SIAM J. APPL. MATH
Vol 33, No 4, December 1977

BIFURCATION OF PERIODIC SOLUTIONS OF INTEGRODIFFERENTIAL SYSTEMS WITH APPLICATIONS TO TIME DELAY MODELS IN POPULATION DYNAMICS*

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Abstract. A Fredholm alternative is proved for a general linear system of Stieltjes integrodifferential equations. This result is used to derive necessary and sufficient conditions for the bifurcation of nontrivial periodic solutions of a nonlinear perturbation of the system containing n parameters. The results are applied to several models from mathematical ecology which describe the dynamics of various species interactions (included are models of mutualistic, competitive and predator-prey interactions) under the influence of time delays. These applications illustrate how, for such models, the existence of multi-dimensional manifolds of periodic solutions of various periods in the presence of unstable equilibria can occur as a result of the presence of time delays at least for birth rates near certain ciritical values.

1. Introduction. Our purpose here is to consider the bifurcation from equilibrium of periodic solutions of a general class of Stieltjes integrodifferential systems which occurs as a function of several parameters appearing in the system. The motivation for this inquiry and for the form of the systems is found in the theory of population dynamics with (possible) time delays.

Volterra, in the 1930's [20], seems to have been the first to consider time delays in the study of interaction species and many others have contributed to the study of such systems since that time (see the bibliography in [14] for a list of references). Several authors have considered the existence of periodic solutions of ecological models for two or more interacting species when time delays are present. The early work of Cunningham and Wangersky [4] on a predator-prey model with a single time lag has received much attention, but is often criticised mathematically [16]. Purely linearized studies of predator-prey interactions with delays can be found in [12], [14], [15], [18] and of two competing species in [10]. Periodic solutions of forced predator-prey interactions with delays has been studied in [6], [11]. The problems of the existence of nonconstant periodic solutions in the presence of an equilibrium was considered for predator-prey models in [2], [8], [13] and for general two species interactions in [7]. A detailed ecological discussion and numerical simulation is made of a three species predator-prey interaction with delays in [3].

The main result of this paper (Theorem 2) asserts the existence of nonconstant periodic solutions which bifurcate from equilibrium as certain parameters pass through critical values for a general system of Stieltjes integrodifferential equations. When applied to a system of the form

$$N_j^{-1}\, dN_j/dt = b_j f_j(N_1, \cdots, N_n), \qquad 1 \leqq j \leqq n, \quad n \geqq 2, \tag{1.1}$$

where f_j is a functional of some sort which may (or may not) involve time lags or time delays, this result generalizes the main result in [7] which deals with the case $n=2$ and f_j linear in its arguments. Most (but not all) models used in the above cited references are of the form (1.1) as are in fact most differential models used in

* Received by the editors July 21, 1976, and in revised form January 15, 1977.
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population dynamics. Some applications of Theorem 2 to such ecological models are given in § 4 where, with one exception, these examples deal with models of $n=3$ species interactions. An example dealing with an $n=2$ predatory-prey interaction is also discussed and related to some recent work of May [14], [15]. A different predator-prey example is studied by means of our approach here in [8] where numerical evidence of our results here may also be found. For further $n=2$ examples see [7].

We do not consider the stability of the bifurcating periodic solutions in this paper. The problem of determining the stability of a nonconstant periodic solution is in general quite difficult for integrodifferential systems (and even for ordinary differential systems). In this regard MacDonald's recent paper [13] should be pointed out. In this paper the bifurcation of periodic solutions is considered for a $n=2$ predator-prey model with delays. MacDonald's approach is to convert the integrodifferential system to a larger differential system (a trick which works only for special kernels and dates back at least to Volterra's work [19]) and then apply Hopf bifurcation techniques, some of which yield the stability of the bifurcating periodic solutions [17]. These results of MacDonald for a predator-prey model seem to be the only analytically obtained stability results for the bifurcating periodic solutions of integrodifferential systems. Numerical evidence of this stability for predator-prey models can be found in [8].

The proof of our main result Theorem 2 is carried out in § 3 by means of Lyapunov–Schmidt expansions. The method and results differ from most bifurcation results in that the problem considered here has many parameters instead of just one. This approach requires a Fredhom alternative for linear Stieltjes integrodifferential systems which is proved in § 2.

Finally we point out that as far as applications to models (1.1) in population dynamics with delays are concerned our main result Theorem 2 is really (nonvacuously) applicable only to systems with $n \geqq 2$. The reason is that in hypothesis (H4) we assume $n \geqq r \geqq 1$ (r is the number of independent, nontrivial periodic solutions of the linearized adjoint problem) in order to avoid an overdetermined set of algebraic equations in the Lyapunov–Schmidt method. Thus, if $n=1$ and f_1 in (1.1) is an expression involving $\int_{-\infty}^{t} d_s k(t-s) N_1(s)$ where $dk(s) \geqq 0$, $k(s) \not\equiv 0$ for all $s \geqq 0$ (as is usually assumed in delay models) then (H4) implies $r=1$ which in turn implies $\mu=0$. In this case Theorem 2 yields only the trivial branch of solutions $b_1=0$, $N_1=c$ where c is an arbitrary constant. As a result of this, Theorem 2 does not apply to the single species model (1.1) with $n=1$, a model which has received a great deal of attention in the literaure.

2. Periodic solutions of linear systems. Our goal in this section is to obtain necessary and sufficient conditions for the existence of nontrivial periodic solutions of a given period p (or, in short, p-period solutions) of the homogeneous system

$$y'(t)=\int_{-\infty}^{t} d_s A(t-s) y(s) \tag{2.1}$$

and to prove a Fredholm alternative for the nonhomogeneous system

$$x'(t)=\int_{-\infty}^{t} d_s A(t-s) x(s)+f(t) \tag{2.2}$$

with p-periodic forcing function $f(t)$.

We assume throughout this paper that the systems have kernels which satisfy the following hypothesis:

(H1) The $n \times n$ matrix $A(t)$ is (or more precisely its entries are) of bounded variation on every finite interval of the half line $t \geqq 0$ and satisfies $\int_0^\infty |dA(t)| < +\infty$.

If $x(t)$ is continuous for all t then so is

$$\mathscr{A}(x) \equiv \int_{-\infty}^{t} d_sA(t-s)x(s) = \int_0^\infty dA(s)x(t-s)$$

for all t [1, p. 144]. As a result of this and of (H1) we see that if $P(p)$ denotes the Banach space of real, n-vector valued functions continuous and p-periodic for all t under the sup norm $|x|_0 = \sup_{0 \leqq t \leqq p} |x(t)|$ then $x \in P(p)$ implies $\mathscr{A}(x) \in P(p)$. We must also consider the *adjoint system*

$$z'(t) = -\int_t^\infty d_sA^T(s-t)z(s) \tag{2.3}$$

where A^T denotes the transpose of A. Reasoning in a fashion similar to that above for the right-hand side of (2.1), we find that (H1) and $z \in P(p)$ imply that the right-hand side of (2.3) lies in $P(p)$.

Let $x \cdot y$ denote the usual inner product on complex Euclidean n-space: $x \cdot y = \sum_1^n x_j\bar{y}_j$ where throughout this paper a bar over a letter means complex conjugation and let $(x(t), y(t)) = p^{-1} \int_0^p x(t) \cdot y(t)\, dt$ for $x, y \in P(p)$.

By a *solution* in $P(p)$ of any of the above systems we mean a function, differentiable for almost all t, which reduces the equation to an identity for almost all t. In view of the above remarks, (H1) implies that a solution in $P(p)$ of any of the above systems is necessarily continuously differentiable.

THEOREM 1. *Assume $A(t)$ satisfies* (H1) *and let $p > 0$ be any given positive real number. Then the following conclusions hold*:

(a) *the homogeneous system* (2.1) *has at most a finite number $r \geqq 0$ of independent nontrivial (i.e. $y(t) \not\equiv 0$) solutions $y^j \in P(p)$*;

(b) *the adjoint system* (2.3) *has exactly r independent nontrivial solutions $z \in P(p)$*;

(c) *if $r = 0$ then the nonhomogeneous system* (2.2) *has, for every $f \in P(p)$, a unique solution $x \in P(p)$*;

(d) *if $r \geqq 1$ then the nonhomogeneous system* (2.2) *has a solution in $P(p)$ if and only if $(f, z) = 0$ for every solution $z \in P(p)$ of the adjoint system* (2.3), *i.e.* $(f, z^j) = 0$, $1 \leqq j \leqq r$ *for any set $z^j \in P(p)$ of r independent solutions of* (2.3);

(e) *if $P_0(p)$, $P_{00}(p)$ denote the Banach subspaces of those $x \in P(p)$ satisfying $(x, y^j) = 0$, $(x, z^j) = 0$ respectively, then for every $f \in P_{00}(p)$ there exists a unique solution $x = Lf \in P_0(p)$ of the nonhomogeneous system* (2.2) *and the operator $L: P_{00}(p) \to P_0(p)$ is linear and compact.*

Proof. (a) To find solutions $y \in P(p)$ of (2.1) we substitute into (2.1) the Fourier series

$$\sum_{m=-\infty}^{+\infty} c_m \exp(im\omega t), \qquad \omega = 2\pi/p, \quad \bar{c}_m = c_{-m}, \tag{2.4}$$

for $y(t)$ where the Fourier coefficients c_m are complex n-vectors. If

$$A_m = \int_0^{\infty} dA_s(s) \exp(-im\omega s) \tag{2.5}$$

then we find that (2.1) yields

$$(A_m - im\omega I)c_m = 0, \qquad -\infty < m < +\infty, \tag{2.6}$$

where I is the $n \times n$ identity matrix. Note that the entries of A_m are bounded independently of m under the hypothesis (H1) and as a result $|\det(A_m - im\omega I)| \to +\infty$ as $|m| \to +\infty$. Consequently $\det(A_m - im\omega I)$ is nonzero for $|m| \geqq m_1 \geqq 0$ for some integer $m_1 \geqq 0$ which implies that $c_m = 0$ for all $|m| \geqq m_1$. This proves (a).

(b) If the Fourier series (2.4) with coefficients d_m in place of c_m is substituted for $z(t)$ into the adjoint system (2.3) we find

$$(A_m^* + im\omega I)\, d_m = 0, \qquad -\infty < m < +\infty, \tag{2.7}$$

where $A_m^* = \bar{A}_m^T$, the complex conjugate transpose of A_m. Since the coefficient matrix for (2.7) is just the conjugate transpose of that for (2.6), equation (2.6) is solvable for some m if and only if (2.7) is. Moreover, the number of independent solutions d_m of (2.7) is the same as that for (2.6). Let $M = \{m: \det(A_m - im\omega I) = 0\}$.

(c) If $f(t) = \sum_{m=-\infty}^{+\infty} f_m \exp(im\omega t)$, $f_{-m} = \bar{f}_m$ and the Fourier series (2.4) for $x(t)$ are substituted into (2.2) we obtain the equations

$$(A_m - im\omega I)c_m = -f_m, \qquad -\infty < m < +\infty, \tag{2.8}$$

to be solved for c_m. If $r = 0$ then by the proof of (a) above each coefficient matrix in (2.8) is invertible and hence (2.8) may be uniquely solved for c_m. Thus (2.4) will define a real valued solution $x \in P(p)$ of (2.2) for these unique c_m provided we can show that this Fourier series defines an absolutely continuous function.

It is clear, since the entries of A_m are bounded uniformly in m, that the determinant and the cofactors of $A_m - im\omega I$ are of order m^n and m^{n-1} respectively. From Cramer's rule we deduce the bounds

$$|c_0| \leqq K f_0 \quad \text{and} \quad m|c_m| \leqq K|f_m| \quad \text{for } m \neq 0$$

for some constant $K > 0$ independent of m. Thus

$$\sum_{m=-\infty}^{+\infty} m^2 |c_m|^2 \leqq K^2 \sum_{m=-\infty}^{+\infty} |f_m|^2 = K^2 |f|_2^2 < +\infty$$

where $|f|_2$ is the L^2 norm of $f \in P(p)$ on $[0, p]$: $|f|_2 = (f, f)^{1/2}$. The Riesz–Fischer theorem implies that $x(t)$ defined by (2.4) lies in L^2 while the above estimate implies $x(t)$ is absolutely continuous [9, p. 129].

(d) This part follows rather straightforwardly from the fact that (2.8) has a solution c_m for $m \in M$ if and only if $f_m \cdot d_m = 0$ for all solutions d_m, $m \in M$ of the adjoint system (2.7) and that in this case there is a unique solution c_m orthogonal to the solution space of (2.6) which satisfies $|c_m| \leqq K|f_m|$, $m \in M$. We deduce the absolute continuity of (2.4) just as in (c).

(e) It follows from (c) and (d) that L is well defined. It is easy to see that L is linear and hence we need only prove that L is compact.

Let $f^n \in P_{00}(p)$ be a bounded sequence $|f^n|_0 \leqq K$ and let $x^n = Lf^n$. From the inequality (2.9) for the Fourier coefficients $c_m^{(n)}$ of x^n and from the Schwarz inequality we obtain for all n the inequality

$$|x^n|_0 \leqq \sum_{m=-\infty}^{+\infty} |c_m^{(n)}| \leqq K^* |f^n|_2$$

for a positive constant $K^* > 0$ independent of n. Since $|f^n|_0 \leqq K$ implies $|f^n|_2 \leqq K$ we see that the sequence $x^n \in P_0(p)$ is uniformly bounded. In addition since each x^n solves (2.2) with forcing function $f^n(t)$ we see that the sequence of derivatives dx^n/dt is uniformly bounded. That x^n has a convergent subsequence now follows from the Ascoli–Arzéla theorem. □

3. A bifurcation theorem. Let R^n denote Euclidean n-space. For notational convenience we define, for two n-vectors $v = \text{col}(v_j)$ and $w = \text{col}(w_j) \in R^n$, the vector product $v * w = \text{col}(v_j w_j) \in R^n$. It is easy to see that

$$v * w = w * v, \qquad v * (w + z) = v * w + v * z.$$

If $A = (a_{jk})$ is an $n \times n$ matrix then we define $v \circ A = (v_j a_{jk})$. Then $v * (Aw) = (v \circ A)w$. We consider the system

$$x'(t) = \lambda * \left(\int_{-\infty}^{t} d_s H(t-s) x(s) + g(x)(t) \right) \tag{3.1}$$

where λ is a constant n-vector, H is an $n \times n$ matrix valued function satisfying (H1) and g is a perturbation functional satisfying the following hypothesis:

(H2) $g: B(\rho) \to P(p)$, $\rho > 0$, $B(\rho) = \{x \in P(p): |x|_0 \leqq \rho\}$ is continuous and $|g(x)(t)|_0 = o(|x|_0)$ near $x = 0$.

Note that $g(0)(t) \equiv 0$ so that $x \equiv 0$ solves (3.1) for all $\lambda \in R^n$.

The theory of § 2 above applies to the linearized system

$$y'(t) = \mu * \int_{-\infty}^{t} d_s H(t-s) y(s) \tag{3.2}$$

with $A = \mu \circ H$. Next we assume that for some given period p that:

(H3) There exists a $\mu \in R^n$ such that the linear homogeneous system (3.2) has a nontrivial p-periodic solution.

In view of the proof of Theorem 1 in § 2 this is equivalent to assuming that the finite set of integers $M = M(\mu)$ (for which the matrix $\mu \circ H_m - im\omega I$, $\omega = 2\pi/p$, $-\infty < m < +\infty$ is singular) is nonempty. By Theorem 1 both (3.2) and its adjoint system

$$z'(t) = -\mu * \int_{t}^{\infty} d_s H^T(s-t) z(s) \tag{3.3}$$

have a finite number $r \geqq 1$ of independent solutions in $P(p)$ which we denote by y^k and $z^k = \text{col}(z_j^{(k)})$, $1 \leqq k \leqq r$, respectively. Let C denote the $r \times n$ matrix given by

$$C = \left(p^{-1} \int_0^p \sum_{q=1}^{n} z_j^{(k)} \int_0^{\infty} y_q(t-s) d_s h_{jq}(s)\, dt \right)$$

for $1 \leqq k \leqq r$, $1 \leqq j \leqq n$ where $H(s)=(h_{jq}(s))$ and $y \in P(p)$ is any solution of (3.2). Finally we need the hypothesis:

(H4) Assume (H3) and let $y \in P(p)$ be any nontrivial solution of the linear homogeneous system (3.2). Assume that $n \geqq r$ and that the $r \times n$ matrix C has rank equal to r.

Note that if $\mu = \text{col}(\mu_j)$ in (H3) is such that $\mu_j \neq 0$ for all $1 \leqq j \leqq n$ then C may be rewritten as $C=(\mu_j^{-1} p^{-1} \int_0^p z_j^{(k)} y_j' \, dt)$ and clearly has the same rank as the $r \times n$ matrix

$$C^* = \left(p^{-1} \int_0^p z_j^{(k)}(t) y_j'(t)\, dt\right). \tag{3.4}$$

Our main result is contained in the following theorem.

THEOREM 2. *Assume that the kernel H and the perturbation p satisfy* (H1) *and* (H2) *respectively. Assume that* (H3) *and* (H4) *hold for some $p>0$ and some p-periodic solution y of the linear homogeneous system* (3.2). *Then there exists a constant $\varepsilon_o>0$ such that the perturbed system* (3.1) *has nontrivial p-periodic solution with Lyapunov–Schmidt expansion*

$$x(t)=\varepsilon y(t)+\varepsilon w(t,\varepsilon) \quad \text{with } \lambda = \mu + \gamma(\varepsilon) \tag{3.5}$$

for $0<|\varepsilon| \leqq \varepsilon_0$ where y and μ are as in (H4) *and* (H3) *and $w \in P_0(p)$, $\gamma \in R^n$ satisfy* $|w(t,\varepsilon)|_0 = O(|\varepsilon|)$, $|\gamma(\varepsilon)| = O(|\varepsilon|)$.

Remark 1. It turns out that (H3) is necessary for the bifurcation as described in Theorem 2 to occur. The added hypotheses (H4) is sufficient to insure the bifurcation.

Remark 2. According to (H4) the matrix C has at least one $r \times r$ nonsingular submatrix. Let $J \subseteq \{1, \cdots, n\}$ denote those subscripts j corresponding to the columns of C forming a nonsingular submatrix. Then it turns out (see the proof below) that the remaining components γ_j, $j \in \{1, \cdots, n\} - J$ are arbitrary, i.e., $\gamma_j = \varepsilon \gamma_j^*$ for any real γ_j^*.

Proof. If we substitute (3.5) into (3.1) and equate the lowest order (i.e. ε) coefficients on both sides of the equation we find that μ and y must satisfy the linear homogeneous system (3.2), which in fact they do by the assumptions (H3) and (H4). The remaining higher order terms in ε yield the nonlinear system (after a cancellation of an ε)

$$\frac{dw(t,\varepsilon)}{dt} = \mu * \int_{-\infty}^{t} d_s H(t-s) w(s,\varepsilon) + \gamma * F(\varepsilon, w) - G(\varepsilon, w) \tag{3.6}$$

where

$$\begin{aligned} F(\varepsilon, w) &\equiv \int_{-\infty}^{t} d_s H(t-s)(y(s)+w(s,\varepsilon)) + \varepsilon^{-1} g(\varepsilon y + \varepsilon w)(t), \\ G(\varepsilon, w) &\equiv -\varepsilon^{-1} \mu * g(\varepsilon y + \varepsilon w)(t) \end{aligned} \tag{3.7}$$

to be solved for $w \in P_0(p)$. If $w \in P_0(p)$ solves (3.6) for some $\gamma \in R^n$ then (3.5) solves (3.1). We will solve (3.6) by means of the Schauder fixed point theorem.

The Fredholm alternative in Theorem 1 implies that in order for (3.6) to have a solution $w \in P(p)$ it is necessary that the conditions

$$(3.8) \qquad (z^k, \gamma * F(\varepsilon, w)) = (z^k, G(\varepsilon, w)), \qquad 1 \leqq k \leqq r,$$

be satisfied. Here, of course the $z^k \in P(p)$ are r independent solutions of the adjoint system (3.3).

Given $w \in P_0(p)$ we attempt to solve (3.8) by an appropriate choice of $\gamma \in R^n$. The equation (3.8) constitutes r linear algebraic equations in n unknowns γ_j. Since $n \geqq r$ (see (H4)), (3.8) has no more equations than unknowns. The coefficient matrix of this system is the $r \times n$ matrix

$$\left(p^{-1} \int_0^p z_j^{(k)}(t)\left[\varepsilon^{-1} g_j(\varepsilon y + \varepsilon w)(t) + \int_{-\infty}^t \sum_{q=1}^n d_s h_{jq}(t-s)(y_q(s) + w_q(s, \varepsilon))\right] dt\right).$$

For the choice $w \equiv 0$, $\varepsilon = 0$, this coefficient matrix reduces to C and hence has rank r by (H4). Consequently the coefficient matrix has rank r for $w \in B_0(\varepsilon_1) = \{w \in P_0(p): |w|_0 \leqq \varepsilon_1\}$ and $|\varepsilon| \leqq \varepsilon_1$ for $\varepsilon_1 > 0$ sufficiently small (and $\varepsilon_1 < \rho$). This means that we may solve (3.8) for $\gamma = \gamma(\varepsilon, w)$ for every $w \in B_0(\varepsilon_1)$ and $0 \leqq |\varepsilon| \leqq \varepsilon_1$ where $n-r$ of the components γ_j are arbitrary. If these $n-r$ components are chosen to that $\gamma_j = O(|\varepsilon|)$ then it is easy to see by Cramer's rule that $\gamma = \gamma(\varepsilon, w)$: $(-\varepsilon_1, \varepsilon_1) \times B_0(\varepsilon_1) \to R^n$ is a continuous operator which has (by (H2)) the property that $|\gamma(\varepsilon, w)| = O(|\varepsilon|)$ uniformly for $w \in B_0(\epsilon_1)$.

Given $w \in B_0(\varepsilon_1)$ let $w^0 = N(\varepsilon, w) \in P_0(p)$ be the unique solution of the linear nonhomogeneous system obtained by substituting w and $\gamma(\varepsilon, w)$ into F and G in (3.6). Here

$$N(\varepsilon, w) = L(\gamma(\varepsilon, w) * F(\varepsilon, w) - G(\varepsilon, w))$$

where L is the compact linear operator of Theorem 1 and hence the operator $N(\varepsilon, w)$: $(-\varepsilon_1, \varepsilon_1) \times B_0(\varepsilon_1) \to P_0(p)$ is completely continuous in w for each ε. If $w \in P_0(p)$ is a fixed point of N for some ε then clearly w solves (3.6). To prove that N has a fixed point for all ε sufficiently small we only need show that for small ε the range of N lies in $B_0(\varepsilon_1)$ and then invoke the Schauder fixed point theorem. To do this we observe that from the definitions of F and G given in (3.7), hypothesis (H2) and the above described order property of γ, it follows that $|\gamma * F - G|_0 = O(|\varepsilon|)$ uniformly for $w \in B_0(\varepsilon_1)$. Thus, since L is a bounded linear operator we conclude that the range of N lies in $B_0(\varepsilon_1)$ for $|\varepsilon| \leqq \varepsilon_0$ for some sufficiently small $\varepsilon_0 < \varepsilon_1$.

Finally, we observe that $|w(\varepsilon)|_0 = |N(\varepsilon, w)|_0 = O(|\varepsilon|)$ since $w(\varepsilon) \in B_0(\varepsilon_1)$, and hence from Cramer's rule we also find that $|\gamma| = O(|\varepsilon|)$. □

4. Some applications. As pointed out in § 1 most models used in discussing the dynamics of interaction species are of the form (1.1) where N_j is some measure of the population size (numbers, biomass, etc.) of the jth species and b_j is the inherent net birth rate (or death rate if $b_j < 0$) at which the population grows (exponentially) in the absence of all constraints. Suppose the function f_j which actually describes the unit growth rate of N_j has the form

$$f_j = f_j\left(\int_{-\infty}^{t} N_1(s)\,d_s k_{j1}(t-s), \cdots, \int_{-\infty}^{t} N_n(s)\,d_s k_{jn}(t-s)\right), \qquad \int_0^\infty dk_{ij}(s) = 1, \quad dk_{ij}(s) \geqq 0,$$

where $f_j(z_1, \cdots, z_n)$: $R^n \to R$. Suppose that the system has an equilibrium $N_j \equiv e_j$, i.e., suppose $f_j(e_1, \cdots, e_n) = 0$, $1 \leqq j \leqq n$, has positive roots $e_j > 0$. If we center the model on this equilibrium by letting $x_j = N_j - e_j$ then (1.1) takes the form (3.1) with $\lambda = \text{col}\,(\lambda_j)$, $\lambda_j = b_j e_j$ and $H(s) = (h_{jk}(s))$ with

$$h_{jk}(s) = \frac{\partial f_j}{\partial z_k}(e_1, \cdots, e_n) k_{jk}(s)$$

provided the f_j have continuous partial derivatives. If further f_j has, say, continuous second order partials at the equilibrium then the remainder term g in (3.1) is higher order in x and consequently satisfies (H2). This means that in order to apply Theorem 2 we need investigate only the necessary properties (namely (H3) and (H4)) of the linearized problem (3.2) with the above described matrix H. If these two hypotheses (H3) and (H4) can be fulfilled for some period p then by Theorem 2 nontrivial p-periodic solutions will bifurcate from the equilibrium e_j for birth rates near the critical values $b_j \sim \beta_j = \mu_j/e_j$ where $\mu = \text{col}\,(\mu_j)$ is as in (H3). For simplicity we will assume that the equilibrium e_j is isolated.

Referring to the linear theory of § 2 we see that (H3) is satisfied by solving the algebraic systems

$$(4.1) \qquad (\mu \circ H_m - im\omega I)c_m = 0, \qquad m \geqq 0,$$

for the complex Fourier coefficients c_m and choosing μ such that not all $c_m = 0$, i.e., such that $\mu \circ H_m - im\omega I$ is singular for some m. Here $\omega = 2\pi/p$ and

$$H_m = \int_0^\infty d_s H(s) \exp(-im\omega s).$$

Since e_j is by assumption an isolated equilibrium it follows that c_0 must be zero and hence $\mu \circ H_0$ must be nonsingular. This means each component of μ must be nonzero. In this case we may divide the jth equation in (4.1) by μ_j to obtain an equivalent system

$$(4.2) \qquad (H_m - im\xi \circ I)c_m = 0, \qquad m > 0,$$

where $\xi = \text{col}\,(\omega\mu_j^{-1}) = \text{col}\,(\xi_j)$. This form of the system is more convenient with which to work in our examples below. Let $M_+ = M_+(\xi)$ be the finite set of indices $m \geqq 0$ for which $H_m - im\xi \circ I$ is singular. As already pointed out $0 \notin M_+$. Let $\rho(m) < n$ be the rank of $H_m - im\xi \circ I$ for $m \in M_+$. Then (4.2) has $\nu(m) = n - \rho(m)$ independent complex solutions $c_m \neq 0$ each of which yields two independent real solutions of (3.2) (see the proof of Theorem 1(d))

$$(4.3) \qquad y(t) = \text{Re}\, c_m \exp(im\omega t) \quad \text{and} \quad y(t) = \text{Im}\, c_m \exp(im\omega t).$$

Thus the number of independent real solutions of the linear systems (3.2) (and (3.3)) is $r = 2\sum_{m \in M_+} \nu(m)$, an even number. Independent solutions of the adjoint system (3.3) are given by

(4.4) $z(t) = \operatorname{Re} \omega^{-1}\xi \circ d_m \exp(im\omega t)$ and $z(t) = \operatorname{Im} \omega^{-1}\xi \circ d_m \exp(im\omega t)$

where $d_m \neq 0$ solves the adjoint system $(H_m^* + im\xi \circ I)\, d_m = 0$, $m > 0$.

Since $\mu_j \neq 0$ for all j, (H4) can be satisfied by consideration of C^* in place of C as pointed out prior to Theorem 2.

To summarize: for the population models considered here, bifurcation of nontrivial p-periodic solutions will occur from an isolated positive equilibrium for $b_j \sim \beta_j = 2\pi/(p\xi_j e_j)$ provided p and ξ can be found for which $M_+ \neq \phi$, $r \leqq n$ and the rank of C^* equals r.

(i) *An example of mutualism.* As pointed out by May [14, p. 224] the simplest, quadratically nonlinear Lotka–Volterra models are wholly unsuitable for even a simple discussion of mutualism since such models lead to ridiculously unstable populations. Many mutualistic interactions involve significant delays (for example, the effect that changes in the populations size of pollinators have on that of the plants which they pollinate will be delayed until at least the next generation of plants) which hopefully will provide a stabilizing effect on the model. (Note that this hope is in contrast to the usual destabilizing effect of time delays.) We will illustrate this mathematically by applying Theorem 2 to a simple (quadratic) mutualistic model of Lotka-Volterra type involving two plant species and one pollinator.

First consider the nondelayed system

$$\begin{aligned} N_1' &= b_1 N_1(-1 - aN_2 + bN_3), \\ N_2' &= b_2 N_2(-1 - cN_1 + N_3), \qquad a, b, c, b_j > 0. \\ N_3' &= b_3 N_3(-1 + N_1 + N_2), \end{aligned} \tag{4.5}$$

Here $N_1 > 0$ and $N_2 > 0$ represent plant species (with population sizes normalized to make the interaction coefficients of the third equation both equal to one) and $N_3 > 0$ represents a common pollinator species (normalized to make its iteraction coefficient with N_2 equal to one). Both plant species benefit from contacts with the pollinator and the pollinator benefits from contacts with either plant species. Note that the plant species inhibit each other as might be expected from their competition for common resources. Also note that in the absence of pollinators ($N_3 \equiv 0$) both plant species die out and vice versa.

We assume that (4.5) has an isolated, positive equilibrium $N_j \equiv e_j > 0$; this is easily seen to occur if and only if

$$a - b + 1 > 0 \quad \text{and} \quad bc + b - 1 > 0. \tag{4.6}$$

If the standard linearization analysis is done on (4.5) at e_j one easily finds that this equilibrium is unstable in the sense that the linearized system has at least one eigenvalue with positive real part. Our purpose here is to show how time delays, if introduced into the model (4.5), can "stabilize" the system for appropriate birth rates b_j. By "stabilize" we mean here something rather crude: that under certain conditions at least one p-periodic solution will exist for at least one period. It is usually the case in applying Theorem 2 and it will in fact be the case in the examples considered here that multi-dimensional manifolds of p-periodic solutions will exist for at least one period p (and usually a continuum of periods p).

Suppose delays are introduced into (4.5) as follows:

$$(4.7)\qquad \begin{aligned} N_1' &= b_1N_1\Big(-1-aN_2+b\int_{-\infty}^{t} d_sk_1(t-s)N_3(s)\Big),\\ N_2' &= b_2N_2\Big(-1-cN_1+\int_{-\infty}^{t} d_sk_2(t-s)N_3(s)\Big),\\ N_3' &= b_3N_3(-1+N_1+N_2),\\ &a, b, c, b_j>0 \quad\text{and}\quad \int_0^{\infty} dk_j(s)=1. \end{aligned}$$

Here, as described above, we have possible delays in the effects felt by the plant species due to contact with pollinators. Assuming (4.6) this delayed system has the same equilibrium $e_j>0$ as (4.5). Following the discussion at the beginning of this section we consider the 3×3 algebraic system (4.2) where for this example

$$H_m-im\xi\circ I=\begin{pmatrix} -im\xi_1 & -a & bE_1\\ -c & -im\xi_2 & E_2\\ 1 & 1 & -im\xi_3\end{pmatrix}$$

where $E_j=E_j(m)=C_j(m)-iS_i(m)$ and

$$C_j(m)=\int_0^{\infty}\cos m\omega s\, dk_j(s),\qquad S_j(m)=\int_0^{\infty}\sin m\omega s\, dk_j(s).$$

We must find $\xi_j>0$ such that the rank $\rho(m)$ of this matrix is two for exactly one $m>0$. Then (H3) holds and $r=2\nu(m)=2<3=n$ holds in (H4). A simple calculation shows that this rank is two if and only if the $\xi_j>0$ satisfy the two equations

$$(4.8a)\qquad m(S_2\xi_1+bS_1\xi_2)=bcC_1+aC_2,$$

$$(4.8b)\qquad m^3\xi_1\xi_2\xi_3+mC_2\xi_1+mbC_1\xi_2+acm\xi_3+bcS_1+aS_2=0.$$

When these conditions hold for some ξ_j and exactly one $m>0$ then (4.2) may be solved for one independent $c_m\neq 0$ which defines the only two independent solutions y of the linearized problem by means of (4.3).

Finally we need that the rank of C^* be $r=2$. To compute C^* (a 2×3 matrix) is a lengthy, but straightforward calculation involving the adjoint system of (4.2) and the resulting adjoint solutions (4.4). It turns out that if one takes y to be the first homogeneous solution in (4.3) then the rank of C^* is two if and only if

$$(4.9a)\qquad -m^2bS_1\xi_2^2+m(aC_2+bcC_1)\xi_2+acS_2\neq 0,$$

$$(4.9b)\qquad -m^2S_2\xi_1^2+m(bcC_1+aC_2)\xi_1+abcS_1\neq 0.$$

We conclude that Theorem 2 applies if (4.8) and (4.9) hold for some $\xi_j>0$. In case (4.9a) (or (4.9b)) we may take γ_2 (or γ_1) to be arbitrary as in Remark 2.

Example 1 (no delays): If $k_1(s)\equiv k_2(s)\equiv u_0(s)$, the unit step function at $s=0$ so that (4.7) reduces to (4.5), then $S_j=0$ and $C_j=1$ for all m. Thus (4.8a) cannot be satisfied for any $\xi_j>0$, $m>0$. Because (4.8) is necessary for bifurcation (see Remark 1) we see that no bifurcation as described in Theorem 2 can occur for our model (4.7) unless delays are genuinely present.

Example 2 (equal constant time lags): Although (4.8) and (4.9) are sufficient for bifurcation under general delays as derived above, let us now simplify, for purpose of illustration, to models with two equal constant time lags: $k_j(s)\equiv u_\tau(s)$ where $\tau>0$. Suppose we choose a period $p>0$ so that

$$\frac{\tau}{p}=\frac{5+8k}{8m_0} \tag{4.10}$$

for some integers $k\geqq 0$ and $m_0\geqq 1$. Then $S_j=C_j=-(1/2)^{1/2}$ and (4.8) reduces to

$$m_0(\xi_1+b\xi_2)=bc+a, \tag{4.11a}$$

$$\xi_3=\frac{(bc+a)2^{1/2}}{m_0^3\xi_1\xi_2+acm_0} \tag{4.11b}$$

for $m=m_0$. If ξ_1 and ξ_2 are chosen so that (4.11a) holds one finds that (4.9b) holds (since in this case $\xi_1<(bc+a)/m_0$). Thus all the hypotheses necessary for Theorem 2 hold with $m=m_0$ if ξ_1, ξ_2 satisfy (4.11a) and ξ_3 is determined by (4.11b). (Note: given ξ_1, ξ_2 and p by (4.10) one can see, with a little effort, that (4.8a) holds only for $m=m_0$ and no other integer.)

We conclude then that nontrivial p-periodic solutions of the constant lag system (4.7) with $k_j=u_\tau$ bifurcate from the unique positive equilibrium guaranteed by (4.6) for periods given by (4.10) at the critical values of the birth rates given by $b_j\sim\beta_j=2\pi/(p\xi_je_j)$ for any $\xi_j>0$ satisfying (4.11).

Note that since there are infinitely many choices for ξ_1,ξ_2 one would expect to see, for given fixed b_j in the model (4.7), infinitely many p-periodic solutions. Furthermore, our choice for p in (4.10) is not required in the analysis and if one carries out the details for arbitrary p one finds that all of this can be done for infinitely many periods p (for example, p close to those determined by (4.10) would do). All of this implies that for a given set of appropriate parameters in the model (4.7) one expects to see multi-dimensional manifolds of periodic solutions. This phenomenon is common in the application of Theorem 2. For another example (but for a different model) see [8] where numerical evidence is also given for this phenomenon.

(ii) *A competition model.* As a second example of the possible stabilizing effects of time delays we consider the model

$$\begin{aligned} N_1'&=b_1N_1(-1-bN_2+aN_3),\\ N_2'&=b_2N_2(-1-dN_1+cN_3),\\ N_3'&=b_3N_3\left(1-\int_{-\infty}^{t}N_3(s)\,dk(t-s)-N_1-N_2\right), \end{aligned} \tag{4.12}$$

$$a,b,c,d,b_j>0 \quad\text{and}\quad \int_0^\infty dk(s)=1.$$

This model serves to describe the dynamics of two (predator) species N_1, N_2 who are in competition for a common (prey) resource N_3. Here we have assumed no self inhibition on the part of the competing species while (following May [15]) the resource N_3 has a self-inhibiting factor (i.e. a finite carrying capacity in the absence of predators) with a possible time delay. If

$$a+b<bc+c, \qquad c+d<ad+a \tag{4.13}$$

then (4.12) has an isolated positive equilibrium $e_i>0$.

If no delay is present: $k(s)\equiv u_0(s)$; then the equilibrium can be shown, by means of the usual linearization analysis to be unstable. This is not inconsistent with the familiar law of competitive exclusion.

Suppose $k(s)\equiv u_\tau(s)$ for $\tau \geqq 0$. Then

$$H_m - im\xi\circ I = \begin{pmatrix} -im\xi_1 & -b & a \\ -d & -im\xi_2 & c \\ -1 & -1 & -E-im\xi_3 \end{pmatrix}$$

$$E=C-iS=\cos m\omega\tau - i\sin m\omega\tau.$$

This matrix is singular for some $\xi_j>0$ and $m>0$ if and only if

$$m^2\xi_1\xi_2C+dbC+ad+bc=0, \tag{4.14a}$$

$$m^3\xi_1\xi_2\xi_3-m^2\xi_1\xi_2S-mc\xi_1-am\xi_2+dbm\xi_3-dbS=0 \tag{4.14b}$$

hold. If p is chosen so that

$$S=\sin m_0\omega\tau>0, \quad -(ad+bc)/(bd)<\cos m_0\omega\tau<0, \quad \omega=2\pi/p, \tag{4.15}$$

for some integer $m_0>0$ then it is easy to see that it is possible to choose $\xi_i>0$ such that (4.14) holds for $m=m_0$ (e.g., $\xi_1>0$ is arbitrary and ξ_2, ξ_3 are determined by (4.14)). Without going into the details here we can also show that the rank of C^* is, as required, equal to two for any allowable values of the parameters and any homogeneous linear solution y.

To summarize: the competition model (4.12) under (4.13) has nontrivial p-periodic solutions bifurcating from its unique positive equilibrium for periods p satisfying (4.15) (which incidently rules out nondelay models $\tau=0$) for values of b_j near the critical values $\beta_j=2\pi/(p\xi_je_j)$ where the constants ξ_j are determined by (4.14) for $m=m_0$. The remarks concerning multi-dimensional manifolds of p-periodic solutions at the end of the preceding example are applicable here.

(iii) *A predator-prey model with continuously distributed delays*. The examples above all involve constant time lags. Undoubtedly more realistic models involve continuously distributed delays of the form $dk(s)=k'(s)\,ds$ [14], [15], [20]. Since our analysis in §§ 2 and 3 also applies to such delays, we conclude with an example of this type.

Consider the predator-prey model

$$N_1' = b_1 N_1\Big(1 - K^{-1}\int_{-\infty}^{t} N_1(s)\, d_s k_1(t-s) - \alpha N_2\Big),$$

(4.16)
$$N_2' = b_2 N_2\Big(-1 + \beta\int_{-\infty}^{t} N_1(s)\, d_s k_2(t-s)\Big),$$

$$K, \alpha, \beta > 0 \quad \text{and} \quad \int_0^\infty dk_j(s) = 1,$$

in which the prey N_1 has a delayed self-inhibition (as in May's model [15]) and the effect on the predator of contracts with prey has a delay (as in Volterra's model [20]). We assume that

(4.17)
$$K\beta > 1$$

so that (4.16) has a positive equilibrium $e_j > 0$.

In the absence of delays: $k_j(s) \equiv u_0(s)$; the system (4.16) is well-known to have a uniformly asymptotically stable equilibrium e_j.

Following May [15] we will assume that the delay k_2 is small compared to k_1. May in fact assumes that $k_2 \equiv u_0$. We will assume that k_2 is "close to" u_0. The presence of delays in (4.16) tends, roughly speaking, to destabilize the equilibrium [2], [5], [8], [14], [15], although May [14], [15] argues for his model (in which $k_2 \equiv u_0$) that if the product $b_1 b_2$ is small enough (compared to the "size" of the delay) then the equilibrium will be stable. We will use Theorem 2 to argue that the system (4.16) may be "stable", in the broader sense used above, for even a wider range of values of $b_1 b_2$.

Since the "carrying capacity" K of the prey N_1 (in the absence of predators $N_2 \equiv 0$) loses its stability as b_1 gets large compared to the "size" of the delay May argues that there is then an overlap interval of values for the delay "size" $\tau > 0$ for which the predator-prey system has a stable equilibrium, while the prey alone, in the absence of the predator, has an unstable equilibrium; roughly $b_1^{-1} < \tau < (b_1 b_2)^{-1/2}$. This points to the possibility that predators may stabilize an otherwise unstable prey population. Our application of Theorem 2 will add to this argument in that this interval may possibly be widened (i.e. $\tau > (b_1 b_2)^{-1/2}$) if by the "stability" of the model we include the broader meaning described above. Such a possibility relating to periodic solutions was briefly mentioned in [15].

For (4.16) we find that

$$H_m - im\xi \circ I = \begin{pmatrix} -im\xi_1 - K^{-1}E_1 & -\alpha \\ \beta E_2 & -im\xi_2 \end{pmatrix}$$

where E_j is the usual Fourier integral for k_j. This matrix is singular for $\xi_j > 0$ if and only if $\xi_j > 0$ can be found such that

$$m\xi_2 C_1 = K\alpha\beta S_2, \qquad m^2\xi_1\xi_2 = \alpha\beta C_2 + K^{-1} m\xi_2 S_1$$

for some integer $m > 0$. Following May suppose the delay due to k_2 is small: $k_2(s) \equiv (1-\varepsilon)u_0(s) + \varepsilon r(s)$, $\int_0^\infty dr(s) = 1$, $\varepsilon > 0$ small. Then

(4.18)
$$m\xi_2 C_1 = \varepsilon K\alpha\beta S_r, \qquad m^2\xi_1\xi_2 = \alpha\beta + K^{-1} m\xi_2 S_1 + \varepsilon(C_r - 1)\alpha\beta,$$

where $C_r - iS_r = \int_0^\infty \exp(-im\omega s)\, dr(s)$, needs to be solved for $\xi_j > 0$. If this can be done then another straightforward but detailed calculation shows that C^* has the required rank of two provided

$$(4.19) \qquad S_2 = \varepsilon S_r \neq 0.$$

Note that this latter technical requirement rules out the possibility of no delays in the predator equation (i.e. (4.19) disallows $\varepsilon = 0$ and hence $k_2 \equiv u_o$). This unfortunately prevents our making an exact comparison with May's results in [15] where $\varepsilon = 0$; however we will still attempt to relate our results to those in [15] by further considering the model for ε small, but nonzero, and also by formally setting $\varepsilon = 0$.

To summarize: if (4.19) holds and if (4.18) holds for some $\xi_j > 0$, $m > 0$ then bifurcation of p-periodic solutions will occur at the critical values β_j of b_j given by the usual formula $\beta_j = 2\pi/(p\xi_j e_j)$.

For example, if we consider May's model [15] in which $dk_1(s) = (\tau^{-2} s \exp(-s/\tau))\, ds$ for $\tau > 0$ we find that $C_1 = a/(a^2+b^2)$, $S_1 = b/(a^2+b^2)$ where $a = 1-(\tau m\omega)^2$, $b = 2\tau m\omega$. Suppose we assume that τ and p are such that

$$2\pi m_0 \tau/p = 1 - \varepsilon$$

for some integer $m_0 > 0$. Then we find for $m = m_0$ that (4.18) and (4.19) hold for $\varepsilon \neq 0$ small if $S_r > 0$ for ξ_j satisfying

$$\xi_1 = \frac{1+S_r}{2m_0 K S_r} + O(\varepsilon), \qquad \xi_2 = \frac{2K\alpha\beta S_r}{m_0} + O(\varepsilon).$$

Hence under these conditions bifurcation will occur.

To compare these results with those of May as discussed above we let $\varepsilon = 0$ in (4.18) and neglect the fact that the technical, sufficiency condition (4.19) fails to hold. We find from (4.18) that $C_1 = 0$ which leads to

$$(4.20) \qquad \tau/p = 1/(2m_0\pi)$$

for some $m_0 > 0$, in which case $\xi_1 > (2m_0 K)^{-1}$ is arbitrary and

$$(4.21) \qquad \xi_2 = 2\alpha\beta K/(m_0(2m_0\xi_1 K - 1)) > 0;$$

here we use the fact that $S_1 = 1/2$. To compare with the results in [15] we must relate the product of the critical values $\beta_1\beta_2$ to the constant τ, which is the time at which maximum delay occurs in k_1. This we do by substituting $\xi_j = 2\pi/(pe_j\beta_j)$, $e_1 = \beta^{-1}$, into (4.21) and using (4.20). This results in a quadratic equation in τ whose only positive root is

$$\tau_0 = \tau_0(\beta_1, \beta_2) = (-e_1\beta_1 + (e_1^2\beta_1^2 + 16K^2\alpha e_2\beta_1\beta_2)^{1/2}/(4K\alpha e_2\beta_1\beta_2).$$

This critical value of the delay τ_0 is precisely that calculated by May [15, eq. (21)] in his stability study of this model. May showed that if $\tau < \tau_0(b_1 b_2)$ then the equilibrium for (4.16) is stable. Note that $\tau_0 = (\beta_1\beta_2)^{-1/2} + O(K^{-1})$ and hence for large carrying capacities K this critical value of the lag is close to $(\beta_1\beta_2)^{-1/2}$ which near bifurcation is close to the "natural" period $(b_1 b_2)^{-1/2}$ of the periodic solutions of the well-known Volterra–Lotka (nondelayed) model.

We see here (at least for $\varepsilon \neq 0$ small) that bifurcation of p-periodic solutions occurs from equilibrium at the critical value $\tau = \tau_0(\beta_1, \beta_2)$, to order ε; and hence for those values of τ, b_j at which periodic solutions of this model exist, by Theorem 2 it is evidently the case that $\tau > \tau_0(b_1, b_2)$, to order ε.

The above analysis concerns the model (4.16) when the lag in the predator equation is small. For the opposite case ($k_1 \equiv u_0$) see [8].

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