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Predator Prey Interactions with Time Delays

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Summary

A general (Volterra-Lotka type) integrodifferential system which describes a predator-prey interaction subject to delay effects is considered. A rather complete picture is drawn of certain qualitative aspects of the solutions as they are functions of the parameters in the system. Namely, it is argued that such systems have, roughly speaking, the following features. If the carrying capacity of the prey is smaller than a critical value then the predator goes extinct while the prey tends to this carrying capacity; and if the carrying capacity is greater than, but close to this critical value then there is a (globally) asymptotically stable positive equilibrium. However, unlike the classical, non-delay Volterra-Lotka model, if the carrying capacity of the prey is too large then this equilibrium becomes unstable. In this event there are critical values of the birth and death rates of the prey and predator respectively (which hitherto have been fixed) at which "stable" periodic solutions bifurcate from the equilibrium and hence at which the system is stabilized. These features are illustrated by means of a numerically solved example.

1. Introduction

The integrodifferential system

$$N_1'(t)=b_1 N_1(t)\left(1-c_{11} N_1(t)-c_{12}\int_0^\infty N_2(t-u)\,dh_1(u)\right)$$

$$N_2'(t)=b_2 N_2(t)\left(-1+c_{21}\int_0^\infty N_1(t-u)\,dh_2(u)\right) \tag{1.1}$$

$$b_i>0,\ c_{ij}>0,\ dh_i(u)\geq 0,\ \int_0^\infty dh_i(u)=1$$

serves to describe the dynamics of two species whose population sizes are $N_i(t)$ (in some appropriate units) and whose interaction is that of a predator N_2 and prey N_1. Here b_1 (or b_2) is the inherent, exponential net birth (or death) rate of the prey (or predator) in the absence of all constraints and c_{11} is the density coefficient for the prey. In the absence of predators (i.e. when $N_2\equiv 0$) N_1 satisfies the well-known logistic equation $N_1'=b_1 N_1(1-c_{11}N_1)$ and hence $N_1(0)>0$ implies that $N_1(t)$ tends to the equilibrium $1/c_{11}$ (i.e. to its so-called "carrying capacity") as $t\to+\infty$; in the absence of prey, $N_2\to 0$ as $t\to+\infty$. On the other hand, when N_1 and N_2 interact, the Stieltjes integrals in (1.1) allow the contacts between predator and prey at (possibly all) past times to effect the growth rates of both species.

Delay effects were first considered in predator-prey systems by Volterra in his well-known book [8]. Volterra set $dh_i(u)=k_i(u)\,du$ and showed that under certain conditions all solutions possess a certain "oscillatory" behavior. If $h_i(u)=s_\tau(u)$, the unit step function at $\tau>0$, then (1.1) is a differential system with constant time lags. Such systems have been studied by a few authors (see [2] and [6] and the references therein) and, although such systems are not as completely understood as systems without time-lag, enough is certainly known to say that such lags can significantly alter the qualitative behavior of solutions. (Also see [1].)

Although the general theory and available analytic techniques for integrodifferential systems are not as well developed as those of differential systems, enough recent work has been done for both general integrodifferential systems (e.g. see [3], [4], [7] and the references therein) as well as those of the form (1.1) (see [1], [5]) to be able to draw a rather complete picture of certain aspects of the qualitative behavior of solutions of (1.1) as they are functions of the parameters in the system. To attempt to do this is the purpose of this paper.

To begin we observe that the only equilibria, $N_i(t)\equiv e_i=\text{constant}$, of (1.1) lying in the right half plane are

$$\begin{aligned} &E_1:\ e_1=1/c_{21},\ \ e_2=(c_{21}-c_{11})/c_{21}\,c_{12} \\ &E_2:\ e_1=1/c_{11},\ \ e_2=0. \end{aligned} \tag{1.2}$$

In the classical, nondelayed case of the Volterra-Lotka equations (i.e. when $h_i(u)=s_0(u)$, the unit step function at $\tau=0$) it is well-known that all positive solutions $N_i>0$ (a) tend to E_2 if $c_{11}>c_{21}$ and (b) tend to E_1 if $0<c_{11}<c_{21}$. Thus, either the equilibrium E_1 is asymptotically stable or the predator goes extinct depending on whether the carrying capacity of the prey is respectively greater than or less than the critical value $1/c_{21}$. In the presence of time delays, however, the situation is a good deal more complicated. In some cases for example E_1 may be unstable [1], [3] and/or nonconstant, periodic solutions may exist [1], [5].

In section 2 and section 4 theorems will be stated and proved which, roughly speaking,support the following general statement concerning (1.1) when delays are present. Case (a) above holds in general for (1.1) when $c_{11}>c_{21}$ regardless of the values of the other parameters or of the nature of the delay integrators $h_i(u)$. This is also true of case (b) provided c_{11} is not too small. However, unlike the classical Volterra-Lotka system, if $c_{11}>0$ is small (all other quantities being held fixed), then the equilibrium E_1 will usually, owing to the presence of delays, become unstable. In the case when c_{11} is small however, there are under certain conditions critical values b_i^0 of the birth and death rates b_1 and b_2 at which nonconstant, periodic limit cycles will bifurcate from E_1. Hence, an equilibrium which is unstable due to the presence of time delays and a large carrying capacity for the prey can be stabilized by an appropriate adjustment of the birth and death rates b_1 and b_2.

All of the above points are illustrated in section 3 by means of a specific, numerically solved system (1.1) with exponentially decaying kernels $k_i(u)$. Although the rigorous mathematical theorems in section 2 only support the above claims "locally", all examples which have been numerically investigated by the author (including the one discussed in section 3 below) indicate that these phenomena are for all practical purposes in fact global in the sense that for fixed values of the parameters in (1.1) every positive solution either tends to E_1 or E_2; or every solution spirals outwardly in an unstable manner; or every solution tends to a periodic limit cycle (not necessarily to the same one). Only for a very narrow range of "borderline" values of the parameters was "mixed" behavior ever observed. For example, see Fig. 1 (e) below where some trajectories spiral outwardly while some spiral inwardly.

2. Theorems

Following Volterra [8] we say that two functions $N_i(t)$ form a *solution* $(N_1(t), N_2(t))$ *of* (1.1) *for* $t>t_0$ for some $t_0>-\infty$ if each $N_i(t)$ is defined for $-\infty<t<+\infty$ and differentiable for $t>t_0$, if each integral in (1.1) is defined for $t>t_0$ and if each equation in (1.1) is identically satisfied for $t>t_0$. Note that any solution of (1.1) for $t>t_0$ is necessarily of one sign for $t>t_0$. This is because $N_i(t)=N_i(t_0)\exp\left(\int_{t_0}^t P_i(s)\,ds\right)$ for $t>t_0$ where the P_i are the parenthetical expressions on the right hand sides of the equations in (1.1). By a *positive solution of* (1.1) *for* $t>t_0$ we mean a solution for $t>t_0$ as defined above for which $N_i(t)>0$ for all $-\infty<t<+\infty$. Positive solutions are of course the only solutions of interest in any ecological application of (1.1). For simplicity we will take $t_0=0$, although all of the following theorems remain valid for an arbitrary $t_0>-\infty$. Thus by a solution or positive solution of (1.1) we will mean a solution or positive solution of (1.1) for $t>0$.

We assume throughout that $h_i(u)$ is of bounded variation of finite intervals.

Theorem 1: *If* $(N_1(t), N_2(t))$ *is a positive solution of* (1.1) *with* $c_{11}>c_{21}$ *then* (N_1, N_2) *approaches* E_2 *as* $t\to+\infty$; *that is,*

$$\lim_{t\to+\infty} N_1(t)=1/c_{11}, \quad \lim_{t\to+\infty} N_2(t)=0.$$

We emphasize that this theorem, which says that the predator goes extinct if the prey's carrying capacity is too small, is valid for any values of the other parameters b_1, b_2 and c_{12} and for any delay integrators h_i. In this regard (1.1) behaves like the classical Volterra-Lotka system.

The next three theorems deal with the case $c_{11}<c_{21}$; i.e. with the case when the equilibrium E_1 lies in the first quadrant. We say that E_1 is *locally stable* [4] if given any $\varepsilon>0$ there exists a $\delta=\delta(\varepsilon)>0$ such that for any solution of (1.1) satisfying $|N_i(t)|\le\delta$ for all $t<0$ it is true that $|N_i(t)|\le\varepsilon$ for all $t\ge 0$. The equilibrium $E_1=(e_1, e_2)$ is *locally asymptotically stable* [4] if it is stable and if there exists a constant $\gamma>0$ for which $|N_i(t)|\le\gamma$ for all $t<0$ implies that $N_i(t)\to e_i$ as $t\to+\infty$.

Theorem 2: *Assume that* $dh_i(u)=k_i(u)\,du$ *in* (1.1) *where* $k_i(u)$ *has a Laplace transform* $k_i^*(s)$ *which is analytic for* $\operatorname{Re} s\ge 0$. *There exists a constant*

$\varepsilon_1 = \varepsilon_1(c_{12}, c_{21}, b_i, k_i) > 0$ such that if c_{11} satisfies $c_{21} - \varepsilon_1 < c_{11} < c_{21}$, then the equilibrium E_1 is locally asymptotically stable.

This theorem is proved by means of the standard technique of linearization about E_1 and an investigation of the resulting linear system of integro-differential equations. For the details of this procedure and for its formal justification we refer the reader to [4]. The stability of the linearized system is determined by means of the location in the complex plane of the roots of the characteristic determinant [7] which for our application here turns out to be $f(s) = s(s + b_1 e_1 c_{11}) + k(s)$ where $k(s) = b_1 b_2 e_1 e_2 c_{12} c_{21} k_1^*(s) k_2^*(s)$. If the roots of $f(s) = 0$ all lie in the left half complex plane $\operatorname{Re} s < 0$ then E_1 is locally asymptotically stable [4], [7] and Theorem 2 is proved in section 4 by showing that this is in fact the case for c_{11} close to, but less than c_{21}.

On the other hand, if $f(s) = 0$ has a root in the right half plane $\operatorname{Re} s > 0$ then E_1 is unstable [3], [4]. As we will see this often happens as c_{11} is taken closer to zero. In order to investigate this possibility we consider $f(s)$ when $c_{11} = 0$; let $f_0(s) = s^2 + k(s)$ where now $k(s) = b_1 b_2 k_1^*(s) k_2^*(s)$. We look for conditions on k_i under which $f_0(s) = 0$ has a root in the right half plane. Under these same conditions $f(s)$ will have roots in the right half plane for c_{11} small.

It is often the case that $k(s)$ is a rational function of s in which case the location of the roots of f_0 (and f) can be carried out by means of the well-known Routh-Hurwitz criteria. For example, see the examples in [3] or section 3 below. To obtain more general criterion, however, we make use of the argument principle and obtain the following theorem.

Theorem 3: *Assume that the integrators h_i satisfy the hypotheses of Theorem 2 and that $f_0(s) = 0$ has no purely imaginary roots $s = i y$, $-\infty < y < +\infty$. If the condition*

$$\arg f_0(+\infty\, i) \neq \pi \tag{2.1}$$

holds, then the equilibrium E_1 is unstable for $0 < c_{11} < \varepsilon_2$ where $\varepsilon_2 = \varepsilon_2(c_{12}, c_{21}, b_i, k_i) > 0$ is some sufficiently small constant.

Here we mean, of course, that $\arg f_0(+\infty\, i) = \lim_{y \to +\infty} \arg f_0(i y)$. Note that $f_0(i y) = -y^2 + k(i y)$ and that $|k_i^*(i y)| \leq 1$ for all y implies that the curve $f_0(i y)$, $y > 0$ lies in the semi-infinite rectangle $-\infty < x \leq b_1 b_2$, $|y| \leq b_1 b_2$ of the complex plane $s = x + i y$. Since $f_0(0) = b_1 b_2$ and $\operatorname{Re} f_0(i y) \to -\infty$ as $y \to +\infty$ it follows that $\arg f_0(+\infty\, i) = (2n+1)\pi$ for some integer $n = 0, \pm 1, \pm 2, \ldots$. According to Theorem 3 all possibilities except $n = 0$ imply the instability of E_1. It will follow from the proof of Theorem 3 in section 4 below that when $n = 0$ no roots of $f_0(s) = 0$ will lie in the right half plane. Hence, since it was assumed that none lie on the imaginary axis, it follows that in this exceptional case all roots lie in the left half plane which implies, as in Theorem 2, that E_1 is locally asymptotically stable. Since all but this one case of infinitely many lead to instability we conclude that it is usually the case that E_1 is unstable for c_{11} small (i.e. for prey with large carrying capacity). In further support of this statement we point out that all examples with specific kernels k_i ever computed by the author, including that in section 3 below and those in [1] and [3], have yielded unstable cases.

Our final result deals with the existence of nonconstant periodic solutions of (1.1) which surround the equilibrium E_1. (By a *p-periodic solution of* (1.1) *for* $t > t_0$ we mean a solution for $t > t_0$ as defined above such that $N_i(t+p) = N_i(t)$ for all t. It is not difficult to see that such a solution is in fact a solution for arbitrary $t_0 > -\infty$ and hence we speak simply of p-periodic solutions of (1.1).) This problem was dealt with for general two species interactions in [5] and we will apply the main results in [5] to (1.1). The theorems in [5] give necessary and sufficient conditions for the bifurcation of p-periodic solutions of (1.1) from E_1 as the birth and death rates b_1 and b_2 respectively vary through critical values $b_1^0 > 0$ and $b_2^0 > 0$. In order to describe the application of these criteria to (1.1) we must introduce some further notation.

For a positive integer $n \geq 1$ and positive period $p > 0$ we define the Fourier-Stieltjes integrals

$$S_{ij} = S_{ij}(n, p) = c_{ij} \int_0^\infty \sin 2\pi n p^{-1} u \, dh_i(u)$$
$$C_{ij} = C_{ij}(n, p) = c_{ij} \int_0^\infty \cos 2\pi n p^{-1} u \, dh_i(u)$$

and the expressions

$$\Sigma_1 = \Sigma_1(n, p) = S_{12} C_{21} + S_{21} C_{12}, \quad \Sigma_2 = \Sigma_2(n, p) = S_{12} S_{21} - C_{12} C_{21}.$$

Theorem 4: *Suppose that the following conditions hold for some integer* $n \geq 1$ *and period* $p > 0$:

$$\Sigma_1(n, p) > 0, \quad \Sigma_2(n, p) < 0, \quad C_{21}(n, p) \neq 0. \tag{2.2}$$

Suppose in addition that either

$$n \Sigma_1(m, p) \neq m \Sigma_1(n, p) \quad \text{or} \quad n^2 \Sigma_1(n, p) \Sigma_2(m, p) \neq m^2 \Sigma_1(m, p) \Sigma_2(n, p) \tag{2.3}$$

for all integers $m \geq 1$, $m \neq n$. *Then for* $c_{11} > 0$ *sufficiently small*:

$$0 < c_{11} < \varepsilon_3 = \varepsilon_3(c_{12}, c_{21}, h_i),$$

there exists a nonconstant, positive p-periodic solution of (1.1) *for values of* b_1, b_2 *sufficiently close to the critical values given by*

$$b_1^0 = -2\pi n c_{21} \Sigma_1(n, p)/p \, c_{11} \Sigma_2(n, p) \tag{2.4}$$

$$b_2^0 = 2\pi n c_{11}/p \, (c_{21} - c_{11}) \Sigma_1(n, p). \tag{2.5}$$

Furthermore, the average of any p-periodic solution of (1.1) *is the equilibrium* E_1; *i.e.* $p^{-1} \int_0^p N_i(t) \, dt = e_i$.

The first two inequalities in (2.2) are in fact necessary for the bifurcation of p-periodic solutions from E_1 [5]. The conditions $C_{21} \neq 0$ and (2.3) are added to guarantee that bifurcation actually occurs. (As those familar with bifurcation theory know, the necessary conditions derived for a given problem by means of examining the corresponding linearized problem are not necessarily sufficient for bifurcation to occur. Hence the need in general for added hypotheses.)

Notice that conditions (2.2) and (2.3) are all inequalities. One would expect from this that if these conditions hold for some n and p then they would hold for this n and all other periods close to p. Thus periodic solutions of (1.1) of various periods p are to be expected for certain values of b_i. This can be observed in the numerically solved example in section 3.

We do not offer any formal theorems concerning the "stability" of the periodic solutions obtained from Theorem 4. The stability question is a difficult one (in fact, the stability of nonconstant periodic solutions of nondelay differential systems is in general a difficult one) and there appears to be no available techniques for approaching it for systems as general as (1.1). Certainly the remarks above concerning the existence of many periodic solutions of different periods rules out global stability properties of any one periodic solution. As is observed numerically in section 3 neither is it true that all solutions are periodic. The best statement we can make based on our numerical investigations is that each and every solution seems to tend orbitally to a periodic solution, but not necessarily each to the same one.

Finally we point out that, as will be seen in the proof in section 4, the smallness of c_{11} is not really necessary in Theorem 4. Technically we will see that the theorem remains valid if $0<c_{11}<c_{21}$ and $c_{11}\neq c_{11}^0$ where $c_{11}^0>0$ is a certain critical value.

3. An Example

System (1.1) was solved numerically for $c_{21}=c_{12}=b_2=1.0$ and $dh_i(u)=\exp(-u)du$. Selected trajectories for selected values of c_{11} and b_1 are shown in Figs. 1 and 2 in such a way as to illustrate the four theorems in section 2 above. Note that the critical value for c_{11} is $c_{21}=1.0$ and that the two equilibria are

$$E_1:\ e_1=1.0, \quad e_2=1.0-c_{11}$$

$$E_2:\ e_1=c_{11}^{-1}, \quad e_2=0.$$

In this example $f_0(s)=s^2+b_1/(s+1)^2$ and it is easy to see by direct calculation that there are roots in the right half plane (or that $\arg f_0(+\infty\, i)=-\pi$) and hence that Theorem 3 applies.

First b_1 was fixed at $b_1=1.0$ and c_{11} was varied. In Figs. 1 (a) and (b) where $c_{11}>1.0$ we see illustrated the global attraction of the equilibrium E_2 (which is approximately (0.5, 0) and (0.9, 0) respectively) as is consistent with Theorem 1. In Fig. 1 (c) where $c_{11}=0.9$ is less than, but close to 1.0 we see the asymptotic stability of $E_1=(1.0,\ 0.1)$ as expected from Theorem 2. This stability still holds for $c_{11}=0.6$ as shown in Fig. 1 (d). However, when c_{11} is as small as 0.4 the equilibrium $E_1=(1.0,\ 0.6)$ has become unstable as the outwardly spiralling trajectory in Fig. 1 (f) demonstrates. This is consistent with Theorem 3. The choice $c_{11}=0.55$ in Fig. 1 (e) shows a borderline case where the larger trajectory spirals inwardly while the smaller trajectory spirals outwardly. In all other cases shown (although for clarity only a few trajectories are drawn) every trajectory computed for a given value of c_{11} possessed the same qualitative behavior as those shown in Fig. 1.

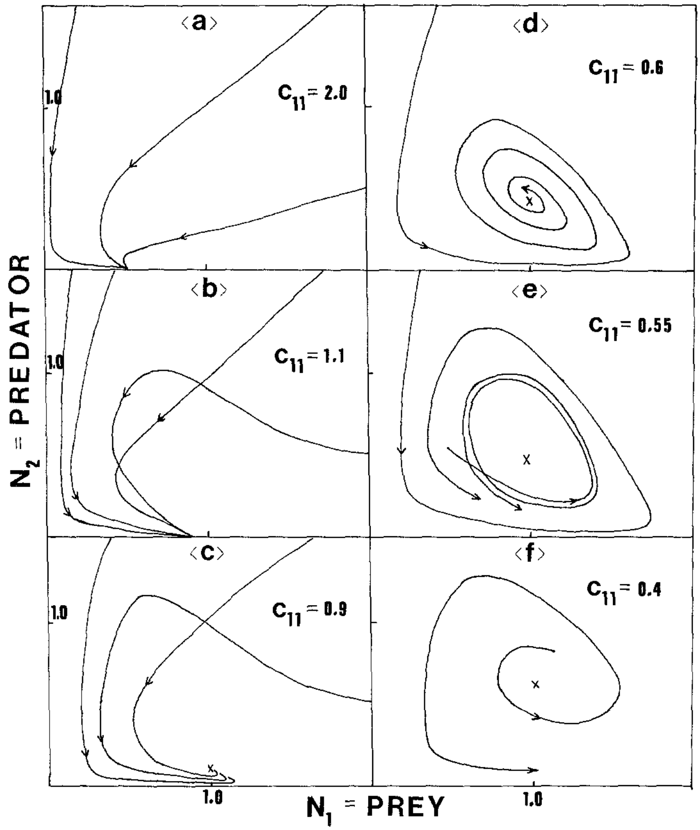

Fig. 1

The results of Theorem 4 are demonstrated by Fig. 2. There we have fixed c_{11} at the value 0.4 which as shown in Fig. 1 (f) is an unstable case when $b_1 = 1.0$. In Fig. 2 the value of b_1 is increased in order to illustrate not only Theorem 4, but how an unstable equilibrium may be "stabilized" by an appropriate adjustment of the birth rate b_1. For the exponential kernels chosen in this example we find that

$$\Sigma_1(n, p) = 2\pi n p^{-1}/(1+(2\pi n p^{-1})^2)^2$$

$$\Sigma_2(n, p) = ((2\pi n p^{-1})^2 - 1)/(1+(2\pi n p^{-1})^2)^2$$

$$C_{21} = (1+(2\pi n p^{-1})^2)^{-1}$$

$$b_1^0 = 5\,(2\pi n p^{-1})^2/(1-(2\pi n p^{-1})^2) \tag{3.1}$$

$$b_2^0 = (1+(2\pi n p^{-1})^2)^2/3. \tag{3.2}$$

The first inequality in hypothesis (2.2) obviously holds as does $C_{21} \neq 0$. The remaining hypothese $\Sigma_2 < 0$ of (2.2) of Theorem 4 clearly holds if

$$2\pi n p^{-1} < 1. \tag{3.3}$$

We take $n=1$ and recall that we have chosen $b_2^0=1.0$. This choice of b_2^0 in (3.2) determines $p \sim 7.34$ which yields $2\pi n p^{-1} = 2\pi p^{-1} \sim 0.86$ and shows that (3.3) holds. Thus, Theorem 4 applies. The critical value for b_1 is found from (3.1) to be $b_1^0 \sim 13.66$.

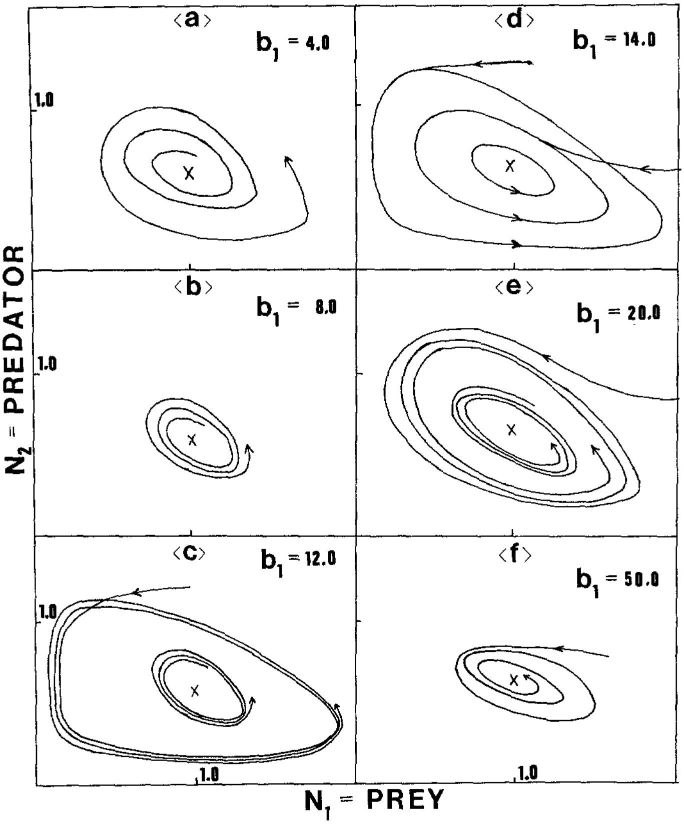

Fig. 2

The graphs in Fig. 2 bear out the above calculations. In Figs. 2 (a), (b) and (c) we see that as b_1 approaches the critical value b_1^0 from below the unstable, outward spirals become progressively tighter until at $b_1 = 14.0$ (which is near the critical value 13.66) periodic solutions are observed, three of which are drawn in Fig. 2 (d). Also drawn in Fig. 2 (d) are two trajectores which, although themselves not periodic, approach periodic trajectories (so quickly in fact that except for a short segment in the graphs they appear indistinguishable from the periodic trajectories). These computer runs were made for $0 \leq t \leq 30$ and it was observed that, very roughly, the periodic trajectories passed through four periods in this time interval. Thus observationally the periods were seen to be very close to 30/4 which is in turn very near the theoretically computed period of 7.34. As b_1 was increased further, inwardly spiralling trajectories were observed (see Figs. 2 (e) and (f)), but it was not clear whether these trajectories approached a nonconstant periodic solution or the equilibrium $E_1=(1.0, 0.6)$. Nonetheless is quite evident that the formerly unstable case for $b_1=1.0$ is stabilized for $b_1 \geq 14.0$.

4. Proofs

For the special case when $h_1(u)=s_0(u)$ and $dh_2(u)=k_2(u)\,du$, Theorem 1 was proved in [1]. The proof in [1] can however be carried out with only the most obvious of modifications for the more general case (1.1). In doing this it is crucial that the integrators h_i be nondecreasing. For brevity here we skip the details of the proof of Theorem 1 and refer the interested reader to the proof of Theorem 2 in [1].

Proof of Theorem 2: This theorem will be proved by showing that the roots of $f(s)=0$ all lie in the left half plane $\operatorname{Re} s<0$ for c_{11} close to, but less than c_{21}. To do this we wish to treat f as a function of c_{11} as well as s and hence we denote $f=f(s, c_{11})=s(s+b_1 e_1 c_{11})+k(s)$ where all other constants are fixed and

$$k(s)=\beta \int_0^\infty e^{-su} k_1(u)\,du \int_0^\infty e^{-su} k_2(u)\,du \tag{4.1}$$

where $\beta=\beta(c_{11})=b_1 b_2 e_2 c_{21}$ since $e_2=e_2(c_{11})$. Here $E_1=(e_1, e_2)$ is given by (1.2). Note that $\beta(c_{21})=0$ since $e_2(c_{21})=0$.

We argue by contradiction. Suppose it is not true that all roots of f satisfy $\operatorname{Re} s<0$ for c_{11} close to, but less than c_{21}. Then we can select sequences $c_{11}^{(n)}$ and s_n such that

$$f(s_n, c_{11}^{(n)})=0, \quad \operatorname{Re} s_n \geq 0, \quad c_{11}^{(n)} \to c_{21}, \quad c_{11}^{(n)} \leq c_{21}.$$

Now $f(s, c_{21})=s(s+b_1)$ has only two roots $s=0$ and $s=-b_1<0$. We distinguish two cases: (i) s_n has a convergent subsequence or (ii) $|s_n| \to +\infty$ as $n \to +\infty$.

(i) Relabeling if necessary we suppose without loss in generality that $s_n \to s_0$. By continuity $0=f(s_n, c_{11}^{(n)}) \to f(s_0, c_{21})$ and hence $f(s_0, c_{21})=0$ which implies, together with $\operatorname{Re} s_n \geq 0$ that $s_0=0$.

A straightforward application of the Implicit Function Theorem (note that $f(0, c_{21})=0$ and $\partial f(0, c_{21})/\partial s=b_1 \neq 0$) shows that the equation $f(s, c_{11})=0$ has a *unique* solution branch $s=s(c_{11})$ satisfying $s(c_{21})=0$ for c_{11} near c_{21}. Taking the implicit derivative of $f(s(c_{11}), c_{11})=0$ with respect to c_{11} and evaluating the result at $c_{11}=c_{21}$, we find that $ds/dc_{11}=dx/dc_{11}=b_2/c_{21}>0$ where $s(c_{11})= =x(c_{11})+i\,y(c_{11})$. Thus for c_{11} close to, but less than c_{21} the only roots of f near zero have negative real parts, in contradiction to $s_n \to 0$, $\operatorname{Re} s_n \geq 0$.

(ii) Suppose $|s_n| \to +\infty$. Then $s_n(s_n+b_1 e_1 c_{11}^{(n)}) \to \infty$. If $0 \leq \operatorname{Re} s_n=x_n \to +\infty$, then because $k(s_n) \to 0$ (see (4.1)) we find the contradiction that $0=f(s_n, c_{11}^{(n)}) \to \infty$. Thus, we conclude that $0 \leq x_n \leq m$ for some constant $m>0$. This means $k_i^*(s_n)$ is bounded and hence that $k(s_n) \to 0$ since $\beta(c_{11}^{(n)}) \to \beta(c_{21})=0$. Again we have the contradiction $0=f(s_n, c_{11}^{(n)}) \to \infty$.

Since both cases lead to contradictions the theorem follows.

Proof of Theorem 3: We wish to show that under the hypotheses of the theorem $f_0(s)$ has at least one root with $\operatorname{Re} s>0$. To do this we apply the argument principle on the half circle $\operatorname{Re} s\geq 0$, $|s|\leq R$ for an arbitrary but fixed radius $R>0$. If $\gamma(R)$ is the boundary of this half circle and if $\nu=\nu(R)\geq 0$ is the number of zeros of f_0 inside the half circle, then

$$\nu(R)=(2\pi i)^{-1}\int_{\gamma(R)}\frac{f_0'(s)}{f_0(s)}\,ds \tag{4.2}$$

where of course $\gamma(R)$ is oriented counterclockwise. The number of roots of f_0 in the right half plane is $\nu_+=\lim_{R\to+\infty}\nu(R)$. Let $\gamma(R)$ be divided into two parts $\gamma(R)=\gamma_1(R)+\gamma_2(R)$ where $\gamma_1(R)$ is the semi-circle $|s|=R$, $\operatorname{Re} s>0$ and $\gamma_2(R)$ is the line segment iy where y runs from R to $-R$. Then $\nu(R)=I_1(R)+I_2(R)$ where

$$I_i(R)=(2\pi i)^{-1}\int_{\gamma_i(R)}\frac{f_0'(s)}{f_0(s)}\,ds.$$

First we consider $I_1(R)$ for large R. Now

$$\frac{f_0'(s)}{f_0(s)}-\frac{2}{s}=\frac{s\,k'(s)-2\,k(s)}{s\,(s^2+k(s))}.$$

For s on $\gamma_1(R)$ it is easy to see that $k(s)$ and $k'(s)$ are bounded: $|k'(s)|\leq M$, $|k(s)|\leq M$. (See the note below added in proof.) Thus,

$$\int_{\gamma_1(R)}|f_0'(s)/f_0(s)-2/s|\,ds\leq(R+2)\,M/(R^2-M)\,\pi\to 0 \text{ as } R\to+\infty.$$

Hence $I_1(R)\to(2\pi i)^{-1}\int_{\gamma_1(R)}2/s\,ds=1$ as $R\to+\infty$.

Consequently from (4.2) and

$$I_2(R)=(2\pi i)^{-1}\int_R^{-R}f_0'(iy)/f_0(iy)\,i\,dy=\big(\arg f(-iR)-\arg f(iR)\big)/2\pi$$

we obtain the result

$$\nu_+=1+\big(\arg f(-\infty i)-\arg f(+\infty i)\big)/2\pi.$$

It is not difficult to see that $f(-yi)=\overline{f(yi)}$ for all y and as a result that $\arg f(-\infty i)=\arg f\overline{(+\infty i)}$. Since $\arg f\overline{(+\infty i)}-\arg f(+\infty i)=-2\arg f(+\infty i)$ we find that

$$\nu_+=1-\arg f(+\infty i)/\pi$$

and Theorem 3 follows from the fact that $\nu_+\neq 0$ if and only if (2.1) holds.

Proof of Theorem 4: Assume that $c_{11}<c_{21}$ so that E_1 lies in the first quadrant. From [5] we find that p-periodic solutions bifurcate from E_1, treating b_1 and b_2 as parameters, only if the 4×4 matrix

$$M_n=\begin{pmatrix}\xi_n & -b_1^0\,e_1\,S_{12} & -b_1^0\,e_1\,c_{11} & -b_1^0\,e_1\,C_{12}\\ b_2^0\,e_2\,S_{21} & \xi_n & b_2^0\,e_2\,C_{21} & 0\\ b_1^0\,e_1\,c_{11} & b_1^0\,e_1\,C_{12} & \xi_n & -b_1^0\,e_1\,S_{12}\\ -b_2^0\,e_2\,C_{21} & 0 & b_2^0\,e_2\,S_{21} & \xi_n\end{pmatrix}$$

where $\xi_n=2\pi n\,p^{-1}$ is singular. If the determinant of this matrix is set equal to zero the result is an equation of the form

$$A\,\beta_1^2 + 2\,B\,\beta_1 + \xi_n^4 = 0 \tag{4.3}$$

where $\beta_i = b_i^0\, e_i$, $B = \xi_n^2\, \Sigma_2\, \beta_2$ and

$$A = (S_{12}^2 + C_{12}^2)(S_{21}^2 + C_{21}^2)\,\beta_2^2 - 2\,c_{11}\,\xi_n\,\Sigma_1\,\beta_2 + c_{11}^2\,\xi_n^2.$$

If we treat (4.3) as a quadratic in β_1 we find that its discriminant is

$$B^2 - A\,\xi_n^4 = -\xi_n^4\,(\Sigma_1\,\beta_2 - c_{11}\,\xi_n)^2 \leq 0$$

and hence that (4.3) can have a real solution β_1 if and only if β_2 is chosen so that this discriminant is zero; i.e. if and only if b_2^0 is given by (2.5). In this case the left hand side of (4.3) becomes a perfect square

$$(\Sigma_2\,\beta_1\,\beta_2 + \xi_n^2)^2 = 0$$

so that β_1 is then uniquely determined. This leads to b_1^0 being given by (5.1). Of course we must have both $b_i^0 > 0$ which means that n and p must be chosen so that $\Sigma_1 > 0$ and $\Sigma_2 < 0$ as required in (2.1).

Finally to complete the proof we refer to [5] for conditions sufficient to insure that bifurcation occurs. First of all it is required that M_m be nonsingular for $m \neq n$. This is insured by (2.3) since these conditions mean that either b_1^0 or b_2^0 is different for all $m \neq n$. Lastly it is required that a certain determinant J involving vectors from the nullspaces of M_n and its transpose as well as the Fourier integrals S_{ij}, C_{ij} be nonzero. The calculation of this determinant is straightforward but rather tedious and consequently we omit the details. It turns out that $J = a\,C_{21} + c_{11}\,b$ where $a = a\,(c_{21}, c_{12}, h_i) > 0$ and $b = b\,(c_{21}, c_{12}, h_i)$ are two very complicated constants in terms of the indicated parameters. In any case we certainly have $J \neq 0$ for c_{11} small if $C_{21} \neq 0$. The existence of p-periodic solutions as stated in Theorem 4 now follows from Theorem 1 in [5].

To compute the averages of N_i (which we denote be $[N_i]$) we divide both sides of the equations in (1.1) by $p\,N_1$, $p\,N_2$ respectively and integrate from 0 to p. If we make use of the fact that

$$p^{-1} \int_0^p \int_0^\infty N_i\,(t-u)\,d h_j(u)\,dt = [N_i] \int_0^\infty d h_j(u) = [N_i]$$

then these manipulations yield, for p-periodic solutions, the equations

$$0 = 1 - c_{11}\,[N_1] - c_{12}\,[N_2]$$

$$0 = -1 + c_{21}\,[N_1].$$

Thus $[N_1] = 1/c_{21}$ and $[N_2] = (c_{21} - c_{11})/c_{21}\,c_{12}$.

Note added in proof: In Theorem 3 we need to assume also that $\int_0^\infty u\,k_i(u)\,du < +\infty$. This insures in the proof that $|\,k_i'(s)|$ is bounded on $\gamma_1\,(R)$.

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