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On the Use of Reducible-Functional Differential Equations in Biological Models

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I. INTRODUCTION

Biological models often lead to systems of delay or functional differential equations and to questions concerning the stability of equilibrium solutions of such equations. The monographs by Cushing [5] and MacDonald [11] discuss a number of examples of such models which describe phenomena from population dynamics, ecology, and physiology. The above-cited work of MacDonald is mainly devoted to the analysis of models leading to functional differential equations which are reducible to systems of ordinary differential equations. For example, consider the system

$$\frac{dX^1(t)}{dt} = \int_0^\infty e^{-\lambda s} X^2(t-s)\, ds, \qquad \frac{dX^2(t)}{dt} = \int_0^\infty e^{-\lambda s} X^1(t-s)\, ds.$$

If we define

$$X^3(t) = \int_0^\infty e^{-\lambda s} X^2(t-s)\, ds$$

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and

$$X^4(t) = \int_0^\infty e^{-\lambda s} X^1(t-s)\,ds,$$

then the above system reduces to the system of ordinary differential equations

$$\frac{dX^1(t)}{dt} = X^3(t), \qquad \frac{dX^2(t)}{dt} = X^4(t),$$

$$\frac{dX^3}{dt} = X^2(t) - \lambda X^3(t), \qquad \frac{dX^4(t)}{dt} = X^1(t) - \lambda X^4(t).$$

A necessary and sufficient condition for the reducibility of a functional differential equation to a system of ordinary differential equations is given by Fargue [6]. Fargue's method is used by MacDonald [10] as well as by Cohen *et al.* [3], Post and Travis [11] and Wörz-Busekros [15], to reduce functional differential equations arising in biological models to systems of ordinary differential equations for which certain stability questions can be answered. An example of the type of biological model with which we are concerned is that of a community of n-interacting species described by the system of functional differential equations

$$\frac{dX^i(t)}{dt} = X^i(t)\left[r_i + \sum_{i=1}^{m} a_{ij} \int_0^T X^j(t-s)\,d\eta_{ij}(s) + G_i(X)\right]. \tag{1}$$

There, X^i is the population of the ith species, r_i is the intrinsic population growth rate of species i, $A = (a_{ij})$ is an interaction matrix, η_{ij} are of bounded variation, and G_i is a higher order-nonlinear function of the X^i and their past histories. The η_{ij} may be atomic at zero as well as elsewhere, hence, both instantaneous and pure delay terms may be present in (1). If $\bar{X} = (\bar{X}^1, \ldots, \bar{X}^n)$, $\bar{X}^i > 0$, is an equilibrium solution of (1), then its local asymptotic stability is determined by the asymptotic stability of the trivial solution of the linearized system

$$\frac{dy^i(t)}{dt} = \bar{X}^i \sum_{j=1}^{n} a_{ij} \int_0^T y^j(t-s)\,d\eta_{ij}(s), \tag{2}$$

$y^i(t) = X^i(t) - \bar{X}^i$. The question that we are addressing is whether the delay terms in Eq. (1), and hence (2), can be replaced by terms of the form

$$b_{ij} y^j(t) + \sum_{k,l=1}^{M,N} \gamma_{ij}^{kl} \int_0^T y^j(t-s)\, g_{kl}(s)\,ds,$$

where

$$g_{kl}(t) = \frac{t^{k-1}}{(k-1)!} e^{-\lambda_l t} \tag{3}$$

and yet have stability of the trivial solution of the linearized system

$$\frac{dZ^i(t)}{dt} = \bar{Z}^i \sum_{j=1}^{n} a_{ij} \left[b_{ij} Z^j(t) + \sum_{k,l=1}^{M,N} \gamma_{ij}^{kl} \int_0^T Z^j(t-s)\, g_{kl}(s)\, ds \right] \tag{4}$$

determine the stability of the trivial of the original system (2).

The advantage of system (4) is that it is reducible to a system of ordinary differential equations [6, 11], and hence, the stability question reduces to that of the location of the zeros of a polynomial. The corresponding stability question for system (2) involves the location of the zeros of an entire function which, even in the case of discrete delays, presents considerable difficulties.

The first result of this paper provides an affirmative answer to the question raised above by noting that, given any linear-retarded functional differential equation and a finite subset of its spectrum defined by $\Lambda = \{\lambda \mid \operatorname{Re} \lambda \geqq \beta, \beta$ real$\}$, it is possible to find a reducible system of functional differential equations whose spectrum exactly coincides with this set. Thus, for the purpose of addressing questions of stability or asymptotic behavior of solutions, the use of reducible-functional differential equations in biological models is theoretically quite general. In practice, however, it can be difficult to find a reducible system whose spectrum coincides exactly with a given subset of the spectrum of a functional differential equation. What is usually obtainable is a reducible system whose spectrum is close to the spectrum of a given functional differential equation. This leaves open the question of how to measure the degree of approximation so that stability properties of the original functional differential equation are reflected in the approximating reducible system. In Theorems 2–4 of this paper we shall give computable-sufficient conditions for the asymptotic stability of the trivial solution of systems of linear-retarded functional differential equations approximated by equations that are reducible to systems of ordinary differential equations. We shall then use these results in Theorems 5 and 6 to analyze the asymptotic stability of the feasible equilibria of a class of population models with hereditary (or memory) terms. Theorem 3 includes, as a special case, the stability result of Bailey and Williams [1] and that reported by Ladde [10], and, in part, overlaps the stability result of Jordan [9], while Theorem 6 gives a generalization to multispecies systems of the stability result for the single-species equation that is proved by Stech [13]. The stability of the single-species equation treated in [13] has also been studied by Hadeler [7] and Walther [14].

The statement and discussion of our results are collected in the next section. In that section we shall also discuss some extensions and the ecological implications of the stability conditions given in Theorems 5 and 6. The proofs of all results are contained in the third section.

2. Stability Conditions

In order to simplify the statements of our theorems we introduce the following notation. We let $C = C([-T, 0], R^n)$ denote the space of continuous functions on $[-T, 0]$ to R^n with the uniform norm topology. For $\phi: R \to R^n$, we define $\phi_t: [-T, 0] \to R^n$ by $\phi_t(-s) = \phi(t-s)$, $s \in [0, T]$. Finally, we formally define a *reducible system* to be a retarded functional-differential equation whose kernel $\eta(s)$ satisfies

$$d\eta_{ij}(s) = \sum_{k,l=1}^{M,N} \gamma_{ij}^{kl} g_{kl}(s)\, ds, \qquad i = 1,..., n, \tag{5}$$

where g_{kl} is given by (3). We let L be a continuous-linear function mapping C into R^n, and consider the linear-retarded functional differential equation

$$\frac{dX(t)}{dt} = L(X_t) = \int_0^T [d\eta(s)]\, X_t(s), \tag{6}$$

where $\eta(s)$, $0 \leqq s \leqq T$, is an $n \times n$ matrix whose elements are of bounded variation. If ϕ is a given function in C, then $X_t(\phi)$ is the unique solution of (6) with $X_0(\phi) = \phi$. Our notation closely follows that of Hale [8], from which reference we shall quote a number of results. The linear-reducible systems take the form

$$\frac{dy^i(t)}{dt} = \sum_{j=1}^{n'} \left[b_{ij} y^j(t) + \sum_{k,l=1}^{M,N} \gamma_{ij}^{kl} \int_{-T}^{t} g_{kl}(t-s)\, y^j(s)\, ds \right] \tag{7}$$

$i = 1,..., n'$, and g_{kl} given by (3). Equations of the form (7) are reducible to a system of ordinary differential equations whose solutions with initial value α we denote by $y(t, \alpha)$, where y is a vector of length $m \geqq n'$.

Theorem 1. *There exists a linear-reducible system* (7) *such that its trivial solution is asymptotically stable if and only if the trivial solution of* (6) *is asymptotically stable. Moreover, for each $\alpha > 0$, there exists an integer m, a reducible system whose differential equation form has dimension m, a* *positive constant K, and continuous-linear maps V and S,* $V: R^m \to R^n$, $S: C \to R^m$, *such that for any* $\phi \in C$

$$|X_t(\phi) - Vy_t(S\phi)| \leqq K\,|\phi|\,e^{-\alpha t}, \qquad t \geqq 0,$$

where $X_t(\phi)$ *solves* (6) *with* $X_0(\phi) = \phi$ *and* $y_t(S\phi)(s) = y(t+s, S\phi)$; *and* $y(t, S\phi)$ *is the solution of the differential equation form of the reducible system with* $y(0, S\phi) = S\phi$.

The implication of Theorem 1 is that in the analysis of questions of local-asymptotic stability or of asymptotic-decay rates, there always exists an appropriate reducible system that can be analyzed instead of the original functional differential equation (6). In this respect, it justifies the widespread use of reducible systems in biomathematical models [3, 5, 11, 12, 14].

The theorem, however, leaves open the question of how to select the correct approximating reducible system. As we shall see in the next section, the general theory of functional differential equations, of which Theorem 1 is a direct consequence, does provide an algorithm for constructing the appropriate reducible system. This algorithm, however, involves the accurate computation of the zeros of the characteristic equation of (6) as well as the corresponding generalized eigenspaces–the very task one seeks to avoid by using the approximating reducible system (7). Consequently, it is desirable to have less general but more readily applicable conditions that will guarantee the stability of the trivial solution of equations approximated by reducible systems. It is the purpose of the next set of results to provide such sufficient conditions.

The results that follow, if stated in their greatest possible generality, would be notationally very involved. Hence, we have chosen to use the general form of the approximating kernel only in the one-dimensional case. In the n-dimensional case we state the results with a special simple form of the kernel which sufficies to illustrate the scope of our methods and avoids complications in the notation. In what follows, we shall use equations with both finite and infinite delays. References [4, 8] give good overviews of the theory of such equations. In particular, the notion of asymptotic stability for equations with finite delay that we employ is the one in [8].

THEOREM 2. *Consider the one-dimensional retarded functional differential equation*

$$\frac{dX(t)}{dt} = aX(t) + \sum_{k,l=1}^{M,N} \gamma_{kl} \int_0^\infty h_{kl}(s)\, X(t-s)\, ds$$
$$+ b \int_0^\infty X(t-s)\, d\mu(s), \tag{8}$$

where $\int_0^\infty |d\mu(s)| = 1$, $h_{kl}(s) = (\lambda_l)^k g_{kl}(s)$, $\lambda_l > 0$, *and* g_{kl} *is a reducible kernel of form* (3). *If* $a < 0$, *and if*

$$|a| - \sum_{k,l=1}^{M,N} |\gamma_{kl}| - |b| > 0, \tag{9}$$

then all roots of the characteristic equation of (8) *have negative-real part. If instead,* $a = 0$, $0 < \int_0^\infty s\,|d\mu(s)| < \infty$, *and*

$$\sum_{k,l=1}^{M,N} \gamma_{kl} + b \int_0^\infty d\mu(s) < 0, \tag{10a}$$

$$-\int_0^\infty \left| \sum_{k,l=1}^{M,N} \gamma^{kl} h^{kl}(s) + b \frac{d\mu(s)}{ds} \right| s\,ds + 1 \geqslant 0, \tag{10b}$$

the same conclusion holds. We note that (10b) *is implied by the simpler condition*

$$-\sum_{k,l=1}^{M,N} \frac{k}{\lambda_1} |\gamma^{kl}| - |b| \int_0^\infty s\,|d\mu(s)| + 1 \geqslant 0. \tag{10c}$$

If in addition to (9) *or* (10), *it is assumed that*

$$\eta(s) = b\mu(s) + \sum_{k,l=1}^{M,N} \int_0^s \gamma^{kl} h_{kl}(s)\,ds$$

is constant for $s > T$, *then the zero solution of* (8) *is asymptotically stable.*

Note that both (9) and (10) are essentially a restriction on the magnitude of the nonreducible term $b \int_0^\infty X(t-s)\,d\mu(s)$ that guarantees stability of the trivial solution. The simpler condition (9) applies only when the instantaneous term $a\,X(t)$ is a damping term. Condition (10) applies to the more general case when an instantaneous term need not be present, or else, when this term is not a damping term. (In this case, the instantaneous term is incorporated into the term $b \int_0^\infty X(t-s)\,d\mu(s)$.) We note in passing that the terms k/λ_1 in (10c) are equal to $\int_0^\infty h_{kl}(s) s\,ds$ and thus (10c) is actually a condition involving the first moment of $d\eta(s)$ analogous to that used by Stech [13].

A special case of condition (9) is obtained when $\gamma_{kl} = 0$ for all k, l and the measure μ in (8) is atomic and of the form $d\mu(s) = \sum c_i \delta_i(s - T_i)\,ds$, where $|c_i| = 1$, δ_i is the Dirac delta, and $T_i > 0$. Equation (8) then becomes a delay-differential equation $dX(t)/dt = aX(t) + \sum (bc_i) X(t - T_i)$, and condition (9) becomes $|a| - \sum |bc_i| > 0$. The result in this special form has been obtained by Bailey and Williams [1]. In the case where $b \int_0^\infty X(t-s)\,d\mu(s) = AX(t) + \int_0^t X(t-s)\,B(s).ds$, where $B \in L^1(0, \infty)$, Theorem 1 in Jordan [9] can be applied to (8) to yield a stability criterion with our Eq. (10b) replaced by $-\int_0^\infty s\,|B(s)|\,ds + |A + \int_0^\infty B(s)\,ds|/[|A| + \int_0^\infty |B(s)|\,ds] \geqslant 0$. This is a stronger restriction than $-\int_0^\infty s\,|B(s)|\,ds + 1 \geqslant 0$, which is the form that (10b) takes in this case. The paper of Jordan [9] and the relation between his results and ours was pointed out to us by M. Asunta Pozio. We now proceed to the n-dimensional versions of Theorem 2 which, as we said above, we state in a special form for notational convenience.

THEOREM 3. *Consider the retarded functional differential equation*

$$\frac{dX^i(t)}{dt} = \sum_{j=1}^{M} \left[a_{ij} X^j(t) + \gamma_{ij} \int_0^\infty \lambda e^{-\lambda s} X^j(t-s)\,ds + b_{ij} \int_0^\infty X^j(t-s)\,d\mu_{ij}(s) \right], \qquad i = 1, 2,..., n, \tag{11}$$

with $\lambda > 0$, $a_{ii} < 0$, $\mu_{ij}\colon [0, \infty) \to R$, *of bounded variation on compact intervals of* $(0, \infty)$, *and* $\int_0^\infty |d\mu_{ij}(t)| = 1$. *If there exist* $d_i > 0$, *such that*

$$|a_{ii}| - d_i^{-1} \left\{ \sum_{\substack{j=1 \\ j\neq i}}^{n} d_j\,|a_{ij}| + \sum_{j=1}^{n} d_j[|b_{ij}| + |\gamma_{ij}|] \right\} > 0, \tag{12}$$

then all roots of the characteristic equation of (11) *have negative-real parts. If, in addition, it is assumed that* $d\eta_{ij}(s) = \gamma_{ij}\lambda e^{-\lambda s}\,ds + b_{ij}\,d\mu_{ij}(s) = 0$ *for* $s > T$, *then the trivial solution of* (11) *is asymptotically stable.*

A special case of Theorem 3 is obtained by setting

$$\begin{aligned} \gamma_{ij} = 0,\ b_{ii} = 0,\ \mu_{ij}(s) &= s/T, \qquad 0 \leqq s \leqq T \\ &= 1, \qquad T < s, \\ a_{ij} = 0 \qquad \text{if} \quad i &\neq j, \quad i, j = 1, 2,..., n. \end{aligned}$$

Condition (12) then becomes

$$|a_{ii}| - d_i^{-1} \sum_{\substack{j=1 \\ j\neq i}}^{n} d_j\,|b_{ij}| > 0, \qquad i = 1, 2,..., n. \tag{13}$$

This condition is equivalent to that given by Ladde [10] for the equation

$$\frac{dX^i(t)}{dt} = a_{ii} X^i(t) + \sum_{j=1}^{n} \int_0^T B_{ij} X^j(t-s)\,ds,$$

where $B_{ij} = b_{ij}/T$. Ladde presents a stability argument using a Lyapunov function of Razumikhin type. This type of argument is difficult to apply because it involves a standard but involved estimate of a quadratic functional on a subset of C defined by the Lyapunov function. The present method of proof proceeds via an analysis of the characteristic equation thus avoiding these difficulties, and applies to the more general equations discussed here.

The condition in (12) is useful when the instantaneous diagonal terms a_{ii} are negative and large compared to the hereditary-delay terms. In that case, it gives an easily computable condition for stability. When that is not the case, we need to use a condition that involves the delayed part of the diagonal terms. Such a condition is given in

THEOREM 4. *Consider the retarded functional differential equation*

$$\frac{dX^i(t)}{dt} = \sum_{j=1}^{n} a_{ij} \int_0^\infty X^j(t-s)\, d\eta_{ij}(s), \tag{14}$$

with η_{ij} *normalized by* $\int_0^\infty |d\eta_{ij}(s)| = 1$, $i, j = 1, 2,..., n$. *Suppose that,* $0 < \int_0^\infty |d\eta_{ij}(s)| < \infty$, *for all i, and*

$$a_{ii} \int_0^\infty d\eta_{ii}(s) < 0, \qquad -|a_{ii}| \int_0^\infty s\, |d\eta_{ii}(s)| + 1 = 0, \tag{15}$$

for $i = 1, 2,..., n$, *and there exist* $d_i > 0$ *such that*

$$\left| a_{ii} \int_0^\infty \cos(sv)\, d\eta_{ii}(s) \right| - d_i^{-1} \sum_{\substack{j \neq i \\ j=1}}^{n} d_j |a_{ij}| > 0, \tag{16}$$

for all real v satisfying

$$|v| \leqq \left[d_i^{-1} \sum_{\substack{j=1 \\ j \neq i}}^{n} d_j |a_{ij}| \right] \Big/ \left[-|a_{ii}| \int_0^\infty s\, |d\eta_{ii}(s)| + 1 \right].$$

Then the roots of the characteristic equation of (14) *have negative-real parts.*

It should be noted that, for the one-dimensional case, conditions (15) and (16) collapse to the condition $-|a_{ii}| \int_0^\infty s\, |d\eta_{ii}(s)| + 1 > 0$, and $a_{ii} \int_0^\infty d\eta_{ii}(s) < 0$. This is the condition derived by Stech [12] for the one-dimensional system, under the added restrictions that $a_{ii} < 0$ and η_{ii} is monotone increasing. In the n-dimensional case, the second condition (16) cannot be dropped since (15) incorporates no information on the off-diagonal terms of the system. We stated Theorem 4 without explicitly exhibiting reducible terms in the right-hand side of Eq. (14). The addition of such terms can be easily done. For example, if we consider the equation

$$\frac{dX^i(t)}{dt} = \sum_{j=1}^{n} \left[\gamma_{ij} \int_0^\infty \lambda e^{-\lambda s} X^j(t-s)\,ds + a_{ij} \int_0^\infty X^j(t-s)\,d\eta_{ij}(s) \right],$$
$$i = 1, 2, \ldots, n,$$

where $\gamma_{ii} + a_{ii} < 0$ and the η_{ij} satisfy the conditions stated in Theorem 6, then stability conditions (15) and (16) are implied by conditions (22) and (23) of Theorem 6. In this circumstance, the stability condition can be viewed as a restriction on the size of the nonreducible terms a_{ij} relative to that of the reducible terms γ_{ij}.

Since Theorem 4 partly overlaps the stability result given by Jordan [9], it is worth considering a simple example where our result predicts stability but where the result in [9] fails to apply. In fact, let

$$\begin{aligned} \frac{dX^1(t)}{dt} &= -2X^1(t-\tfrac{1}{4}) + X^2(t-\tfrac{1}{4}), \\ \frac{dX^2(t)}{dt} &= X^1(1-\tfrac{1}{4}) - 2X^2(t-\tfrac{1}{4}). \end{aligned} \tag{17}$$

This system is of the form (14) with $a_{11} = a_{22} = -2$, $a_{12} = a_{21} = 1$, and $d\eta_{ij}(s) = \delta(s-\frac{1}{4})\,ds$. Since $-|a_{ii}| \int_0^\infty s\,|d\eta_{ii}(s)| + 1 = -2\int_0^\infty s\delta(s-\frac{1}{4})\,ds + 1 = \frac{1}{2} > 0$, condition (15) of Theorem 4 is satisfied. In order to check condition (16) we first note that the appropriate restriction on $|v|$ is, $|v| \leqslant \sum_{j \neq i, j=1}^{2} |a_{ij}| / [1 + a_{ii} \int_0^\infty s d\eta_{ii}(s)]$, which implies

$$|v| \leqslant 2.$$

So, since $\cos(v/4)$ is a monotone decreasing function of $|v|$ for $|v| \leqslant 2$, we have

$$\begin{aligned} \left| a_{ii} \int_0^\infty \cos(sv)\,d\eta_{ii}(s) \right| - \sum_{\substack{j \neq i \\ j \neq i}}^{2} |a_{ij}| &= 2\cos(v/4) - 1 \\ &> 2\cos(1/2) - 1 > 0. \end{aligned}$$

So, condition (16) is satisfied, and by Theorem 4, (0, 0) is an asymptotically stable solution of Eqs. (17).

On the other hand, Theorem 1 of [9] requires the condition (condition H_4 in [9])

$$\int_0^\infty s\,|a_{ii}\,d\eta_{ii}(s)| \leqslant \left(\left|\int_0^\infty a_{ii}\,d\eta_{ii}(s)\right| - \sum_{\substack{j\neq i\\ j=1}}^{2}\int_0^\infty |a_{ij}d\eta_{ij}(s)|\right)\Big/\sum_{j=1}^{2}\int_0^\infty |a_{ij}\,d\eta_{ij}(s)|.$$

In our particular example (17) the left-hand side of this inequality is easily seen to be equal to $\frac{1}{2}$ while the right-hand side is equal to $(\frac{1}{2}-\frac{1}{4})/(\frac{1}{2}+\frac{1}{4})=\frac{1}{3}$. So, this inequality fails, and Theorem 1 of [9] does not apply to Eq. (17). We note that even though Jordan [9] restricts his attention to the case where $d\eta_{ij}(s)=b_{ij}(s)\,ds$, $b_{ij}\in L^1(0,\infty)$, his stability result does apply to the more general kernels we have been considering here.

We now give two direct applications of our results to some model equations from the theory of population dynamics. Again, for notational convenience, we state the results with only a simple reducible kernel incorporated in the equations.

THEOREM 5. *Consider the functional differential equations*

$$\frac{dX^i(t)}{dt} = X^i(t)\left[r_i + \sum_{j=1}^{n}\left\{a_{ij}X^j(t) + \gamma_{ij}\int_0^\infty \lambda e^{-\lambda s}X^j(t-s)\,ds + b_{ij}\int_0^\infty X^j(t-s)\,d\mu_{ij}(s)\right\}\right], \qquad i=1,2,\dots,n \tag{18}$$

with $\lambda>0$, $a_{ii}<0$, $\mu_{ij}\colon[0,\infty)\to R$ *of bounded variation,* $\int_0^\infty |d\mu_{ij}(s)|=1$, *and* $\eta_{ij}(s)=b_{ij}\mu_{ij}(s)-\gamma_{ij}e^{-\lambda s}$ *obeying* $\eta_{ij}(s)=$ *constant for* $s>T$. *Assume that* (18) *has an isolated feasible equilibrium* $\bar{X}=(\bar{X}^1,\dots,\bar{X}^n)$, $\bar{X}^i>0$. *Suppose that there exist* $d_j>0$ *with*

$$|a_{ii}|d_i^{-1}\left[\sum_{\substack{j\neq i\\ j=1}}^{n} d_j|a_{ij}| + \sum_{j=1}^{n} d_j(|b_{ij}|+|\gamma_{ij}|)\right]>0, \tag{19}$$

$$i=1,2,\dots,n,$$

then $\bar{X}$ *is locally asymptotically stable.*

We note that the addition of a higher order-nonlinear term on the right-hand side of (18) does not alter the result. Also, exactly the same result holds for the more general equation

$$\frac{dX^i(t)}{dt} = L_i(X_t^i)\left[r_i + \sum_{j=1}^{n}\left\{a_{ij}\int_{-t}^{0} X^j(t+s)\,d\mu_{ij}(s)\right.\right.$$
$$\left.\left. + \gamma_{ij}\int_{-t}^{0} X^j(t+s)\,\lambda e^{\lambda s}\,ds\right\}\right],$$

where $L_i: C \to R^n$ is linear and continuous and $L_i(\bar{X}^i) > 0$. (Here $L_i(\bar{X}^i)$ denotes L_i operating on the function which is identically equal to $\bar{X}^i$ on $[-T, 0]$.) This type of generalization of the interacting species equation may be useful in modeling populations where the removal rates depend on past histories. Equations of this type do come up naturally in models of epidemics (see, e.g., Busenberg and Cooke [2] for the discussion and analysis of such a model) because of the delays due to the incubation periods for particular infections.

Our next result treats the case where the a_{ii} are not necessarily negative.

THEOREM 6. *Consider the retarded functional differential equation*

$$\frac{dX^i(t)}{dt} = X^i(t)\left[r_i + \sum_{j=1}^{n}\left\{a_{ij}\int_{0}^{\infty} X^j(t-s)\,d\eta_{ij}(s)\right.\right.$$
$$\left.\left. + \gamma_{ij}\int_{0}^{\infty} X^j(t-s)\,\lambda e^{-\lambda s}\,ds\right\}\right], \qquad i = 1, 2,..., n, \tag{21}$$

with $a_{ii}\int_0^\infty d\eta_{ii}(s) + \gamma_{ii} < 0$, $\int_0^\infty |d\eta_{ij}(s)| = 1$, $a_{ij}\eta_{ij}(s) - \gamma_{ij}e^{-\lambda s}$ *constant for* $s > T$, *and* $\lambda > 0$, $i, j = 1, 2,..., n$. *Assume that* (21) *has an isolated feasible equilibrium* $\bar{X} = (\bar{X}^1,..., \bar{X}^n)$, $\bar{X}^i > 0$, *and suppose that there exist constants* $d_j > 0$, $j = 1, 2,..., n$ *such that for all* $i = 1, 2,..., n$

$$-\bar{X}^i\,|a_{ii}|\int_0^\infty s\,|d\eta_{ii}(s)| - \bar{X}^i\,|\gamma_{ii}|/\lambda + 1 > 0, \tag{22}$$

and,

$$\left|a_{ii}\int_0^\infty \cos(vs)\,d\eta_{ii}(s) + \gamma_{ii}\int_0^\infty \cos(vs)\,\lambda e^{-\lambda s}\,ds\right|$$
$$- d_i^{-1}\sum_{\substack{j=1\\ j\neq i}}^{n} d_j[|a_{ij}| + |\gamma_{ij}|] > 0, \tag{23}$$

for all real v *such that*

$$|v| \leqq \left[d_i^{-1}\sum_{\substack{j=1\\ j\neq i}}^{n} \bar{X}^i d_j(|a_{ij}| + |\gamma_{ij}|)\right]\Big/\left[1 - \bar{X}^i\,|a_{ii}|\int_0^\infty s\,|d\eta_{ii}(s)|\right.$$
$$\left. - \bar{X}^i\,|\gamma_{ii}|/\lambda\right].$$

Then $\bar{X}$ *is locally asymptotically stable.*

We again note that the addition of a higher order-nonlinear term does not change the result. Also, if the intrinsic-population growth terms $X^i(t)\, r_i$ are given the more general form $L_i(X_t^i)\, r_i$, where each $L_i\colon C \to R^n$ is linear and continuous with $L_i(\bar{X}^i) > 0$, then a similar result holds with $\bar{X}^i$ in Eq. (22) replaced by $L_i(\bar{X}^i)$. The restriction that $a_{ij}\eta_{ij}(s) - \gamma_{ij}\, e^{-\lambda s}$ be constant for $s > T$ is needed only so we may use the concept of asymptotic stability given in [8].

The biological implications of Theorems 5 and 6 can be summarized by saying that the feasible equilibrium will be locally asymptotically stable if intraspecific regulation of population densities is stronger than some positive-linear combination of the effect of interspecific interaction. When the governing equations are completely reducible to ordinary differential equations, then the result of Post and Travis [12] shows that the stability of the equilibrium is global in this case. Our results give only local stability of the feasible equilibrium and our methods of proof, via linearization about the equilibrium, cannot be generalized to yield global results. On the other hand, these last two theorems, do handle more general systems than in [12], and, as in that reference, give conditions that are interpretable in ecological terms which are verifiable in a finite number of algebraic steps.

In a number of biological applications delay equations with a reducible kernel have been used to analyze the local (Hopf) bifurcation of a periodic solution from a feasible equilibrium. Examples of such analysis are given in [3, 11]. Again, the question naturally arises about how large a class of delay equation can be replaced by equations with equations with reducible kernels and still preserve the properties of Hopf bifurcation. In order to answer this question, we consider the retarded functional-differential equations parameterized by the real parameter α,

$$\frac{dX(t)}{dt} = L(\alpha)\, X_t + f(\alpha, X_t), \tag{24}$$

and follow Hale in assuming that $L\colon R \times C \to R^n$ is continuously differentiable in α, $L(\alpha)\colon C \to R^n$ is linear and continuous, $f(\alpha, \phi) + L(\alpha, \phi)$ has continuous first and second derivatives in α, ϕ for $\alpha \in R$, $\phi \in C$; $f(\alpha, 0) = 0$ for all α and $f_\phi(\alpha, 0) = 0$ for all α, where $f_\phi(d, 0)$ is the derivative of f with respect to ϕ at $\phi = 0$. Finally, assume that:

(H1) The linear equation $dX(t)/dt = L(0)\, X_t$ has a simple purely imaginary characteristic root $\lambda_0 = iy_0 \neq 0$ and all characteristic roots $\lambda_j \neq \lambda_0$, $\lambda_j \neq \bar{\lambda}_0$ satisfy $\operatorname{Re} \lambda_j < 0$.

(H2) $\operatorname{Re} \lambda'(0) = \operatorname{Re} d\lambda(\alpha)/d\alpha\,|_{\alpha=0} > 0$.

Under these hypotheses, Hale [8, Chapter 11, Theorem 1.1] shows that, as the parameter α is increased in a neighborhood of 0 from a negative to a positive value, a nontrivial-periodic solution of (24) *bifurcates* at $\alpha = 0$. The above-quoted theorem in [8] provides the detailed technical meaning of the situation described above and we shall not repeat it here. Our purpose here is to show that there exists a system whose linear part is reducible

$$dX(t)/dt = L_R(\alpha)\, X_t + f(\alpha, X_t), \tag{25}$$

which can be used to analyze this local bifurcation of periodic solutions instead of the system (24). We have the following result:

THEOREM 7. *Consider the system* (24) *with the restrictions stated above. Then there exists a system with reducible-linear part* (25), *satisfying the same restrictions and such that* (H1) *and* (H2) *are satisfied by* (24) *if and only if they are satisfied by* (25).

This result provides a justification of the use of reducible kernels in the analysis of the local bifurcation of periodic solutions in biological models. Again, it may be useful to give simple sufficient conditions for the adequacy of special forms of Eq. (25) arising in biomathematics in describing the phenomenon of Hopf bifurcation for nonreducible equations that they approximate. We shall not, however, pursue this question here.

3. PROOFS OF THE STABILITY RESULTS

The two general results, Theorems 1 and 7, rely on similar techniques for their verification and we start by giving their proofs.

Proof of Theorem 1. We start by showing that, given any constant square matrix B, there exists a reducible system whose differential equation form is equivalent via a similarity transformation to $y'(t) = By(t)$. In order to see this, let E be the nonsingular matrix which reduces B to Jordan canonical form, and B_{λ_j} be the kth Jordan block ($j = j(k)$) of $E^{-1}BE$ with λ_j the only eigenvalue of this block (which we assume to be an $m_k \times m_k$ matrix. Our claim will be established if we construct a reducible system whose differential equation form has B_{λ_j} as its matrix. But, the system

$$\frac{dy^1(t)}{dt} = \lambda_j y^1(t), \quad \frac{dy^l(t)}{dt} = \lambda_j y^l(t) + y^{l-1}(t), \quad l = 2, 3, \ldots, m_k \tag{26}$$

is the differential equation form of the reducible system

$$\frac{du(t)}{dt} = \lambda_j u(t),$$

$$\frac{dv(t)}{dt} = \lambda_j v(t) + \int_{-T}^{t} g_{m_k-2}(t-s)\, u(s)\, ds, \qquad m_k > 2$$

$$= \lambda_j v(t) + u(t), \qquad m_k = 2$$

obtained by defining $y^1 = u$, $y_{m_k} = v$, and $y^{l+1}(t) = \int_{-T}^{t} g_1(t-s)\, y^1(s)\, ds$, for $l = 1, 2,..., m_k - 2$, where $g_1(t) = (t^{l-1}/(l-1)!)\, e^{\lambda_1 t}$.

We also note that given m_k constants $a_1, a_2,..., a_{m_k}$ there always exist $\phi \in C$ with $\phi(0) = a_1$, $y^{l+1}(0) = \int_{-T}^{0} g_1(-s)\, \phi(s)\, ds = a_1$, so any arbitrary-initial vector can be obtained for (26). The entire matrix $E^{-1}BE$ is now obtained by constructing a system which consists of a single vector whose components are obtained from a sequential stringing together of the components of systems of the form (26) starting with the first component of the first Jordan block and ending with the last component of the final Jordan block of $E^{-1}BE$.

We can now complete the proof of our result by using [8, Theorems 2.1 and 4.1, Chapter 7]. Specifically, given $\alpha > 0$, let $\Lambda = (\lambda_1,..., \lambda_p)$, where λ_i are the roots of the characteristic equation of (6) obeying $\operatorname{Re} \lambda_i > -\alpha$; and let $m_1,..., m_p$ be the respective multiplicities of these roots. From the theory of retarded function differential equations, we know that Λ is a finite set and that $m_1,..., m_p$ are positive integers. Using the theorems quoted above, decompose C into the direct sum $C = P_\Lambda \oplus Q_\Lambda$, such that, if $\phi \in C$, there exist positive constants K and γ such that the solution $X_t(\phi) = X_t(\phi^P \Lambda) + X_t(\phi^Q \Lambda)$, $\phi = \phi^P \Lambda \oplus \phi^Q \Lambda$, obeys

$$|X_t(\phi^Q \Lambda)| \leqq K e^{(-\alpha-\gamma)t}\, |\phi^Q \Lambda| \leqq K e^{-\alpha t}\, |\phi|, \qquad t \geqq 0. \tag{27}$$

Also, if $m = m_1 + m_2 + \cdots + m_p$, there exists a constant $m \times m$ matrix B_Λ, an $n \times m$ matrix Φ_Λ whose entries are continuous functions in $C([-T, 0], R)$, and a constant vector $a \in R^m$ such that

$$X_t(\phi^P \Lambda)(s) = \Phi_\Lambda(s)\, e^{B_\Lambda t} a = \Phi_\Lambda(0)\, e^{B_\Lambda(t+s)} a, \qquad s \in [-T, 0]. \tag{28}$$

Our notation here follows that of [8], where these results are proved.

Now, construct a reducible system whose differential equation is $E^{-1}B_\Lambda E$, as was done above, then the solution y of this differential equation with initial value $E^{-1}a$ obeys $Ey(t+s, E^{-1}a) = e^{B_\Lambda(t+s)}a$, which when substituted in (28) yields

$$X_t(\phi^P \Lambda)(s) = \Phi_\Lambda(0)\, Ey(t+s, E^{-1}a). \tag{30}$$

Now, $\Phi_\Lambda(0)E$ is an $n \times m$ matrix with real entries which we denote by V. Also, letting $\pi_{P_\Lambda} : \phi \to \phi^P \Lambda$, again from the results of [8] quoted above we have $\phi^P \Lambda = \Phi_\Lambda a$, $a \in R^m$. Let $U: \phi_\Lambda a \to a$ and let E^{-1} denote the linear map induced by the $m \times m$ matrix E^{-1}, then $S = E_0^{-1} U_0 \pi_{P_\Lambda}: C \to R_m$ is a linear-continuous map obeying $S\phi = E^{-1} a$. With all this notation, (30) can now be written as $X_t(\phi^P \Lambda)(s) = Vy(t+s, S\phi)$. Hence, $X_t(\phi)(s) - Vy(t+s, S\phi) = X_t(\phi^Q \Lambda)(s)$, and the estimate (27) completes the proof of Theorem 1.

From the proof of this result it is fairly clear that, even though the theorem provides a method of constructing reducible systems that provide appropriate approximations to delay functional differential equation systems, the method of construction is not at all easy to apply. In fact, the construction of the matrices C_Λ and B_Λ, and the projections π_{P_Λ} require an intimate knowledge of the roots of the characteristic equation of (6) as well as the generalized eigenspaces corresponding to these roots. These are the very tasks one seeks to avoid when using reducible systems, so this result is mainly of theoretical import. It is also clear from the proof that this result is a direct consequence of known facts about functional differential equations.

Proof of Theorem 7. From the proof of Theorem 1, we know that for each $\alpha \in R$ we can construct a reducible linear part $L_R(\alpha)\phi$, $\phi \in C$, such that the spectrum of the linear-differential system corresponding to $dY(t)/dt = L_R(0)\, Y_t$ is identical to that part of the spectrum of $dX(t)/dt = L(0)\, X_t$ which lies on the imaginary axis. These roots are all simple, by hypothesis; so, since $L(\alpha)$ is twice continuously differentiable in α, using the same ideas as in [8, Chap. 7, Lemma 2.2], we can show that there exists $\alpha_0 > 0$, and simple characteristic roots $\lambda_j(\alpha)$ of $L(\alpha)$ such that $\lambda_j(0)$ coincide with the imaginary roots of $L(0)$ and $\lambda_j(\alpha)$ are twice continuously differentiable for $|\alpha| < \alpha_0$. Now, construct the reducible system with matrix $B(\alpha)$ consisting of diagonal blocks of the form

$$B_j = \begin{bmatrix} \operatorname{Re} \lambda_j & -\operatorname{Im} \lambda_j \\ \operatorname{Im} \lambda_j & \operatorname{Re} \lambda_j \end{bmatrix} \quad \text{which have the Jordan form} \quad \begin{bmatrix} \lambda_j & 0 \\ 0 & \bar{\lambda}_j \end{bmatrix}.$$

Of course, since we are dealing with a real system, the λ_j occur in conjugate pairs. Now, the entries in $B_j(\alpha)$ are twice continuously differentiable in α, hence, $B(\alpha)$ is twice continuously differentiable in α, $|\alpha| < \alpha_0$, and hence, so is the coefficient matrix of the linear-differential system corresponding to the reducible system $dY(t)/dt = L(\alpha)\, Y_t$. The spectrum of this differential-equation system, for α near zero, coincides with the part of the spectrum of (24) which enters in hypotheses (H1) and (H2). This completes the proof of Theorem 7.

The same remarks that were made after the proof of Theorem 1 on the lack of practicality of this method of reduction apply to this case as well. We now proceed to the

Proof of Theorem 2. The characteristic equation of (8) is

$$\Delta(z) = z - a - \sum_{k,l=1}^{M,N} \gamma^{kl} \int_0^\infty h_{kl}(s)\, e^{-zs}\, ds - b \int_0^\infty e^{-zs}\, d\mu(s)$$

$$= z - a - \sum_{k,l=1}^{M,N} \gamma^{kl} \left[\frac{\lambda_1}{\lambda_1 + z}\right]^k - b \int_0^\infty e^{-zs}\, d\mu(s).$$

If $\operatorname{Re} z \geqq 0$, $|\int_0^\infty e^{-zs}\, d\mu(s)| \leqq \int_0^\infty |d\mu(s)| = 1$, and since $\lambda_1 > 0$, $|\lambda_1/(\lambda_1 + z)|^k \leqq 1$. So, if $\Delta(z) = 0$ we have $\operatorname{Re} z \leqq a + \sum_{k,l=1}^{M,N} |\gamma^{kl}| + |b|$, so, since $a < 0$, by condition (9) we get $\operatorname{Re} z < 0$, and this completes the first part of Theorem 2.

We next consider the case where $a = 0$, $\gamma^{kl} < 0$, $0 < \int_0^\infty |d\mu(s)| s < \infty$. The characteristic equation in this case can be written in the form

$$\Delta(z) = z - \int_0^\infty e^{-zs} \left[\sum_{k,l=1}^{M,N} \gamma^{kl} h^{kl}(s)\, ds + b d_\mu(s)\right] = z - \int_0^\infty e^{-zs}\, d\zeta(s),$$

and conditions (10a) and (10b) become

$$\int_0^\infty d\zeta(s) < 0, \qquad -\int_0^\infty s\, |d\zeta(s)| + 1 \geqslant 0.$$

Now, $z = 0$ is not a root of Δ since

$$\Delta(0) = -\int_0^\infty d\zeta(s) > 0,$$

while if $z = u + iv$, $u \geqslant 0$, $v \neq 0$ is a root we have

$$0 = |\operatorname{Im} \Delta(u + iv)| = \left| v + \int_0^\infty e^{-us} \sin(vs)\, d\zeta(s) \right|$$

$$= |v| \left| 1 + \int_0^\infty e^{-us} \frac{\sin(vs)}{vs} s d\zeta(s) \right|.$$

Now, if $s d\zeta(s) = 0$ a.e. for $s \geqslant 0$, we get from the above relation the contradiction $|v| = 0$. Otherwise, we have

$$0 \geqslant |v| \left[1 - \int_0^\infty \left|\frac{\sin(vs)}{vs}\right| s\, |d\zeta(s)|\right] > |v| \left[1 - \int_0^\infty s\, |d\zeta(s)|\right] \geqslant 0,$$

which is again a contradiction. In the above sequence of inequalities, the strict inequality follows from the fact that $|\sin(vs)/vs| < 1$ for $vs \neq 0$, and for some $s > 0$, $s d\zeta(s) \neq 0$ a.e.

So, from this we see that Δ has no roots with nonnegative-real parts when conditions (10a) and (10b) hold. Finally, the fact that (10c) implies (10b) follows from the relation

$$\begin{aligned}\int_0^\infty \left| \sum_{k,l}^{M,N} \gamma^{kl} h^{kl}(s) + b \frac{d\mu(s)}{ds} \right| s\, ds &\leqslant \sum_{k,l}^{M,N} |\gamma^{kl}| \int_0^\infty h^{kl}(s) s\, ds + |b| \int_0^\infty s\,|d\mu(s)| \\ &= \sum_{k,l}^{M,N} \frac{k}{\lambda_l} |\gamma^{kl}| + |b| \int_0^\infty s\,|d\mu(s)|.\end{aligned}$$

This completes the proof of Theorem 2.

Proof of Theorem 3. Let D be the positive-diagonal matrix in the hypothesis of the theorem, and consider the characteristic matrix Δ of the differential equation for the transformed variable $Y = D^{-1}X$. The (i, j)th entry $\Delta_{ij}(z)$ of $\Delta(z)$ is given by

$$\Delta_{ii}(z) = a_{ii} - z + \frac{\lambda\gamma_{ii}}{\lambda + z} + b_{ii} \int_0^\infty e^{-zs}\, d\mu_{ii}(s), \qquad i = 1, 2,\dots, n,$$

$$\Delta_{ij}(z) = d_i^{-1} d_j \left\{ a_{ij} + \frac{\lambda\gamma_{ij}}{\lambda + z} + b_{ij} \int_0^\infty e^{-zs}\, d\mu_{ij}(s) \right\},$$

$$i \neq j, \qquad i, j = 1, 2,\dots, n.$$

From Gershgorin's theorem, the values of z for which the equation $\Delta(z)\, y = 0$ holds for a nontrivial vector y must lie in the union of the disks

$$D_i = \left\{ \omega : |a_{ii} - \omega| \leqq d_i^{-1} \sum_{\substack{j \neq i \\ j=1}}^{n} d_j\, |a_{ij}| + \sum_{j=1}^{n} d_j \left| \frac{\lambda\gamma_{ij}}{\lambda + z} + b_{ij} \int_0^\infty e^{-zs}\, d\mu_{ij}(s) \right| \right\}.$$

Now, suppose that $\operatorname{Re} z \geqq 0$, and z is a characteristic root of this equation. Then, for at least one value of i we have

$$|a_{ii} - z| \leqq d_i^{-1} \sum_{\substack{j \neq i \\ j=1}}^{n} d_j\, |a_{ij}| + \sum_{j=1}^{n} d_j \left[\left| \frac{\lambda\gamma_{ij}}{\lambda + z} \right| + |b_{ij}| \right] \Bigg\} \tag{32}$$

since $|\int_0^\infty e^{-zs}\, d\mu_{ij}(s)| \leqq \int_0^\infty |d\mu_{ij}(s)| = 1$ when $\operatorname{Re} z \geqq 0$. Since $\lambda > 0$ and $\operatorname{Re} z \geqq 0$, $|\lambda\gamma_{ij}/(\lambda + z)| \leqq |\gamma_{ij}|$, and (32) becomes

$$|a_{ii} - z| \leqq d_i^{-1} \left\{ \sum_{\substack{j \neq i \\ j=1}}^{n} d_j |a_{ij}| + \sum_{j=1}^{n} d_j [|\gamma_{ij}| + |b_{ij}|] \right\} < |a_{ii}|,$$

the last inequality following from condition (12). This, of course, is impossible since $a_{ii} < 0$ is real and $\operatorname{Re} z \geqq 0$. Consequently, all the roots of the characteristic equation $\det \Delta(z) = 0$ have negative-real parts, and Theorem 3 is proved.

Proof of Theorem 4. We again start by transforming to the variable $Y = D^{-1}X$, and consider (14) with coefficients $d_i^{-1} d_j a_{ij}$ instead of a_{ij}. The characteristic matrix Δ of this system has rows Δ_{ij} given by

$$\Delta_{ii}(\omega) = a_{ii} \int_0^\infty e^{-\omega s}\, d\eta_{ii}(s) - \omega, \qquad i = 1, 2, \ldots, n;$$

$$\Delta_{ij}(\omega) = d_i^{-1} d_j a_{ii} \int_0^\infty e^{-\omega s}\, d\eta_{ij}(s), \qquad i \neq j, \quad i = 1, 2, \ldots, n.$$

Using the same arguments as in the previous proof, we know that any root z of the characteristic equation $\det \Delta(z) = 0$ must satisfy the following relation for some value of $i = 1, 2, \ldots, n$ and for constants $K_j = K_j(z)$ with $|K_j| \leqq 1$:

$$z - a_{ii} \int_0^\infty e^{-zs}\, d\eta_{ii}(s) + d_i^{-1} \sum_{j \neq i} d_j K_j a_{ij} \int_0^\infty e^{-zs}\, d\eta_{ij}(s) = 0. \qquad (33)$$

We first note that $z = 0$ cannot satisfy this relation, since it then reduces to

$$\left| a_{ii} \int_0^\infty d\eta_{ii}(s) \right| \leqq d_i^{-1} \sum_{j \neq i} d_j |a_{ij}| < \left| a_{ii} \int_0^\infty d\eta_{ii}(s) \right|$$

the last inequality following from (16) with $v = 0$. Now, if $z^* = iv \neq 0$ is a pure imaginary root of the characteristic equation, then consider the function g defined by

$$g(z) = z - a_{ii} \int_0^\infty e^{-zs}\, d\eta_{ii}(s) + d_i^{-1} \sum_{j \neq i} d_j K_j a_{ij} \int_0^\infty e^{-zs}\, d\eta_{ij}(s),$$

where $K_j = K_j(iv)$, are complex constants with $|K_j| \leqq 1$. Clearly, $g(iv) = 0$, because of this choice of K_j. So, considering the real and imaginary parts of $g(iv)$ we get the relations

$$-a_{11}\int_0^\infty \cos(vs)\, d\eta_{ii}(s)$$

$$= \operatorname{Re}\left[d_i^{-1} \sum_{j\neq i} d_j K_j a_{ij} \int_0^\infty e^{-ivs}\, d\eta_{ij}(s)\right], \tag{34}$$

and

$$v\left[1 + a_{ii}\int_0^\infty \frac{\sin(vs)}{v}\, d\eta_{ii}(s)\right]$$

$$= \operatorname{Im}\left[d_i^{-1} \sum_{j\neq i} d_j K_j a_{ij} \int_0^\infty e^{-ivs}\, d\eta_{ij}(s)\right]. \tag{35}$$

Now, from (35) we get

$$|v| \left| -|a_{ii}| \int_0^\infty s\,|d\eta_{ii}(s)| + 1 \right| \leqq |v| \left| 1 + a_{ii}\int_0^\infty \frac{\sin(vs)}{vs} s\, d\eta_{ii}(s) \right|$$

$$\leqq d_i^{-1} \sum_{\substack{j=1\\ j\neq i}}^{n} d_j\,|a_{ij}|$$

and hence, v satisfies the restriction in (16). Now, from (34) we get

$$\left| a_{ii}\int_0^\infty \cos(vs)\, d\eta_{ii}(s) \right| \leqq d_i^{-1} \sum_{j\neq i} d_j\,|a_{ij}|,$$

which contradicts (16). Thus g cannot have a pure imaginary root, and neither does the characteristic equation of (14).

We now replace (16) by the same equation except that a_{ij} for $i \neq j$ is replaced by ha_{ij}, $0 \leqq h \leqq 1$. If $h = 1$, we of course return to our original equation. Also, conditions (15) and (16) imply the same conditions when for $i \neq j$ the a_{ij} are replaced by ha_{ij}, $0 \leqq h \leqq 1$. So, the characteristic equations of all these systems cannot have pure-imaginary roots, Also, the characteristic function $\det(\Delta_h(z))$ is continuous in (h, z) in $[0, 1] \times [\operatorname{Re} z \geqq 0]$ and analytic for (h, z) in $[0, 1] \times [\operatorname{Re} z > 0]$. Specifically, for $h = 0$, we have the characteristic equation

$$\det(\Delta_0(z)) = \prod_{i=1}^{n} \left[a_{ii}\int_0^\infty e^{-zs}\, d\eta_{ii}(s) - z\right] = 0,$$

whose zeros coincide with those of the equations

$$a_{ii}\int_0^\infty e^{-zs}\, d\eta_{ii}(s) - z = 0, \qquad i = 1, 2,\dots, n.$$

But, as we have seen in the proof of Theorem 2, these last equations have no roots z with $\operatorname{Re} z \geqq 0$ whenever the restrictions

$$a_{ii} \int_0^\infty d\eta_{ii}(s) < 0, \qquad -|a_{ii}| \int_0^\infty s\,|d\eta_{ii}(s)| + 1 > 0, \qquad i = 1, 2,..., n,$$

hold. That is, of course, condition (15) of our hypotheses, so the characteristic equation $\det(\Delta_0(z)) = 0$ has no nonnegative roots. Now, the roots of $\det \Delta_h(\lambda)$ are continuous functions of h, and since $\det \Delta_h(\lambda)$, $0 \leqslant h \leqslant 1$, has not roots with zero-real part, there does not exist h^* in the interval $[0, 1]$, where $\det \Delta_{h^*}$ has a root with positive-real parts. For, otherwise, there will exist some h with $0 \leqslant h \leqslant h^*$, for which $\det \Delta_h$ must have a pure-imaginary root. So, $\det \Delta = \det \Delta_1$ has no roots with positive real part and Theorem 2 is established.

Proof of Theorem 5. Let $y^i = X^i - \bar{X}^i$ and linearize the transformed equations (16) about $y^i = 0$ to get the equations

$$\frac{dy^i(t)}{dt} = \sum_{j=1}^{n} \left\{ \bar{X}^i a_{ij} y^j(t) + \bar{X}^i \gamma_{ij} \int_0^\infty \lambda e^{-\lambda s} y^j(t-s)\, ds \right.$$
$$\left. + \bar{X}^i b_{ij} \int_0^\infty y^j(t-s)\, d\mu_{ij}(s) \right\}, \qquad i = 1, 2,..., n. \tag{36}$$

From Theorem 3, we see that condition (19) implies that the trivial solution of (36) is asymptotically stable. This completes the proof of the theorem.

Proof of Theorem 6. Again let $y^i = X^i - \bar{X}^i$ and linearize the transformed equations (21) about $y = 0$ to get the equations

$$\frac{dy^i(t)}{dt} = \sum_{j=1}^{n} \left\{ \bar{X}^i a_{ij} \int_0^\infty y^j(t-s)\, d\eta_{ij}(s) \right.$$
$$\left. + \bar{X}^i \gamma_{ij} \int_0^\infty y^j(t-s)\, \lambda e^{-\lambda s}\, ds \right\}. \tag{37}$$

This can be rewritten in the form

$$\frac{dy^i(t)}{dt} = \bar{X}^i(a_{ii} + \gamma_{ii}) \int_0^\infty y^i(t-s) d\left[\frac{-a_{ii}\eta_{ii}(s) + \gamma_{ii} e^{-\lambda s}}{-a_{ii} - \gamma_{ii}}\right]$$
$$+ \sum_{\substack{j \neq i \\ j=1}}^{n} \bar{X}^i(|a_{ij}| + |\gamma_{ij}|)$$
$$\times \int_0^\infty y^j(t-s) d\left[\frac{a_{ij}\eta_{ij}(s) - \gamma_{ij} e^{-\lambda s}}{|a_{ij}| + |\gamma_{ij}|}\right]. \tag{38}$$

Equation (38) is in the form treated in Theorem 4, and conditions (22) and (23) imply that (15) and (16) hold, so zero is an asymptotically stable solution of (38), and Theorem 6 is proved.

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