Stable Limit Cycles of Time Dependent Multispecies Interactions

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ABSTRACT

The standard differential system which models the interaction of n species is considered under the assumption that the coefficients (i e , the net birth rates, the self-inhibition coefficients and the interaction coefficients) are all periodic functions of time Conditions are given which guarantee the existence of a stable periodic limit cycle The basic result implies, roughly, that if an $n-1$ species subcommunity with a stable periodic limit cycle exists and if the interactions of the system are sufficiently weak, then the addition of the nth species will result in a stable periodic limit cycle provided its average net birth rate is larger than and close to a specified critical value, on the other hand, if this average is less than but close to the critical value, then the nth species will not survive and the system will stabilize on the limit cycle of the subcommunity Starting with basic results concerning periodic solutions of the one species case, we apply our basic result in a "bootstrapping" manner to derive a corollary which, roughly speaking, states that if at least one species has a positive average net birth rate and if the interactions are sufficiently weak, then a multispecies community will have a stable, positive limit cycle provided that the average net birth rates of the remaining species lie in certain specified ranges

1 INTRODUCTION

Consider the well-known system of differential equations

$$N_i' = N_i\left(b_i + \sum_{j=1}^{n} a_{ij}N_j\right), \qquad 1 \leqslant i \leqslant n, \tag{1 1}$$

which serves as a model for the interaction of n species whose sizes (e g , numbers, biomasses, etc) $N_i = N_i(t)$ are functions of time t Here b_i is the inherent net birth rate of the ith species in the absence of any interaction with the other species (as accounted for by the interaction coefficients a_{ij}, $i \neq j$) and any self-inhibition (as accounted for by the coefficients a_{ii}, which are assumed to be nonpositive) Our purpose here is to consider this model under the assumption that the coefficients $b_i = b_i(t)$, $a_{ij} = a_{ij}(t)$ are periodic functions of time, this assumption seems reasonable in consideration of the obvious periodic fluctuations that such ecological systems would naturally be subjected (e g , such seasonal effects as weather, temperature, food supplies, hunting and mating habits, etc) Our main aim is to give conditions under which a stable, periodic positive solution $N_i > 0$ of (1 1) exists The approach taken is the same as that used by the author in [3] in his study of time dependent predator-prey systems [a special case of (1 1) when $n = 2$] namely, positive periodic solutions of (1 1) are sought which bifurcate from some such solution for some subcommunity consisting of $n-1$ species [which we take, without loss of generality, to be the first $n-1$ species $N_1, \ldots, N_{n-1}$ in (1 1)] The free parameter (denoted by μ) is taken to be the time average of the net birth rate of the remaining species The results of this approach are contained in Theorem 1 below, which, roughly speaking, concludes that a positive periodic solution of (1 1) exists for certain values of μ provided the interactions of the subcommunity are sufficiently weak Stability considerations are taken up in Theorem 2, where, under the assumption that the full system (1 1) is weakly interacting, the bifurcation described in Theorem 1 is shown to exhibit an exchange of stability This means, roughly speaking, that if μ is larger than but close to a certain critical value μ^*, then the periodic solution given by Theorem 1 is (locally) uniformly asymptotically stable, and that, on the other hand, if this average μ is less than but close to μ^*, then the periodic solution of the subcommunity is (locally) uniformly asymptotically stable as a solution of (1 1) This latter case means that the nth species will become extinct, while the remaining species will tend to the periodic solution of the subcommunity It also follows from Theorem 1 below that no positive periodic solution of (1 1) for which the size of the nth species is small exists except for μ close to μ^*

Because the results in Theorem 1 rely on the existence of a positive, periodic solution of a subcommunity, certain results for the case of $n = 1$ species are of interest In [2] the time dependent logistic model

$$N_1' = N_1 \{ b_1(t) + a_{11}(t) N_1 \}$$

is shown to have a positive, globally uniformly asymptotically stable periodic solution if b_1 and a_{11} are periodic, a_{11} is negative, and the average of b_1 is positive Using this result, we apply Theorem 1 to (1 1) for $n = 2$ and obtain positive limit cycles for two species interactions These limit cycles are then used in Theorem 1 to obtain positive limit cycles for $n = 3$ species, which in turn are used for $n = 4$ species, and so forth This repetitive argument is used to derive the Corollary in Sec 2 below, which (roughly) says that (1 1) has a positive stable limit cycle if the system is weakly interacting, if at least one species has a positive average net birth rate, and if the remaining average net birth rates lie in certain intervals (These intervals are described in terms of certain weighted averages of the periodic limit cycles of the subcommunities)

2 RESULTS

Let P denote the Banach space of continuous functions of period p under the norm $|N_i|_0 = \max_{-\infty<t<+\infty}|N_i(t)|$ Throughout this paper the period p will be arbitrary, but fixed Let R denote the set of all real numbers, and let P_n denote the n-fold Cartesian product of P with itself By a *positive solution* $N=(N_i)$ of (1 1) in P_n we mean differentiable functions $N_i \in P$ satisfying (1 1) such that $N_i > 0$ for all $t \in R$ and $1 \leqslant i \leqslant n$ It will be convenient for us to separate out the nth component of the vector N, which we do by means of the notation $N=(N_i, N_n)$, where we tacitly assume $1 \leqslant i \leqslant n-1$ We will refer to the subsystem

$$N_i' = N_i\left(b_i + \sum_{j=1}^{n-1} a_{ij}N_j\right), \qquad 1 \leqslant i \leqslant n-1, \tag{2 1}$$

as the *reduced system* (or as the *subcommunity*) of (1 1) If N_i, $1 \leqslant i \leqslant n-1$, solve the reduced system, then clearly $N=(N_i, 0)$ solves (1 1) and vice versa, so that we may simply refer to solutions of (1 1) with $N_n \equiv 0$ as solutions of the reduced system Let

$$[b_i] = p^{-1}\int_0^p b_i(t)\,dt$$

denote the average of $b_i(t)$, and write

$$b_n(t) = [b_n] + p_n(t), \qquad [p_n] = 0$$

By a *continuum* $C \subseteq R \times P_n$ is meant a set which cannot be written as the union of two disjoint, nonempty open sets By a *positive continuum* we will mean a continuum such that $(\mu, N) \in C$ implies $N_i > 0$ for all $t \in R$ and all $1 \leqslant i \leqslant n$

We will need the following hypotheses

(H1) *$b_i, a_{ij} \in P$ with $a_{ii}(t) \leqslant -m < 0$ for all $t \in R$ and $1 \leqslant i \leqslant n$ and for some constant $m > 0$,*

(H2) *the reduced system* (2 1) *has a solution $N^* = (N_i^*, 0) \in P_n$ with $N_i^* > 0$ for all $t \in R$ and $1 \leqslant i \leqslant n-1$*

DEFINITION

For the $n \times n$ system (1 1) with $n \geqslant 2$ let

$$\alpha_n = \max\{|a_{ij}|_0 \quad 1 \leqslant i,j \leqslant n, i \neq j\}$$

Let $\alpha_1 = 0$

The constant α_n very crudely measures the strength of the interactions amongst the species in system (1 1) Systems with α_n small (in some sense) will be called *weakly interacting systems* By α_{n-1} we mean the corresponding constant for the reduced system (2 1) Our basic result is contained in the following theorem

THEOREM 1

Assume that (H1) *holds and that* $b_i(t)$, $1 \leqslant i \leqslant n-1$, *and* $p_n(t)$ *are given functions in* P *with* $[p_n] = 0$

(a) *There exists a constant* $\varepsilon > 0$ *(depending only on* m *and* $|b_i|_0$ *for* $1 \leqslant i \leqslant n-1$) *such that if* (H2) *holds for* $\alpha_{n-1} < \varepsilon$, *then there exists a positive continuum* $C \subset R \times P_n$ *whose closure contains* (μ^*, N^*),

$$\mu^* = -\sum_{j=1}^{n-1} [a_{nj} N_j^*],$$

with the property that $(\mu, N) \in C$ *implies* $N \in P_n$ *is a positive solution of* (1 1) *with* $[b_n] = \mu$ [*i e* , $b_n(t) = \mu + p_n(t)$]

(b) *If in addition* $|a_{nj}|_0 < \varepsilon$, $1 \leqslant j \leqslant n-1$, *then for* $(\mu, N) \in C$ *it follows that* $\mu > \mu^*$

(c) *Assume further that* $|a_{in}(t)| \neq 0$ *for all* $t \in R$ *and* $1 \leqslant i \leqslant n-1$ *Then for* $(\mu, N) \in C$ *we have*

$$\operatorname{sgn}(N_i - N_i^*) = \operatorname{sgn} a_{in}, \qquad 1 \leqslant i \leqslant n-1, \quad t \in R,$$

where $\operatorname{sgn} r = r/|r|$ *for* $0 \neq r \in R$

Part (c) of this theorem states that the periodic solutions of (1 1) given in part (a) have the property that each of the first $n-1$ species is greater or smaller in size (for each t) than it would be in the absence of the nth species, depending on whether the nth species respectively increases or inhibits its growth rate (i e , whether the nth species serves as a prey or a predator for this species)

Note that for the special case of two species ($n = 2$) the weak interaction assumption $0 = \alpha_1 < \varepsilon$ is automatically fulfilled in part (a) This special case for predator-prey interactions ($a_{12} < 0$, $a_{21} > 0$) is studied in detail in [3]

For the weak interaction systems considered in Theorem 1 we have the following stability results

THEOREM 2

(a) *Suppose* (H1) *holds There exists a constant* $\varepsilon > 0$ *such that if* $N \in P_n$ *is a positive solution of* (1 1) *for* $\alpha_n < \varepsilon$, *then* N *is* (*locally*) *uniformly asymptotically stable*

(b) *Suppose* (H1) *and* (H2) *hold, and suppose* $[b_n] < \mu^*$ *Then for* α_{n-1} *sufficiently small* $N^* = (N_i^*, 0) \in P_n$ *is* (*locally*) *uniformly asymptotically stable as a solution of* (1 1)

Considering hypothesis (H2), we may view Theorems 1 and 2 as giving conditions under which a species N_n may be added to a weakly interacting community of $n-1$ species $N_1, \ldots, N_{n-1}$, which possess a stable periodic limit cycle, and result in a community of n species with a stable periodic limit cycle The conditions are that all interactions be sufficiently weak and that the average net birth rate of the added species be appropriate Using this result together with the results in [2] for $n=1$, we may derive a corollary concerning stable limit cycles of (1 1) in terms of the average birth rates of all species This is done as follows from [2] we have the existence of a positive periodic solutions $N_1^* \in P$ of

$$N_1' = N_1 (b_1 + a_{11} N_1)$$

provided a_{11} satisfies (H1) and $[b_1] > 0$ Applying Theorems 1 and 2, we deduce that any system of $n=2$ species formed by the interaction of a second species has a stable limit cycle $N_2^* \in P_2$ provided the interaction is weak enough and $[b_2]$ is large enough, specifically, $\mu_2^* < [b_2] < \mu_2^{**}$ for some $\mu_2^{**} > \mu_2^* = -[a_{21} N_1^*]$, $\mu_2^{**} \leqslant +\infty$ Using N_2^* to fulfill (H2), we may again apply Theorems 1 and 2 to (1 1) for $n=3$, and so forth Clearly by repeating this argument $n-1$ times we will have proved the following result

COROLLARY

Suppose b_i, a_{ij} *satisfy* (H1) *and suppose* $[b_1] > 0$ *There exists a constant* $\varepsilon > 0$ *and* $n-1$ *intervals* $I_i = (\mu_i^*, \mu_i^{**})$, $\mu_i^* < \mu_i^{**} \leqslant +\infty$, $2 \leqslant i \leqslant n$, *such that if* $\alpha_n < \varepsilon$ *then* (1 1) *has a* (*locally*) *uniformly asymptotically stable, positive periodic solution provided* $[b_i] \in I_i$ *for all* $2 \leqslant i \leqslant n$

In this corollary, of course, we have that

$$\mu_i^* = -\sum_{j=1}^{i-1} [a_{ij} N_{ij}^*], \qquad 2 \leqslant i \leqslant n,$$

where $N_i = (N_{ij}) \in P_i$ is the positive solution of the subcommunity obtained by eliminating the species $N_{i+1}, \ldots, N_n$ [i e, the reduced system obtained by setting $N_{i+1} \equiv \cdots \equiv N_n \equiv 0$ in (1 1)]

REMARK

The continuum C in Theorem 1 consists of elements $(\mu, N) \in R \times P_n$ near the bifurcation point (μ^*, N^*) (cf the proof in Sec 3 below) Actually from the results in [5] we find that C has a global extension $C_\infty \supseteq C$ which is an unbounded continuum in $R \times P_n$ Moreover, from the *a priori* bounds in Lemma 5 below, we can assert that the projection of C_∞ onto R is unbounded and contains μ^* in its closure We cannot, however, be assured in general that all the periodic solutions of (1 1) corresponding to elements on C_∞ are positive solutions In fact the results in [3] for predator-prey interactions (especially the numerical results) indicate that this is not the case for this particular type of system, in this case positive periodic solutions exist for $\mu^* < \mu < \mu^{**} < +\infty$ and do not exist for $\mu > \mu^{**}$ for a certain constant $\mu^{**} < +\infty$ (although nonpositive solutions do exist for $\mu > \mu^{**}$) On the other hand, the results in [2] for the one species case $n = 1$ show that in this special case C_∞ contains all positive solutions and that (1 1) does have a positive, periodic solution for all $\mu > \mu^* = 0$

3 PROOFS

We will prove Theorem 1 by reformulating the problem of solving (1 1) in P_n as an operator equation suitable for the application of certain standard techniques from bifurcation theory To do this we will need the preliminary facts which are stated in the following list of lemmas

LEMMA 1

(a) *Consider the scalar* ($n = 1$) *differential equation* $z' = a(t)z$ *for* $a \in P$ *In order for a nontrivial solution* $z \in P$ *to exist it is necessary and sufficient that* $[a] = 0$

(b) *If* $[a] \neq 0$, *then the nonhomogeneous scalar equation* $z' = a(t)z + f(t)$, $a \in P$, *has for each* $f \in P$ *a unique solution* $z \in P$, *and the operator* $Lf = z$ *is a compact linear operator from* P *into* P

LEMMA 2

(a) *Consider the* $(n-1) \times (n-1)$ *linear system*

$$z_i' = \sum_{j=1}^{n-1} c_{ij}(t) z_j, \qquad 1 \leqslant i \leqslant n-1, \tag{3 1}$$

where $c_{ij} \in P$ *and* $[c_{ii}] \neq 0$, $1 \leqslant i \leqslant n-1$ *There exists a constant* $\varepsilon > 0$ *such that if* $|c_{ij}|_0 < \varepsilon$ *for all* $1 \leqslant i,j \leqslant n-1$, $i \neq j$, *then* (3 1) *has no nontrivial solution in* P_{n-1}

(b) *Hence the nonhomogeneous system*

$$z_i' = \sum_{j=1}^{n-1} c_{ij}(t) z_j + f_i, \qquad 1 \leqslant i \leqslant n-1,$$

has, for each $f_i \in P$, *a unique periodic solution* $z \in P_{n-1}$ *Moreover, the linear operator* $Lf = z$ *is compact from* P_{n-1} *into* P_{n-1}

Proofs Parts (b) of both lemmas are well-known results [4, p 223] Lemma 1(a) follows easily from the fact that an antiderivative of a is periodic if and only if $[a]=0$ To prove Lemma 2(a) we observe that each scalar equation $z_i' = c_{ii} z_i$, by assumption, satisfies the hypotheses of Lemma 1 Thus, the system (3 1) can be reformulated as the operator equation $z = Lz$, where $Lz = \left(L_i(\sum_{j \neq i} c_{ij} z_j)\right)$ and L_i is the compact linear operator guaranteed by Lemma 1(b) Clearly, for ϵ small enough the operator L is a contraction on P_n, and consequently the only solution of $z = Lz$ in P_n is $z=0$ ■

LEMMA 3

Suppose $N \in P_n$ *is a positive solution of* (1 1) *Then*

$$[b_i] + \sum_{j=1}^{n} \left[a_{ij} N_j \right] = 0$$

Proof Functions in P_n are bounded, and hence

$$\lim_{t \to +\infty} t^{-1} \int_0^t \frac{N_i'}{N_i} dt = \lim_{t \to +\infty} t^{-1} \log \frac{N_i(t)}{N_i(0)} = 0$$

From (1 1) we have on the other hand that

$$\lim_{t \to +\infty} t^{-1} \int_0^t \frac{N_i'}{N_i} dt = [b_i] + \sum_{j=1}^{n} \left[a_{ij} N_j \right] \qquad ■$$

The next lemma is given in preparation for the *a priori* estimate established in Lemma 5

LEMMA 4

The algebraic inequalities

$$0 \leqslant \xi_i \leqslant A + B \sum_{j \neq i}^{n} \xi_j, \qquad B \leqslant \frac{1}{6(n-1)}, \qquad 1 \leqslant i \leqslant n, \quad n \geqslant 2$$

for constants $A, B > 0$ *imply* $0 \leqslant \xi_i \leqslant 2A$, $1 \leqslant i \leqslant n$

Proof (by induction) For $n=2$ we have

$$0 \leqslant \xi_i \leqslant A + B\xi_j, \qquad i \neq j, \quad 0 < B \leqslant \tfrac{1}{6},$$

thus, $0 \leqslant \xi_i \leqslant A + B(A + B\xi_i)$, or

$$0 \leqslant \xi_i \leqslant A(1+B)(1-B^2)^{-1} = A(1-B)^{-1} < 2A$$

for $i=1$ or 2

Suppose the lemma is true for $n=k$ and consider the case $n=k+1$ We have then that

$$0 \leqslant \xi_i \leqslant A + B \sum_{j \neq i}^{k+1} \xi_j, \qquad 0 < B \leqslant \frac{1}{6k} \tag{3 2}$$

Let i be arbitrary but fixed, $2 \leqslant i \leqslant k+1$, and reconsider these inequalities in the form

$$0 \leqslant \xi_j \leqslant (A + B\xi_i) + B \sum_{m \neq j\ i}^{k+1} \xi_m$$

for all $2 \leqslant j \leqslant k+1, j \neq i$ Since these inequalities are k in number, we may apply the induction hypothesis with $A + B\xi_i$ replacing A, note that $B \leqslant 1/6k$ implies $B \leqslant 1/6(k-1)$ Thus, we conclude that

$$0 \leqslant \xi_j \leqslant 2(A + B\xi_i), \qquad j \neq i$$

The inequalities (3 2) now in turn imply

$$0 \leqslant \xi_i \leqslant A + 2kB(A + B\xi_i)$$

or

$$0 \leqslant \xi_i \leqslant A(1+2kB)(1-2kB^2)^{-1}$$

which, because $0 < B \leqslant 1/6k$ implies $(1+2kB)(1-B)^{-1} \leqslant 2$ and because i was arbitrary, immediately yields the assertion of the lemma for $n=k+1$ ■

LEMMA 5

Let $N^* = (N_i^*) \in P_n$ be a positive solution of the reduced system (2 1) *with $\alpha_{n-1} \leqslant m/6(n-2)$ [where m is as in* (H1)] *Then*

$$|N_i^*|_0 \leqslant 2Bm^{-1}, \tag{3 3}$$

where $B = \max\{|b_i|_0 \ \ 1 \leqslant i \leqslant n-1\}$

Proof Let i be an arbitrary but fixed integer such that $1 \leqslant i \leqslant n-1$ Choose a t_i such that $N_i^*(t_i) = |N_i^*|_0$, $N_i^{*\prime}(t_i) = 0$, $1 \leqslant i \leqslant n-1$ From (2 1) we have that

$$b_i(t_i) + \sum_{j=1}^{n-1} a_{ij}(t_i) N_j^*(t_i) = 0$$

for each i Thus, for each i

$$|a_{ii}(t_i) N_i^*(t_i)| \leqslant B + \alpha_{n-1} \sum_{j \neq i}^{n-1} |N_j^*|_0,$$

and (H1) implies

$$|N_i^*|_0 = N_i^*(t_i) \leqslant Bm^{-1} + \alpha_{n-1} m^{-1} \sum_{j \neq 1}^{n-1} |N_j^*|_0$$

Lemma 4 now implies (3 3) ■

Proof of Theorem 1

(a) We begin by making the change of variables

$$x_i = N_i - N_i^*, \qquad 1 \leqslant i \leqslant n-1, \tag{3 4}$$

in (1 1), where $(N_i^*) \in P_{n-1}$ is the solution of the reduced system (2 1) guaranteed by (H2) This results in the system

$$x_i' = x_i \left(b_i + \sum_{j=1}^{n-1} a_{ij} N_j^* \right) + N_i^* \left(\sum_{j=1}^{n-1} a_{ij} x_j + a_{in} N_n \right) + f_i, \qquad 1 \leqslant i \leqslant n-1, \tag{3 5a}$$

$$N_n' = N_n \left(b_n + \sum_{j=1}^{n-1} a_{nj} N_j^* \right) + f_n \tag{3 5b}$$

for the unknowns (x_i, N_n), where

$$f_i = f_i(x_i, N_n) = x_i \left(\sum_{j=1}^{n-1} a_{ij} x_j + a_{in} N_n \right), \qquad 1 \leqslant i \leqslant n-1,$$

$$f_n = f_n(x_i, N_n) = N_n \left(\sum_{j=1}^{n-1} a_{nj} x_j + a_{nn} N_n \right)$$

Note that

$$f_i = o(|(x_i, N_n)|_0), \qquad 1 \leqslant i \leqslant n$$

Now let θ be any constant for which

$$\theta \neq -\sum_{j=1}^{n-1} [a_{nj} N_j^*],$$

and set $\lambda = [b_n] - \theta$, so that we may substitute $b_n = \lambda + \theta + p_n$ into (3 5b) and obtain

$$N_n' = N_n \left(\theta + p_n + \sum_{j=1}^{n-1} a_{nj} N_j^* \right) + \lambda N_n + f_n \tag{3 5b'}$$

Since

$$\left[\theta + p_n + \sum_{j=1}^{n-1} a_{nj} N_j^* \right] = \theta + \sum_{j=1}^{n-1} [a_{nj} N_j^*] \neq 0,$$

we see that we may in turn rewrite (3 5b′) in the operator form

$$N_n = L_1(\lambda N_n + f_n), \qquad N_n \in P, \tag{3 6}$$

where L_1 is the compact linear operator guaranteed by Lemma 1(b) Substitution of (3 6) into (3 5a) yields the $(n-1)\times(n-1)$ system

$$x_i' = x_i \left(b_i + \sum_{j=1}^{n-1} a_{ij} N_j^* \right) + N_i^* \left(\sum_{j=1}^{n-1} a_{ij} x_j \right) + \lambda N_i^* a_{in} L_1 N_n + g_i, \tag{3 7}$$

where

$$g_i = g_i(\lambda, (x_i, N_n)) = N_i^* a_{in} L_1 f_n + f_i(x_i, \lambda L_1 N_n + L_1 f_n) = o(|(x_i, N_n)|_0)$$

uniformly in λ (on compact subintervals of R) The related linear system

$$z_i' = z_i \left(b_i + \sum_{j=1}^{n-1} a_{ij} N_j^* \right) + N_i^* \left(\sum_{j=1}^{n-1} a_{ij} z_j \right), \qquad 1 \leqslant i \leqslant n-1,$$

has the form (3 1) with diagonal coefficient

$$c_{ii} = b_i + \sum_{j=1}^{n-1} a_{ij} N_j^* + a_{ii} N_i^*,$$

thus by Lemma 3 applied to the reduced system (2 1) [instead of (1 1)] we find that

$$[c_{ii}] = [a_{ii} N_i^*] < 0, \qquad 1 \leqslant i \leqslant n-1$$

We now make use of Lemma 2(a) in order to conclude that this linear system has no nontrivial solution in P_{n-1} if each $|N_i^* a_{ij}|_0$, $1 \leqslant i,j \leqslant n-1$, $i \neq j$, is sufficiently small Making use of the *a priori* bound derived in Lemma 5, we can guarantee this condition by assuming $\alpha_{n-1} \leqslant \varepsilon$ for some small $\varepsilon > 0$ Lemma 2 now implies that (3 7) can be reformulated as the operator equation

$$x = L\{\lambda(N_i^* a_{in} L_1 N_n) + g(\lambda, x, N_n)\}, \tag{3 8}$$

where L is a compact linear operator from P_{n-1} into P_{n-1}, and where $x = (x_i)$ and $g = (g_i)$ for $1 \leqslant i \leqslant n-1$ The two operator equations (3 6) and (3 8) together constitute an equivalent operator formulation of (3 5a) and (3 5b)—or, in other words, of (1 1) on P_n Letting

$$y = (x, N_n) \in P_n, \qquad Ay = (LN_i^* a_{in} L_1 N_n, L_1 N_n),$$

$$G(\lambda, y) = (Lg(\lambda, x, N_n), L_1 f_n)$$

we find that (3 6) and (3 8) can be written simply as the operator equation

$$y = \lambda Ay + G(\lambda, y), \qquad y \in P_n, \quad \lambda \in R, \tag{3 9}$$

where A is a linear, compact operator from P_n into P_n and G is (for each fixed $\lambda \in R$) a completely continuous operator from P_n into P_n such that $G = o(|y|_0)$ near $y = 0$ uniformly in λ on compact subintervals of R

To summarize $y = (y_i) \in P_n$ solves (3 9) for some $\lambda \in R$ if and only if $N = (N_i) = (y_i + N_i^*, y_n) \in P_n$ solves (1 1) with $b_n(t) = \lambda + \theta + p_n(t)$

Clearly $y = 0$ solves (3 9) for all $\lambda \in R$, but this is just the "trivial" solution $N = (N_i^*, 0)$ of (1 1) Thus, we wish to solve (3 9) for nontrivial solutions $y \neq 0$ As is well known, nontrivial solutions of (3 9) can bifurcate from $y = 0$ only for λ near characteristic values of the linearized problem

$$y = \lambda Ay, \qquad y \in P_n \tag{3 10}$$

In order to find these characteristic values we observe that solving (3 10) is equivalent to solving, for some $\lambda \in R$, the linearized version of (3 5a)–(3 5b′) for a nontrivial solution $y = (x_i, N_n) \in P_n$

$$x_i' = x_i\left(b_i + \sum_{j=1}^{n-1} a_{ij} N_j^*\right) + N_i^*\left(\sum_{j=1}^{n-1} a_{ij} x_j + a_{in} N_n\right), \qquad 1 \leqslant i \leqslant n-1 \tag{3 11a}$$

$$N_n' = N_n\left(\lambda + \theta + p_n + \sum_{j=1}^{n-1} a_{nj} N_j^*\right) \tag{3 11b}$$

Now if $N_n \equiv 0$ in (3 11), then from (3 11a), $\alpha_{n-1} \leqslant \varepsilon$, and Lemma 2(a) follows $x_i \equiv 0$ for $1 \leqslant i \leqslant n-1$, i e, $y \equiv 0$ Thus, to have a nontrivial solution we must have $N_n \neq 0$ Moreover, the converse is true if $N_n \neq 0$ solves (3 11b) in P and is substituted into (3 11a), we may then solve the resulting system uniquely [by Lemma 2(b)] for $x=(x_i) \in P_{n-1}$ Thus, (3 11) has a nontrivial solution in P_n if and only if (3 11b) has a nontrivial solution in P Equation (3 11b) has a nontrivial solution in P if and only if [by Lemma 1(a)] $\lambda = \lambda_0$, where

$$\lambda_0 = -\theta - \sum_{j=1}^{n-1} \left[a_{nj} N_j^* \right] \tag{3 12}$$

Moreover, when $\lambda = \lambda_0$, Eq (3 11b) has one independent solution in P which, in the manner just described, yields one independent solution $(x_i, N_n) \in P_n$ of (3 11), thus, A has one and only one characteristic value λ_0, which is given by (3 12) and for which $\ker(I - \lambda_0 A)$ is one dimensional

Next we argue that λ_0 is in fact a simple characteristic value Suppose $y^* \in \ker(I-\lambda_0 A)^2$ Then $y^{**} = (I-\lambda_0 A)y^* \in \ker(I-\lambda_0 A)$, and hence $y^{**} = ky^0$ for some constant k, where $y^0 \neq 0$ spans $\ker(I-\lambda_0 A)$ Thus $k\lambda_0 A y^0 = y^* - \lambda_0 A y^*$, or $\lambda_0 A(ky^0 + y^*) = y^*$, an equation which implies amongst other things that the nth component of y^* satisfies the nonhomogeneous version of the scalar equation (3 11b) with $\lambda = \lambda_0$ and the "forcing term" $\lambda_0 k y_n^0$ added to the right hand side (y_n^0 is the nth component of y^0) Since (3 11b) with $\lambda = \lambda_0$ has a nontrivial periodic solution y_n^0, it follows from well-known facts concerning periodic differential equations [4] that $\lambda_0 k y_n^0$ must be orthogonal to the adjoint solution $1/y_n^0$ This, together with $\lambda_0 \neq 0$, implies $k=0$ and hence $y^{**}=0$ Thus $y^* \in \ker(I-\lambda_0 A)$ which implies that $\ker(I-\lambda_0 A)^2 \subseteq \ker(I-\lambda_0 A)$ Inasmuch as the opposite set inclusion is obvious, we have shown that these two kernels are identical This proves that λ_0 is simple

It follows from well-known bifurcation results that a continuum $C \subset R \times P_n$ of solutions (λ, y) of (3 9) exists whose closure contains $(\lambda_0, 0)$ (e g, see [5]) We next show that C consists [near the bifurcation point $(\lambda_0, 0)$] of two subcontinua both of whose closures contain $(\lambda_0, 0)$ and one of which contains positive solutions (the other contains negative solutions) of (1 1)

We investigate the solutions in C using the standard Liapunov-Schmidt expansion [6]

$$\begin{aligned} &\lambda = \lambda_0 + \lambda_1 \beta + \cdots, \\ &y = y_1 \beta + y_2 \beta^2 + \cdots, \qquad y_i = (x^{(i)}, N_n^{(i)}), \end{aligned} \tag{3 13}$$

for β a small parameter Substituting these expansions into (3 9) or equivalently into (3 5a)–(3 5b′), and equating the coefficients of like powers of β, we obtain a sequence of linear systems to be solved in P_n recursively for λ_i and y_i. The first system is just the linear system (3.11), hence λ_0 is given by (3.12), and y_1 is any nontrivial solution of (3.11) in P_n. It follows from (3.11b) that $N_n^{(1)}$ is of one sign, without loss of generality we take $N_n^{(1)}>0$ for all $t\in R$, and hence for $\beta>0$ small, $y=(x,N_n)$ has a positive nth component. In addition, for $\beta>0$ small we have that x is near zero and hence that N_i is near N_i^* for $1\leqslant i\leqslant n-1$. Since $N_i^*\in P$ is positive by (H2), it is bounded away from zero. These facts imply that N_i is positive for $1\leqslant i\leqslant n-1$.

If we let $\mu=\lambda+\theta$, we have proved part (a).

(b) Next we show that $\lambda_1>0$. Then, since positive solutions correspond to $\beta>0$ in (3.13), we see that they are associated with $\lambda>\lambda_0$ or $\mu=\lambda+\theta>\lambda_0+\theta=\mu^*$ as required. To find λ_1 we need to equate β^2 coefficients in (3.5a)–(3.5b′) after the substitution of (3.13). This results in the linear, nonhomogeneous system consisting of (3.5a) with f_i evaluated at y_1 and the scalar equation

$$N_n'=N_n\left(\lambda_0+\theta+p_n+\sum_{j=1}^{n-1}a_{nj}N_j^*\right)+\lambda_1N_n^{(1)}+f_n(x_i^{(1)},N_n^{(1)}) \qquad (3.14)$$

to be solved by $y_2\in P_n$. Again it is easy to see that this system has a solution in P_n if and only if (3.14) has a solution in P. Since the homogeneous equation associated with (3.14) has periodic solutions (by the way λ_0 was chosen), Eq. (3.14) can be solved in P if and only if the nonhomogeneous term in (3.14) is orthogonal to the adjoint solution $1/N_n^{(1)}$ [4]. This leads us to

$$\lambda_1=-\left[a_{nn}N_n^{(1)}\right]-\sum_{j=1}^{n-1}\left[a_{nj}x_j^{(1)}\right] \qquad (3.15)$$

Clearly, by (H1) we have that $\lambda_1>0$ if each $|a_{nj}|_0$ is sufficiently small.

(c) To investigate the sign of the solution $y=(x,N_n)$ for small β, we consider more closely the leading coefficient $y_1\in P_n$ in (3.13), which, as already pointed out, is a nontrivial solution of the linear, homogeneous system (3.11) with $\lambda=\lambda_0$ and with $N_n^{(1)}$ taken to be positive [as a solution of (3.11b)]. The first $n-1$ components $x^{(1)}=(x_i^{(1)})$ of y_1 constitute the unique periodic solution of the nonhomogeneous system (3.11a) obtained by letting $N_n=N_n^{(1)}\in P$. Next we point out that if [a]<0 in Lemma 1(a), then the operator L is positive, i.e., $Lf>0$ for all $t\in R$ if $f>0$ for all $t\in R$. This follows from the fact that the Green's function for L in this case is a positive function (see [4, p. 225]). Thus, if a_{in} is of one sign, then the unique periodic solution z_i of the scalar equation

$$z_i'=z_i\left(b_i+\sum_{j=1}^{n-1}a_{ij}N_j^*+\quad a_{ii}N_i^*\right)+a_{in}N_i^*N_n^{(1)}$$

is of the same sign But standard continuity results for differential equations imply that $|x_i - z_i|_0 \to 0$ as the coefficients $|a_{ij}|_0 \to 0$, $1 \leqslant i,j \leqslant n-1$, $i \neq j$ (here we again use Lemma 5) Thus, for α_{n-1} sufficiently small we have $\operatorname{sgn} x_i = \operatorname{sgn} z_i = \operatorname{sgn} a_{in}$ ■

Proof of Theorem 2

(a) Let $\bar{N} \in P_n$ be any positive solution of (1 1) Then $\bar{N} = (\bar{N}_i)$ is bounded away from zero for all t Let $w_i = (N_i - \bar{N}_i)/\bar{N}_i$ in (1 1) Then

$$w_i' = \sum_{j=1}^{n} \left(a_{ij}\bar{N}_j\right) w_j + o(|w|) \tag{3 17}$$

Because $\bar{N}_i$ is bounded away from zero, it is not difficult to see that $\bar{N}$ is uniformly asymptotically stable if and only if $w=0$ is a uniformly asymptotically stable solution of (3 17) Using standard linearization theorems [4] we can assert that $w=0$ is a locally uniformly asymptotically stable solution of (3 17) if the linear system

$$w_i' = \sum_{j=1}^{n} \left(a_{ij}\bar{N}_j\right) w_j$$

is uniformly asymptotically stable, a sufficient condition for which is

$$a_{ii}\bar{N}_i + \sum_{j \neq i} |a_{ij}\bar{N}_j| \leqslant -\delta < 0 \tag{3 18}$$

for all $1 \leqslant i \leqslant n$, $t \in R$ and some constant $\delta > 0$ [1, p 59] Using (H1) and Lemma 5 we see that (3 18) is fulfilled for α_n sufficiently small

(b) Let $w_i = (N_i - N_i^*)/N_i^*$ for $1 \leqslant i \leqslant n-1$ and $w_n = N_n$ in (1 1) Then upon again ignoring terms of order $o(|w|)$ we obtain the linearized system

$$w_i' = \left(\sum_{j=1}^{n-1} a_{ij}N_j^*\right) w_i + a_{in}w_n, \qquad 1 \leqslant i \leqslant n-1, \tag{3 19a}$$

$$w_n' = \left(\mu + p_n + \sum_{j=1}^{n-1} a_{nj}N_j^*\right) w_n \tag{3 19b}$$

We want to argue that this linear system is uniformly asymptotically stable for $\mu < \mu^*$ Equation (3.19b) is a linear, scalar, periodic equation whose periodic coefficient has negative average when $\mu < \mu^*$ This implies that w_n tends exponentially to zero as $t \to +\infty$ Substituting w_n into (3 19a) we obtain an $(n-1)\times(n-1)$ linear nonhomogeneous periodic system for w_i, $1 \leqslant i \leqslant n-1$, whose forcing term $a_{in}w_n$ is exponentially decaying and whose related homogeneous system is [similarly to the case (a)] uniformly asymptotically stable for α_{n-1} sufficiently small Thus all w_i tend exponentially to zero as $t \rightarrow +\infty$, i e , under these conditions (3 19) is uniformly asymptotically stable ■

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