \\ \gamma a_1 & a_2 \end{pmatrix}.$$

Then, it follows from [27] that the eigenvalues of $DP(E_0)$ have magnitude less than one, and thus, E_0 is locally asymptotically stable.

To establish global asymptotic stability of E_0 , note that the inherent projection matrix $B(0)$ of the system (2.2) is nonnegative, irreducible, and primitive. Therefore we know that $B(0)$ has a positive, simple, and strictly dominant eigenvalue r . Also, since $\mathcal{R}_0 < 1$, it follows from [6] (Theorem 1.1.3, pg. 10) that $r < 1$ and $\lim_{t \rightarrow \infty} B^t(0) = 0$. Since (2.2) has the property

$$x \leq y \text{ implies } B(x) \geq B(y),$$

where vector and matrix inequalities hold componentwise, we have that for any $x(0)$, $0 \leq x(1) = B(x(0))x(0) \leq B(0)x(0)$. Repeating this process we get that $0 \leq x(t) = \prod_{i=0}^{t-1} B(x(i))x(0) \leq B^t(0)x(0) \rightarrow 0$ as $t \rightarrow \infty$. Thus, E_0 is globally asymptotically stable. This completes the proof of (a).

(b) Assume $\mathcal{R}_0 > 1$. This implies that $F(0) > 1$ and a unique interior steady state E_1 exists. For simplicity, for the remainder of this proof, we will write $S_1(\bar{J})$ as S_1 and $S_2(\bar{A})$ as S_2 .

Define the map $P : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ to be the right side of (2.1). Linearizing the system (2.1) and evaluating the resulting Jacobian matrix at $E_1 = (\bar{J}, \bar{A})$ gives us

$$DP(E_1) = \begin{pmatrix} (1 - \gamma)(S_1 + S'_1 \bar{J}) & b \\ \gamma(S_1 + S'_1 \bar{J}) & S_2 + S'_2 \bar{A} \end{pmatrix}.$$

To show local asymptotic stability of E_1 , we need to show that the following inequalities hold (see Theorem 2.37 in [11]):

$$|\text{tr}(DP(E_1))| < 1 + \det(DP(E_1)) < 2. \quad (2.6)$$

It is clear that $\text{tr}(DP(E_1)) > 0$ and $\det(DP(E_1)) < 1$. Thus, we only need to check $\text{tr}(DP(E_1)) < 1 + \det(DP(E_1))$. Note first that from (2.4) we have $1 = F(\bar{J})$. Therefore,

$$\begin{aligned} & 1 + \det(DP(E_1)) - \text{tr}(DP(E_1)) \\ &= -(1 - \gamma)S'_1 \bar{J} - S'_2 \bar{A} + (1 - \gamma)S_1 S'_2 \bar{A} + (1 - \gamma)S'_1 \bar{J} S_2 + (1 - \gamma)S'_1 \bar{J} S'_2 \bar{A} - b\gamma S'_1 \bar{J} \\ &= -S'_2 \bar{A}(1 - (1 - \gamma)S_1) - S'_1 \bar{J}(1 - \gamma)(1 - (S_2 + S'_2 \bar{A})) - b\gamma S'_1 \bar{J} > 0 \end{aligned}$$

since $0 < S_2 + S'_2 \bar{A} < 1$ by (H1), $0 < \gamma \leq 1$, and \bar{J}, \bar{A} , and b are all positive. Thus (2.6) holds, and E_1 is locally asymptotically stable.

Now we will establish global attractivity of E_1 by following an approach similar to that in [1]. Since $DP(x)$ is a nonnegative matrix for all x , we have that $P(x)$ is

monotone. Also every solution starting on the boundary of \mathbb{R}_+^2 , but not in E_0 , enters the positively invariant set $\text{int}(\mathbb{R}_+^2)$ in at most two time steps. Thus, it suffices to show that the result holds for solutions in $\text{int}(\mathbb{R}_+^2)$. Pick $x(0) = (J(0), A(0)) \in \text{int}(\mathbb{R}_+^2)$. Since all solutions enter the compact set K in at most two time steps, it is enough to consider $x(0) \in \text{int}(\mathbb{R}_+^2) \cap K$, where K is defined by (2.5). Clearly, $E_1 \in K$. Define $d \equiv \sup K$ (the maximal element in K). Then we have that $P(d) \leq d$. Now, since $B(0)$ is an irreducible non-negative matrix, we know that the spectral radius $r > 1$ of $B(0)$ is an eigenvalue with a corresponding positive eigenvector v such that $B(0)v = rv$. Also, $\forall \epsilon > 0$ sufficiently small, we have $P(\epsilon v) = r\epsilon v + o(\epsilon) \geq \epsilon v$, as $r > 1$. Therefore, given $x(0) \in \text{int}(\mathbb{R}_+^2) \cap K$, we can choose $\epsilon > 0$ sufficiently small such that

$$c \equiv \epsilon v \leq x(0) \text{ and } c \leq P(c).$$

Hence, by Lemma 1, we have that E_1 is globally attractive, and therefore globally asymptotically stable. This concludes the proof of (b).

2.2 Seasonal breeding

We now assume that breeding is seasonal and we let the birth rate $b(t)$ be periodic of period 2. So, we assume $b(0) = 0, b(1) = \hat{b} > 0, b(2) = 0, b(3) = \hat{b}, \dots$. The net reproductive number $\hat{\mathcal{R}}_0$ for the seasonal breeding case is more subtle than in the continuous breeding case. We will use similar techniques to the ones used in [10] to define $\hat{\mathcal{R}}_0$. To motivate the construction of $\hat{\mathcal{R}}_0$, consider the periodic linear system

$$x(t+1) = M(t)x(t), \tag{2.7}$$

where

$$M(t) = \begin{pmatrix} (1-\gamma)a_1 & b(t) \\ \gamma a_1 & a_2 \end{pmatrix}.$$

With $b(t)$ defined above, we have that

$$M(2t) = M_0 = \begin{pmatrix} (1-\gamma)a_1 & 0 \\ \gamma a_1 & a_2 \end{pmatrix} = G_0 + T$$

and

$$M(2t+1) = M_1 = \begin{pmatrix} (1-\gamma)a_1 & \hat{b} \\ \gamma a_1 & a_2 \end{pmatrix} = G_1 + T,$$

where $G_0 \equiv 0$, and $G_1 = \begin{pmatrix} 0 & \hat{b} \\ 0 & 0 \end{pmatrix}$, and T is given by (2.3). Therefore, the projection matrix over a full cycle composed of two time units is given by the constant matrix

$$\bar{M} = M_1 M_0 = (G_1 + T)T = G_1 T + T^2 = \hat{G} + \hat{T},$$

where $\hat{G} = G_1 T$ represents the fertility matrix over a full cycle, and $\hat{T} = T^2$ represents the transition matrix over a full cycle (two time units). Thus, the net reproductive

number of (2.7) is the positive strictly dominant eigenvalue of the matrix $\hat{G}(I - \hat{T})^{-1}$. Applying the above approach to our model (2.1), we define $\hat{\mathcal{R}}_0$ to be

$$\hat{\mathcal{R}}_0 \equiv \frac{\hat{b}\gamma a_1(1 + (1 - \gamma)a_1 a_2)}{(1 - a_2^2)(1 - (1 - \gamma)^2 a_1^2)}.$$

Although $\hat{\mathcal{R}}_0$ is defined mathematically, it has the biological interpretation of the expected number of offspring produced by an individual over the course of its life. To see this clearly, let $\gamma = 1$. Then

$$\hat{\mathcal{R}}_0 = \frac{\hat{b}a_1}{1 - a_2^2} = \hat{b}a_1(1 + a_2^2 + a_2^4 + \dots).$$

The even powers of a_2 in $\hat{\mathcal{R}}_0$ reflect the fact that adults must survive two time units with a probability of a_2^2 in order to reproduce repeatedly.

Now using a similar argument as in the continuous case, we see that there exists a compact set \hat{K} such that every forward solution enters this set in at most two time steps and remains there forever.

Let $J(0) = J^*$ and $A(0) = A^*$ be given positive real numbers. Then

$$\begin{cases} J(1) = (1 - \gamma)S_1(J^*)J^* \\ A(1) = \gamma S_1(J^*)J^* + S_2(A^*)A^*, \end{cases}$$

as $b(0) = 0$, which gives us

$$\begin{cases} J(2) = \hat{b}(\gamma S_1(J^*)J^* + S_2(A^*)A^*) + (1 - \gamma)S_1((1 - \gamma)S_1(J^*)J^*)((1 - \gamma)S_1(J^*)J^*) \\ A(2) = \gamma S_1((1 - \gamma)S_1(J^*)J^*)((1 - \gamma)S_1(J^*)J^*) + \\ \quad S_2(\gamma S_1(J^*)J^* + S_2(A^*)A^*)(\gamma S_1(J^*)J^* + S_2(A^*)A^*). \end{cases}$$

Now, in order for a solution $(J(t), A(t))$ of (2.1) to be periodic with period 2, we must have

$$\begin{cases} J^* = J(2) \\ A^* = A(2). \end{cases} \quad (2.8)$$

Therefore, solving the first equation of (2.8) for A^* and substituting it into the second equation, we see that a periodic solution must satisfy

$$\begin{aligned} 1 = & (1 - \gamma)^2 S_1(J^*)S_1((1 - \gamma)S_1(J^*)J^*)(1 - S_2(A^*)S_2(\gamma S_1(J^*)J^* + S_2(A^*)A^*)) \\ & + \hat{b}\gamma S_1(J^*)(1 + (1 - \gamma)S_2(A^*)S_1((1 - \gamma)S_1(J^*)J^*)) \\ & + S_2(A^*)S_2(\gamma S_1(J^*)J^* + S_2(A^*)A^*) \equiv \hat{F}(J^*). \end{aligned}$$

Using similar calculations as before, one can show that $\hat{F}'(J) < 0$ and $\lim_{J \rightarrow \infty} \hat{F}(J) = 0$. Thus, if $\hat{F}(0) > 1$, which is equivalent to $\hat{\mathcal{R}}_0 > 1$, then (2.1) has a nontrivial unique 2-cycle exists and is given by

$$\{(J^*, A^*), ((1 - \gamma)S_1(J^*)J^*, \gamma S_1(J^*)J^* + S_2(A^*)A^*)\}. \quad (2.9)$$

The following theorem summarizes the stability analysis of (2.1) with periodic birth rate.

Theorem 2.2. Let $b(2t) = 0$ and $b(2t + 1) = \hat{b} > 0$, for $t = 0, 1, \dots$

(a) If $\hat{\mathcal{R}}_0 < 1$, then $E_0 = (0, 0)$ is globally asymptotically stable.

(b) If $\hat{\mathcal{R}}_0 > 1$, then the 2-periodic solution \hat{E}_1 given by (2.9) is globally asymptotically stable.

Proof: (a) Assume $\hat{\mathcal{R}}_0 < 1$. Let $E_0 = (0, 0)$. Define the map $P : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ to be the right side of (2.1). From [4], the local stability of E_0 can be determined by investigating the eigenvalues of the product of matrices

$$D_0 = \begin{pmatrix} (1-\gamma)a_1 & 0 \\ \gamma a_1 & a_2 \end{pmatrix} \begin{pmatrix} (1-\gamma)a_1 & \hat{b} \\ \gamma a_1 & a_2 \end{pmatrix} = \begin{pmatrix} (1-\gamma)^2 a_1^2 & \hat{b}(1-\gamma)a_1 \\ (1-\gamma)\gamma a_1^2 + \gamma a_1 a_2 & \hat{b}\gamma a_1 + a_2^2 \end{pmatrix}.$$

We will use condition (2.6) to show that the eigenvalues of D_0 have magnitude less than one. It is clear that $\text{tr}(D_0) > 0$ and $\det(D_0) < 1$. Thus, we only need to check $\text{tr}(D_0) < 1 + \det(D_0)$. To this end,

$$\text{tr}(D_0) - \det(D_0) = (1-\gamma)^2 a_1^2 (1 - a_2^2) + \hat{b}\gamma a_1 (1 + (1-\gamma)a_1 a_2) + a_2^2 < 1,$$

since $\hat{\mathcal{R}}_0 < 1$. Therefore, E_0 is locally asymptotically stable.

We now establish the global attractivity of E_0 . From (2.1), we see that

$$J(2t + 1) = (1 - \gamma)S_1(J(2t))J(2t) \quad (2.10)$$

as $b(2t) = 0$, and

$$A(2t + 1) = \gamma S_1(J(2t))J(2t) + S_2(A(2t))A(2t). \quad (2.11)$$

From this, we get

$$\begin{aligned} J(2t + 2) &= \hat{b}\gamma S_1(J(2t))J(2t) + \hat{b}S_2(A(2t))A(2t) \\ &\quad + (1-\gamma)^2 S_1((1-\gamma)S_1(J(2t))J(2t))S_1(J(2t))J(2t) \end{aligned}$$

and

$$\begin{aligned} A(2t + 2) &= \gamma(1-\gamma)S_1((1-\gamma)S_1(J(2t))J(2t))S_1(J(2t))J(2t) \\ &\quad + S_2(\gamma S_1(J(2t))J(2t) + S_2(A(2t))A(2t)) \times \\ &\quad (\gamma S_1(J(2t))J(2t) + S_2(A(2t))A(2t)). \end{aligned}$$

Let $\tau + i = 2(t + i)$ for $i \geq 0$. Then we get the system

$$\begin{cases} J(\tau + 1) = \hat{b}(\gamma S_1(J(\tau))J(\tau) + S_2(A(\tau))A(\tau)) \\ \quad + (1-\gamma)^2 S_1((1-\gamma)S_1(J(\tau))J(\tau))S_1(J(\tau))J(\tau) \\ A(\tau + 1) = \gamma(1-\gamma)S_1((1-\gamma)S_1(J(\tau))J(\tau))S_1(J(\tau))J(\tau) \\ \quad + S_2(\gamma S_1(J(\tau))J(\tau) + S_2(A(\tau))A(\tau)) \times \\ \quad (\gamma S_1(J(\tau))J(\tau) + S_2(A(\tau))A(\tau)) \end{cases} \quad (2.12)$$

which can be written as

$$x(\tau + 1) = \hat{B}(x(\tau))x(\tau). \quad (2.13)$$

Here $x(\tau) = (J(\tau), A(\tau))^T$ and \hat{B} has the form

$$\hat{B}(x) = \begin{pmatrix} \hat{B}_{11} & \hat{B}_{12} \\ \hat{B}_{21} & \hat{B}_{22} \end{pmatrix}$$

where

$$\begin{aligned} \hat{B}_{11} &= \hat{b}\gamma S_1(J) + (1 - \gamma)^2 S_1((1 - \gamma)S_1(J)J)S_1(J) \\ \hat{B}_{12} &= \hat{b}S_2(A) \\ \hat{B}_{21} &= \gamma(1 - \gamma)S_1((1 - \gamma)S_1(J)J)S_1(J) + \gamma S_1(J)S_2(\gamma S_1(J)J + S_2(A)A) \\ \hat{B}_{22} &= S_2(\gamma S_1(J)J + S_2(A)A)S_2(A). \end{aligned}$$

Therefore, the inherent projection matrix $\hat{B}(0)$ of the system (2.13) is given by

$$\hat{B}(0) = \begin{pmatrix} \hat{b}\gamma a_1 + (1 - \gamma)^2 a_1^2 & \hat{b}a_2 \\ \gamma(1 - \gamma)a_1^2 + \gamma a_1 a_2 & a_2^2 \end{pmatrix}$$

Note the $\hat{B}(0)$ is nonnegative, irreducible, and primitive. Thus, by a similar argument as in the proof of Theorem 2.1, we have E_0 is globally attractive for (2.12). Thus, $\lim_{t \rightarrow \infty} J(2t) = 0$ and $\lim_{t \rightarrow \infty} A(2t) = 0$. As a result, we get $\lim_{t \rightarrow \infty} J(2t + 1) = 0$ and $\lim_{t \rightarrow \infty} A(2t + 1) = 0$. Hence, E_0 is globally asymptotically stable. This completes the proof of (a).

(b) Assume $\hat{\mathcal{R}}_0 > 1$. We know that (2.1) has a nontrivial, unique period-2 solution \hat{E}_1 given by (2.9). For the remainder of this proof, for simplicity, we will write $S_1(J^*)$ as S_1 , $S_2(A^*)$ as S_2 , $(1 - \gamma)S_1(J^*)J^*$ as \hat{J} , $\gamma S_1(J^*)J^* + S_2(A^*)A^*$ as \hat{A} , $S_1((1 - \gamma)S_1(J^*)J^*)$ as \hat{S}_1 , and $S_2(\gamma S_1(J^*)J^* + S_2(A^*)A^*)$ as \hat{S}_2 . The local stability of \hat{E}_1 can be determined by investigating the eigenvalues of the product of matrices

$$D_1 = \begin{pmatrix} (1 - \gamma)(S_1 + S_1'J^*) & 0 \\ \gamma(S_1 + S_1'J^*) & S_2 + S_2'A^* \end{pmatrix} \begin{pmatrix} (1 - \gamma)(\hat{S}_1 + \hat{S}_1'\hat{J}) & \hat{b} \\ \gamma(\hat{S}_1 + \hat{S}_1'\hat{J}) & \hat{S}_2 + \hat{S}_2'\hat{A} \end{pmatrix}$$

We need to show condition (2.6) holds. It is clear that $\text{tr}(D_1) > 0$. Now, to establish $\det(D_1) < 1$ and $\text{tr}(D_1) < 1 + \det(D_1)$ requires some complicated calculations the details of which are provided in the appendix. Thus, we have that \hat{E}_1 is locally asymptotically stable.

Now we need to show that \hat{E}_1 is globally attracting. Define the map $\hat{P} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ to be the right side of (2.12). The Jacobian matrix $D\hat{P}(x)$ is given by

$$D\hat{P}(x) = \begin{pmatrix} D\hat{P}_{11} & D\hat{P}_{12} \\ D\hat{P}_{21} & D\hat{P}_{22} \end{pmatrix}$$

where

$$\begin{aligned}
D\hat{P}_{11} &= \hat{b}\gamma(S_1(J) + S'_1(J)J) \\
&\quad + (1-\gamma)^2(S_1(J) + S'_1(J)J)(S_1((1-\gamma)S_1(J)J) \\
&\quad + (1-\gamma)^2S_1(J)JS'_1((1-\gamma)S_1(J)J)((1-\gamma)(S_1(J) + S'_1(J)J)) \\
D\hat{P}_{12} &= \hat{b}(S_2(A) + S'_2(A)A) \\
D\hat{P}_{21} &= \gamma(1-\gamma)(S_1(J) + S'_1(J)J)(S_1((1-\gamma)S_1(J)J)) \\
&\quad + \gamma(1-\gamma)S_1(J)JS'_1((1-\gamma)S_1(J)J)((1-\gamma)(S_1(J) + S'_1(J)J)) \\
&\quad + \gamma(S_1(J) + S'_1(J)J)(S_2(\gamma S_1(J)J + S_2(A)A) \\
&\quad + S'_2(\gamma S_1(J)J + S_2(A)A)(\gamma(S_1(J) + S'_1(J)J))(\gamma S_1(J)J + S_2(A)A)) \\
D\hat{P}_{22} &= (S_2(A) + S'_2(A)A)(S_2(\gamma S_1(J)J) + S_2(A)A) \\
&\quad + S'_2(\gamma S_1(J)J + S_2(A)A)(S_2(A) + S'_2(A)A)(\gamma S_1(J)J + S_2(A)A).
\end{aligned}$$

Combining like terms and using arguments as above which rely on assumption (H1), it is not difficult to show that $D\hat{P}(x)$ is a nonnegative matrix for all x . Therefore, $\hat{P}(x)$ is monotone. Note that \hat{P} has a unique, positive fixed point (J^*, A^*) as $\hat{\mathcal{R}}_0 > 1$. Following a similar argument in Theorem 2.1 (b), we have that (J^*, A^*) is the globally attractive fixed point for (2.12). Thus, we have that $\lim_{t \rightarrow \infty} J(2t) = J^*$ and $\lim_{t \rightarrow \infty} A(2t) = A^*$. Consequently, from (2.10)-(2.11) we have $\lim_{t \rightarrow \infty} J(2t+1) = (1-\gamma)S_1(J^*)J^*$ and $\lim_{t \rightarrow \infty} A(2t+1) = \gamma S_1(J^*)J^* + S_2(A^*)A^*$. Thus, \hat{E}_1 is globally asymptotically stable.

3 Comparing seasonal and continuous breeding

In this section, we provide a comparison between seasonally breeding and continuously breeding populations. In particular, we focus on two questions: 1) Is seasonal breeding advantageous? 2) How does the length of the breeding season influence such an advantage?

3.1 Period-2 versus continuous birth rate

We are interested in knowing whether there are birth rate values b for which seasonal breeding is advantageous over continuous breeding (i.e., results in higher average of total population in the long term). Note that during a full cycle (two time units) each adult in a population with a continuous breeding strategy produces $b + b = 2b$ juveniles, while each adult in a population with a seasonal birth strategy produces $0 + \hat{b} = \hat{b}$ juveniles. To compare the two reproduction strategies on an equal basis, we let $\hat{b} = 2b$. Therefore, an adult belonging to a population with either of the two reproduction strategies will produce $2b$ juveniles in a full cycle. In this case, Theorems 2.1 and 2.2 require, respectively, that

$$b > \frac{(1-a_2)(1-(1-\gamma)a_1)}{\gamma a_1} \quad \text{and} \quad b > \frac{(1-a_2^2)(1-(1-\gamma)^2 a_1^2)}{2\gamma a_1(1+(1-\gamma)a_1 a_2)}.$$

for the population to persist. It is not hard to check that

$$\frac{(1-a_2^2)(1-(1-\gamma)^2 a_1^2)}{2(1+(1-\gamma)a_1 a_2)} < (1-a_2)(1-(1-\gamma)a_1).$$

Thus, for birth rates satisfying

$$\frac{(1 - a_2^2)(1 - (1 - \gamma)^2 a_1^2)}{2\gamma a_1(1 + (1 - \gamma)a_1 a_2)} < b < \frac{(1 - a_2)(1 - (1 - \gamma)a_1)}{\gamma a_1}$$

the seasonally breeding population survives while the one with continuous breeding goes to extinction. Hence, for such values of birth rates the seasonal breeding is advantageous.

To understand the effects of γ (which in effect is related to the length of the juvenile stage) on these birth rate values, let

$$g(\gamma) = \frac{(1 - a_2^2)(1 - (1 - \gamma)^2 a_1^2)}{2\gamma a_1(1 + (1 - \gamma)a_1 a_2)} \quad \text{and} \quad f(\gamma) = \frac{(1 - a_2)(1 - (1 - \gamma)a_1)}{\gamma a_1}.$$

Observe that $g'(\gamma) < 0$ and $f'(\gamma) < 0$. Therefore, for $0 < \gamma \leq 1$, we have that

$$g(\gamma) > g(1), f(\gamma) > f(1).$$

Thus, smaller γ values (i.e., longer juvenile stage) cause a shift in the interval of birth rates b where seasonal breeding is advantageous to the right.

Next we provide numerical results showing that for low birth rates the periodic solution has total population average larger than that of the continuous solution, while for large birth rates, the opposite happens. For the following examples, we will use $\gamma = 0.75$, $S_1(J) = a_1/(1 + k_1 J)$ and $S_2(A) = a_2/(1 + k_2 A)$ where $a_1 = 0.1$, $k_1 = 0.01$, $a_2 = 0.8$, and $k_2 = 0.1$. The initial conditions used are $J(0) = 0$ and $A(0) = 1$. First, we let $b = 2.5$. Then for continuous breeding, we get $\mathcal{R}_0 = 0.96 < 1$, hence the population goes to extinction as $t \rightarrow \infty$. For seasonal breeding, we get that $\hat{\mathcal{R}}_0 = 1.06 > 1$, thus the population persists. Therefore, seasonal breeding is clearly advantageous for the low birth rate $b = 2.5$. In Figure 1, we let $b = 3$. In this case both populations persist, but the seasonal reproduction strategy is advantageous as it results in higher total population average for large t values. We then let $b = 20$ and present the results in Figure 2. In this case continuous breeding is advantageous. In Figure 3, we provide the bifurcation diagrams for the continuous and seasonal birth rates (with the birth rate used as a bifurcation parameter). This diagram shows that for the above choice of parameters the seasonal breeding is advantageous for birth rates b in the (approximate) interval $[2.35, 12]$ and deleterious for birth rates $b > 12$.

3.2 Length of breeding season effect

We want to understand how the length of breeding season influences the dynamics of (2.1). Thus, for definiteness, we assume that the cycle length is one year divided into p time units where the breeding season length is equal to one time unit. So, during the p time units adults produce during one time unit and not produce for $p - 1$ time units. Therefore, the birth rate function satisfies $b(0) = 0, b(1) = 0, \dots, b(p - 2) = 0, b(p - 1) = \hat{b}$. For simplicity we assume throughout this section that $\gamma = 1$ in (2.1).

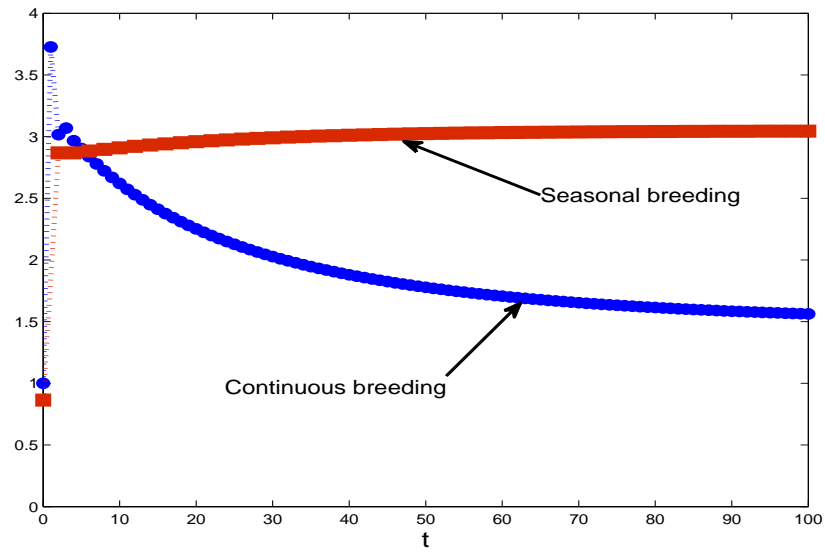


Figure 1: A plot of the total population for the seasonal and continuous birth rates. For seasonal birth rate, the cycle average is plotted.

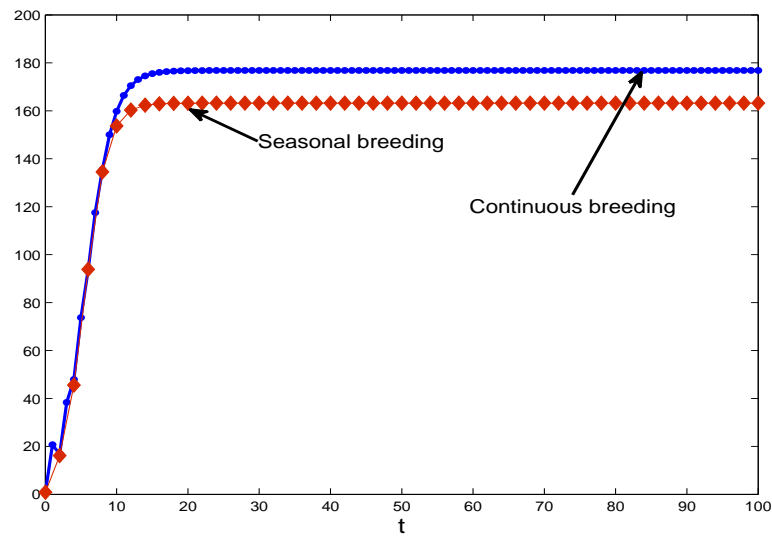


Figure 2: A plot of the total population for the seasonal and continuous birth rates. For seasonal birth rate, the cycle average is plotted.

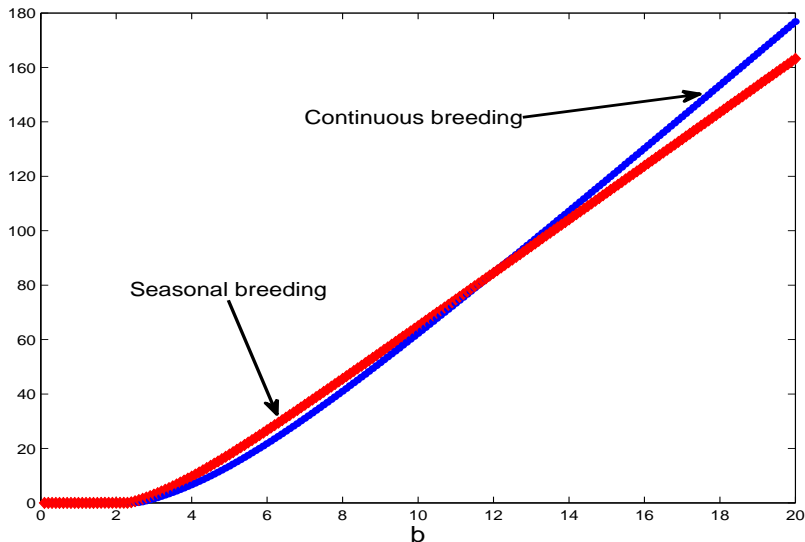


Figure 3: Bifurcation diagrams for the continuous and seasonal birth rates. The bifurcation diagram of the seasonal case is the cycle average of the total population.

Thus, following a similar approach as in Section 2, the net reproductive number can be derived as follows: Let $\hat{G} = G_1 T^{p-1}$ and $\hat{T} = T^p$, where

$$T = \begin{pmatrix} 0 & 0 \\ a_1 & a_2 \end{pmatrix} \quad \text{and} \quad G_1 = \begin{pmatrix} 0 & \hat{b} \\ 0 & 0 \end{pmatrix}.$$

Then the inherent projection matrix over of full cycle composed of p time units can be written as $\hat{G} + \hat{T}$. Thus, the net reproductive number is the positive strictly dominant eigenvalue of $\hat{G}(I - \hat{T})^{-1}$, which is given by

$$\hat{\mathcal{R}}_0 = \frac{\hat{b} a_1 a_2^{p-2}}{1 - a_2^p}.$$

Note that for $p = 2$, the net reproductive number reduces to the one discussed in Section 2.2 (when $\gamma = 1$). Using similar arguments as before, one can show that if $\hat{\mathcal{R}}_0 < 1$, then the population goes to extinction. Letting $\hat{b} = pb$ (so that each adult produces pb juveniles in one year in both continuous and seasonal populations), and comparing this to the continuous case, we see that if

$$\frac{1 - a_2^p}{pa_2^{p-2}} < 1 - a_2, \quad (3.1)$$

then there are values of b for which $\hat{\mathcal{R}}_0 > 1$ while $\mathcal{R}_0 < 1$. If the opposite inequality holds, then there are b values for which the continuously breeding population survives while the one with seasonal breeding goes to extinction. Simple calculations reveal that (3.1) holds for $p = 2$ only. Thus, for model (2.1) periods $p > 2$ (i.e., shorter breeding season) result in disadvantage for low birth rates.

4 Conclusion

In this paper, we develop and analyze a general discrete juvenile-adult population model with time-dependent birth rate and nonlinear survivorship rates. We show that the survival of a population with either continuous or seasonal breeding depends on the inherent net reproductive number of the population, which is the expected number of juvenile recruits per juvenile per life time. Although the inherent net reproductive number is well-known for the continuous breeding case, we show that for the seasonal breeding case with period 2 birth rate satisfying $b(2t) = 0$ and $b(2t + 1) = \hat{b}$, the inherent net reproductive number is the positive strictly dominant eigenvalue of the matrix $\hat{G}(I - \hat{T})^{-1} = G_1 T(I - T^2)^{-1}$. This form reflects the fact in order for an adult to transition to the next cycle, it must survive two time units, hence the T^2 . We show that for continuous breeding, the model has a unique globally asymptotically stable positive equilibrium provided the net reproductive number is larger than one. If it is smaller than one, then the extinction equilibrium is globally asymptotically stable. We also show that when breeding is seasonal, there exists a unique globally asymptotically stable periodic solution provided the net reproductive number is larger than one. When this value is less one, the population goes to extinction.

In section 3, we give conditions on the birth rate where the population with seasonal breeding survives while that with continuous breeding becomes extinct. We show that for low birth rates, seasonal breeding produces a total population average larger than that of continuous breeding. This is due to the fact that the inherent net reproductive number for seasonal breeding $\hat{\mathcal{R}}_0$ with $\hat{b} = 2b$ is larger than the inherent net reproductive number for continuous breeding \mathcal{R}_0 . So it is possible for low birth rates b that continuous breeders become extinct while seasonal breeders survive. We also show in section 3 that smaller γ values (i.e., longer juvenile stage) cause a shift in the interval of birth rates b where seasonal breeding is advantageous to the right. This is because for small γ values, there are less juveniles making the transition into the adult stage in one time unit. Therefore for the population to persist, the birth rates must be larger to compensate for the smaller fraction of juveniles making transition to adults.

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Appendix

To establish local asymptotic stability of the period-2 solution in Theorem 2.2 (b) we must show $1 - \det(D_1) > 0$ and $\text{tr}(D_1) - \det(D_1) - 1 < 0$. After lengthy calculations and combining like terms, we get $1 - \det(D_1) = (1) + (2) + (3) + (4) + (5) + (6) + (7) + (8) + (9) + (10) > 0$ where:

$$(1) = \gamma(1 - \gamma)AbJS'_1S'_2(\hat{S}_1 + \hat{S}'_1\hat{J})$$

$$(2) = -(1 - \gamma)^2AJ\hat{A}\hat{S}'_2S'_1S'_2(\hat{S}_1 + \hat{S}'_1\hat{J})$$

$$\begin{aligned}
(3) &= \gamma(1-\gamma)bS_2((\hat{S}_1 + \hat{S}'_1\hat{J})(S_1 + S'_1J) + S_1\hat{S}_1) \\
(4) &= \gamma bS_1(1 - (1-\gamma)AS'_2(\hat{S}_1 + \hat{S}'_1\hat{J})) \\
(5) &= -(1-\gamma)^2AS'_2\hat{S}_2(\hat{S}_1 + \hat{S}'_1\hat{J})(S_1 + S'_1J) \\
(6) &= -(1-\gamma)^2JS_2S'_1(\hat{S}_1 + \hat{S}'_1\hat{J})(\hat{S}_2 + \hat{S}'_2\hat{A}) \\
(7) &= -(1-\gamma)^2\hat{A}\hat{S}'_2S_1(\hat{S}_1 + \hat{S}'_1\hat{J})(S_2 + S'_2A) \\
(8) &= \hat{S}_2S_2(1 - (1-\gamma)^2S_1\hat{S}_1) \\
(9) &= (1-\gamma)^2\hat{S}_1S_1(1 - \hat{S}_2S_2) \\
(10) &= -(1-\gamma)^2\hat{S}_2S_1S_2\hat{J}\hat{S}'_1.
\end{aligned}$$

Also, we have that $\text{tr}(D_1) - \det(D_1) - 1 = (11) + (12) + (13) + (14) + (15) + (16) + (17) + (18) + (19) + (20) + (21) + (22) + (23) < 0$ where:

$$\begin{aligned}
(11) &= \gamma(1-\gamma)Ab\hat{S}_1S'_2(S_1 + S'_1J) \\
(12) &= -(1-\gamma)^2AJ\hat{S}_1S'_1S'_2(\hat{S}_2 + \hat{S}'_2\hat{A}) \\
(13) &= \gamma(1-\gamma)bJS'_1S_2(\hat{S}_1 + \hat{S}'_1\hat{J}) \\
(14) &= -(1-\gamma)^2J\hat{A}\hat{S}'_2S'_1S_2(\hat{S}_1 + \hat{S}'_1\hat{J}) \\
(15) &= \gamma(1-\gamma)b\hat{J}\hat{S}'_1S_1(S_2 + S'_2A) \\
(16) &= -(1-\gamma)^2A\hat{J}\hat{S}'_1\hat{S}_2S'_2(S_1 + S'_1J) \\
(17) &= A\hat{S}_2S'_2(1 - (1-\gamma)^2\hat{S}_1S_1) \\
(18) &= (1-\gamma)^2\hat{S}'_1S_1(\hat{J} - \hat{J}S_2\hat{S}_2) \\
(19) &= (1-\gamma)^2JS'_1(\hat{S}_1 + \hat{S}'_1\hat{J})(1 - S_2\hat{S}_2) \\
(20) &= \hat{A}\hat{S}'_2(S_2 + S'_2A)(1 - (1-\gamma)^2S_1(\hat{S}_1 + \hat{S}'_1\hat{J})) \\
(21) &= bJ\gamma S'_1 \\
(22) &= \gamma(1-\gamma)AbJ\hat{A}\hat{J}\hat{S}'_1S'_1S'_2 \\
(23) &= -(1-\gamma)^2AJ\hat{A}\hat{J}\hat{S}'_1\hat{S}'_2S'_1S'_2.
\end{aligned}$$

Thus, we have that E_1 is locally asymptotically stable.