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CONTENTS

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VOLTERRA INTEGRODIFFERENTIAL EQUATIONS IN POPULATION DYNAMICS

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VOLTERRA INTEGRODIFFERENTIAL EQUATIONS IN POPULATION DYNAMICS

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Introduction

Integrodifferential equations appear quite early in the mathematical development of theoretical population dynamics in the pioneering work of such mathematicians as V. Volterra and V. A. Kostitzin. In their attempts to model the growth of populations by means of differential equations these early investigators were quick to point out that the current growth rate of a population is unlikely to depend only on the current population size or, put another way, that growth rates are unlikely to respond instantaneously (or even "quickly") to changes in population sizes or densities. This led Volterra in particular to include functionals of (Volterra) integral type in what have become the classical differential models of population dynamics and mathematical ecology (equations such as the logistic equation, the famous predator-prey system of Volterra and the well-known Volterra-Lotka competition model). Much of this early work involving integrodifferential equations in population dynamics can be found in the recent collection of papers edited by Scudo and Ziegler (1978). Despite this early interest in and recognition of the importance of temporal response delays, the formulation, analysis and use of differential models which attempt to incorporate delays in them has lagged considerably behind that of nondelay models which ignore response delays. Nonetheless the inevitable presence and the often significant importance of response delays is widely recognized by population biologists as can be seen by the frequency of reference to such delays in textbooks (e.g. see

Ricklefs (1974) and Pianka (1978)) to say nothing of the more technical and specialized literature.

In recent years there has been an increasing mathematical interest in the study of biological models which incorporate response delays in them. This is especially true of single species growth models in which delays have been successfully used to model certain phenomena, for example the failure of some species to follow the classical logistic curve (typically insect species, but also some species of small mammals and birds, see e.g. Slobodkin (1961), May (1974,1976), Maynard Smith (1975), May et. al. (1974)). This is also true, although to a lesser extent, for some multi-species interactions (May (1973), Caswell (1972)). This more recent interest in single species models with delays, starting with the work of Wright (1955), Kakutani and Markus (1962) and Jones (1962) on the lag logistic equation*, has stimulated a great deal of mathematical research on such questions as the stability of equilibria and the existence of nontrivial periodic solutions of first order differential equations with time lags and, to a lesser extent, of equations with the biologically more reasonable case of more general delay response functionals. There has been corresponding less work of this nature done on systems with response delays, even though it is rare that a species (especially in nature) is isolated from interactions with other species and response delays obviously must play a role in the dynamics of these interacting species as well.

One aspect of the study of delays in population growth models which in my opinion has been on the whole very inadequately treated is that of the careful derivation of the delay model with regard to the biological or physical mechanism causing the delay and to how exactly this affects the growth rate. While some mechanisms which cause response delays are rather obvious even to a

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*I will use the term "lag" for instantaneous time delays while reserving the word "delay" for the more general case of a distributed delay.

casual observer, others are very subtle and complex. Perhaps gestation and maturation periods (or taken together, the "generation time") are the first to come to mind as causes of response delays in the growth rate to any change in population densities in that they result in a delayed response in the birth rate. Such delay mechanisms are often mentioned for example in context with the lag logistic equation (e.g. May (1976)) which, however, is an illustration of my point here since, as I will show below, the lag or delay logistic equation is altogether inappropriate as a model involving delays caused by gestation and/or maturation periods.

There are of course a great many other causes of delayed responses in population growth rates. In fact, the delay logistic equation was first proposed by Volterra (see Scudo and Ziegler (1978,pages 47-49)) to account for delays in the response of a population's death rate to changes in density as might be caused by an accumulation of pollutants (itself a functional of density) over past times. Volterra was in fact interested in a specific species of bacteria whose own metabolism results in the accumulation of toxic substances. Other causes of response delays which have been mentioned in the literature include differential resource consumption with respect to age structure, hunger threshold levels, migration and diffusion of populations, markedly differing birth rates in interaction species and delays in behavioral responses to a changing environment (including changes in density of prey or predators or competing species). And there are others.

Thus, if it is hoped to study and understand the effects of a response delay caused by a particular mechanism or a particular type of mechanism, then one must, given the complexity of biological interactions and the diversity of delay causing mechanisms, use some care in deriving the model and see to it that the delay in the model is affecting the appropriate vital parameters in an appropriate manner. Obviously this modeling procedure may not be so simple as to "stick a time delay" into a familiar nondelay model.

To quote Ricklefs (1974,p.488): "A population can be reduced much more rapidly by death than it can be built up by reproduction" and as a result "time lags might be expected to occur primarily in stabilizing processes involving reproduction rather than death, because death is an immediate response to environmental change". Thus it seems particularly appropriate to concentrate attention on gestation and maturation periods as primary causes of response delays (although there certainly can be others which are significant). This will, however, result in models which are not of the type obtained from so-called Kolomogorov-type differential equations ($P'/P = f(P)$) with delays placed in the per capita growth rate response functional f such as are most often considered (such as the delay logistic and the other models considered in Cushing (1977a) .

My purpose in these lectures is to derive some integrodifferential models for both single species and interacting species growth which allow for the inclusion of response delays in birth and death rates, including those caused by gestation and maturation periods, and to study in a little detail a few special cases of primary importance in mathematical ecology, namely single species growth, competition between two species and predator-prey interactions. Special, but not exclusive, attention will be paid to gestation and maturation periods and for this reason the models will be derived from a general dynamical model of age structured populations.

Since a central theme here is the role played by response delays, I will frequently be guided in the analysis by the desire to see what effects such delays have on the resulting dynamics, particularly if these effects are unusual. In this respect the "significance" of the response delay is, of course, a major concern and depends on what aspect of the dynamics one is interested in. Moreover, this question not only involves the "length" of the delay (in a time scale relative to other vital parameters) but also such things as the magnitude of the delayed effects when they are at last felt, which vital parameters are affected by the delayed response, the "spread of the delay period" and the exact manner in which the delayed terms affect the growth rate.

Chapter 1: SOME MODELS FOR POPULATION GROWTH

I would like to take as a starting point a dynamical model for age structured populations which is based on the so-called von Foerster equation (1.1) below. By taking into account the age structure of a population this model avoids the unrealistic assumption of a fixed constant age distribution within the population, an assumption which is inherently made in "lumped parameter" models for total population numbers based on ordinary differential equations (such as those of Kolomogorov type mentioned above). This assumption is for example particularly unsuitable for species in which there are important fluctuations in birth or death rates, fluctuations forced either by the physical environment or interactions with other species or caused by natural life cycles within the species. In such a model we can explicitly account for and study the effects of, in particular, maturation and gestation delays.

In this approach it is assumed that the population can be described by a (differentiable) density (of females) function $n(t,a) \geq 0$ of chronological age a and time t which are assumed measured on the same scale. Thus, if one assumes that the only way in which individuals can leave the population is by death (i.e. there is no emigration) then $\partial n/\partial t + \partial n/\partial a$ represents the change in an age cohort as a function of time. If then the death or removal rate is assumed proportional to density, one arrives at the von Foerster equation

$$(1.1) \qquad \partial n/\partial t + \partial n/\partial a + dn = 0 , \quad a > 0 , \quad -\infty < t < +\infty$$

where $d \geq 0$ is the (per unit density per unit time) death or removal rate. This death rate would reasonably be assumed to be a function of time, of age and, in a density regulated population, of the density n. Equation (1.1) accounts for the removal of individuals from the population. One must now account for the addition of individuals to the population which is assumed here to be only by births (of females) to members of the popluation (i.e. there is no immigration). Since by definition a newborn individual has age $a = 0$, this is done by means of the birth equation

$$(1.2) \qquad n(t,0) = \int_0^{\infty} m(a)n(t,a)\,da \ , \quad -\infty < t < +\infty$$

where $m \geq 0$ is the age specific <u>maternity function</u> (per unit density) which, although it is not explicitly stated in (1.2), might also be assumed to depend on time and, in a density regulated population, on the density n as well. Equation (1.2) assumes that reproduction is instantaneous in the sense that the number of (female) individuals born at time t to individuals of ages a to $a + da$ is proportional to the density n at time t. If, in order to take into account a possible gestation period between conception and birth, one considers m to be a <u>fertility</u> or <u>fecundity function</u> which is defined so that $m(t,a)n(t,a)da$ is the number of fertilized eggs (which ultimately result in births) produced at time t by females of ages a to $a + da$ then equation (1.2) is replaced by the equation

$$(1.3) \qquad n(t,0) = \int_{-\infty}^{t} g(t-s) \int_0^{\infty} m(s,a)n(s,a)\,da\,ds \ , \quad -\infty < t < +\infty$$

where $g(s) \geq 0$, $\int_0^\infty g(s)ds = 1$, is a <u>gestation probability density function</u> describing the probability that an egg fertilized at some time (and which ultimately results in a live birth of a female) will produce an addition to the population at s units of time later.

In the formulation of the model above initial conditions of the form $n(0,a) = n_0(a)$, $a \geq 0$, have been ignored. Instead it is assumed that such initial conditions contribute transient effects as $t \to +\infty$, that the population has been dynamically evolving for a long (in fact, an infinite amount of) time, and that it is the long term asymptotic behavior as $t \to +\infty$ of the population density which is of interest. With the "initial state placed at $t = -\infty$" in this manner the above equations are, as indicated, to be solved for $-\infty < t < +\infty$ instead of for $t > 0$. If, on the other had, an initial value problem is considered, it turns out that the models ultimately to be considered here will change only in that $-\infty$ will be replaced by 0 in certain integrals and a forcing function will appear in the equations which tends to zero as $t \to +\infty$ (and in fact will have compact support if the function m, d, g and n_0 do). Thus the models studied here are the "limiting equations" of those derivable from the initial value problems. The benefit of ignoring the initial conditions from the outset is the avoidance of a great amount of technical detail and cumbersome formulas.

The linear autonomous version of problem (1.1)-(1.2) when d and m, as shown, do not depend on t or n leads by an integration along characteristics (for the associated initial value problem) to the linear renewal equation for the birth rate function $B(t) := n(t,0)$. The linear renewal equation has of course a long and rich history in population dynamics and other subjects. In recognition of the nonlinearities inherent in density regulated population dynamics there is a growing interest in nonlinear versions of this model (e.g. see Rotenberg (1975), Gurtin and MacCamy (1974), Oster (1978), Hoppenstaedt (1975)).

The replacement of (1.2) by (1.3) allows the additional possibility of a gestation period. The only work I know of on such a model is that of Swick (1976,1977) who considers existence, uniqueness and boundedness questions for the case of a gestation lag (where g(s) is the Dirac delta function $\delta_T(s)$) much along the lines of Gurtin and MacCamy's (1974) work on (1.1)-(1.2).

My goal here however is not to study any of these models per se but to derive from them integrodifferential models for the total population size

$$P(t) := \int_0^\infty n(t,a)\,da \ . \tag{1.4}$$

If one is interested in modeling the dynamics of several interacting species then one has model equations as above for each species' density and these are coupled by the assumption that the vital parameters d and m depend on the densities of the other species. These models can be shown (as we'll see below) to yield, under the assumption that vital parameters are independent of age, to yield general ordinary differential (or functional) equation models for the total population size P, including the familiar classical equations of population dynamics. But even in this case the above model has the advantage that the age structure of the population can be recovered. Moreover, by discretizing independent variables one can obtain familiar difference equation models (such as the frequently used Leslie matrix models). Thus, the von Foerster age structure model constitutes a nice unifying set of modeling equations in population dynamics.

From now on it is assumed that the death rate $d = d(t) \geq 0$ is a function of time, either explicitly or implicitly through a dependence on population size $P(t)$, and that the fertility function $m = m(t,a) \geq 0$ is a function of age and time (again possibly implicitly through a dependence on $P(t)$). In doing this, without being specific with the notation, the possible dependence of d and m on $P(t)$ is permitted to be that of a functional of population sizes over possibly past times. Note that the death rate d is assumed not to depend on age a. This admittedly unreasonable assumption (which is often made in specific models, e.g. see Oster (1978), Oster and Takahashi (1974)) is made here purely for mathematical reasons and many of the manipulations to follow are not valid without it. Nonetheless, age dependence is permitted in the fecundity function m, which of course allows one to study the effects of maturation periods. This assumption might be considered appropriate for a species in which there is greater variation in fecundity with age than in the death rate with age.

Let $B(t) := n(t,0)$ denote the birth rate at time t. From (1.1) one gets

$$n(t,a) = B(t-a)\exp\left(-\int_0^a d(t-a+\sigma)\,d\sigma\right)\ , \quad a > 0,\ -\infty < t < +\infty \tag{1.5}$$

which together with (1.4) and the birth equation (1.3) yields

$$B(t) = P'(t) + d(t)P(t) \tag{1.6}$$

$$B(t) = \int_{-\infty}^{t} g(t-s)\int_0^\infty m(s,a)B(s-a)\exp\left(-\int_0^a d(s-a+\sigma)\,d\sigma\right) da\,ds\ . \tag{1.7}$$

As it will ultimately be assumed that both d and m depend on total population size, equations (1.6) and (1.7) constitute a system of two coupled equations for P and B. The system (1.6)-(1.7) is equivalent to the uncoupled system consisting of (1.6) and the equation

$$P'(t) + d(t)P(t) =$$
$$\int_{-\infty}^{t} g(t-s)\int_0^\infty m(s,a)\{P'(s-a) + d(s-a)P(s-a)\}\exp\left(-\int_0^a d(s-a+\sigma)\,d\sigma\right) da\,ds$$

which , after an integration by parts, reduces to

$$\begin{aligned} &P'(t) + d(t)P(t) = \\ &\int_{-\infty}^{t} g(t-s)\left\{m(s,0)P(s) + \int_0^\infty m_a(s,a)P(s-a)\exp\left(-\int_0^a d(s-a+\sigma)\,d\sigma\right) da\right\} ds \end{aligned} \tag{1.8}$$

In doing the integration by parts it was assumed that the expression $m(t,a)P(t-a)\exp(-\int_0^a d(t-a+\sigma)d\sigma)$ vanishes at $a = +\infty$ for all $-\infty < t < +\infty$, which would be the case for example if $m(t,+\infty) \equiv 0$ (a reasonable biological assumption is in fact that $m(t,a) \equiv 0$ for all t whenever $a \geq a_0$ for some age a_0) or if $\lim_{a\to\infty} \exp(-\int_0^a d(s-a+\sigma)d\sigma) = 0$ and $P(t)$ is bounded (e.g. when $d \equiv$ constant).

Equation (1.8) is an integrodifferential equation for the total population

$P(t)$, a bounded solution of which defines a birth rate function $B(t)$ by means of (1.6) which then in turn defines the population age dependent density $n(t,a)$ by means of (1.5). If d and m are also functionals of total population size $P(s)$ for $s \le t$, which one might denote by $d = d(t,P_t)$, $m = m(t,a,P_t)$, then (1.8) becomes the rather complicated nonlinear integrodifferential equation

$$\text{(1.9)} \qquad \begin{aligned} &P'(t) + d(t,P_t)P(t) = \\ &\int_{-\infty}^{t} g(t-s)\{m(s,0,P_s)P(s) + \int_0^\infty m_a(s,a,P_s)P(s-a)\exp(-\int_0^a d(s-a+\sigma, \\ &\qquad\qquad P_{s-a+\sigma})\, d\sigma)\, da\}ds \ . \end{aligned}$$

This equation can be used to derive specific models which incorporate delays due to gestation periods as described by the probability distribution function $g(s)$, to maturation periods as described by m as a function of age a and/or to delay responses in the death or fecundity functions d and m as they are functions of P_t .

As a special case, if gestation and maturation periods are ignored by assuming that $g(s)$ is the Dirac delta function at $T = 0$ (or alternatively by deriving from (1.2) in place of (1.3)) and by assuming that $m = m(t,P_t)$ is independent of age a, then (1.9) reduces to the equation

$$\text{(1.10)} \qquad P'(t) = (m(t,P_t) - d(t,P_t))P(t)$$

a very general functional differential equation of Kolomogorov type. In particular, the choices $m \equiv \text{constant} > 0$, $d = \delta + \mu P(t) + \gamma\int_0^\infty k(s)P(t-s)ds$, $\delta > 0$, $k(s) \ge 0$ leads to a delay logistic equation considered by Volterra and by Kostitizin (see Scudo and Ziegler (1978,p.47-56)).

Or, as another case, if the only delay of interest is caused by a gestation period so that $m = m(t,P)$ is independent of age a and if d and m respond instantaneously to total population changes, (1.9) becomes

$$(1.11)\qquad P'(t) + d(t,P(t))P(t) = \int_{-\infty}^{t} g(t-s)m(s,P(s))P(s)\,ds\ .$$

Another special case I will consider is the case when d is a constant, when there is no gestation period and when $m = m(t,a,P(t))$ with $m(t,0,P) = 0$. This results in the integrodifferential equation

$$(1.12)\qquad P'(t) + dP(t) = \int_{0}^{\infty} m_a(t,a,P(t))P(t-a)\exp(-da)\,da\ .$$

In the following chapters I will consider some questions concerning the stability or instability of equilibrium population sizes, unforced oscillations in a constant environment and forced oscillations in a periodically varying environment for single species in isolation and for some special two species interactions. In the case of interacting species, one has a system of equations (1.9) for each individual species which are coupled by the assumption that each species' death and fecundity functions depend on the total population sizes of other species as well as its own.

The more fundamental mathematical questions of existence and uniqueness of solutions of (1.9) will not be treated here. It is not difficult to prove standard type theorems (involving Lipschitz conditions) when the solution is prescribed $P(t) = P_0(t)$ for $t \leq 0$.

Another fundamental question as far as models in population dynamics is concerned is that of the positivity of solutions. When $P_0(t) > 0$ implies $P(t) > 0$ for $t > 0$ for the general equation (1.9) is an open problem. In general this positivity property fails to be true since m_a may change sign. For the special case (1.11) of a gestation delay we have

THEOREM 1. _Suppose there exist constants_ $0 \leq c_1 < c_2 \leq +\infty$ _such that for all_ $t \geq 0$

$$(1.13)\qquad m(t,P) = 0 \ \underline{\text{for}}\ 0 \leq P \leq c_1 \ \underline{\text{and}}\ P \geq c_2,\ m(t,P) > 0\ \underline{\text{for}}\ c_1 < P < c_2.$$

Suppose $g(t) > 0$ for $t > 0$. If $P(t)$ is a solution of (1.11) for which $P(t) > 0$ when $t \leq 0$, then $P(t) > 0$ for as long as it exists for $t > 0$.

Proof. Let $t^* > 0$ be the first point at which $P(t^*) = 0$. Then $P'(t^*) \leq 0$ and (1.11) implies $\int_{-\infty}^{t^*} m(s,P(s))g(t^*-s)P(s)ds = 0$ (and $P'(t^*) = 0$) which in turn implies $0 \leq P(t) \leq c_1$ for all $-\infty < t \leq t^*$. Thus from (1.11) on the interval $0 < t \leq t^*$ follows $P'(t) + d(t,P(t))P(t) = 0$. This implies together with $P(t^*) = 0$ that $P(t) \equiv 0$ for $0 \leq t \leq t^*$ which is a contradiction to t^* being the first zero of $P(t)$. This contradiction implies no first zero t^* exists. §§

Note that the condition (1.13) permits the fecundity to drop to zero for small and/or large population sizes.

An obvious positivity theorem can be stated analogously for systems of equations (2.11) for several species.

Chapter 2: STABILITY AND SINGLE SPECIES MODELS

Suppose that the death rate $d = d(P_t)$ and the fecundity function $m = m(a,P_t)$ do not depend explicitly on time t. Then (1.9) has an equilibrium solution $P(t) \equiv P_0$ if and only if either $P_0 = 0$ or P_0 solves

$$(2.1) \qquad R := \int_0^\infty m(a,P_0)\exp(-d(P_0)a)\, da = 1 .$$

The number R is called the net reproductive rate (at equilibrium) and can be interpreted as the expected number of (female) offspring per female during her lifespan (under the assumption that the population is held at the equilibrium level P_0). Equation (2.1), which means that the population is at exact replacement, is an equation to be solved for $P_0 > 0$.

If any functional dependence of d or m is of Volterra integral form

$$P_t = \int_0^\infty K(s)P(t-s)\, ds \quad , \qquad \int_0^\infty |K(s)|\, ds < +\infty$$

and if $x(t) := P(t) - P_0$ then an $n \times n$ system of equations of the general form (1.9) will reduce, after ignoring all "higher order" terms in x, to an integrodifferential system of the form[*]

$$(2.2) \qquad x'(t) + Cx(t) + \int_0^{\infty} B(s)x(t-s)\,ds = 0 \;, \quad B_1 := \int_0^{\infty} |B(s)|ds < +\infty$$

for some constant $n \times n$ matrix C and an $n \times n$ matrix kernel $B(t)$. Associated with this equation is the characteristic equation

$$D(z) := \det(zI + C + B^*(z)) = 0$$

where $B^*(z)$ is the Laplace transform of $B(t)$. If

$$(2.3) \qquad D(z) \neq 0 \quad \text{for all} \quad \operatorname{Re} z \geq 0$$

then all solutions of

$$(2.4) \qquad x'(t) + Cx(t) + \int_0^t B(t-s)x(s)\,ds = f(t)$$

tend to zero as $t \to +\infty$ for any bounded continuous $f(t)$ which tends to zero as $t \to +\infty$ (Miller (1972)). For equation (2.2) this means that all solutions which are bounded for $t \leq 0$ tend to zero as $t \to +\infty$ since $f(t) = \int_t^{\infty} B(s)x(t-s)ds \to 0$. If a functional in x is added to equation (2.4) which is higher order in x (i.e. is $o(|x|_0)$ where $|x|_0 := \sup_{t \geq 0}|x(t)|$ uniformly in $t \geq 0$) then the resulting equation is locally asymptotically stable in the sense that if $|f|_0$ is small then all solutions for which $|x(0)|$ is small are themselves small for all $t \geq 0$ and tend to zero as $t \to +\infty$ (Cushing (1975)). For systems of equations (1.9) this means that if $x(t) = P(t) - P_0$ is small for $t \leq 0$ then $x(t)$ is small for $t > 0$ and $P(t) \to P_0$ as $t \to +\infty$. In this sense the equilibrium P_0 will be called

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[*] In order to keep the technical details to a minimum the explicit description of the domains and smoothness of the various functions (such as d and m) will not be stated. It is assumed that there is enough smoothness to carry out the linearization above. For simplicity all kernels are continuous.

locally asymptotically stable. (The consideration of initial conditions defined for all $t \leq 0$ can be avoided by posing an initial value problem for the von Foerster equation (1.1) as mentioned in Chapter 1 in which case integrodifferential systems of the form (2.4) for $t > 0$ will be obtained straight away.) The equilibrium P_0 is <u>unstable</u> if $D(z) = 0$ has a root satisfying $\mathrm{Re}\, z > 0$.

Under the assumption that $B^*(z)$ is analytic for $\mathrm{Re}\, z \geq 0$ and that $D(z)$ has no roots with $\mathrm{Re}\, z = 0$ the number of roots $\nu(R)$ of $D(z)$ inside a semi-circle $|z| \leq R$, $\mathrm{Re}\, z \geq 0$ is given by the argument principle $\nu(R) = (1/2\pi i)\int_{\gamma(R)} D'(z)/D(z)dz$ where $\gamma(R)$ is the boundary of the semi-circle. Consider now the case of a single equation (1.9) in which case we write $C = c$, $B(t) = b(t)$ and $b_1 := \int_0^\infty |b(s)|ds$. Then

$$\frac{D'(z)}{D(z)} - \frac{1}{z} = \frac{b^{*\prime}(z)}{D(z)} - \frac{c + b^*(z)}{zD(z)}$$

and on the curve $\gamma_1(R)$: $|z| = R$, $\mathrm{Re}\, z \geq 0$ for $R > |c| + b_1$

$$\left|\int_{\gamma_1(R)} \frac{c + b^*(z)}{zD(z)}\, dz\right| \leq \frac{|c| + b_1}{R - |c| - b_1}\,\pi$$

$$\left|\int_{\gamma_1(R)} \frac{b^{*\prime}(z)}{D(z)}\, dz\right| \leq \frac{R}{R - |c| - b_1} \int_{\theta=-\pi/2}^{\pi/2} |b^{*\prime}(Re^{i\theta})|\, d\theta$$

since $|b^*(z)| \leq b_1$ for $\mathrm{Re}\, z \geq 0$. From Theorem B.1 of Appendix B follows

$$\lim_{R\to+\infty} \int_{\gamma_1(R)} \frac{D'(z)}{D(z)}\, dz = \lim_{R\to+\infty}\int_{\gamma_1(R)} \frac{1}{z}\, dz = \pi i\ .$$

Thus the number of roots ν of $D(z)$ in the right half plane $\mathrm{Re}\, z \geq 0$ equals $\nu = \lim_{R\to+\infty}\nu(R) = \frac{1}{2} + \lim_{R\to+\infty}(\arg D(-iR) - \arg D(iR))/2\pi$.

If $D(0) = c + \int_0^\infty b(s)ds < 0$ then $D(z) = 0$ obviously has a positive real root $z = x > 0$ since $D(x) \to +\infty$ as $x \to +\infty$. In this case (2.2) is unstable. Suppose then that $D(0) > 0$ and that we choose the principle argument $\arg D(0) = 0$. Then since $D(\overline{z}) = \overline{D(z)}$ it follows that $\arg D(-iR) =$

$-\arg D(iR)$ and $\nu = \frac{1}{2} - \frac{1}{\pi}\arg D(+i\infty)$ where $\arg D(+i\infty) := \lim_{R\to+\infty} \arg D(iR)$. Consequently $\arg D(+i\infty) = (1 - 2\nu)\pi/2$ for some nonnegative integer $\nu \geq 0$. But $D(iR) = iR + c + b^*(iR)$ and hence $\lim_{R\to+\infty} \operatorname{Im} D(iR) = +\infty$ since $b^*(iR) := C(R) - iS(R)$ where

$$C(R) := \int_0^\infty b(s)\cos Rs\, ds \qquad , \qquad S(R) := \int_0^\infty b(s)\sin Rs\, ds$$

is bounded as a function of R. This means $\nu = 2m$ must be even.

THEOREM 2. (i) *If* $D(0) = c + \int_0^\infty b(s)ds < 0$ *then the equilibrium* P_0 *of equation* (1.9) *is unstable.*

(ii) *Suppose that* $D(0) > 0$, *that* $b_2 := \int_0^\infty s|b(s)|ds < +\infty$ *and that* $D(z) := z+c+b^*(z)$ *has no purely imaginary roots. Then* $\arg D(+i\infty) = \frac{\pi}{2} - 2m\pi$ *for some integer* $m \geq 0$ *and the equilibrium* P_0 *of equation* (1.9) *is locally asymptotically stable if* $m = 0$ *and unstable if* $m \geq 1$.

This very general stability criterion (which is a generalization of Theorem 3.3, page 31 in Cushing (1977a) in which $c = 0$) can be used to prove virtually all stability theorems found in the literature. For example, if $D(0) > 0$ then P_0 is locally asymptotically stable under any one of the following circumstances:

(a) $c + C(R) \geq 0$ for all $R \geq 0$

(b) $b(+\infty) = b'(+\infty) = 0$ and $c + \int_0^\infty b''(s)(1-\cos Rs)ds \geq 0$ for all $R \geq 0$

(c) whenever $c + C(R) = 0$ then $R \geq S(R)$

(d) $R \geq S(R)$ for all $R \geq 0$

(e) $b(s) \geq 0$, $0 < \int_0^\infty sb(s)\, ds \leq 1$.

Since $D(iR) = c + C(R) + i(R - S(R))$ it is easily seen that (a) or (c) imply that $D(iR)$ does not "wind around" $z = 0$ for $R \geq 0$ and hence that $\arg D(+i\infty) = \pi/2$. Condition (b) follows from (a) after two integrations by parts and yields a theorem of Walther (1975) when $c = 0$, $b''(s) \geq 0$. Condition (d) obviously follows from (c). Condition (e) follows from (d) since it implies that $\operatorname{Im} D(iR) = R - S(R)$ is an increasing function of R. Condition (e) implies a theorem of Stech (1978).

To illustrate these results consider the delay logistic equation

$$(2.5) \qquad P'(t) = P(t)\left(r - \mu P(t) - \gamma\int_0^\infty k(s)P(t-s)\,ds\right)$$

where $r > 0$, $\mu \geq 0$, $\gamma \geq 0$ and $k(s) \geq 0$, $\int_0^\infty k(s)ds = 1$. This equation has equilibria $P_0 = 0$ and $P_0 = r/(\mu + \gamma) > 0$ provided $\mu + \gamma \neq 0$. Clearly $P_0 = 0$ is unstable since the linearization is $P' = P$. Assuming that $\int_0^\infty sk(s)ds < +\infty$ we may apply Theorem 1 to the characteristic equation $D(z) = z + \mu P_0 + \gamma P_0 k^*(z) = 0$. More specifically (a), (b) and (e) above imply that <u>the delay logistic</u> (2.5) <u>has a locally asymptotically stable equilibrium</u> $P_0 = r/(\mu + \gamma)$ <u>if any one of the following conditions hold</u>:

(i) $\gamma < \mu$ (ii) $k(+\infty) = k'(+\infty) = 0$, $k''(s) \geq 0$ (iii) $\int_0^\infty sk(s)ds \leq \frac{\mu + \gamma}{\gamma r}$.

The first stability condition (i) (Miller (1966)) means that the magnitude of those density effects on the death rate which are delayed is less than those which act instantaneously. Condition (iii) is entirely different; it means that the "length" of the delay as measured by the first moment of the delay kernel $k(s)$ is small regardless of the relative magnitudes of γ and μ. Condition (ii) is yet different in that it implies stability purely on the basis of the "shape" of the delay kernel (in this case $k(s)$ is concave) independently of the vital parameters r, μ and γ. Condition (ii) is probably the least interesting since it implies k is montonically decreasing and hence such a kernel represents a case of "lingering effects" or "fading memory" rather that a "genuine" delay. (Such a stability condition has recently been used in a predator-prey system by Leung (1979).)

These three stability conditions illustrate how the effects of delays can be studied or measured in a variety of ways.

Condition (i) actually implies the global attractibility of the positive equilibrium (with respect to positive solutions, Miller (1966)). The ideas of Miller (1966) have been considerable generalized in a recent paper of Artstein and Karakostas (1979) where conditions in the spirit of (i) are shown to imply the global attractibility of a positive equilibrium of a general functional equation. Global stability is also considered by Wörz-Busekros (1978) using Liapunov functions for equations involving special kernels $k(s)$, namely kernels which are linear combinations of polynomials times decaying exponentials. These very interesting global results, however, do not seem to apply or at least have not been applied to non-Kolomogorov type models such as (1.9).

The equation (1.9) derived in Chapter 1 is obviously quite complicated in a general setting. I want therefore only to consider the special cases (1.11) and (1.12) in order to gain some insight into the effects of gestation and maturation periods separately. Before doing this, however, it is possible to make a couple of simple observations about (1.9). First of all, $P_0 = 0$ is always an equilibrium . Secondly, if (1.9) is linearized at $P_0 = 0$ under the assumption that $d = d(P_t)$, $m = m(a,P_t)$ are independent of time, one obtains the linear equation

$$x'(t) + d_0x(t) = \int_{-\infty}^{t} (m_0(0)g(t-s) + k(t-s))x(s)\,ds$$

where $k(t) = \int_0^t g(t-s)m_0'(s)\exp(-d_0s)ds$ and where $d_0 = d(0) \geq 0$, $m_0(a) = m(a,0) \geq 0$. The characteristic equation is then $(z + d_0)(1 - g^*(z)m_0^*(z+d_0)) = 0$ whose roots are $z = -d_0$ and those of $g^*(z)m_0^*(z+d_0) = 1$. Since for $\text{Re } z \geq 0$ we have $|g^*(z)| \leq 1$, $|m_0^*(z+d_0)| \leq \int_0^\infty m_0(s)\exp(-d_0s)ds := R_0$ where R_0 can be interpreted as the net reproductive rate when the population is near zero. Thus there are no roots satisfying $\text{Re } z \geq 0$ if $R_0 < 1$ and $d_0 > 0$ which leads us to the reasonable and general conclusion that <u>if the net reproductive rate drops below replacement for small population sizes then small populations will go extinct</u> ($P_0 = 0$ is locally asymptotically stable).

As a first special case I would like to consider the effects of a maturation period, but in the absence of a (significant) gestation period or any other response delay. Consider then the equation (1.12) and assume there exists a positive equilibrium $P_0 > 0$ (i.e. P_0 solves (2.1)). The death rate is assumed constant: $d = \text{constant} > 0$. The fecundity function $m = m(a,P) \geq 0$ is assumed independent of time t and is assumed to satisfy the following:

$$(2.6)\quad m(0,P) \equiv 0,\ m_P(a,P_0) \leq 0\ (\not\equiv 0),\ m_P(0,P_0) = 0,\ m_P(+\infty,P_0) \text{ exists .}$$

These mean in essence that newborns have zero fecundity and that any increase in total population, at least near equilibrium, cannot result in increased fecundity for any age group. The linearization at P_0 leads to

$$x'(t) + d(1 - P_0 \int_0^\infty m_P(a,P_0)e^{-da}da)x(t) = \int_0^\infty m_a(a,P_0)e^{-da}x(t-a)\,da$$

whose characteristic equation reduces to (after a division by $z + d$)

$$(2.7)\qquad (z + d(1 - P_0 \int_0^\infty m_P(a,P_0)e^{-da}da))/(z + d) = m_0^*(z+d)$$

where $m_0^*(z)$ is the Laplace transform of $m_0(a) = m(a,P_0)$. If z is a root of (2.7) with $\text{Re } z \geq 0$ then from (2.6) the left hand side of (2.7) is strictly greater than one in absolute value. But by (2.1) it follows that $|m_0^*(z+d)| \leq \int_0^\infty m(a,P_0)e^{-da}da = 1$ for $\text{Re } z \geq 0$. This contradiction implies that (2.7) has no roots satisfying $\text{Re } z \geq 0$.

THEOREM 3. Under the assumptions (2.6) on the fecundity function m any positive equilibrium of (1.12) is locally asymptotically stable.

Since the conditions (2.6) are quite general and also very reasonable biologically we conclude that maturation periods per se are not likely to cause instabilities.

A typical example is (see Hoppensteadt (1975))

$$(2.8)\quad m = b\beta(a)\{1-P\}_+\ ,\ \beta(0) = 0,\ \beta(a) \geq 0,\ \int_0^\infty \beta(a)da = 1,\ \beta(+\infty) \text{ exists, } b>0$$

where $\{x\}_+ = x$ if $x \geq 0$ and zero if $x < 0$. Without loss in generality I have assumed that the total population is measured in units such that the fecundity (of all age classes) drops to zero when the population size reaches unity. The constant b will be referred to as the *modulus of fecundity*. For this example, $P_0 = (R_0-1)/R_0$ where $R_0 = b\beta^*(d) = b\int_0^\infty \beta(a)\exp(-da)da$ is the net reproductive rate and thus $P_0 > 0$ if and only if $R_0 > 1$ (a condition which we saw above to be necessary for the instability of the zero equilibrium state). By Theorem 3 this positive equilibrium is locally asymptotically stable when it exists, namely when $R_0 > 1$.

Suppose that in the example (2.8) the fecundity age distribution function $\beta(a)$ is given by one of the functions

$$\beta_n(a) = \left(\frac{n}{T}\right)^{n+1} \frac{1}{n!} a^n e^{-na/T} \quad , \quad n = 1,2,3,\ldots. \tag{2.9}$$

where $T > 0$ is the *age of maximum fecundity*. The integer n measures the *"length" of the period of active reproduction*. An increase in n shortens this period of active reproductivity while a decrease in n lengthens it. In this case $\beta^*(d) = \beta^*_n(d) = n^{n+1}(dT+n)^{-n-1}$ and the (low population level) net reproductive rate becomes $R_0 = R_0(n,dT,b) = bn^{n+1}(dT+n)^{-n-1}$. Solving (2.1) for the equilibrium P_0 one finds that $P_0 = P_0(n,dT,b) = (R_0-1)/R_0$. Note that P_0 increases (decreases) as R_0 increases (decreases) and is positive if and only if $R_0 > 1$. It is interesting to study for this example the dependence of P_0 on n, dT and b. This can be done by means of Theorem B.2 of Appendix B. Suppose we pose the problem of trying to obtain a maximum positive equilibrium P_0. From Theorem B.2 it is seen that in this example the equilibrium P_0 is positive if

$$b\,e^{-dT} > 1 \quad \text{and} \quad n \geq N \geq 1 \tag{2.10}$$

for a certain first integer N. Furthermore

(i) for fixed $dT \leq 2$ and b satisfying (2.10) the equilibrium $P_0 = P_0(n,dT,b)$ monotonically increases to $P_\infty = (be^{-dT}-1)/be^{-dT} < 1$ with $n \geq N$;

(ii) for fixed $dT > 2$ and b satisfying (2.10) the equilibrium P_0 increases to a maximum for some $n_0 \geq N$ after which it decreases to P_∞ with increasing n;

(iii) for fixed n and dT, P_0 increases with b;

(iv) for fixed b and n, P_0 increases with decreasing dT.

The last two statemnts (iii) and (iv) lead to the rather intiutively obvious conclusion that in order to maximize the population equilibrium the modulus of fecundity b should be increased and the death rate d should be decreased. The first two statements (i) and (ii) lead to the following theoretical conclusions: if a species matures sexually at an early age (relative to its expected lifespan, i.e. T is small relative to $1/d$) then it can always increase its equilibrium size by narrowing its active reproductive period (i.e. by increasing n). If however it reaches sexual maturity late then there is an optimal length to its reproductive period which produces a maximal equilibrium population size. The case (ii) would seem to be an exceptional case however. This is because e^{-da} is the probability of surviving to at least age a and hence expected survival is to age $1/d$. The condition $dT > 2$ means that the age of maximum reproductivity T is twice the expected life span $1/d$.

Whereas a maturation period delay does not cause instabilities in the models above, a gestation period can cause instabilities, as will be seen in the next chapter.

Chapter 3: SINGLE SPECIES OSCILLATIONS IN A CONSTANT ENVIRONMENT

Consider the model (1.11) with a gestation period delay when $d = d(P) \geq 0$ and $m = m(P) \geq 0$ are independent of age a and time t. This equation has a positive equilibrium P_0 if and only if $m(P_0) = d(P_0) \geq 0$ has a solution $P_0 > 0$ (see (2.1) in which $R = m(P_0)/d(P_0)$). A linearization of (1.11) about P_0 yields the equation

$$x'(t) + (d_0 + P_0 d_0')x(t) = (d_0 + P_0 m_0') \int_{-\infty}^{t} g(t-s)x(s)\, ds \quad ,$$

where $d_0 = d(P_0)$, $d_0' = d'(P_0)$ and $m_0' = m'(P_0)$, whose characteristic equation is

$$(3.1) \qquad D(z) := z + (d_0 + P_0 d_0') - (d_0 + P_0 m_0')g^*(z) = 0 \quad .$$

The stability criteria of Chapter 2 can be applied to this equation with $c = d_0 + P_0 d_0'$ and $b(s) = -(d_0 + P_0 m_0')g(s)$. That $P_0 > 0$ can be unstable, unlike the case of the maturation delay model (1.12) considered in Chapter 2, can be easily illustrated by an example.

Suppose that d = constant > 0 and $m = b\{1 - P\}_+$, b = constant > 0. Then $P_0 = (b - d)/b > 0$ if and only if $b > d$. Since $d_0' = 0$, $m_0' = -b$ we find

$$D(z) = z + d - (2d - b)g^*(z) \quad .$$

The stability criteria of Chapter 2 (following Theorem 2) can be applied to this equation. For example, from (a), (b) and (e) respectively we find that P_0 in this example is asymptotically stable if $d < b < 3d$ or if $g(+\infty) = g'(+\infty) = 0$, $g''(s) \geq 0$ and $b > 2d$ or if $b > 2d$ and $\int_0^\infty sg(s)ds < 1/(b-2d)$ respectively.

To see that P_0 can be unstable in this example, consider the special case when the gestation period probability density function is $g(s) = T^{-2}se^{-s/T}$, $T > 0$. Then $g^*(z) = (zT + 1)^{-2}$ and it is easy to show by investigating the roots of $D(z)$ that P_0 is asymptotically stable if $b < b_0$ and is unstable if $b > b_0$ where b_0 is given by

$$(3.2) \qquad b_0 = 2Td^2 + 6d + \frac{2}{T} \quad .$$

Note that this critical value b_0 of the modulus of fecundity b is large for both small and large gestation delays T (unlike the case of the famous delay logistic equation where $b_0 \to 0$ as $T \to +\infty$; see May (1974, p.98)). Note also that b_0 attains a minimum of $10d$ at $T = 1/d$, in other words the smallest critical value of the modulus of fecundity occurs when the gestation period in length is equal to the expected lifespan of an individual. This suggests that instabilities due to gestation delays are more likely in species which die immediately after reproduction.

Loss of equilibrium stability suggests the possibility of nontrivial sustained oscillations. Sustained oscillations in a constant environment, whether caused by a gestation period or whether caused by some other mechanism, are of great interest to population biologists. Although all population data invariably possess fluctuations, the regularity of the fluctuations of certain populations have intrigued ecologists for many years. Regular "cycles" have been reported, just to mention a few cases, in populations of the Snowshoe Hare, Canadian Lynx, many species of voles and lemmings, the Prairie Chicken, the Ruffed Grouse, Muskrat and many other (particularly Arctic) small mammals and birds as well as certain insect species including the Sheep Blowfly, water fleas of the genus Daphnia and several strains of beetles. Any regularity in population fluctuations can of course be due to a great many causes, some of the more obvious being regular daily or seasonal oscillation in abiotic environmental factors such as temperature, weather conditions, availability of food and water or other resources, etc. An intriguing aspect of many observed cycles, however, is that they often track no apparent environmental periodicity. For example, small herbivores such as voles and lemmings often have approximately three to four year cycles while larger herbivores such as the hare, lynx and grouse often have approximately ten year cycles (Ricklefs (1974)). Oscillations can also be attributed to interactions with other species even in an otherwise constant environment such as is suggested by the famous Volterra predator-prey model. Laboratory experiments with insects (e.g. see Slobodkin (1961), Nicholson (1954)) have shown, on the other hand, that it is also poosible for a single isolated species to have sustained population oscillations in a constant environment. This possibility for inherent oscillations is of interest to population biologists as one possible explanation of certain observed cycles.

For mathematicians who are interested in the study of models arising from population dynamics the question of the existence of periodic solutions and the nature of these solutions is of course an interesting and challenging one. The topics of the existence and bifurcation of periodic solutions, their periods and amplitudes, beats, resonance, synchronization and many others are familiar topics in other applied fields. Most of these topics are virtually unexplored with respect to models in population dynamics.

Consider now the question of the onset of oscillations accompanying the loss of stability in a single species model in a constant environment. I want to treat this question as one of a bifurcation phenomenon for the autonomous integrodifferential equation (1.9) by means of the following very general theorem (Cushing (1979b)).

THEOREM 4. *Suppose that the linear equation*

$$y'(t) + \sum_{i=1}^{2} \alpha_i \int_0^\infty y(t-s)\, dh_i(s) = 0 \tag{3.3}$$

has exactly two independent p-periodic solutions $y_i(t)$ *for isolated values of the constant* α_i *and for integrators* $h_i(s)$ *of finite total variation. Suppose that the operator* $S(x,\lambda_1,\lambda_2)$ *satisfies hypothesis H3 of Appendix A with* $Y = C^0(p)$ *and* $X = C^1(p)$, *the Banach spaces of continuous and continuously differentiable p-periodic functions under the usual supremum norms and that* $S(x,\lambda_1,\lambda_2) = o(||x||_0+||x'||_0)$ *near* $x = 0$ *uniformly on bounded* λ_1,λ_2 *sets. Then the equation*

$$x'(t) + \sum_{i=1}^{2} \alpha_i \int_0^\infty x(t-s)dh_i(s) = - \sum_{i=1}^{2} \lambda_i \int_0^\infty x(t-s)dh_i(s) + S(x,\lambda_1,\lambda_2) \tag{3.4}$$

has p-periodic solutions of the form $x(t) = \varepsilon(y(t) + z(t,\varepsilon))$, $\lambda_i = \lambda_i(\varepsilon)$ *for small* $|\varepsilon|$ *with* $z(t,0) \equiv 0$, $\lambda_i(0) = 0$, z *is orthogonal to* y_i *and where* y *is any given nontrivial linear combination of the* y_i .

Proof. Let L and T be operators defined by the left and right sides of (3.4) respectively. Let $X = C^1(p)$ be the Banach space of continuously differentiable p-periodic functions under the norm $||x||_0 + ||x'||_0$ and let $Y = C^0(p)$ be the Banach space of continuous p-periodic function under the supremum norm $||x||_0 = \sup_{-p \leq t \leq p} |x(t)|$. The linear operator $L: X \to Y$ is Fredholm (Cushing (1977b)) and H1 of Appendix A holds. Take $h = 0$ in equation (A.1) and note that T is independent of ε in Theorem A of Appendix A (see the REMARK in Appendix A). A Fourier analysis shows that (3.3) has exactly $m = 2$ independent p-periodic solutions for isolated α_i if and only if the following condition are met:

(3.5) $C_1(1) \neq C_2(1)$ and $\sum_1 := C_1(1)S_2(1) - S_1(1)C_2(1) \neq 0$

$$(3.6)\quad \begin{cases} \text{either } C_1(1)C_2(n) \neq C_1(n)C_2(1) \text{ or } n\sum_1 \neq C_1(1)S_2(n) - C_2(1)S_1(n) \\ \text{for all integers } n \geq 2 \end{cases}$$

(3.7) $\alpha_1 = -\omega C_2(1)/\sum_1$ and $\alpha_2 = \omega C_1(1)/\sum_1$ where $\omega = 2\pi/p$

where $C_i(n) := \int_0^\infty \cos n\omega s \, dh_i(s)$, $S_i(n) := \int_0^\infty \sin n\omega s \, dh_i(s)$. These two independent solutions are $y_1 = \sin \omega t$ and $y_2 = \cos \omega t$. The null space of the adjoint equation

$$y'(t) - \sum_{i=1}^{2} \alpha_i \int_0^\infty y(t+s) \, dh_i(s) = 0$$

is also spanned by $\sin \omega t$, $\cos \omega t$. Thus $d = \det(\frac{1}{p} \int_0^p \int_0^\infty y_i(t-s) dh_j(s) y_i(t) \, dt)$ which turns out to equal $d = -(k_1^2 + k_2^2)\sum_1/4 \neq 0$ if $y(t) = k_1 y_1 + k_2 y_2$, $k_1^2 + k_2^2 \neq 0$. Thus, the final hypothesis H4 holds and Theorem Ai applies. §§

REMARKS (1) Although this general bifurcation theorm appears different from the familiar Hopf-type bifurcation theorems because it involves two bifurcation parameters λ_i instead of just one, it is actually more general than Hopf bifurcation in that one-parameter Hopf-type bifurcation theorems are derivable from Theorem 4 if (as is usually done in the proof of Hopf bifurcation theorems anyway) the unknown period is introduced into the equation as a second bifurcation parameter by means of a rescaling of the variable t. This will involve, however, greater technical details and hypotheses (e.g. on h_i) and require a further nondegeneracy condition. For further discussion of the relationship between Theorem 4 and Hopf bifurcation see Cushing (1978a,1979b).

Note that the nondegeneracy condition $d \neq 0$ is always fulfilled in the above application of Theorem A .

Hopf-type bifurcation theorem can be found in papers by Kazarinoff and Wan (1978), Stech (1979) and Simpson (1979).

(2) In the applications to be considered here the integrators will either have the form $dh(s) = k(s)ds$ or $h(s) = u_0(s)$, the unit step function at $s = 0$. The generality of Theorem 4 allows also for instantaneous time lags ($h(s) = u_T(s)$) and multi-lags. For examples see Cushing (1978a,1979b).

(3) From Theorem A of Appendix A, x and λ have the smoothness in ε possessed by S. This allows one to substitute ε expansions for x and λ into the integrodifferential equations in order to calculate lower order approximations to solutions by means of the usual procedure of eliminating secular terms.

(4) The question of the (orbital) stability of the bifurcating periodic solutions is not addressed in Theorem 4. Stability theorems analogous to (and actually generalizations of) the classical Hopf bifurcation theorems for differential systems have been proved for integrodifferential systems (see Stech (1979), Simpson (1979) and their references). These theorems assert that the bifurcating periodic solution is stable if a certain (in principle calculatable) number δ is negative and unstable if $\delta > 0$. The number δ depends on the nonlinearities as well as the ingredients of the linearized system (the critical values α_i, the nontrivial solutions of the linearization and those of its adjoint) and although formulas and/or procedures have been given in the literature for the calculation of δ they are unfortunately

notoriously lengthy, very tedious and rarely practical or useful in anything but the simplest of examples. One can, of course, get an idea of the stability of the periodic solutions from numerical integrations. §§

Suppose that Theorem 4 above is applied to the gestation delay model (1.11) with the linear fecundity function as in the above example, namely to

$$(3.8) \qquad P'(t) + dP(t) = \int_{-\infty}^{t} g(t-s)b\{1 - P(s)\}_{+}P(s)\, ds$$

where $d > 0$, $b > 0$. This model has equilibrium $P_0 = (b-d)/b$. Let $x = P-P_0$ and $\mu_1 = d$, $\mu_2 = b-2d$, $\mu_i = \alpha_i + \lambda_i$. Then (for x small) (3.8) becomes

$$(3.9) \quad x' + \alpha_1 x + \alpha_2\int_{-\infty}^{t} g(t-s)x(s)ds = -\lambda_1 x - \lambda_2\int_{-\infty}^{t} g(t-s)x(s)ds$$
$$-(\alpha_2 + 2\alpha_1 + \lambda_2 + 2\lambda_1)\int_{-\infty}^{t} g(t-s)x^2(s)ds ,$$

an equation of the form (3.4) to which Theorem 4 applies. Thus, model (3.8) will have a bifurcating branch of nontrivial p-periodic solutions for values of $b = b_0 + \beta_1(\varepsilon)$ and $d = d_0 + \beta_2(\varepsilon)$ provided the linearized equation has exactly two nontrivial p-periodic solutions. This will occur provided (3.5)-(3.7) hold for some $p > 0$ where in this case $C_1(n) = 1$, $S_1(n) = 0$ for all n, that is provided the following condition are met: $C_2(1) \neq 1$, $S_2(1) \neq 0$ and

$$(3.10) \quad \text{either } C_2(n) \neq C_2(1) \text{ or } nS_2(1) \neq S_2(n) \text{ for all integers } n \geq 2$$

$$(3.11) \quad b_0 = \omega(1 - 2C_2(1))/S_2(1) \quad , \quad d_0 = -\omega C_2(1)/S_2(1) \quad , \quad \omega = 2\pi/p$$

where $C_2(n) := \int_0^\infty g(s)\cos n\omega s\, ds$ and $S_2(n) := \int_0^\infty g(s)\sin n\omega s\, ds$. In order to have $b_0 > d_0 > 0$ it is also necessary that

$$(3.12) \qquad S_2(1) > 0 \quad , \quad C_2(1) < 0 \quad .$$

(Note: $|C_2(n)|$ and $|S_2(n)| \leq \int_0^\infty g(s)ds = 1$.)

Thus (3.8) has a branch of p-periodic solutions bifurcating from the equilibrium $P_0 = P_0(\varepsilon,p) = (b-d)/b$ for $b = b_0(p) + \beta_1(\varepsilon,p)$, $d = d_0(p) + \beta_2(\varepsilon,p)$ for a period $p > 0$ provided that (3.10) and (3.12) hold for this p. Here the dependence on p is explicitly indicated. Since (3.10) and (3.12) are inequalities they in general will hold for an interval of periods p so that the branches found here form a two parameter family of periodic solutions.

As a specific example, consider again the case $g(s) = T^{-2}se^{-s/T}$, $T > 0$. In this case $C_2(n) = (1-(n\omega T)^2)/(1+(n\omega T)^2)^2$, $S_2(n) = 2n\omega T/(1+(n\omega T)^2)^2$ so that (3.12) holds if and only if $\omega T > 1$ or in other words for periods satisfying

$$p < 2\pi T .$$

That the second inequality in (3.10) holds is easily checked. Bifurcation thus occurs for b and d at the critical values given by

$$(3.13) \qquad b_0 = \frac{(\omega T)^4 + 4(\omega T)^2 - 1}{2T} \quad , \quad d_0 = \frac{(\omega T)^2 - 1}{2T} \quad , \quad \omega = 2\pi/p.$$

This <u>bifurcation curve</u> C , which in nonparametric form (i.e. when ω is eliminated) is just the parabola (3.2) found from the stability analysis, is plotted in FIGURE 1.

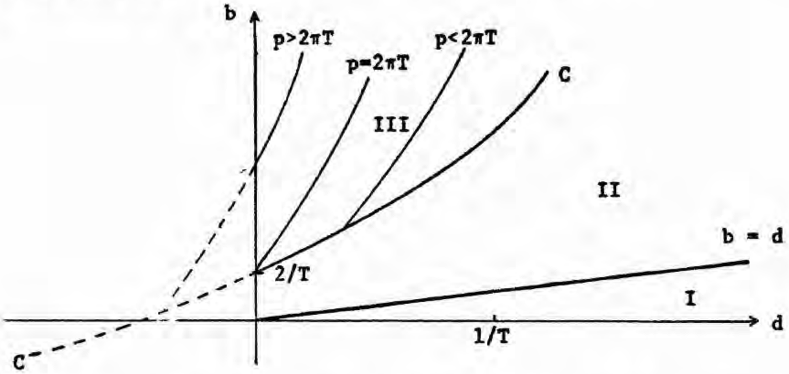

FIGURE 1: For equation (3.8) with $g(s) = T^{-2}se^{-s/T}$, $P_0 = 0$ is asymptotically stable in region I and unstable in II,III. $P_0 = (b-d)/b$ is positive in II,III, is asymptotically stable in II and is unstable in III. The steep curves above and emanating from the parabolic bifurcation curve C are the curves along which bifurcation occurs in spaces of fixed period.

A substitution of series expansions in ε

$$x = P - P_0 = \varepsilon y + \varepsilon^2 z + \varepsilon^3 w + \dots \quad , \qquad \lambda_i = \varepsilon \gamma_i + \beta_i \varepsilon^2 + \dots$$

into equation (3.9) yields, by equating coefficients of corresponding powers of ε, a hierarchy of linear problems for $y, z, w, \dots$ whose orthogonality conditions for the nonhomogeneities determine the constants $\gamma_i, \beta_i, \dots$. It is easy to show by this procedure that in this example both $\gamma_i = 0$ (so that the bifurcation is "one-sided"). These quantities are functions of p. For example when $p = 2\pi T$ and $y = \cos t$ one finds that

$$x = \varepsilon \cos t + \varepsilon^2 \left(-\frac{1}{2} + \frac{1}{12}\cos 2t + \frac{1}{12}\sin 2t\right) + \dots \quad ,$$

$\beta_1 = 7/150T$ and $\beta_2 = 76/75T$ so that in the original variables

$$P(t) = 1 + \varepsilon \cos t + \varepsilon^2 \left(-\frac{157}{300} + \frac{1}{12}\cos 2t + \frac{1}{12}\sin 2t\right) + \dots$$

$$b = \frac{2}{T} + \frac{83}{75T}\varepsilon^2 + \dots \quad , \quad d = \frac{7}{150T}\varepsilon^2 + \dots \quad , \quad P_0 = 1 - \frac{7}{300}\varepsilon^2 + \dots \quad .$$

Note that the average $p^{-1}\int_0^p P(t)dt = 1 - (157/300)\varepsilon^2 + \dots$ of the oscillation is less than that of the equilibrium $P_0 = 1 - (7/300)\varepsilon^2 + \dots$. It can be shown in this example that these bifurcating periodic solutions are orbitally stable.

Note that if only one of the parameters is varied, say b is varied while d is held fixed, then bifurcation occurs at C for a critical value b_0 given by (3.13) or (3.2) with a period which now varies and increases with b (see FIGURE 1) starting at a critical period p obtained by solving for p in the second equation of (3.13). This is typical Hopf-type bifurcation with a typical bifurcation diagram as shown in FIGURE 2.

A similar analysis for delay models of Kolomorgorov type (1.10) (i.e. neglecting age structure and gestation periods) is given by Cushing (1977a). Some examples involving two delays are worked out also by Cushing (1979b).

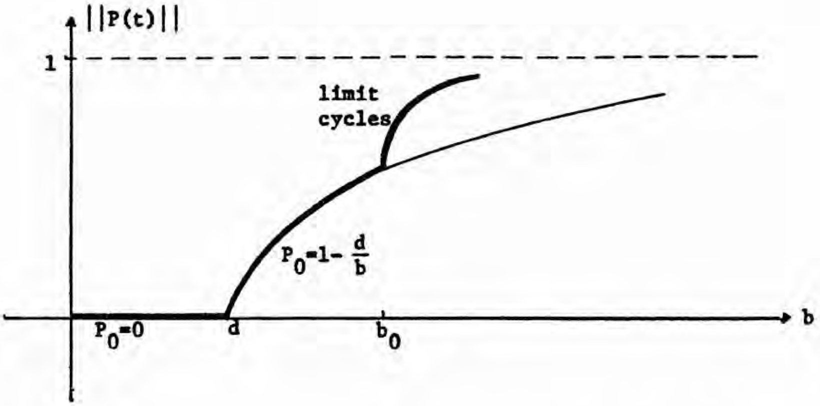

FIGURE 2: The bifurcation diagram for equation (3.8) with d held fixed and b varied. The dark line represents stable equilibria and stable periodic solutions.

It is interesting to compare the bifurcation phenomenon above for a gestation delay model (3.8) with that of a similar model with response delays in the death rate (and/or maturity function) as in the classic delay logistic. Consider the delay logistic equation (2.5) with P measured in units so that $\gamma = 1$. The characteristic equation of the linearization at $P_0 = r(1+\mu)^{-1}$ is $z + \mu P_0 + P_0 k^*(z) = 0$ which, when $k(s) = T^{-2}se^{-s/T}$, reduces (for $z \neq 1/T$) to the cubic equation

$$T^2z^3 + T(2 + T\mu r(1+\mu)^{-1})z^2 + (1 + 2T\mu r(1+\mu)^{-1})z + r = 0$$

whose roots are easily shown by the Hurwitz criteria to all lie in the left half complex plane

for all $r > 0$ provided $\mu > 1/8$

for $0 < r < r_-$ or $r > r_+$ provided $0 < \mu < 1/8$

where $r_{\pm} = (1+\mu)(1-4\mu \pm (1-8\mu)^{1/2})/4T\mu^2$. For $r = r_{\pm}$ there are purely imaginary roots $z = \pm i\omega_0$ for $\omega_0 = T^{-1}(1+2T\mu r_{\pm}(1+\mu)^{-1})^{1/2}$. For $r_- < r < r_+$ the equilibrium is unstable. Thus one has a bifurcation occuring at $r = r_-$ and at $r = r_+ > r_-$ (whose branches presumably join). The bifurcation picture analogous to that given in FIGURE 1 for this delay logistic equation when $0 < \mu < 1/8$ is shown in FIGURE 3. Note that $r_+ \to +\infty$, $r_- \to 2/T$ and $\omega T \to 1$ as $\mu \to 0$.

By way of comparison between the gestation delay model (3.8) and the delay logistic (2.5) note that for large inherent death rates d bifurcation occurs earlier (for smaller modulus of fecundity b) in the delay logistic while the opposite is the case for small d. For small d bifurcation not only occurs for smaller b in the gestation delay model but it results in oscillations with a longer period.

The existence of nontrivial periodic solutions of integrodifferential equations of the type we have been considering (as well as of other delay models) has frequently been used in a qualitative way to explain sustained oscillations observed in some animal species. Going further than this, some (e.g. see May (1976), Maynard Smith (1975)) have obtained remarkably close fits to certain oscillatory data using delay models, although this is often done with simple models (such as the lag logistic equation) which do not, in spite of the good fit to data, offer much specific explanation of the biological mech-

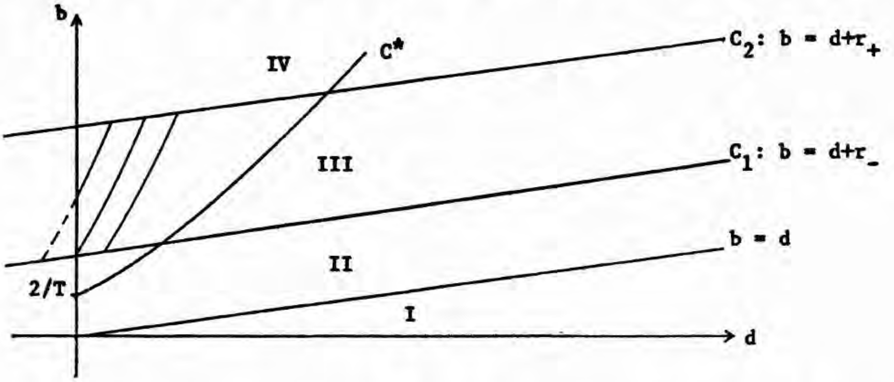

FIGURE 3: The bifurcation diagram for the delay logistic (2.5) with $0<\mu<1/8$ showing the bifurcation curves C_1, C_2. The bifurcation curve C* of the gestation delay model (3.8) is also drawn from FIGURE 1 for comparison purposes. $P_0=0$ is stable in I. $P_0>0$ is stable in II, IV and unstable in III. Also $\gamma = 1$.

anisms involved. Since gestation and maturation delays as well as other age dependent phenomena have been specifically cited as agents causing oscillations in certain insect populations (Nicholson (1951), Slobodkin (1961), Maynard Smith (1975)) it would be of interest to do similar data fitting using some of the models considered here. This kind of quantitative use of delay models has only begun in population dynamics.

Chapter 4: SINGLE SPECIES OSCILLATIONS IN A PERIODIC ENVIRONMENT

Although it is possible, as we have seen in the previous Chapter 3, for an isolated species to exhibit inherent oscillations in density, it is undoubtedly true that an at least equally, if not in many cases a more important, cause of such oscillations in nature is the presence of some sort of environmental periodicity. Such environmental fluctuations express themselves in models of the type being considered here by the explicit appearance of time t in the parameters of the equation. If the model parameters depend periodically on t then there arises first of all the interesting mathematical question of the existence of a periodic solution....a solution which presumably plays the role played by the equilibrium in the autonomous equations and which, if stable (another interesting mathematical question), plays the role of a "periodically varying carrying capacity". Beyond this, a host of other questions arise which are virtually unexplored in a population dynamical setting. For example, given the possibility of inherent oscillations in conjunction with environmental forcing periodicites there arise questions concerning reasonance effects, beats, sub- and ultraharmonics and the question of which period will the population predominately track and with what amplitude and average. Which vital parameter oscillations play the most significant role in the resulting dynamics and in what way? Are there bifurcations of further periodicities at critical parameter values? What effect does different phases in vital parameter oscillations have?

Many of these questions are studied (mainly numerically) in an interesting paper of Nisbet and Gurney (1976) for the special case of the lag logistic equation with sinusoidal oscillations in the inherent growth rate and the carrying capacity. Some quite general theorems concerning the existence and stability of positive periodic solutions have been obtained for functional equations of Kolomogorov type (1.10) by means of bifurcation theory by Cushing (1977a, 1978b), by means of limiting equation techniques by Artstein and Karakostas (1979) and by means of multi-time scale perturbation techniques by Simpson (1979).

In this chapter I will confine myself to the mathematical problem of the existence of periodic solutions of integrodifferential equations in which the parameters exhibit small amplitude periodic oscillations and to a very brief study of some of their properties. This will be done by another application of Theorem A in Appendix A where ε will be the amplitude of these oscillations.

Suppose that the death rate d and fecundity m in the general model (1.9) are subjected to a p-periodic oscillation in time of amplitude ε in such a way that when $\varepsilon = 0$ equation (1.9) has a positive equilibrium $P_0 > 0$ (satisfying (2.1)). If one sets $x = P - P_0$ in (1.9) there results in general an equation of the form to which Theorem A can be applied. Rather than attempt to do this in any general way I will consider as an example a gestation delay model.

Suppose that in equation (3.8) the constants d and b are replaced by $d + \varepsilon\alpha\cos(\omega_e t+\phi)$ and $b + \varepsilon\cos\omega_e t$ respectively where $\alpha \geq 0$, $\omega_e > 0$ and ϕ are constants:

$$(4.1)\quad P'(t) + (d+\varepsilon\alpha\cos(\omega_e t+\phi))P(t) = (b+\varepsilon\cos\omega_e t)\int_{-\infty}^{t} g(t-s)\{1-P(s)\}_+ P(s)\,ds\ .$$

Thus the inherent death and birth rates are subjected to $p_e = 2\pi/\omega_e$ periodic oscillations about constant values with amplitudes proportional to ε and a phase difference of ϕ. When $\varepsilon = 0$ we have the equilibrium $P_0 = (b-d)/b$

so that we assume $b > d$. If $x = P - P_0$ then

$$(4.2) \quad x'(t) + dx(t) + (b-2d)\int_{-\infty}^{t} g(t-s)x(s)ds = T(x,\varepsilon) + \varepsilon h(t)$$

$$h(t) := P_0(db^{-1}\cos\omega_e t - \alpha\cos(\omega_e t+\phi))$$

$$T(x,\varepsilon) := -b\int_{-\infty}^{t} g(t-s)x^2(s)ds + \varepsilon(-x(t)\alpha\cos(\omega_e t+\phi)$$
$$+ \cos\omega_e t\int_{-\infty}^{t} g(t-s)((1-2P_0)x(s) - x^2(s))ds)$$

an equation to which Theorem A(ii) in Appendix A immediately applies (on the Banach spaces of p_e-periodic functions used in the proof of Theorem 4) provided that the linear homogeneous equation

$$(4.3) \qquad x'(t) + dx(t) + (b-2d)\int_{-\infty}^{t} g(t-s)x(s)\, ds = 0$$

has no nontrivial p_e-periodic solutions in which case

$$(4.4) \qquad y'(t) + dy(t) + (b-2d)\int_{-\infty}^{t} g(t-s)y(s)\, ds = h(t)$$

has a unique p_e-periodic solution (Cushing (1977b)).

THEOREM 5. If the average inherent birth and death rates b and d, $b > d$, are such that (4.3) has no nontrivial p_e-periodic solutions, then (4.1) has for each small $|\varepsilon|$ a p_e-periodic solution of the form $P(t) = P_0 + \varepsilon y(t) + \varepsilon z(t,\varepsilon)$ where y is the unique p_e-periodic solution of (4.4).

Higher order terms can be found in the usual manner by substitution of the ε-expansion for P into (4.1), equating coefficients of like powers of ε and solving the resulting hierarchy of linear nonhomogeneous equations. This can be of use if some specific property of P is sought. Several examples of this will now be considered.

(a) First, consider the question of the average $av(P)$ of $P(t)$ over one period. It is easy to see from (4.4) that $av(y) = 0$ since $av(h) = 0$. More specifically, the solution of (4.4) has the form $y = A\cos\omega_e t + B\sin\omega_e t$

for constants A and B. Thus $\mathrm{av}(P) = P_0 + \varepsilon\,\mathrm{av}(z)$ or if $z = \varepsilon(w + O(\varepsilon))$ then $\mathrm{av}(P) = P_0 + \varepsilon^2\mathrm{av}(w) + O(\varepsilon^3)$. Here w is the unique p_e-periodic solution of the linear nonhomogeneous equation obtained from the $O(\varepsilon^2)$ terms in (4.2), namely

$$(4.5) \qquad w'(t) + dw(t) + (b-2d)\int_{-\infty}^{t} g(t-s)w(s)\,ds = \bar{h}(t)$$

$$\bar{h}(t) := -b\int_{-\infty}^{t} g(t-s)y^2(s)ds + \cos\omega_e t\int_{-\infty}^{t} g(t-s)(1-2P_0)y(s)ds - y(t)\alpha\cos(\omega_e t+\phi)$$

an integration of which over one period p_e yields $\mathrm{av}(w) = (b-d)^{-1}\mathrm{av}(\bar{h})$. The average $\mathrm{av}(\bar{h})$ is found by computing A and B, a straightforward but rather tedious job in general.

Suppose we consider the special case $\alpha = 0$ in (4.1) when the death rate is constant in time. Then it turns out that

$$(4.6) \qquad A = \frac{\beta}{\Omega}(d - \delta C(1)) \quad , \qquad B = \frac{\beta}{\Omega}(\omega_e + \delta S(1))$$

$$\beta := P_0(1 - P_0) > 0 \ , \quad \Omega := (d - \delta C(1))^2 + (\omega_e + \delta S(1))^2 > 0$$

$$\delta := b(1 - 2P_0) = 2d - b$$

and that

$$(4.7) \qquad 2\mathrm{av}(\bar{h}) = -b(A^2 + B^2) + (1 - 2P_0)(AC(1) - BS(1))$$

where $C(1)$, $S(1)$ are the Fourier cosine and sine integrals of $g(s)$ as in the previous Chapter 3. The question of whether $\mathrm{av}(P)$ is greater than or less than the unperturbed (constant environment) equilibrium P_0 is determined by the sign of $\mathrm{av}(\bar{h})$ in that $\mathrm{sign}(\mathrm{av}(P) - P_0) = \mathrm{sign}\ \mathrm{av}(\bar{h})$ for small $|\varepsilon|$. The answer to this simple question remains unclear, even after the simplifications made so far, because the formulas (4.6)-(4.7) remain rather complicated. That there is no single answer can be shown, however, by some further special cases.

(i) Suppose $C(1) \to 1$ *and* $S(1) \to 0$ *as* $\omega_e = 2\pi/p_e \to 0$. *Then given*

$b > d$ <u>there exists a</u> $p_0 > 0$ <u>such that</u> $p_e > p_0$ <u>implies that</u> $av(P) < P_0$ <u>for small</u> $|\varepsilon|$. This is because that since $\Omega \to (d-b)^2$ as $\omega_e \to 0$ it is straightforward from (4.6)-(4.7) to show that $2av(\bar{h}) \to -d(b-d)/b^3$.

We conclude that for environmental fluctuations of large periods density oscillations occur with average less than the constant environment equilibrium.

<u>(ii)</u> Since $C(1) \to 0$ and $S(1) \to 0$ $\omega_e \to +\infty$ (by the Riemann-Lebesgue lemma; see Hewitt and Stromberg (1961,p.481)), <u>given</u> $b > d$ <u>there exists a</u> $p_0 > 0$ <u>such that</u> $0 < p_e < p_0$ <u>implies that</u> $av(P) < P_0$ <u>for small</u> $|\varepsilon|$. This is because it turns out that $2av(\bar{h}) = (\beta/\Omega)^2 b^{-1}\Gamma$ where $\Gamma = \Gamma(\omega_e) = -b^2(d^2+\omega_e^2) + \delta(2b^2+\Omega/\beta)(dC(1)-\delta S(1))-\delta^2(b^2+\Omega/\beta)(C^2(1)+S^2(1))$ and hence $\Gamma(\omega_e) = -b^2\omega_e^2 + O(\omega_e^\sigma)$, $\sigma < 2$. Thus $av(\bar{h}) < 0$ for ω_e large.

We conclude that for environmental oscillations of very short period density oscillations occur again with average less than the constant environment equilibrium.

<u>(iii)</u> Finally we ask whether it is possible under suitable circumstances that $av(P) > P_0$. At least one case for which this occurs is the case of small d. For if b and ω_e are held fixed while $d \to 0$ it turns out that

$$2\,av(\bar{h}) = d\left(\frac{\omega_e S(1) - b(S^2(1)+C^2(1))}{b(b^2C^2(1) + (\omega_e - bS(1))^2)} + O(d)\right) .$$

Thus <u>if</u> $\omega_e > 0$ <u>is such that</u> $S(1) > 0$ <u>and if</u> $b < \omega_e S(1)/(S^2(1)+C^2(1))$ <u>then there exists a</u> $d_0 > 0$ <u>such that</u> $0 < d < d_0$ <u>implies</u> $av(P) > P_0$ <u>for small</u> $|\varepsilon|$. Note that the constraint on b implies $b < \omega_e/S(1)$ and recall that $\omega_e/S(1)$ is the critical bifurcation value of b corresponding to $d = 0$ for period p_e (see Theorem 4). Thus b and d satisfying these conditions yield, in a constant environment ($\varepsilon = 0$), an asymptotically stable equilibrium P_0. The requirement that $S(1) > 0$ means that some delay must be present.

The gestation delay distribution given by $g(s) = T^{-2}se^{-s/T}$ satisfies all the conditions of the three results (i-iii) above.

Case (iii) is perhaps the most interesting for it says that *under certain circumstances a gestation delay can result in an average population density which is greater than the constant environment equilibrium.* A similar analysis on the correponding nondelay model ($g(s) = \delta_0(s)$) shows that under the same circumstances $\mathrm{av}(P) < P_0$ for $|\varepsilon|$ small, so that it is the gestation delay in this model which has caused a larger average population density.

(b) Consider now the question of the amplitude of the oscillations in (4.1). Again suppose $\alpha = 0$. To order $O(\varepsilon)$ these oscillations about P_0 have amplitude $M = (A^2+B^2)^{1/2}$ which from (4.6) equals $M = \beta/\Omega^{1/2}$. Observe first of all that $\Omega \to 0$ and hence $M \to +\infty$ as $d \to d_0 := -\omega_e C(1)/S(1)$ and $b \to b_0 := \omega_e(1-2C(1))/S(1)$. But d_0, b_0 are the critical values of d, b at which the linear equation (4.3) has nontrivial p_e-periodic solutions (and at which bifurcation occurs in a constant environment, see (3.11)). This *resonance-like* phenomenon implies then that large oscillations are likely to result in (4.1) for average death and birth rates d, b nearer these critical values.

(c) Finally consider the amplitude M (to order $O(\varepsilon)$) as a function of the gestation delay. More specifically, suppose $g(s) = T^{-2}se^{-s/T}$ and conseder $M = M(T)$ as a function of $T > 0$. For simplicity assume that time is measured in units for which the environmental period is $p_e = 2\pi$ (i.e. $\omega_e = 1$). In this case we find that

$$\Omega = \Omega(T) = (2d-b)\Gamma(T) + d^2 + 1 > 0\ , \quad \Gamma(T) := (2dT^2 + 4T - b)/(T^2+1)^2\ .$$

Then $\Omega(0+) = (b-d)^2 + 1$ and $\Omega(+\infty) = d^2 + 1$ which imply that

$$(4.8)\quad M(0+) = d(b-d)/b^2((b-d)^2+1)^{1/2}\ , \quad M(+\infty) = d(b-d)/b^2(d^2+1)^{1/2}.$$

Furthermore an investigation of $\Gamma' = d\Gamma/dT$ shows that $\Gamma' > 0$ for $T < T_0$ and $\Gamma' < 0$ for $T > T_0$ for some critical $T_0 > 0$. Thus sign $d\Omega/dT = \text{sign}(2d-b)$ for $T < T_0$ but sign $d\Omega/dT = -\text{sign}(2d-b)$ for $T > T_0$. Since $M' = dM/dT = -\beta\Omega'/2\Omega^{3/2}$ it follows that

$$\text{sign } M' = \begin{cases} -\text{sign}(2d-b) & \text{for } T < T_0 \\ \text{sign}(2d-b) & \text{for } T > T_0 . \end{cases}$$

Consequently two different cases occur as illustrated in FIGURE 4. Note that if $b < 2d$ then the presence of a gestation delay decreases the amplitude of the oscillations while if $b > 2d$ such a delay increases the amplitude.§§

Time delays are generally considered to cause adverse effects: instabilities, oscillations and so on. It is interesting to note two effects caused by the gestation delay in the above examples which might be considered as "positive". Namely, the periodic oscillation in population density due to a periodic fluctuation in the inherent birth rate (as modeled by (4.1) with $\alpha = 0$) can under certain circumstances have its average increased and its amplitude decreased by a gestation delay (or by a lengthening of this delay).

Up to this point we have been considering the problem of environmentally forced oscillations under the assumption that there is no inherent (constant environment) oscillation such as was considered in Chapter 3. If b and d

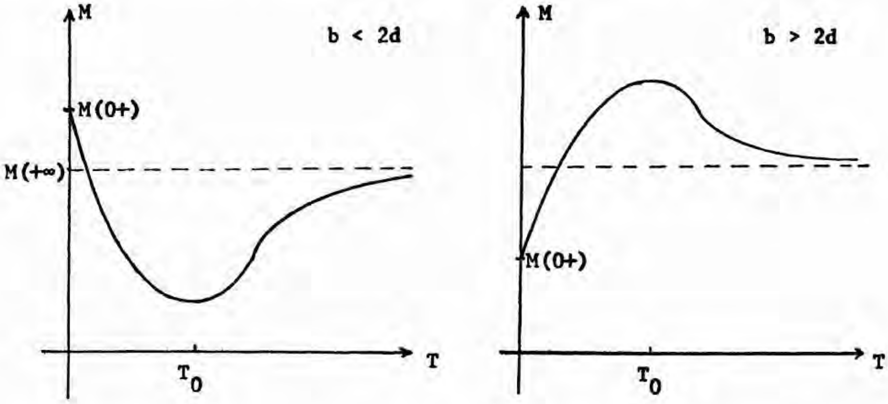

FIGURE 4: The amplitude $M=M(T)$ (to order $O(\varepsilon)$) of the periodic oscillations in the solution of the gestation delay model (4.1) with $\alpha=0$, $\omega_e=1$ and $g(s) = T^{-2}s\exp(-s/T)$ as plotted against T.

are such that inherent ($\varepsilon = 0$ in (4.1)) oscillations occur then there arise the questions not only of the existence of a periodic solution of (4.1) but the nature of its properties....questions such as that of its period and amplitude, whether it more closely tracks the inherent or environmental periodicities and how these depend on the nature of the delay.

Suppose for simplicity from now on that the environmental periodicity is $p_e = 2\pi$, *i.e.* $\omega_e = 1$. If (4.3) has for $b = b_0$, $d = d_0$ two independent periodic solutions $y_1(t)$, $y_2(t)$ of period $p = 2m_0\pi/n_0$ where $m_0 \neq n_0$ are positive integers, then we can write (as in Chapter 3) $x = P - P_0$, $\mu_1 = d$ and $\mu_2 = b - 2d$ and set $\mu_i = \alpha_i + \lambda_i(\varepsilon)$ where $\alpha_1 = d_0$, $\alpha_2 = b_0 - 2d_0$ so that equation (4.1) (or (4.2)) reduces to the equation

$$(4.9) \quad x'(t) + \alpha_1 x(t) + \alpha_2 \int_{-\infty}^{t} g(t-s)x(s)\,ds = T(x,\lambda,\varepsilon) + \varepsilon h(t)$$

$$h(t) := (\alpha_1+\alpha_2)\alpha_1(2\alpha_1+\alpha_2)^{-2}\cos t$$

$$\begin{aligned} T(x,\lambda,\varepsilon) := {} & -\lambda_1 x(t) - \lambda_2 \int_{-\infty}^{t} g(t-s)x(s)ds - (2\alpha_1+\alpha_2+2\lambda_1+\lambda_2)\int_{-\infty}^{t} g(t-s)x^2(s)ds \\ & -\varepsilon(\alpha_2+\lambda_2)(2\alpha_1+\alpha_2+2\lambda_1+\lambda_2)^{-1}\cos t\int_{-\infty}^{t} g(t-s)x(s)ds \\ & -\varepsilon\cos t\int_{-\infty}^{t} g(t-s)x^2(s)ds + \varepsilon\left(\frac{(\mu_1+\mu_2)\mu_1}{(2\mu_1+\mu_2)^2} - \frac{(\alpha_1+\alpha_2)\alpha_1}{(2\alpha_1+\alpha_2)^2}\right)\cos t\ . \end{aligned}$$

The critical constants b_0, d_0 are given by (3.11) where $\omega = n_0/m_0$ and where $C_2(1)$, $S_2(1)$ are replaced respectively by

$$(4.10) \quad C_0 := \int_0^\infty g(s)\cos n_0 s/m_0\,ds\ , \quad S_0 := \int_0^\infty g(s)\sin n_0 s/m_0\,ds.$$

Theorem A of Appendix A applies to (4.9) with $m = 2$, but now on the Banach spaces of periodic functions of the common period $p_c = 2m_0\pi$ of the y_i and h (i.e. of the inherent and environmental periodicities). The nondegeneracy condition H4 holds because d is exactly as in Theorem 4. The reason we have assumed $m_0 \neq n_0$ is to fulfill the hypothesis H2 of Appendix A.

THEOREM 6. *Equation* (4.1) *with* $\alpha = 0$ *has periodic solutions of the common period* $p_c = 2m_0\pi$ (*of the inherent and environmental periodicities*) *for small* $|\varepsilon|$ *and* $b = b_0 + \beta_1(\varepsilon)$, $d = d_0 + \beta_2(\varepsilon)$, $\beta_1(0) = 0$ *where* b_0, d_0 *are given by* (3.11) *with* $\omega = 1$ *and* $S_2(1)$, $C_2(1)$ *replaced by* S_0, C_0 *in* (4.10).

Note that if $m_0 > 1$ then these oscillations are subharmonic, i.e. of a period longer than the forcing environmental period.

To the lowest order in ε this $2m_0\pi$-periodic solution of (4.9) satisfies

$$y'(t) + \alpha_1 y(t) + \alpha_2 \int_{-\infty}^{t} g(t-s)y(s)\,ds = h(t) \tag{4.11}$$

whose general $2m_0\pi$-periodic solution is

$$y(t) = A\cos n_0 t/m_0 + B\sin n_0 t/m_0 + y_e(t), \quad y_e(t) = A_e\cos t + B_e\sin t$$

for arbitrary A and B* where y_e is the environmentally forced response whose coefficients A_e, B_e are determined by solving (4.11). The amplitude $M = (A_e^2 + B_e^2)^{1/2}$ of this forced response is $M = \Psi/\Omega^{1/2}$ where

$$\Psi := (b_0 - d_0)d_0/b_0^2 > 0\ , \quad \Omega := (d_0 + (b_0 - 2d_0)C_e)^2 + (1 - (b_0 - 2d_0)S_e)^2 > 0$$

$$C_e := \int_0^\infty g(s)\cos s\,ds \quad , \quad S_e := \int_0^\infty g(s)\sin s\,ds\ .$$

Suppose we let $g(s) = T^{-2}se^{-s/T}$ and treat the forced response amplitude $M = M(T)$ as a function of $T > 0$. In order to see how M changes with T consider $M'(T) = (2\Psi'\Omega - \Psi)/2\Omega^{3/2}$. In this case

$$b_0 = ((\omega_0 T)^4 + 4(\omega_0 T)^2 - 1)/2T\ , \quad d_0 = ((\omega_0 T)^2 - 1)/2T\ , \quad \omega_0 = n_0/m_0$$

$$C_e = (1 - T^2)/(1 + T^2)^2 \quad , \quad S_e = 2T/(1 + T^2)^2\ .$$

(a) Consider the case $d_0 \approx 0$ (i.e. $T \approx m_0/n_0$). Then $b_0 \approx 2n_0/m_0$, $\Omega \approx 4n_0^6(n_0^2 - m_0^2)^2/m_0^2(n_0^2 + m_0^2)^4 > 0$ and $d_0' \approx n_0^2/m_0^2$. Consequently $\Psi \approx 0$ and

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*The β_1 and hence b and d depend on the choice of A and B.

$\Psi' = n_0/2m_0 > 0$ which implies that $M'(T) > 0$ for $d_0 = 0$.

We conclude that *for small death rates* d *and for inherent birth rates* b *near* $2/T$ *the amplitude of the forced environmental response increases with increasing gestation delay*. From this we would expect to find that under these circumstances the oscillations will tend to track more and more the forced environmental periodicity with increasing gestation delay.

(b) Suppose we consider the case when T is very large. A straightforward computation shows that $\Psi' = (b_0-2d_0)b_0^{-1}(d_0/b_0)'$ and that for large T this expression is negative. Consequently, $M'(T) < 0$ for large T.

We conclude that *for large gestation delays the amplitude of the forced environmental response decreases as the delay increases*. Thus, under these circumstances we expect to find the oscillations tracking the natural period. §§

Although only a gestation delay model has been considered in this chapter (and a special one (4.1) at that) it should be clear how the analysis here using Theorem A of Appendix A would apply to other models. For example, the age dependent, maturation delay model (1.12) can be subjected to a very similar analysis (although in this case, as was seen in Chapter 2, there would be no inherent sustained oscillation in a constant environment and hence no resonances or subharmonics in the forced periodic environmental case).

Chapter 5: PREDATOR-PREY INTERACTIONS AND RESPONSE DELAYS

Except in artificial situations it is very unlikely that a species will exist in isolation from interactions with other species. The other species with which a given species interacts could of course be viewed simply as one part of the environment of the given species whose model equations as in the previous chapters would then reflect this part, as well as the abiotic part, of the environment. The subject of ecology, on the other hand, attempts to study the dynamics of such interacting species as a coupled system.

Traditionally, ecological interactions have been classified on the basis of a small number of types of two species interactions. While it is true that a given species is also unlikely to interact with only one other species, these two species interaction models seem to have proved fruitful as a means, albeit elementary and simplified, of organizing the thinking, analysis and discussion of the otherwise frightfully complex real world of multi-species population dynamics. The types of two species interactions which play the central role in population dynamics are predator-prey interactions and competitive interactions. In this and the following chapter I will explore some topics concerning these two ecological interactions when response delays are present.

Response delays appeared early in the modeling of predator-prey interactions. Volterra was quick to point out that whereas contact between predator and prey might (at least for the species he had in mind) result in a more or less instantaneous decrease in the prey population, the resulting increase (if any) in the predator population might be significantly delayed because, if for no other reason, the reproduction of the predator would not occur instantaneously. This led Volterra to modify his now famous predator-prey model so as to include a Volterra integral term of the type we have been considering here. The resulting integrodifferential model as well as many other differential delay predator-prey models of Kolomogorov type (and some not of this type) have been analysed in the literature (for a reference list see Cushing (1977a)). It would be impossible here because of space limitation to summarize adequately this work and therefore I will restrict my attention to some models which, while admittedly special in nature, nonetheless illustrate many typical features of predator-prey models with response delays.

<u>(a)</u> <u>Stability</u> <u>of</u> <u>equilibria.</u> Predator-prey models typically have several equilibria. The "positive" equilibria (in which both prey and predator equilibrium states are positive) are important in that their stability reflects the possible coexistence of the species. In addition there is usually at least one equilibrium state in which the predator state is zero and that of the prey is

positive. If stable such an equilibrium, which arises under the assumption that the prey has an inherent carrying capacity in the absence of predators, suggests the impossibility of coexistence. The situation which is typical in many (if not most) predator-prey models is the following: the null equilibrium (which represents the absence of both species) is unstable if the prey has a positive inherent growth rate at low population levels or a net reproductive rate greater than one. For small inherent prey carrying capacity there is no stable positive equilibrium and the predator goes to extinction while the prey population tends to this inherent carrying capacity. In this sense the prey cannot "support" the predator. On the other hand, if this carrying capacity exceeds a certain threshold level, there exists a stable positive equilibrium which then implies possible coexistence. As the prey carrying capacity is increased further, however, the stability of this positive equilibrium is "weakened" (in the sense that eigenvalues move to the right in the complex plane) or even lost altogether. This has been referred to as the "paradox of enrichment" (Rosenzweig (1971)). If in fact this stability is lost then there arises the question of the existence of a limit cycle, a phenomenon considered quite important in predator-prey dynamics. These assertions are easily demonstrable in the simpler classical models. Many have been proved for quite general models (Cushing (1976a,1979a)).

To illustrate these phenomena I will consider a specific predator-prey model involving a maturation delay as derived from the age dependent theory of Chapter 1. This model is possibly of some interest in and of itself because, first of all, as far as I know there is no predator-prey model in the literature which deals specifically with maturation period delays and secondly the model exhibits some unusual phenomena.

Let V denote the prey (or victim) population and P the predator. Assume that each species has a constant death rate independent of age. The prey's fecundity function will be taken to be $m_v = b_v\{1-c_1V-c_2P\}_+$ and that of the predator to be $m_p = b\beta(a)V$, $\int_0^\infty \beta(a)da = 1$, in equation (1.12). Here $c_i \geq 0$, b_v and b are positive constants and $\beta(a) \not\equiv 0$ is a nonnegative, continuously differentiable L^1 function of $a \geq 0$ for which $\beta(0) = 0$. These admittedly simplified assumptions mean that the age dependent fecundity of the predator for any age group increases linearly with total prey population size (dropping to zero for all ages when no prey are present); that the prey fecundity is age independent and decreases linearly with an increase of either total prey or total predator population sizes (dropping to zero for large populations, namely for $c_1V+c_2P \geq 1$); and that in the absence of predators the dynamics of the prey is governed by the single species nondelay logistic equation. From (1.10) and (1.12) we arrive at the system

$$(5.1) \qquad \begin{aligned} V' &= rV(1 - V/K - \alpha P) \\ P' + dP &= b \int_0^\infty \beta'(a) V(t)P(t-a)e^{-da}\, da \end{aligned}$$

for a constant predator death rate d and where $r = b_v - d_v$ (d_v being the prey inherent death rate) is assumed positive and $K = r/c_1 > 0$, $\alpha = c_2/r > 0$. The constants K, r are the prey inherent carrying capacity (in the absence of predators) and growth rate (in the absence of predators and interspecies competition) respectively. Since there is no prey response delay this particular model would only be suitable if the predator response delay due to its maturation period is considerably longer than any prey response delays. An illustration might be a vegetation-herbivore interaction in which the vegetation regeneration time is short compared to the maturation period of the herbivore.

The system (5.1) has three equilibria $V = V_0$, $P = P_0$:

(1) $V_0 = P_0 = 0$ (2) $V_0 = K$, $P_0 = 0$ (3) $V_0 = 1/R$, $P_0 = (KR-1)/\alpha KR$

where $R := b\int_0^\infty \beta(a)e^{-da}da$.

Linearization at the null equilibrium (1) shows that this equilibrium is always unstable since $r > 0$. (If $r < 0$, (1) is asymptotically stable so that both species go to extinction).

Linearization at the equilibrium (2) leads to a characteristic equation $(z+r)(z+d)(1-bK\beta^*(z+d)) = 0$ which has roots $\mathrm{Re}\, z \geq 0$ if and only if $1 - bK\beta^*(z+d) = 0$ does. Since $|b\beta^*(z+d)| \leq b\int_0^\infty \beta(a)e^{-da}da = R$ for $\mathrm{Re}\, z \geq 0$ we see that there are no roots with $\mathrm{Re}\, z \geq 0$ when

$$(5.2) \qquad K < 1/R \ .$$

Thus (5.2) implies that equilibrium (2) is (locally) asymptotically stable. Note that (5.2) also implies equilibrium (3) is not positive.

Suppose now that equilibrium (3) is positive, i.e. $K > 1/R$. Linearization at this equilibrium yields a characteristic equation

$$(5.3) \quad D(z) := (z+r/RK)(z+d)(1-b\beta^*(z+d)/R) + dr(1-1/KR) = 0 \ .$$

It is difficult in general to study the possibility of roots with $\mathrm{Re}\, z \geq 0$ of this equation. We will consider two cases: K close to $1/R$ and K large.

<u>(i)</u> For $K = 1/R$, $D(z)$ reduces to $D_0(z) := (z+r)(z+d)(1-b\beta^*(z+d)/R)$. Suppose that there exist sequences K_n, z_n such that

$$(5.4) \quad K_n > 1/R, \ K_n \to 1/R, \ \mathrm{Re}\, z_n \geq 0, \ D(z_n) = 0 \quad \text{for all } n \ .$$

From (5.3) and Theorem C.2 of Appendix C it follows that z_n must be bounded so that (extracting a subsequence if necessary) $z_n \to z_0$ for some z_0 with $\mathrm{Re}\, z_0 \geq 0$. By continuity $D_0(z_0) = 0$ and Theorem C.1 of Appendix C implies $z_0 = 0$. Thus we have sequences satisfying (5.4) and $z_n \to 0$.

Next we argue that the existence of these sequences contradicts the implicit function theorem. Treating D as a function of K as well as z we consider the equation $D(z,K) = 0$ to be solved for complex $z = z(K)$ near $(z,K) = (0,1/R)$. Easy calculations show that $D(0,1/R) = 0$, $D_z(0,1/R) = (drb/R)\int_0^\infty \beta(a) e^{-da}da > 0$ and $D_K(0,1/R) = drR$. The implicit function theorem implies that there exists a <u>unique</u> solution branch $z = z(K)$ of equation (5.3) which satisfies $z(1/R) = 0$. An implicit differentiation shows that $z'(1/R) = -R^2(b\int_0^\infty a\beta(a)e^{-da}da)^{-1} < 0$ and hence for $K > 1/R$, but near $1/R$, it follows that $\operatorname{Re} z(K) < 0$. This yields the desired contradiction.

THEOREM 7. *For the predator-prey model* (5.1) *with predator maturation period delay the null equilibrium is unstable and the equilibrium* (2) *is (locally) asymptotically stable if* $K < 1/R$. *The positive equilibrium* (3) *is (locally) asymptotically stable if* $K > 1/R$ *is close to* $1/R$ *(and if* $\int_0^\infty a\beta(a)da < +\infty$).

As an example, take the fecundity age distribution function $\beta(a) = \beta_n(a)$ as given in (2.9). We have seen that stable coexistence occurs only if K exceeds the threshold value $K_{cr} := 1/R$. For this example $K_{cr}^{(n)} = (dT+n)^{n+1}/bn^{n+1}$. Suppose that we view all parameters except T, n as fixed and study $K_{cr}^{(n)}$ as a function of these fecundity age distribution parameters T, n. This can be done by the results of Appendix B. Recall that T is the age of maximum fecundity and n (inversely) measures the "length" of the active reproductive age period. A decrease in the threshold value $K_{cr}^{(n)}$ promotes the survival of the predator in the sense that the predator then survives for a smaller prey carrying capacity K and its equilibrium population is increased. The converse is true if the threshold increases. Consequently we arrive at the following conclusions on the basis of this simple model:

for a fixed "length" n *of the active reproductive age period, a predator promotes its survival by decreasing its age* T *of maximum fecundity;*

for a given age $T \leq 2/d$ *of maximum fecundity, a predator promotes its survival by narrowing its active reproductive age period (increasing* n);

for a given age $T > 2/d$ *of maximum fecundity, a predator promotes its survival by having an optimal "length"* n *for its active reproductive period;*

$K_{cr}^{(n)} \to e^{dT}/b$ *as* $n \to +\infty$ *and thus for a very narrowly defined age period of active reproductivity the threshold is approximately* e^{dT}/b .

(ii) As $K \to +\infty$, $D(z)$ given by (5.3) reduces to $D_\infty(z) = z(z+d)(1-b\beta^*(z+d)/R) + dr$. More precisely, $D(z)$ approaches $D_\infty(z)$ uniformly on compact subsets of the right half plane $\operatorname{Re} z \geq 0$ as $K \to +\infty$. This means, first of all, by Hurwitz's theorem that if $D_\infty(z) = 0$ has a root $\operatorname{Re} z > 0$ then so does $D(z) = 0$ for large K.

Secondly, suppose that $D_\infty(z) \neq 0$ for $\operatorname{Re} z \geq 0$. Assume K_n, z_n are sequences for which $\operatorname{Re} z_n \geq 0$, $D(z_n) = 0$ for $K = K_n$ and $K_n \to +\infty$. Then by (5.3) and Theorem C.2 of Appendix C, z_n is bounded so that (extracting a subsequence if necessary) $z_n \to z_0$, $\operatorname{Re} z_0 \geq 0$. By continuity $D_\infty(z_0) = 0$. This contradiction to our assumption implies $D(z) \neq 0$, $\operatorname{Re} z \geq 0$, for large K.

Note that $D_\infty(z) = 0$ is the characteristic equation for the system

$$(5.5) \quad V' = rV(1 - \alpha V), \; P' + dP = b\int_0^\infty \beta'(a)V(t)P(t- \;)e^{-da}\,da$$

linearized at the positive equilibrium $V_0^\infty = 1/R$, $P_0^\infty = 1/\alpha$. This system is obtained formally by letting $K = +\infty$ in (5.1). It models the case when there is no prey self-inhibition term, i.e. prey increases exponentially without bound in the absence of predators.

We have shown the following: suppose $D_\infty(z) \neq 0$ for $\operatorname{Re} z = 0$. If $D_\infty(z) = 0$ has a root $\operatorname{Re} z > 0$ then equilibrium (3) of (5.1) is unstable for large K. On the other hand, if $D_\infty(z) = 0$ has no root $\operatorname{Re} z > 0$ then equilibrium (3) of (5.1) is (locally) asymptotically stable for large K. *That is, roughly speaking, for large K the stability property of equilibrium (3) of (5.1) is that of the positive equilibrium V_0^∞, P_0^∞ of (5.5).*

That the positive equilibrium of (5.5) can be either asymptotically stable or unstable can be seen by the following example. Take $\beta(a) = T^{-2}ae^{-a/T}$ in which case $D_\infty(z) = z(z+d)(1-(dT+1)^2(zT+dT+1)^{-2})+dr$ whose roots satisfying $\operatorname{Re} z \geq 0$ are the same as those of the quartic polynomial

$$T^2z^4 + (3dT^2+2T)z^3 + (d(2d+r)T^2+2dT)z^2 + 2dTr(dT+1)z + dr(dT+1)^2 = 0 .$$

All coefficients are positive. A straightforward calculation of the Hurwitz determinants H_i, $1 \leq i \leq 4$, shows that $H_1 = T^2 > 0$, $H_2 > 0$ and $H_4 = dT(dT+1)^2 H_3$ where $H_3 = drT^2(dT+1)p(T)$, $p(T) = d^2(3d+2r)T^3 - d^2T^2 - 8dT - 4$. Note that $H_3 > 0$ for large T, but $H_3 < 0$ for small T.

Thus *the positive equilibrium* $V_0^\infty = 1/R$, $P_0^\infty = 1/\alpha$ *of* (5.5) *with* $\beta(a) = T^{-2}ae^{-a/T}$ *is unstable for small* $T > 0$ *and (locally) asymptotically stable for large* $T > 0$. This is a rather unusual conclusion in that whereas large delays are usually destabilizing agents large response delays in this example promote stability. This conclusion suggests that under at least some circumstances a predator should have a substantial maturation period in order to promote its stable coexistence with the prey.

For the original model (5.3) *with* $\beta(a) = T^{-2}ae^{-a/T}$ *it follows that for large* T *and large enough* $K > 0$ *equilibrium* (3) *is (locally) asymptotically stable while for small* T *and large enough* K *it is unstable*.

In this example the positive equilibrium (3) loses its stability as the prey carrying capacity K increases provided the "maturation period" T is small. This suggest the bifurcation of a limit cycle at some critical value of the prey carrying capacity K.

(b) Oscillations. The subject of predator-prey oscillations is an important one of central interest in ecology which, as such, has a considerably large literature. Volterra's original interest in mathematical ecology was in fact stimulated by reported oscillations in certain fish species in the Mediterranean Sea and his famous predator-prey model, in which all solutions periodic, has been used as a possible theoretical explanation of this phenomenon. This model, however, has been heavily criticized mainly on the grounds of its marginal (structural) stability. It is considered of more interest that predator-prey models exhibit limit cycle behavior and one can find an abundance of such models appearing in the literature. The sources of these oscillations can be found in a great variety of causes arising from many mechanisms. If we divide

oscillations into the two broad categories of the environmentally forced and the inherent, unforced oscillations then the latter has by far received the most attention. Limit cycle behavior due simply to the nature of the interaction in a constant environment is of special interest in predator-prey theory (as it is in other subjects) and can be demonstrated using biologically quite simple models involving (nondelay) differential equations. Forced oscillations, which can superimpose with these inherent oscillations to produce interesting oscillatory phenomena, can arise from many causes, some obvious (e.g. daily, monthly and seasonal cycles in the natural environment) and some more subtle (e.g. complicated nutrient cycles). Such models have been much less studied.

Response delays fit into this picture as another possible source of oscillations. While such delays are repeatedly mentioned in standard ecology texts as a primary source of oscillations it is only rather recently that predator-prey models with delays have been mathematically investigated for oscillatory solutions. For the constant environment case this has usually been done by bifurcation analyses which have been carried out using a variety of approaches (Cushing (1977a,1976a), Kazarinoff and Wan (1976), Simpson (1979)). It is clear from this work that response delays can cause sustained predator-prey oscillations and can do so in a model which otherwise would not show such oscillations. Essentially all of these investigations, while often general enough to apply to other models, have dealt with Kolomogorov type models with delays in fecundity or death rate responses to changes in densities of either prey or predator.

Oscillations due to periodicities in environmental parameters have been studied by Cushing (1976b,1977c) for models without delays although, as pointed out by Cushing (1976b), it is easy to extend the techniques and results to models with delays.

Gestation and maturation period delays do not seem to have been studied explicitly in the literature. There is not enough space here however to undertake an investigation of oscillations caused by such delays, so I will accordingly confine myself to the specific maturation delay model (5.1). One way in which the bifurcation of nontrivial solutions from a positive equilibrium can be rigorously investigated is by means of Theorem A in Appendix A along the lines of what is done for other models by Cushing (1977a,1979b). Such bifurcation occurs of course only at those values of the parameters at which the linearized system has nontrivial periodic solutions, in other words at which the characteristic equation (5.3) has purely imaginary roots $z = i\omega$, $\omega \neq 0$. It is only this linear problem which will be considered here.

Equation (5.3) has a solution $z = i\omega$, $\omega \neq 0$ if and only if

$$(dr/RK-\omega^2)(1-bC/R) - \omega bS(d+r/RK)/R + dr(1 - 1/KR) = 0$$

$$bS(dr/RK-\omega^2)/R + \omega(d+r/RK)(1-bC/R) = 0$$

where $C = C(\omega) := \int_0^\infty \beta(a)e^{-da}\cos \omega a da$, $S = S(\omega) := \int_0^\infty \beta(a)e^{-da}\sin \omega a da$. This can be seen by setting $z = i\omega$ in (5.3), equating real and imaginary parts to zero and rearranging terms. Letting $\xi = r/K$ we can solve the second equation for ξ and the first equation for r to obtain

$$\text{(5.6)} \quad \begin{aligned} \xi &= \omega R(\omega bS-d(R-bC))/(dbS+\omega(R-bC)) \ , \quad (\xi := r/K) \\ dR^2 r &= b(\omega S+dC)\xi + \omega bdRS + \omega^2(R-bC) \ . \end{aligned}$$

Thus we have $p = 2\pi/\omega$ periodic solutions of the linearization of (5.1) for K,r given by (5.6). It is necessary that $\omega > 0$ be chosen so that $\xi > 0$, $r > 0$. Note that $R > bC$ follows from the definitions of R and C.

We expect from the stability analysis in <u>(a)</u> above for the special case $\beta(a) = T^{-2}a\exp(-a/T)$ that oscillations occur when T is small and K is large. In this special case $S = 2\omega T(dT+1)/((dT+1)^2+(\omega T)^2)^2$, $C = ((dT+1)^2-(\omega T)^2)/((dT+1)^2+(\omega T)^2)^2$. Equations (5.6) define large positive critical values of K, r for T and $p = 2\pi/\omega$ small. To see this let $T \to 0+$, $\omega \to +\infty$ in such a way that $\omega T = \theta =$ constant > 0. Then $S \to 2\theta/(1+\theta^2)^2 > 0$, $C \to (1-\theta^2)/(1+\theta^2)^2$ and it is easy to see from (5.6) that $\xi = O(\omega)$ and $r = O(\omega^2)$ as $\omega \to +\infty$. Thus we expect bifurcation of nontrivial large frequency oscillations in (5.1) from equilibrium (3) for large K and r. §§

In conclusion, we have found that a typical situation for the predator-prey model (5.3) with age dependent fecundity in the predator species would be roughly speaking the following: *for inherent prey carrying capacity* K *less than the critical threshold value* $K_{cr} := 1/R$ *the predator goes to extinction while the prey population tends to* K; *for* $K > K_{cr}$, *but close to* K_{cr}, *there is a stable positive equilibrium indicating predator-prey coexistence*; *and under certain circumstances for* K *large the predator-prey system exhibits nontrivial periodic oscillations*.

Chapter 6: TWO SPECIES COMPETITION

The theory of two species competing for the same resources plays an extremely important role in present day ecology, both applied and theoretical. The role played by response delays in competitive interactions has not, however, been investigated to the extent that it has been for predator-prey interactions. In a short note (see Scudo and Ziegler (1978,p.48)) Volterra mentions in passing the possibility of delays in what is now called the Lotka-Volterra competition model. Such Kolomogorov type delay equations which model two competing species were studied in a book by Cushing (1977a) where some general conclusions are drawn. Competition models with gestation or maturation delays do not seem to have been studied in the literature.

The classical Lotka-Volterra competition model is

(6.1) $P_i' = r_iP_i(1 - c_{ii}P_i - c_{ij}P_j)$, $1 \leq i \neq j \leq 2$, $r_i > 0$, $c_{ii} > 0$, $c_{ij} > 0$.

In order to give direction to our thinking the well-known basic properties of this system are summarized as follows: the null equilibrium $P_i = 0$ is unstable; the equilibrium $P_i = 1/c_{ii}$, $P_j = 0$ is (locally) asymptotically stable if $c_{ji} > c_{ii}$ and unstable if $c_{ji} < c_{ii}$; and a positive equilibrium exists if and only if both $c_{ii} > c_{ji}$ or both $c_{ii} < c_{ji}$ $(1 \leq i \neq j \leq 2)$, the first case of which yields (local) asymptotic stability and the second of which yields instability. These conclusions, as elementary as they are, constitute the first step towards the formulation of the principles of competitive exclusion, ecolobical niche and limiting similarity in present day theoretical ecology. The extent to which these conclusions remain true when the per capita growth rate response (i.e. the parenthetical expression in (6.1)) is replaced by a delay functional of Volterra integral form is briefly investigated by Cushing (1977a) along with the possibility of sustained oscillations. In this chapter I will investigate, in more detail than was done in this earlier work, a delay version of the classical system (6.1) to see not only to what extent the above features of the nondelay system hold true, but also to point out some unusual phenomena due to the delays. Also a new model of competition in age structured populations with a corresponding maturation delay will be considered.

(a) Suppose that unlike the case modeled by (6.1) we assume that, in the absence of the other species, each species grows according to a delay logistic equation and consequently that in isolation each species may be stable or may be unstable and oscillate according to the results of Chapters 2 and 3. Assume that there is no other significant delay so that (6.1) is replaced by

(6.2) $P_i' = r_iP_i(1 - c_{ii}\int_0^\infty k_i(s)P_i(t-s)ds - c_{ij}P_j)$, $1 \leq i \neq j \leq 2$

where $k_i(s) \geq 0$, $\int_0^\infty k_i(s)ds = 1$. This system has the same equilibria $P_i = e_i$ as the nondelay system (6.1), namely

(1) $e_1 = e_2 = 0$ (2) $e_i = 1/c_{ii}$, $e_j = 0$, $1 \leq i \neq j \leq 2$ (3) $e_i = (c_{jj} - c_{ij})/\Delta$

where $\Delta = c_{11}c_{22} - c_{12}c_{21}$. The null equilibrium (1) is obviously unstable. Linearization of (6.2) at equilibrium (2) leads to the characteristic equation $D_i(z) := (z - r_j(c_{ii} - c_{ji})/c_{ii})h_i(z) = 0$ where $h_i(z) := z + r_i k_i^*(z)$. The function $h_i(z)$ is the characteristic function for the equilibrium $1/c_{ii}$ of the delay logistic for the species P_i in isolation. We conclude that if species P_i is stable in isolation (i.e. $1/c_{ii}$ is locally asymptotically stable) then equilibrium (2) of (6.2) is unstable when $c_{ji} < c_{ii}$ and (locally) asymptotically stable if $c \quad > c_{ii}$. This conclusion is exactly that for the nondelay model (6.1). If however species P_i is unstable in isolation then equilibrium (2) of (6.2) is unstable, since roots of $h_i(z)$, $\text{Re } z \geq 0$, are roots of $D_i(z)$.

Assume now that equilibrium (3) is positive. This equilibrium was studied by Cushing (1977a,p.80) who showed first of all that if $\Delta < 0$ then a positive equilibrium (3) is unstable (as in the nondelay case (6.1)). However, unlike the nondelay case (6.1), equilibrium (3) is not otherwise stable. It was shown by Cushing (1977a) that if $\Delta > 0$ and c_{ij} are both small, then the positive equilibrium (3) is (locally) asymptotically stable provided both species in isolation are; on the other hand equilibrium (3) is unstable if at least one species in isolation is unstable.

The inequality $c_{ji} < c_{ii}$ ($> c_{ii}$) means that interspecies competition is stronger (weaker) than intraspecies competition. The net result of the above is then, just as in the nondelay case, two competing species can coexist only if interspecies competition is stronger than interspecies competition (provided for coexistence one requires an asymptotically stable equilibrium).

Unlike the nondelay case (6.1) there is in (6.2) the possibility of sustained oscillations. This can be investigated by means of Theorem A in Appendix A as a bifurcation phenomenon from the (assumed existent) positive equilibrium (3). To do this we first center the problem on equilibrium (3) by setting $x_i = P_i - e_i$ after which system (6.2) can be written in the form of (A.1) with $h = 0$, $m = 2$ and $Lx := \mathrm{col}(x_i' + r_i^0 e_i c_{ii} \int_0^\infty k_i(s) x_i(t-s)ds + r_i^0 e_i c_{ij} x_j)$, $T(x,\lambda) := \mathrm{col}(-e_i c_{ii} \lambda_i \int_0^\infty k_i(s) x_i(t-s)ds - e_i c_{ij} \lambda_i x_j - (r_i^0 + \lambda_i)(c_{ii} x_i \int_0^\infty k_i(s) x_i(t-s)ds + c_{ij} x_i x_j)$ where $\lambda = \mathrm{col}(\lambda_i)$. Suppose that the $r_i^0 > 0$ are chosen so that $Lx = 0$ has exactly $m = 2$ independent p-periodic solutions y_1, y_2 given by the real and imaginary parts of $a \exp(i\omega t)$, $\omega = 2\pi/p$, where $a = \mathrm{col}(a_i)$. Let the two independent p-periodic solutions of the adjoint system $L_a x = 0$, where $L_a x := \mathrm{col}(x_i' - r_i^0 e_i c_{ii} \int_0^\infty k_i(s) x_i(t+s)ds - r_j^0 e_j c_{ji} x_j)$ be given by the real and imaginary parts of $b \exp(i\omega t)$, $b = \mathrm{col}(b_i)$. It turns out that (see Cushing (1979b)) in H4 of Appendix A

$$(6.3) \qquad d = (\omega^2/4r_1^0 r_2^0)(k_1^2 + k_2^2)\,\mathrm{Im}\; a_1 \bar{a}_2 \bar{b}_1 b_2$$

for the homogeneous solution $y = k_1 y_1 + k_2 y_2$, $k_1^2 + k_2^2 \neq 0$. By Theorem A of Appendix A we see that *if* $d \neq 0$ *then* (6.2) *has nontrivial p-periodic solutions of the form* $P_i = e_i + \varepsilon y + \varepsilon z(\varepsilon)$ *for* $r_i = r_i^0 + \lambda_i(\varepsilon)$ *as described in Theorem A of Appendix A.*

To be more specific suppose we consider the case of similar species: $c_{ii} = 1/K$, $c_{ij} = \beta$ and $k_1(s) \equiv k_2(s)$. Then (6.2) reduces to the system

$$(6.4) \qquad P_i' = r_i P_i (1 - K^{-1} \int_0^\infty k_i(s) P_i(t-s)ds - \beta P_j)$$

with $e_i = e = K/(1+K\beta) > 0$. As pointed out above this positive equilibrium is unstable if $\Delta = (1/K)^2 - \beta^2 < 0$ or $K\beta > 1$.

It is easy to show that the linearization of (6.4) at the positive equilibrium has solution $a \exp(in\omega t)$ if and only if (Cushing (1977a,p.167))

$$(6.5) \quad \begin{aligned} &(a)\ n^2 \xi_1 \xi_2 - (e/K)S(n)n\xi_1 - (e/K)S(n)n\xi_2 + e^2(\beta^2 + (S^2(n) - C^2(n)/K^2) = 0 \\ &(b)\ nC(n)(\xi_1 + \xi_2)/K = 2eS(n)C(n)/K^2 \end{aligned}$$

$$C(n) := \int_0^\infty k(s) \cos n\omega s \, ds \quad , \qquad S(n) := \int_0^\infty k(s) \sin n\omega s \, ds$$

where $\xi_i = \omega/r_i^0$. Since we want exactly $m = 2$ independent solutions we need to solve (6.5) for $\xi_i > 0$ when $n = 1$ such that (6.5) fails to hold for $n \geq 2$. Assume $C(1) \neq 0$ in which case (6.5b) reduces to $\xi_1 + \xi_2 = 2eS(1)/K$ which implies the necessary condition $S(1) > 0$. Solving this equation for ξ_2 and substituting the result into (6.5a) we obtain the quadratic

$$\xi_1^2 - 2(eS(1)/K)\xi_1 + e^2((S^2(1) + C^2(1))/K - \beta^2) = 0$$

to be solved for real $\xi_1 > 0$. A straightforward investigation of the roots of this quadratic shows that both roots $\xi_i > 0$ if and only if

$$\text{(6.6)} \qquad 0 < C^2(1) < (K\beta)^2 < S^2(1) + C^2(1)$$

in which case there are two symmetric solution pairs $\xi_1 = \xi^{\pm}$, $\xi_2 = \xi^{\mp}$

$$\text{(6.7)} \qquad \xi^{\pm} = e(S(1) \pm \sqrt{(\beta K)^2 - C^2(1)}\,)/K > 0 .$$

Thus for $r_i^0 = \omega/\xi_i$ the linearized system $Lx = 0$ has nontrivial p-periodic solutions $a \exp(i\omega t)$ for, as it turns out, $a = \mathrm{col}(-er_1^0\beta, i\omega+er_1^0(C(1) - iS(1))/K)$ and the adjoint system has solutions $b \exp(i\omega t)$ for $b = \mathrm{col}(-er_2^0\beta, -i\omega+er_1^0(C(1) + iS(1))/K)$. A straightforward calculation shows that

$$d = e^3\omega^5\beta^2(k_1^2+k_2^2)C(1)(S(1) - \xi_1 K/e)/2\xi_1^4\xi_2^2K^2 \neq 0$$

which is nonzero by (6.6) and (6.7).

We have left only to guarantee that $Lx = 0$ has no more than $m = 2$ independent p-periodic solutions, i.e. that (6.5) does not hold for $n \geq 2$ and the ξ_i chosen above. A simple way to do this is to require that (6.5b) fail for $n \geq 2$, i.e. that

$$\text{(6.8)} \qquad nC(n)S(1) \neq C(n)S(n) , \quad n \geq 2.$$

THEOREM 8. *If* $p = 2\pi/\omega$ *is a period for which* $S(1) > 0$, (6.6) *and* (6.8) *hold then the delay competition model* (6.4) *has nontrivial p-periodic solu-*

tions of the form $P_i = e + \varepsilon y_i + \varepsilon z_i(\varepsilon)$ *for* $r_i = \omega/\xi_i + \lambda_i(\varepsilon)$, $z(0) = \lambda(0) = 0$, *where* $\xi_1 = \xi^{\pm}$, $\xi_2 = \xi^{\mp}$ *are given by* (6.7).

I will not carry out a stability analysis here but will only note that stable bifurcation, as a general rule of thumb, usually occurs when there is a loss of stability of the equilibrium or an exchange of stability from a stable equilibrium to a limit cycle. It has already been pointed out above that the equilibrium $P_i = e$ is already unstable if $K\beta > 1$. Suppose then that $K\beta < 1$ so that the equilibrium is asymptotically stable for the nondelay case (6.1). In order to have the bifurcation described above under the constraint (6.6) it is clearly necessary that $C^2(1) \neq 1$ ($C^2(1) \leq 1$ follows from the assumptions on $k(s)$).

As an illustration take $k(s) = T^{-2}se^{-s/T}$. Then $C(n) = (1-(n\omega T)^2)/(1+(n\omega T)^2)^2$, $S(n) = 2n\omega T/(1+(n\omega T)^2)^2$ so that $S(1) > 0$ and $C^2(1) < 1$ hold. If $n\omega T \neq 1$ for $n \geq 2$ then (6.8) holds. The bifurcation curve C of critical values $r_i^0 = \omega/\xi_i$ of r_i for the values $T = K = 1$, $\beta = 1/2$ is drawn in FIGURE 5. In this case condition (6.6) reduces to $\omega < 1$ and $\omega^4 + 4\omega^2 - 1 > 0$ or in other words $2\pi < p < 12.93$. In the absence of the other

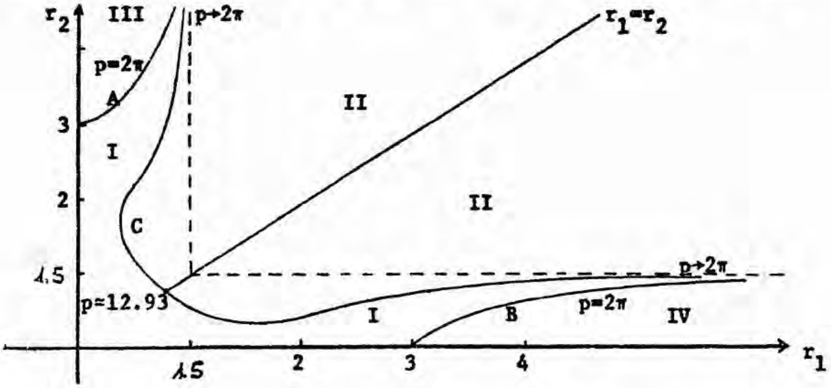

FIGURE 5: The bifurcation curve C of critical values of r_i in the competition model (6.4) with $K=1$, $\beta=1/2$ and $k=s\exp(-s)$ is symmetric with respect to r_1, r_2. The positive equilibrium $P_i=2/3$ is asymptotically stable in Region I and unstable in II, III and IV. On the hyperbolic curves A and B (where $C(1)=0$) the linearized problem has nontrivial 2π-periodic solutions, but the nondegeneracy condition fails so it is not clear whether bifurcation occurs or not.

species each species has a stable equilibrium ($K = 1$) if $r_i < 2$, but bifurcating oscillations and an unstable equilibrium for $r_i > 2$ (Cushing (1977a)).

From this specific example we can draw some conclusions concerning competing species with self-density response delays which, in the absence of such delays, would be in stable coexistence: it is possible that (1) *a species which is unstable and oscillatory in isolation can have a stable equilibrium when placed in interaction with a competitor* (i.e. (r_1, r_2) can be in region I of FIGURE 5 while r_1 or $r_2 > 2$); (2) *for large enough inherent growth rates, the positive equilibrium which is stable in the absence of delays will be unstable in the presence of delays and the species will exhibit limit cycle behavior*; (3) *for each species the onset of instability can occur for smaller inherent growth rates than would occur for one or both in isolation* (part of the curve C in FIGURE 5 lies inside the square $0 < r_i < 2$) but in this case the period of oscillation is longer ($12.93 > 2\pi$); and (4) *two species stable in isolation can be unstable in competition* (part of region II in FIGURE 5 lies in the square $0 < r_i < 2$). In fact any species, stable or not (fix r_i), when placed in competion with another with a large inherent growth rate (r_j large) will be unstable.

(b) We now consider competition between two age structured populations as modeled by (1.12) under the assumption that the effect of the competition is to decrease linearly the fecundity of each species. Thus, we consider

$$(6.9) \qquad P_i' + d_iP_i = b_i \int_0^\infty \beta_i'(a)e^{-d_ia}P_i(t-a)da \, \{1 - c_{ii}P_i - c_{ij}P_j\}_+$$

for $\beta_i(a) \geq 0$, $\int_0^\infty \beta_i(a)da = 1$, $d_i > 0$, $c_{ii} > 0$, $c_{ij} > 0$, $1 \leq i \neq j \leq 2$, which has three equilibria $P_i = e_i$ given by

$$(1)\ e_i = 0 \quad (2)\ e_i = (R_i - 1)/R_ic_{ii},\ e_j = 0 \quad (3)\ e_i = \left(c_{jj}\left(1 - \frac{1}{R_i}\right) - c_{ij}\left(1 - \frac{1}{R_j}\right)\right)/\Delta$$

where $\Delta = c_{11}c_{22} - c_{12}c_{21}$ and $R_i = b_i\int_0^\infty \beta_i(a)\exp(-d_ia)da$. Linearization at the null equilibrium (1) yields the characteristic equation

$$D(z):= (z + d_1)(z + d_2)(1 - b_1\beta_1^*(z+d_1))(1 - b_2\beta_2^*(z+d_2)) = 0$$

Inasmuch as $|\beta_i^*(z+d_i)| \le \int_0^\infty \beta_i(a)\exp(-d_i a)da$ for $\operatorname{Re} z \ge 0$ we see that if both net reproductive rates $R_i < 1$ then $D(z) \ne 0$ for $\operatorname{Re} z \ge 0$ and (1) is asymptotically stable. Linearization at equilibrium (2) results in a characteristic function $D(z):= (z+d_j)h_j(z)h_i(z)$, $1 \le i \ne j \le 2$, $h_j(z):= z + d_i R_i - (b_i/R_i)(z+d_i)\beta_i^*(z+d_i)$, $h_i(z):= 1 - b_i(1-c_{ji}e_i)\beta_j^*(z+d_j)$ and hence the roots of $D(z)$ are $-d_j < 0$ and those of $h_i(z)$, $h_j(z)$. The equation $h_j(z) = 0$ is the characteristic equation of the linearized isolated species P_i at its equilibrium $P_i = (R_i-1)/R_i c_{ii}$ and hence has no roots $\operatorname{Re} z \ge 0$ according to the analysis in Chapter 2. Thus the stability of equilibrium (2) in the competition model (6.9) is determined by the roots of $h_i(z) = 0$. Note that this says that whether species j (locally) goes extinct (i.e (2) is stable) depends on its own maturation delay $\beta_j(a)$.

THEOREM 9. *If both* $R_i < 1$ *then the null equilibrium* (1) *is* (*locally*) *asymptotically stable* (*and both species go extinct*). *If* $\int_0^\infty a\beta_j(a)e^{-d_j a}da < +\infty$ *and* $R_i > 1$ *for* $i = 1$ *or* 2 $(j \ne i)$ *then equilibrium* (2) *is* (*locally*) *asymptotically stable if either of the following conditions hold*: (a) $c_{ii}R_i/(R_i-1) > c_{ji} > c_{ii}R_i(1-1/b_i)/(R_i-1)$ *or* (b) c_{ji} *is greater than but close to* c_{ii} .

Note that (a) implies $c_{ji} > c_{ii}$ since $R_i < b_i$.

Proof. Condition (a) implies $|b_i(1-c_{ji}e_i)| < 1$. For $\operatorname{Re} z \ge 0$, $|\beta_j^*(z+d_j)| \le \int_0^\infty \beta_j(a)da = 1$. Thus $h_i(z) \ne 0$ and hence $D(z) \ne 0$ for $\operatorname{Re} z \ge 0$.

Secondly consider (b). Treat $h_i = h_i(z,c_{ji})$ as a function of z, c_{ji}. Suppose there exist sequences such that $c_{ji}^n \ge c_{ii}$, $c_{ji}^n \to c_{ii}$, $\operatorname{Re} z_n \ge 0$ for which $h_i(z_n,c_{ji}^n) = 0$. By theorem B.2 of Appendix B, z_n must be bounded so that without loss in generality $z_n \to z_0$, $\operatorname{Re} z_0 \ge 0$. By continuity $h_i(z_0,c_{ii}) = 0$ which implies $\beta^*(z_0+d_j) = \beta^*(d_j)$ and hence $z_0 = 0$. But this contradicts the implicit function theorem, which (because $h_i(0,c_{ii}) = 0$, $\partial h_i(0,c_{ii})/\partial z = \int_0^\infty a\beta_j(a)\exp(-d_j a)da/\int_0^\infty \beta_j(a)\exp(-d_j a)da > 0$, $\partial h_i(0,c_{ii})/\partial c_{ji} = b_i e_i R_j/b_j > 0$)

implies the existence of a unique branch of solutions $z = z(c_{ji})$, $z(c_{ii}) = 0$ for c_{ji} near c_{ii} satisfying $z'(c_{ii}) < 0$ and hence $\operatorname{Re} z(c_{ji}) \geq 0$ for c_{ji} greater than but near c_{ii}. §§

Theorem 9 shows that equilibrium (2) has a similar threshold property to that in models (6.1) and (6.2). One question which arises, however, is whether equilibrium (2) remains stable for c_{ji} large. That it can, unlike the case of (6.1) or (6.2), lose its stability for large c_{ji} can be seen in the following example. Suppose $\beta_j(a) = \beta_i(a)$ is given by (2.9). Then $\beta_j^*(z) = (n/(zT+n))^{n+1}$ and $R_i = b_i(n/(d_iT+n))^{n+1}$ so that $R_i > 1$ requires $b_i > ((d\ T+n)/n)^{n+1}$. In this case $h_i(z) = 0$ if and only if $b_i(1-c_{ji}\ e_i) = ((zT+d_jT+n)/n)^{n+1}$. From Theorem C.3 of Appendix C we see that equilibrium (2) in this example is asymptotically stable if and only if $(d_jT+n)/n > |b_i(1-c_{ji})e_i|^{1/(n+1)}$ if $1-c_{ji}e_i > 0$ or $|b_i(1-c_{ji})e_i|^{1/(n+1)}\cos\pi/(n+1)$ if $1-c_{ji}e_i < 0$ which is equivalent to $c_{ii} < c_{ji} < c_n^0 := e_i^{-1}+((d_jT+n)/n)^{n+1}/b_ie_i \cos^{n+1}(\pi/(n+1))$. Thus for $c_{ji} < c_{ii}$ or $c_{ji} > c_n^0$ the equilibrium (2) in this example is unstable and for $c_{ii} < c_{ji} < c_n^0$ it is (locally) asymptotically stable. When $n = 1$, $c_1^0 = +\infty$ and equilibrium (2) remains stable for all $c_{ji} > c_{ii}$. But for more narrowly defined maturation periods $n \geq 2$ there is a loss of stability at c_n^0 as well as at c_{ii}. The loss of stability at c_{ii} is not of Hopf type since as c_{ji} passes through c_{ii} a real root crosses the imaginary axis at $z = 0$. But as c_{ji} passes through c_n^0, $n \geq 2$, the loss of stability is of Hopf type as two purely imaginary conjugate roots cross into the right half plane (at $z = i(d_jT+n)\tan\pi/(n+1)$). Note that as $n \to +\infty$, $R_i \to b_i\exp(-d_jT)$ (which must be assumed > 1) and $c_n^0 \to c_{ii}(b_i+\exp(d_jT)/(b_i-e^{d_jT})$.

Finally we briefly consider equilibrium (3) which we assume is positive. The characteristic equation is $D(z) = 0$ where

$$D(z) := (z+d_1)(z+d_2)g_1(z)g_2(z) + \sum_{i=1}^{2} d_ie_iR_ic_{ii}(z+d_i)g_i(z) + d_1d_2e_1e_2R_1R_2\Delta$$

where $g_i(z) := 1-b_i\beta_i^*(z+d_i)/R_i$. Since $D(x) = O(x^2)$ for large real $x > 0$

and $D(0) < 0$ if $\Delta < 0$ we see that equilibrium (3) is unstable if $\Delta < 0$.

Note that in the above example with $n \geq 2$ all four nonnegative equilibria are unstable under strong interspecies competition, i.e. for c_{ji} large.

Suppose now that $\Delta > 0$ and consider again the case of similar species: $c_{ii} = \alpha_1 > 0$, $c_{ji} = \alpha_2 > 0$, $b_i = b > 0$, $d_i = d > 0$ and $\beta_i(a) \equiv \beta(a)$. Then $\Delta = \alpha_1^2 - \alpha_2^2 > 0$ implies $\alpha_1 > \alpha_2$. It follows that $R_i = R > 0$, $g_i(z) = g(z) = 1-b\beta^*(z+d)/R$ and $e_i = e$. Then $D(z) = ((z+d)g(z)+deR\alpha_1)^2-(deR\alpha_2)^2 = 0$ implies, since $R = b\beta^*(d)$, that $\beta^*(z+d)/\beta^*(d) = (z+d+deR(\alpha_1 \pm \alpha_2))/(z+d)$. Since the abolute value of the right hand side is strictly greater than one for $\mathrm{Re}\, z \geq 0$ while the left hand side is less than or equal to one it follows that $D(z) \neq 0$ for $\mathrm{Re}\, z \geq 0$.

THEOREM 10. *Suppose that equilibrium* (3) *of the competition model* (6.9) *is positive. If* $\Delta < 0$ *this equilibrium is unstable. If* $\Delta > 0$ *in the case of similar species* ($b_1 = b_2$, $c_{11} = c_{22}$, $c_{12} = c_{21}$, $\beta_1(a) \equiv \beta_2(a)$), *then this equilibrium* (3) *is (locally) asymptotically stable*.

APPENDIX A

Let X, Y denote real normed linear spaces and suppose $L: X \to Y$ is a bounded linear operator with nullspace $N(L)$ and range $R(L)$. Consider

$$(A.1) \qquad Lx = T(x,\lambda,\varepsilon) + \varepsilon h, \qquad h \in R(L)$$

to be solved for $(x,\lambda) \in X \times R^m$, $m \geq 0$, as a function of the real parameter $\varepsilon \in R^1$ near $\varepsilon = 0$. For conciseness we allow $m = 0$ to mean T is independent of λ in which case (A.1) is to be solved for x as a function of ε. Assume that the following hypotheses hold:

H1: $R(L)$, $N(L)$ are closed and admit (continuous) projections and
$0 \leq \mathrm{codim}\, R(L) = m < +\infty$;

H2: $y \in X$ is such that $Ly = h$;

H3: $T: D := X \times R^m \times R^1 \to Y$ is an operator for which $T(\varepsilon x,\lambda,\varepsilon) = \varepsilon\overline{T}(x,\lambda,\varepsilon)$ for all $(x,\lambda,\varepsilon) \in D$ where $\overline{T}: D \to Y$ is $q \geq 1$ times continuously Frechet differentiable in (x,λ,ε) with $\overline{T}(y,0,0) = 0$, $\overline{T}_x(y,0,0) = 0$ for y as in H2.

Let M be a closed subspace of X complementary to $N(L)$ and let $A: R(L) \to M$ be a bounded right inverse of L. (Such M and A are guaranteed by H1.) Let $P: Y \to R(L)$ be a (continuous) projection. Then $I-P$ is a (continuous) projection of Y onto the m-dimensional subspace $N(P)$ complementary to $R(L)$ and as a result if $m \geq 1$ then for y as in H2, for $z \in M$, for $\lambda \in R^m$ and for $\varepsilon \in R^1$ the element $(I-P)\overline{T}(y+z,\lambda,\varepsilon)$ has $m \geq 1$ real components $c = c(z,\lambda,\varepsilon): M \times R^m \times R^1 \to R^m$ with respect to a fixed basis of $N(P)$. Note that c has the smoothness properties of $\overline{T}$ and by H3 that $c(0,0,0) = c_z(0,0,0) = 0$. If $m \geq 1$ we need the further hypothesis

H4: $d := \det c_\lambda(0,0,0) \neq 0$.

<u>THEOREM A</u>. (i) <u>If</u> $m \geq 1$ <u>assume</u> H1-H4 <u>hold</u>. <u>Then there exists an</u> $\varepsilon_0 > 0$ <u>such that</u> (A.1) <u>has a solution of the form</u> $x = \varepsilon(y+z(\varepsilon))$, $\lambda = \lambda(\varepsilon)$ <u>for</u> $\varepsilon \in I := \{\varepsilon \in R^1 : |\varepsilon| \leq \varepsilon_0\}$ <u>where</u> y <u>is as in</u> H3, $z: I \to M$ <u>and</u> $\lambda: I \to R^m$ <u>are</u> $q \geq 1$ <u>times continuously Frechet differentiable operators with</u> $z(0)=\lambda(0)=0$.

(ii) <u>If</u> $m = 0$ <u>assume</u> H1-H3 <u>hold</u>. <u>Then equation</u> (A.1) <u>has a solution of the form</u> $x = \varepsilon(y+ z(\varepsilon))$ <u>as described in</u> (i).

<u>Proof</u>. Substitute $x = \varepsilon(y+z)$ for $z \in M$ and $Ly = h$ into (A.1). The resulting equation is equivalent to the two equations

$$z - AP\overline{T}(y+z,\lambda,\varepsilon) = 0 \tag{A.2}$$

$$c(z,\lambda,\varepsilon) = 0 \tag{A.3}$$

for $(z,\lambda,\varepsilon) \in M \times R^m \times R^1$. Clearly $(z,\lambda,\varepsilon) = (0,0,0)$ solves both of these equations. Equation (A.2) is uniquely solvable for $z = z(\lambda,\varepsilon)$ near $(\lambda,\varepsilon) = (0,0)$ by means of the implicit function theorem. When $m \geq 1$ and this solution is substituted into (A.3) the resulting equation in (λ,ε) is also uniquely solvable for $\lambda = \lambda(\varepsilon)$ near $\varepsilon = 0$ by means of the implicit function theorem and by H4. §§

REMARK: This theorem permits $h = 0$ and also permits T to be independent of ε. In this case the theorem yields as a corollary the multi-parameter bifurcation theorems of Cushing (1979b,1979c) where $0 \neq y \in N(L)$ and it is assumed that $N(L) \neq \{0\}$ so that H2 is fulfilled and the solutions are nontrivial $x \neq 0$ (even though in this case $x = 0$ is a solution for all λ).

APPENDIX B

THEOREM B.1. If $k(s)$ *is continuously differentiable for* $s \geq 0$, $k_1 := \int_0^\infty |k(s)|ds < +\infty$ *and* $k_2 := \int_0^\infty s|k(s)|ds < +\infty$ *then* $\lim_{R\to+\infty}\int_{-\pi/2}^{\pi/2}|k^{*\prime}(Re^{i\theta})|d\theta = 0$.

Proof. Given $\varepsilon > 0$ let $T > 0$ be so small that $0 \leq \int_0^T s|k(s)|ds < \varepsilon$. For $z = Re^{i\theta}$, $-\pi/2 < \theta < \pi/2$, $|k^{*\prime}(z)| = |\int_0^\infty e^{-zs}sk(s)ds| \leq \varepsilon + e^{-RT\cos\theta}\int_T^\infty s|k(s)|ds$ and hence $\limsup_{R\to+\infty}|k^{*\prime}(Re^{i\theta})| \leq \varepsilon$ which, since $\varepsilon > 0$ is arbitrary, implies $\lim_{R\to+\infty}|k^{*\prime}(Re^{i\theta})| = 0$, $-\pi/2 < \theta < \pi/2$. Since $|k^*(Re^{i\theta})| \leq k_1 < +\infty$ for all $R > 0$, $-\pi/2 \leq \theta \leq \pi/2$, the assertion of this theorem follows from Lebesgue's dominated convergence theorem. §§

Theorem B.1 makes hypothesis (4.34) in Theorem 4.12 of Cushing (1977a,p89) unnecessary.

THEOREM B.2. The function $f(x) := bx^{x+1}(a+x)^{-x-1}$ *for* $x > 0, a > 0, b > 0$ *has the following properties*: $f(0+) = 0$, $f(+\infty) = be^{-a}$ *and if* $a \leq 2$ *then* $f'(x) > 0$ *while if* $a > 2$ *then* $f'(x) > 0$ *for* $0 < x < x_0$ *and* $f'(x) < 0$ *for* $x > x_0$ *where* $x_0 < a/(a-2)$ *is the unique number such that* $f'(x_0) = 0$.

Proof. $f(0+) = 0$ is obvious and $f(+\infty) = be^{-a}$ follows from a straightforward application of l'Hopital's rule to $(x+1)\ln(x/(a+x))$. A differentiation shows that $f'(x) = -f(x)g(x)$ where $g(x) := \ln((x+a)/x) - (x+1)/(x^2+ax)$. It is easy to show that $g(0+) = -\infty$ and $g(+\infty) = 0$. Moreover, $g'(x) = a(a+(2-a)x)/x^2(x+a)^2$. Thus $a \leq 2$ implies $g(x) < 0$ and hence $f'(x) > 0$ for all

$x \geq 0$. If $a > 2$ then $g(x)$ increases for $x < a/(a-2)$ and then decreases (to zero) for $x > a/(a-2)$ which implies that there exists a unique x_0 less than $a/(a-2)$ such that $g(x) < 0$ for $x < x_0$ and $g(x) > 0$ for $x > x_0$.§§

APPENDIX C

Assume that $\beta(a) \geq 0$ is continuously differentiable for $a \geq 0$ and satisfies $\int_0^\infty \beta(a)da < +\infty$.

THEOREM C.1. *The only root of* $1 - b\beta^*(z+d)/R = 0$ *where* $b > 0$ *and* $R = b\int_0^\infty e^{-da}\beta(a)da$ *satisfying* $\operatorname{Re} z \geq 0$ *is* $z = 0$.

Proof. Since $R = b\beta^*(d)$ this equation reduces to $\beta^*(z+d) = \beta^*(d)$ for $\operatorname{Re} z \geq 0$, the real part of which (setting $z = x + iy$) yields the equation $\int_0^\infty e^{-da}\beta(a)(e^{-xa}\cos ya - 1)da = 0$. This latter equation implies, for $x \geq 0$, that $x = y = 0$. §§

THEOREM C.2. *Suppose* z_n *is a sequence for which* $\operatorname{Re} z_n \geq 0$ *and* $z_n \to +\infty$. *Then there exists a subsequence such that* $\lim_{n\to+\infty}\beta^*(z_n+d) = 0$.

Proof. If the set of $x_n = \operatorname{Re} z_n \geq 0$ is unbounded then there is a subsequence for which $x_n = \operatorname{Re} z_n \to +\infty$. The result follows from $|\beta^*(z_n+d)| \leq \int_0^\infty\beta(a)\exp(-x_n a)da$ and the dominated convergence theorem.

If x_n is bounded then there exists a convergent subsequence. Let $x_n \to x_0$, $x_0 \geq 0$. Define $w_n = x_0 + iy_n$ where $y_n = \operatorname{Re} z_n$. From Hewitt and Stromberg (1965,p.401) follows $\beta^*(w_n+d) \to 0$ as $n \to +\infty$. If γ_n is the circle with center at w_n+d of radius $\rho = d/2$ (so that γ_n lies in the half plane $\operatorname{Re} z \geq d/2$ on which $\beta^*(z)$ is bounded: $|\beta^*(z)| \leq M$, $\operatorname{Re} z \geq d/2$) then we get from Cauchy's integral theorem that

$$\beta^*(z_n+d) - \beta^*(w_n+d) = (2\pi i)^{-1}\int_{\gamma_n} \beta(\xi)\,\frac{w_n - z_n}{(\xi-z_n-d)(\xi-w_n-d)}\,d\xi$$

For large enough n (so that $|\xi-z_n-d| \geq \rho/2$, $\xi \in \gamma_n$) we have the estimate

$$|\beta^*(z_n+d) - \beta^*(w_n+d)| \leq 2M|w_n - z_n|/\rho = 2M|x_n - x_0|/\rho \quad .$$

Thus $\beta^*(z_n+d) \to 0$ as $n \to +\infty$. §§

THEOREM C.3. The equation $(z + a)^k = b$ for a and b real and for k a positive integer has all roots with $\mathrm{Re}\, z < 0$ if and only if

$$a > \begin{cases} b^{1/k} & \text{when } b \geq 0 \\ |b|^{1/k}\cos \pi/k & \text{when } b < 0 \end{cases} .$$

Proof Clearly

$$\mathrm{Re}\, z = -a + |b|^{1/k} \begin{cases} \cos 2\pi m/k & \text{when } b \geq 0 \\ \cos(2m+1)\pi/k & \text{when } b < 0 \end{cases}$$

where $0 \leq m \leq k-1$. The maximum of $\cos 2\pi m/k$ is one (occuring for $m = 0$) while that of $\cos(2m+1)\pi/k$ is $\cos \pi/k$ (occuring for $m = 0$). §§

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