

## ON THE OSCILLATORY NATURE OF SOLUTIONS OF GENERAL PREDATOR–PREY MODELS WITH TIME DELAYS

J. M. CUSHING

Department of Mathematics, Building #89, University of Arizona, Tucson, Arizona 85721, U.S.A.

(Received 7 January 1977)

*Key words:* Predator–prey models, time delays, stability, divergent oscillations.

### 1. INTRODUCTION

VOLTERRA [1] was the first to study mathematically the effects of time delays on predator–prey interactions. He did this by modifying the famous Volterra–Lotka predator–prey model in such a way as to describe interactions between the two species which are in general functionals (of Volterra integral form) of past population sizes. Volterra then proved that all solutions of this integrodifferential model oscillate about a unique positive equilibrium, but he did not consider the question of whether these oscillations converge or diverge. (See [2] for an English presentation of the work of Volterra). In this work of Volterra there is no term to account for self inhibition of either species on its own per unit growth rate and consequently the prey, in the absence of predators, grows exponentially without bound. If a finite carrying capacity were to be assumed for the prey then one might expect the oscillations described Volterra's model to converge in keeping with the stabilizing nature of such effects. This however may or may not be true, depending on various trade-off possibilities amongst the parameters in the system [4–7].

May [7] considers Volterra's model under the assumption that there are significant delays in the self inhibition effects of the prey. May's analysis is carried out in terms of the inherent (unconstrained) birth and death rates of the prey and predators respectively and a measure of the delay in the self inhibition term. It is concluded in [7] (also see [6]), amongst other things, that if the delay measure is small (for fixed values of the birth and death rates) then the equilibrium is stable (i.e. the oscillations converge) while on the other hand if the delay measure is large then the equilibrium is unstable (i.e. the oscillations diverge). Mathematically speaking May's analysis is purely a linear analysis carried out on a specific model with a specific delay functional form. The divergence of the oscillations or the possibility of periodic oscillations was not established for the nonlinear model.

Our purpose here is to study a very general predator–prey model with very general delay characteristics and to show that for 'small delays' (for fixed values of the inherent birth and death rates of the prey and predator respectively) the equilibrium is locally stable while for 'large delays' the solutions tend to have divergent oscillations (at least for a finite time interval after the initial time reference). In the latter case we will obtain, by singular perturbation techniques, a first order approximation to the divergent oscillations valid on short time intervals. For divergent oscillations (at least of significant magnitude) it is only reasonable to consider a finite time interval since populations of small sizes are subject to extinction or other drastic phenomena caused by random effects unaccounted for in the model. Moreover, differential models assume sufficiently large

populations sizes for their validity. Thus, we only concern ourselves with finite time intervals in the case of divergent oscillations whether or not these oscillations are unbounded as  $t \rightarrow +\infty$ .

One would expect, of course, for intermediate values of the delay to see sustained, but bounded oscillations or even exactly periodic solutions. The bifurcation of periodic solutions from equilibrium at critical values of the delay and the birth and death rates has been studied in [5, 8, 9] and although only models with quadratic interactions are considered in these references the mathematical analysis, proofs and theorems there still apply to the more general models we consider below. (This is because the bifurcation analysis in [8, 9] only depends on the interactions being higher order.) For this reason we will not explicitly consider the existence of periodic solutions here.

2. GENERAL PREDATOR-PREY DELAY MODELS

We consider the following integrodifferential system

$$\begin{aligned} N_1'/N_1 &= b_1 g_1 \left( \int_{-\infty}^t N_1(s) k_{11}(t-s) ds, \int_{-\infty}^t N_2(s) k_{12}(t-s) ds \right) \\ N_2'/N_2 &= b_2 g_2 \left( \int_{-\infty}^t N_1(s) k_{21}(t-s) ds \right) \end{aligned} \tag{2.1}$$

for  $t > 0$  under the assumptions.

- (a)  $k_{ij}(t) \in C^0(\mathbf{R}_+, \mathbf{R}_+^1)$ ,  $k_{ij}(t) \geq 0$ ,  $\int_0^t k_{ij}(t) dt = 1$ ,  $b_i > 0$ ;
- (b)  $g_1(e_1, e_2) = g_2(e_1) = 0$  for some  $e_i \in \mathbf{R}^1$ ,  $e_i > 0$ ,  $g_1(0, 0) = 1$ ,  $g_2(0) = 1$ ;
- (c)  $g_1(\zeta, \eta)$  and  $g_2(\zeta)$  are twice continuously differentiable in their arguments in a neighborhood of  $\zeta = e_1$ ,  $\eta = e_2$  and  $\zeta = e_1$  respectively
- (d)  $\partial g_1(e_1, e_2)/\partial \zeta < 0$ ,  $\partial g_1(e_1, e_2)/\partial \eta < 0$ ,  $\partial g_2(e_1)/\partial \zeta > 0$ . (2.2)

Here  $' = d/dt$  and,  $\mathbf{R}^k$  is  $k$ -dimensional Euclidean space.

(2.2) the solution  $N_i = e_i$  is an equilibrium in the neighborhood of which the interaction between the species whose population sizes  $N_i(t)$  are governed as functions of time  $t$  by (2.1) is that of a predator  $N_2$  and prey  $N_1$ . The constants  $b_1$  and  $-b_2$  are (by 2.2b) the inherent birth and death rates of the prey and predator respectively. The functions  $k_{ij}(t)$  describe the precise manner in which the past population sizes effect the per unit growth rate of each species and are accordingly referred to as the *delay kernels*.

Actually our analysis below is valid for models of other general forms as well. This is because the techniques we use involve an investigation of the linearized system (which could be the same for the other general models) and utilize only the fact that the model is a higher order perturbation of this linearization. For example the theorems below remain valid for the more general system with the integrals in (2.1) replaced by integrals of the form

$$\int_{-\infty}^t f(N_i(s))k(t-s) ds$$

under the restrictions in (2.2) together with obvious restrictions on the kernels  $f$  of the sort necessary to make this a predator-prey model, at least near some equilibrium.

The delay model considered by Volterra in [1] is obtained from the general model (2.1) by letting  $g_i$  be linear in its arguments.

Each delay kernel  $k_{ij}(t)$  weighs the effect of the past population size of the  $j$ th species on the

growth rate of the  $i$ th species. We now suppose that some measure  $T_{ij} \geq 0$  of the length of this delay is determined. For example, a frequently used kernel in delay models is  $k_{ij}(t) = a_{ij}^{-2} t \exp(-t/a_{ij})$  for some constant  $a_{ij} > 0$  [5-7]. Since the unique maximum of this kernel occurs at  $t = a_{ij}$  one might reasonably take  $T_{ij} = a_{ij}$ . Other means of measuring the delay represented by a delay kernel are also conceivable; e.g.  $T_{ij} = \int_0^\infty t k_{ij}(t) dt$  (the first moment of  $k_{ij}$ ) or  $\int_0^{T_{ij}} k(t) dt = 1/2$  (since  $\int_0^\infty k_{ij}(t) dt = 1$ ). As far as the qualitative features which we will study here are concerned it does not matter in the least how  $T_{ij}$  is specifically defined and hence we simply assume it has been determined in some meaningful way for each kernel  $k_{ij}$ . (For that matter, it does not matter that  $T_{ij}$  measures the 'length' of the delay, but could just as well be some other measure of the delay effects, e.g. of their 'magnitude'). Finally we assume that these three non-negative numbers  $T_{ij}$  are averaged or otherwise combined to yield a positive constant  $T > 0$  which is in some way a reasonable and meaningful measure of the total delay present in the system modelled by (2.1). Again we do not wish or need to be specific here, but only need to assume that  $T$  is calculated in some reasonable manner.

In order to introduce explicitly the delay measure  $T > 0$  into the analysis of (2.1) we choose  $T$  as the unit of time and make the change of variable  $t' = t/T$ . If (2.1) is then rewritten as a system for  $\bar{N}_i(t') = N_i(t'T)$  one finds that the resulting system has exactly the form of (2.1) with  $b_i$  replaced by  $b_i T$  and the delay kernels  $k_{ij}(t)$  replaced by  $T k_{ij}(t'T)$ . Thus, without loss in generality we consider, in place of (2.1), the system

$$\begin{aligned} N_1'/N_1 &= b_1 T g_1 \left( \int_{-\infty}^t N_1(s) k_{11}(t-s) ds, \int_{-\infty}^t N_2(s) k_{12}(t-s) ds \right) \\ N_2'/N_2 &= b_2 T g_2 \left( \int_{-\infty}^t N_1(s) k_{21}(t-s) ds \right) \end{aligned} \tag{2.3}$$

where  $k_{ij}$  and  $g_i$  still satisfy (2.2) and where the total delay represented by these delay kernels is now equal to one. For simplicity we have suppressed the primes on the new time variable.

We wish to study the solutions of (2.3) as they are functions of the parameters  $\beta_i = b_i T$ .

Since predator-prey interaction models are stable when no delays are present we expect the equilibrium  $N_i = e_i$  of (2.3) to be stable for  $\beta_i$  small. If (2.3) is linearized at the equilibrium (a procedure justified in [10]) and the resulting linear integrodifferential system is analysed by means of its characteristic equation [11] we can verify the expected stability as stated in the following theorem. The details of this proof are given in Section 4 below.

**THEOREM 1.** In addition to (2.2) suppose that  $\int_0^\infty t k_{ij}(t) dt < +\infty$ . Then there exist constants  $\beta_0^i = \beta_0^i(g_i, k_{ij}) > 0$  such that  $0 < \beta_i = b_i T < \beta_0^i$  implies that the equilibrium  $N_i = e_i$  of (2.1) is (locally) asymptotically stable.

By *locally asymptotically stable* we mean that for solutions with initial values  $N_i(t) = N_i^0(t)$ ,  $t \leq 0$  sufficiently close to equilibrium, say  $|N_i^0(t) - e_i| \leq \delta$ ,  $t \leq 0$ , it follows that  $N_i(t) - e_i \rightarrow 0$  as  $t \rightarrow +\infty$ .

In order to study the opposite case when  $\beta_i = b_i T$  are both large we introduce an auxiliary, small parameter  $\varepsilon > 0$  and write  $\beta_i = \alpha_i/\varepsilon^2$  for arbitrary, but fixed constants  $\alpha_i > 0$ . Since only a finite time interval after the initial time  $t = 0$  would be of interest in the case of divergent oscillations we change the time scale in such a way as to magnify small time intervals:  $u = t/\varepsilon$ . After making this change of variables in (2.3) we look for solutions of order  $\varepsilon$  near the equilibrium. The

results are contained in the following Theorem 2, the details of whose proof appear in Section 4 below.

**THEOREM 2.** In addition to (2.2) assume that  $k_{ij} \in C^1$  in some neighborhood of  $t = 0$ ,  $k_{12}(0) > 0$ ,  $k_{21}(0) > 0$ . Let  $t_0 > 0$  and  $\alpha_i > 0$  be arbitrary but fixed given constants. Let  $y_i^0(t)$  be arbitrary, integrable functions defined for  $t \leq 0$  which have compact support.

There exists a constant  $\varepsilon_0 = \varepsilon_0(t_0) > 0$  such that for all  $\varepsilon$  satisfying  $0 < \varepsilon < \varepsilon_0$  the solution of (2.3) with  $b_i T = \alpha_i/\varepsilon^2$  subject to the initial conditions

$$N_i(t) = e_i \exp(\varepsilon y_i^0(t/\varepsilon)), \quad t \leq 0$$

is of the form

$$N_i(t) = e_i \exp(\varepsilon y_i(t/\varepsilon) + \varepsilon z_i(t/\varepsilon, \varepsilon)), \quad 0 \leq t \leq \varepsilon t_0$$

where  $z_i(u, \varepsilon) = 0$  for  $u \leq 0$ ,  $|z_i(u, \varepsilon)| = O(\varepsilon)$  uniformly for  $0 \leq u \leq t_0$  and where  $y_i(u)$  is the unique solution of the elementary initial value problem (4.8)–(4.9) below (and hence has the divergent oscillatory form (4.10)).

The functions (4.10) exhibit, in general, divergent oscillations and hence so do the first order (in  $\varepsilon$ , that is to say in  $T^{-1/2}$ ) approximations to  $N_i$  given by

$$N_i(t) \sim e_i \exp(\varepsilon y_i(t/\varepsilon)), \quad 0 \leq t \leq \varepsilon t_0.$$

Thus Theorem 2 says roughly that solutions starting near equilibrium tend to oscillate in a divergent manner, at least for a finite time interval.

The conditions  $k_{ij}(0) > 0$ ,  $i \neq j$  mean that at least some instantaneous effects are present in the interaction of  $N_1$  and  $N_2$ . These are, however, merely technical requirements and since these constants may be arbitrarily small in comparison to the later delayed effects represented by  $k_{ij}(t)$ ,  $i \neq j$  for values of  $t > 0$  these conditions do not actually make any strong restriction one way or the other with regard to the nature of the delay in the system. The real restriction on the delay is in the requirement that  $\varepsilon > 0$  be small and hence that both  $b_i T$  be large. This may for example be thought of as meaning that the delay measure  $T$  is large compared to both the prey's inherent birth rate  $b_1$  and the predator's inherent death rate  $b_2$ .

### 3. A NUMERICALLY INTEGRATED EXAMPLE

The system

$$\begin{aligned} N_1'/N_1 &= 4\varepsilon^{-2} \left( 1 - \frac{1}{2} \int_{-\infty}^t N_1(s)(t-s)e^{-(t-s)} ds - \frac{1}{2} \int_{-\infty}^t N_2(s)e^{-(t-s)} ds \right) \\ N_2'/N_2 &= 2\varepsilon^{-2} \left( -1 + \int_{-\infty}^t N_1(s)e^{-(t-s)} ds \right) \end{aligned} \quad (3.1)$$

was integrated numerically for various choices of  $\varepsilon > 0$ . (This was done by converting the system to a differential system of higher order by repeated differentiations and substitutions making use of the special nature of the delay kernels appearing in (3.1).) Here, in keeping with the remarks in [6, 7], we have chosen an example for which the prey birth rate is larger (in fact double) the predator's death rate and for which the delay kernels  $k_{12}(t) = k_{21}(t) = \exp(-t)$  and  $k_{11}(t) = t \exp(-t)$  are appropriate to the requirement that the delay effects in the self inhibition of the prey be more significant than those in the interactions between the two species. This is because

$k_{ij}(t)$ ,  $i \neq j$  is monotonically decreasing while  $k_{11}(t)$  increases until  $t = 1$  and only after this time does it monotonically decrease. This model has a unique positive equilibrium  $N_i(t) = 1$  and all of the hypotheses on the delay kernels in both Theorems in Section 2 are fulfilled. Consequently we expect to see convergent oscillations for  $\varepsilon$  'large' and divergent oscillations for  $\varepsilon$  'small', all taking place around  $N_i = 1$ .

The results of our numerous computer integrations may be summarized as follows. For values of  $\varepsilon$  greater than, but not 'close' to  $\varepsilon = 2$  the solutions show what are definitely convergent oscillations about equilibrium, the damping of the oscillations growing stronger with increasing  $\varepsilon$ . This is illustrated in Figs 1(a) and (b). As  $\varepsilon$  was decreased to values 'near'  $\varepsilon = 2$  the oscillations became sustained (either they were apparently periodic or, more often, apparently asymptotic

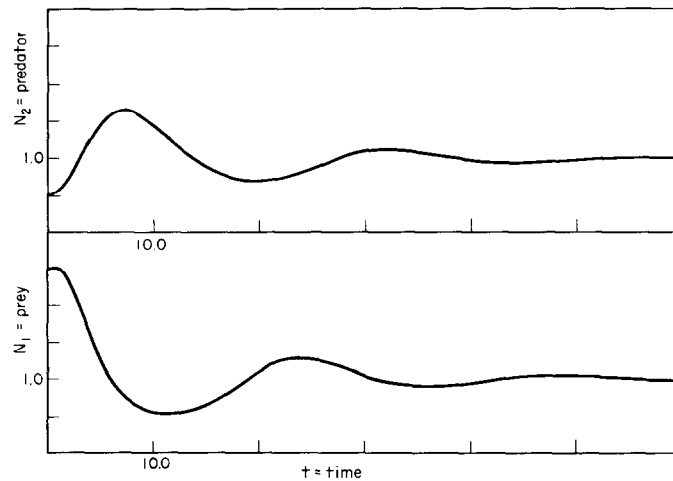


Fig. 1(a). Convergent oscillations of a solution of (3.1) for  $\varepsilon = 3.0$ .

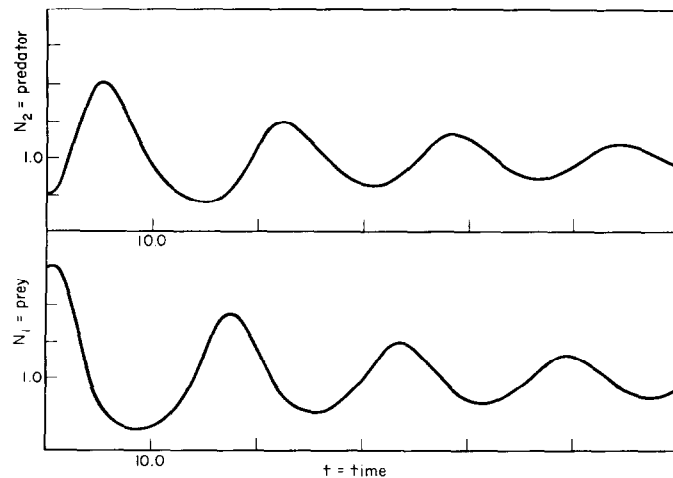


Fig. 1(b). Convergent oscillations of a solution of (3.1) for  $\varepsilon = 2.4$ .

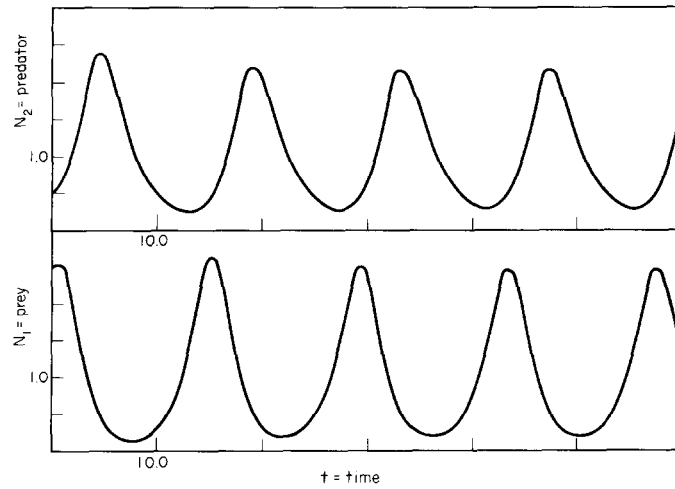


Fig. 2. Sustained oscillations of a solution of (3.1) for  $\varepsilon = 2.1$ .

to periodic oscillations). This is predicted by the theorems of [8] and is illustrated by a single case in Fig. 2 for  $\varepsilon = 2.1$ . When  $\varepsilon$  was further decreased to values less than  $\varepsilon = 2$  the oscillations became divergent, even for solutions starting near equilibrium, in such a way that ultimately the solutions spend larger and larger time intervals very near zero, followed by sharper peaks of increasing magnitude. This is illustrated in Figs. 3 (a) and (b). All of these qualitative features were found to be independent of the initial states chosen.

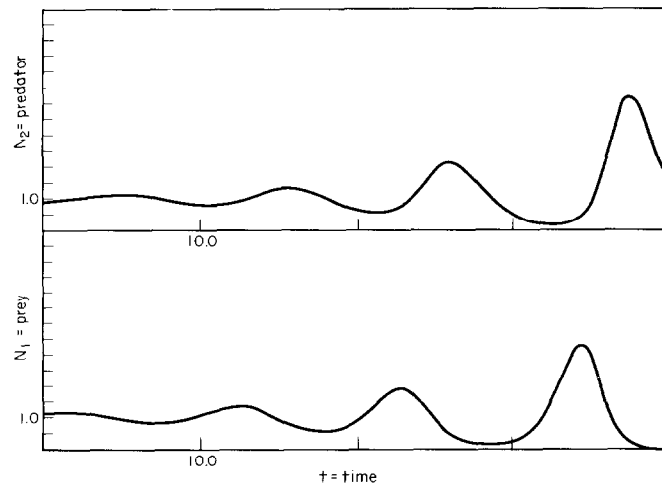


Fig. 3(a). Divergent oscillations of a solution of (3.1) for  $\varepsilon = 1.8$ .

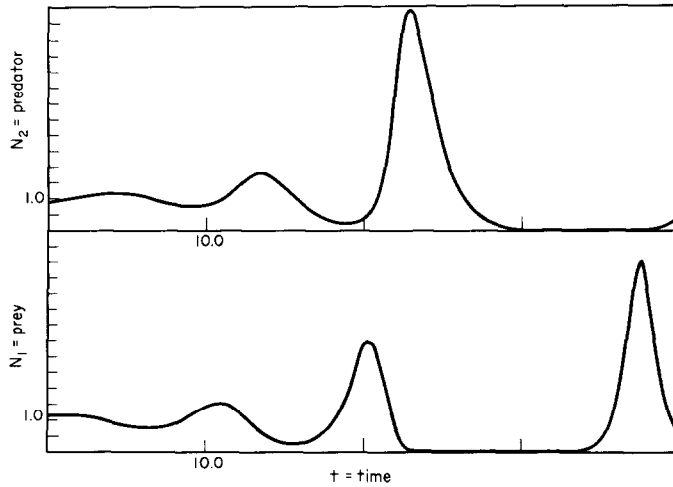


Fig. 3(b). Divergent oscillations of a solution of (3.1) for  $\varepsilon = 1.6$ .

4. PROOFS OF THEOREMS 1 AND 2

(a) We begin the proof of Theorem 1 with a lemma.

LEMMA. Assume (2.2) and  $\int_0^\infty tk_{11}(t) dt < +\infty$  hold. There exists a constant  $\theta_0 > 0$  such that the equation

$$z + \theta k_{11}^*(z) = 0, \quad k_{11}^*(z) = \int_0^\infty e^{-zt} k_{11}(t) dt$$

has no roots satisfying  $\text{Re } z \geq 0$  provided  $0 < \theta < \theta_0$ .

*Proof.* Define  $q(z, \theta) = z + \theta k_{11}^*(z)$  and note that  $q(0, 0) = 0$ ,  $q_z(0, 0) = 1$ . By the implicit function theorem there exists a *unique* continuously differentiable solution branch of  $q(z, \theta) = 0$ :

$$z = z(\theta), \quad z(0) = 0, \quad |\theta| < \theta_0, \quad \theta_0 > 0.$$

Moreover, an implicit differentiation of  $q(z(\theta), \theta) = 0$  yields  $z'(0) = -1$  so that

$$\text{Re } z(\theta) < 0, \quad 0 < \theta < \theta_0. \tag{4.1}$$

Suppose that the assertion of the lemma is false. Then there exist sequences  $\theta_n > 0$ ,  $\theta_n \rightarrow 0$ ,  $\text{Re } z_n \geq 0$ ,  $n = 1, 2, \dots$  such that  $q(z_n, \theta_n) = 0$ . Since  $z_n = -\theta_n k_{11}^*(z_n)$  and since  $|k_{11}^*(z_n)| \leq 1$  for  $\text{Re } z_n \geq 0$  we find that  $z_n \rightarrow 0$  as  $n \rightarrow +\infty$ . But  $\text{Re } z_n \geq 0$  then contradicts (4.1) and the uniqueness of the solution branch  $z(\theta)$ .

We set  $x_i = N_i - e_i$  in (2.3) and neglect all terms which are higher order in  $x_i$ . If we denote

$$c_{11} = -\partial g_1(e_1, e_2)/\partial \xi > 0, \quad c_{12} = -\partial g_1(e_1, e_2)/\partial \eta > 0, \quad c_{21} = dg_2(e_1)/d\xi > 0$$

then we arrive at the linearized system

$$\begin{aligned} x'_1 &= -b_1 T \left( e_1 c_{11} \int_0^t x_1(t-s)k_{11}(s) ds + e_1 c_{12} \int_0^t x_2(t-s)k_{12}(s) ds \right) \\ x'_2 &= b_2 T e_2 c_{21} \int_0^t x_1(t-s)k_{21}(s) ds. \end{aligned} \tag{4.2}$$

Here we have also ignored inhomogeneous terms which tend to zero as  $t \rightarrow +\infty$ . According to established results for integrodifferential systems [10, 11] the equilibrium  $N_i = e_i$  is locally asymptotically stable as a solution of (2.3) provided  $x_i = 0$  is asymptotically stable for (4.2) and the latter is true if (and only if) there exist no zeros of the characteristic equation  $p(z) = 0$  satisfying  $\text{Re } z \geq 0$  where

$$\begin{aligned} p(z) &= z(z + \beta_1 e_1 c_{11} k_{11}^*(z)) + \beta_1 \beta_2 e_1 e_2 c_{12} c_{21} k_{12}^*(z) k_{21}^*(z) \\ k_{ij}^*(z) &= \int_0^\infty e^{-zt} k_{ij}(t) dt. \end{aligned}$$

We wish to show that this is in fact true for  $\beta_i$  sufficiently small.

Let  $\beta_0^1 = \theta_0/e_1 c_{11}$  where  $\theta_0$  is as in the Lemma and choose any  $\beta_1$  such that  $0 < \beta_1 < \beta_0^1$ . We consider  $p$  as a function of both  $z$  and  $\beta_2$ :  $p = p(z, \beta_2)$ . Suppose that it is not true that  $p$  has no roots  $\text{Re } z \geq 0$  for  $\beta_2$  sufficiently small. We desire to reach a contradiction. Under this assumption there exist sequences  $\beta_2(n)$  and  $z_n$  such that

$$\beta_2(n) > 0, \quad \beta_2(n) \rightarrow 0, \quad \text{Re } z_n \geq 0, \quad p(z_n, \beta_2(n)) = 0.$$

It is clear that  $z_n$  unbounded implies that  $p(z_n, \beta_2(n))$  is unbounded. Thus, it must be the case that the sequence  $z_n$  is bounded. Without loss in generality we assume that  $z_n \rightarrow z_0$  for some limit  $z_0$ ; clearly  $\text{Re } z_0 \geq 0$ . By continuity

$$p(z_0, 0) = z_0(z_0 + \beta_1 e_1 c_{11} k_{11}^*(z_0)) = 0.$$

By the way  $\beta_0^1$  was chosen we have from the Lemma that expression in the parentheses cannot vanish and hence  $z_0 = 0$ . Thus

$$z_n \rightarrow 0, \quad \text{Re } z_n \geq 0, \quad p(z_n, \beta_2(n)) = 0, \quad \beta_2(n) \rightarrow 0, \beta_2(n) > 0. \tag{4.3}$$

We will reach the desired contradiction by showing that (4.3) contradicts the implicit function theorem. Note that  $p(0, 0) = 0$ ,  $p_z(0, 0) = \beta_1 e_1 c_{11} \neq 0$  and hence there exists a *unique* solution branch

$$z = z(\beta_2), \quad z(0) = 0, \quad |\beta_2| < \beta_2^0, \beta_2^0 > 0$$

of  $p(z, \beta_2) = 0$ . An implicit differentiation of  $p(z(\beta_2), \beta_2) = 0$  yields  $z'(0) = -e_2 c_{12} c_{21} / c_{11} < 0$  so that  $\text{Re } z(\beta_2) < 0$  for  $0 < \beta_2 < \beta_2^0$ . This contradicts (4.3) and concludes the proof of Theorem 1.

(b) To prove Theorem 2 we make the following change of variables:

$$u = t/\varepsilon, \quad \bar{x}_i(u) = x_i(u\varepsilon), \quad x_i(t) = \ln N_i(t)/e_i$$

where  $\varepsilon > 0$  is a small parameter. If these substitutions are made into (2.3) together with



$\beta_i = b_i T = \alpha_i / \varepsilon^2$  we obtain the system

$$\begin{aligned} \bar{x}'_1 &= \alpha_1 \varepsilon^{-1} g_1 \left( \varepsilon e_1 \int_{-\infty}^u k_{11}(\varepsilon(u-s)) \exp(\bar{x}_1(s)) ds, \varepsilon e_2 \int_{-\infty}^u k_{12}(\varepsilon(u-s)) \exp(\bar{x}_2(s)) ds \right) \\ \bar{x}'_2 &= \alpha_2 \varepsilon^{-1} g_2 \left( \varepsilon e_1 \int_{-\tau}^u k_{21}(\varepsilon(u-s)) \exp(\bar{x}_1(s)) ds \right) \end{aligned} \tag{4.4}$$

where now  $' = d/du$ . We look for a solution of (4.4) in the form

$$\bar{x}_i(u) = \varepsilon y_i(u) + \varepsilon z_i(u, \varepsilon), \quad 0 \leq u \leq t_0 \tag{4.5}$$

for a fixed  $t_0 > 0$  where  $y_i(u) = y_i^0(u)$  is given for  $u \leq 0$  and where  $z_i(u, \varepsilon) = 0, u \leq 0$ , and  $|z_i(u, \varepsilon)| = O(\varepsilon)$  uniformly on  $0 \leq u \leq t_0$ . If we write

$$k_{ij}(t) = \mu_{ij} + m_{ij}(t), \quad \mu_{ij} = k_{ij}(0) \geq 0, \quad m_{ij}(t) = O(t)$$

and substitute (4.5) into (4.4) we obtain, by equating terms of order  $\varepsilon$ , the following linear system for  $y_i$  (after a cancellation of a factor of  $\varepsilon$ )

$$\begin{aligned} y'_1 &= -\alpha_1 \left( e_1 c_{11} \mu_{11} \int_0^u y_1(s) ds + e_2 c_{12} \mu_{12} \int_0^u y_2(s) ds + \kappa_1 \right) \\ y'_2 &= \alpha_2 \left( e_1 c_{21} \mu_{21} \int_0^u y_1(s) ds + \kappa_2 \right) \end{aligned} \tag{4.6}$$

where

$$\begin{aligned} \kappa_1 &= e_1 c_{11} \mu_{11} \int_{-\infty}^0 y_1^0(s) ds + e_2 c_{12} \mu_{12} \int_{-\infty}^0 y_2^0(s) ds \\ \kappa_2 &= e_2 c_{21} \mu_{21} \int_{-\infty}^0 y_1^0(s) ds. \end{aligned}$$

The higher order terms in  $\varepsilon$  yield a nonlinear system to be solved for  $z_i$ :

$$\begin{aligned} z'_1 &= -\alpha_1 \left( e_1 c_{11} \mu_{11} \int_0^u z_1(s) ds + e_2 c_{12} \mu_{12} \int_0^u z_2(s) ds \right) + \varepsilon^{-1} f_1(\varepsilon y_i + \varepsilon z_i) \\ z'_2 &= \alpha_2 e_1 c_{21} \mu_{21} \int_0^u z_1(s) ds + \varepsilon^{-1} f_2(\varepsilon y_i + \varepsilon z_i) \end{aligned} \tag{4.7}$$

where  $f_i = f_i(\xi) \in C^2(\mathbf{R}_+^1, \mathbf{R}^1)$ ,  $f_i(0) = f'_i(0) = 0$ . Thus  $|f_i(\xi)| = o(|\xi|)$  and  $f_i$  satisfies a local Lipschitz condition

$$|f_i(\xi_1) - f_i(\xi_2)| \leq L_i(\xi) |\xi_1 - \xi_2|, \quad |\xi_i| \leq \rho, L_i = O(\varepsilon^2)$$

for some  $\rho > 0$ . If  $Y(u, s)$  is the fundamental matrix of the linear system (4.6) [10, 11] and if we write  $\bar{f} = \text{col}(f_1, f_2)$ ,  $\bar{z} = \text{col}(z_1, z_2)$  then (4.7) is equivalent to the integral equation

$$\bar{z}(u) = \int_0^u Y(u, s) \varepsilon^{-1} \bar{f}(\varepsilon y_i + \varepsilon z_i) ds \equiv N(\bar{z}, \varepsilon), \quad 0 \leq u \leq t_0.$$

Let  $B(t_0)$  denote the Banach space of continuous vector valued functions  $\bar{z}(u)$  on  $0 \leq u \leq t_0$

under the usual supremum norm  $|\bar{z}|_0 = \sup_{0 \leq u \leq t_0} |\bar{z}(u)|$ . Let  $S(r) = \{\bar{z} \in B(t_0) : |\bar{z}|_0 \leq r\}$ ,  $r > 0$ . Given any  $\bar{y} = \text{col}(y_1, y_2) \in B(t_0)$  the above described properties of  $f_i$  imply that  $|N(\bar{z}, \varepsilon) - N(\bar{z}^*, \varepsilon)|_0 \leq L(\varepsilon)|\bar{z} - \bar{z}^*|_0$  for  $\bar{z}, \bar{z}^* \in S(r)$  and some constant  $0 < L(\varepsilon) = O(\varepsilon)$ . Thus there exists a constant  $\varepsilon_0 > 0$  such that  $0 < \varepsilon < \varepsilon_0$  implies that  $N$  is a contraction mapping from  $S(r)$  into itself. As a result, for small  $\varepsilon$  the system (4.7) may be uniquely solved for  $z_i(u, \varepsilon)$  once  $y_i$  is given. It follows immediately from the above integral equation for  $\bar{z}$  that  $|\bar{z}|_0 = O(\varepsilon)$  uniformly on the finite interval  $0 \leq u \leq t_0$ .

To finish the proof of Theorem 2 we need only prove that (4.6) is solvable for  $y_i$  and that the solutions have the desired properties.

System (4.6) has a unique solution, for the initial values  $y_i^0(0)$ , which is defined on  $0 \leq u \leq t_0$  [3]. A simple sequence of differentiations and substitutions shows that both of the solutions  $y_i$  must satisfy the same higher order equation

$$y^{(iv)} + Ay'' + By = 0 \quad (4.8)$$

where  $A = \alpha_1 e_1 c_{11} \mu_{11} \geq 0$ ,  $B = \alpha_1 \alpha_2 e_1 e_2 c_{12} c_{21} \mu_{12} \mu_{21} > 0$  subject to initial conditions

$$\begin{aligned} y_i(0) &= y_i^0(0), & y_1'(0) &= -\alpha_1 \kappa_1, & y_2'(0) &= \alpha_2 \kappa_2 \\ y_1''(0) &= -\alpha_1 [e_1 c_{11} \mu_{11} y_1^0(0) + e_2 c_{12} \mu_{12} y_2^0(0)] \\ y_2''(0) &= \alpha_2 e_1 c_{21} \mu_{21} y_1^0(0), & y_2^{(3)}(0) &= -\alpha_1 \alpha_2 e_1 c_{21} \mu_{21} \kappa_1 \\ y_1^{(3)}(0) &= -\alpha_1 (\alpha_1 e_1 c_{11} \mu_{11} \kappa_1 + \alpha_2 e_2 c_{12} \mu_{12} \kappa_2). \end{aligned} \quad (4.9)$$

It is not difficult to show that the characteristic quartic polynomial associated with (4.8) has two roots in the right- and two roots in the left-hand plane (note that  $B > 0$ ):  $\delta_j \pm \gamma_j i$ ,  $j = 1, 2$  where  $\delta_1 < 0$ ,  $\delta_2 > 0$ ,  $\gamma_j > 0$ . Thus the solutions  $y_i(u)$  have the general form

$$y_i(u) = e^{\delta_1 u} (K_i^1 \cos \gamma_1 u + K_i^2 \sin \gamma_1 u) + e^{\delta_2 u} (K_i^3 \cos \gamma_2 u + K_i^4 \sin \gamma_2 u) \quad (4.10)$$

where of course the constants  $K_i^j$  are determined by the initial conditions (4.9). Since  $\delta_2 > 0$  these solutions in general exhibit divergent oscillations.

#### REFERENCES

1. VOLTERRA V., *Lecons sur la Théorie Mathématique de la Lutte par la Vie*. Gauthier-Villars, Paris (1931).
2. RESCIGNO A. & RICARDSON I. W., The deterministic theory of population dynamics, in *Foundations of Mathematical Biology* (Edited by ROBERT ROSEN) pp. 283-360. Academic Press, New York (1973).
3. MILLER R. K., *Nonlinear Volterra Integral Equations*. Benjamin Press, Menlo Park Ca. (1971).
4. BOWNS, J. M. & CUSHING J. M., On the behavior of solutions of predator-prey equations with hereditary terms, *Math. Biosci.* **26**, 41-54 (1975).
5. CUSHING J. M., Predator-prey interactions with time delays, *J. math. Biol.* **3**, 369-380 (1976)
6. MAY R. M., *Stability and Complexity in Model Ecosystems*, 2nd edn. Monographs in Population Biology 6, Princeton U. Press, New Jersey (1974).
7. MAY R. M., Time-delay versus stability in population models with two and three trophic levels, *Ecology* **54**, 315-325 (1973).
8. CUSHING J. M., Periodic solutions of two species interaction models with lags, *Math. Biosci.* **31**, 143-156 (1976).
9. CUSHING J. M., Bifurcation of periodic solutions of integrodifferential systems with applications to time delay models in population dynamics, to appear in *SIAM J. appl. Math.*
10. CUSHING J. M., An operator equation and bounded solutions of integrodifferential systems, *SIAM J. math. Anal.* **6**(3), 433-445 (1975).
11. MILLER R. K., Asymptotic stability and perturbations for linear Volterra integrodifferential systems, in *Delay and Functional Differential Equations and Their Applications* (Edited by K. SCHMITT) pp. 257-268. Academic Press, New York (1972).