

A Three-Stage Discrete-Time Population Model: Continuous Versus Seasonal Reproduction

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(Received 00 Month 200x; revised 00 Month 200x; in final form 00 Month 200x)

Abstract. We consider a three-stage discrete-time population model with density-dependent survivorship and time-dependent reproduction. We provide stability analysis for two types of birth mechanisms: continuous and seasonal. We show that when birth is continuous there exists a unique globally stable interior equilibrium provided that the inherent net reproductive number is greater than unity. If it is less than unity then extinction is the population's fate. We then analyze the case when birth is a function of period two and show that the unique 2-cycle is globally attracting when the inherent net reproductive number is greater than unity. While if it is less than unity the population goes to extinction. The two birth types are then compared. It is shown that for low birth rates the adult average number over a one year period is always higher when reproduction is continuous. Numerical simulations suggest that this remains true for high birth rates. Thus periodic birth rates of period two are deleterious for the three stage population model. This is different from the results obtained for a two-stage model discussed by Ackleh and Jang (*J. Diff. Equ. Appl.* (13):261-274, 2007) where it was shown that for low birth rates seasonal breeding results in higher adult averages.

Keywords: Three-stage discrete models, continuous breeding, seasonal breeding, global stability

AMS Subject Classification: 92D25, 39A11

1. Introduction

Several researchers have focused in recent years on the dynamics of nonautonomous discrete-time models and the advantage of seasonal versus continuous breeding in terms of maximizing the total population number or the total number of adults over a fixed time period [4–10, 12, 13, 15]. These studies were motivated by an experimental system which investigated the responses of populations of the flour beetle, *Tribolium castaneum*, cultured in a series of regularly fluctuating environments. Therein, it was observed that population density declined as environmental period lengthened [14].

Motivated by an urban population of green treefrogs that we are studying [16], we recently developed the following juvenile-adult model for a seasonally breeding population [1]:

$$\begin{cases} x_{t+1} = b_t y_t \\ y_{t+1} = \frac{x_t}{a + k_1 x_t} + \frac{y_t}{c + k_2 y_t} \\ x_0, y_0 > 0, \end{cases}$$

where the parameters a, c, k_1 and k_2 are assumed to be positive. Moreover, since $\frac{1}{a + k_1 x_t}$ represents the

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fraction of the juveniles x_t present at time t that survive one unit of time and appear as adults at time $t + 1$, we assumed $a > 1$ for the model to be biologically meaningful (note that $1/a$ is the inherent survivorship of juveniles). Similarly, we assume that the parameter $c > 1$. The function b_t represents the time-dependent birth rate.

In that paper we focused on the following question: given that an adult recruits a fixed number of juveniles in one year, is it advantageous (in terms of maximizing the total number of adults over a period of one year) to reproduce continuously or seasonally? To answer this question we investigated the model dynamics for two types of recruitment: continuous (i.e., $b_t = b > 0$ for $t = 0, 1, 2, \dots$) and periodic with period two (i.e., $b_0 = \hat{b} = 2b, b_1 = 0, b_2 = \hat{b}, \dots$).

Our analysis showed that for low birth rates the population which produces seasonally may survive while the one which reproduces continuously will go to extinction. Thus seasonal breeding is beneficial for such values of birth rates. Furthermore, we show that for low values of birth rates where both populations persist, the adults for the continuously breeding population have lower average over a one year period than the one that produces seasonally. Therefore, seasonal reproduction is beneficial in this case. However, for high birth rates this conclusion reverses and it is shown that breeding continuously results in higher adult averages over a one year period.

The purpose of this paper is to continue this investigation for a three-stage discrete time model. In Section 2 we present the model and we analyze the continuous breeding case and show that if the inherent net reproductive number is less than unity then the population goes to extinction while if it is greater than unity then the unique interior equilibrium is globally asymptotically stable. We then analyze the seasonal breeding with period-two and show that if the inherent net reproductive number is less than unity then the population becomes extinct while if it is greater than unity the unique 2-cycle is globally attracting. At the end of this section we compare the two birth types and show that in this case (unlike the two-stage model) breeding seasonally seems to always be deleterious. In Section 3 we provide concluding remarks.

2. Model Development and Analysis

We develop a theoretical model describing the dynamics of a population which engages in seasonal breeding and is divided into three stages: a juvenile stage, nonbreeding (sexually immature) stage, and breeding (adult) stage. To this end, denote by x_t the number of juveniles at time t , by y_t the number of nonbreeding individuals at time t and by z_t the number of adults at time t . We assume that the juvenile and nonbreeding stages are less than or equal to one time unit (i.e., all juveniles and nonbreeders move into the next stage within one time step). Assume that competition occurs within each stage. We then obtain the following nonautonomous three-stage discrete model:

$$\begin{cases} x_{t+1} = b_t z_t \\ y_{t+1} = s_1(x_t) x_t \\ z_{t+1} = s_2(y_t) y_t + s_3(z_t) z_t \\ (x_0, y_0, z_0) \in \mathbb{R}_+^3 \setminus \{(0, 0, 0)\} \end{cases} \quad (2.1)$$

where b_t is the per-capita birth rate of the breeding adults and s_i is the survivorship rate of stage i . We assume that s_i satisfies the following assumption:

$$(H1) \quad s_i \in C^1[0, \infty), s_i(0) = a_i, 0 < a_i < 1, s'_i(x) < 0, \frac{d(s_i(x)x)}{dx} > 0, \lim_{x \rightarrow \infty} s_i(x) = 0, \text{ and } \lim_{x \rightarrow \infty} s_i(x)x = \hat{a}_i < \infty \text{ for } i = 1, 2, 3.$$

Such an assumption is satisfied, for example, by a Beverton-Holt type of survivorship function. Before we start analyzing model (2.1) we recall the following result (see Theorem 1.10 in [11]) which will be used in the sequel. Consider a $k + 1$ order nonlinear difference equation of the form

$$x_{n+1} = F(x_n, x_{n-1}, \dots, x_{n-k}), n = 0, 1, 2, \dots, \quad (2.2)$$

where $F \in C(I^{k+1}, \mathbb{R})$ and I is an open interval of \mathbb{R} .

Theorem 2.1 *Let $x^* \in I$ be an equilibrium of (2.2). Suppose F satisfies the following two conditions:*

- (a) F is non-decreasing in each of its arguments, and
- (b) F satisfies $(u - x^*)[F(u, u, \dots, u) - u] < 0$ for all $u \in I \setminus \{x^*\}$.

Then x^ is a global attractor of all solutions of (2.2).*

2.1. Continuous breeding

In this subsection we consider model (2.1) with continuous breeding. In particular, we assume that in model (2.1) $b_t \equiv b$, a positive constant. Clearly solutions of system (2.1) remain positive. The system always has a trivial steady state $E_0 = (0, 0, 0)$. The z -component of a nontrivial steady state $(\bar{x}, \bar{y}, \bar{z})$, $\bar{z} > 0$, must satisfy

$$1 = bs_2(s_1(bz)bz)s_1(bz) + s_3(z). \tag{2.3}$$

Notice the right hand side of (2.3) is a strictly decreasing function of z by (H1), with value $ba_1a_2 + a_3$ when $z = 0$, and approaches 0 as z goes to infinity. Therefore, (2.3) has a positive solution if and only if $ba_1a_2 + a_3 > 1$. Consequently, (2.1) has an interior steady state $E_1 = (\bar{x}, \bar{y}, \bar{z})$ if and only if

$$ba_1a_2 + a_3 > 1, \tag{2.4}$$

where \bar{z} solves (2.3), $\bar{x} = b\bar{z}$, and $\bar{y} = s_1(\bar{x})\bar{x}$. The interior steady state is unique whenever it exists. Clearly (2.4) is equivalent to

$$R_0 := \frac{ba_1a_2}{1 - a_3} > 1, \tag{2.5}$$

where R_0 is the inherent net reproductive number. Using Theorem 2.1 the asymptotic dynamics of system (2.1) can be understood and are summarized below.

Theorem 2.2 *If $R_0 < 1$, then (2.1) has only the trivial steady state $E_0 = (0, 0, 0)$ which is globally asymptotically stable. If $R_0 > 1$, then E_0 is unstable and (2.1) has another equilibrium $E_1 = (\bar{x}, \bar{y}, \bar{z})$ which is globally asymptotically stable in the interior of \mathbb{R}_+^3 .*

Proof. Suppose $R_0 < 1$. Let (x_t, y_t, z_t) be a solution of (2.1). Since $y_{t+1} \leq a_1x_t$ and $z_{t+1} \leq a_2y_t + a_3z_t$ for $t \geq 0$, consider the following linear system

$$\begin{aligned} X_{t+1} &= bZ_t \\ Y_{t+1} &= a_1X_t \\ Z_{t+1} &= a_2Y_t + a_3Z_t. \end{aligned} \tag{2.6}$$

The eigenvalues λ of the above coefficient matrix \mathbf{A} satisfy $p_0(\lambda) = \lambda^3 - a_3\lambda^2 - ba_1a_2 = 0$. It is clear that $p_0(1) > 0$, $p_0(-1) < 0$, and $1 - b^2a_1^2a_2^2 > ba_3a_1a_2$ by our assumption of $R_0 < 1$. It follows from the Jury conditions [2] that E_0 is locally asymptotically stable. Since \mathbf{A} is nonnegative and irreducible with spectral radius less than unity, we have $\lim_{t \rightarrow \infty} \mathbf{A}^t = 0$ and hence $\lim_{t \rightarrow \infty} X_t = \lim_{t \rightarrow \infty} Y_t = \lim_{t \rightarrow \infty} Z_t = 0$. As a result, all solutions of (2.1) converge to E_0 and E_0 is globally asymptotically stable.

Suppose now $R_0 > 1$. It is clear that E_0 is unstable by the above analysis. We first verify that E_1 is locally asymptotically stable. The linearization of (2.1) with respect to E_1 yields the following Jacobian

matrix $J(E_1)$:

$$J(E_1) = \begin{pmatrix} 0 & 0 & b \\ J_{21} & 0 & 0 \\ 0 & J_{32} & J_{33} \end{pmatrix},$$

where $J_{21} = s'_1(\bar{x})\bar{x} + s_1(\bar{x})$, $J_{32} = s'_2(\bar{y})\bar{y} + s_2(\bar{y})$, and $J_{33} = s'_3(\bar{z})\bar{z} + s_3(\bar{z})$. The eigenvalues λ of $J(E_1)$ satisfy $p_1(\lambda) = \lambda^3 - J_{33}\lambda^2 - bJ_{21}J_{32} = 0$. In the following we shall verify the three Jury conditions [2]: $p_1(1) > 0$, $p_1(-1) < 0$, and $1 - b^2J_{21}^2J_{32}^2 - |bJ_{33}J_{21}J_{32}| > 0$.

Observe that $J_{21} > 0$, $J_{32} > 0$, and $J_{33} > 0$ by our assumptions of (H1). Since \bar{z} satisfies (2.3), $\bar{x} = b\bar{z}$, and $\bar{y} = s_1(\bar{x})\bar{x}$, we have by (2.3) that

$$1 = bs_2(\bar{y})s_1(\bar{x}) + s_3(\bar{z}). \tag{2.7}$$

Substituting the above expression of 1 in $p_1(1) = 1 - J_{33} - bJ_{21}J_{32}$ yields

$$p_1(1) = -s'_3(\bar{z})\bar{z} - bs'_1(\bar{x})s_2(\bar{y})\bar{x} - bs'_2(\bar{y})\bar{y}[s'_1(\bar{x})\bar{x} + s_1(\bar{x})] > 0.$$

It is also clear that

$$p_1(-1) = -1 - J_{33} - bJ_{21}J_{32} < 0$$

as $J_{21} > 0$, $J_{32} > 0$, and $J_{33} > 0$. We proceed to verify the last inequality $1 - b^2J_{21}^2J_{32}^2 - |bJ_{33}J_{21}J_{32}| > 0$, which is equivalent to $B := 1 - b^2J_{21}^2J_{32}^2 - bJ_{21}J_{32}J_{33} > 0$. For notational convenience, we rewrite $s_1(\bar{x})$ by s_1 , $s_2(\bar{y})$ by s_2 and $s_3(\bar{z})$ by s_3 . Replacing 1 by the square of the right hand side of (2.3), i.e.,

$$1 = b^2s_1^2s_2^2 + 2bs_1s_2s_3 + s_3^2,$$

then

$$B = b^2s_1^2s_2^2 + 2bs_1s_2s_3 + s_3^2 - b^2J_{21}^2J_{32}^2 - bJ_{21}J_{32}J_{33}. \tag{2.8}$$

Notice $b^2s_1^2s_2^2 - b^2J_{21}^2J_{32}^2 = [bs_1s_2 + bJ_{21}J_{32}][bs_1s_2 - bJ_{21}J_{32}]$, where $bs_1s_2 + bJ_{21}J_{32} > 0$, and $bs_1s_2 - bJ_{21}J_{32} = -bs'_1\bar{x}(s'_2\bar{y} + s_2) - bs_1s'_2\bar{y} > 0$. Furthermore, $2bs_1s_2s_3 + s_3^2 - bJ_{21}J_{32}J_{33} = 2bs_1s_2s_3 + s_3^2 - bJ_{21}J_{32}s'_3\bar{z} - bJ_{21}J_{32}s_3$. The only negative terms in the above expression are

$$-bs'_1s'_2s_3\bar{x}\bar{y} \text{ and } -bs_1s_2s_3,$$

where $-bs_1s_2s_3$ can be cancelled out by one of the $2bs_1s_2s_3$ in (2.8) and $-bs'_1s'_2s_3\bar{x}\bar{y}$ can be combined with the positive term $-bs'_1s_3[s'_2\bar{y} + s_2]\bar{x} > 0$. This proved that E_1 is locally asymptotically stable.

To show that E_1 is globally attracting in the interior of \mathbb{R}_+^3 , we apply Theorem 2.1. Notice system (2.1) can be converted into the following third order scalar difference equation:

$$z_{t+3} = s_2(s_1(bz_t)bz_t)s_1(bz_t)bz_t + s_3(z_{t+2})z_{t+2}. \tag{2.9}$$

Since $ba_1a_2 + a_3 > 1$, (2.9) has a unique positive steady state \bar{z} . It is sufficient to prove that \bar{z} is globally attracting for (2.9) in $(0, \infty)$. Let

$$g(x, y, z) = s_2(s_1(bx)bx)s_1(bx)bx + s_3(z)z.$$

Then

$$\frac{\partial g}{\partial x} = b[s'_1(bx)bx + s_1(bx)][s_2(s_1(bx)bx) + s'_2(s_1(bx)bx)s_1(bx)bx] > 0,$$

$$\frac{\partial g}{\partial y} = 0 \text{ and } \frac{\partial g}{\partial z} = s'_3(z)z + s_3(z) > 0$$

for all $x > 0, y > 0, z > 0$. Moreover,

$$(z - \bar{z})[g(z, z, z) - z] = (z - \bar{z})[bs_2(s_1(bz)bz)s_1(bz) + s_3(z) - 1]z < 0$$

for $z > 0$ and $z \neq \bar{z}$ by (2.3). Hence \bar{z} is globally attracting for (2.9) in $(0, \infty)$ by Theorem 2.1 and consequently E_1 is globally attracting for (2.1). This completes the proof. ■

2.2. Seasonal breeding

In this subsection we assume that breeding is seasonal where the function b_t in (2.1) is periodic with period two. Specifically, we set $b_0 = 0, b_1 = \hat{b} > 0, b_2 = 0, b_3 = \hat{b}, \dots$. Let $(x_0, y_0, z_0) \in \mathbb{R}_+^3 \setminus \{0, 0, 0\}$ be given. It is clear that $(x_t, y_t, z_t) \in \mathbb{R}_+^3 \setminus \{0, 0, 0\}$ for $t > 0$. Moreover, $x_1 = 0, y_1 = s_1(x_0)x_0, z_1 = s_2(y_0)y_0 + s_3(z_0)z_0, x_2 = \hat{b}z_1, y_2 = 0$ and $z_2 = s_2(y_1)y_1 + s_3(z_1)z_1$. Therefore, if (x_0, y_0, z_0) is a part of a 2-cycle, then we have $x_2 = x_0, y_2 = y_0 = 0$ and $z_2 = z_0 = s_2(s_1(x_0)x_0)s_1(x_0)x_0 + s_3(s_3(z_0)z_0)s_3(z_0)z_0$. As a result, if $z_0 \neq 0$, then z_0 must satisfy

$$1 = s_2(s_1(\hat{b}s_3(z)z)\hat{b}s_3(z)z)s_1(\hat{b}s_3(z)z)\hat{b}s_3(z) + s_3(s_3(z)z)s_3(z). \tag{2.10}$$

Let

$$h(z) = \hat{b}s_3(z)z.$$

Then $h(0) = 0, \lim_{z \rightarrow \infty} h(z) < \infty$ and $h'(z) > 0$ for $z \geq 0$ by (H1). Let $H(z)$ denote the right hand side of (2.10) and $X = s_1(h(z))h(z)$. Then

$$H(0) = \hat{b}a_1a_2a_3 + a_3^2, \lim_{z \rightarrow \infty} H(z) = 0$$

and

$$\begin{aligned} H'(z) &= s'_2(X)s_1(h(z))\hat{b}s_3(z)[s'_1(h(z))h(z) + s_1(h(z))]h'(z) \\ &\quad + s_2(X)s'_1(h(z))\hat{b}s_3(z)h'(z) + \hat{b}s_2(X)s_1(h(z))\hat{b}s'_3(z) \\ &\quad + s'_3(s_3(z)z)s_3(z)[s'_3(z)z + s_3(z)] + s_3(s_3(z)z)s'_3(z) < 0, \end{aligned}$$

for all $z \geq 0$ as $h' > 0$ and s_i satisfies (H1) for $i = 1, 2, 3$. We conclude that (2.10) has a positive solution z^* if and only if

$$\hat{b}a_1a_2a_3 + a_3^2 > 1. \tag{2.11}$$

Condition (2.11) is equivalent to

$$\hat{R}_0 := \frac{\hat{b}a_1a_2a_3}{1 - a_3^2} > 1, \tag{2.12}$$

where \hat{R}_0 is the inherent net reproductive number for the seasonal population. Therefore, (2.1) has a unique 2-cycle $\{(x^*, 0, z^*), (0, s_1(x^*)x^*, s_3(z^*)z^*)\}$ if and only if (2.12) holds, where z^* satisfies (2.10) and

$$x^* = \hat{b}s_3(z^*)z^*.$$

Theorem 2.3 *If $\hat{R}_0 < 1$, then $E_0 = (0, 0, 0)$ is globally asymptotically stable for (2.1).*

Proof. We first show that E_0 is globally attracting by using a simple comparison method. Observe that $x_{2t+1} = 0$ for $t \geq 0$ and $y_{2t} = 0$ for $t \geq 1$. Also

$$y_{2t+1} \leq a_1x_{2t}, x_{2t} \leq \hat{b}z_{2t-1}, \text{ and } z_{2t+1} \leq a_3z_{2t}$$

imply

$$x_{2t+2} \leq \hat{b}z_{2t+1} \leq \hat{b}a_3z_{2t} \text{ and } z_{2t+2} \leq a_2y_{2t+1} + a_3z_{2t+1} \leq a_1a_2x_{2t} + a_3^2z_{2t},$$

i.e.,

$$x_{2t+2} \leq \hat{b}a_3z_{2t} \text{ and } z_{2t+2} \leq a_1a_2x_{2t} + a_3^2z_{2t}$$

for $t \geq 1$. Letting $n + i = 2(t + i)$ for $i \geq 0$, consider the following linear system of difference equations:

$$\begin{aligned} A_{n+1} &= \hat{b}a_3B_n \\ B_{n+1} &= a_1a_2A_n + a_3^2B_n \end{aligned}$$

with $A_1 = x_2$ and $B_1 = z_2$, i.e.,

$$\begin{pmatrix} A_{n+1} \\ B_{n+1} \end{pmatrix} = \begin{pmatrix} 0 & \hat{b}a_3 \\ a_1a_2 & a_3^2 \end{pmatrix} \begin{pmatrix} A_n \\ B_n \end{pmatrix}.$$

The eigenvalues of the above coefficient matrix satisfy

$$\lambda^2 - a_3^2\lambda - \hat{b}a_1a_2a_3 = 0.$$

It is clear that $-\hat{b}a_1a_2a_3 < 1$, and $a_3^2 < 1 - \hat{b}a_1a_2a_3$ under the assumption $\hat{R}_0 < 1$. It follows that $\lim_{n \rightarrow \infty} A_n = \lim_{n \rightarrow \infty} B_n = 0$. Therefore $\lim_{t \rightarrow \infty} x_{2t+2} = \lim_{t \rightarrow \infty} z_{2t+2} = 0$ and as a result, $\lim_{t \rightarrow \infty} y_{2t+1} \leq a_1 \lim_{t \rightarrow \infty} x_{2t} = 0$ and $\lim_{t \rightarrow \infty} z_{2t+1} \leq a_3 \lim_{t \rightarrow \infty} z_{2t} = 0$. We conclude that E_0 is globally attracting. It remains to show that E_0 is locally asymptotically stable.

Since system (2.1) is periodic with period two, the local stability of E_0 depends on the product of the matrices [3]:

$$\begin{pmatrix} 0 & 0 & 0 \\ a_1 & 0 & 0 \\ 0 & a_2 & a_3 \end{pmatrix} \begin{pmatrix} 0 & 0 & \hat{b} \\ a_1 & 0 & 0 \\ 0 & a_2 & a_3 \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & a_1\hat{b} \\ a_1a_2 & a_2a_3 & a_3^2 \end{pmatrix}.$$

Denote the resulting product matrix by J_0 . Then the eigenvalues of J_0 are 0 and eigenvalues of \hat{J}_0 , where

$$\hat{J}_0 = \begin{pmatrix} 0 & a_1\hat{b} \\ a_2a_3 & a_3^2 \end{pmatrix}.$$

Since $tr \hat{J}_0 = a_3^2$ and $det \hat{J}_0 = -\hat{b}a_1a_2a_3$, we see that $|tr \hat{J}_0| < 1 + det \hat{J}_0 < 2$. Therefore all the eigenvalues of J_0 have modulus less than 1. Hence E_0 is locally asymptotically stable and thus E_0 is globally asymptotically stable. ■

Suppose now $\hat{R}_0 > 1$. Then it follows from the proof of Theorem 2.3 that E_0 is unstable. Moreover, (2.1) has a unique 2-cycle:

$$\{(x^*, 0, z^*), (0, s_1(x^*)x^*, s_3(z^*)z^*)\},$$

where z^* satisfies (2.10) and $x^* = \hat{b}s_3(z^*)z^*$. In the following we show that the 2-cycle is globally asymptotically stable.

Theorem 2.4 *If $\hat{R}_0 > 1$, then the 2-cycle is globally asymptotically stable for system (2.1) in the interior of \mathbb{R}_+^3 .*

Proof. We first prove that the 2-cycle is locally asymptotically stable. Recall that its stability depends on the eigenvalues of the product of the matrices [3]:

$$\begin{pmatrix} 0 & 0 & 0 \\ s'_1(x^*)x^* + s_1(x^*) & 0 & 0 \\ 0 & a_2 s'_3(z^*)z^* + s_3(z^*) & 0 \end{pmatrix} \begin{pmatrix} 0 & 0 & \hat{b} \\ a_1 & 0 & 0 \\ 0 & a_{32} & a_{33} \end{pmatrix},$$

where

$$a_{32} = s'_2(s_1(x^*)x^*)s_1(x^*)x^* + s_2(s_1(x^*)x^*)$$

and

$$a_{33} = s'_3(s_3(z^*)z^*)s_3(z^*)z^* + s_3(s_3(z^*)z^*).$$

Denote the resulting product matrix by J_1 . Then

$$J_1 = \begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & A \\ a_1a_2 & B & C \end{pmatrix},$$

where

$$A = \hat{b}[s'_1(x^*)x^* + s_1(x^*)] > 0, B = [s'_3(z^*)z^* + s_3(z^*)]a_{32}$$

and

$$C = [s'_3(z^*)z^* + s_3(z^*)]a_{33}.$$

The eigenvalues of J_1 consist of 0 and the roots of $\lambda^2 - C\lambda - AB = 0$. For the 2-cycle to be locally asymptotically stable, it is necessary and sufficient that $|C| < 1 - AB < 2$. Observe that $a_{32} > 0, a_{33} > 0$ by (H1) and we have $AB > 0$. Thus $1 - AB < 2$ is trivially true. It remains to verify $|C| < 1 - AB$ which reduces to $C < 1 - AB$ as $C > 0$. Using $x^* = \hat{b}s_3(z^*)z^*$, abbreviate $s_i(z^*)$ by s_i and $s'_i(z^*)$ by s'_i , and rewrite z^* by $x, C < 1 - AB$ is equivalent to

$$\begin{aligned} &1 - \hat{b}[s'_1(\hat{b}s_3x)\hat{b}s_3x + s_1(\hat{b}s_3x)](s'_3x + s_3)[s'_2(s_1(\hat{b}s_3x)\hat{b}s_3x)s_1(\hat{b}s_3x)\hat{b}s_3x \\ &+ s_2(s_1(\hat{b}s_3x)\hat{b}s_3x)] - (s'_3x + s_3)[s'_3(s_3x)s_3x + s_3(s_3x)] > 0. \end{aligned}$$

The only negative terms in the above expression are

$$-\hat{b}s_1(\hat{b}s_3x)s_3s_2(s_1(\hat{b}s_3x)\hat{b}s_3x) - s_3s_3(s_3x)$$

and

$$-\hat{b}s'_1(\hat{b}s_3x)\hat{b}s_3xs'_3xs_2(s_1(\hat{b}s_3x)\hat{b}s_3).$$

Replacing 1 by the right hand side of the equilibrium equation (2.10), we see that the first two negative terms can be canceled out by the terms in the equilibrium equation while the last negative term can be combined with $-\hat{b}s'_1(\hat{b}s_3x)\hat{b}s_3xs_3s_2(s_1(\hat{b}s_3x)\hat{b}s_3x)$ to yield a positive term

$$-\hat{b}s'_1(\hat{b}s_3x)\hat{b}s_3xs_2(s_1(\hat{b}s_3x)\hat{b}s_3x)[s'_3x + s_3].$$

Therefore $C < 1 - AB$ holds and the 2-cycle is locally asymptotically stable.

It remains to show that the 2-cycle is globally attracting in the interior of \mathbb{R}_+^3 . The proof is similar to the proof of Theorem 2.2. Let $(x_0, y_0, z_0) \in \mathbb{R}_+^3 \setminus \{(0, 0, 0)\}$ be given. Observe that $x_{2t+1} = 0$ for $t \geq 0$ and $y_{2t} = 0$ for $t \geq 1$. It follows that for $t \geq 1$

$$x_{2t+2} = bs_3(z_{2t})z_{2t}$$

and

$$z_{2t+2} = s_2(s_1(x_{2t})x_{2t})s_1(x_{2t})x_{2t} + s_3(s_3(z_{2t})z_{2t})s_3(z_{2t})z_{2t}.$$

Let $n + i = 2(t + i)$ for $i \geq 0$. We obtain the following system of first order difference equations:

$$\begin{aligned} x_{n+1} &= bs_3(z_n)z_n \\ z_{n+1} &= s_2(s_1(x_n)x_n)s_1(x_n)x_n + s_3(s_3(z_n)z_n)s_3(z_n)z_n \end{aligned} \tag{2.13}$$

for $n \geq 1$. The system is equivalent to the following second order scalar equation:

$$\begin{aligned} z_{n+2} &= s_2(s_1(\hat{b}s_3(z_n)z_n)\hat{b}s_3(z_n)z_n)s_1(\hat{b}s_3(z_n)z_n)\hat{b}s_3(z_n)z_n \\ &\quad + s_3(s_3(z_{n+1})z_{n+1})s_3(z_{n+1})z_{n+1}. \end{aligned} \tag{2.14}$$

Let the right hand side of (2.14) be denoted by $f(x, y)$, i.e.,

$$f(x, y) = s_2(s_1(\hat{b}s_3(x)x)\hat{b}s_3(x)x)s_1(\hat{b}s_3(x)x)\hat{b}s_3(x)x + s_3(s_3(y)y)s_3(y)y$$

and $Y = s_1(\hat{b}s_3(x)x)\hat{b}s_3(x)x$. Then

$$\frac{\partial f}{\partial x} = [s'_2(Y)s_1(\hat{b}s_3(x)x)\hat{b}s_3(x)x + s_2(Y)] \times$$

$$\{s'_1(\hat{b}s_3(x)x)\hat{b}[s'_3(x)x + s_3(x)]\hat{b}s_3(x)x + s_1(\hat{b}s_3(x)x)\hat{b}[s'_3(x)x + s_3(x)]\} > 0.$$

Similarly,

$$\frac{\partial f}{\partial y} = s'_3(s_3(y)y)s_3(y)y[s'_3(y)y + s_3(y)] + s_3(s_3(y)y)[s'_3(y)y + s_3(y)] > 0.$$

Furthermore, (2.14) has a unique interior steady state z^* as $\hat{b}a_1a_2a_3 + a_3^2 > 1$. It is clear that

$$(u - z^*)[f(u, u) - u] = (u - z^*)[s_2(s_1(\hat{b}s_3(u)u)\hat{b}s_3(u)u)s_1(\hat{b}s_3(u)u)\hat{b}s_3(u) + s_3(s_3(u)u)s_3(u) - 1]u < 0.$$

It follows from Theorem 2.1 that $\lim_{n \rightarrow \infty} z_n = z^*$. Hence $\lim_{t \rightarrow \infty} x_{2t} = x^*$ and $\lim_{t \rightarrow \infty} y_{2t+1} = s_1(x^*)x^*$. That is, the even subsequence (x_{2t}, y_{2t}, z_{2t}) of the solution converges to $(x^*, 0, z^*)$ and the odd subsequence $(x_{2t+1}, y_{2t+1}, z_{2t+1})$ converges to $(0, s_1(x^*)x^*, s_3(z^*)z^*)$. Since $(x_0, y_0, z_0) \neq (0, 0, 0)$ is arbitrary, we see that the 2-cycle is globally attracting in the interior of \mathbb{R}_+^3 . Therefore the 2-cycle is globally asymptotically stable for (2.13) in the interior of \mathbb{R}_+^3 . ■

2.3. Comparison between continuous and seasonal breeding

For the rest of this section we assume that in a continuous or seasonal breeding population an adult reproduces the same number of juveniles in one year period. Thus, we let $\hat{b} = 2b$. We are interested to see for what values of b is continuous breeding (seasonal breeding) advantageous in terms of maximizing the average number of adults over a one year period.

a) Persistence of population with continuous reproduction

Since $\hat{b} = 2b$, then Theorem 2.2 and Theorem 2.4 require respectively that

$$b > \frac{1 - a_3}{a_1a_2}, \quad \text{and} \quad b > \frac{1 - a_3^2}{2a_1a_2a_3}.$$

Since (recall that $a_3 < 1$)

$$\frac{1 - a_3}{a_1a_2} < \frac{1 - a_3^2}{2a_1a_2a_3}$$

it follows that Theorem 2.2 applies, and hence there exists a survival interior steady state on interval of average birth rates b , namely

$$\left(\frac{1 - a_3}{a_1a_2}, \frac{1 - a_3^2}{2a_1a_2a_3}\right),$$

for which the population in the periodic case goes extinct. This shows that for this range of birth rates continuous reproduction is advantageous.

b) Comparison of the breeding adults for periodic and constant birth rates

Differentiate both sides of equilibrium equation (2.3) with respect to b yields $\frac{d\bar{z}}{db} = \bar{A}/\bar{B}$, where

$$\bar{A} = -[s_1(bz) + s_1'(bz)bz][s_2(s_1(bz)bz) + s_2'(s_1(bz)bz)s_1(bz)bz] < 0$$

and

$$\bar{B} = bs_2(s_1(bz)bz)bs_1'(bz) + s_3'(z) + b^2s_1(bz)s_2'(s_1(bz)bz)[s_1'(bz)bz + s_1(bz)] < 0.$$

Therefore $\frac{d\bar{z}}{db} > 0$ for $b \geq \frac{1 - a_3}{a_1a_2}$. Similarly, letting $\hat{b} = 2b$ in (2.10) and differentiate both sides of (2.10)

with respect to b resulting in $\frac{dz^*}{db} = C^*/D^*$, where

$$D^* = s_2'(X^*)s_1(2bs_3(z)z)2bs_3(z)2b[s_3'(z)z + s_3(z)][s_1(2bs_3(z)z) + s_1'(2bs_3(z)z)2bs_3(z)]$$

$$+ s_2(X^*)2bs_3(z)s_1'(2bs_3(z)z)2b[s_3'(z)z + s_3(z)]$$

$$+ s_2(X^*)s_1(2bs_3(z)z)2bs_3'(z) + s_3'(s_3(z)z)s_3(z)[s_3'(z)z + s_3(z)] + s_3(s_3(z)z)s_3'(z) < 0$$

and

$$C^* = -s_2'(X^*)s_1(2bs_3(z)z)2bs_3(z)\{s_1'(2bs_3(z)z)2bs_3(z)z2s_3(z)z + s_1(2bs_3(z)z)2s_3(z)z\}$$

$$+ s_2(X^*)2bs_3(z)s_1'(2bs_3(z)z)2s_3(z)z + s_2(X^*)s_1(2bs_3(z)z)2s_3(z) < 0,$$

with $X^* = s_1(2bs_3(z)z)2bs_3(z)z$. Therefore $\frac{dz^*}{db} > 0$ for $b \geq \frac{1 - a_3^2}{2a_1a_2a_3}$. Since $\lim_{b \rightarrow (\frac{1 - a_3^2}{2a_1a_2a_3})^+} z^*(b) = 0$, we conclude that when $b > \frac{1 - a_3^2}{2a_1a_2a_3}$ but sufficiently close to $\frac{1 - a_3^2}{2a_1a_2a_3}$, the constant birth rate has a higher breeding adult equilibrium value, i.e., $\bar{z} > z^* > \frac{z^* + s_3(z^*)z^*}{2}$. Therefore, constant birth rate is more advantageous.

We provide numerical results verifying our theoretical conclusions. In Figure 1, we choose a set of parameters that results in the continuous birth population converging to a positive equilibrium while the population with period-two birth rate going to extinction. In this case $R_0 = 1.0125 > 1$ while $\hat{R}_0 = 0.9 < 1$. Increasing the birth rate, we present the results in Figure 2. In this case $R_0 = 1.5 > 1$ while $\hat{R}_0 = 1.333 > 1$. Thus, both populations survive. One converges to a positive equilibrium and the other converges to a positive 2-cycle. Clearly, the equilibrium value for adults z_t is larger than the average 2-cycle. Thus continuous reproduction is advantageous for this birth rate value.

3. Concluding Remarks

In this paper we have shown that for the three-stage discrete-time population model (2.1) a periodic birth rate with period two is deleterious for low birth rates as it will result in smaller average of adults in comparison with a continuous birth rate even though in both cases each adult reproduces the same number of juveniles per year. Numerical simulations of model (2.1) suggest that this conclusion remains true for large birth rates. This is in contrast with the result for a two stage discrete model which shows that when birth rates are low seasonal reproduction is advantageous while when birth rates are high continuous breeding is advantageous. The reason for this is that for a juvenile to become a breeding adult it has to survive two time units (two stages). Thus, a period two birth rate is not enough to compensate for this. Therefore, the seasonally breeding population needs to concentrate its breeding over a shorter time period. However, this period cannot be too short. If for example, the seasonal population resorts to a period three birth rate then numerical simulations of model (2.1) suggest that the conclusion is similar to that of the two stage model with period two birth rate [1]. That is for low birth rates the three stage model with period three birth rate results in higher adult averages than the continuous breeding population (see Figure 3 for an example).

Similarly if the birth rate has period four then seasonal breeding results in higher adult averages for low birth rates. However, if the birth rate has period five then our numerical simulations suggest that seasonal breeding is always deleterious. Thus, the conclusion is similar to a period two birth rate.

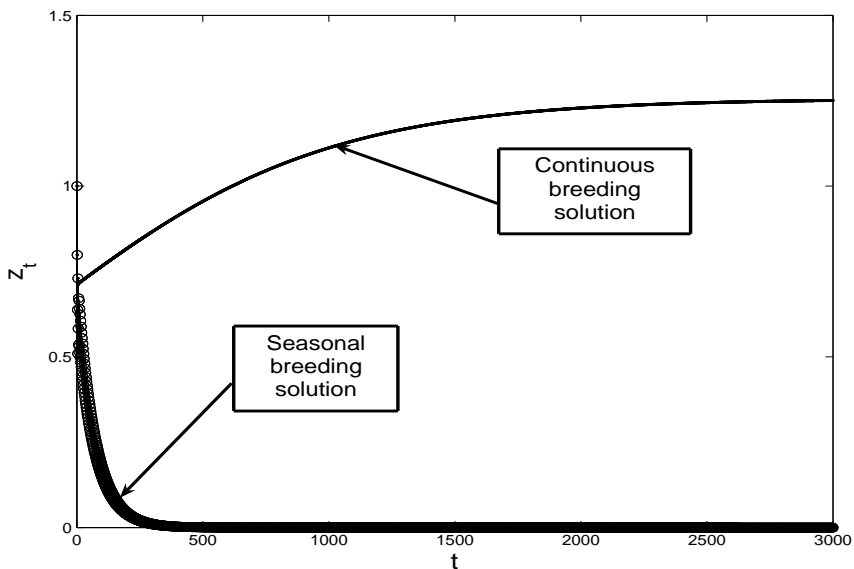


Figure 1. A comparison between continuous and seasonal breeding with period two birth rate for model (2.1). The survivorship functions are $s_1(x) = a_1/(1 + k_1x)$, $s_2(y) = a_2/(1 + k_2y)$, $s_3(z) = a_3/(1 + k_3z)$ with parameter values $a_1 = 0.3$, $a_2 = 0.5$, $a_3 = 0.8$, $k_1 = 0.001$, $k_2 = 0.0015$, $k_3 = 0.002$ and $b = 1.35$ and $\tilde{b} = 2b = 2.7$. The initial conditions are given by $x_0 = 0$, $y_0 = 0$, and $z_0 = 1$.

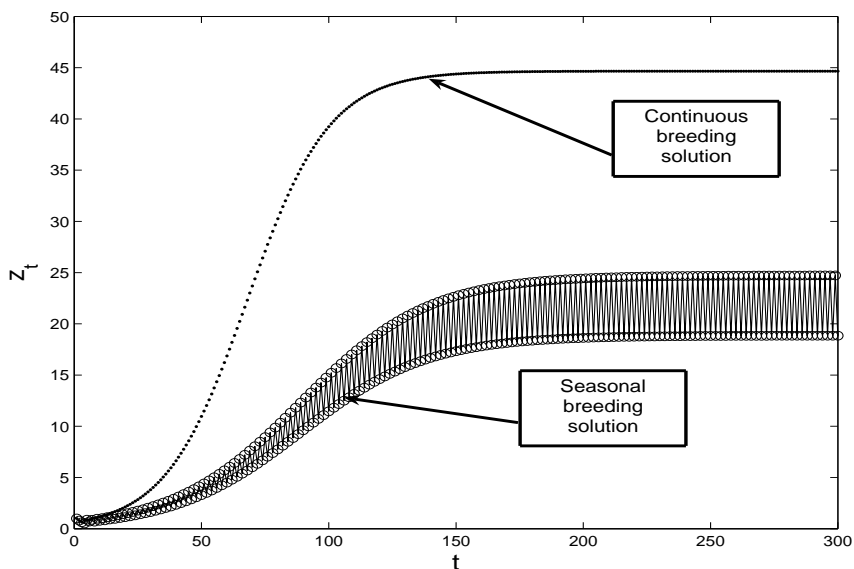


Figure 2. A comparison between continuous and seasonal breeding with period two birth rate for model (2.1). The survivorship functions are $s_1(x) = a_1/(1 + k_1x)$, $s_2(y) = a_2/(1 + k_2y)$, $s_3(z) = a_3/(1 + k_3z)$ with parameter values $a_1 = 0.3$, $a_2 = 0.5$, $a_3 = 0.8$, $k_1 = 0.001$, $k_2 = 0.0015$, $k_3 = 0.002$ and $b = 2$ and $\tilde{b} = 2b = 4$. The initial conditions are given by $x_0 = 0$, $y_0 = 0$, and $z_0 = 1$.

If the population with three stages have a seasonal breeding of period three, i.e., $b_0 = 0$, $b_1 = 0$, $b_2 = \tilde{b} > 0$, $b_3 = 0$, $b_4 = 0$ and $b_5 = \tilde{b} \dots$, then one can show that by defining $\tilde{R}_0 := \frac{ba_1a_2}{1 - a_3^3}$ the inherent net reproductive number for this population, a unique 3-cycle exists provided that $\tilde{R}_0 > 1$. We conjecture that this 3-cycle is globally attracting provided that $\tilde{R}_0 > 1$. While if $\tilde{R}_0 < 1$ then the population becomes extinct. These results should follow by using a similar argument as in Section 2 (which involves lengthy computations). Thus, if $\tilde{b} = 3b$ (i.e., each individual reproduces in one season the same number of juveniles

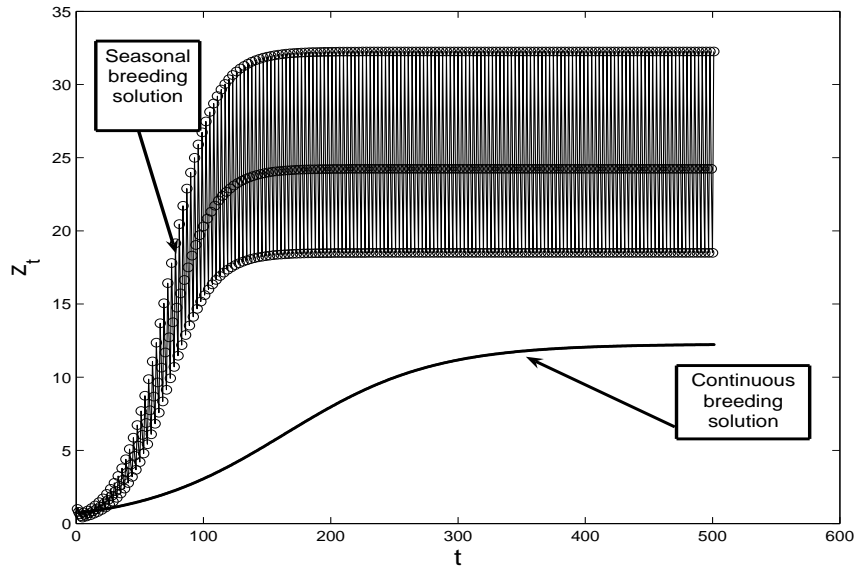


Figure 3. A comparison between continuous and seasonal breeding with period three birth rate for model (2.1). The survivorship functions are $s_1(x) = a_1/(1 + k_1x)$, $s_2(y) = a_2/(1 + k_2y)$, $s_3(z) = a_3/(1 + k_3z)$ with parameter values $a_1 = 0.3$, $a_2 = 0.5$, $a_3 = 0.8$, $k_1 = 0.001$, $k_2 = 0.0015$, $k_3 = 0.002$ and $b = 1.5$ and $\bar{b} = 3b = 4.5$. The initial conditions are given by $x_0 = 0$, $y_0 = 0$, and $z_0 = 1$.

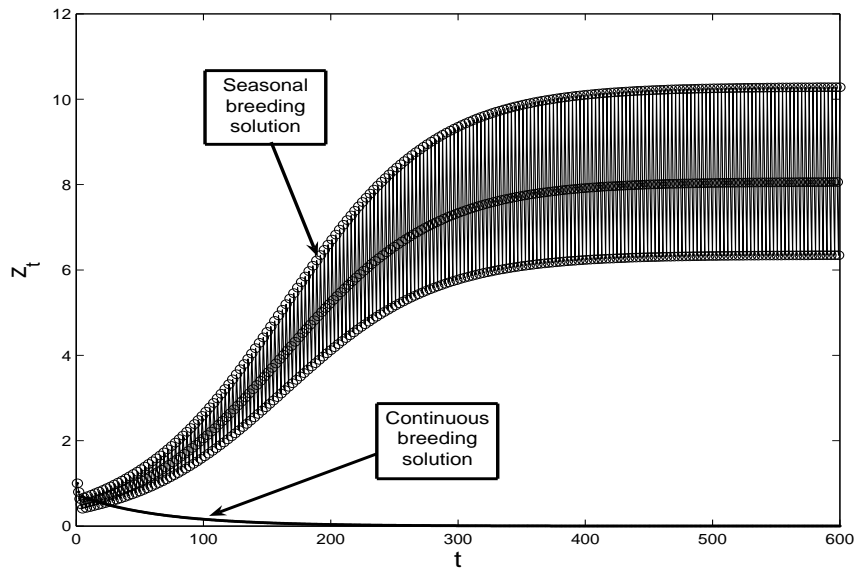


Figure 4. A comparison between continuous and seasonal breeding with period three birth rate for model (2.1). The survivorship functions are $s_1(x) = a_1/(1 + k_1x)$, $s_2(y) = a_2/(1 + k_2y)$, $s_3(z) = a_3/(1 + k_3z)$ with parameter values $a_1 = 0.3$, $a_2 = 0.5$, $a_3 = 0.8$, $k_1 = 0.001$, $k_2 = 0.0015$, $k_3 = 0.002$ and $b = 1.2$ and $\bar{b} = 3b = 3.6$. The initial conditions are given by $x_0 = 0$, $y_0 = 0$, and $z_0 = 1$.

as an individual who reproduces continuously breeds in an entire year) then both populations persist if:

$$b > \frac{1 - a_3}{a_1 a_2}, \quad \text{and} \quad b > \frac{1 - a_3^3}{3a_1 a_2}.$$

However, since (recall that $a_3 < 1$)

$$\frac{1 - a_3}{a_1 a_2} > \frac{1 - a_3^3}{3a_1 a_2}$$

then for

$$\frac{1 - a_3^3}{3a_1a_2} < b < \frac{1 - a_3}{a_1a_2}$$

the seasonal population persists while the continuous breeding population goes to extinction. In Figure 4 we present a numerical example for this case. Here, the inherent net reproductive numbers are $R_0 = 0.9$ and $\tilde{R}_0 = 1.1066$.

Acknowledgement: The work of A.S. Ackleh is partially supported by the National Science Foundation under grant # DUE-0531915.

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