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A discrete two-stage population model: continuous versus seasonal reproduction

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A discrete two-stage model which describes the dynamics of a population where juveniles and adults compete for different resources is developed. A motivating example is the green tree frog (*Hyla cinerea*) where tadpoles and adult frogs feed on separate resources. First, continuous breeding is assumed and the asymptotic behavior of the resulting autonomous model is fully analyzed. It is shown that the unique interior equilibrium is globally asymptotically stable when the inherent net reproductive number is greater than one. However, when the inherent net reproductive number is less than one, the population becomes extinct. Then a seasonal breeding described by a periodic birth rate with period 2 is assumed. It is proved that for this nonautonomous model a period two solution is globally asymptotically stable when the inherent net reproductive number is greater than one and when the inherent net reproductive number is less than one the population becomes extinct. Finally, the advantage (in terms of maximizing the number of juveniles and adults in the population over a fixed time period) of having a seasonal breeding is studied by comparing the average of the juvenile and adult numbers of the periodic solution for the nonautonomous model to the equilibrium solution of the autonomous model. Our results indicate that for high birth rates the equilibrium of the autonomous model is higher than the average of the two cycle solution. Therefore, all other factors being equal, seasonal breeding appears to be deleterious to populations with high birth rates. However, for low birth rates seasonal breeding can be beneficial. It is also shown that for a range of birth rates the nonautnomous model is persistent while the solution to the autonomous model goes to extinction.

Keywords: Discrete two-stage model; Seasonal versus continuous reproduction; Inherent net reproductive number; Global stability

1. Introduction

Many populations engage in seasonal breeding versus continuous breeding. The cost of winter breeding, presumably, overweigh the benefits. This hypothesis is well accepted [3,4]. Energy availability in the winter is generally low. Therefore, many animal populations restrict their reproductive activities to specific times of the year when food is abundant and survival and reproductive success is high [20]. In addition to seasonal breeding, many populations also have their juveniles and adults compete for different resources. Anurans are a good example of such populations. They have a bi-phasic lifestyle, living on land and in water at different stages in their life cycle. Tadpoles feed on algae while frogs feeds on crickets, wax worms, mealworms, small silkworms, red worms, moths, and flies. Therefore, in this population intra-competition within each stage occurs.

In this paper, we develop a two-stage discrete model which describes the dynamics of a seasonally breeding population with stage specific competition. We fully analyze this model when breeding is continuous and when breeding is seasonal (Section 2). In particular, we show

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that the continuous breeding model has a globally asymptotically stable equilibrium. While we prove that the model with seasonal breeding has a globally asymptotically stable periodic solution. We then ask the following question: all other factors being equal, is seasonal reproduction (assuming within a season an adult individual reproduce the same number of juveniles as in continuous breeding during a year) advantageous in terms of maximizing the average number of juvenile and adult individuals over a fixed time period? To answer this question we compare the equilibrium solution to that of the average of the periodic solution. The results show that for a high birth rates the seasonal reproduction is deleterious. While for low birth rates seasonal breeding is beneficial. Also our results indicate that for a range birth rates seasonal reproduction is advantageous in the sense that for such birth rates the autonomous population becomes extinct while the seasonal population is uniformly persistent with respect to the origin.

2. Model development and analysis

This work is motivated by our interdisciplinary project for understanding the dynamics of the green tree *Hyla cinerea*. In March 2003 we set up a long term monitoring program of this population at ponds located near the USGS National Wetlands Research Center in Lafayette, Louisiana. We have combined statistics and data collected using a mark-recapture technique to obtain population estimates in these ponds (for more details see Ref. [21]). The green tree frog has a tadpole stage of approximately 2 months (55–65 days). Its breeding season varies according to temperature. Within moderate climates the breeding season includes late spring months, early summer and mid-summer months. In warmer, southern environments the breeding season can be as long as March–October. However, our calling data indicate that in these ponds the breeding season is from March to August (6 months).

  Our interest here is to develop a theoretical model which describes the dynamics of a population which is divided into two stages: juveniles and adults and engages in seasonal breeding. To this end, denote by $x(t)$ the number of juveniles at time t and by $y(t)$ the number of adults at time t. We assume that the juvenile stage is less than or equal 6 months and choose the time step equal to the breeding season of 6 months (note that all surviving juveniles move into the adult stage within one time step). Assume that juveniles compete with each other but not with adults and similarly adults compete with each other but not with juveniles. Assume further that Beverton–Holt type function is used to model this competition. Let $b(t)$ be the time-dependent birth rate. We then obtain the following two-stage discrete model:

$$
\begin{cases}
x(t + 1) = b(t)y(t) \\
y(t + 1) = \dfrac{x(t)}{a + k_1 x(t)} + \dfrac{y(t)}{c + k_2 y(t)} \\
(x(0), y(0)) \in \mathbb{R}_+^2 \setminus \{(0,0)\},
\end{cases}
\tag{2.1}
$$

where the parameters a, c, k_1 and k_2 are assumed to be positive. Moreover, since $1/(a + k_1 x(t))$ represents the 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 assume $a > 1$ for the model to be biologically meaningful. Similarly, we assume that the parameter $c > 1$. We define $s_j = 1/a$,

the inherent survivorship fraction of juveniles, and $s_a = 1/c$, the inherent survivorship fraction of adults.

We are interested in theoretically understanding whether seasonal reproduction is advantageous or not. Therefore, we will analyze the model equation (2.1) for two cases. The first one is assuming that $b(t) = b$ a positive constant and the second case is $b(t)$ being periodic with period 2. Before we start analyzing the model equation (2.1) we recall the following result (see Theorem 1.10 in Ref. [15]) which will be used in the sequel. Consider a $k + 1$ order nonlinear difference equation of the form

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

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 equation* (2.2). *Suppose F satisfies the following two conditions:*

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

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

2.1 Continuous breeding

In this section we consider the model equation (2.1) with continuous breeding. That is we assume throughout this section that in the model equation (2.1) $b(t) = b$, a positive constant. Clearly solutions of system (2.1) remain nonnegative. The system always has a trivial steady state $E_0 = (0, 0)$. The *y*-component of a nontrivial steady state $(\bar{x}, \bar{y})$, $\bar{y} > 0$, must satisfy

$$1 = \frac{b}{a + k_1 by} + \frac{1}{c + k_2 y}. \tag{2.3}$$

Consequently, equation (2.1) has an interior steady state $E_1 = (\bar{x}, \bar{y})$ if and only if

$$\frac{b}{a} + \frac{1}{c} > 1, \tag{2.4}$$

where $\bar{y}$ solves equation (2.3) and $\bar{x} = b\bar{y}$. The interior steady state is unique whenever it exists.

Observe that since $c > 1$ inequality (2.4) is equivalent to

$$\frac{b}{a} \frac{1}{1 - (1/c)} > 1,$$

and the left hand side of the above inequality can be rewritten as

$$\frac{b}{a} \frac{1}{1 - (1/c)} = b/a(1 + (1/c) + (1/c^2) + \cdots) = bs_j + bs_j s_a + bs_j s_a^2 + \cdots.$$

Therefore,

$$\mathcal{R}_0 \equiv \frac{b}{a} \frac{1}{1 - (1/c)}$$

represents the inherent net reproductive number of the population. It is the expected number of juvenile recruits per juvenile per life time. Using Theorem 2.1 the asymptotic dynamics of system (2.1) can be understood and are summarized below.

THEOREM 2.2. *Suppose that $b(t) = b$ for $t = 0, 1, \ldots,$ then we have the following results:*

(a) *If $\mathcal{R}_0 < 1$, then equation (2.1) has only the trivial steady state $E_0 = (0,0)$ which is globally asymptotically stable.*

(b) *If $\mathcal{R}_0 > 1$, then in addition to E_0, equation (2.1) has another equilibrium $E_1 = (\bar{x}, \bar{y})$ which is globally asymptotically stable.*

Proof.

(a) Suppose $\mathcal{R}_0 < 1$. It is clear that equation (2.1) has only the trivial steady state E_0. Linearization of system (2.1) at E_0 yields the following Jacobian matrix

$$J(E_0) = \begin{pmatrix} 0 & b \\ 1/a & 1/c \end{pmatrix}.$$

Since the spectral radius of $J(E_0)$, $((1/c) + \sqrt{(1/c^2) + 4b/a})/2$, is less than 1, and equation (2.1) satisfies inequality (1.22) in Ref. [6], E_0 is globally asymptotically stable by Ref. [6].

(b) Suppose now $\mathcal{R}_0 > 1$. Let $(x(t), y(t))$ be an arbitrary solution of equation (2.1). Notice that

$$y(t) \le \frac{1}{k_1} + \frac{1}{k_2}$$

and

$$x(t) \le b \left(\frac{1}{k_1} + \frac{1}{k_2} \right)$$

for all t large. Hence solutions of equation (2.1) are bounded.

Since $\mathcal{R}_0 > 1$, it follows from an earlier discussion that system (2.1) has two nonnegative equilibria $E_0 = (0, 0)$ and $E_1 = (b\bar{y}, \bar{y})$. The linearization of equation (2.1) at E_1 yields the following Jacobian matrix

$$J(E_1) = \begin{pmatrix} 0 & b \\ \dfrac{a}{(a + k_1 b\bar{y})^2} & \dfrac{c}{(c + k_2\bar{y})^2} \end{pmatrix}.$$

Since $\mathrm{tr} J(E_1) > 0$ and $\det J(E_1) < 0$, to show local asymptotic stability of E_1 it is enough to prove $\mathrm{tr} J(E_1) < \det J(E_1) + 1$ by the Jury conditions [2,11]. Replacing 1 by the right hand side of equation (2.3) evaluated at $y = \bar{y}$, we see that $\mathrm{tr} J(E_1) < \det J(E_1) + 1$ is

equivalent to

$$\frac{c}{(c + k_2\bar{y})^2} - \frac{1}{c + k_2\bar{y}} < \frac{b}{a + k_1 b\bar{y}} - \frac{ab}{(a + k_1 b\bar{y})^2},$$

which is clearly true. Therefore E_1 is locally asymptotically stable.

Furthermore, equation (2.1) is equivalent to the following second order scalar difference equation

$$y(t + 2) = \frac{by(t)}{a + k_1 by(t)} + \frac{y(t + 1)}{c + k_2 y(t + 1)} \tag{2.5}$$

with

$$y(1) = \frac{x(0)}{a + k_1 x(0)} + \frac{y(0)}{c + k_2 y(0)} > 0$$

for a given $(x(0), y(0)) \in \mathbb{R}_+^2 \backslash \{(0,0)\}$. Clearly $\bar{y}$ is a steady state solution of equation (2.5). Let

$$G(u, v) = \frac{bu}{a + k_1 bu} + \frac{v}{c + k_2 v} \quad \text{for} \quad u, v \geq 0.$$

Then $(\partial G/\partial u) > 0$, $(\partial G/\partial v) > 0$ for all $u, v \geq 0$, and

$$(u - \bar{y})[G(u, u) - u] = (u - \bar{y})\left[\frac{b}{a + k_1 bu} + \frac{1}{c + k_2 u} - 1\right]u < 0$$

for all $u > 0, u \neq \bar{y}$ by equation (2.3). Hence solutions of equation (2.5) converge to $\bar{y}$ by Theorem 2.1. As a consequence, solution $(x(t), y(t))$ of equation (2.1) converges to $E_1 = (b\bar{y}, \bar{y})$. This completes the proof of (b) as the solution was arbitrary. $\qquad\square$

Remark. Although from the global asymptotic result it follows that the system is uniformly persistent with respect to the origin, the general theory in [6, Theorem 1.2.1] and [19, Theorem 3] can be applied to system (2.1) to prove uniform persistence.

2.2 Seasonal breeding

In this section we assume that breeding is seasonal. That is we assume that the function $b(t)$ in equation (2.1) is periodic with period 2. Specifically, $b(0) = \hat{b} > 0$, $b(1) = 0$, $b(2) = \hat{b}$, $b(3) = 0$, ... Let $(x(0), y(0)) \in \mathbb{R}_+^2 \backslash \{(0,0)\}$ be given. Then

$$\begin{cases} x(1) = \hat{b}y(0) \\ y(1) = \dfrac{x(0)}{a + k_1 x(0)} + \dfrac{y(0)}{c + k_2 y(0)}, \end{cases}$$

and

$$\begin{cases} x(2) = 0 \\ y(2) = \dfrac{\hat{b}y(0)}{a + k_1 \hat{b}y(0)} + \dfrac{\dfrac{x(0)}{a + k_1 x(0)} + \dfrac{y(0)}{c + k_2 y(0)}}{c + k_2\left(\dfrac{x(0)}{a + k_1 x(0)} + \dfrac{y(0)}{c + k_2 y(0)}\right)}. \end{cases}$$

If the solution $(x(t), y(t))$ is periodic with period 2, we must have

$$
\begin{cases}
x(0) = 0 \\[2ex]
y(0) = \dfrac{\hat{b}y(0)}{a + k_1\hat{b}y(0)} + \dfrac{\dfrac{y(0)}{c + k_2 y(0)}}{c + \dfrac{k_2 y(0)}{c + k_2 y(0)}}.
\end{cases}
$$

If $y(0) > 0$, then $y(0)$ must satisfy

$$
1 = \frac{\hat{b}}{a + k_1 \hat{b} y} + \frac{1}{c^2 + c k_2 y + k_2 y}. \tag{2.6}
$$

Equation (2.6) has a unique positive solution y^* if and only if

$$
\frac{\hat{b}}{a} + \frac{1}{c^2} > 1. \tag{2.7}
$$

In this case, system (2.1) has a unique nontrivial 2-cycle

$$
\left\{ (0, y^*), \left(\hat{b}y^*, \frac{y^*}{c + k_2 y^*} \right) \right\}.
$$

Similar to the autonomous model, equation (2.7) is equivalent to $(\hat{b}/a)(1/(1 - (1/c^2))) > 1$. The left hand side of this inequality can be written as:

$$
\frac{\hat{b}}{a} \frac{1}{1-(1/c^2)} = \hat{b}/a(1 + (1/c^2) + (1/c^4) + \cdots).
$$

Thus, we define

$$
\hat{\mathcal{R}}_0 \equiv \frac{\hat{b}}{a} \frac{1}{1 - (1/c^2)} = \hat{b}s_j + \hat{b}s_j s_a^2 + \hat{b}s_j \left(s_a^2\right)^2 + \cdots
$$

It is the inherent net reproductive number of the population for the periodic birth rate (this is because in order to reproduce repeatedly an adult must suffer two survivorship events with a probability s_a^2). The asymptotic dynamics of system (2.1) (depending on $\hat{\mathcal{R}}_0$) can be summarized below.

THEOREM 2.3. *Suppose that $b(2t) = \hat{b}$, $b(2t + 1) = 0$ for $t = 0, 1, \ldots$, then we have the following results:*

(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 $\{(0, y^*),(\hat{b}y^*, y^*/(c + k_2 y^*))\}$ is globally asymptotically stable.*

Proof. We start by proving (b) first. To this end, suppose $\hat{\mathcal{R}}_0 > 1$. Let $(x(t), y(t))$ be a solution of equation (2.1). Notice that $y(t) > 0$ for $t \geq 1$ and

$$
y(t + 2) = \frac{b(t)y(t)}{a + k_1 b(t)y(t)} + \frac{y(t + 1)}{c + k_2 y(t + 1)}
$$

for $t \geq 0$. Since $x(2t) = 0$ for $t \geq 1$, we have by equation (2.1) that

$$y(2t + 1) = \frac{y(2t)}{c + k_2 y(2t)}$$

and

$$y(2t) = \frac{\hat{b} y(2t - 2)}{a + k_1 \hat{b} y(2t - 2)} + \frac{y(2t - 1)}{c + k_2 y(2t - 1)}$$

for $t \geq 1$. Hence

$$y(2t) = \frac{\hat{b} y(2t - 2)}{a + k_1 \hat{b} y(2t - 2)} + \frac{y(2t - 2)}{c^2 + ck_2 y(2t - 2) + k_2 y(2t - 2)} \tag{2.8}$$

for $t \geq 2$. The above second order difference equation has the nontrivial steady state y^* by the assumption $\hat{\mathcal{R}}_0 > 1$. Since equation (2.8) has the same form as equation (2.5) and $y(2) > 0$, we conclude that solutions of equation (2.8) converge to y^* by Theorem 2.1, i.e. solution $(x(t), y(t))$ of equation (2.1) satisfies $\lim_{t \to \infty} x(2t) = 0$ and $\lim_{t \to \infty} y(2t) = y^*$. Consequently, $\lim_{t \to \infty} x(2t + 1) = \hat{b} y^*$, and since $y(2t + 1) = y(2t)/(x + k_2 y(2t))$ for $t \geq 1$, we have $\lim_{t \to \infty} y(2t + 1) = y^*/(c + k_2 y^*)$. This shows that solutions of equation (2.1) converge to the 2-cycle $\{(0, y^*), (\hat{b} y^*, y^*/(c + k_2 y^*))\}$.

Furthermore, the local stability of the 2-cycle depends on the eigenvalues of the product of the matrices [11]

$$\hat{J} = \begin{pmatrix} 0 & b(0) \\ 1/a & \dfrac{c}{(c + k_2 y^*)^2} \end{pmatrix} \begin{pmatrix} 0 & b(1) \\ \dfrac{a}{(a + k_1 \hat{b} y^*)^2} & \dfrac{c}{\left(c + \frac{k_2 y^*}{c + k_2 y^*}\right)^2} \end{pmatrix}$$

$$= \begin{pmatrix} \dfrac{a\hat{b}}{(a + k_1 \hat{b} y^*)^2} & \dfrac{\hat{b} c}{\left(c + \dfrac{k_2 y^*}{c + k_2 y^*}\right)^2} \\ \dfrac{ac}{(c + k_2 y^*)^2 (a + k_1 \hat{b} y^*)^2} & \dfrac{c^2}{(c + k_2 y^*)^2 \left(c + \dfrac{k_2 y^*}{c + k_2 y^*}\right)^2} \end{pmatrix}.$$

Similar to the proof of Theorem 2.2(b), we have $\det \hat{J} = 0$ and

$$\operatorname{tr} \hat{J} = \frac{a\hat{b}}{(a + k_1 \hat{b} y^*)^2} + \frac{c^2}{(c + k_2 y^*)^2 \left(c + \dfrac{k_2 y^*}{c + k_2 y^*}\right)^2} > 0.$$

Replacing 1 by the right hand side of equation (2.6) evaluated at $y = y^*$, it can be shown that $\operatorname{tr} \hat{J} < 1$. Consequently, the 2-cycle is locally asymptotically stable. Therefore, the 2-cycle is globally asymptotically stable.

To prove (a), suppose $\hat{\mathcal{R}}_0 < 1$. It follows from equation (2.8) that

$$y(2t) \leq \frac{\hat{b}}{a} y(2t - 2) + \frac{1}{c^2} y(2t - 2)$$

for $t \geq 2$. We consider the following second order scalar difference equation for $t \geq 2$

$$\begin{cases} z(2t) = \frac{\hat{b}}{a}z(2t-2) + \frac{1}{c^2}z(2t-2) \\ z(2) = y(2). \end{cases}$$

Its corresponding characteristic equation is $\lambda^2 - ((\hat{b}/a) + (1/c^2)) = 0$. Therefore, we have $\lim_{t\to\infty}z(2t) = 0$ as $\hat{\mathcal{R}}_0 < 1$. Hence $\lim_{t\to\infty}y(2t) = \lim_{t\to\infty}x(2t) = 0$, and as a result, $\lim_{t\to\infty}y(2t+1) = \lim_{t\to\infty}x(2t+1) = 0$. Therefore, solutions converge to $E_0 = (0,0)$ if $\hat{\mathcal{R}}_0 < 1$. Now, the local stability of E_0 can be determined by the eigenvalues of the product of the matrices [11]

$$J = \begin{pmatrix} 0 & b(0) \\ 1/a & 1/c \end{pmatrix} \begin{pmatrix} 0 & b(1) \\ 1/a & 1/c \end{pmatrix} = \begin{pmatrix} \hat{b}/a & \hat{b}/c \\ 1/ac & 1/c^2 \end{pmatrix}.$$

It is clear that $\det J = 0$ and $\operatorname{tr} J = (\hat{b}/a) + (1/c^2) < 1$ by the assumption $\hat{\mathcal{R}}_0 < 1$. Thus it follows that E_0 is locally asymptotically stable. Consequently, E_0 is globally asymptotically stable. $\square$

Remark. Parallel to the earlier remark on the autonomous model, system (2.1) is also uniformly persistent when birth rate is seasonal. This follows directly from the global asymptotic stability of the nontrivial 2-cycle as proved in Theorem 2.3(b). However, letting $z(t) = y(2t)$ for $t \geq 1$ in equation (2.8), one obtains a one-dimensional autonomous difference equation for the even subsequence (in y) of the original system (2.1) and similar procedure can be applied for the odd subsequence. Using the technique developed by Cushing [6] and Kon *et al.* [19] one can also conclude uniform persistence of system (2.1).

2.3 Comparison between continuous and seasonal breeding

Motivated by some recent work in Refs. [7–9,12–14], our next goal is to understand whether seasonal breeding is advantageous or not. There are many comparison questions between continuous and seasonal reproduction one can ask about the model equation (2.1). For example, are there values for the birth rate such that the population with periodic birth rate persists while the one with continuous birth rate go to extinction? Do both juvenile and adult averages x and y decrease (or increase) with fluctuating birth rates? Does the average of the total population (i.e. $x + y$) decrease (or increase)? Does a weighted average $w_1 x + w_2 y$ for positive w_1 and w_2 increase (or decrease)? Does the reproductive stage y (adults) decrease (or increase)?

The most recent literature concerning such problems was motivated by an observed increase of the total population size in an experimental system [18]. Thus in the papers [5,16,17] the authors consider the average total population size $x + y$ as a comparison criterion. In this paper, we address the first two questions posed above. We point out that the component wise comparison posed in the second question is a more strict criterion than the ones discussed in the remaining questions. Thus the results obtained here will apply to these other criteria such as the total population $x + y$ or the weighted average $w_1 x + w_2 y$ or the reproductive stage y.

To compare the two cases on an equal basis, we assume for the rest of this section that $\hat{b} = 2b$. Clearly in this case for both the continuous and seasonal breeding models each adult produces $2b$ juveniles within a one-year period.

(a) *Persistence of population with periodic birth rate*

Since $\hat{b} = 2b$, then Theorems 2.2 and 2.3 require, respectively, that

$$b > a\left(1 - \frac{1}{c}\right), \quad \text{and} \quad b > \frac{1}{2}a\left(1 - \frac{1}{c^2}\right).$$

Since (recall that $c > 1$)

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

it follows that Theorem 2.3 applies, and hence there exists a survival 2-cycle on interval of average birth rates b, namely

$$\frac{1}{2}a\left(1 - \frac{1}{c^2}\right) < b < a\left(1 - \frac{1}{c}\right),$$

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

(b) *Comparison of the averages of x and y for periodic and constant birth rates*

Here we show that the average of juveniles and adults increase for the seasonal reproduction for birth rates which are low while decreases when the birth rates are high. This shows that seasonal reproduction is advantageous for low birth rates. To this end since $\hat{b} = 2b$, then equation (2.6) becomes

$$1 = \frac{2b}{a + 2k_1 by} + \frac{1}{c^2 + ck_2 y + k_2 y}, \tag{2.9}$$

which is equivalent to

$$1 = \frac{b}{\frac{a}{2} + k_1 by} + \frac{1}{c^2 + ck_2 y + k_2 y}.$$

Solving for equation (2.3) explicitly yields

$$\bar{y} = \frac{(bk_1 + bk_2 - ak_2 - bck_1) + \sqrt{(bk_1 + bk_2 - ak_2 - bck_1)^2 - 4bk_1k_2(ac - bc - a)}}{2bk_1k_2}.$$

Similarly, solving for equation (2.9) we have

$$y^* = \frac{\hat{C} + \sqrt{\hat{C}^2 - 8bk_1k_2(c + 1)(ac^2 - 2bc^2 - a)}}{4bk_1k_2(c + 1)},$$

where $\hat{C} = 2bk_1 + 2bk_2 + 2bck_2 - ak_2 - ack_2 - 2bc^2k_1$.

Since $\bar{y}$ satisfies equation (2.3), differentiating both sides of equation (2.3) with respect to b yields

$$0 = \frac{a - k_1 b^2 \frac{d\bar{y}}{db}}{(a + k_1 b\bar{y})^2} - \frac{k_2 \frac{d\bar{y}}{db}}{(c + k_2\bar{y})^2}.$$

Hence

$$\frac{d\bar{y}}{db} = \frac{a(c + k_2\bar{y})^2}{k_1 b^2(c + k_2\bar{y})^2 + k_2(a + k_1 b\bar{y})^2} > 0$$

for $b \geq a(1 - (1/c))$. Similarly, differentiate both sides of equation (2.9) with respect to b, we have

$$0 = \frac{2a - 4b^2 k_1 \frac{dy^*}{db}}{(a + 2bk_1 y^*)^2} - \frac{(c + 1)k_2 \frac{dy^*}{db}}{(c^2 + ck_2 y^* + k_2 y^*)^2}.$$

Therefore

$$\frac{dy^*}{db} = \frac{2a(c^2 + ck_2 y^* + k_2 y^*)^2}{4b^2 k_1(c^2 + ck_2 y^* + k_2 y^*)^2 + (c + 1)k_2(a + 2bk_1 y^*)^2} > 0$$

for $b \geq (a/2)(1 - (1/c^2))$.

As $\bar{y}$ and y^* are increasing functions of b and solutions of equation (2.1) are bounded, we see that $\lim_{b \to \infty} \bar{y}(b) = \bar{y}(\infty)$ and $\lim_{t \to \infty} y^*(b) = y^*(\infty)$ both exist. A direct computation yields

$$\bar{y}(\infty) = \frac{k_1 + k_2 - ck_1}{2k_1 k_2} + \frac{\sqrt{(k_1 + k_2 - ck_1)^2 + 4ck_1 k_2}}{2k_1 k_2}$$

and

$$y^*(\infty) = \frac{k_1 + k_2 + ck_2 - c^2 k_1}{2k_1 k_2(c + 1)} + \frac{\sqrt{(k_1 + k_2 + ck_2 - c^2 k_1)^2 + 4k_1 k_2 c^2(c + 1)}}{2k_1 k_2(c + 1)}.$$

Since

$$\frac{k_1 + k_2 - ck_1}{2k_1 k_2} = \frac{k_1 + k_2 + ck_2 - c^2 k_1}{2k_1 k_2(c + 1)}$$

and

$$\frac{\sqrt{(k_1 + k_2 + ck_2 - c^2 k_1)^2 + 4k_1 k_2 c^2(c + 1)}}{2k_1 k_2(c + 1)} < \frac{\sqrt{(k_1 + k_2 - ck_1)^2 + 4ck_1 k_2}}{2k_1 k_2},$$

we have $y^*(\infty) < \bar{y}(\infty)$. Consequently,

$$y^*(b) < \bar{y}(b) \quad \text{for all } b \text{ sufficiently large}.$$

On the other hand, it is easy to see that $\lim_{b \to (a(1-(1/c)))^+} \bar{y}(b) = 0$, and since $\lim_{b \to a(1-(1/c))} bk_1 k_2(c + 1)(ac^2 - 2bc^2 - a) = a^2/c(c^2 - 1)k_1 k_2(2c - 1 - c^2) < 0$, we have $\lim_{b \to a(1-(1/c))} y^*(b) > 0$. In particular,

$y^*(b) > 2\bar{y}(b)$ for $b > a(1 - (1/c))$ but sufficiently close to $a(1 - (1/c))$.

Now, if $y^* < \bar{y}$ (which is true for high birth rates b), then

$$\frac{\hat{b}y^* + 0}{2} = by^* < b\bar{y} = \bar{x}$$

and

$$\frac{1}{2}\left(y^* + \frac{y^*}{c + k_2 y^*}\right) < \frac{1}{2}\left(\bar{y} + \frac{\bar{y}}{c + k_2 \bar{y}}\right) < \bar{y}.$$

Therefore, the periodic environment is deleterious. If $y^* > 2\bar{y}$ (which is true for birth rates b sufficiently close to $a(1 - (1/c))$), then

$$\frac{2by^* + 0}{2} = by^* > 2b\bar{y} > \bar{x},$$

and

$$\frac{1}{2}\left(y^* + \frac{y^*}{c + k_2 y^*}\right) > \frac{1}{2}\left(2\bar{y} + \frac{2\bar{y}}{c + 2k_2 \bar{y}}\right) > \bar{y}$$

Therefore, the periodic environment is advantageous.

We use a numerical example to demonstrate our finding. Let $a = 3$, $c = 2$, $k_1 = 0.001$, and $k_2 = 0.01$. Then clearly $\mathcal{R}_0 = (b/a)(1/(1 - (1/c))) > 1$ for $b > 1.5$ and $\hat{\mathcal{R}}_0 = (2b/a) \times (1/(1 - (1/c^2))) > 1$ for $b > 1.125$. We plot $\bar{y}$ and y^* as a function of the parameter b in figure 1 together with the ratio $\bar{y}/y^*$. Since $y^* < \bar{y}$ for $b > 24.04$, the periodic environment is deleterious to the population if b is greater than around 24.04. When b is between 1.5 and 3.05 the periodic environment is advantageous since $y^* > 2\bar{y}$ for this range of birth rates. Our theory is inconclusive as whether the periodic environment is deleterious or not for b larger than 3.05 and less than 24.04. However, simulation results of the model equation (2.1) indicate that periodic environment produces larger averages of juveniles and adults and thus is advantageous for b in the interval (1.5, 3.376).

3. Concluding remarks

All other factors being equal, we showed that for high birth rates the seasonal breeding is deleterious. While for low births rate it is beneficial. However, this is a first attempt and indeed a simplification of reality, that is to say, all other factors may not be equal. For example, survival success may be lower in harsh winter seasons due to risk of infections because of insufficient energy reserve being available to sustain immunity. Stress can compromise immune system [1,10]. To investigate the effect of both periodic survival rate and seasonal breeding one can modify the model developed in this paper as follows:

$$\begin{cases} x(t + 1) = b(t)y(t) \\ y(t + 1) = \gamma_1(t)\dfrac{x(t)}{a + k_1 x(t)} + \gamma_2(t)\dfrac{y(t)}{c + k_2 y(t)} \\ (x(0), y(0)) \in \mathbb{R}_+^2 \setminus \{(0,0)\}, \end{cases} \qquad (3.10)$$
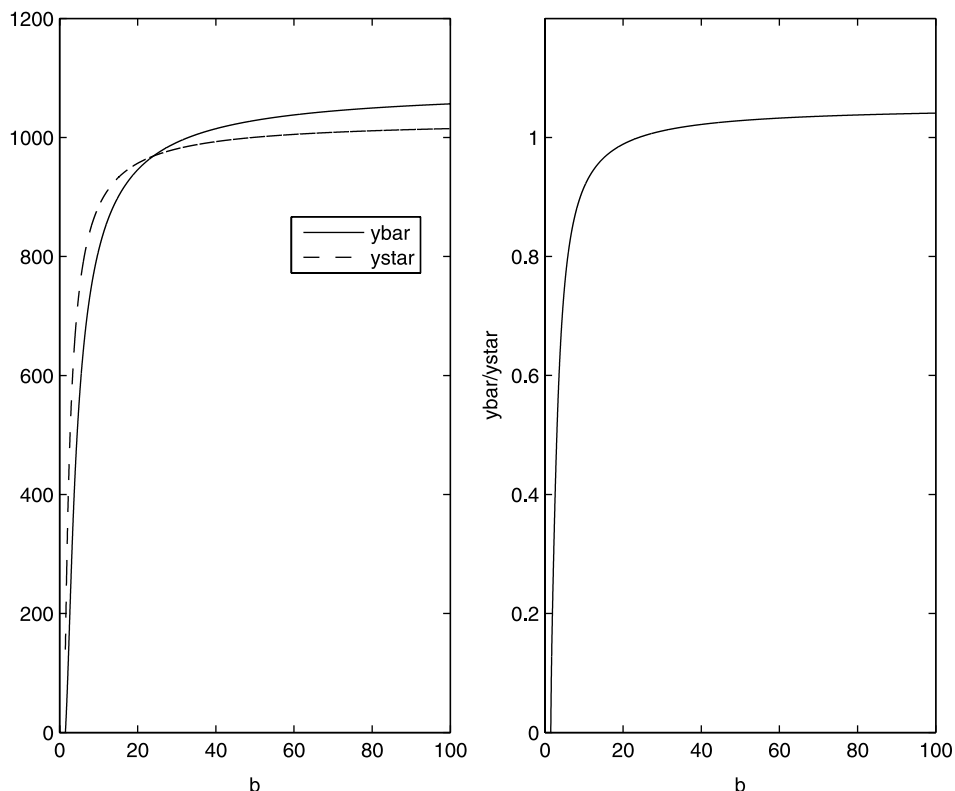
Figure 1. Using parameter values $a = 3$, $c = 2$, $k_1 = 0.001$, and $k_2 = 0.01$ we plot in the left figure $\bar{y}$ and y^* as functions of b, the birth rate. While in the right figure we plot the ratio $\bar{y}/y^*$. Note that $y^* < \bar{y}$ when b is larger than 24.04 and $y^* > \bar{y}$ when b is between 1.5 and 24.04. Furthermore, $y^* > 2\bar{y}$ when $1.5 \leq b \leq 3.05$.

where $0 \leq \gamma_1(t) \leq 1$ and $0 \leq \gamma_2(t) \leq 1$ are periodic functions which are low in winter and high(er) during warm weather.

Simulation results show that the model (3.10) with continuous breeding will produce larger juvenile and adult population numbers for high birth rates. Hence, in this sense, the conclusion would be similar to the models discussed in Section 2. In figure 2 we present a comparison of the solution of equation (3.10) with $b(t) = b = 10$ (i.e. continuous reproduction) with the solution of equation (3.10) when $b(t)$ is periodic with period 2. Specifically, $b(0) = \hat{b} = 2b > 0$, $b(1) = 0$, $b(2) = \hat{b}$, $b(3) = 0$, ... The functions $\gamma_1(t)$ and $\gamma_2(t)$ are chosen to be periodic with period 2, where $\gamma_1(0) = 1$, $\gamma_1(1) = 0.6$, $\gamma_1(2) = 1$, ..., and $\gamma_2(0) = 1$, $\gamma_2(1) = 0.8$, $\gamma_2(2) = 1$, ... The initial conditions are chosen as $x(0) = 100$ and $y(0) = 10$ while the rest of the parameters are given as follows: $a = 3, c = 2, k_1 = 0.001$, and $k_2 = 0.01$. Clearly the average of juveniles and adults for the continuous breeding case is larger than those for the seasonal breeding case. This seems true for high values for b. However, if we set b to small values (e.g. $b = 2.1$) this conclusion is reversed. Therefore, seasonal breeding is beneficial for low values of b.

Finally, we point out that our current work is focused on improving this model to better fit the dynamics of the green tree frog (*Hyla cinerea*). In particular, not all frogs are reproductive. In fact, green tree frogs become sexually mature when they are around one year of age. Therefore, we plan to modify equation (2.1) to include an additional equation which describes the dynamics of nonreproductive frogs. This will result in a new system composed
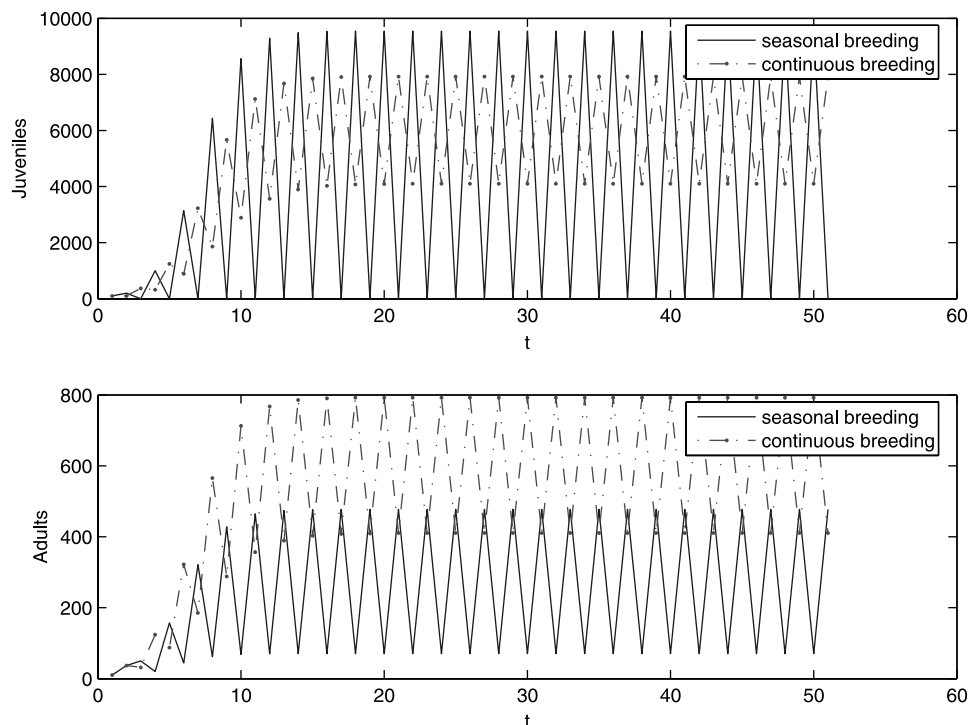
Figure 2.   A comparison between continuous and seasonal breeding for the model equation (3.10).

of three difference equations which model the dynamics of juveniles, nonreproductive adults, and reproductive adults. We also plan to extend this investigation to competition modeled by Ricker type of functions.

Acknowledgements

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