

Periodic Solutions of Two Species Interaction Models with Lags

J. M. CUSHING

Department of Mathematics, University of Arizona, Tucson, Arizona 85721

ABSTRACT

The classical Volterra–Lotka system of differential equations modeling the interaction of two species is considered under the assumption that the interaction and/or density inhibition terms may possess time lags (of a very general nature). Under the assumption that there exists a positive equilibrium, sufficient conditions are given which guarantee the existence of nonconstant, positive periodic solution. These conditions are algebraic in nature and are easily and straightforwardly applied. A few specific examples (namely, some predator-prey and competing species models) are discussed and are used to illustrate how lags are able to alter significantly the general dynamics of the classical equations. The mathematical approach is to construct periodic solutions which bifurcate from the equilibrium (using the net birth rates as free parameters) by making use of Liapunov–Schmidt type expansions, an approach which requires the proof of a Fredholm-type alternative for Stieltjes integrodifferential systems.

1. INTRODUCTION

The classical Volterra–Lotka differential system often used to describe the interaction of two species is given by

$$N_i' = N_i(b_i - d_{ii}N_i + d_{ij}N_j), \quad 1 \leq i, j \leq 2, \quad i \neq j, \quad (1.1)$$

where $N_i = N_i(t)$ is some measure of the population size of the i th species and time t , b_i is the inherent net birth rate of the i th species in the absence of any constraints, $d_{ii} \geq 0$ is the inhibition coefficient measuring the constraining effects of the i th species upon itself, and d_{ij} , $i \neq j$, is the interaction coefficient measuring the effect of the j th species upon the growth rate of the i th species. The signs of the constants b_i and d_{ij} characterize the type of ecological interactions described by (1.1). For example, b_1 and $d_{21} > 0$ with b_2 and $d_{12} < 0$ represent a predator-prey relationship, while $b_i > 0$ with $d_{ij} < 0$

represents a competition interaction. We will not, however, except in some examples in Sec. 3, place any particular constraints on the signs of these coefficients.

In his book on population dynamics [10], Volterra offers a modification of (1.1) which accounts for possible lag effects in the interaction of the species. This he does by considering the system

$$N'_i = N_i \left(b_i - d_{ii} \int_0^\infty N_i(t-s) dh_{ii}(s) + d_{ij} \int_0^\infty N_j(t-s) dh_{ij}(s) \right) \quad (1.2)$$

for $1 \leq i, j \leq 2$, $i \neq j$, where

$$\int_0^\infty dh_{ij}(s) = 1, \quad 1 \leq i, j \leq 2. \quad (1.3)$$

[Actually Volterra considers the special case $dh_{ij}(s) = k_{ij}(s) ds$.] In this model the effects on the growth rate of one species of contacts with either itself or the other species are accumulated over past time. Formally (1.1) is derivable from (1.2) by letting $h_{ij}(t)$ be the unit step function $u_0(t)$ at $t=0$, i.e., by assuming all interaction effects are concentrated at the present time t . If h_{ij} is taken to be the unit step function $u_{\tau_{ij}}(t)$ at $t = \tau_{ij} > 0$, then (1.2) reduces to a system with instantaneous, constant time lags. Notice that equilibria $N_i = e_i$ of both (1.1) and (1.2) lying in the first quadrant $e_i > 0$, if such exist, are found by solving the same pair of linear, algebraic equations:

$$\begin{aligned} d_{11}e_1 - d_{12}e_2 &= b_1, \\ -d_{21}e_1 + d_{22}e_2 &= b_2. \end{aligned} \quad (1.4)$$

The presence of lag effects accounted for by the integral expressions in (1.2) can, of course, significantly alter the dynamical behavior of the interaction. For example, it was shown by the author in [2] that the predator-prey system considered by Volterra in [10] possesses (for certain reasonable integrators h_{ij}) an unstable equilibrium, unlike the nonlag predator-prey model. It is shown further below in Sec. 3 that this system possesses, however, a periodic solution surrounding the unstable equilibrium. [This behavior was also predicted in [1] by using certain approximations to the system (1.2).] Thus, lag factors are able to destabilize an otherwise stable equilibrium while giving rise to nonconstant, periodic solutions. Such dynamical behavior seems to be of some interest to ecologists [7, 8] and has been accomplished using differential, nonlag models by (in some cases rather artificially) adding higher order terms to the model (1.1) [4, 5, 8, 12]. Here we will show that such dynamical behavior can result from lag effects using the original models proposed by Volterra.

Our purpose here is to give conditions under which the integrodifferential system (1.2) possesses nonconstant, positive ($N_i > 0$) periodic solutions which bifurcate from the equilibrium e_i . These conditions are contained in Theorems 1 and 2 of Sec. 2. In Sec. 3 several examples are worked out to support the rough statement that such solutions of (1.2) will exist if the “delayed” interaction effects are in some sense more predominant than the “present” interaction effects. Theorems 1 and 2 are proved in Sec. 4. Because our approach uses a Liapunov-Schmidt expansion technique, we need a Fredholm alternative for periodic solutions of linear Stieltjes integrodifferential systems. This alternative is established in Sec. 5.

2. RESULTS

In everything below we let (v_i) denote two dimensional vectors (v_1, v_2) . Let $B(p)$ denote the Banach space of continuously differentiable, p -periodic functions under the norm $|f|_1 = |f|_0 + |f'|_0$, where $|f|_0 = \max_{0 \leq t \leq p} |f(t)|$. For convenience we rewrite (1.2) in the form

$$N'_i = |b_i| N_i \left(\delta_i - c_{ii} \int_0^\infty N_i(t-s) dh_{ii} + c_{ij} \int_0^\infty N_j(t-s) dh_{ij} \right),$$

$$1 \leq i, j \leq 2, \quad i \neq j, \quad (2.1)$$

where $\delta_i = b_i/|b_i| = \pm 1$ and $c_{ij} = d_{ij}/|b_i|$. We assume throughout that the integrators h_{ij} satisfy (1.3); this implies in particular that $\int_0^\infty f(t-s) dh_{ij} \in B(p)$ for all $f \in B(p)$. With regard to the coefficients c_{ij} we assume that (2.1) has a unique equilibrium in the first quadrant, i.e., from (1.4), that the following conditions hold:

H1:

$$\Delta = c_{11}c_{22} - c_{12}c_{21} \neq 0, \quad e_1 = (\delta_1c_{22} + \delta_2c_{12})/\Delta > 0,$$

$$\text{and } e_2 = (\delta_1c_{21} + \delta_2c_{11})/\Delta > 0.$$

Define, for fixed p and any integer $n \geq 1$, the numbers

$$S_{ij}(n) = e_i c_{ij} \int_0^\infty \sin 2n\pi p^{-1}s dh_{ij}, \quad C_{ij}(n) = e_i c_{ij} \int_0^\infty \cos 2n\pi p^{-1}s dh_{ij}$$

for $1 \leq i, j \leq 2$, and the 2×2 matrices

$$S(n) = \begin{pmatrix} 2n\pi p^{-1} - \lambda_1 S_{11} & \lambda_1 S_{12} \\ \lambda_2 S_{21} & 2n\pi p^{-1} - \lambda_2 S_{22} \end{pmatrix},$$

$$C(n) = \begin{pmatrix} -\lambda_1 C_{11} & \lambda_1 C_{12} \\ \lambda_2 C_{21} & -\lambda_2 C_{22} \end{pmatrix},$$

where λ_i are as yet unspecified positive constants. Let

$$M(n) = \begin{pmatrix} S(n) & C(n) \\ -C(n) & S(n) \end{pmatrix},$$

and let $M^*(n)$ denote the transpose of the 4×4 matrix $M(n)$. We will need the following hypothesis:

H2:

For some $\lambda_i > 0$ and period $p > 0$, the matrix $M(n)$ is singular (but not identically zero) for some integer $n = n_0 \geq 1$, and nonsingular for $n \neq n_0$.

If H2 holds, let the vectors (a_1, a_2, b_1, b_2) and $(a_1^*, a_2^*, b_1^*, b_2^*)$ lie in the null spaces of $M(n_0)$ and $M^*(n_0)$ respectively. Define the two periodic functions $y^j(t) = (y_i^j(t)) \in B(p) \times B(p)$ for $j = 1, 2$ by

$$\begin{aligned} y_i^1(t) &= a_i \cos 2n_0\pi p^{-1}t + b_i \sin 2n_0\pi p^{-1}t, \\ y_i^2(t) &= -b_i \cos 2n_0\pi p^{-1}t + a_i \sin 2n_0\pi p^{-1}t, \quad i = 1, 2, \end{aligned} \quad (2.2)$$

and the two periodic functions $w^j(t) = (w_i^j(t)) \in B(p) \times B(p)$ for $j = 1, 2$ by

$$\begin{aligned} w_i^1(t) &= a_i^* \cos 2n_0\pi p^{-1}t + b_i^* \sin 2n_0\pi p^{-1}t, \\ w_i^2(t) &= -b_i^* \cos 2n_0\pi p^{-1}t + a_i^* \sin 2n_0\pi p^{-1}t, \quad i = 1, 2. \end{aligned} \quad (2.3)$$

Finally let $[f] = p^{-1} \int_0^p f(t) dt$, let $y = (y_i)$ be any linear combination of y^1 and y^2 : $y = K_1 y^1 + K_2 y^2$, $K_1^2 + K_2^2 \neq 0$, and define the operators

$$\Gamma_i(y) \equiv e_i \left(-c_{ii} \int_0^\infty y_i(t-s) dh_{ii} + c_{ij} \int_0^\infty y_j(t-s) dh_{ij} \right), \quad 1 \leq i, j \leq 2, \quad i \neq j.$$

Let J denote the determinant of the 2×2 matrix $([\Gamma_i w^j])$, where $1 \leq i, j \leq 2$. Our main result is contained in the following theorem.

THEOREM 1

Suppose both H1 and H2 hold and suppose $J \neq 0$. Then the system (2.1) has a nonconstant, p -periodic positive solution $N_i > 0$ whose average is $[N_i] = e_i$ for net birth rates b_i for which $|b_i|$ is sufficiently close to λ_i .

More specifically, under these conditions there exists a constant $\varepsilon_0 > 0$ such that (2.1) has for all $|\varepsilon| \leq \varepsilon_0$ a p -periodic solution of the form $N_i = e_i + \varepsilon y_i + \varepsilon z_i(\varepsilon)$ for $z_i \in B(p)$, $|z_i(\varepsilon)|_1 = O(\varepsilon)$ with $|b_i| = \lambda_i + \mu_i(\varepsilon)$, where $\mu_i = O(\varepsilon)$ and $z \cdot y^j \equiv [z_1 y_1^j + z_2 y_2^j] = 0$ for $j = 1$ and 2 .

The hypotheses H2 and $J \neq 0$ depend of course on the integrators h_{ij} (amongst other things). In an important special case we can explicitly relate these hypotheses to the integrators h_{ij} ; this is the case when $c_{ii} = d_{ii} = 0$ for both $i = 1, 2$ (i.e., when neither species inhibits its own growth rate).

THEOREM 2

If $c_{11} = c_{22} = 0$ and $c_{12}c_{21} \neq 0$, then H2 and $J \neq 0$ hold (and hence Theorem 1 applies) if and only if H1 and the following conditions hold:

$$\Sigma_1(n) \equiv C_{12}S_{21} + C_{21}S_{12} = 0 \tag{2.4a}$$

$$\Sigma_2(n) \equiv S_{12}S_{21} - C_{12}C_{21} > 0 \tag{2.4b}$$

$$C_{12}S_{21} \neq 0 \tag{2.4c}$$

for some period $p > 0$ and some integer $n = n_0 \geq 1$, and in addition

$$n_0 \Sigma_2(n) \neq n \Sigma_2(n_0) \tag{2.5}$$

for all $n \neq n_0$ which satisfy (2.4). In this case the constants λ_i can be chosen in any manner such that

$$\lambda_1 \lambda_2 = (2n_0 \pi p^{-1})^2 / \Sigma_2(n_0). \tag{2.6}$$

Remark 1. In order for H2 to hold it is necessary that some lag effects be present in (2.1). One can see this by setting $h_{ij} = u_0$ so that (2.1) reduces to the unlagged system (1.1). In this case $S_{ij} = 0$, $C_{ij} = 1$ for all $1 \leq i, j \leq 2$, and one finds that

$$\det M(n) \equiv D(n) = (2n\pi p^{-1})^2 \{ (2n\pi p^{-1})^2 + (\lambda_1 e_1 c_{12} + \lambda_2 e_2 c_{21})^2 \} \neq 0$$

for all $n \geq 1$. Although the failure of the conditions H2 and $J \neq 0$ does not necessarily rule out the existence of periodic solutions of (2.1), the singularity of M is necessary for the bifurcation of periodic solutions from equilibrium as described in Theorem 1. Thus we see that some lag effects are necessary in (2.1) if such a bifurcation is to occur.

The presence of lags, however, does not necessarily imply that bifurcation will occur or even that H2 will hold (as can be seen in some of the examples in Sec. 3 below). In fact if $h_{ij}(t) = u_0(t) + \eta h_{ij}^*(t)$, then $\det M(n) = D(n) + O(\eta)$, so that $\det M(n) \neq 0$ for η a small constant. Thus lag effects must be "more significant" than nonlag effects in order for H2 to hold.

Remark 2. The question of stability of the periodic solutions found in Theorem 1 is a difficult one to answer in general. The usual linearization approach leads one to a linear, homogeneous system of "nonautonomous"

Stieltjes integrodifferential equations for which stability techniques are not in general available. (Even the case of nonautonomous differential systems without lags can be a difficult one in general.) Some limited techniques are available for such systems (for Riemann integrals [2,9]); we do not, however, wish to consider this problem here. Nonetheless, one can say that since the periodic solutions in Theorem 1 bifurcate from the equilibrium solution e_i , one is likely to have an "exchange of stability", as is so often the case in bifurcation theory; that is to say, very roughly, that as the parameter $|b_i|$ varies and passes through the value λ_i , the stability or instability of the equilibrium is likely to change, as is that of the periodic solutions. Techniques for testing the stability of the equilibrium are more readily available [2,9].

3. SOME EXAMPLES

We assume in this section that all integrators h_{ij} are monotone nondecreasing, so that $dh_{ij}(s) \geq 0$ for all s . The category of ecological interaction described by the model (2.1) is then determined by the signs of the constants c_{ij} . The two theorems in Sec. 2 are of course sufficiently general to cover a great variety of interesting examples (variety in category and in lag integrators h_{ij}). We will, however, restrict our attention here to a few examples, all of which exhibit in some sense marked differences from the corresponding classical, nonlagged differential model (1.1).

(a) SOME COMPETING SPECIES MODELS

Suppose we take $c_{ii} = 0$, $c_{ij} < 0$ and $b_i > 0$. In this model each species grows exponentially in the absence of the other and inhibits the growth of the other when interaction occurs. The equilibrium in this case is $e_i = -1/c_{ji} > 0$, $j \neq i$, and hence H1 holds. To obtain nonconstant periodic solutions of (2.1) from Theorem 2, we may use the criteria of Theorem 3 for this problem.

As a first example, suppose $h_{ij} = u_{\tau_i}$, $i \neq j$, for some constant time lag $\tau_i > 0$, so that (2.1) reduces to the system

$$N_i' = b_i N_i \{1 + c_{ij} N_j(t - \tau_j)\}, \quad j \neq i, \quad 1 \leq i, j \leq 2.$$

Let Z^+ be the set of positive integers. We find that $C_{ij} = e_i c_{ij} \cos 2n\pi p^{-1} \tau_i$ and $S_{ij} = e_i c_{ij} \sin 2n\pi p^{-1} \tau_i$, and hence

$$\Sigma_1(n) = \sin 2n\pi p^{-1} (\tau_1 + \tau_2), \quad \Sigma_2(n) = -\cos 2n\pi p^{-1} (\tau_1 + \tau_2),$$

so that (2.4) and (2.5) hold if p and $\tau_i > 0$ are chosen so that $(\tau_1 + \tau_2)p^{-1} = (2k - 1)/2n_0$ for some $k, n_0 \in Z^+$. For such lags τ_i the system (2.1) will have p -periodic solutions for birth rates b_i for which the product $b_1 b_2$ is near

the constant $(2n_0\pi p^{-1})^2$. Note that $\tau_i = 0$ is ruled out as a choice for the lags; the unlagged system (1.1) which results from this choice has, in fact, an unstable equilibrium, and each solution has the property that $N_i \rightarrow 0$ as $t \rightarrow +\infty$ for one and only one $i = 1$ or 2 . This is of course consistent with the familiar law of competitive exclusion, which says that two species competing for the same resource cannot both survive. Our results say, on the other hand, that if time lags are present, then two competing species may very well coexist (for appropriate birth rates) in the sense that, besides the equilibrium, there may exist nonconstant period solutions.

Probably a more realistic model would be one with continuously distributed lags: $dh_{ij}(s) = k_{ij}(s)ds$, $k_{ij} \geq 0$ for all s . Since lag effects due to encounters s time units ago should tend to zero as $s \rightarrow +\infty$, kernels such as $c_{ij}k_{ij}(s) = e^{-\delta_i s}$ or $se^{-\delta_i s}$ with $\delta_i > 0$ are reasonable. In the first case (2.4a) yields $\delta_1^2 + \delta_2^2 = 0$, an impossibility, and hence no periodic solutions bifurcate from equilibrium. However, for the second choice, one finds from Theorem 3 that p -periodic solutions exist if

$$\delta_1 \neq \delta_2 \quad \text{and} \quad \delta_1 \delta_2 (2\pi p^{-1})^2 = n_0^2$$

for some $n_0 \in \mathbb{Z}^+$ and if $b_1 b_2$ is near $\delta_1^4 \delta_2^4 / (\delta_1 + \delta_2)^2$. Notice that the two cases differ in that the first has monotonically decreasing lag effects, while the second has lag effects which increases to a maximum before decaying exponentially to zero. This supports the rough "rule of thumb" that periodic solutions bifurcate from equilibrium when the lag effects are more significant in some sense than present effects.

(b) *A PREDATOR-PREY MODEL*

The following predator-prey model was considered by Volterra in [10]:

$$\begin{aligned} N_1' &= b_1 N_1 (1 - c_{11} N_1 + c_{12} N_2), \\ N_2' &= b_2 N_2 \left(-1 + c_{21} \int_0^\infty N_1(t-s) dh_{21}(s) \right), \end{aligned} \tag{3.1}$$

$$b_i, c_{21} > 0 \quad \text{and} \quad c_{12} < 0 \quad \text{and} \quad c_{11} < c_{21}.$$

(Actually Volterra considered this model with $c_{11} = 0$, whereas we have assumed $c_{11} > 0$; i.e., we assume that the prey has a finite carrying capacity in the absence of predators.) Here we have put $h_{11} = h_{12} = u_0$ in (1.1). The system (3.1) has an equilibrium given by

$$e_1 = \frac{1}{c_{21}} > 0, \quad e_2 = \frac{c_{11} - c_{21}}{c_{21} c_{12}} > 0,$$

and hence H1 holds. With regards to H2 a straightforward calculation shows that $\det M(n)$ is a quadratic polynomial in λ_1 which has a positive root if and only if $\lambda_2 = -2n\pi p^{-1}c_{11}/c_{12}S_{21}$, in which case this root is $\lambda_1 = 2n\pi p^{-1}S_{21}/e_1c_{11}C_{21}$. Thus, we need $S_{21} > 0$, $C_{21} > 0$, in which case if λ_i and p satisfy these relationships for some integer $n = n_0$, then H2 holds. One can also calculate $J = (K_1^2 + K_2^2)e_1e_2c_{11}^2c_{21}/S_{21} \neq 0$ so that Theorem 1 yields the existence of p -periodic solutions if b_i is close to the values of λ_i given above. The condition $S_{21} > 0$ cannot be met for nonlag models, since $h_{21} = u_0$ implies that $S_{21} = 0$. The conditions that S_{21} and C_{21} be positive roughly demand that significant lag effects must be present in the model. As a specific illustration of these results, consider the case $c_{21}dh_{21}(s) = (\alpha + \beta)e^{-\delta s}ds$ for constants $\delta > 0$ and $\alpha, \beta \geq 0$ ($\alpha^2 + \beta^2 \neq 0$), which implies that $S_{21} > 0$ for any α, β, δ and that $C_{21} > 0$ if and only if $(\alpha + \beta\delta)\delta^2 + (2n_0\pi p^{-1})(\beta\delta - \alpha) > 0$. Thus, given α, β, δ , one may choose $n_0 = 1$ and any p large enough so that this inequality holds, and obtain p -periodic solutions for b_i close to λ_i as calculated from the formulas above. For this specific kernel one can show, using the methods in [2] (the case $c_{11} = 0$ is worked out in [2]) that the equilibrium for (3.1) is *unstable*. Thus, unlike the nonlag classical predator-prey model, which has a globally attracting, stable equilibrium, this lag model has an unstable equilibrium surrounded by nonconstant periodic solutions (for certain birth rates). See [1] for other results concerning this model.

4. PROOF OF THEOREM 1 AND 2.

(a)

Let $x_i = N_i - e_i$. Into the system (2.1) we make the substitutions $x_i = \epsilon y_i + \epsilon z_i(\epsilon)$, $z_i = O(\epsilon)$ and $|b_i| = \lambda_i + \mu_i(\epsilon)$, $\mu_i = O(\epsilon)$. The first order terms in ϵ in the resulting expression yield the linear homogeneous system

$$y_i' = \lambda_i \Gamma_i(y), \quad 1 \leq i \leq 2, \quad (4.1)$$

for y_i , and the higher order terms in ϵ yield the nonlinear system

$$z_i' = \lambda_i \Gamma_i(z) + F_i, \quad 1 \leq i \leq 2, \quad (4.2)$$

for $z = (z_i)$, where $F_i = F_i(z, \mu_i, \epsilon)$ is given by

$$F_i(z, \mu_i, \epsilon) = \mu_i \{ \Gamma_i(z) + \Gamma_i(y) \} + \epsilon(\lambda_i + \mu_i)(y_i + z_i)\Gamma_i(y + z). \quad (4.3)$$

Our goal is to show that H2 implies that (4.1) has a p -periodic solution y given by (2.2), and that $J \neq 0$ implies that, for certain $\mu_i = O(\epsilon)$, (4.2) has a p -periodic solution z satisfying $z \cdot y^j = 0$ for $j = 1, 2$.

First, we consider (4.1). Referring to Theorem 5.1 in Sec. 5 below (using $\Delta \neq 0$ in H1), we see by part (c) that [since the matrix $Q(n)$ is for (4.1) just the matrix $M(n)$] the system (4.1) has two independent p -periodic solutions y^j given by (2.2) under the hypothesis H2.

Next, consider (4.2). Given $z \in B(p) \times B(p) \equiv B^2$ such that $z \cdot y^j = 0$, we determine μ_i such that the orthogonality conditions

$$F \cdot w^j = 0 \quad \text{for } j = 1, 2 \tag{4.4}$$

hold where $F = (F_i)$ and the w^j are given by (2.3). These conditions are certainly necessary for solutions of (4.2), as we know from Theorem 3 in Sec. 5 below. To solve these two equations we will use the implicit function theorem [6]. Since $\mu_i = \epsilon = z = 0$ solves (4.4) (because then $F = 0$) and since the Jacobian of (4.4) with respect to μ_i evaluated at $\mu_i = \epsilon = z = 0$ is just J , we have from the assumption that $J \neq 0$ the existence of a solution $\mu_i = \mu_i(\epsilon, z)$ defined for $\epsilon, |z_i|_1 \leq \epsilon^*$ for some $\epsilon^* > 0$ satisfying $\mu_i(0, 0) = 0$. If $\epsilon = 0$ in (4.4), one obtains a linear, homogeneous system for $\mu_i(0, z)$ whose coefficient matrix has determinant $J(z)$ such that $J(0) = J \neq 0$. Thus, for ϵ^* smaller (if necessary), we have $J(z) \neq 0$ for $|z_i|_1 \leq \epsilon^*$, which implies that $\mu_i(0, z) = 0$ for all such z . Moreover, since the right hand side of (4.4) has continuous (Fréchet) derivatives in μ_i, ϵ and z_i of all orders, it follows that μ_i has continuous derivatives of all orders in ϵ and z_i [6]. Since $\mu_i(0, z) = 0$ for small z , we have that $\partial \mu_i(0, z) / \partial z_j = 0$ for $j = 1, 2$ and small z .

Let $B_0^2(p) = \{f \in B^2(p) : f \cdot y^j = 0, j = 1, 2\}$, a Banach subspace of $B^2(p)$. For $z \in B_0^2(p)$ the integrodifferential system (4.2), with $\mu_i = \mu_i(\epsilon, z)$ substituted into (4.3), can be reformulated as the operator equation

$$z = G(\epsilon, z), \quad z \in S(\epsilon^*), \tag{4.5}$$

where $G = (G_i) = LF$, L is the bounded linear operator on $B(p) \times B(p)$ of Theorem 3 below, and $S(\epsilon^*) = \{z \in B_0^2(p) : |z_i|_1 \leq \epsilon^*\}$. We now wish to argue that (4.5) has a solution z by means of the contraction principle. Since $G(0, z) = 0$ for all $z \in S(\epsilon^*)$, it follows that $|G_i(0, z)|_1 \leq \epsilon^*$ for $\epsilon \leq \epsilon_0$ for some $\epsilon_0 > 0$. Thus, $G(\epsilon, z)$ maps $S(\epsilon^*)$ into itself for every $\epsilon \leq \epsilon_0$. From (4.3) and $\partial \mu_i(0, z) / \partial z_j = 0$ on $S(\epsilon^*)$, it follows that $\partial G_i(0, z) / \partial z_j = 0$ on $S(\epsilon^*)$. Thus, for ϵ_0 smaller (if necessary), G is a contraction on $S(\epsilon^*)$ for each $\epsilon \leq \epsilon_0$. The unique solution thus guaranteed for (4.5) yields a solution of (2.1) as described in Theorem 1.

Finally we consider the average of $N_i \in B(p)$. Clearly

$$\left[\int_0^\infty N_i(t-s) dh_y(s) \right] = [N_i] \int_0^\infty dh_y(s) = [N_i]$$

for $1 \leq i, j \leq 2$. Using this fact, dividing both sides of (1.2) by pN_i and integrating from 0 to p , one obtains

$$0 = b_i - c_{ii}[N_i] + c_{ij}[N_j], \quad 1 \leq i, j \leq 2, \quad i \neq j,$$

which [because (1.4) has, by H1, a unique solution e_i] implies that $[N_i] = e_i$. This completes the proof of Theorem 1.

(b)

To prove Theorem 2 we consider $M(n)$ and J when $c_{ii} = 0$ for both $i = 1, 2$. The determinant of $M(n)$ turns out in this case to be $\det M(n) = (\lambda_1 \lambda_2)^2 P(\xi)$, where the polynomial $P(\xi)$ is given by

$$P(\xi) = \xi^2 + 2(C_{12}C_{21} - S_{12}S_{21})\xi + (S_{12}^2 + C_{12}^2)(S_{21}^2 + C_{21}^2),$$

and where $\xi = (2n\pi p^{-1})^2 / \lambda_1 \lambda_2$. Thus, $M(n)$ is singular if and only if $P(\xi) = 0$ for some nonzero, positive real root ξ . The roots of P are $\xi = \Sigma_2(n) \pm \Sigma_1(n) (-1)^{1/2}$, and hence H2 holds if and only (2.4a, b) and (2.5) hold, in which case $\xi = \Sigma_2(n_0)$ [which in turn implies (2.5)]. The condition (2.5) guarantees that for this choice of λ_i the matrix $M(n)$ is nonsingular for $n \neq n_0$.

Finally we consider the requirement that $J \neq 0$. From the definition of J we have for $\mu_i = z = \varepsilon = 0$ that

$$J = \xi^{-1} (K_1^2 + K_2^2) (C_{12}S_{21} - S_{12}C_{21}) = 2\xi^{-1} (K_1^2 + K_2^2) C_{12}S_{21}.$$

Here we have made use of (2.4a) as well as the fact that $c_{ii} = 0$ implies that the vector

$$(a_1^*, a_2^*, b_1^*, b_2^*) = \left(-\frac{\lambda_2 S_{21}}{2n_0 \pi p^{-1}}, 1, -\frac{\lambda_2 C_{21}}{2n_0 \pi p^{-1}}, 0 \right)$$

lies in the null space of the transpose matrix $M^*(n_0)$. This vector was used in J for w^j as defined in (2.3). Thus, $J \neq 0$ if and only if (2.4c) holds.

5. A FREDHOLM ALTERNATIVE

Consider the linear integrodifferential systems

$$y'_i = L_i(y), \quad i = 1, 2, \quad (\text{H})$$

$$z'_i = L_i(z) + f_i(t), \quad i = 1, 2, \quad (\text{NH})$$

where $y = (y_i)$ and

$$L_i(y) = \int_0^\infty y_i(t-s) dm_{ii}(s) + \int_0^\infty y_j(t-s) dm_{ij}(s), \quad 1 \leq i, j \leq 2, \quad i \neq j,$$

$$-\infty < \mu_{ij} = \int_0^\infty dm_{ij}(s) < +\infty.$$

For a fixed period p and for all integers, define the numbers

$$B_{ij} = B_{ij}(n) = \int_0^\infty \sin 2n\pi p^{-1}s \, dm_{ij}(s),$$

$$A_{ij} = A_{ij}(n) = \int_0^\infty \cos 2n\pi p^{-1}s \, dm_{ij}(s)$$

and the matrices $B(n) = (B_{ij}(n))$, $A(n) = (A_{ij}(n))$ and

$$Q(n) = 2n\pi p^{-1}I + \begin{pmatrix} B(n) & A(n) \\ -A(n) & B(n) \end{pmatrix},$$

where I is the 4×4 identity matrix. Let $Q^*(n)$ denote the transpose of $Q(n)$.

THEOREM 3

(a) If (H) has no nontrivial solution $y_i \in B(p)$, then (NH) has, for each $f_i \in B(p)$, a unique solution $z_i \in B(p)$.

(b) Assume $\mu_{11}\mu_{22} - \mu_{12}\mu_{21} \neq 0$. The system (H) has a solution in $B(p)$ for some p if and only if $Q(n)$ is singular for some integer $n \in \mathbb{Z}^+$.

(c) Suppose that $Q(n)$ is singular (but nonzero) for $n = n_0 \geq 1$ and that $Q(n)$ is nonsingular for $n \neq n_0$. Then the null space of $Q(n_0)$ and $Q^*(n_0)$ are both two dimensional, and (H) has two (and only two) independent solutions $y^j = (y_i^j)$, $j = 1, 2$ in $B(p)$, given by

$$y_i^1 = a_i(n_0)\cos 2n_0\pi p^{-1}t + b_i(n_0)\sin 2n_0\pi p^{-1}t,$$

$$y_i^2 = -b_i(n_0)\cos 2n_0\pi p^{-1}t + a_i(n_0)\sin 2n_0\pi p^{-1}t,$$

respectively, where the vector $(a_1(n_0), a_2(n_0), b_1(n_0), b_2(n_0))$ lies in the null space of $Q(n_0)$.

(d) Under the assumptions of part (c), (NH) has a solution $z_i \in B(p)$ if and only if the orthogonality conditions

$$f \cdot w^j = 0, \quad j = 1, 2 \tag{0}$$

hold, where $f = (f_i)$ and

$$w_i^1 = a_i^*(n_0)\cos 2n_0\pi p^{-1}t + b_i^*(n_0)\sin 2n_0\pi p^{-1}t,$$

$$w_i^2 = -b_i^*(n_0)\cos 2n_0\pi p^{-1}t + a_i^*(n_0)\sin 2n_0\pi p^{-1}t.$$

Here the vector $(a_1^*(n_0), a_2^*(n_0), b_1^*(n_0), b_2^*(n_0))$ lies in the null space of $Q^*(n_0)$. If (0) is met, then (H) has a unique solution $z_i \in B(p)$ satisfying $z \cdot y^j = 0$, $j = 1, 2$, and the operator defined by $Lf = z$ is a continuous linear operator from B_0^2 into itself.

Proof.

(a) For $f_i \in B(p)$ we have the Fourier series

$$f_i(t) = \alpha_i(0) + \sum_{n=1}^{\infty} \{ \alpha_i(n) \cos 2n\pi p^{-1}t + \beta_i(n) \sin 2n\pi p^{-1}t \}.$$

If these series and the series

$$z_i = a_i(0) + \sum_{n=1}^{\infty} \{ a_i(n) \cos 2n\pi p^{-1}t + b_i(n) \sin 2n\pi p^{-1}t \} \quad (5.1)$$

are substituted into (NH) and if the coefficients of like terms are then equated, one finds that (NH) will have a solution $z_i \in B(p)$ if and only if the equations

$$m_{i1}a_1(0) + m_{i2}a_2(0) = \alpha_i(0), \quad i = 1, 2, \quad (5.2)$$

$$\begin{aligned} 2n\pi p^{-1}b_i(n) &= A_{i1}a_1(n) - B_{i1}b_1(n) + A_{i2}a_2(n) - B_{i2}b_2(n) + \alpha_i(n), \\ -2n\pi p^{-1}a_i(n) &= B_{i1}a_1(n) + A_{i1}b_1(n) + B_{i2}a_2(n) + A_{i2}b_2(n) + \beta_i(n), \end{aligned} \quad i = 1, 2 \quad (5.3)$$

are satisfied by the a_i and b_i for all $n \geq 1$.

First consider (5.2). Since (H) is assumed to have no nontrivial periodic solution in $B(p)$, it follows that $\mu_{11}\mu_{22} - \mu_{12}\mu_{21} \neq 0$; for otherwise (H) would have constant (but nonzero) solutions. Thus, (5.2) implies that the $a_i(0)$ are uniquely determined.

Next consider (5.3). If $\theta = (a_1(n), a_2(n), b_1(n), b_2(n))$, then the linear algebraic system (5.3) may be written in the matrix form $Q(n)\theta = \eta$, where $\eta = (-\beta_1(n), -\beta_2(n), \alpha_1(n), \alpha_2(n))$. Since (H) is assumed to have no nontrivial solutions in $B(p)$, it follows that $Q(n)$ is nonsingular for all n [for otherwise the homogeneous system associated with (5.3) would have nontrivial solutions which when used in (5.1) would yield a nontrivial solution in $B(p)$ of (H)]. Thus, (5.3) may be solved uniquely for every $n \geq 1$, and its solutions when substituted in (5.1) yield a unique formal solution in $B(p)$ of (NH).

Finally we must argue that this formal Fourier series converges to a function in $B(p)$. Using Cramer's rule together with the definition of $Q(n)$ and the fact that all B_{ij}, A_{ij} are bounded independently of n , one easily finds the estimates

$$\begin{aligned} |a_i(0)| &\leq K|\alpha_i(0)|, \\ |a_i(n)|, |b_i(n)| &\leq n^{-1}K \sum_{i=1}^2 |\alpha_i(n)| + |\beta_i(n)|, \quad n \geq 1, \end{aligned} \quad (5.4)$$

for some constant $K > 0$ independent of n . Since $f_i \in B(p)$ implies $\alpha_i^2(0) + \sum_n \alpha_i^2(n) + \beta_i^2(n) < +\infty$, $i = 1, 2$ [3], it follows from (5.4) (and Hölder's inequality) that

$$\sum_{n=1}^{\infty} n^2 a_i^2(n) + n^2 b_i^2(n) < +\infty, \quad i = 1, 2.$$

Thus, the Fourier series for z_i given by (5.1) defines an absolutely continuous function [3] which, by its construction, satisfies (H) almost everywhere. But the right hand side of (H) is continuous, so that we can further conclude that z_i is continuously differentiable; i.e., $z_i \in B(p)$.

(b) If $\alpha_i(n) = \beta_i(n) = 0$ for all $i = 1, 2$ and $n \geq 1$, then $\eta = 0$ for all $n \geq 1$, and clearly a nontrivial solution $y_i \in B(p)$ of (H) exists if and only if $Q(n)$ is singular for some $n \geq 1$.

(c) Under the stated assumptions, the null space of $Q(n_0)$ is either one, two or three dimensional. Since $Q(n_0)\theta = 0$, $\theta \neq 0$, implies $Q(n_0)\theta' = 0$ where $\theta' = (-b_1(n_0), -b_2(n_0), a_1(n_0), a_2(n_0)) \neq 0$, we see that the nullity must in fact be two. (It is easily shown that θ and θ' are independent.) Since the rank of a matrix is that of its transpose, $Q^*(n_0)$ also has nullity two.

(d) As is well known, $Q(n_0)\theta = \eta$ is solvable if and only if η is orthogonal to the null space of $Q^*(n_0)$. If θ^* is in the null space of $Q^*(n_0)$, then so is $\theta^{*'}$, and hence this condition is that η be orthogonal to both θ^* and $\theta^{*'}$, which is equivalent to (0). There is, of course, a unique solution which is orthogonal to both θ and θ' ; this vector yields by means of (5.1) a unique solution z_i of (NH) which satisfies $z \cdot y^j = 0$ for $j = 1, 2$.

Finally we consider the continuity of the operator $Lf = z$, which is clearly linear from B_0^2 into itself. Suppose $f^k = (f_i^k)$ is a sequence of functions converging to zero in B_0^2 as $k \rightarrow +\infty$. We must show that $|z_i^k|_1 \rightarrow 0$ as $k \rightarrow +\infty$, where $(z_i^k) = Lf^k$. Certainly for each fixed k , (5.4) holds for all $n \neq n_0$ and for K independent of k . For $n = n_0$ the estimate (5.4) will still hold for that solution of (5.3) which is orthogonal to both θ and θ' . With this choice for $n = n_0$ we have that (5.4) holds for all $n \geq 1$ and k :

$$|a_i^k(n)|, |b_i^k(n)| \leq n^{-1}K \sum_{i=1}^2 |\alpha_i^k(n)| + |\beta_i^k(n)|, \quad i = 1, 2. \quad (5.5)$$

From the definition (5.1) of the solution z_i^k we have

$$|z_i^k|_0 \leq |a_i^k(0)| + \sum_{n=1}^{\infty} |a_i^k(n)| + |b_i^k(n)|.$$

Since the sum $\alpha_i^2(0) + \sum_n \alpha_i^2(n) + \beta_i^2(n)$ is equal to the L^2 norm $|f_i|_2$ of f_i , we deduce from this last inequality and from (5.5) (by use of Hölder's inequality) that $|z_i^k|_0 \leq K^*(|f_1^k|_2 + |f_2^k|_2)$, $i = 1, 2$, for some constant $K^* > 0$ independent of k . Thus, since $|f_i^k|_1 \rightarrow 0$ implies $|f_i^k|_2 \rightarrow 0$ as $k \rightarrow +\infty$, we find that $|z_i^k|_0$ as $k \rightarrow +\infty$, $i = 1, 2$. Since z_i^k solves (NH), this fact in turn implies that $|dz_i^k/dt|_0 \rightarrow 0$ and hence $|z_i^k|_1 \rightarrow 0$ as $k \rightarrow +\infty$.

REFERENCES

- 1 J. M. Bownds and J. M. Cushing, On the behavior of solutions of predator-prey equations with hereditary terms, *Math. Biosci.* **26**, 41–54 (1975).
- 2 J. M. Cushing, An operator equation and bounded solutions of integrodifferential systems, *SIAM J. Math. Anal.* **6** (3), 433–445 (1975).
- 3 R. E. Edwards, *Fourier Series: A Modern Introduction*, Holt, Rinehart and Winston, New York, 1967.
- 4 H. I. Freedman, A perturbed Kolomogorov-type model for the growth problem, *Math. Biosci.* **23**, 127–149 (1975).
- 5 H. I. Freedman and Paul Waltman, Periodic solutions of perturbed Lotka–Volterra systems, *Proc. Int. Conf. on Differ. Equations* (H. A. Antosiewicz, Ed.), Academic, New York, 1975, pp. 312–316.
- 6 T. H. Hildebrandt and Lawrence M. Graves, Implicit functions and their differentials in general analysis, *Trans. Am. Math. Soc.* **29**, 127–153 (1927).
- 7 G. E. Hutchinson, Theory of competition between two social species, *Ecology* **28**, 319–321 (1947).
- 8 R. M. May, Limit cycles in predator-prey communities, *Science* **177**, 900–902 (1972).
- 9 R. K. Miller, Structure of solutions of unstable linear Volterra integrodifferential equations, *J. Differ. Equations* **15**, 129–157 (1974).
- 10 V. Volterra, *Leçons sur la Théorie Mathématique de la Lutte par la Vie*, Gauthier-Villars, Paris, 1931.
- 11 P. E. Waltman, The equations of growth, *Bull Math. Biophys.* **26**, 39–43 (1964).
- 12 P. Wangersky and W. J. Cunningham, Time lag in predator-prey population models, *Ecology* **38**, 136–139 (1957).