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Periodically Forced Nonlinear Systems of Difference Equations

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Dedicated to Gerry Ladas on his sixtieth birthday

The existence of nontrivial ($x \neq 0$) periodic solutions of a general class of periodic nonlinear difference equations is proved using bifurcation theory methods. Specifically, the existence of a global continuum of nontrivial periodic solutions that bifurcates from the trivial solution ($x = 0$) is proved. Conditions are given under which the nontrivial solutions are positive. A prerequisite Fredholm and adjoint operator theory for linear periodic systems is developed. An application to population dynamics is made.

Keywords: Nonlinear difference equations; Periodic difference equations; Periodic solutions; Global bifurcation

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1 INTRODUCTION

Systems of difference equations of the form

$$x(t+1) = Px(t), \quad t = 0, 1, 2, \ldots$$

(often called "matrix" equations) have found widespread application to a variety of fields, most notably to population dynamics [1,3–5].

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When the "projection matrix" $P = P(x(t))$ depends on the population state vector $x(t)$, the system is nonlinear. If P does not depend explicitly on t and the equation is "autonomous", then equilibria play a central role. In population dynamics, this is the case when the external environment and all demographic vital rates are constant in time (common modeling assumptions). The general theory of equilibria for nonlinear matrix equations is well developed [3–5]. A nonautonomous case of interest is when the projection matrix P is periodically dependent on t. This arises in population dynamics, for example, when periodic fluctuations occur in environmental or demographical parameters. Such fluctuations can be due to seasonal or daily environmental periodicities (e.g. in resource availability), periodic life cycles stages (e.g. birth and death rates), etc. In this case the projection matrix takes the form $P = P(t, x)$ where $P(t, x)$ is periodic in t with some integer period p. For equations of this form one is interested in the existence and stability of p-periodic solutions (in place of equilibria). Since the equation has the trivial p-periodic solution $x(t) \equiv 0$, the concern is with nontrivial p-periodic solutions and, in applications such as in population dynamics, with nonnegative or positive p-periodic solutions.

Applying bifurcation theory to a general class of difference equations containing a parameter (Eq. (11) (which includes matrix equations as a special case)), Henson [6] proved the existence of a continuum of nontrivial solutions that bifurcates from the trivial solution as the parameter is varied through a critical value. The result in [6] is local in that it establishes the existence of nontrivial p-periodic solutions only near the bifucation point. Our goal in this paper is to prove that this bifurcating continuum of nontrivial p-periodic solutions exists globally (Theorem 2). Furthermore, for the special case of matrix equations, we give conditions under which the continuum consists of positive solutions (Theorem 3).

We begin in Section 2 with some prerequisite linear theory. This theory is a Hilbert space reformulation and extension of the Fredholm theory for linear systems given in [6]. Our main results are proved in Section 3 for a class of difference equations that contain a parameter, namely equations of the form (11). Finally, an application to population dynamics is given in Section 4.

2 SOME LINEAR THEORY FOR PERIODIC MAPS

A Fredholm theory for systems of difference equations is proved in [6]. In this section we develop a Fredholm theory from a different point of view. We formulate the theory on a Hilbert space of sequences in terms of a related adjoint problem.

Let Z denote the set of integers. For $i, j \in Z \cup \{-\infty, +\infty\}$, define the subsets of integers

$$Z[i,j] \doteq \{n \in Z \mid i \le n \le j\},$$
$$Z(i,j] \doteq \{n \in Z \mid i < n \le j\},$$
$$Z[i,j) \doteq \{n \in Z \mid i \le n < j\},$$
$$Z(i,j) \doteq \{n \in Z \mid i < n < j\}.$$

For a positive integer $n \in Z[1, +\infty)$, let R^n denote the set of all $n \times 1$ (column) vectors of real numbers and $R^{n \times n}$ the set of all $n \times n$ matrices consisting of real numbers. For a positive integer $p \in Z[1, +\infty)$ define the linear spaces of p-periodic, "forward" p-periodic and "backward" p-periodic sequences:

$$S_p \doteq \{x\colon Z \to R^n \mid x(t+p) = x(t)\ \forall t \in Z\},$$
$$S_p^+ \doteq \{x\colon Z[0, +\infty) \to R^n \mid x(t+p) = x(t)\ \forall t \in Z[0, +\infty)\},$$
$$S_p^- \doteq \{x\colon Z(-\infty, p-1] \to R^n \mid x(t) = x(t-p)\ \forall t \in Z(-\infty, p-1]\}.$$

These spaces are finite dimensional Hilbert spaces under the inner product

$$\langle x, y \rangle \doteq \sum_{t=0}^{p-1} x(t) \cdot y(t), \tag{1}$$

where $x \cdot y$ denotes the usual inner product in R^n. Finally, let M_p denote the set of p-periodic sequences of $n \times n$ matrices, i.e.

$$M_p \doteq \{A\colon Z \to R^{n \times n} \mid A(t+p) = A(t)\ \forall t \in Z\}.$$

Consider the initial value problem

$$\begin{aligned} x(t+1) &= A(t)x(t) + h(t), \quad t \in Z[0, +\infty), \\ x(0) &= x_0, \end{aligned} \tag{2}$$

where the coefficient matrix $A(t)$ and $h(t)$ are p-periodic, i.e.

$$A \in M_p \quad \text{and} \quad h \in S_p. \tag{3}$$

We are interested in the existence of forward p-periodic solutions of (2), i.e. the existence of sequences $x \in S_p^+$ that satisfy the equations in (2).

We begin by developing formulas for the solutions of homogeneous and nonhomogeneous linear initial value problems. Given an integer $s \in Z$ and an initial vector $x_s \in R^n$, we can write the unique (forward) solution of the homogeneous initial value problem

$$\begin{aligned} x(t+1) &= A(t)x(t), \quad t \in Z[s, +\infty), \\ x(s) &= x_s \end{aligned}$$

as

$$x(t) = X(t,s)x_s, \quad t \in Z[s, +\infty),$$

where the "fundamental solution matrix" $X(t,s)$ is defined for $t \in Z[s, +\infty)$ by

$$X(t,s) = \begin{cases} A(t-1)A(t-2)\cdots A(s+1)A(s) & \text{for } t \in Z[s+1, +\infty), \\ I & \text{for } t = s. \end{cases} \tag{4}$$

Here I is the $n \times n$ identity matrix.

Given an integer $s \in Z$ and an initial vector $x_s \in R^n$, we can write the unique (forward) solution of the nonhomogeneous initial value problem

$$\begin{aligned} x(t+1) &= A(t)x(t) + h(t), \quad t \in Z[s, +\infty), \\ x(s) &= x_s \end{aligned}$$

as

$$x(t) = \begin{cases} X(t,s)x_s + \sum_{i=s}^{t-1} X(t, i+1)h(i) & \text{for } t \in Z[s+1, +\infty), \\ x_s & \text{for } t = s. \end{cases} \tag{5}$$

This formula is called the "variation of constants" formula.

LEMMA 1 *Suppose that* $x: Z[0, +\infty) \to R^n$ *satisfies the nonhomogeneous initial value problem* (2). *Then* $x \in S_p^+$ *if and only if* $x(p) = x(0)$.

Proof For $x \in S_p^+$, the condition $x(p) = x(0)$ follows by definition. Conversely, suppose that $x(p) = x(0)$. A straightforward calculation shows that $z: Z[0, +\infty) \to R^n$ defined by $z(t) \doteq x(t+p)$ also satisfies (2) and consequently (by uniqueness) $z(t) = x(t)$ for all $t \in Z[0, +\infty)$. It follows that x is forward p-periodic and hence lies in S_p^+.

The unique solution of the homogeneous initial value problem

$$\begin{aligned} x(t+1) &= A(t)x(t), \quad t \in Z[0, +\infty), \\ x(0) &= x_0 \end{aligned} \tag{6}$$

is given by $x(t) = X(t, 0)x_0$. Let $\ker(I - X(p, 0))$ denote the kernel (nullspace) of the $n \times n$ matrix $I - X(p, 0)$. By Lemma 1 the solution of (6) is (forward) p-periodic if and only if $x_0 \in \ker(I - X(p, 0))$.

The set of (forward) p-periodic solutions of (6), i.e. the set of solutions with initial vectors $x_0 \in \ker(I - X(p, 0))$, is a finite dimensional subspace of S_p^+ whose dimension is equal to $\dim \ker(I - X(p, 0))$. The initial value problem (6) has a "nontrivial" (forward) p-periodic solution if and only if $\dim \ker(I - X(p, 0)) > 0$, i.e. if and only if 1 is an eigenvalue of $I - X(p, 0)$ and x_0 is an associated right eigenvector.

The initial value problem

$$\begin{aligned} y(s-1) &= y(s)A(s) \quad \text{for } s \in Z(-\infty, p-1], \\ y(p-1) &= y_p \end{aligned} \tag{7}$$

will be called the "adjoint problem" associated with (6). Here $y^{\mathrm{T}}: Z(-\infty, p-1] \to R^n$ where $y^{\mathrm{T}}(t)$ denotes the transpose of $y(t)$ (thus, $y(t)$ is a $1 \times n$ row vector). The unique solution of the adjoint problem (7) is given by

$$y(s) = y_p X(p, s+1) \quad \text{for } s \in Z(-\infty, p-1].$$

The solution $y(s)$ of the adjoint problem (7) is (backward) p-periodic if $y(s) = y(s-p)$ for all $s \in Z(-\infty, p-1]$. A proof similar to that given for Lemma 1 shows that the solution of (7) is (backward) p-periodic if and only if $y(p-1)=y(-1)$, i.e. if and only if $y_p^{\mathrm{T}} \in \ker(I-X^{\mathrm{T}}(p,0))$. The set of (backward) p-periodic solutions of the adjoint problem (7), i.e. the set of solutions with initial vectors satisfying $y_p^{\mathrm{T}} \bullet \ker(I-X^{\mathrm{T}}(p,0))$, is a finite dimensional Hilbert space whose dimension is equal to $\dim\ker(I-X^{\mathrm{T}}(p,0))=\dim\ker(I-X(p,0))$. The adjoint problem (7) has a nontrivial (backward) p-periodic solution if and only if $\dim\ker(I-X(p,0))>0$, i.e. if and only if 1 is an eigenvalue of $I-X^{\mathrm{T}}(p,0)$ and y_p^{T} is an associated eigenvector (i.e. y_p is a left eigenvector of $I-X(p,0)$).

To conclude these preliminaries we return to the nonhomogeneous initial value problem (2) and the existence of p-periodic solutions. By Lemma 1 the solution of (2) is (forward) p-periodic if and only if the initial condition x_0 satisfies the linear algebraic equation

$$(I-X(p,0))x_0=\sum_{i=0}^{p-1}X(p,i+1)h(i).$$

This equation is uniquely solvable for $x_0\in R^n$ if and only if $\dim\ker(I-X(p,0))=0$. If $\dim\ker(I-X(p,0))>0$, then this equation has a solution if and only if the right-hand side is orthogonal to all vectors in $\ker(I-X^{\mathrm{T}}(p,0))$, i.e. if and only if

$$y_p\sum_{i=0}^{p-1}X(p,i+1)h(i)=0, \quad \forall y_p^{\mathrm{T}}\in I-X^{\mathrm{T}}(p,0) \tag{8}$$

Since $y(i)=y_pX(t,i+1)$ is a p-periodic solution of the adjoint problem (7) we have arrived at the following result.

THEOREM 1 *Consider the nonhomogeneous initial value problem* (2) *with p-periodic coefficients* (3).

(a) *If the associated homogeneous initial value problem* (6) *has no nontrivial (forward) p-periodic solution* (*i.e.* $\dim\ker(I-X(p,0))=0$), *then* (2) *has a unique (forward) p-periodic solution. This solution is given by the initial condition*

$$x_0=(I-X(p,0))^{-1}\sum_{i=0}^{p-1}X(p,i+1)h(i). \tag{9}$$

(b) *If the associated homogeneous initial value problem* (6) *has a nontrivial* (*forward*) *p-periodic solution* (*i.e.* $\dim\ker(I - X(p,0)) > 0$), *then* (2) *has a* (*forward*) *p-periodic solution if and only if* $h(t)$ *is orthogonal to all* (*backward*) *p-periodic solutions of the adjoint problem* (7) (*i.e. if and only if* (8) *holds*).

This theorem is a reformulation in terms of adjoint solutions of Theorem 1 in [6]. In the first alternative (a), the unique (forward) p-periodic solution of (2) is given by the variation of constants formula

$$x(t) = \begin{cases} x_0 + \sum_{i=0}^{t-1} X(t, i+1)h(i) & \text{for } t \in Z(1, +\infty), \\ x_0 & \text{for } t = 0, \end{cases}$$

with x_0 given by (9). This formula can be written

$$x(t) = \sum_{i=0}^{p-1} G(t,i)h(i),$$

where the "Green's function" $G : Z[0, +\infty) \times Z[0, p-1]$ is defined given by

$$G(t,i) = \begin{cases} (I - X(p,0))^{-1}X(p, i+1) + X(t, i+1) & \text{for } 0 \le i < t, \\ (I - X(p,0))^{-1}X(p, i+1) & \text{for } 0 \le t \le i \le p-1. \end{cases}$$

Under the assumption that there exist no nontrivial p-periodic solution of the homogeneous initial value problem (6), i.e. that $\dim\ker(I - X(p,0)) = 0$, the "solution" operator

$$G : S_p^+ \to S_p^+ \tag{10}$$

defined by the Green's function $G(t,s)$, namely by $G(h) \doteq \sum_{i=0}^{p-1} G(t,i)h(i)$, is linear, bounded and compact (since S_p^+ is finite dimensional). For $h \in S_p^+$, $x = G(h)$ is the unique (forward) p-periodic solution of the nonhomogeneous initial value problem (2).

3 A GLOBAL BIFURCATION THEOREM

We are interested in the existence of (forward) p-periodic solutions of periodically forced, nonlinear equations containing a parameter.

Specifically, we will consider nonlinear equations of the form

$$x(t+1) = A(t)x(t) + \lambda B(t)x(t) + h(t, \lambda, x(t)), \quad t \in Z[0, +\infty), \quad (11)$$

where

$$A, B \in M_p \quad \text{and} \quad \lambda \in R$$

and h is "higher order" in x, i.e.

$$h : Z \times R \times \Omega \to S_p^+ \text{ is continuous;}$$

$$\|h(t, \lambda, x)\| = o(\|x\|) \quad \text{near } x = 0 \text{ uniformly on finite } \lambda \text{ intervals.}$$

Here the norm $\|\cdot\|$ is defined by $\|x\| = \langle x, x\rangle^{1/2}$ and Ω is an open neighborhood of $x = 0$ in S_p^+.

A "*p-periodic solution pair*" of (11) is a pair $(\lambda^*, x^*) \in R \times S_p^+$ such that $x = x^*(t)$ is a (forward) p-periodic solution of (11) with $\lambda = \lambda^*$. A pair $(\lambda, 0)$ is a p-periodic solution pair for all $\lambda \in R$ and will be called a "*trivial solution pair*". A solution pair (λ, x) for which $x \neq 0$ will be called a "*nontrivial solution pair*". Let N_p^+ denote the set of nontrivial p-periodic solution pairs of (11) and let $cl\left(N_p^+\right)$ denote its closure in S_p^+.

We assume (6) has no nontrivial p-periodic solution, i.e.

$$\dim \ker(I - X(p, 0)) = 0,$$

where $X(t, s)$ is the fundamental matrix (4) associated with the coefficient matrix $A(t)$. Then, as far as p-periodic solutions are concerned, the nonlinear equation (11) is equivalent to the operator equation

$$x = \lambda Lx + g(\lambda, x)$$

where $L : S_p^+ \to S_p^+$ is the linear operator that maps $x(t)$ to $G(B(t)x(t))$ and $g : \Omega \times R \to S_p^+$ is the nonlinear operator that maps (λ, x) to $G(h(t, \lambda, x(t)))$. Here G is the linear operator (10) defined by the Green's function associated with the coefficient matrix $A(t)$. Because G is a compact operator, it follows that L is compact and that g is completely continuous (i.e. continuous and compact). Moreover, the assumption on h implies that $\|g(\lambda, x)\| = o(\|x\|)$ near $x = 0$ uniformly on finite λ intervals.

We are now in a position to apply a general global bifurcation result of Rabinowitz [9]. To do this we need to consider the characteristic values λ of the operator L, i.e. those values of λ such that

$$x = \lambda Lx \quad \text{for some } 0 \neq x \in S_p^+.$$

By construction λ is a characteristic value of L if and only if the associated characteristic sequence $0 \neq x \in S_p^+$ is a nontrivial (forward) p-periodic solution of the linear equation

$$x(t+1) = A(t)x(t) + \lambda B(t)x(t), \quad t \in Z[0, +\infty), \tag{12}$$

in which case λ will be called a "*characteristic value of* (12)" and x its associated p-periodic "*characteristic solution*". Let $X(t, s, \lambda)$ denote the fundamental solution matrix associated with the coefficient $A(t) + \lambda B(t)$. Note that $X(t, s)$ above (and in the previous section) is the same as $X(t, s, 0)$. A characteristic value λ is called "*odd*" if the dimension of associated space of characteristic solutions is odd, i.e. if and only if $\dim\ker(I - X(p, 0, \lambda))$ is odd; if this dimension is equal to one, λ is called "*simple*". The following result follows directly from Corollary 1.12 in [9].

THEOREM 2 *Suppose $\lambda_0 \neq 0$ is an odd characteristic value and $\lambda = 0$ is not a characteristic value of* (12). *Then $cl(N_p^+)$ contains a continuum C_p^+ (i.e. a closed connected set) with the following properties*:

(a) $(\lambda_0, 0) \in C_p^+$;
(b) *C_p^+ either connects to the boundary of $R \times \Omega$ or contains a trivial pair $(\lambda^*, 0) \in C_p^+$ for some odd characteristic value $\lambda^* \neq \lambda_0$.*

Because part (a) implies the continuum C_p^+ intersects the set of trivial solutions, we say that $(\lambda_0, 0)$ is a "*bifurcation point*". Part (b) is referred to as the Rabinowitz Alternative. Because it implies that the continuum C_p^+ either connects to the boundary of $R \times \Omega$ or to another bifurcation point $(\lambda^*, 0)$, the theorem is referred to as a "global" bifurcation result. By "connects to" is meant that there exists a sequence of solution pairs in C_p^+ that approaches the boundary of $R \times \Omega$. This includes the possibility that C_p^+ "connects to ∞", i.e. is unbounded in $R \times S_p^+$. To be unbounded means that one of the components λ or x in the pair (λ, x) is unbounded for pairs lying in C_p^+. Often in applications the second alternative in (b) can be ruled out and $\Omega = S_p^+$, in which case alternative (b) implies that there exists an unbounded continuum of nontrivial p-periodic solutions that bifurcates from the trivial solution at $\lambda = \lambda_0$. This means that either the spectrum of λ values or the amplitudes $\|x\|$ from solution pairs on the continuum C_p^+ is an unbounded interval (or both).

As a special case, consider the nonlinear matrix equation

$$x(t+1) = P(t, \lambda, x(t))x(t), \quad t \in Z[0, +\infty), \tag{13}$$

where

$$\begin{aligned}&\text{for each } t \in Z[0, +\infty) \text{ and } \lambda \in R\\ &\quad P(t, \lambda, \cdot) : \Omega \to M_p \text{ is continuously differentiable.}\end{aligned} \tag{14}$$

Here Ω is an open neighborhood of the nonnegative cone $K \doteq \{x \in S_p^+ \colon x(t) \geq 0 \text{ for } t \in Z[0, +\infty)\}$. These types of equations arise in population dynamics in which P is a projection matrix that maps a population distribution vector x from one time step to the next; see Section 4 below for an example. Write

$$P(t, \lambda, x) = P_0(t, \lambda)x + r(t, \lambda, x),$$

$$\|r(t, \lambda, x)\| = O(\|x\|) \quad \text{near } x = 0 \text{ uniformly on finite } \lambda \text{ intervals},$$

and assume that P_0 is linear in λ, so that

$$P_0(t, \lambda) = A(t) + \lambda B(t). \tag{15}$$

Then (13) has the form (11) and Theorem 2 applies to this problem.

In applications to population dynamics, one is interested in positive solutions $x(t)$. In order to obtain results concerning the positivity of solutions on the continuum C_p^+, we make two further assumptions:

$$\begin{aligned}&\text{if } 0 \leq x \in S_p^+ \text{ solves (13), then}\\ &\quad \text{either } x(t) > 0 \text{ or } x(t) = 0 \text{ for all } t \in Z[0, +\infty)\end{aligned} \tag{16}$$

and

> there exists a simple characteristic value λ_0 of (12) whose associated characteristic p-periodic solution is positive $x_0(t) > 0$ and no other characteristic value has a nonnegative characteristic p-periodic solution. (17)

THEOREM 3 Assume (14–17). *Suppose* $\lambda = 0$ *is not a characteristic value of* (12). *Then the continuum* C_p^+ *from Theorem* 2 *contains an unbounded subcontinuum* P_p^+ *such that* $(\lambda, x) \in P_p^+/\{(\lambda_0, 0)\}$ *implies* x *is a positive p-periodic solution of* (13).

Proof It follows from the local bifurcation result of [6] that, in a neighborhood of the bifurcation point $(\lambda_0, 0)$, the continuum C_p^+ of Theorem 2 can be parameterized by $x(t) = \varepsilon x_0(t) + y(t, \varepsilon)$ where $\|y(t, \varepsilon)\| = o(|\varepsilon|)$ for ε small. Thus, locally near the bifurcation point, C_p^+ consists of two subcontinua defined by $\varepsilon > 0$ and $\varepsilon < 0$ respectively. From (17) we see that the first of these subcontinua, which we denote by P_p^+, contains, with the exception of the trivial solution for $\varepsilon = 0$, positive solutions. Because λ_0 is simple, Theorem 1.40 of [9] implies P_p^+ also satisfies the alternative (b) in Theorem 2.

First we argue that the set (continuum of) solutions x arising from pairs on the continuum P_p^+ cannot leave the positive cone K (except at the bifurcation point $(\lambda_0, 0)$). If this were not the case, then there would exist a solution pair (λ', x') with $\lambda' \neq \lambda_0$ and x' lying on the boundary ∂K of the cone K. By assumption (16), it would follow that $x' = 0$. Moreover, since P_p^+ is a continuum there would exist a sequence $(\lambda_n, x_n) \in P_p^+$ with $x_n \in K$ such that $(\lambda_n, x_n) \to (\lambda', 0)$. Since S_p^+ is finite dimensional, we can assume (without loss in generality) that the limit

$$\lim_{n \to +\infty} \frac{x_n}{\|x_n\|} = y' \geq 0$$

exists. From $x_n = \lambda_n L x_n + g(\lambda_n, x_n)$ we obtain

$$\lim_{n \to +\infty} \frac{x_n}{\|x_n\|} = \lim_{n \to +\infty} \left[\lambda_n L\left(\frac{x_n}{\|x_n\|}\right) + \frac{g(\lambda_n, x_n)}{\|x_n\|} \right],$$

$$y' = \lambda' L y',$$

that is to say, $\lambda' \neq \lambda_0$ is a characteristic value with a nonnegative characteristic solution $y' \geq 0$. This is a contradiction to assumption (17).

By the same argument, the second alternative in part (b) of Theorem 2 is ruled out. This leaves us with the fact that the continuum P_p^+ connects to the boundary of $R \times \Omega$. Since Ω is an open neighborhood of the cone K, it follows that P_p^+ must connect to ∞, i.e. be unbounded.

Theorems 2 and 3 are existence theorems. The stability of those p-periodic solutions from the continuum C_p^+ lying in a neighborhood of the bifurcation point $(\lambda_0, 0)$ is studied in [6], where conditions are given sufficient for an exchange of stability to occur between the continuum of trivial solutions and the continuum C_p^+.

4 AN APPLICATION TO POPULATION DYNAMICS

The following system of three difference equations has been applied to the dynamics of laboratory cultures of flour beetles:

$$\begin{aligned}
x_1(t+1) &= bx_3(t)\exp[-c_{\mathrm{ea}}x_3(t) - c_{\mathrm{el}}x_1(t)],\\
x_2(t+1) &= (1-\mu_{\mathrm{l}})x_1(t),\\
x_3(t+1) &= x_2(t)\exp\left[-c_{\mathrm{pa}}x_3(t)\right] + (1-\mu_{\mathrm{a}})x_3(t).
\end{aligned}$$

In these equations $x_1(t)$, $x_2(t)$ and $x_3(t)$ are the number of larvae, pupae and adult beetles at time t (the time unit is two weeks), $\mu_{\mathrm{l}} < 1$ and $\mu_{\mathrm{a}} < 1$ are the larval and adult mortality probabilities (per unit time); the positive constants c_{ea}, c_{el} and c_{pa} are the "cannibalism coefficients" expressing mortality of eggs and pupae due to cannibalism by adults and larvae; and $b > 0$ is the larval recruitment rate (per adult) in the absence of cannibalism. In order to study the effects of a periodically fluctuating habitat on beetle dynamics, such as in the experiments of Jillson [8], the assumption that cannibalism rates are inversely proportional to flour volume was introduced into this model in [2,7]. (This assumption has been validated in laboratory experiments [2].) This modification results in the periodic system

$$\begin{aligned} x_1(t+1) &= bx_3(t)\exp\left[-\frac{c_{\mathrm{ea}}}{v(t)}x_3(t) - \frac{c_{\mathrm{el}}}{v(t)}x_1(t)\right], \\ x_2(t+1) &= (1-\mu_{\mathrm{l}})x_1(t), \\ x_3(t+1) &= x_2(t)\exp\left[-\frac{c_{\mathrm{pa}}}{v(t)}a(t)\right] + (1-\mu_{\mathrm{a}})x_3(t), \end{aligned} \tag{18}$$

where $0 < v \in S_p^+$ is a positive p-periodic sequence with mean equal to one. Only the case of period $p = 2$ cycles is considered in [2,7] (although the experiments in [8] were done for other periods as well). We will consider a general integer period p and use the larval recruitment rate as the bifurcation parameter. More exactly, we use the bifurcation parameter

$$\lambda = b - \frac{1}{2}\frac{\mu_{\mathrm{a}}}{1-\mu_{\mathrm{l}}}.$$

The system (18) is of the form (13) with

$$P(t,\lambda,x) = \begin{pmatrix} 0 & 0 & \left(\frac{1}{2}\mu_{\mathrm{a}}/(1-\mu_{\mathrm{l}}) + \lambda\right)\exp[-(c_{\mathrm{ea}}/v(t))x_3(t) - (c_{\mathrm{el}}/v(t))x_1(t)] \\ 1-\mu_{\mathrm{l}} & 0 & 0 \\ 0 & \exp[-(c_{\mathrm{pa}}/v(t))x_3(t)] & 1-\mu_{\mathrm{a}} \end{pmatrix}$$

The linear part of this projection matrix

$$P_0(t,\lambda) = \begin{pmatrix} 0 & 0 & \frac{1}{2}\mu_{\mathrm{a}}/(1-\mu_{\mathrm{l}}) + \lambda \\ 1-\mu_{\mathrm{l}} & 0 & 0 \\ 0 & 1 & 1-\mu_{\mathrm{a}} \end{pmatrix}$$

$$= \begin{pmatrix} 0 & 0 & \frac{1}{2}\mu_{\mathrm{a}}/(1-\mu_{\mathrm{l}}) \\ 1-\mu_{\mathrm{l}} & 0 & 0 \\ 0 & 1 & 1-\mu_{\mathrm{a}} \end{pmatrix} + \lambda \begin{pmatrix} 0 & 0 & 1 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

is a *constant* Leslie matrix (and hence p-periodic). Clearly assumptions (14) and (15) are satisfied.

Consider assumption (16). Suppose that $x(t) \geq 0$ is a nonnegative p-periodic solution of (18). If $x_3 > 0$ at some $t' \in Z[0, +\infty)$, then from (18) we find that x_1 and x_2 are positive at $t' + 1$ and hence x_1, x_2, and x_3 are positive for all $t \geq t' + 2$. We conclude that if x_3 is positive at some time, then x is positive for all $t \in Z[0, +\infty)$. If, on the other hand, $x_2 > 0$ at some $t' \in Z[0, +\infty)$, then from (18) we find that $x_3 > 0$ at $t' + 1$ and, as just shown, this in turn implies x is positive for all $t \in Z[0, +\infty)$. Finally, if $x_1 > 0$ at some $t' \in Z[0, +\infty)$, then from (18) we find that $x_2 > 0$ at $t' + 1$ and, as just shown, this implies x is positive for all $t \in Z[0, +\infty)$. We conclude, then, that unless $x = 0$ for all $t \in Z[0, +\infty)$ it must be the case that $x > 0$ for all $t \in Z[0, +\infty)$. This verifies assumption (16) for the system (18).

The final assumptions in Theorem 2 concern the nontrivial p-periodic solutions of the linear matrix equation (12), i.e.

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & \frac{1}{2}\mu_a/(1-\mu_l) + \lambda \\ 1-\mu_l & 0 & 0 \\ 0 & 1 & 1-\mu_a \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \end{pmatrix}. \quad (19)$$

Since the coefficient matrix is irreducible and primitive (its fourth power is strictly positive), the Perron/Frobenius theorem implies that it has a strictly dominant, positive, simple eigenvalue $\xi > 0$ with a positive eigenvector

$$v = \begin{pmatrix} v_1 \\ v_2 \\ v_3 \end{pmatrix} > 0$$

and that there exists no other nonnegative eigenvector (for any eigenvalue). This means that the positive periodic solutions of the linear equation (19) can be obtained only when ξ equals 1 and in this case the solutions are the equilibrium eigenvector solutions given by the associated positive eigenvectors. The dominant eigenvalue equals 1 if and only if $\lambda = \lambda_0 = \frac{1}{2}\mu_a/(1-\mu_l)$. For this (and only for this) value of λ does (12) have a positive p-periodic solution. This proves that assumption (17) holds for the system (18).

Finally, when $\lambda = 0$, the dominant eigenvalue of the coefficient matrix in (19) is less than 1. Consequently all solutions of (19) tend to 0 as $t \to +\infty$ and in particular none are p-periodic. This implies that $\lambda = 0$ is not a characteristic value.

Theorem 3 now applies to the system (18). It follows that there exists an unbounded continuum of positive p-periodic solutions that bifurcates from the trivial solution at $\lambda = \frac{1}{2}\mu_a/(1-\mu_l)$, i.e. at $b = \mu_a/(1-\mu_l)$.

The local analysis given in [7] for the case $p = 2$ shows that the positive period-2 solutions on the bifurcating continuum exists for $b > \mu_a/(1-\mu_l)$ and are (locally asymptotically stable). The direction of bifurcation and local stability for periods $p > 2$ have not been studied for this model, although the general results in [6] show that the usual exchange of stability principle holds. Stability (or instability) results for positive periodic solutions outside a neighborhood of the bifurcation point have not been obtained.

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