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PERIODIC TIME-DEPENDENT PREDATOR-PREY SYSTEMS*

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Abstract. The general system of differential equations describing predator-prey dynamics is modified by the assumption that the coefficients are periodic functions of time. By use of standard techniques of bifurcation theory, as well as a recent global result of Rabinowitz, it is shown that this system has a periodic solution (in place of an equilibrium) provided the long term time average of the predator's net, unihibited death rate is in a suitable range. The bifurcation is from the periodic solution of the time-dependent logistic equation for the prey (which results in the absence of any predator). Numerical results which clearly show this bifurcation phenomenon are briefly discussed.

1. Introduction. The classical predator-prey model

$$N_1' = N_1(b_1 - c_{11}N_1 - c_{12}N_2),$$
$$N_2' = N_2(-b_2 + c_{21}N_1 - c_{22}N_2), \tag{1.1}$$

where $' = d/dt$ describes the dynamics of a predator-prey interaction where N_1 and N_2 measure, in some convenient units (such as number of individuals, biomass, etc.), the prey and predator population sizes respectively. Here b_1, $-b_2$ are the inherent net birth rates (i.e., the birth rates in the absence of any constraints) per unit of population per unit time of the prey and predator respectively; c_{ij} for $i \neq j$ measures the effect (on the corresponding growth rate in (1.1)) of the interaction of the two species; and c_{ii} is the self-inhibition (or logistic) coefficient. In this classical model all coefficients are constants and

$$c_{ii} \geqq 0, \quad b_i > 0 \quad \text{and} \quad c_{ij} > 0 \quad \text{for } i \neq j. \tag{1.2}$$

Our concern in this paper is with the more general case when these coefficients are functions of time t, or more specifically, periodic functions of time. Such a generalization seems a natural one considering the oscillations to which any ecological parameter might quite naturally be exposed (for example, those due to seasonal effects of weather, food supply, mating habits, hunting or harvesting seasons, etc.). Although, to the author's knowledge, such time-dependent systems have not been studied in any generality, the time dependence of the coefficients was a suggested (but unexplored) explanation for the oscillatory data obtained by Utida in his experimental studies [9]. Our goal is to establish the existence of a positive $N_i > 0$, periodic solution for such a time-varying predator-prey system. The trajectories of this solution in the phase plane of N_1, N_2 will take the place of the equilibria solutions of the classical systems (1.1).

To motivate not only the type of results we will obtain but also the approach and method of proof, we consider for a moment the classical system (1.1) with constant coefficients satisfying (1.2). If $c_{11} > 0$, then it is easy to see that (1.1) has

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two equilibrium solutions in the right half-plane $N_1 > 0$ given by

$$E_1 = \left(\frac{b_1c_{22}+b_2c_{12}}{c_{11}c_{22}+c_{12}c_{21}}, \frac{b_1c_{21}-b_2c_{11}}{c_{11}c_{22}+c_{12}c_{21}}\right),$$

$$E_2 = \left(\frac{b_1}{c_{11}}, 0\right).$$

The equilibrium E_1 lies in the first or fourth quadrant if

$$b_1c_{21}-b_2c_{11} > 0 \quad \text{or} \quad < 0$$

respectively. In order to motivate our approach to the time-dependent system, we wish to recognize within this constant coefficient case a bifurcation phenomenon. Towards this end we treat b_2 (the predator's inherent net death rate in the absence of all constraints and all prey) as a free parameter. Then we observe the following: (i) for $b_2 > b_1c_{21}/c_{11}$ there is no equilibrium in the first quadrant; (ii) for $b_2 < b_1c_{21}/c_{11}$ the equilibrium E_1 lies in the first quadrant; (iii) E_1 and E_2 coincide for $b_2 = b_1c_{21}/c_{11}$; and (iv) for all b_2 the equilibrium E_2 remains fixed. Thus, with b_2 as a parameter we may view E_1 as an equilibrium which bifurcates from the stationary equilibrium E_2. With these facts in mind, together with the powerful general techniques available for studying bifurcation phenomena, we will prove the existence of periodic solutions of the time-dependent system (1.1) treating the average $[b_2]$ of $b_2(t)$ as a parameter. The point of bifurcation (played by E_2 above) should be, of course, a positive periodic solution of (1.1) when $N_2 \equiv 0$; i.e., of the time-dependent logistic equation

$$N_1' = N_1(b_1 - c_{11}N_1). \tag{1.3}$$

This equation has such a solution when $[b_1] > 0$ and $c_{11} = c_{11}(t) > 0$ for all t [2].

Our results are given in Theorem 2. We also discuss very briefly the stability of the periodic solutions of (1.1) found in Theorem 2. In § 3 we give numerical results for a periodic example of (1.1) which quite clearly show the bifurcation of the periodic solutions (as the average of b_2 varies) as well as their global asymptotic stability (as is the case for E_1 above). Our results are formally proved in § 4.

In a recent paper [6] Pimbley uses bifurcation theory to prove the existence of periodic solutions of a certain predator-prey model. There is no overlap with our results here, however, since Pimbley considers a different question for a different model. Specifically, Pimbley considers the problem of nonconstant periodic solutions in the presence of an equilibrium for an autonomous model, while we consider the question of periodic solutions of nonautonomous models in the absence of equilibria. If the equilibrium in Pimbley's model is viewed as a branch of a bifurcation from the single species equilibrium as suggested above for (1.1) with constant coefficients, then from the point of view of bifurcation theory, Pimbley's study is one of secondary bifurcation in the autonomous case. Our concern here, on the other hand, is with the primary bifurcation from the single species "time-varying carrying capacity", but in the nonautonomous case.

2. Results. Let B denote the Banach space of continuous, ω-periodic functions under the supremum norm: $|N|_0 = \sup_{0 \leq t \leq \omega} |N(t)|$. Throughout this paper ω

is an arbitrary, but fixed period. We will also consider the product space $B \times B$ which is a Banach space under the norm $|(N_1, N_2)|_0 = |N_1|_0 + |N_2|_0$. For N defined on $[0, \omega]$ we define average of N to be

$$[N] = \omega^{-1} \int_0^\omega N(s)\, ds.$$

We begin with an existence and uniqueness theorem for the logistic equation (1.3).

THEOREM 1. *Suppose that* $b_1, c_{11} \in B$ *satisfy* $[b_1] > 0$ *and* $c_{11}(t) > 0$ *for all* t. *Then* (1.3) *has one and only one solution* $N_1 \in B$ *satisfying* $N_1 > 0$ *for all* t.

By a solution of (1.3) (or (1.1)) in B (or in $B \times B$) we mean functions which are in addition differentiable.

Let $N_1^*(t) \in B$ denote the unique solution of (1.3) as described and guaranteed by Theorem 1. Our main results are contained in the following theorem.

THEOREM 2. *Suppose that* $b_i, c_{ij} \in B$, *that* $[b_1] > 0$ *and* $c_{ij} \geqq 0$ *for all* t, *and that* $c_{11}, c_{12} > 0$, $c_{21} \not\equiv 0$ *for all* t.

(a) *There is a constant* b_0, $0 \leqq b_0 < [c_{21}N_1^*]$, *such that for each* $b_2 \in B$ *satisfying* $b_0 \leqq [b_2] < [c_{21}N_1^*]$ *there exists a solution* $(N_1, N_2) \in B \times B$ *of* (1.1) *satisfying* $0 < N_1 < N_1^*$, $N_2 > 0$ *for all* t.

(b) *If in addition* $c_{22} > 0$ *for all* t, *then* $b_0 \leqq 0$.

Part (a) of this theorem is local in nature in that solutions in B are guaranteed only for $[b_2]$ near (and less than) the number $[c_{21}N_1^*]$. Part (b) asserts that b_2 may lie anywhere in the full interval $[0, c_{21}N_1^*)$ if the predator has a logistic coefficient c_{22} bounded away from zero. In the case of constant coefficients, this added assumption on c_{22} is not necessary for the validity of part (b) and in fact periodic solutions (namely, E_1) exists for b_2 in the whole interval $[0, c_{21}b_1/c_{11})$ even if $c_{22} = 0$. The proof of part (b) given below in § 4 definitely requires the condition $c_{22} > 0$; this is pointed out in § 4. Moreover, numerical results carried out by the author as described in § 3 below give, for the specific systems considered, no definite indication of the existence of a periodic solution when $c_{22} \equiv 0$ and $[b_2]$ is near zero. This seems to indicate that the condition $c_{22} > 0$ may not be eliminated from part (b) of Theorem 2, although it may be the case that this condition could be weakened.

When all coefficients are constants, this theorem is consistent with the above discussed observations where the periodic solution, whose existence is asserted in Theorem 2, is just the equilibrium E_1 and where the condition $[b_2] < [c_{21}N_1^*]$ reduces to $b_1c_{21} - b_2c_{11} > 0$ (since in this case $N_1^* = b_1/c_{11}$). In this case E_1 is (globally) uniformly asymptotically stable. In the more general case with coefficients lying in B one would hope that the solutions lying in $B \times B$ guaranteed by Theorem 2 possess some stability properties. It is not our purpose here to study this stability question in depth, although we will offer a few simple observations.

Suppose $(\bar{N}_1, \bar{N}_2) \in B \times B$ is a solution of (1.1) as described in Theorem 2, and suppose we linearize (1.1) about this solution; i.e., let $x_i = N_i - \bar{N}_i$, make this substitution into (1.1) and drop all terms in x_i of order two or more. This results in the system

$$\begin{aligned} x_1' &= (\bar{N}_1'/\bar{N}_1 - c_{11}\bar{N}_1)x_1 + (-c_{12}\bar{N}_1)x_2, \\ x_2' &= (c_{21}\bar{N}_2)x_1 + (\bar{N}_2'/\bar{N}_2 - c_{22}\bar{N}_2)x_2. \end{aligned} \tag{2.1}$$

Well-known theorems tell us that if this linear system is uniformly asymptotically stable, then the same is true (locally) of $(\bar{N}_1, \bar{N}_2)$ for (1.1) [1], [4]. If we further let $y_i = x_i/\bar{N}_i$, then (2.1) becomes

$$y_1' = (-c_{11}\bar{N}_1)y_1 + (-c_{12}\bar{N}_2)y_2, \qquad (2.2)$$
$$y_2' = (c_{21}\bar{N}_1)y_1 + (-c_{22}\bar{N}_2)y_2,$$

and (2.1) is uniformly asymptotically stable if and only if (2.2) is also. In general it is difficult to determine the stability properties of a nonautonomous system such as (2.2), even in this case where all the coefficients are ω-periodic. Certainly the average of the trace of (2.2) is negative, and hence at least one characteristic exponent has negative real part, but, as is usually the case, the other characteristic exponent is difficult to locate in general. One well-known technique which does yield some stability criteria for (2.2) is that which uses a certain "measure" $\mu(A(t))$ of the coefficient matrix $A(t) = (a_{ij}(t))$ of the system; μ depends on the vector norm used and for the norm $|(v_i, v_2)| = |v_1| + |v_2|$ is given by [1]

$$\mu(A(t)) = \max\{a_{11} + |a_{21}|, a_{22} + |a_{12}|\}$$
$$= \max\{(c_{21} - c_{11})\bar{N}_1, (c_{12} - c_{22})\bar{N}_2\}.$$

If $Y(t)$ is a fundamental matrix for (2.2), then [1]

$$|Y(t)Y^{-1}(s)| \leqq \exp\left(\int_s^t \mu(A(u))\right) du,$$

and hence (2.2) is uniformly asymptotically stable (i.e., $|Y(t)Y^{-1}(s)|$ decays exponentially to zero as $t \to +\infty$) if

$$c_{21} - c_{11} < 0, \quad c_{12} - c_{22} < 0 \qquad (2.3)$$

for all t. Under these conditions, the solution $(\bar{N}_1, \bar{N}_2)$ will be (locally) uniformly asymptotically stable. If the same technique is applied to (2.1) with the vector norm $|(v_1, v_2)| = \max|v_i|$, in which case $\mu(A(t)) = \max\{a_{11} + |a_{12}|, a_{22} + |a_{21}|\}$ [1], then one arrives at the criteria

$$c_{12}\bar{N}_2 - c_{11}\bar{N}_1 < 0, \qquad c_{21}\bar{N}_1 - c_{22}\bar{N}_2 < 0 \qquad (2.4)$$

in place of (2.3). Although these criteria do give stability results for the periodic solutions of (1.1), they are rather restrictive; both demand in the dynamics of the interaction that the self-inhibiting effects of both species are the more significant factors.

Next we consider the stability of the "trivial" solution $(N_1, N_2) = (N_1^*, 0)$. If we let $x_1 = N_1 - N_1^*$ in (1.1), ignore terms of order two or more in x_1 and N_2, and let $y_1 = x_1/N_1^*$ we find that

$$y_1' = (-c_{11}N_1^*)y_1 + (-c_{12})N_2, \qquad (2.5)$$
$$N_2' = (-b_2 + c_{21}N_1^*)N_2.$$

Just as with the case above, if this linear system is (locally) uniformly asymptotically stable, then the solution $(N_1^*, 0)$ will be also. From the second equation for

N_2 in (2.5) we have

$$N_2(t)=N_2(0)\exp([c_{21}N_1^*-b_2]t)\exp\left(\int_0^t p(s)\,ds\right),$$

where $p(t)=c_{21}N_1^*-b_2-[c_{21}N_1^*-b_2]$; note that $[p]=0$ and hence that $\int_0^t p(s)\,ds\in B$. Thus, for $[b_2]>[c_{21}N_1^*]$ we find that N_2 tends exponentially to zero as $t\to+\infty$. Since $[c_{11}N_1^*]\geqq c_0[N_1^*]>0$ for some constant $c_{11}(t)\geqq c_0>0$, it is easily seen that the same is true for y_1, and hence that (2.5) is uniformly asymptotically stable provided $[b_2]>[c_{21}N_1^*]$. Clearly (2.5) (and hence that solution $(N_1^*, 0)$ for the nonlinear system (1.1) [1]) is unstable if $[b_2]<[c_{21}N_1^*]$.

Thus, as is often the case in bifurcation theory, we see an *exchange of stability* from one branch of solutions to another as the parameter $[b_2]$ passes through its critical value. These stability results are summarized in the following theorem.

THEOREM 3. *Assume the hypotheses of Theorem* 2. (a) *If* $[b_2]>[c_{21}N_1^*]$, *then the trivial solution* $(N_1^*, 0)$ *of* (1.1) *is* (*locally*) *uniformly asymptotically stable.* (b) *If* $[b_2]<[c_{21}N_1^*]$, *then this trivial solution is unstable. In this case, however, the nontrivial periodic solution whose existence is guaranteed by Theorem* 2 *is* (*locally*) *uniformly asymptotically stable, at least if either* (2.3) *or* (2.4) *holds.*

Ecologically, Theorem 3 says that if the net death rate of the predator is too large, then the predator will go extinct while the prey will tend to its time-varying carrying capacity $N_1^*(t)$. On the other hand, if this death rate is small enough, then coexistence is possible. We suspect that the conditions (2.3) or (2.4) necessary for this latter statement can be weakened and that the exchange of stability described in Theorem 3 occurs under, in fact, more general conditions.

We make one final remark concerning stability. If all coefficients in (1.1) lie in B but are sufficiently close to constants satisfying (1.2), and if $b_1c_{21}-b_2c_{11}>0$ for these constants, then well-known perturbation (or small parameter) techniques [4] imply that $(N_1, N_2)\in B\times B$ is uniformly asymptotically stable (since E_1 is). In fact, under these very restrictive conditions on the coefficients one can also deduce the existence of $(N_1\, N_2)\in B\times B$ near E_1 using known theorems [4].

The proof of Theorem 2 part (a) involves sufficiently general techniques that this result is valid for systems of more generality than (1.1). The proof given in § 4 below remains essentially unchanged for the functional equations

$$N_1'=N_1(b_1-c_{11}N_1-F_{12}(t, N_2)),$$
$$N_2'=N_2(-b_2+F_{21}(t, N_1)-F_{22}(t, N_2))$$

for any continuous operators provided (compare the hypotheses of Theorem 2) only that $F_{ij}=0(|N|_0)$ near $N=0$, that F_{ij} possesses a Fréchet derivative F'_{ij} at $N=0$ which satisfies $F'_{ij}N\geqq 0$ and $\not\equiv 0$ for all t and all $N\in B$, $N\geqq 0$, and that $F'_{12}N>0$ for all t and all $N\in B$, $N>0$. Note that the operators F_{ij} may involve time-lags or integral operators (continuously distributed time-lags or hereditary effects). See [3] for a general study of such systems for functionals involving time-lags and their possible secondary bifurcations. These functionals may involve quadratic terms in N_1 or N_2 as in the model considered by Pimbley in [6].

With regard to further generalizations of Theorems 2 we point out that the more general case of almost periodic coefficients can be treated similarly in order

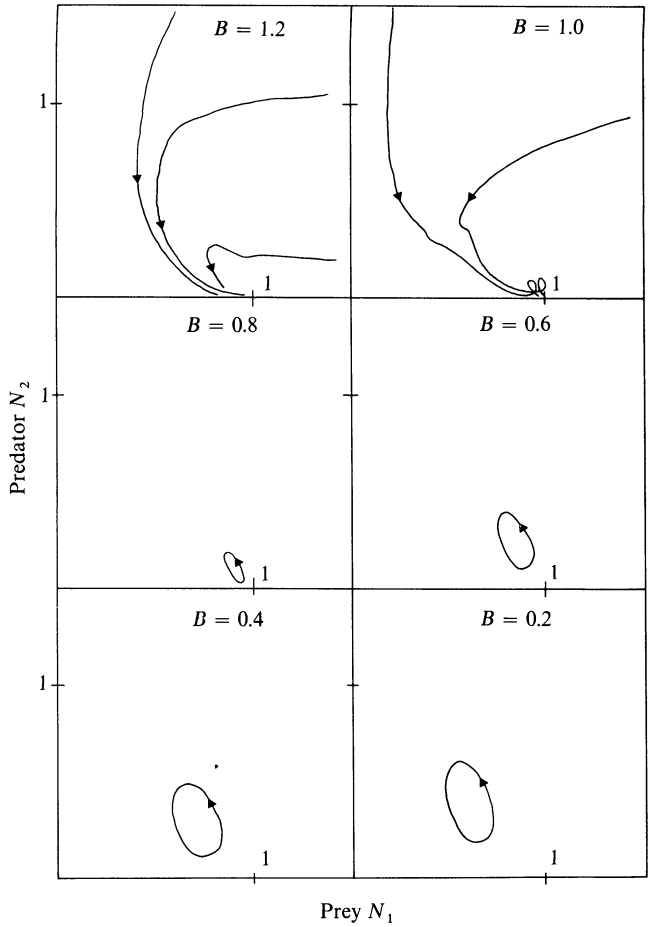

FIG. 1

to obtain the results of part (a) (provided the technical assumption that $c_{21}N_1^* - [c_{21}N_1^*]$ has a bounded antiderivative is met). Technically the proof of Theorem 2 in § 4 fails for the case of almost periodic coefficients because the linear operator L in Lemma 1 is not compact; L is, however, bounded and hence Theorem 1(a) can be proved using standard Lyapunov–Schmidt expansion techniques (e.g., as in [6], [8]). This requires complicated details which we prefer not to give here. The global results in [6] would not be available using this approach, and consequently the global assertion in Theorem 2(b) is left open for the case of almost periodic coefficients. The remarks concerning stability and in particular, Theorem 3 remain valid for almost periodic solutions provided that they are, when positive, bounded away from zero.

3. Some numerical results. System (1.1) was investigated numerically for the coefficients

$$b_2 = B - \tfrac{1}{2}\sin t, \qquad b_1 = c_{ij} = 1 + \tfrac{1}{2}\sin t;$$

these coefficients satisfy all the hypotheses of Theorem 1 and 2 with $\omega = 2\pi$. Equation (1.3) has the 2π-periodic solution $N_1^* \equiv 1$ so that, according to Theorem 2(b), system (1.1) should have 2π-periodic solutions for at least each $B \in [0, 1)$ (since, in this case, $[c_{21}N_1^*] = [c_{21}] = 1$). Actually 2π-periodic solutions lying in the first quadrant were found for all $B \in (-1, 1)$ examined; see Figs. 1 and 2. One can see quite clearly in Fig. 1 the bifurcation of the periodic loops from the point $(1, 0)$ as B passes from values larger than one, through the value one, to values less than one. The numerical evidence also indicated that the periodic solutions are globally asymptotically stable; this is illustrated in Fig. 3 where several trajectories are graphed for the value $B = 0.6$ in addition to the periodic solution. For $B \leqq -1$ and $B \geqq 1$ the solutions $(N_1, N_2) = (0, 1)$ and $(1, 0)$ were found respectively to be globally attracting in the first quadrant; several trajectories for each $B \leqq -1$ and $B \geqq 1$ are drawn in Figs. 1 and 2 to illustrate this fact.

The system with these same coefficients, except that $c_{22} \equiv 0$, was also solved numerically for many values of B. Again 2π-periodic solutions were clearly seen to bifurcate from $(1, 0)$ for B less than, but near one. However, in this case, unlike

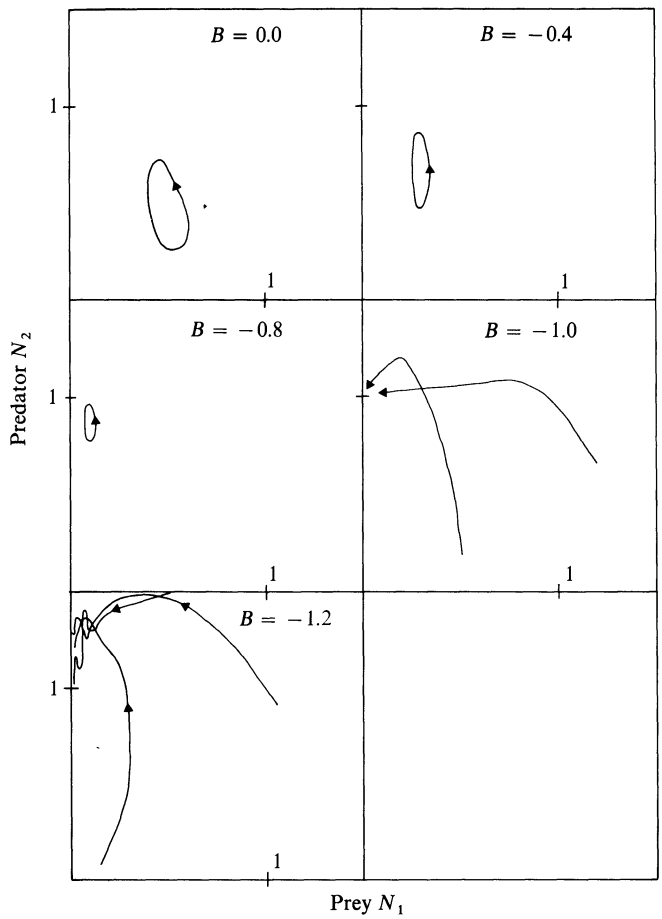

FIG. 2

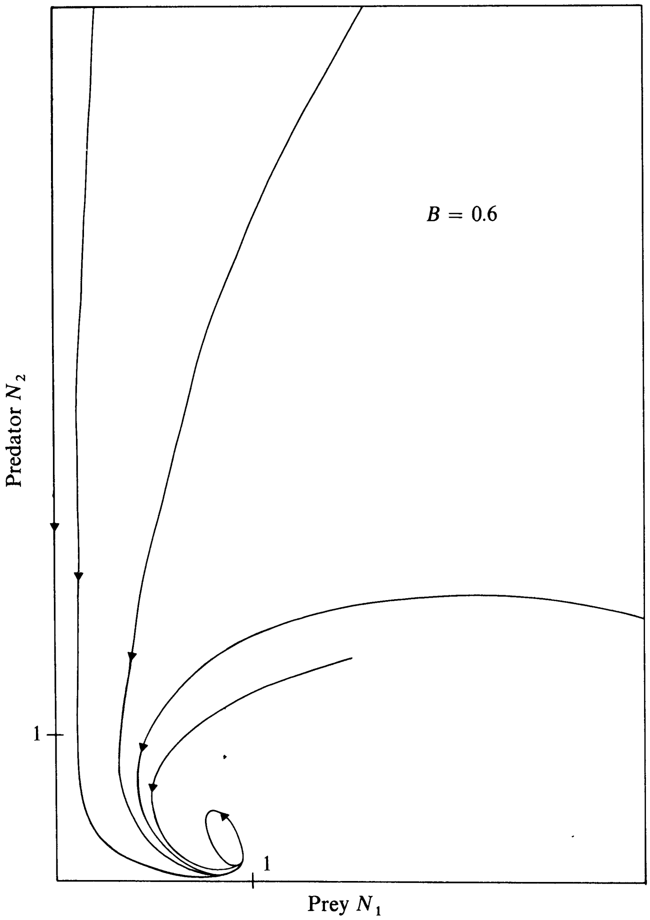

FIG. 3

the case above when $c_{22} \neq 0$ as graphed in Figs. 1–3, we found that as B approaches zero from above the periodic trajectories disappear; at least no clear-cut evidence was found of periodic trajectories for B near zero (specifically, for $B < 0.2$) and, moreover, the N_2 components of the solutions grow seemingly without bound as $B \to 0$. It was also found numerically in this case that for B nonpositive, $N_2 \to +\infty$ and $N_1 \to 0$ (which is consistent with the case of constant coefficients and $c_{22} = 0$). These facts seem to indicate that in order to be guaranteed periodic solutions for all $[b_2]$ in the full interval $[0, [c_{21}N_1^*])$ in Theorem 2(b) it is necessary to require at least that $c_{22} \neq 0$. Hence the necessity of a condition like $c_{22} > 0$ as appears in Theorem 2(b).

4. Proofs.

Proof of Theorem 1. That a positive solution $N_1 \in B$ exists is shown in [2]; we have thus only to prove that this solution is unique. First we make an observation concerning a certain weighted average of N_1. Dividing both sides of (1.3) by N_1, integrating from 0 to ω, and dividing the result by ω we find that $0 = [b_1 - c_{11}N_1]$ or

$$[b_1] = [c_{11}N_1]. \tag{4.1}$$

Turning now to the uniqueness question, we suppose that N^*, $N^{**} \in B$ are different solutions of (1.3) satisfying $N^* > 0$, $N^{**} > 0$ for all t. Let $N = N^* - N^{**}$. Since the uniqueness of solutions of initial value problems for (1.3) implies that if $N^* = N^{**}$ for some t then $N^* = N^{**}$ for all t, and since N^*, N^{**} are assumed to be different, we conclude that $N \neq 0$ for all t. Assume without loss of generality that $N > 0$ for all t. From (1.3) we have that

$$N' = N(b_1 - c_{11}N^* - c_{11}N^{**})$$

for all t. Dividing both sides by N and integrating from 0 to ω we find from this equation, upon dividing by ω, that

$$0 = [b_1] - [c_{11}N^*] - [c_{11}N^{**}]. \tag{4.2}$$

But N^*, N^{**} solve (1.3) and hence satisfy (4.1). Taken together, (4.1) and (4.2) imply the contradiction $[b_1] = 0$. □

Before proving Theorem 2 we state and prove some lemmas.

LEMMA 1. *Suppose* $a_{ij} \in B$. (a) *If* $[a_{22}] \neq 0$, $[a_{11}] \neq 0$, *then the linear homogeneous system*

$$\begin{aligned} y_1' &= a_{11}y_1 + a_{12}y_2, \\ y_2' &= a_{22}y_2 \end{aligned} \tag{4.3}$$

has no nontrivial solution in $B \times B$. *In this case the nonhomogeneous system*

$$\begin{aligned} x_1' &= a_{11}x_1 + a_{12}x_2 + f_1, \\ x_2' &= a_{22}x_2 + f_2 \end{aligned} \tag{4.4}$$

has, for every $(f_1, f_2) \in B \times B$, *a unique solution* $(x_1, x_2) \in B \times B$ *and the operator* $L: B \times B \to B \times B$ *defined by* $(x_1, x_2) = L(f_1, f_2)$ *is linear and compact.*

(b) *If* $[a_{22}] = 0$ *and* $[a_{11}] \neq 0$, *then* (4.3) *has exactly one independent solution in* $B \times B$.

Proof. (a) Since

$$y_2 = y_2(0) \exp\left(\int_0^t a_{22}(s)\, ds\right) \tag{4.5}$$

the condition $[a_{22}] \neq 0$ implies that $y_2 \notin B$ unless $y_2 \equiv 0$. But then $y_1 = y_1(0) \exp\left(\int_0^t a_{11}(s)\, ds\right)$ and $[a_{11}] \neq 0$ in turn implies $y_1 \notin B$ unless $y_1 \equiv 0$.

In this case $x_2' = a_{22}x_2 + f_2$ has a unique solution $x_2 \in B$ and the operator $L_2: B \to B$ defined by $x_2 = L_2 f_2$ is linear and compact [4]. Furthermore, $x_1' = a_{11}x_1 + f_3$ for $f_3 \in B$ has a unique solution (since $[a_{11}] \neq 0$) in B and $x_1 = L_1 f_3$ defines a linear, compact operator $L_1: B \to B$. Thus, (4.4) has a unique solution in $B \times B$ given by $(x_1, x_2) = L(f_1, f_2)$, where

$$L(f_1, f_2) \equiv (L_1(a_{12}L_2 f_2 + f_1), L_2 f_2). \tag{4.6}$$

(b) Under the stated assumptions, y_2 as given by (4.5) lies in B for all initial conditions $y_2(0)$. Now if $[a_{11}] \neq 0$, then $z' = a_{11}z$ has no nontrivial solution in B and hence

$$y_1' = a_{11}y_1 + a_{12}y_2(0) \exp\left(\int_0^t a_{22}\, ds\right)$$

has a unique solution in B. This defines a one-parameter family of solutions (y_1, y_2) of (4.3) which since (4.3) is linear and homogeneous is actually a one-dimensional subspace of $B \times B$. □

LEMMA 2. *Suppose* $a \in B$ *and* $[a]=0$. *Then* $x' = ax + f$, $f \in B$, *has a solution* $x \in B$ *if only if* $[f \exp(-\int_0^t a(s)\,ds)] = 0$.

Proof. See [4, p. 226].

Proof of Theorem 2. Let $x_1 = N_1 - N_1^*$, $x_2 = N_2$ in (1.1). Then

$$\begin{aligned} x_1' &= (b_1 - 2c_{11}N_1^*)x_1 - c_{12}N_1^*x_2 + g_1(x_1, x_2), \\ x_2' &= (c_{21}N_1^* - b_2)x_2 + g_2(x_1, x_2), \end{aligned} \tag{4.7}$$

where

$$g_1(x_1, x_2) = -c_{11}x_1^2 - c_{12}x_1x_2,$$
$$g_2(x_1, x_2) = c_{21}x_1x_2 - c_{22}x_2^2.$$

Notice that since $c_{21}N_1^* \geqq 0$, but $\not\equiv 0$, we have that

$$[c_{21}N_1^*] > 0. \tag{4.8}$$

Define

$$p_2(t) = b_2(t) - \lambda, \qquad \lambda = [b_2]. \tag{4.9}$$

Then $b_2 = p_2 + \lambda$ and $[p_2] = 0$. With these new symbols (4.7) becomes

$$\begin{aligned} x_1' &= (b_1 - 2c_{11}N_1^*)x_1 - c_{12}N_1^*x_2 + g_1(x_1, x_2), \\ x_2' &= (c_{21}N_1^* - p_2)x_2 - \lambda x_2 + g_2(x_1, x_2). \end{aligned} \tag{4.10}$$

The linear homogeneous system

$$y_1' = (b_1 - 2c_{11}N_1^*)y_1 - c_{12}N_1^*y_2,$$
$$y_2' = (c_{21}N_1^* - p_2)y_2$$

satisfies the hypotheses of part (a) of Lemma 1; this is because by (4.8), (4.9) and (4.1) we have

$$[a_{22}] = [c_{21}N_1^* - p_2] = [c_{21}N_1^*] \neq 0,$$
$$[a_{11}] = [b_1 - 2c_{11}N_1^*] = -[b_1] \neq 0.$$

Consequently we have available the compact linear operator $L: B \times B \to B \times B$ given by (4.6). Using L we can equivalently write system (4.10) as the operator equation

$$(x_1, x_2) = \lambda L^*(x_1, x_2) + G(x_1, x_2), \tag{4.11}$$

where

$$L^*(x_1, x_2) = (L_1(c_{12}N_1^*L_2x_2), -L_2x_2),$$
$$G(x_1, x_2) = (L_1(-c_{12}N_1^*L_2g_2(x_1, x_2) + g_1(x_1, x_2)), L_2g_2(x_1, x_2)).$$

Here $L^*: B \times B \to B \times B$ is linear and compact and $G: B \times B \to B \times B$ is continuous and compact (since L_1 and L_2 are compact) and satisfies $G = o(|(x_1, x_2)|_0)$ near

(0, 0). This operator equation (4.11) is consequently of the type to which standard bifurcation theorems and techniques apply. A nontrivial solution $(x_1, x_2) \neq (0, 0)$ of (4.11) in $B \times B$ for some $\lambda \in R$ (R is the set of reals) yields a solution $(N_1, N_2) = (x_1 + N_1^*, x_2)$ of the predator-prey system (1.1) for $[b_2] = \lambda$. Solutions $(N_1, N_2) \neq (N_1^*, 0)$ will be called nontrivial solutions of (1.1).

To prove part (a) of Theorem 2 we apply well-known local bifurcation techniques to (4.11). As is well known [5], bifurcation can occur only at the nontrivial solutions of the linearized problem

$$(4.12) \qquad (y_1, y_2) = \lambda L^*(y_1, y_2), \qquad (y_1, y_2) \neq (0, 0), \qquad \lambda \in R.$$

If $(y_1, y_2) \in B \times B$ is a solution of (4.12) for some $\lambda \in R$, then by the very manner in which L^* was defined, (y_1, y_2) solves the system

$$(4.13) \qquad \begin{aligned} y_1' &= (b_1 - 2c_{11}N_1^*)y_1 - c_{12}N_1^*y_2, \\ y_2' &= (c_{21}N_1^* - p_2 - \lambda)y_2, \end{aligned}$$

and conversely. Using Lemma 1 above we see that (4.13) and hence (4.12) has a nontrivial solution in $B \times B$ if and only if $\lambda = \lambda^*$ where

$$(4.14) \qquad \lambda^* = [c_{21}N_1^*].$$

If $\lambda = \lambda^*$ then, by part (b) of Lemma 1, (4.12) has one independent solution in $B \times B$. A well-known result [5], [7] implies that bifurcation in fact occurs at this simple eigenvalue; hence there exists a continuum $\mathscr{C} = \{(\lambda; x_1, x_2)\} \subseteq R \times B \times B$ of nontrivial solutions of (4.12) such that the closure $\bar{\mathscr{C}}$ of $\mathscr{C}$ contains $(\lambda^*; 0, 0)$. This continuum gives rise to a continuum $C = \{(\lambda; N_1, N_2)\} \subseteq R \times B \times B$ of nontrivial solutions of (1.1) whose closure $\bar{C}$ contains the bifurcation point $(\lambda^*; N_1^*, 0)$.

To see that solutions in C correspond to solutions (N_1, N_2) of (1.1) with all the properties described in Theorem 2, we investigate the nature of the continuum $\mathscr{C}$ near the bifurcation point $(\lambda^*; 0, 0)$ by expanding λ and (x_1, x_2) in Lyapunov–Schmidt series [8]:

$$\begin{aligned} \lambda &= \lambda^* + \lambda_1 \varepsilon + \cdots, \\ x_i &= x_{i1}\varepsilon + x_{i2}\varepsilon^2 + \cdots, \qquad i = 1 \text{ and } 2, \end{aligned}$$

for $x_{ij} \in B$ where ε is a small parameter. If we substitute these series into the differential system (4.10) and equate coefficients of ε and ε^2 we find that

$$(4.15) \qquad \begin{aligned} x_{11}' &= (b_1 - 2c_{11}N_1^*)x_{11} - c_{12}N_1^*x_{21}, \\ x_{21}' &= (c_{21}N_1^* - p_2 - \lambda^*)x_{21} \end{aligned}$$

and

$$(4.16) \qquad \begin{aligned} x_{12}' &= (b_1 - 2c_{11}N_1^*)x_{12} - c_{12}N_1^*x_{22} - c_{11}x_{11}^2 - c_{12}x_{11}x_{21}, \\ x_{22}' &= (c_{21}N_1^* - p_2 - \lambda^*)x_{22} - \lambda_1 x_{21} + c_{21}x_{11}x_{21} - c_{22}x_{21}^2 \end{aligned}$$

respectively. Thus, $(x_{11}, x_{21}) \in B \times B$ must be a solution of (4.12). We choose the specific solution satisfying the initial conditions $x_{21}(0) = 1$. Then

$$x_{21} = \exp \int_0^t (c_{21}N_1^* - p_2 - \lambda^*)\, ds > 0.$$

Moreover $x_{11} < 0$ for all t. (This is because $[b_1 - 2c_{11}N_1^*] < 0$ implies that the Green's function for the first equation in (4.13) is positive.) Using Lemma 2 on the second equation of (4.16) we find that

$$\lambda_1 = [c_{21}x_{11} - c_{22}x_{21}] < 0.$$

Thus we see (also refer to [7]) that near the bifurcation point $(\lambda^*; 0, 0)$ (say, for $|\lambda - \lambda^*| < b_0$) the continuum C has two (subcontinua) branches corresponding to $\varepsilon > 0$, $\varepsilon < 0$ respectively:

$$\mathscr{C}^+ = \{(\lambda; x_1, x_2) \in \mathscr{C} : \lambda^* - b_0 \leqq \lambda < \lambda^*, x_1 < 0, x_2 > 0\},$$

$$\mathscr{C}^- = \{(\lambda; x_1, x_2) \in \mathscr{C} : \lambda^* < \lambda \leqq \lambda^* + b_0, x_1 > 0, x_2 < 0\}.$$

It is the solutions on C^+ which prove the theorem, part (a), since $\lambda^* - b_0 \leqq \lambda < \lambda^*$ is equivalent to $[c_{21}N_1^*] - b_0 \leqq [b_2] < [c_{21}N_1^*]$. We have left only to show that $N_1 = x_1 + N_1^* > 0$ for all t. This is easy, for if b_0 is small, then N_1 is near N_1^* in the sup norm of B; thus since $N_1^* > 0$ is bounded away from zero, so is N_1.

(b) We prove the second part of Theorem 2 by applying a global alternative of Rabinowitz [7, Thm. 4.1] from which follows the existence of a continuum $C_\infty^+ \subset R \times B \times B$ of nontrivial solutions which locally coincides with C^+ and which either is unbounded in $R \times B \times B$ or bifurcates from another trivial solution $(\lambda^{**}; N_1^*, 0)$ for $\lambda^{**} \neq \lambda^*$. However, since λ^{**} must then be a characteristic value of L (i.e., there must exist a nontrivial solution of (4.12) for $\lambda = \lambda^{**}$) and since it follows from Lemma 1 applied to (4.13) that λ^* is the only possible such value of λ, we conclude that the second alternative is impossible and that as a result the continuum C_∞^+ is unbounded. This implies that if $\Lambda \subseteq R$ is the projection of C^+ onto R and if $X \subseteq B \times B$ is the projection of C^+ onto $B \times B$, then at least one of these two continua must be unbounded. Now we establish several facts about C_∞^+ and Λ and about solutions of (1.1).

(i) *If* (N_1, N_2) *solves* (1.1), *then both* N_i *are of one* (*but not necessarily of the same*) *sign*. This is because $N_1(t) = N_1(0) \exp(\int_0^t g(s)\, ds)$ where $g(s) = b_1 - c_{11}N_1 - c_{12}N_2$. A similar argument works for N_2.

(ii) *If* $(\lambda; N_1, N_2) \in C_\infty^+$, *then* $N_2 > 0$ *for all* t. Since $N_2 > 0$ for solutions near the bifurcation point $(\lambda^*; N_1^*, 0)$ (where C_∞^+ coincides with C^+) and since C_∞^+ is a continuum we have by (i) that if $N_2 < 0$ for some solution at some time then there would exist a solution of C_∞^+ for which $N_2 \equiv 0$. For this solution we would have, by Theorem 1, that $N_1 \equiv N_1^*$ in contradiction to the fact that C_∞^+ contains no such trivial solutions.

(iii) *If* $(\lambda; N_1, N_2) \in C^+$ *with* $\lambda \in [0, \lambda^*)$, *then* $N_1 > 0$ *for all* t. Suppose N_1 were negative for all t. Then, since C_∞^+ is a continuum, there would exist a $\lambda' \in (\lambda, \lambda^*)$ for which $N_1 \equiv 0$ (recall that $N_1 > 0$ is near the bifurcation point). For this solution we find that

$$N_2' = N_2(-b_2 - c_{22}N_2)$$

which, by (ii) and the same argument used to deduce (4.1), implies the contradiction

$$0 < [c_{22}N_2] = -[b_2] = -\lambda' \leqq 0.$$

(iv) *If for some* $(\lambda; N_1, N_2) \in C_\infty^+$ *we have* $N_1 < 0$, *then* $[0, \lambda^*) \subseteq \Lambda$. The proof of (iii) shows that $\lambda < 0$ and hence that Λ contains negative reals. Since Λ is a continuum (interval) whose closure contains λ^* the result follows.

(v) *If* $(\lambda; N_1, N_2) \in C_\infty^+$ *and* $N_1 > 0$ *then for some constants* $c, d > 0$ *independent of* $(\lambda; N_1, N_2)$ *the estimate* $|(N_1, N_2)|_0 \leqq c\lambda + d$ *holds.* Let t' be chosen so that $N_1(t') = |N_1|_0$ and $N_1'(t') = 0$. From the first equation of (1.1) we have that for $t = t'$,

$$b_1(t') - c_{11}(t')N_1(t') - c_{12}(t')N_2(t') = 0,$$

and hence (since $N_2 > 0$ by (ii)) we have

$$|N_1|_0 = N_1(t') \leqq |b_1|_0/\alpha, \tag{4.17}$$

where α is a constant for which $c_{11}(t) \geqq \alpha > 0$ for all t.

For N_2 we do something very similar: let t' be such that $N_2(t') = |N_2|_0$ and $N_2'(t') = 0$. From the second equation in (1.1) we have that

$$-N_2(t') = (b_2(t') - c_{21}(t')N_1(t'))/c_{22}(t').$$

If β is such that $c_{22}(t) \geqq \beta > 0$ for all t, this easily yields the estimate

$$|N_2|_0 \leqq (|b_2|_0 + |c_{21}|_0 |N_1|_0)/\beta.$$

Since $|(N_1, N_2)|_0 = |N_1|_0 + |N_2|_0$ we find from this estimate together with (4.17) the desired estimate with

$$c = \beta^{-1} \quad \text{and} \quad d = |b_1|_0 \alpha^{-1} + (|p_2|_0 + |c_{21}|_0 |b_1|_0 \alpha^{-1})\beta^{-1}.$$

(vi) *If for every* $(\lambda; N_1, N_2) \in C_\infty^+$ *it is true that* $N_1 > 0$ *for all* t, *then* Λ *is an unbounded interval, bounded above.* By (v), if Λ were bounded, then X would also be bounded in contradiction to the above stated fact that at least one of these is unbounded. Suppose now that Λ were unbounded above so that we can find a solution $(\lambda; N_1, N_2) \in C_\infty^+$ with $N_1 > 0$, $N_2 > 0$ and

$$\lambda > |c_{21}|_0 |b_1|_0 \alpha^{-1} + |p_2|_0 + 1.$$

From the second equation in (1.1) and from the estimate (4.17), we find that $N_2' < -N_2$ which contradicts $N_2 \in B$.

We are now able to prove that $[0, \lambda^*) \subseteq \Lambda$ as required in part (b) of Theorem 2. There are two cases: either $N_1 > 0$ for all solutions on C_∞^+ or $N_1 < 0$ for some solution on C_∞^+. In the first case, (vi) implies the desired set inclusion while (iv) yields the same result in the second case.

At this point we have proved that for any $\lambda = [b_2] \in [0, \lambda^*)$, there exists a solution $(N_1, N_2) \in B \times B$ of (1.1) satisfying $N_1 > 0$ and $N_2 > 0$. All that remains to prove of part (b) of Theorem 2 is that $N_1 < N_1^*$ for all t and all such solutions.

Consider the subcontinuum of C_∞^+ obtained by restricting λ to $[0, \lambda^*)$. Near the bifurcation point λ^* we know (part (a)) that $N_1 < N_1^*$ for all t. Suppose that this inequality fails to hold for some $\lambda \in [0, \lambda^*)$. Then since C_∞^+ is a continuum, we could find a $\lambda' \in [0, \lambda^*)$ such that the estimates $0 < N_1 \leqq N_1^*$, $N_2 > 0$ hold for all t and such that $N_1(t') = N_1^*(t')$ for some t'. The first equation in (1.1) implies for

$t = t'$ that

$$N_1' = N_1(b_1 - c_{11}N_1) - c_{12}N_1N_2 = N_1^{*\prime} - c_{12}N_1N_2 < N_1^{*\prime}.$$

Thus the difference $N_1 - N_1^*$ vanishes and has a strictly negative derivative at $t = t'$. This implies the contradiction $N_1 < N_1^*$ for $t < t'$ but near t'. □

To prove part (b) of Theorem 2 we use an estimate $|(N_1, N_2)|_0 \leqq \lambda c + d$ where $c_{22} \geqq \beta > 0$. The numerical results discussed in § 3 above seem to indicate that such an estimate may not be valid if $c_{22} \equiv 0$.

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