

FORCED ASYMPTOTICALLY PERIODIC SOLUTIONS OF PREDATOR-PREY SYSTEMS WITH OR WITHOUT HEREDITARY EFFECTS*

J. M. CUSHING†

Abstract. Volterra's two-species predator-prey integro-differential model, which describes the dynamics of predator-prey interactions when continuously accumulating lag effects are considered, is modified by the addition of forcing or control functions (as well as by the use of Stieljes integrals in place of Riemann integrals so as to include in the analysis models with discrete time lags). It is shown that for appropriate choices of these control functions (viz., functions which are asymptotically periodic with a certain determinant condition being satisfied by the periodic parts) the model possesses infinitely many asymptotically periodic solutions for small logistic loads and hereditary (or lag) effects. For certain special cases (in particular, the classical differential model with no lag effects) the existence of periodic solutions is proved. The method of proof is to introduce a small constant ϵ into selected parameters of the system and to construct, by the contraction principle, solutions which are perturbations off of a given periodic solution of the classical Volterra-Lotka model (which corresponds to $\epsilon = 0$).

1. Introduction. It is well known that all solutions satisfying $x_i > 0$ (or, equivalently, initiating in the first quadrant) of the classical two-species predator-prey system

$$(1.1) \quad \begin{aligned} x'_1 &= x_1(a_1 - c_1x_2), & a_1, c_1 &> 0, \\ x'_2 &= x_2(-a_2 + b_2x_1), & a_2, b_2 &> 0, \end{aligned}$$

are periodic; this was proved by Volterra [12], who was one of the original investigators of this system. With the introduction of logistic loads (or carrying capacities)

$$\begin{aligned} x'_1 &= x_1(a_1 - b_1x_1 - c_1x_2), & b_1 &\geq 0, \\ x'_2 &= x_2(-a_2 + b_2x_1 - c_2x_2), & c_2 &\geq 0, \end{aligned}$$

the system has a globally (in the first quadrant) asymptotically stable equilibrium for $b_1 > 0$ small (b_1 is small in order to place the equilibrium in the first quadrant). This follows from the fact that the constant of motion for (1.1) [12], [10] is a Lyapunov function with negative definite trajectory derivative for this system.

Volterra [12, Chap. 4] also introduced hereditary effects into the system by consideration of the integro-differential system

$$\begin{aligned} x'_1 &= x_1(a_1 - c_1x_2), \\ x'_2 &= x_2\left(-a_2 + \int_{t_0}^t k_2(t-s)x_1(s) ds\right), \end{aligned}$$

where $k_2 \geq 0$ satisfies $\int_0^\infty k_2(s) ds < \infty$ and $t_0 = -\infty$. This added feature significantly complicates the behavior of the solutions and as a result not a great deal is known in general about their long-term behavior. Volterra [12] showed that for $t_0 = -\infty$

* Received by the editors October 17, 1974, and in revised form May 5, 1975.

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

the solutions possess a certain "oscillatory" property around the equilibrium point $(\sigma_1, \sigma_2) = (a_2/(b_1 + \int_0^\infty k_2 ds), a_1/c_1)$. In [5] it is shown that for $t_0 = 0$, this critical point is unstable, at least for certain kernels k_2 . Even with the introduction of logistic loads, the system may be unstable (although their long-term time averages are still this critical point) as is shown numerically and by the use of certain nonlinear approximations in [2]; these two approaches also show that "limit cycles" frequently exist in these unstable cases. The mathematical question of the existence of "limit cycles" for these hereditary models is an interesting open question. In this paper we consider the problem of the existence of "limit cycles" for forced or controlled systems. It will be shown that for suitable control functions, "many" solutions approach a periodic state as $t \rightarrow +\infty$ whose period is independent of the initial state.

Specifically, we consider the more general system

$$(1.2) \quad \begin{aligned} x_1' &= x_1 \left[a_1 - c_1 x_2 - b_1 \int_{t_0}^t x_1(s) d\alpha_{11}(t-s) - d_1 \int_{t_0}^t x_2(s) d\alpha_{12}(t-s) \right] \\ &\quad + f_1(t), \\ x_2' &= x_2 \left[-a_2 + b_2 x_1 - c_2 \int_{t_0}^t x_2(s) d\alpha_{21}(t-s) + d_2 \int_{t_0}^t x_1(s) d\alpha_{22}(t-s) \right] \\ &\quad + f_2(t), \end{aligned}$$

where $a_i, c_1, b_2 > 0$; $d_i, c_2, b_1 \geq 0$; and where $\alpha_{ij}(t)$ is nondecreasing and satisfies $\int_0^\infty d\alpha_{ij}(t) = 1$. If $d\alpha_{ij}(s) = k_{ij}(t) dt$, then we get continuously distributed lag (or hereditary) effects from this term. If $\alpha_{ij}(t) = u_\tau(t)$, the unit step function at $\tau > 0$, then we have an instantaneous lag effect; if $\tau = 0$ we have no lag effect for this term. We are interested in finding conditions under which periodic or asymptotically periodic (this term will be made precise below) solutions exist for an appropriate choice of $f_i(t)$. We will consider this problem for small hereditary or lag terms (i.e., for b_1, c_2 and d_i small) and small forcing terms f_i as made explicit below. The forcing terms f_i may be thought of as describing immigration and/or emigration, or some external (state-independent) control (e.g., harvesting and/or seeding), or just "noise" effecting the growth of the populations as might be unaccounted for in the other terms.

It has been suggested [1], [6] that because (1.1) is critically stable it is ecologically undesirable and that a more reasonable model would possess an unstable critical point together with a stable limit cycle. Recent authors [6], [7], [11] have accomplished this by adding state-dependent perturbations to (1.1) of an appropriate type. Our results here can be related to theirs in that we prove the existence of "limit cycles" (for the even more general hereditary problem (1.2)) for appropriate state-independent perturbations f_i .

Our main result, Theorem 1, describes a large class of functions f_i for which infinitely many asymptotically periodic solutions exist at least for small logistic loads and hereditary effects. The only restrictions on the f_i are that they be asymptotically periodic and that their periodic parts satisfy a certain determinant condition. This theorem does not exclude the differential, nonhereditary case $\alpha_{ij} = u_0$; however, in this case, as well as in the hereditary case when $t_0 = -\infty$, we can also assert the existence of periodic solutions by using only slight modifications of the proof of Theorem 1. These results are stated in Theorem 2.

2. Results. We consider the following integro-differential system:

$$\begin{aligned}
 (2.1) \quad x'_1 &= x_1 \left[a_1 - c_1 x_2 - \varepsilon b_1 \int_{t_0}^t x_1(s) d\alpha_{11}(t-s) - \varepsilon d_1 \int_{t_0}^t x_2(s) d\alpha_{12}(t-s) \right] \\
 &\quad + \varepsilon f_1(t), \\
 x'_2 &= x_2 \left[-a_2 + b_2 x_1 - \varepsilon c_2 \int_{t_0}^t x_2(s) d\alpha_{21}(t-s) + \varepsilon d_2 \int_{t_0}^t x_1(s) d\alpha_{22}(t-s) \right] \\
 &\quad + \varepsilon f_2(t),
 \end{aligned}$$

where we have introduced a small parameter ε to emphasize that the logistic coefficients and hereditary effects are to be small; here $a_i, c_1, b_2 > 0$ and $b_1, c_2, d_i \geq 0$ are fixed constants. We will look for forcing terms, also of order ε , which yield asymptotically periodic solutions. More specifically, if we let $\bar{x} = \text{col}(x_1, x_2)$ and $|\cdot|$ be any vector norm in R^2 , then we desire solutions in the Banach space $P(\omega) \oplus E_\beta$, for some ω and β , where E_β is the Banach space of vector-valued functions continuous in $t \geq t_0$ for which $|\bar{x}|_\beta = \sup_{t \geq t_0} |\bar{x}(t)| \exp(\beta t) < +\infty$ and where $P(\omega)$ is the Banach space of continuous vector-valued functions which are ω -periodic in $t \geq t_0$ under the norm $|\bar{x}| = \sup_{[0, \omega]} |\bar{x}(t)|$. Let $|\cdot|_{\omega, \beta} = |\cdot|_\omega + |\cdot|_\beta$ be the norm on $P(\omega) \oplus E_\beta$; then the projections P_1 and P_2 onto $P(\omega)$ and E_β respectively are bounded, linear operators.

If $\bar{y} = \text{col}(y_1, y_2), y_i > 0$, is a solution of the classical Volterra-Lotka predator-prey differential system (1.1), then we will have occasion to consider the linear, nonautonomous homogeneous system $\bar{z}' = A(t)\bar{z}$, where

$$(2.2) \quad A(t) = \begin{pmatrix} a_1 - c_1 y_2(t) & -c_1 y_1(t) \\ b_2 y_2(t) & -a_2 + b_2 y_1(t) \end{pmatrix}.$$

Let $Z(t)$ be a fundamental matrix of this system. This system is the variational system of (1.1) with respect to $\bar{y}(t)$. As is well known [3], such a variational system has at least one ω -periodic solution, where ω is the period of \bar{y} , and hence that the adjoint system does also. This means $Z^{-1}(t)$ has at least one ω -periodic row which we assume, without loss in generality, to be the first row. Let $Z^{-1}(t) = (z_{ij}(t))$. The set of initial conditions giving rise to ω -periodic solutions of $z' = A(t)z$ forms a linear subspace of R^2 of dimension $d = 1$ or 2 which we denote by V . If $\bar{p} = \text{col}(p_1, p_2) \in P(\omega)$, define the matrix

$$M(Z^{-1}; \bar{p}) = \begin{pmatrix} \int_0^\omega z_{11} p_1 ds & \int_0^\omega z_{12} p_2 ds \\ \int_0^\omega z_{21} p_1 ds & \int_0^\omega z_{22} p_2 ds \end{pmatrix}.$$

THEOREM 1. Assume $\int_0^\infty e^{\beta s} d\alpha_{ij}(s) < +\infty$ for $1 \leq i, j \leq 2$ for some $\beta > 0$. Given any solution \bar{y} of the classical predator-prey system (1.1) satisfying $y_i > 0$, any vector $\bar{v} \in V$, any $\bar{q} = \text{col}(q_1, q_2) \in E_\beta$, and any $\bar{p} = \text{col}(p_1, p_2) \in P(\omega)$ (where ω is the period of \bar{y}), there exists a constant $\varepsilon_0 = \varepsilon_0(\bar{y}, \bar{v}, b_i, c_i, d_i, \alpha_{ij}, \bar{p}, \bar{q}) > 0$ for which the following are true: (a) Suppose $d = 2$ and hence $V = R^2$. If \bar{p} is such that

$\det M(Z^{-1}; \bar{p}) \neq 0$, then for all $|\varepsilon| \leq \varepsilon_0$ there exist “amplitudes” α_1, α_2 such that the predator-prey system (2.1), with forcing terms $f_i = \alpha_i p_i + q_i, i = 1$ and 2 , has a solution $\bar{x} \in P(\omega) \oplus E_\beta$ satisfying $(P_1 \bar{x})(0) = \bar{y}(0) + \varepsilon \bar{v}$. This solution has the form $\bar{x} = \bar{y} + \varepsilon \bar{w}(\varepsilon)$ for a unique $\bar{w}(\varepsilon) \in P(\omega) \oplus E_\beta$ where $\bar{w}(\varepsilon) = O(|\varepsilon|)$. The amplitudes have the form $\alpha_i = \alpha_i^0 + O(|\varepsilon|)$ where $\alpha_i^0 = \alpha_i^0(\bar{y}, \bar{p}, b_1, c_2, d_i, \alpha_{ij})$ are constants given by (3.7) below.

(b) Suppose $d = 1$. If p_i is such that $\int_0^\omega z_{1i} p_i ds \neq 0$ for either $i = 1$ or 2 , then for each arbitrarily chosen, but fixed $f_j, j \neq i$, and all $|\varepsilon| \leq \varepsilon_0$, there exists an “amplitude” α_i such that (2.1) with $f_i = \alpha_i p + q_i$ has a solution $\bar{x} \in P(\omega) \oplus E_\beta$ with the same properties as in (a). In this case α_i^0 is given by (3.8) below.

We point out that, as indicated, the amplitudes α_i are independent of $\bar{v} \in R^2$. The function \bar{w} is, however, dependent on \bar{v} as well as all of the other parameters. It is not difficult to see that this dependence is continuous since \bar{w} is the fixed point of a certain contraction, as will be shown in the proof.

If $t_0 = -\infty$, then the proof of Theorem 1 can be slightly modified to prove a further result concerning periodic solutions.

THEOREM 2. *If $t_0 = -\infty$ and the added assumption on α_{ij} is dropped, then the conclusions of Theorem 1 hold with E_β replaced by the empty set \emptyset .*

Remarks. 1. It is well known that the long-term time average $[\bar{y}]$ of solutions $\bar{y}(t)$ of (1.1) is the critical point $\bar{y}_0 = \text{col}(a_2/b_2, a_1/c_1)$; i.e.,

$$[\bar{y}] = \lim_{t \rightarrow +\infty} t^{-1} \int_0^t \bar{y}(s) ds = \omega^{-1} \int_0^\omega \bar{y}(s) ds = \bar{y}_0.$$

Since the long-term time average of functions in E_β is zero we have, for the solutions of (2.1) found in Theorem 1, that $[\bar{x}] = \bar{y}_0 + \varepsilon [P_1 \bar{w}]$, where $[P_1 \bar{w}] = \omega^{-1} \int_0^\omega \bar{w} ds$ and, hence, $[\bar{x}] = \bar{y}_0 + O(|\varepsilon|)$.

2. Both theorems above are applicable in the differential case $\alpha_{ij} = \sum_{n=1}^m u_{\tau_n}, \tau_n \geq 0$ and, hence, give conditions under which forced differential predator-prey systems, with (or without) multiple constant time lags, have asymptotically periodic or periodic solutions.

3. Since $[\bar{y}] = y_0$ as noted in Remark 1, it follows easily that the integral of the trace of $A(t)$ is ω -periodic. Thus, by the Jacobi-Liouville theorem, $\det Z(t) = \det Z(0) \exp(\int_0^t \text{tr} A(s) ds)$ is ω -periodic. Consequently, since the first row of $Z^{-1}(t)$ was assumed ω -periodic, we have that the first column of $Z(t)$ is ω -periodic. If we define

$$\Pi = \begin{cases} \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}, & \text{if } d = 1, \\ \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}, & \text{if } d = 2, \end{cases}$$

then $Z(t)\Pi$ and $\Pi Z^{-1}(t)$ are ω -periodic.

4. If in Theorem 1 or 2 we choose \bar{y} to be the equilibrium solution $(a_2/b_2, a_1/c_1)$ (and hence consider forced periodic solutions near equilibrium), then the system $\bar{z}' = A(t)\bar{z}$ is easily seen to have an ω -periodic fundamental matrix and hence $d = 2$. This alternative in Theorems 1 and 2 is consequently seen to be nonvacuous. Numerical studies carried out by the authors of [6], [7] seem to

indicate that if \bar{y} is not the equilibrium, then $d = 1$; in fact, on the basis of their results, it is conjectured (private communication) that for such \bar{y} one always has $d = 1$. This remains, however, an open question. If this conjecture is true, then part (b) of Theorems 1 and 2 would be applicable in all cases when \bar{y} is not taken to be the equilibrium solution of (1.1).

5. A careful reading of the proof below shows that the hypothesis $\int_0^\infty e^{\beta t} d\alpha_{ij}(t) < +\infty$ can be replaced by $\int_0^\infty g(t) d\alpha_{ij}(t) < +\infty$, where g is a continuous, real-valued function such that $g(t) > 0$ and $g(t) \int_t^\infty (1/g(s)) ds \leq K < +\infty$ for some K and all $t \geq 0$. In this case we change E_β to $E_g = \{x : |x|_g = \sup_{t \geq 0} |x(t)|g(t) < +\infty\}$. Such Banach spaces appear frequently in the theory of Volterra integral equations [4].

6. Given Z^{-1} (i.e., given \bar{y}) there certainly exist $\bar{p} \in P(\omega)$ for which $\det M(Z^{-1}; \bar{p}) \neq 0$ (or $\int_0^\omega z_{1i} p_i dt \neq 0$). For example, as \bar{y} is chosen closer to the equilibrium \bar{y}_0 of (1.1), the coefficient matrix $A(t)$ in (2.2) tends to

$$\begin{pmatrix} 0 & -a_1 \\ a_2 & 0 \end{pmatrix};$$

consequently, the fundamental matrix Z tends to

$$Z(t) = \begin{pmatrix} \cos \sigma t & -\frac{\sigma}{a_2} \sin \sigma t \\ \frac{\sigma}{a_1} \sin \sigma t & \cos \sigma t \end{pmatrix}$$

and

$$Z^{-1}(t) = \begin{pmatrix} \cos \sigma t & \frac{\sigma}{a_2} \sin \sigma t \\ -\frac{\sigma}{a_1} \sin \sigma t & \cos \sigma t \end{pmatrix}$$

where $\sigma = (a_1 a_2)^{1/2}$. Also the period ω tends to $\omega_0 = 2\pi\sigma^{-1}$. Thus, if we let $\Delta = \sup_{t \geq 0} |\bar{y} - y_0|$, we find that $\det M(Z^{-1}; \bar{p}) = \det D_0 + O(\Delta)$, where the matrix $D_0 = (D_{ij})$ is given by

$$D_0 = \begin{pmatrix} \int_0^{\omega_0} p_1 \cos \sigma s ds & -\frac{\sigma}{a_2} \int_0^{\omega_0} p_2 \sin \sigma s ds \\ -\frac{\omega}{a_1} \int_0^{\omega_0} p_1 \sin \sigma s ds & \int_0^{\omega_0} p_2 \cos \sigma s ds \end{pmatrix}.$$

If $\det D_0 \neq 0$, then $\det M(Z^{-1}; \bar{p}) \neq 0$ for small Δ . For example, one could take $\bar{p} = \text{col}(\cos \sigma t, \cos \sigma t)$, in which case $D_0 = \pi\sigma^{-1}I$, $\det D_0 = \pi\sigma^{-1} \neq 0$, and $\det M(Z^{-1}; \bar{p}) = \pi\sigma^{-1} + O(\Delta) \neq 0$ for Δ small. This would be applicable when, for example, \bar{y} is taken to be at equilibrium in which case $\Delta = 0$ (see Remark 4)). Also $\int_0^{\omega_0} z_{1i} p_i dt = D_{1i} + O(\Delta)$. If $D_{1i} \neq 0$ for either $i = 1$ or 2 , then $\int_0^{\omega_0} z_{1i} p_i dt \neq 0$ for Δ small. One could take \bar{p} as above, for example, and obtain $D_{11} = \pi\sigma^{-1}$ (and $D_{12} = 0$), which would be applicable in the event that $d = 1$ (see Remark 4).

7. Since \bar{y} lies in the first quadrant, the same is true for the solutions $\bar{x} = \bar{y} + \varepsilon \bar{w}$ found in Theorems 1 and 2 for ε sufficiently small.

8. Finally, we point out that Theorems 1 and 2 apply when we take $b_1 = d_1 = c_2 = d_2 = 0$. The results then concern the nonhomogeneous (forced)

3. Proofs. The proofs will be carried out with the aid of some lemmas.

LEMMA 1. Given any solution $\bar{y}(t)$ of (1.1), let $A(t)$ be given by (2.2). Let $\bar{\psi} \in P(\omega) \oplus E_\beta$, where ω is the period of \bar{y} and suppose

$$(3.1) \quad \prod \int_0^\omega Z^{-1}(s) P_1 \bar{\psi}(s) ds = \bar{0}.$$

Then $\bar{z}' = A(t)\bar{z} + \bar{\psi}(t)$ has a manifold of solutions in $P(\omega) \oplus E_\beta$ of dimension d .

Proof. Writing $\bar{\psi} = P_1 \bar{\psi} + P_2 \bar{\psi}$ we consider the two systems

$$(3.2) \quad \bar{z}' = A(t)\bar{z} + P_i \bar{\psi}, \quad i = 1, 2.$$

The general solution of $\bar{z}' = A(t)\bar{z} + \bar{\psi}(t)$ is given by $z = Z(t)\bar{v} + \bar{z}^{(1)} + \bar{z}^{(2)}$, where $\bar{z}^{(i)}$ are any particular solutions of (3.2) and where $\bar{v} \in V$ is arbitrary. We will show that there exist particular solutions $\bar{z}^{(1)} \in P(\omega)$ and $\bar{z}^{(2)} \in E_\beta$ and, hence, that this manifold of solutions $z \in P(\omega) \oplus E_\beta$.

Now (3.2) has a ω -periodic solution for $i = 1$ if and only if $P_1 \bar{\psi}$ is orthogonal to the ω -periodic solutions of the adjoint system [8]. But this is exactly the assumption (3.1) made on $P_1 \bar{\psi}$. Thus, $\bar{z}^{(1)}$ can be chosen in $P(\omega)$; and this can be done such that $|\bar{z}^{(1)}| \leq K_1 |P_1 \bar{\psi}|$ for some constant $K_1 > 0$. Define

$$\bar{z}^{(2)} = -Z(t) \int_t^\infty Z^{-1}(s) P_2 \bar{\psi}(s) ds.$$

If this integral is sufficiently convergent, a straightforward calculation shows that $\bar{z}^{(2)}$ solves (3.2) for $i = 2$. But we claim the integral is absolutely convergent; in fact, we claim $\bar{z}^{(2)} \in E_\beta$.

Since $\int_0^\omega \text{tr } A(t) dt = 0$, it follows that both characteristic exponents of $Z(t)$ are purely imaginary. This means that $|Z(t)Z^{-1}(s)| \leq A + B|t-s|$ for some constants $A, B > 0$ and all t, s . Thus, for $P_2 \bar{\psi} \in E_\beta$ we have

$$|\bar{z}^{(2)}(t)| e^{\beta t} \leq |P_2 \bar{\psi}|_\beta e^{\beta t} \int_t^\infty (A + B(s-t)) e^{-\beta s} ds = |P_2 \bar{\psi}|_\beta \beta^{-2} (A\beta + B).$$

Consequently, we have that $\bar{z}^{(2)} \in E_\beta$. Thus $\bar{z}^{(2)}$ solves (3.2) for $i = 2$ and clearly satisfies $|\bar{z}^{(2)}|_\beta \leq K_2 |P_2 \bar{\psi}|_\beta$ for some constant $K_2 > 0$. \square

Since $Z(t)\bar{v} = Z(t)\Pi\bar{v}$ for $\bar{v} \in V$, we also have (Remark 3) that $|Z(t)\bar{v}| \leq K_3 |\bar{v}|$ for $\bar{v} \in V$ for some constant $K_3 > 0$. From the above proof we can write the solutions of $\bar{z}' = A(t)\bar{z} + \bar{\psi}(t)$ lying in $P(\omega) \oplus E_\beta$ when (3.1) holds as

$$(3.3) \quad \bar{x} = Z(t)\bar{v} + L\bar{\psi},$$

where $\bar{v} \in V$ and $L\bar{\psi} \in P(\omega) \oplus E_\beta$, $|L\bar{\psi}|_{\omega, \beta} \leq |L| |\bar{\psi}|_{\omega, \beta}$ for a constant $|L| > 0$ ($|L| = \max K_i$).

LEMMA 2. If $\bar{\psi}(t) \in P(\omega) \oplus E_\beta$, then for $t_0 = -\infty$ or $t_0 = 0$,

$$\int_{t_0}^t \bar{\psi}(s) dK(t-s) \in P(\omega) \oplus E_\beta$$

for any continuous matrix K for which $\int_0^\infty e^{\beta s} dK(s) < +\infty$.

Proof. Write $\int_{t_0}^t \bar{\psi}(s) dK(t-s) = I_1(t) + I_2(t) + I_3(t)$, where

$$I_1(t) = \int_{-\infty}^t P_1 \bar{\psi}(s) dK(t-s),$$

$$I_2(t) = - \int_{-\infty}^{t_0} P_1 \bar{\psi}(s) dK(t-s),$$

$$I_3(t) = \int_{t_0}^t P_2 \bar{\psi}(s) dK(t-s).$$

First, $I_1 \in P(\omega)$ follows from $P_1 \bar{\psi} \in P(\omega)$ as is seen by the calculation

$$I_1(t+\omega) = \int_{-\infty}^{t+\omega} P_1 \bar{\psi}(s) dK(t+\omega-s) = \int_{-\infty}^t P_1 \bar{\psi}(s+\omega) dK(t-s) = I_1(t).$$

Also, $I_2 = 0 \in E_\beta$ for $t_0 = -\infty$ and, for $t_0 = 0$,

$$|I_2(t)|e^{\beta t} \leq |P_1 \bar{\psi}|_\omega \int_t^{+\infty} dK(s) e^{\beta t} \leq |P_1 \bar{\psi}|_\omega \int_0^{+\infty} e^{\beta s} dK(s) < +\infty$$

for all $t \geq 0$ implies $I_2 \in E_\beta$. Finally, for all $t \geq t_0$,

$$\begin{aligned} |I_3(t)| e^{\beta t} &\leq |P_2 \bar{\psi}|_\beta \int_{t_0}^t e^{-\beta s} dK(t-s) e^{\beta t} \\ &\leq |P_2 \bar{\psi}|_\beta \int_0^{t-t_0} e^{\beta s} dK(s) \\ &\leq |P_2 \bar{\psi}|_\beta \int_0^{+\infty} e^{\beta s} dK(s) < +\infty \end{aligned}$$

so that $I_3 \in E_\beta$. \square

Proof of Theorem 1. Substitution of $\bar{x} = \bar{y} + \varepsilon \bar{w}$ into (2.1) yields, taking into account that \bar{y} solves (1.1), the following system for \bar{w} :

$$(3.4) \quad \bar{w}' = A(t)\bar{w} + \bar{g}(t) + \varepsilon \bar{h}(t, \bar{w}) + \bar{f}(t),$$

where

$$\begin{aligned} g_1(t) &= -b_1 y_1 \int_0^t y_1(s) d\alpha_{11}(t-s) - d_1 y_1 \int_0^t y_2(s) d\alpha_{12}(t-s), \\ g_2(t) &= -c_2 y_2 \int_0^t y_2(s) d\alpha_{21}(t-s) + d_2 y_2 \int_0^t y_1(s) d\alpha_{22}(t-s), \\ h_1(t, \bar{w}) &= -w_1 \left[b_1 \int_0^t (y_1 + \varepsilon w_1) d\alpha_{11}(t-s) + d_1 \int_0^t (y_2 + \varepsilon w_2) d\alpha_{12}(t-s) \right] \\ &\quad - y_1 \left[b_1 \int_0^t w_1 d\alpha_{11}(t-s) + d_1 \int_0^t w_2 d\alpha_{12}(t-s) \right], \\ h_2(t, \bar{w}) &= w_2 \left[-c_2 \int_0^t (y_2 + \varepsilon w_2) d\alpha_{21}(t-s) + d_2 \int_0^t (y_1 + \varepsilon w_1) d\alpha_{22}(t-s) \right] \\ &\quad - y_1 \left[c_2 \int_0^t w_2 d\alpha_{12}(t-s) - d_2 \int_0^t w_1 d\alpha_{22}(t-s) \right]. \end{aligned}$$

We wish to solve (3.4) for $\bar{w} \in P(\omega) \oplus E_\beta$. This we will do by substituting $\bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{f}$ for $\bar{\psi}$ in (3.2) which, if $\bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{f}$ were known and satisfied (3.1), would be solvable. Since \bar{w} is unknown, this creates an operator equation to be solved for \bar{w} ; namely,

$$(3.5) \quad \bar{w} = Z\bar{v} + L(\bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{f}).$$

In order that the right-hand side of (3.5) make sense, it is necessary that $\bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{f}$ satisfy the orthogonality conditions (3.1) and in addition that it lie in $P(\omega) \oplus E_\beta$ for any $\bar{w} \in P(\omega) \oplus E_\beta$. That the latter property holds is easily checked using Lemma 2 and the facts that sums and products of scalar asymptotically ω -periodic functions are also asymptotically ω -periodic. To fulfill (3.1) we choose the amplitudes, $\bar{\alpha} = \text{col}(\alpha_1, \alpha_2)$ as described in Theorem 1, appropriately. (a) Suppose $d = 2$. If $\bar{f}(t) = \text{col}(\alpha_1 p_1 + q_1, \alpha_2 p_2 + q_2)$, then given $\bar{w} \in P(\omega) \oplus E_\beta$ the condition (3.1) becomes a 2×2 linear, nonhomogeneous algebraic system for α_1, α_2 whose coefficient matrix is $M(Z^{-1}; \bar{p})$. Since it is assumed that \bar{p} is chosen so that this matrix is nonsingular, the system has a unique solution $\alpha_1 = \alpha_1(\bar{w})$, $\alpha_2 = \alpha_2(\bar{w})$. Furthermore, using Cramer's rule and the fact that the nonhomogeneous term is

$$(3.6) \quad - \int_0^\omega Z^{-1}(s)[\bar{g}(s) + \varepsilon \bar{h}(\bar{w})] ds,$$

one easily sees that $\alpha_i(\bar{w})$ are continuous in \bar{w} and that $\alpha_i(\bar{w}) = \alpha_i^0 + O(|\varepsilon|)$, where

$$(3.7) \quad \alpha_1^0 = \frac{(\int_0^\omega [z_{21}g_1 + z_{22}g_2] ds)(\int_0^\omega z_{12}p_2 ds) - (\int_0^\omega [z_{11}g_1 + z_{12}g_2] ds)(\int_0^\omega z_{22}p_2 ds)}{\det M(Z^{-1}; \bar{p})},$$

$$\alpha_2^0 = \frac{(\int_0^\omega [z_{11}g_1 + z_{12}g_2] ds)(\int_0^\omega z_{21}p_1 ds) - (\int_0^\omega [z_{21}g_1 + z_{22}g_2] ds)(\int_0^\omega z_{11}p_1 ds)}{\det M(Z^{-1}; \bar{p})}.$$

Choosing α_i in this manner, we have that $\bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{f} = \bar{g} + \varepsilon \bar{h}(\bar{w}) + \bar{p}_\alpha(\bar{w}) + \bar{q}$ (where $\bar{p}_\alpha(\bar{w}) = \text{col}(\alpha_1(\bar{w})p_1, \alpha_2(\bar{w})p_2)$) satisfies (3.1), and that (3.5) defines an operator equation to be solved for $\bar{w} \in P(\omega) \oplus E_\beta$, the solution of which solves (3.4).

(b) Suppose $d = 1$. In this case, given \bar{w} , (3.1) is simply one linear equation in the two unknowns α_1, α_2 . As assumed, $\int_0^\omega z_{1i}p_i ds \neq 0$ for either $i = 1$ or 2 ; this implies that (3.1) is uniquely solvable for α_i (in terms of the other $\alpha_j, j \neq i$, which is assumed arbitrary, but fixed). In this case,

$$(3.8) \quad \alpha_i^0 = \frac{-\int_0^\omega (z_{11}g_1 + z_{12}g_2) ds - \alpha_j^0 \int_0^\omega z_{ij}p_j ds}{\int_0^\omega z_{1i}p_i ds}$$

In what follows we write, in either case, $\alpha_1 = \alpha_1(\bar{w})$ and $\alpha_2 = \alpha_2(\bar{w})$ although in case (b) we have $\alpha_j(\bar{w}) \equiv \text{const}$.

Before proceeding, we observe that because $\bar{h}(\bar{w})$ as defined above involves only linear or quadratic expressions in the components of \bar{w} , it is easily seen that for all $\bar{w}, \bar{w}^* \in B(R) = \{\zeta \in P(\omega) \oplus E_\beta : |\zeta|_{\omega, \beta} \leq R\}$, where $R > 0$ is any fixed real, we have that

$$|\bar{h}(\bar{w}) - \bar{h}(\bar{w}^*)|_{\omega, \beta} \leq K_1 |\bar{w} - \bar{w}^*|_{\omega, \beta},$$

where $K_1 = K_1(\bar{y}, d_i, c_i, b_i, R, \alpha_{ij}) > 0$ is some constant. Furthermore, by Cramer's rule, considering the form of the nonhomogeneous term (3.8) in the system for α_i , we have also that

$$|\bar{\alpha}(\bar{w}) - \bar{\alpha}(\bar{w}^*)|_{\omega, \beta} \leq K_2 |\bar{w} - \bar{w}^*|_{\omega, \beta},$$

where $K_2 = K_2(\bar{y}, d_i, c_i, b_i, R, \alpha_{ij}) > 0$.

We wish to solve the operator equation (3.5) by use of the contraction principle and by use of the appearance of the small parameter ε . Considering how the $\alpha_i(\bar{w})$ were chosen above, we rewrite (3.5) as $\bar{w} = O\bar{w}$, where

$$O\bar{w} \equiv Z\bar{v} + L(\bar{g} + \bar{p}_\alpha^0 + \bar{q}) + \varepsilon L(\bar{h}(\bar{w}) + \bar{p}_\alpha^1(\bar{w})).$$

Here we have defined $\bar{p}_\alpha(\bar{w}) = \bar{p}_\alpha^0 + \bar{p}_\alpha^1(\bar{w})$, where $\bar{p}_\alpha^0 = \text{col}(\alpha_1^0 p_1, \alpha_2^0 p_2)$. Then $\bar{p}_\alpha^1(\bar{w}) = \text{col}((\alpha_1(\bar{w}) - \alpha_1^0) p_1, (\alpha_2(\bar{w}) - \alpha_2^0) p_2)$ satisfies

$$|\bar{p}_\alpha^1(\bar{w}) - \bar{p}_\alpha^1(\bar{w}^*)|_{\omega, \beta} \leq K_3 |\bar{w} - \bar{w}^*|_{\omega, \beta}$$

for $\bar{w}, \bar{w}^* \in B(R)$, where $K_3 = K_3(\bar{y}, d_i, b_i, c_i, R, p_i, \alpha_{ij}) > 0$. Thus we have

$$|O\bar{w} - O\bar{w}^*|_{\omega, \beta} \leq \varepsilon |L| K_4 |\bar{w} - \bar{w}^*|_{\omega, \beta}$$

for $\bar{w}, \bar{w}^* \in B(R)$, where $K_4 = \max(K_1, K_3)$. Consequently, O is a contraction on $B(R)$ if $|\varepsilon| \leq \varepsilon_0 = (2|L|K_4)^{-1}$. Note that $\varepsilon_0 = \varepsilon_0(\bar{y}, k_i, c_i, b_i, R, \bar{p})$.

Finally, to insure that O maps $B(R)$ into itself, we simply make R so large that $R/2 \geq |Z\bar{v}|_{\omega, \beta} + |L|(|\bar{g}|_{\omega, \beta} + |\bar{p}^0|_{\omega, \beta} + |\bar{q}|_{\omega, \beta})$. Then

$$|O\bar{w}|_{\omega, \beta} \leq R/2 + \varepsilon |L| K_4 |\bar{w}|_{\omega, \beta} \leq R/2 + R/2 = R.$$

As a result, O has a fixed point \bar{w} in $B(R)$ which solves (3.4). Hence $\bar{x} = \bar{y} + \varepsilon \bar{w}$ solves the original problem (2.1). Since R depends on $\bar{v}, \bar{y}, \bar{p}, \bar{q}, b_i, c_i, d_i, \alpha_{ij}$, it follows that ε_0 depends on all of these parameters. \square

Proof of Theorem 2. Since the operators

$$\int_{-\infty}^t \psi(s) d\alpha_{ij}(t-s) = \int_0^\infty \psi(t-s) d\alpha_{ij}(s)$$

obviously map scalar ω -periodic functions into scalar ω -periodic functions and hence $\bar{h}(\bar{w})$ maps $P(\omega)$ into itself, the above proof can be carried out as stated with $P(\omega) \oplus E_\beta$ replaced by $P(\omega)$. In this case, $P_2 \equiv 0$ throughout. \square

Acknowledgment. The author would like to thank the referee for his many helpful suggestions.

REFERENCES

[1] F. ALBRECHT, H. GATZKE AND H. WAX, *Stable limit cycles in prey-predator populations*, Science, 181 (1973), pp. 1073-1074.
 [2] J. M. BOWNS AND J. M. CUSHING, *On the behavior of solutions of predator-prey equations with hereditary terms*, Math. Biosci., 26 (1975), pp. 41-54.
 [3] E. A. CODDINGTON AND N. LEVINSON, *Theory of Ordinary Differential Equations*, McGraw-Hill, New York, 1955.
 [4] C. CORDUNEANU, *Integral Equations and Stability of Feedback Systems*, Mathematics in Science and Engineering Series, vol. 104, Academic Press, New York, 1973.

- [5] J. M. CUSHING, *An operator equation and bounded solutions of integro-differential systems*, SIAM J. Math. Anal., 6 (1975), pp. 433–445.
- [6] H. I. FREEDMAN AND P. WALTMAN, *Perturbation of two-dimensional predator-prey equations*, this Journal, 28 (1975), pp. 1–10.
- [7] ———, *Perturbation of two-dimensional predator-prey equations with an unperturbed critical point*, this Journal, 29 (1975), pp. 719–733.
- [8] A. HALANAY, *Differential Equations: Stability, Oscillations, Time Lags*, Math. in Science and Engineering series, vol. 23, Academic Press, New York, 1966.
- [9] R. M. MAY, *Limit cycles in predator-prey communities*, Science, 177 (1972), pp. 900–902.
- [10] E. N. MONTROLL, N. S. GOEL AND S. C. MAITRA, *On the Volterra and Other Nonlinear Models of Interacting Populations*, Academic Press, New York, 1971.
- [11] E. SAMUELSON, *A universal cycle?*, Operations Researchverfahren, 3 (1967), pp. 307–320.
- [12] V. VOLTERRA, *Leçons sur la Théorie Mathématique de la Lutte par la Vie*, Gauthier-Villars, Paris, 1931.