Discrete Three-Stage Population Model: Persistence and Global Stability Results

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Abstract

A general three stage discrete-time population model is studied. The inherent net reproductive number for this model is derived. Global stability of the origin is established provided that the inherent net reproductive number is less than one. If it is larger than one the existence of a unique positive fixed point is proved and the persistence of the system is established. Finally, for certain parameter ranges global stability of the positive fixed point is proved.

1 Introduction

Linear and nonlinear matrix models have played a central role in understanding the dynamics of many populations (see [5, 11] and the reference therein) including endangered species [4], invasive species [19] and species with rich dynamical behavior. A recent well-known such model, is the nonlinear discrete three-stage LPA model developed in [7] to describe the dynamics of a flour beetle population. The nonlinearities in this model account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults and are of the Ricker type [3, 5]. The resulting deterministic model and its stochastic counterparts were very successful in predicting experimentally observed dynamics of flour beetles including cyclic and chaotic behavior [8, 9, 10, 13]. This work has enriched the literature with yet another example of the predictive power of such models.

The purpose of this paper is to theoretically study a matrix model which describes the dynamics of a general closed (no immigration or migration) population composed of individuals having one of the following three-stages: 1) juveniles, 2) sexually immature adults (nonbreeders), and 3) reproductive adults (breeders). In addition, it is assumed that juveniles depend on different resources than adults. Thus, no competition for resources takes place between them. Such life history is typical of amphibians where larvae which are called tadpoles metamorphose into adults, where the adults are composed of sexually immature and mature individuals. Also, for many amphibians

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tadpoles are herbivorous, while adults are carnivorous. Thus, juveniles and adults depend on different resources. A particular amphibian example which motivated this theoretical study is the green tree frog (*Hyla cinerea*) which we have been monitoring since 2004 [18].

Stage structured models similar to the one presented here have been applied recently to describe the dynamics of amphibian populations [23]. The model presented in [23] assumes that the population is divided into two stages, namely juveniles and adults (where all adults are reproductive). In contrast with the three dimensional matrix model considered here, such a simplifying assumption results in a two dimensional nonlinear matrix population model which is related to a general class of juvenile-adult models studied recently in [12]. The model in [23] was applied to two amphibian species *Bufo boreas* and *Ambystoma macrodactylum* with different reproductive strategies (the former species has a clutch size more then 100 times larger the latter one). Local stability of the interior equilibrium was established and elasticity analysis was used to determine the most influential stage survival rate on amphibian declines, a problem which was extensively discussed in [6, 22].

In contrast with a two dimensional counterpart, the (Beverton-Holt type) nonlinearities in the three dimensional model presented here -which are due to competition between sexually mature and immature adults- generally lead to a non-monotone discrete dynamical system. For monotone systems, global stability can often be established, thanks to the availability of a well-developed theory, see [20] and cited references therein for a review. Non-monotone systems on the other hand lack a similar theory, and their global stability analysis is therefore usually more complicated. Our approach will be as follows. We first note that for a particular choice of some of the parameters in the model, the system is monotone, and global stability can be established. Secondly, we show that when the parameters are perturbed slightly away from their above critical values, global stability is preserved despite the fact that the perturbation destroys monotonicity of the model.

This paper is organized as follows. In section 2 we present the discrete model. In section 3 we prove persistence for the general model and provide an existence-uniqueness result for an interior fixed point. In sections 4 and 5 we establish global stability results for special cases of the model. Finally, concluding remarks are provided in section 6.

2 The discrete model

As mentioned above, the discrete model we consider describes the dynamics of a population divided into three stages where juveniles compete for one resource while nonbreeders and breeders compete for another. The model is given by the following system of difference equations:

$$
\begin{array}{rcl}
J(t+1) & = & bB(t) + (1-\gamma_1)s_1(J(t))J(t) \\
N(t+1) & = & \gamma_1 s_1(J(t))J(t) + (1-\gamma_2)s_2(N(t)+B(t))N(t) \\
B(t+1) & = & \gamma_2 s_2(N(t)+B(t))N(t) + s_2(N(t)+B(t))B(t).
\end{array}
\tag{1}
$$

The state variables $J(t), N(t), B(t)$ represent the number of juveniles, non-breeders and breeders, respectively, at time t. The parameter $b > 0$ is the birth rate, while $\gamma_1, \gamma_2 \in (0, 1]$ represent the fraction (in one time unit) of juveniles that become non-breeders and non-breeders that become breeders, respectively. The functions s_1 and s_2 are the survivorship functions of juveniles (tadpoles) and non-breeders/breeders (adults), respectively. We assume that s_i, $i = 1, 2$, satisfy the following assumption:

($\Sigma 1$) $s_i \in C^1[0, \infty)$, $s_i(0) = a_i$, $0 < a_i < 1$, $\dfrac{d}{dz}s_i(z) < 0$, $\dfrac{d}{dz}(s_i(z)z) > 0$, $\lim\limits_{z \to \infty} s_i(z) = 0$, and $\lim\limits_{z \to \infty} s_i(z)z = \hat{a}_i < \infty$ for $i = 1, 2$.

The assumption ($\Sigma 1$) is satisfied, for example, by the following Beverton-Holt function:
$$s_i(z) = \frac{a_i}{1 + k_i z}, \quad i = 1, 2.$$

The above difference equation system (1) can be written in the following matrix form:
$$x(t + 1) = A(x(t))x(t) \tag{2}$$
where $x(t) = (J(t), N(t), B(t))^T$ and the projection matrix A has the form:
$$A(x) = \begin{pmatrix} (1 - \gamma_1)s_1(J) & 0 & b \\ \gamma_1 s_1(J) & (1 - \gamma_2)s_2(N + B) & 0 \\ 0 & \gamma_2 s_2(N + B) & s_2(N + B) \end{pmatrix}.$$

Note that
$$x \leq y, \text{ implies } A(y) \leq A(x). \tag{3}$$

3 Existence-uniqueness of interior fixed point and persistence

In this section we prove the existence of a unique interior fixed point for the model (1) and show that the system is persistent. We first begin by finding the inherent net reproductive number. To this end, following [5, 11] we let
$$G = \begin{pmatrix} (1 - \gamma_1)a_1 & 0 & 0 \\ \gamma_1 a_1 & (1 - \gamma_2)a_2 & 0 \\ 0 & \gamma_2 a_2 & a_2 \end{pmatrix}$$
and
$$F = \begin{pmatrix} 0 & 0 & b \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}.$$
Note that the inherent projection matrix of the nonlinear system
$$A(0) = \begin{pmatrix} (1 - \gamma_1)a_1 & 0 & b \\ \gamma_1 a_1 & (1 - \gamma_2)a_2 & 0 \\ 0 & \gamma_2 a_2 & a_2 \end{pmatrix} = F + G.$$

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Thus, the inherent net reproductive number R_0 is the positive, simple and strictly dominant eigenvalue of $F(I - G)^{-1}$. Simple calculations show that

$$R_0 = \frac{b\gamma_1\gamma_2 a_1 a_2}{(1 - (1 - \gamma_1)a_1)(1 - (1 - \gamma_2)a_2)(1 - a_2)}. \tag{4}$$

When necessary we will use the notation $A(0, (\gamma_1, \gamma_2))$ and $R_0(\gamma_1, \gamma_2)$ to indicate the dependency of $A(0)$ and R_0 on γ_1 and γ_2. We now have the following result:

Lemma 1. *Suppose $R_0(\gamma_1, \gamma_2) < 1$ then the origin $E_0 = (0, 0, 0)$ is a globally asymptotically stable fixed point of system (1).*

Proof. Since the inherent projection matrix, $A(0)$, of system (2) is nonnegative, irreducible and primitive, it has a positive, simple and strictly dominant eigenvalue r. Furthermore, since $R_0 < 1$ it follows from [11] (Theorem 1.1.3, page 10) that $r < 1$ and $\lim_{t\to\infty} A^t(0) = 0$. Now, for any $x(0)$ we have that $0 \leq x(1) = A(x(0))x(0) \leq A(0)x(0)$ by (3), and repeating this we get that $0 \leq x(t) \leq A^t(0)x(0)$. Since $A^t(x(0))x(0)$ converges to 0 as $t \to \infty$, the conclusion follows.

$\square$

We now establish the existence and uniqueness of an interior fixed point as follows:

Theorem 1. *Suppose $R_0(\gamma_1, \gamma_2) > 1$ then (1) has a unique interior fixed point $E^* = (J^*, N^*, B^*)$.*

Proof. A positive fixed point of (1) is a point $(J^*, N^*, B^*) \in \text{int}(\mathbb{R}^3_+)$ that satisfies

$$\begin{aligned}
J &= bB + (1 - \gamma_1)s_1(J)J \\
N &= \gamma_1 s_1(J)J + (1 - \gamma_2)s_2(N + B)N \\
B &= \gamma_2 s_2(N + B)N + s_2(N + B)B.
\end{aligned} \tag{5}$$

From the first equation in (5) we get:

$$h(J) := (1 - (1 - \gamma_1)s_1(J))J = bB.$$

It is easy to see that $h'(J) > 0$, $h(0) = 0$, and $\lim_{J\to\infty} h(J) = \infty$. Thus, $h : [0, \infty) \to [0, \infty)$ is one to one and onto. Therefore, $J(B) = h^{-1}(bB)$. Furthermore, $\lim_{B\to\infty} J(B) = \infty$, $J(0) = 0$ and $J'(B) > 0$. Observe also that

$$J = \frac{bB}{1 - (1 - \gamma_1)s_1(J)}. \tag{6}$$

Now letting $W = N + B$ and adding the second and the third equations of (5) we get

$$W = N + B = \gamma_1 s_1(J)J + s_2(N + B)(N + B) = \gamma_1 s_1(J)J + s_2(W)W.$$

Thus,

$$\tilde{h}(W) := (1 - s_2(W))W = \gamma_1 s_1(J)J.$$

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Therefore, noticing that $\tilde{h}'(W) > 0$ by ($\Sigma 1$), and arguing as above we get that W can be solved as a function of B. In particular, $W(B) = \tilde{h}^{-1}(\gamma_1 s_1(J(B))J(B))$ and $W(0) = 0$. Furthermore, using ($\Sigma 1$) once again it follows by implicit differentiation that $W'(B) > 0$.

Using the notation $s_1(J) = s_1$ and $s_2(W) = s_2$ we get from adding the second and third equations of (5)

$$N(1 - s_2) = \gamma_1 s_1 J + (s_2 - 1)B.$$

Solving for N yields

$$N = \frac{\gamma_1 s_1 J + (s_2 - 1)B}{1 - s_2}. \tag{7}$$

Plugging the equations (6) and (7) for J and N into the B equation of (5) results in

$$B = \frac{\gamma_1 \gamma_2 s_1 s_2 b B}{(1 - s_2)(1 - (1 - \gamma_1)s_1)} + (1 - \gamma_2)s_2 B$$

Since we are interested in the existence and uniqueness of a positive equilibrium dividing by B we obtain:

$$1 = \frac{\gamma_1 \gamma_2 s_1 s_2 b}{(1 - s_2)(1 - (1 - \gamma_1)s_1)} + (1 - \gamma_2)s_2.$$

This is equivalent to

$$1 = \gamma_1 \gamma_2 s_1 s_2 b + (1 - \gamma_1)s_1(1 - s_2) + s_2 + (1 - \gamma_2)s_2(1 - s_2)(1 - (1 - \gamma_1)s_1)$$

$$\tag{8}$$

$$= \hat{H}(J(B), W(B))) := H(B).$$

Clearly, any interior equilibrium must satisfy (8).

Now differentiating $H(B)$ with respect to B we see that

$$H' = \gamma_1 \gamma_2 s_1' J' s_2 b + \gamma_1 \gamma_2 s_1 s_2' W' b + s_1' J'(1 - s_2)(1 - \gamma_1) - s_2' W'(1 - \gamma_1)s_1 + s_2' W'$$

$$+ (1 - \gamma_2)s_2' W'(1 - s_2)(1 - (1 - \gamma_1)s_1)) - (1 - \gamma_2)s_2 s_2' W'(1 - (1 - \gamma_1)s_1))$$

$$- (1 - \gamma_2)s_2(1 - s_2)(1 - \gamma_1)s_1' J'$$

$$= \gamma_1 \gamma_2 s_1' J' s_2 b + \gamma_1 \gamma_2 s_1 s_2' W' b + s_1' J'(1 - \gamma_1)(1 - s_2)(1 - (1 - \gamma_2)s_2)$$

$$+ s_2' W'(1 - (1 - \gamma_1)s_1) - (1 - \gamma_2)s_2' W' s_2(1 - (1 - \gamma_1)s_1)$$

$$+ (1 - \gamma_2)s_2' W'(1 - s_2)(1 - (1 - \gamma_1)s_1)$$

$$= \gamma_1 \gamma_2 s_1' J' s_2 b + \gamma_1 \gamma_2 s_1 s_2' W' b + s_1' J'(1 - \gamma_1)(1 - s_2)(1 - (1 - \gamma_2)s_2)$$

$$+ s_2' W'(1 - (1 - \gamma_1)s_1)(1 - (1 - \gamma_2)s_2) + (1 - \gamma_2)s_2' W'(1 - s_2)(1 - (1 - \gamma_1)s_1) < 0,$$

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since $J' > 0$, $W' > 0$ and $s_i' < 0$, $i = 1, 2$. Therefore, H is a decreasing function. Also note that $\lim_{B \to \infty} H(B) = 0$. Thus, it follows that if $H(0) > 1$ then there exists a unique B^* such that $1 = H(B^*)$. (Clearly, $H(0) > 1$ is equivalent to $R_0(\gamma_1, \gamma_2) > 1$). From this and the above established relations between W, J and B it follows that there exists a unique interior equilibrium $E^* = (J^*, N^*, B^*)$. $\qquad \square$

The next result establishes boundedness of solutions uniformly in the parameters.

Lemma 2. *There is a compact set $K \subset \mathbb{R}_+^3$ such that every forward solution sequence of (1) enters K in at most 2 time steps, and remains in K forever after.*

Proof. It is clear that $\mathbb{R}_+^3$ is forward invariant. Consider now the dynamics of $W(t + 1) = N(t + 1) + B(t + 1)$ then from ($\Sigma 1$) we have

$$W(t + 1) = \gamma_1 s_1(J(t))J(t) + s_2(W(t))W(t) \leq \gamma_1 \hat{a}_1 + \hat{a}_2 \leq \hat{a}_1 + \hat{a}_2, \quad \forall t = 0, 1, \ldots,$$

so that in particular

$$N(t), B(t) \leq \hat{a}_1 + \hat{a}_2, \quad \forall t = 1, 2, \ldots$$

Therefore

$$J(t + 1) \leq b(\hat{a}_1 + \hat{a}_2) + (1 - \gamma_1)\hat{a}_1, \quad \forall t = 1, 2, \ldots,$$

hence

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

The conclusion of the lemma follows by defining

$$K = \{(J, N, B) \in \mathbb{R}_+^3 \mid J \in [0, (b + 1)\hat{a}_1 + b\hat{a}_2], N, B \in [0, \hat{a}_1 + \hat{a}_2] \}.$$

$\qquad \square$

Next we show that if the net reproductive number is greater than one then the origin is unstable and system (1) is uniformly persistent.

Theorem 2. *Suppose $R_0(\gamma_1, \gamma_2) > 1$, then (1) has an unstable fixed point at the origin. Moreover, it is uniformly persistent.*

Proof. Since $R_0(\gamma_1, \gamma_2) > 1$ it follows from Theorem 1.1.3 in [11] that $A(0)$ has a positive strictly dominant eigenvalue $r > 1$. This shows that the origin is unstable. Uniform persistence will follow from an application of Theorem 4.1 in [16]. Using the notation of that paper we let $\mathcal{H} = \mathbb{R}_+^3$, $\mathcal{Y} = \mathrm{bd}(\mathbb{R}_+^3)$, and f denote the map on the right hand side of (1). Then clearly $f(\mathcal{H} \setminus \mathcal{Y}) \subset \mathcal{H} \setminus \mathcal{Y}$ since $\mathrm{int}(\mathbb{R}_+^3)$ is positively invariant for the system (1). By Theorem 2.1 in [15] and using Lemma 2, it follows that there exists a global attractor X in $\mathcal{H}$. Let M be the maximal compact invariant set in $\mathcal{Y}$. Here, $M = \{(0, 0, 0)\}$. Uniform persistence follows if we can prove that

1. M is isolated in X.

2. $W^s(M) \subset \mathcal{Y}$,

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where $W^s(M)$, the stable set of M, denotes the set of points whose solution sequence for (1) converges to M. In fact, we will prove the stronger result that M is a repeller which by Theorem 2.1 in [16] is equivalent to showing

1. M is isolated in $\mathcal{H}$.

2. $W^s(M) \subset M$.

To prove that M is a repeller we will construct a continuous function $P : \mathbb{R}^3_+ \to \mathbb{R}_+$ which is 0 on M. Furthermore, there is a neighborhood U of M such that for all $x \in U \setminus M$, there exists a $t > 0$ where $P(f^t(x)) > P(x)$. Let us now construct P. Since $A(0)$ is non-negative and irreducible, its dominant eigenvalue r (which is larger than 1) has a corresponding left eigenvector $p > 0$, i.e.,

$$p'A(0) = rp'.$$

Pick $r^* \in (1, r)$ such that $p'A(0) - r^*p' > 0$. Then by continuity of $A(x)$, there exists a neighborhood U of M in $\mathcal{H}$ such that

$$p'A(x) - r^*p' > 0.$$

Define $P : \mathbb{R}^3_+ \to \mathbb{R}_+$ as follows:
$$P(x) = p'x.$$

Then $P(x) = 0$ for $x \in U$ iff $x \in M$, and positive elsewhere in U. Moreover,

$$P(f(x)) = p'A(x)x > r^*p'x > P(x), \quad \forall x \in U \setminus M.$$

This establishes that system (1) uniformly persistent, i.e. there is some $\eta > 0$ such that $\liminf_{t \to \infty} J(t), N(t), B(t) \geq \eta$ for all nonzero orbits in $\mathbb{R}^3_+$. $\qquad \square$

4 Global stability for the case $\gamma_1 = \gamma_2 = 1$

Throughout this section we assume that $\gamma_1 = \gamma_2 = 1$. We begin by establishing a convergence result for monotone maps. Consider a map $T : \mathbb{R}^n \to \mathbb{R}^n$. We say that T is monotone if $x \leq y$ implies that $T(x) \leq T(y)$. Here, $x \leq y$ denotes the usual, componentwise partial order on $\mathbb{R}^n$.

Lemma 3. *Let $T : \mathbb{R}^n \to \mathbb{R}^n$ be a continuous, monotone map and $a \leq b$ be points in $\mathbb{R}^n$. If $a \leq T(a)$ and $T(b) \leq b$, and if T has a unique fixed point x^* in the order interval $[a, b] := \{x \in \mathbb{R}^n \mid a \leq x \leq b\}$, then every solution sequence of the discrete system*

$$x(t+1) = T(x(t)), \tag{9}$$

starting in $[a, b]$, converges to x^*.

Proof. Note that the assumptions on T imply that

$$a \leq T(a) \leq T(b) \leq b,$$

so by induction the solutions sequences starting in a and b are non-decreasing and non-increasing respectively. Since they also remain in the compact set $[a, b]$, they must converge, and since T is continuous, the limits must be fixed points of T in $[a, b]$. As there is only one fixed point x^* in $[a, b]$, both limits are the same and equal to x^*. Now for an arbitrary $x \in [a, b]$, we have that $a \leq x \leq b$, hence monotonicity of T implies that $T^k(a) \leq T^k(x) \leq T^k(b)$ for all $k = 1, 2, \dots$. This, and the fact that $T^k(a), T^k(b) \to x^*$ as $k \to \infty$, implies that $T^k(x) \to x^*$, concluding the proof. $\square$

The inherent net reproductive number for the case $\gamma_1 = \gamma_2 = 1$ is given by

$$R_0(1, 1) = \frac{ba_1a_2}{1 - a_2}. \tag{10}$$

If $R_0 > 1$ then by Theorem 1 there exists a unique positive equilibrium $E^* = (J^*, N^*, B^*)$ where B^* solves (8) (see proof of Theorem 1) which here simplifies to

$$1 = bs_2(s_1(bB)bB + B)s_1(bB) + s_2(s_1(bB)bB + B), \tag{11}$$

$J^* = bB^*$, and $N^* = s_1(J^*)J^*$. We sometimes write $E^*(1, 1)$ to denote the unique positive fixed point for the case $\gamma_1 = \gamma_2 = 1$.

Lemma 4. *Let* $R_0(1, 1) = \dfrac{ba_1a_2}{1 - a_2} > 1$. *Then, the unique positive fixed point* $E^*(1, 1) = (J^*(1, 1), N^*(1, 1), B^*(1, 1))$ *of system* (1) *is locally asymptotically stable.*

Proof. Let $W^* = N^* + B^*$. The linearized system at (J^*, N^*, B^*) has the following coefficient matrix:

$$A^* = \begin{pmatrix} 0 & 0 & b \\ A_{21}^* & 0 & 0 \\ 0 & A_{32}^* & A_{33}^* \end{pmatrix},$$

where $A_{21}^* = s_1'(J^*)J^* + s_1(J^*)$, and $A_{32}^* = A_{33}^* = s_2'(W^*)W^* + s_2(W^*)$. The characteristic polynomial associated with this matrix is given by $Q(s) = s^3 - A_{33}^*s^2 - bA_{21}^*A_{32}^* = 0$. In the following we shall verify that the following three Jury conditions [3] hold and conclude that the roots of this polynomial have magnitude less then 1:

1) $Q(1) > 0$, 2) $Q(-1) < 0$, and 3) $1 - b^2(A_{21}^*)^2(A_{32}^*)^2 - |bA_{33}^*A_{21}^*A_{32}^*| > 0$.

To this end, observe that $A_{21}^* > 0$, $A_{32}^* > 0$, and $A_{33}^* > 0$ by our assumption ($\Sigma 1$). Since B^* satisfies (11), $J^* = bB^*$, and $N^* = s_1(J^*)J^*$, we have by (11) that

$$1 = bs_2(W^*)s_1(J^*) + s_2(W^*). \tag{12}$$

Substituting the above expression of 1 in $Q(1) = 1 - A_{33}^* - bA_{21}^*A_{32}^*$ yields

$$Q(1) = -s_2'(W^*)W^* - bs_1'(J^*)J^*s_2(W^*) - bs_2'(W^*)W^*[s_1'(J^*)J^* + s_1(J^*)] > 0.$$

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It is also clear that
$$Q(-1) = -1 - A_{33}^* - bA_{21}^* A_{32}^* < 0$$
as $A_{21}^* > 0$, $A_{32}^* > 0$, and $A_{33}^* > 0$. We proceed to verify the last inequality $1 - b^2 (A_{21}^*)^2 (A_{32}^*)^2 - |bA_{33}^* A_{21}^* A_{32}^*| > 0$, which is equivalent to $\xi := 1 - b^2 (A_{21}^*)^2 (A_{32}^*)^2 - bA_{21}^* A_{32}^* A_{33}^* > 0$. For notational convenience, we rewrite $s_1(J^*)$ by s_1 and $s_2(W^*)$ by s_2. Replacing 1 by the square of the right hand side of (11), i.e.,
$$1 = b^2 s_1^2 s_2^2 + 2bs_1 s_2^2 + s_2^2,$$
then
$$\xi = b^2 s_1^2 s_2^2 + 2bs_1 s_2^2 + s_2^2 - b^2 (A_{21}^*)^2 (A_{32}^*)^2 - bA_{21}^* A_{32}^* A_{33}^*. \tag{13}$$
Notice $b^2 s_1^2 s_2^2 - b^2 (A_{21}^*)^2 (A_{32}^*)^2 = [bs_1 s_2 + bA_{21}^* A_{32}^*][bs_1 s_2 - bA_{21}^* A_{32}^*]$, where $bs_1 s_2 + bA_{21}^* A_{32}^* > 0$, and $bs_1 s_2 - bA_{21}^* A_{32}^* = -bs_1' J^* (s_2' W^* + s_2) - bs_1 s_2' W^* > 0$. Furthermore,
$$
\begin{aligned}
2bs_1 s_2^2 + s_2^2 - bA_{21}^* A_{32}^* A_{33}^* &= 2bs_1 s_2^2 + s_2^2 - bA_{21}^* A_{32}^* s_2' W^* - bA_{21}^* A_{32}^* s_2 \\
&> 2bs_1 s_2^2 + s_2^2 - bA_{21}^* A_{32}^* s_2 = 2bs_1 s_2^2 - b(s_1' J^* + s_1)(s_2' W^* + s_2) s_2 \\
&= 2bs_1 s_2^2 + s_2^2 - bs_1' s_2' J^* W^* s_2 - bs_1' J^* s_2^2 - bs_1 s_2' W^* s_2 - bs_1 s_2^2 \\
&> bs_1 s_2^2 + s_2^2 - bs_1' s_2' J^* W^* s_2 - bs_1' J^* s_2^2 \\
&= bs_1 s_2^2 + s_2^2 - bs_1' s_2 J^* [s_2' W^* + s_2] > 0.
\end{aligned}
$$
Thus, $\xi > 0$. This completes the proof that E^* is locally asymptotically stable. $\qquad\square$

Next we prove that if the net reproductive number is larger than one then the unique positive fixed point is globally attractive.

Theorem 3. *Suppose that* $R_0(1,1) = \dfrac{ba_1 a_2}{1 - a_2} > 1$. *Then every solution of* (1) *starting in* $\mathbb{R}_+^3 \setminus \{(0,0,0)\}$ *converges to* $E^*(1,1) = (J^*(1,1), N^*(1,1), B^*(1,1))$.

Proof. Notice that every solution starting on the boundary of $\mathbb{R}_+^3$, but not in $(0,0,0)$ enters the positively invariant set $\text{int}(\mathbb{R}_+^3)$ in at most 2 time steps, so it is enough to establish the lemma for solutions in $\text{int}(\mathbb{R}_+^3)$. Pick $x(0) = (J(0), N(0), B(0)) \in \text{int}(\mathbb{R}_+^3)$. In fact, by Lemma 2 it suffices to consider $x(0) \in \text{int}(\mathbb{R}_+^3) \cap K$. The unique positive fixed point $E^* = (J^*, N^*, B^*)$ clearly belongs to K. Define $b := \sup K$ (this is the maximal element in K). Then again by Lemma 2 we have that $T(b) \leq b$ (where $T(x)$ denotes the right hand side of (1), which is clearly monotone since $DT(x)$ is a nonnegative matrix for all x). Since $A(0)$ is an irreducible non-negative matrix, its spectral radius r (which we know is larger than 1) is an eigenvalue with a corresponding positive eigenvector v:
$$A(0)v = rv.$$
In addition, for all $\epsilon > 0$ sufficiently small, there holds that
$$T(\epsilon v) = r\epsilon v + o(\epsilon) \geq \epsilon v,$$
since $r > 1$. Now for a given $x(0)$ in $\text{int}(\mathbb{R}_+^3) \cap K$, we can pick a sufficiently small $\epsilon > 0$ such that
$$a := \epsilon v \leq x(0) \text{ and } a \leq T(a).$$
The conclusion now follows from an application of Lemma 3. $\qquad\square$

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The global asymptotic stability of the unique interior fixed point (J^*, N^*, B^*) follows from Theorem 3 and Lemma 4 (local asymptotic stability and global attractivity).

5 Global stability results for a perturbation around $\gamma_1 = \gamma_2 = 1$

We start with an auxiliary result that establishes that the origin is a repeller for (1), uniform in the parameters.

Lemma 5. *Let $R_0(1, 1) = \dfrac{ba_1 a_2}{1 - a_2} > 1$. Then the fixed point at the origin for system (1) is a repeller, uniform in the parameter $\gamma = (\gamma_1, \gamma_2)$, near $(1, 1)$. More precisely, there is an open neighborhood $\mathcal{N}_0$ of 0 in $\mathbb{R}_+^3$, and constants $g_i \in (0, 1)$, $i = 1, 2$, such that for every $x(0) \neq 0$ and every $\gamma \in [g_1, 1] \times [g_2, 1]$, there is some $\bar{t} = \bar{t}(x(0), \gamma) \geq 0$ such that*

$$T_\gamma^t(x(0)) \notin \mathcal{N}_0, \quad \forall t \geq \bar{t},$$

where $x(t) = (J(t), N(t), B(t))$, and $T_\gamma(x(t))$ denotes the right hand side of system (1).

Proof. The proof will follow from an application of a result due to Fonda -see Corollary 2.2 in [16]- applied to the following extended system.

$$
\begin{aligned}
J(t+1) &= bB(t) + (1 - \gamma_1(t))s_1(J(t))J(t) \\
N(t+1) &= \gamma_1(t)s_1(J(t))J(t) + (1 - \gamma_2(t))s_2(N(t) + B(t))N(t) \\
B(t+1) &= \gamma_2(t)s_2(N(t) + B(t))N(t) + s_2(N(t) + B(t))B(t) \\
\gamma(t+1) &= \gamma(t).
\end{aligned}
\tag{14}
$$

Obviously all solution sequences of (1) can be embedded in solution sequences of (14). Notice that the right hand side of this system can be rewritten in pseudo-linear form:

$$
\begin{pmatrix} A(x(t), \gamma(t)) & 0 \\ 0 & I_2 \end{pmatrix} \begin{pmatrix} x(t) \\ \gamma(t) \end{pmatrix}
$$

with

$$
A(x, \gamma) = \begin{pmatrix} (1 - \gamma_1)s_1(J) & 0 & b \\ \gamma_1 s_1(J) & (1 - \gamma_2)s_2(N + B) & 0 \\ 0 & \gamma_2 s_2(N + B) & s_2(N + B) \end{pmatrix}.
$$

Let's reconsider $A(0, (1, 1))$ (which is equal to the matrix $A(0)$ above), which has a spectral radius $r > 1$ by our assumption. Since this matrix is nonnegative and irreducible, there is a vector $p > 0$ such that $p'A(0, (1, 1)) = rp'$. Consequently, there is some $r^* \in (1, r)$ such that $p'A(0, (1, 1)) - r^* p' > 0$. In fact, by continuity of $A(x, \gamma)$, there are $\epsilon > 0$ and $f_i \in (0, 1)$ such that

$$p'A(x, \gamma) - r^* p' > 0, \quad \forall x \in B_\epsilon^+(0), \quad \forall \gamma \in (f_1, 1] \times (f_2, 1],$$

where $B_\epsilon^+(0) := \{x \in \mathbb{R}_+^3 \mid |x| < \epsilon\}$. Let $g_i = (f_i + 1)/2$ for $i = 1, 2$, set $z = (x, \gamma)$, and let $Z := \mathbb{R}_+^3 \times [g_1, 1] \times [g_2, 1]$. Then Z is invariant for system (14), and we restrict the dynamics to Z henceforth. Define the continuous function $P : Z \to \mathbb{R}_+$ as follows

$$P(z) = p'x.$$

Let $M := \{(0, 0, 0)\} \times [g_1, 1] \times [g_2, 1]$. Then clearly M is compact and invariant, and $Z \setminus M$ is positively invariant for (14). Moreover $P(z) = 0$ iff $z \in M$. Finally, observe that (we slightly abuse notation by also denoting the right hand side of (14) by T),

$$P(T(z)) = p'A(z)x > r^*p'x > P(z), \quad \forall z \in U \setminus M,$$

where
$$U := B_\epsilon^+(0) \times [g_1, 1] \times [g_2, 1]$$

is a neighborhood of M in Z. Therefore, all conditions of Corollary 2.2 in [16] hold, and hence M is a repellor for (14). This concludes the proof of this Lemma. $\square$

Theorem 4. *Let* $R_0(1, 1) = \dfrac{ba_1 a_2}{1 - a_2} > 1$. *Then there is a continuous map* $E^* : \Gamma \to$ int$(\mathbb{R}_+^3)$ *with* $\Gamma = (\gamma_1^l, 1] \times (\gamma_2^l, 1]$ *for some* $\gamma_i^l \in (0, 1)$, $i = 1, 2$ *and* $E^*(\gamma_1, \gamma_2) = (J^*(\gamma_1, \gamma_2), N^*(\gamma_1, \gamma_2), B^*(\gamma_1, \gamma_2))$ *is locally asymptotically stable and globally attractive fixed point of* (1) *with respect to nonzero initial conditions.*

Proof. The proof follows from an application of Theorem 2.1 in [21]. Using the notation from that theorem, we let $X = \mathbb{R}_+^3$, $U = \mathbb{R}_+^3 \setminus \{(0, 0, 0)\}$, $\Lambda = [g_1, 1] \times [g_2, 1]$ (see Lemma 5), $\lambda_0 = (1, 1)$ and $x_0 = (J^*, N^*, B^*)$. Clearly, all the needed smoothness requirements hold. The conditions on the unperturbed map follow from Lemma 4 (locally asymptotically stable positive fixed point) and Lemma 3 (globally attractive positive fixed point). Condition (H1) in that paper holds by setting for all $\lambda \in \Lambda$, $B_\lambda = K \cap (\mathbb{R}_+^3 \setminus \mathcal{N}_0)$, where K follows from Lemma 2 and $\mathcal{N}_0$ from Lemma 5. Condition (H2) holds by the compactness of B_λ and by Lemma 5. This concludes the proof. $\square$

6   Concluding remarks

In this paper we have studied a three-stage structured population model. We have established persistence results for the full model and global stability of the positive fixed point only for γ_1 and γ_2 in an interval near one. The global attractivity result given in Theorem 3 can be extended to the case where $\gamma_1 \in (0, 1]$ and $\gamma_2 = 1$, since in this case the map defined by the right hand side of (1) is still monotone. The main difficulty in studying the global attractivity of the positive fixed point for the full model (1) is that the nonlinear map governing the system is not monotone when $0 < \gamma_2 < 1$. Thus, the theory developed for monotone systems (see for example, [14, 20]) and used to study global attractivity of other stage structured models (e.g., [1, 2, 17]) does not apply. Currently, no proof of global convergence to the unique positive fixed point is known in case $\gamma_1, \gamma_2 \in (0, 1]$ when the inherent net reproductive

number $R_0(\gamma_1, \gamma_2)$ is larger than one, although a large number of simulations we performed suggest that this might be the case.

We remark that the results in sections 3-5 can be extended to the following system of difference equations:

$$
\begin{array}{rcl}
J(t+1) & = & bB(t) + (1 - \gamma_1)s_1(J(t))J(t) \\
N(t+1) & = & \gamma_1 s_1(J(t))J(t) + (1 - \gamma_2)s_2(N(t) + B(t))N(t) \\
B(t+1) & = & \gamma_2 s_2(N(t) + B(t))N(t) + s_3(N(t) + B(t))B(t),
\end{array}
\tag{15}
$$

where s_i, $i = 1, 2, 3$ satisfy (Σ1), provided that the following assumption holds:

(Σ2) $0 < s_2(0) \le s_3(0) < 1$ and $s_2'(x) \le s_3'(x)$ for $x \in (0, \infty)$.

Clearly assumption (Σ2) implies that $s_2(x) \le s_3(x)$ for $x \in [0, \infty)$, which states that the survivorship of an individual in the nonbreeding stage is at most as high as that of an individual in the breeding stage. This may happen, for instance, if the older reproductive individuals (in comparison with newly metamorphosed juveniles) are better at avoiding predators (perhaps due to their larger size and stronger muscles, ability to move faster, or knowledge of predator locations), hence, increasing their chance of survival. Furthermore, individuals in the nonbreeding stage may suffer more severe density effects than individuals in the breeding stage, due to breeders being better competitors for food/resources than nonbreeders.

Similarly, the results in sections 3-5 can also be extended to the case where non-breeders are better competitors than breeders, and instead of (Σ2) the following condition is satisfied by s_i, $i = 2, 3$:

(Σ3) $0 < s_3(0) \le s_2(0) < 1$ and $s_3'(x) \le s_2'(x)$ for $x \in (0, \infty)$,

which implies that $s_3(x) \le s_2(x)$ for $x \in [0, \infty)$. Such a scenario may occur because reproduction requires the expenditure of immense amounts of energy leaving reproductive individuals more vulnerable to environmental conditions in comparison with nonreproductive adults and hence reducing their survival chances .

The proof of Theorem 1 changes slightly and only requires that (Σ1) holds ((Σ2) or (Σ3) are not needed here). But (Σ1) together with either (Σ2) or (Σ3) are required to establish monotonicity of system (15) for the case $\gamma_1 \in (0, 1]$ and $\gamma_2 = 1$. We defer the details to the Appendix.

We conclude this paper by pointing out that frogs reproduce seasonally. Thus, the birth rate is generally described by a periodic function which is positive during the reproduction season and zero otherwise. This results in a non-autonomous version of (1) where b is replaced with $b(t)$. Our future efforts will focus on studying the long term behavior of solutions to (1) with a periodic birth rate of this form.

Appendix

First notice that for (15) the inherent net reproductive number changes to

$$R_0(\gamma_1, \gamma_2) := \frac{b\gamma_1\gamma_2 a_1 a_2}{(1-(1-\gamma_1)a_1)(1-(1-\gamma_2)a_2)(1-a_3)}. \tag{16}$$

Theorem 5. *Let $(\Sigma1)$ hold for $i = 1, 2, 3$. Suppose $R_0(\gamma_1, \gamma_2) > 1$ then (15) has a unique interior fixed point $E^* = (J^*, N^*, B^*)$.*

Proof. A positive fixed point of (1) is a point $(J^*, N^*, B^*) \in \text{int}(\mathbb{R}^3_+)$ that satisfies

$$
\begin{aligned}
J &= bB + (1-\gamma_1)s_1(J)J \\
N &= \gamma_1 s_1(J)J + (1-\gamma_2)s_2(N+B)N \\
B &= \gamma_2 s_2(N+B)N + s_3(N+B)B.
\end{aligned}
\tag{17}
$$

From the first equation in (17) we get:

$$h(J) := (1 - (1-\gamma_1)s_1(J))J = bB.$$

Arguing as in the proof of Theorem 1, we have $J(B) = h^{-1}(bB)$ where $\lim_{B\to\infty} J(B) = \infty$, $J(0) = 0$ and $J'(B) > 0$. Observe also that

$$J(B) = \frac{bB}{1 - (1-\gamma_1)s_1(J(B))}. \tag{18}$$

Define $W = N + B$ and solve the second equation of (15) for N:

$$N(W, B) = \frac{\gamma_1 s_1(J(B))J(B)}{1 - (1-\gamma_2)s_2(W)}. \tag{19}$$

Thus, adding the second and the third equations of (17) we get

$$W = \gamma_1 s_1(J)J + s_2(W)N + s_3 B.$$

Then

$$\tilde{h}(W, B) := W - s_2(W)N(W, B) - s_3(W)B - \gamma_1 s_1(J(B))J(B) = 0,$$

and notice that $\tilde{h}(0, 0) = 0$. Now

$$\tilde{h}_W = 1 - s_2'(W)N(W, B) - s_2(W)N_W(W, B) - s_3'(W)B$$

and

$$\tilde{h}_B = -s_2(W)N_B(W, B) - s_3(W) - \gamma_1 s_1'(J(B))J'(B)J(B) - \gamma_1 s_1(J(B))J'(B).$$

From (19) it follows that $N_W(W, B) < 0$ and $N_B(W, B) > 0$ for any $(W, B) > 0$. Thus, $\tilde{h}_W > 0$ and $\tilde{h}_B < 0$. Now, applying the Implicit Function Theorem we get

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that there is a smooth $W(B)$ with $W(0) = 0$, $\tilde{h}(W(B), B) = 0$ and $W'(B) > 0$ for all $B > 0$.

Plugging the equations (18) and (19) for J and N into the B equation of (17) results in

$$B = \frac{\gamma_1 \gamma_2 s_1 s_2 b B}{(1 - (1 - \gamma_1)s_1)(1 - (1 - \gamma_2)s_2)} + s_3 B$$

As we are interested in a positive fixed point dividing by B we obtain:

$$1 = \frac{\gamma_1 \gamma_2 s_1 s_2 b}{(1 - (1 - \gamma_1)s_1)(1 - (1 - \gamma_2)s_2)} + s_3.$$

This is equivalent to

$$1 = \gamma_1 \gamma_2 s_1 s_2 b + (1 - \gamma_1)s_1 + (1 - \gamma_2)s_2(1 - (1 - \gamma_1)s_1)$$

$$+ s_3(1 - (1 - \gamma_1)s_1)(1 - (1 - \gamma_2)s_2) \tag{20}$$

$$= \hat{H}(J(B), W(B))) := H(B).$$

It clear that any interior equilibrium must satisfy (20).

Now differentiating $H(B)$ with respect to B and using the positivity of W' and J' together with a similar calculation as in the proof of Theorem 1 we get $H' < 0$. Also note that $\lim_{B \to \infty} H(B) = 0$. Thus, it follows that if $H(0) > 1$ then there exists a unique B^* such that $1 = H(B^*)$. (Clearly, $H(0) > 1$ is equivalent to $R_0(\gamma_1, \gamma_2) > 1$). From this and the above established relations between W, J and B it follows that there exists a unique interior equilibrium $E^* = (J^*, N^*, B^*)$. $\qquad \square$

Finally, it is not difficult to show that if $\gamma_1 \in (0, 1]$ and $\gamma_2 = 1$, then system (15) is monotone provided that ($\Sigma 2$) or ($\Sigma 3$) holds.

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