Simple Mathematical Models for Cannibalism: A Critique and a New Approach

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ABSTRACT

We show how to incorporate a functional response in recent models of Gurtin, Levine, and others for egg cannibalism. Starting from a relatively complicated model with vulnerability spread over an age interval of finite duration ϵ, we arrive at a much simpler model by passing to the limit $\epsilon \downarrow 0$. It turns out that survivorship through the vulnerable stage is implicitly determined by the solution of a scalar equation. Subsequently we study the existence and stability of steady states, and we find (analytically in a simple case, numerically in more general situations) curves in a two-dimensional parameter space where a nontrivial steady state loses its stability and a periodic solution arises through a Hopf bifurcation.

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1. INTRODUCTION

The incorporation of age or stage structure into mathematical models for the dynamics of biological populations creates the possibility of describing complicated inter- and intraspecific interactions. But the roads to realistic models and to tractable models are seldom parallel, and the would-be modeler is confronted with conflicting forces. Thus computer simulations of truly realistic quantitative models may be supplemented by analytic studies of relatively simple strategic models in order to enhance a qualitative understanding.

In a successful attempt to keep the analytic complexity of an age-dependent prey-predator model within bounds, Gurtin and Levine [7] have intro-

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duced a rather clever idea. They translate the observation that some species only eat those individuals of a prey population which are in an early stage of their life cycle (e.g., eggs or larvae) into the mathematical assumption that predation only affects the rate of recruitment of the prey population. So if $b(t)$ denotes the rate of prey offspring production and $P(t)$ the size of the predator population, the rate of prey recruitment is given by $b(t)R(b(t), P(t))$, where R denotes the fraction of newborns that survive predation during an instantaneous (i.e., infinitesimally short) interaction with the predator population. In a subsequent publication [8] they identify the prey and the predator population so as to consider the qualitative effects of cannibalism. Under various ad hoc mathematical assumptions on the function R, they studied the existence and stability of steady states and the existence of periodic solutions. In a follow-up, Frauenthal [4] has, among other things, tried to specify R starting from a saturating functional response as it arises from well-known mechanistic submodels for the predation process propounded by Holling [9, 10] and others. This is not an easy fill-in exercise, because these mechanistic submodels produce a predation rate that depends on prey *number* (or, more precisely, number per unit of area), whereas $b(t)$ describes the *rate* at which potential victims of cannibalism are produced (per unit of area). Frauenthal ignores this difficulty and ends up with an unconvincing specification, where, in order to avoid *negative* rates of recruitment, he has to add an extra ad hoc rule. Gurtin and Levine [7] also neglect this problem, while Thompson, DiBiasio, and Mendes [13] suggest a modification that, although negative rates of recruitment are no longer possible, still does not solve the basic problem.

This difficulty has prompted us to investigate the rationale of Gurtin and Levine's approach in some more detail. We first formulate a mathematical model of density-dependent cannibalism in which the young of age $0 \leqslant a \leqslant \epsilon$ are potential victims and subsequently take the limit $\epsilon \downarrow 0$. Since a functional response is easily built into the original model (although there are several ways to fill in the details; moreover, the whole construction presupposes that the predation process has a time scale which is very short relative to ϵ), we obtain a limiting model which admits a precise interpretation. Surprisingly, the determination of the survivorship through the vulnerable stage involves, in the limit, the (implicit) solution of a scalar equation. *A posteriori* this equation is easily interpreted as a consistency condition.

For the sake of clarity we present our approach in the context of one specific model, viz., a cannibalism model. It should be clear, however, that the method of deriving a functional response relation for instantaneous interaction applies more generally. We intend to elaborate other examples in future publications.

Our study of the cannibalism model concentrates on the existence and the stability of steady states. There appears to be a unique positive steady state for relevant parameter values. We establish complementary regions in a two-dimensional parameter space where this steady state is stable or unstable. The transition from one region to the other is characterized by a pair of complex conjugate roots of the characteristic equation crossing the imaginary axis and, consequently, by the (Hopf) bifurcation of a periodic solution. Thus our findings confirm the belief that cannibalism may promote oscillations.

Finally, we address the question of the biological relevance of our limiting model. Egg cannibalism has been extensively studied in stored-product organisms (see, for instance, Fujii [5] and the references given there), where a vulnerable egg stage may last a few days out of a life cycle of several weeks. We therefore investigate whether the results for our mathematically simple "limiting model" will remain valid for small positive values of ϵ. In Appendix I we present a formal proof that the processes of local linearization and taking the limit $\epsilon \downarrow 0$ are interchangeable, thereby guaranteeing that, except close to the stability boundary, (in)stability in the limiting model guarantees (in)stability for ϵ positive but small.

2. THE MODEL OF EGG CANNIBALISM AND ITS SIMPLIFICATION

Let $n(t,\cdot)$ denote the age distribution of a biological population at time t. The time evolution of this distribution is described by the McKendrick equation

$$\frac{\partial}{\partial t}n(t,a)+\frac{\partial}{\partial a}n(t,a)=-\mu(t,a)n(t,a) \tag{2.1}$$

provided with the boundary condition

$$n(t,0)=b(t). \tag{2.2}$$

Formulation of a dynamical model amounts to a specification of the age-specific death rate μ and the birth rate b. We assume a density-independent reproduction process and take

$$b(t)=\int_0^\infty B(a)n(t,a)\,da, \tag{2.3}$$

where $B(a)$ is the expected number of births to an individual of age a per unit of time. In order to incorporate cannibalistic effects we assume that

$$\mu(t,a)=\nu(a)+C(a)k(t)\Phi(c(t)), \tag{2.4}$$

where

$\nu(a)$ is the age-specific "natural" death rate,
$C(a)$ is the attack rate as a function of the age of the victim,
$k(t)$ is the effective number of cannibals,
$c(t)$ is the effective number of potential victims of cannibalism,
$\Phi(c(t))$ is the correction factor for density-dependent effects.

The functional response (i.e. the number of prey eaten per predator per unit of time) is given by

$$\int_0^\infty C(a)\,n(t,a)\,da\,\Phi(c(t)).$$

Introducing furthermore

$K(a)$, a dimensionless age-specific index of cannibalistic activity,
$Q(a)$, the "handling" time as a function of the age of the victim,

we choose c and k to be given by

$$c(t)=\int_0^\infty C(a)\,Q(a)\,n(t,a)\,da, \tag{2.5}$$

$$k(t)=\int_0^\infty K(a)\,n(t,a)\,da, \tag{2.6}$$

and we interpret *a posteriori* the words "effective number" to be a shorthand for these weighted averages. Thus our formulation includes an age-dependent version of Holling's [9] "secretary" model, and we may take for Φ the well-known type II factor $\Phi(c)=1/(1+c)$. If, on the other hand, the functional response is determined by limitations of the digestive capacity (Holling [10], Metz and van Batenburg [11]), we may use Q to describe the digestion time as a function of the age of the victim. Note that, since only the products CQn and $k\Phi Cn$ occur in the equation, one may normalize the functions (and even choose their dimensions) in various ways. We will assume that $\Phi(0)=1$ and $\lim_{c\to\infty}c\Phi(c)=1$ (the latter is effectively a normalization of c).

A basic feature of these assumptions is that the influence of the age of the aggressor on the interaction is completely described by the index K entering in the definition (2.6) of k. In Appendix II we briefly discuss a more general setup.

Equations (2.1), (2.2) can be supplemented with an initial condition

$$n(0,a)=\psi(a) \tag{2.7}$$

which determines the solution in the region $a>t$. However, for our present purposes it is better to neglect initial conditions and view n as being determined by (2.1)–(2.2) with $-\infty < t < +\infty$. Thus we can express n explicitly in terms of b, k, and c:

$$n(t,a) = b(t-a)\exp\left\{-\int_0^a [\nu(\sigma) + k(t-a+\sigma) \times \Phi(c(t-a+\sigma))C(\sigma)]\,d\sigma\right\}, \tag{2.8}$$

where the factor

$$\exp\left\{-\int_0^a k(t-a+\sigma)\Phi(c(t-a+\sigma))C(\sigma)\,d\sigma\right\} \tag{2.8a}$$

accounts for the effects of cannibalism. The basic idea now is to let the support of the attack rate C shrink to the point $a = 0$, while at the same time the integral of C remains bounded away from zero [so as to prevent the factor (2.8a) from converging to one, corresponding to cannibalism becoming negligible]. In other words, we let the age interval in which the young suffer from cannibalism become infinitesimally short, but at the same time increase the risk per unit of time of falling victim to cannibalism in such a way that the total risk remains positive. We choose for C a fixed multiple of a δ-function approximation:

$$C(a) = \frac{1}{\epsilon}h\left(\frac{a}{\epsilon}\right), \tag{2.9}$$

where h is some nonnegative function with support in $[0,1]$ such that

$$\int_0^1 h(\sigma)\,d\sigma = \theta, \tag{2.10}$$

The dimensionless parameter θ is the "product" of the attack rate and the length of the vulnerable stage. So it can be considered as a vulnerability index.

Next we calculate limits when $\epsilon \downarrow 0$. We use the suffix ϵ to express the dependence on ϵ explicitly in our notation. Assuming that b_ϵ, c_ϵ, and k_ϵ converge to b_0, c_0, and k_0 when $\epsilon \downarrow 0$, we find for each fixed $a > 0$

$$\begin{aligned}\lim_{\epsilon\downarrow 0} n_\epsilon(t,a) &= \lim_{\epsilon\downarrow 0} b_\epsilon(t-a)\exp\left\{-\int_0^a \nu(\sigma)\,d\sigma - \int_0^{a/\epsilon} k_\epsilon(t-a+\epsilon\tau) \times \Phi(c_\epsilon(t-a+\epsilon\tau))h(\tau)\,d\tau\right\}\\ &= b_0(t-a)\exp\left\{-\theta k_0(t-a)\Phi(c_0(t-a)) - \int_0^a \nu(\sigma)\,d\sigma\right\}.\end{aligned}$$

Since $n_\epsilon(t,0) = b_\epsilon(t) \to b_0(t)$ as $\epsilon \downarrow 0$, we observe nonuniform convergence: the limits $\epsilon \downarrow 0$ and $a \downarrow 0$ are not interchangeable. Indeed, as $\epsilon \downarrow 0$, $n_\epsilon(t,\cdot)$ develops a discontinuity at $a = 0$ which corresponds precisely to the reduction of the rate of production of offspring $b_0(t)$ to the rate of recruitment $b_0(t)\exp\{-\theta k_0(t)\Phi(c_0(t))\}$. In the integrals (2.3) and (2.6) the developing discontinuity of $n_\epsilon(t,\cdot)$ is harmless and we can safely pass to the limit. But in the integral (2.5) the kernel C blows up in precisely the region where $n_\epsilon(t,\cdot)$ becomes discontinuous, so we have to be careful. From

$$\begin{aligned} c_\epsilon(t) = \int_0^1 & h(\sigma) Q(\epsilon\sigma) b_\epsilon(t-\epsilon\sigma) \\ & \times \exp\left\{ -\int_0^{\epsilon\sigma} \nu(\tau)\, d\tau - \int_0^\sigma k_\epsilon(t-\epsilon\sigma+\epsilon\tau) \right. \\ & \qquad \left. \times \Phi(c_\epsilon(t-\epsilon\sigma+\epsilon\tau)) h(\tau)\, d\tau \right\} d\sigma \end{aligned}$$

we derive

$$\begin{aligned} c_0(t) &= Q(0) b_0(t) \int_0^1 h(\sigma) \exp\left\{ -k_0(t)\Phi(c_0(t)) \int_0^\sigma h(\tau)\, d\tau \right\} d\sigma \\ &= \frac{Q(0) b_0(t)}{k_0(t)\Phi(c_0(t))} \left\{ 1 - \exp[-\theta k_0(t)\Phi(c_0(t))] \right\}. \end{aligned}$$

We now drop the suffix nought and summarize and discuss our conclusions. By formal calculations we have found that in the limit $\epsilon \downarrow 0$ the age distribution is completely independent of the function h and given by

$$n(t,a) = b(t-a)\, e^{-\theta k(t-a)\Phi(c(t-a))} e^{-\int_0^a \nu(\sigma)\, d\sigma}, \tag{2.11}$$

where b and k are still given by the formulas (2.3) and (2.6), but c is implicitly determined as a function of b and k by the nonlinear scalar equation

$$\frac{c\Phi(c)}{Q(0)} = \frac{1}{k} b\left(1 - e^{-\theta k \Phi(c)}\right). \tag{2.12}$$

The left-hand side is the formal limit of the functional response $\Phi(c)\int_0^\infty C(a) n(\cdot,a)\, da$, and the right-hand side is, indeed, the number of young eaten per unit of time per cannibal. Thus one can interpret (2.12) as a consistency condition.

Of course the form of Φ has to ensure that, given $b(t)$ and $k(t)$, $c(t)$ is uniquely determined by (2.12). Assuming that $c\Phi(c)$ is increasing for $c > 0$, while $\Phi(c)$ is nonincreasing for $c > 0$, we see that c is uniquely found as the intersection of an increasing and a nonincreasing curve (with opposite ordering of the endpoints, i.e. for $c = 0$ and for $c = +\infty$). In view of our interpretation of Φ, these assumptions are very reasonable indeed.

Finally we prefer to scale k and K with a factor θ and to introduce

$$\alpha = \frac{1}{\theta Q(0)}. \tag{2.13}$$

Effectively this amounts to putting $\theta = 1$ in the formulas above while replacing (2.12) by

$$\alpha c \Phi(c) = \frac{1}{k} b(1 - e^{-k\Phi(c)}). \tag{2.14}$$

As a side remark we note that (2.11) is equivalent to

$$\begin{aligned} \frac{\partial}{\partial t} n(t,a) + \frac{\partial}{\partial a} n(t,a) &= -\nu(a) n(t,a), \\ n(t,0) &= b(t) e^{-k(t)\Phi(c(t))}. \end{aligned} \tag{2.15}$$

3. LOCAL STABILITY OF STEADY STATES

The simplified model takes the form of a system of two Volterra convolution integral equations involving an implicitly defined nonlinear function:

$$\begin{aligned} b(t) &= \gamma \int_0^\infty g(a) b(t-a) e^{-k(t-a)\Phi(c(t-a))} \, da, \\ k(t) &= \rho \int_0^\infty h(a) b(t-a) e^{-k(t-a)\Phi(c(t-a))} \, da, \\ \alpha c(t) \Phi(c(t)) &= \frac{b(t)}{k(t)} (1 - e^{-k(t)\Phi(c(t))}). \end{aligned} \tag{3.1}$$

Here γ and ρ are chosen such that the functions

$$g(a) = \frac{1}{\gamma} B(a) e^{-\int_0^a \nu(\sigma) \, d\sigma} \tag{3.2}$$

and

$$h(a) = \frac{1}{\rho} K(a) e^{-\int_0^a \nu(\sigma) \, d\sigma} \tag{3.3}$$

have integral one. Thus γ is the expected number of offspring of a newly recruited individual (i.e., an individual which is at the beginning of its life but has already escaped from the danger of cannibalism), and ρ is an indicator for the strength of the cannibalistic interaction (recalling the scaling of K, we note that $\rho = \theta\kappa$, where θ is the vulnerability index and κ is the expected time to be spent on cannibalistic activities by newly recruited individuals during their entire future life span).

We refer to Diekmann and van Gils [2] for a detailed account of a qualitative theory of such systems, including a discussion of the incorporation of initial conditions, the principle of linearized stability, and the Hopf bifurcation theorem.

Steady states are found from

$$\begin{aligned} b &= \gamma b e^{-k\Phi(c)}, \\ k &= \rho b e^{-k\Phi(c)}, \\ \alpha c \Phi(c) &= \frac{b}{k}\left(1 - e^{-k\Phi(c)}\right). \end{aligned} \tag{3.4}$$

This system admits the trivial solution $b = k = c = 0$ (for $k = 0$ we interpret the third equation as $\alpha c = b$). Nontrivial solutions have to satisfy

$$\begin{aligned} e^{-k\Phi(c)} &= \frac{1}{\gamma}, \\ \frac{b}{k} &= \frac{\gamma}{\rho}, \\ c\Phi(c) &= \frac{\gamma - 1}{\alpha\rho}. \end{aligned} \tag{3.5}$$

From our assumptions on $c\Phi(c)$ it follows that the third equation has a unique positive solution $c = c^*$ provided that

$$1 < \gamma < 1 + \alpha\rho. \tag{3.6}$$

Since $\alpha = 1/\theta Q(0)$ and $\rho = \theta\kappa$, the product $\alpha\rho$ equals the quotient $\kappa/Q(0)$ of the expected time spent on cannibalistic activities and the handling time. Hence this quantity is the *maximal* number of young eaten during the entire lifetime, and $\gamma - \kappa/Q(0)$ is the *minimal* net contribution to the recruitment. Clearly the population will grow without bound if this contribution exceeds one, and thus the restriction (3.6) has a straightforward biological interpretation. Of course the restriction will disappear if one introduces an extra density-dependent effect so as to bring about a "carrying capacity" even in the absence of cannibalism, but we will not do so here (see Frauenthal [4]).

In the special case

$$\Phi(c) = \frac{1}{1+c} \tag{3.7}$$

we find explicitly

$$c^* = \frac{\gamma - 1}{\alpha\rho - \gamma + 1}. \tag{3.8}$$

Given c^*, we find k from the first equation and subsequently b from the second:

$$k^* = \frac{\ln\gamma}{\Phi(c^*)} = \frac{\alpha\rho\ln\gamma}{\gamma - 1} c^*, \tag{3.9}$$

$$b^* = \frac{\gamma\ln\gamma}{\rho\Phi(c^*)} = \frac{\alpha\gamma\ln\gamma}{\gamma - 1} c^*. \tag{3.10}$$

The trivial steady state is stable for $0 < \gamma < 1$ (in fact global) and unstable for $\gamma > 1$. The nontrivial steady state is stable for γ slightly larger than one. The question arises whether or not the nontrivial steady state loses its stability as γ is further increased and/or other parameters are varied.

Linearization about the nontrivial steady state leads to the *characteristic equation*

$$(q + \gamma\ln\gamma - \gamma + 1)\bar{g}(\lambda) - q\ln\gamma\bar{h}(\lambda) = q + 1 + \ln\gamma - \gamma, \tag{3.11}$$

where

$$q = -\alpha\rho\frac{\Phi^2(c^*)}{\Phi'(c^*)} \tag{3.12}$$

and a bar denotes the Laplace transform

$$\bar{g}(\lambda) = \int_0^\infty e^{-\lambda\tau} g(\tau)\, d\tau \tag{3.13}$$

With Φ given by (3.7) one finds

$$q = \alpha\rho = \frac{\kappa}{Q(0)}, \tag{3.14}$$

and consequently we interpret q as yet another measure for the strength of the cannibalistic interaction.

Our plan is now to study for given functions g and h the curve in the (γ, q)-plane which separates the stability domain, where all roots of (3.11) lie in the left half plane, from the instability domain, where some roots lie in the right half plane. Exploiting the fact that (3.11) is linear in q we can write

$$q = \frac{(\gamma \ln \gamma - \gamma + 1)\bar{g}(\lambda) + \gamma - 1 - \ln \gamma}{1 + \ln \gamma \bar{h}(\lambda) - \bar{g}(\lambda)}. \tag{3.15}$$

The condition for the right-hand side to be real is, for $\gamma \neq 1$,

$$\begin{aligned} &[\operatorname{Im} \bar{g}(\lambda) \operatorname{Re} \bar{h}(\lambda) - \operatorname{Re} \bar{g}(\lambda) \operatorname{Im} \bar{h}(\lambda)](\gamma \ln \gamma - \gamma + 1) \\ &\quad + \operatorname{Im} \bar{h}(\lambda)(\ln \gamma - \gamma + 1) + \operatorname{Im} \bar{g}(\lambda)(\gamma - 1) = 0, \end{aligned} \tag{3.16}$$

and under this condition we have

$$q = \frac{(\gamma \ln \gamma - \gamma + 1) \operatorname{Re} \bar{g}(\lambda) + \gamma - 1 - \ln \gamma}{1 + \ln \gamma \operatorname{Re} \bar{h}(\lambda) - \operatorname{Re} \bar{g}(\lambda)} \tag{3.17}$$

if $1 + \ln \gamma \operatorname{Re} \bar{h}(\lambda) = -\operatorname{Re} \bar{g}(\lambda) \neq 0$, and

$$q = \frac{(\gamma \ln \gamma - \gamma + 1) \operatorname{Im} \bar{g}(\lambda)}{\ln \gamma \operatorname{Im} \bar{h}(\lambda) - \operatorname{Im} \bar{g}(\lambda)} \tag{3.18}$$

otherwise [unless $\ln \gamma \operatorname{Im} \bar{h}(\lambda) - \operatorname{Im} \bar{g}(\lambda) = 0$ as well, in which case the right-hand side is not defined]. In search for purely imaginary roots we put $\lambda = i\omega$, $\omega \in \mathbb{R}$. The idea now is to solve (3.16) for ω for given values of γ (in general there are many solutions) and subsequently determine the corresponding value of q from (3.17) or (3.18). In the next section we present results obtained by a numerical implementation of this idea, but in the rest of this section we restrict ourselves to the special case $h = g$ (if both B and K are step functions, this condition simply means that an individual practises cannibalism if and only if it is reproductive).

If $h = g$, (3.16) simplifies to the γ-independent equation

$$\operatorname{Im} \bar{g}(\lambda) = 0. \tag{3.19}$$

Given a root $\lambda = i\omega$, the formula (3.17) defines q as a function of γ [note that the denominator of (3.18) is always zero now; consequently zeros of the denominator of (3.17) correspond to true singularities of q]. Defining

$$z = \operatorname{Re} \bar{g}(i\omega) \tag{3.20}$$

and

$$H(\gamma)=\frac{z(\gamma\ln\gamma-\gamma+1)+\gamma-1-\ln\gamma}{1+z(\ln\gamma-1)}, \tag{3.21}$$

we rewrite (3.17) as $q=H(\gamma)$. Clearly $\gamma=e^{(z-1)/z}$ is a singular point of H.

The biologically relevant region of parameter space is defined by the inequalities $1<\gamma<1+q$ [in view of (3.14) and (3.6), the second is obvious when Φ is given by (3.7), but it can be derived under the less restrictive assumption that $c\Phi(c)$ is strictly increasing]. Some straightforward but lengthy calculations show that with $q=H(\gamma)$:

(1) these constraints are *not* satisfied whenever $z\geqslant 0$, or $z<0$ and $1<\gamma<e^{(z-1)/z}$;

(2) the constraints are satisfied when $z<0$ and $e^{(z-1)/z}<\gamma<\infty$; in this case $H''(\gamma)>0$, $H(\gamma)\uparrow+\infty$ for $\gamma\downarrow e^{(z-1)/z}$, and $H(\gamma)=\gamma-1/z+o(1)$ for $\gamma\to+\infty$.

Of course, there may be many solutions to $\operatorname{Im}\bar{g}(i\omega)=0$ such that $\operatorname{Re}\bar{g}(i\omega)<0$. From

$$\frac{d}{dz}H(\gamma)=\frac{\ln^2\gamma}{[1-z(1-\ln\gamma)]^2}>0, \tag{3.22}$$

we conclude that the curves $q=H(\gamma)$ are nested (in particular they do not intersect) and that the outer one corresponds to the minimal value of z. We summarize our results in the following

THEOREM

Let $g=h$, *and assume that* $z<0$, *where*

$$z=\min\{\operatorname{Re}\bar{g}(i\omega)\,|\operatorname{Im}\bar{g}(i\omega)=0\}.$$

The stability boundary of the nontrivial steady state is given by $q=H(\gamma)$, $e^{(z-1)/z}<\gamma<\infty$, *where* H *is the convex function defined in* (3.21).

We refer to Figure 1(c) for the graph of H when $z\approx-0{,}44$.

Now consider a path in (γ,q) parameter space which intersects the stability boundary transversally. Along this path a pair of conjugate simple roots of (3.11) crosses the imaginary axis at $\pm i\omega$ with positive speed, and all other roots of (3.11) lie in the left half plane. The Hopf bifurcation theorem implies that the loss of stability of the steady state is accompanied by the "creation" of a periodic solution. Locally this periodic solution may either live *subcritically* (i.e., for parameter values in the stability domain) or

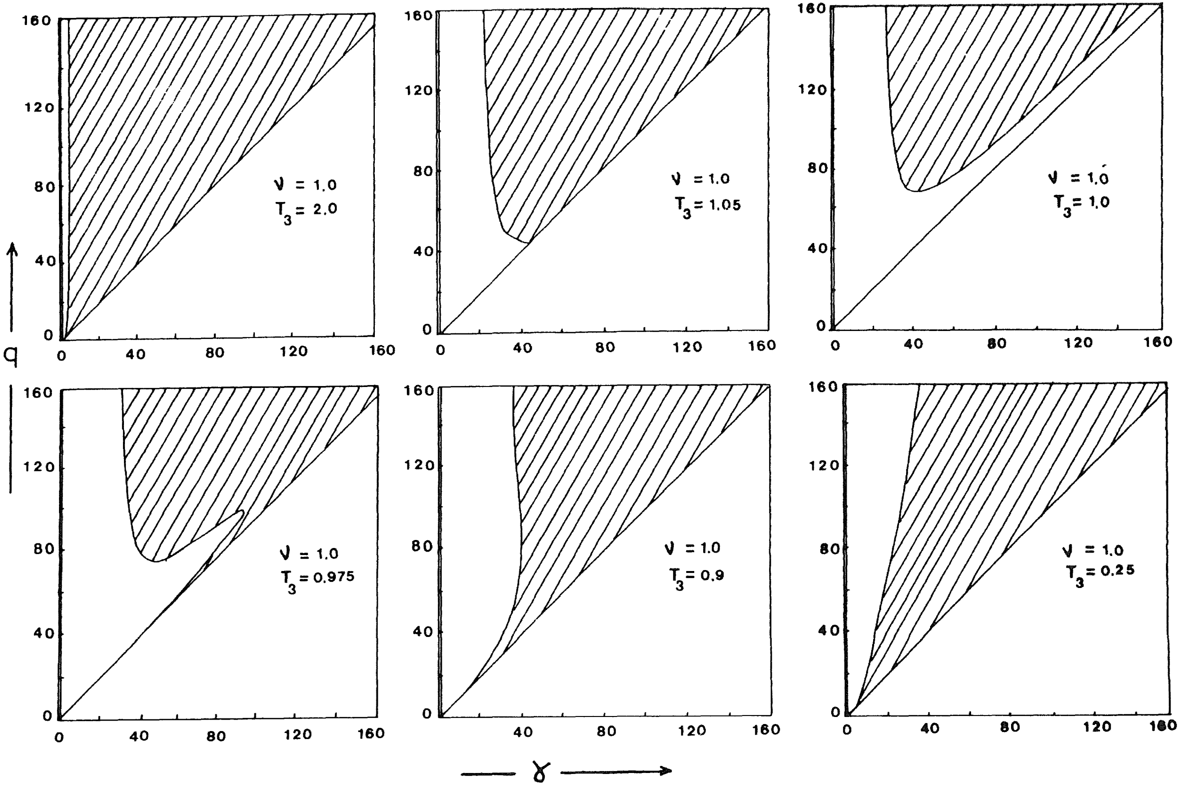

FIG 1. The stability boundary for various values of T_3, the age at which cannibalistic activity starts. The steady state is unstable in the hatched region and does not exist below the line $q = \gamma - 1$.

supercritically (i.e., for parameter values in the instability domain). The principle of the exchange of stability implies that the periodic solution will be unstable in the first case and stable in the second. Again we refer to Diekmann and van Gils [2] for a detailed formulation and derivation of these results. In Appendix III we present an explicit formula for the direction of bifurcation and we apply this formula with Φ given by (3.7) and a special choice of g.

Although the stability boundary depends only on γ and the product $q = \alpha\rho$ and not on ρ itself, the coefficients in the Taylor expansion of the periodic solution do depend on ρ. However, numerical evaluation of the formula shows that for all values of ρ supercritical bifurcation to a stable periodic solution occurs. See Appendix III.

4. NUMERICAL RESULTS: SOME ILLUSTRATIVE EXAMPLES INVOLVING DELAY-DIFFERENTIAL EQUATIONS

In our numerical work we take both B and K to be block functions, while the death rate is taken to be a constant. More precisely we choose

$$
\begin{aligned}
g(a) &= \begin{cases} \dfrac{\nu e^{-\nu a}}{e^{-\nu T_1} - e^{-\nu T_2}} & \text{if} \quad T_1 \leqslant a \leqslant T_2, \\ 0 & \text{elsewhere,} \end{cases} \\
h(a) &= \begin{cases} \dfrac{\nu e^{-\nu a}}{e^{-\nu T_3} - e^{-\nu T_4}} & \text{if} \quad T_3 \leqslant a \leqslant T_4, \\ 0 & \text{elsewhere.} \end{cases}
\end{aligned}
\tag{4.1}
$$

where ν and T_i, $i = 1,2,3,4$, are nonnegative parameters. In fact we always took $T_1 = 1$ (this amounts to choosing the length of the infertile period as the unit of time) and $T_2 = \infty$ (i.e., fertility does not cease at old age).

Figures 1, 2, and 3 present stability boundaries for various values of T_3 and T_4, which were obtained numerically by the procedure outlined in the preceding section. We have chosen to take $\nu = 1$ in these series; in additional calculations it was found that variations of ν hardly change the *form* of the stability boundary, although they do change the precise location in the sense that the stability domain becomes smaller when ν is increased.

In the first series we investigate the influence of T_3, the age at which cannibalistic activity starts, by fixing T_4 at $+\infty$ and gradually reducing T_3 from 2.0 to 0.25. For $T_3 = 1$ we are in the case $g = h$, and consequently Figure 1(c) illustrates the Theorem of the last section. The striplike part of the stability domain along the line $q = \gamma - 1$ is clearly very special to the case $g = h$ as we can make it disappear by perturbing T_3 only slightly away from one. On the contrary, the asymptote-like vertical boundary at the upper left

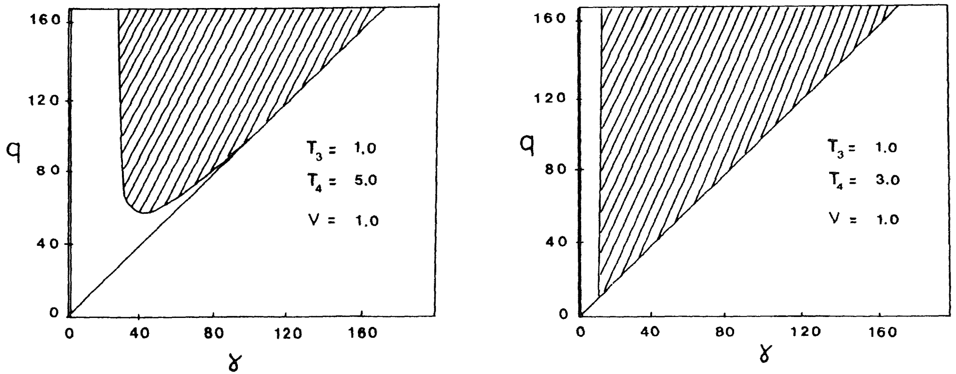

FIG. 2. The stability boundary for two values of T_4, the end of the cannibalistic period.

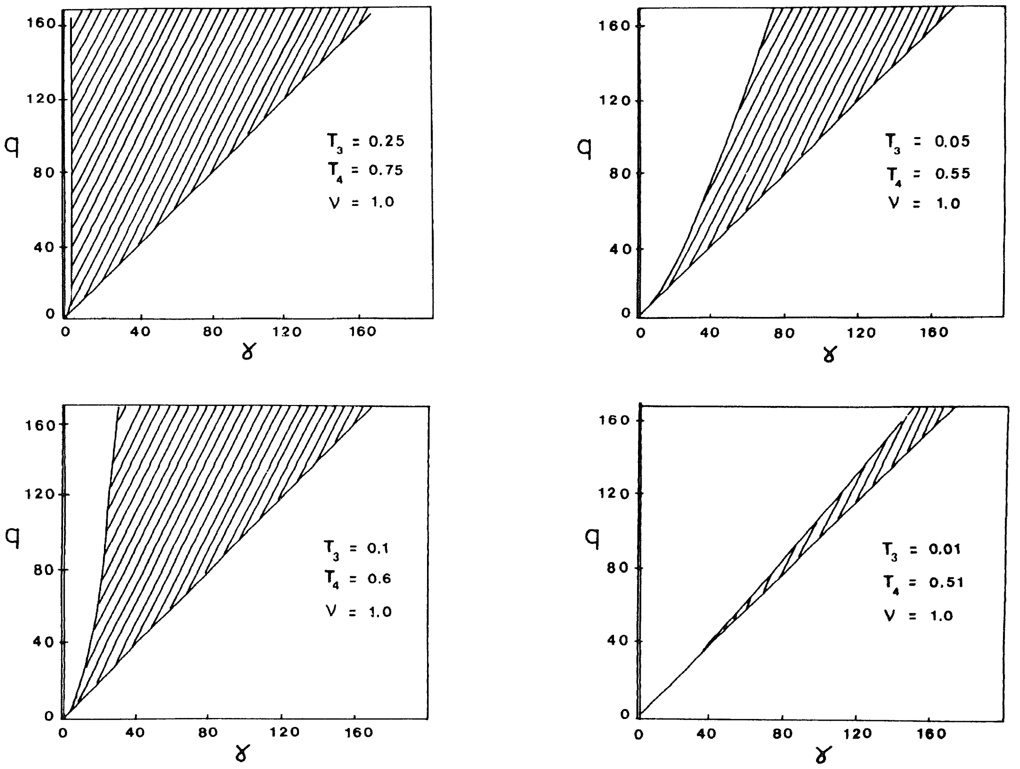

FIG. 3. The stability boundary for various values of T_3 but now with a fixed length $T_4 - T_3 = 0.5$ of the cannibalistic period.

side appears to be rather robust. A phenomenon not shown in Figure 1, but found in the numerical analysis, is that the period of the bifurcating periodic solutions along this part of the boundary increases with increasing T_3.

In the second figure we consider the effect of an upper bound for the cannibalistic age interval by fixing T_3 at 1 and taking for T_4 respectively 5 and 3 [note that Figure 1(c) corresponds to $T_4 = \infty$]. It appears that the instability domain expands when T_4 is decreased. [Caution: when interpreting this result one should keep in mind that the parameter ρ, i.e. the integral of $K(a)\exp[-\int_0^a \nu(\sigma)\,d\sigma]$, is kept fixed when q is fixed and that K was scaled with the vulnerability index θ.]

In the third series the length $T_4 - T_3$ of the cannibalistic age interval is fixed at 0.5, while T_3 is reduced from 0.25 to 0.01 in order to investigate the effect of cannibalistic activities of immature individuals. The stability domain expands considerably. A remarkable feature, not shown in the figure, is that the frequency ω increases from $\omega \approx 6$ for $T_3 = 0.25$ to $\omega \approx 50$ for $T_3 = 0.01$.

In order to test, confirm, and extend the results obtained from the analysis of the characteristic equation, we have done some numerical studies of the dynamical behavior. When the kernels are given by (4.1), one can reduce the system (3.1) of Volterra integral equations to a system of delay differential equations. Indeed, with $T_1 = 1$ and $T_4 = \infty$ the equation for b can be rewritten as

$$b(t) = \gamma \int_{-\infty}^{t-1} g(t-a)\, b(a)\, e^{-k(a)\Phi(c(a))}\, da, \tag{4.2}$$

and, since $g'(a) = -\nu g(a)$ for $a > 1$, one obtains upon differentiation

$$b'(t) = \gamma\nu b(t-1)\, e^{-k(t-1)\Phi(c(t-1))} - \nu b(t). \tag{4.3}$$

Similarly one finds

$$k'(t) = \rho\nu b(t-T_3)\, e^{-k(t-T_3)\Phi(c(t-T_3))} - \nu k(t) \tag{4.4}$$

when $T_4 = \infty$, and

$$k'(t) = \frac{\rho\nu}{e^{-\nu T_3} - e^{-\nu T_4}} \Big\{ e^{-\nu T_3} b(t-T_3)\, e^{-k(t-T_3)\Phi(c(t-T_3))} - e^{-\nu T_4} b(t-T_4)\, e^{-k(t-T_4)\Phi(c(t-T_4))} \Big\} - \nu k(t) \tag{4.5}$$

when $T_4 < \infty$. Figures 4, 5, and 6 present solutions of the system (4.3)–(4.4) with initial data $b(t) = k(t) = 0$ for $t < 0$, and a short input pulse of newborn individuals immediately after $t = 0$, for various values of the parameters and with $\Phi(c) = 1/(1+c)$. These solutions were obtained by means of the program SOLVER [14].

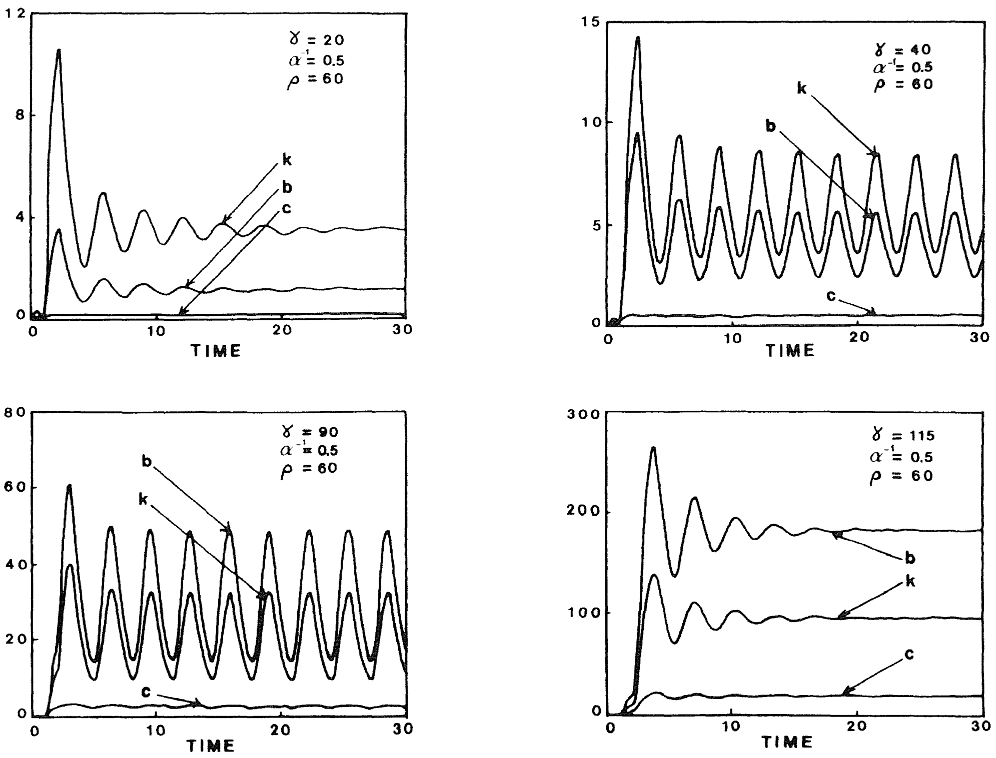

FIG. 4. Numerical solutions for parameters corresponding to various points on a horizontal line $q = \alpha\rho = 120$ in the parameter space of Figure 1(c).

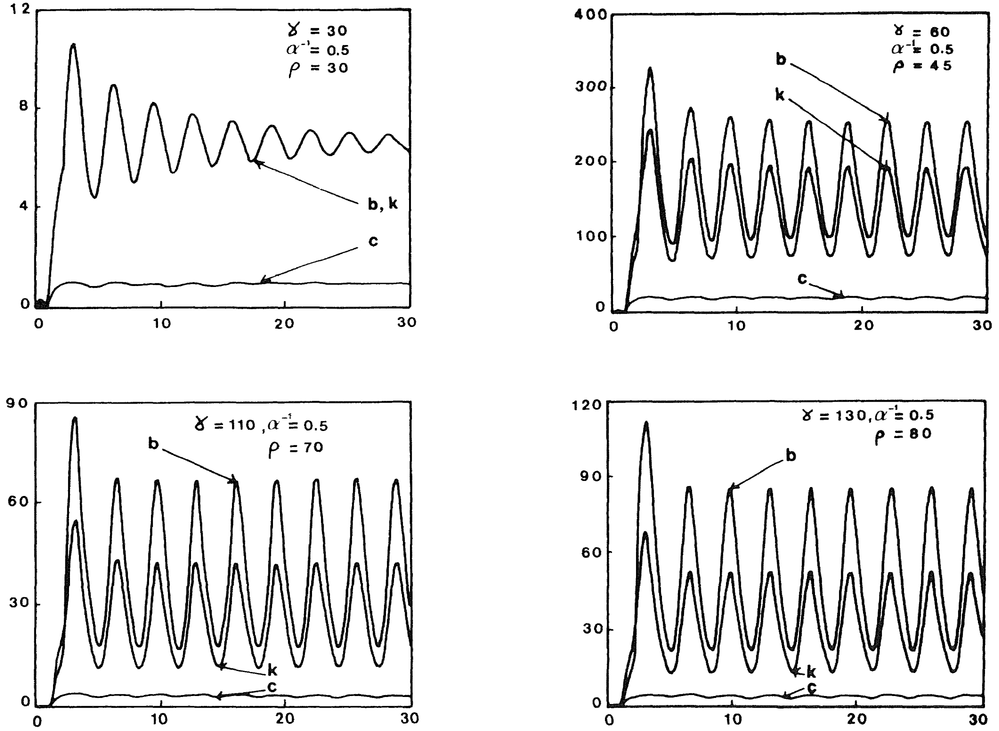

FIG. 5. Numerical solutions for parameters corresponding to various points on a diagonal line $q = 30 + \gamma$ in the parameter space of Figure 1(c).

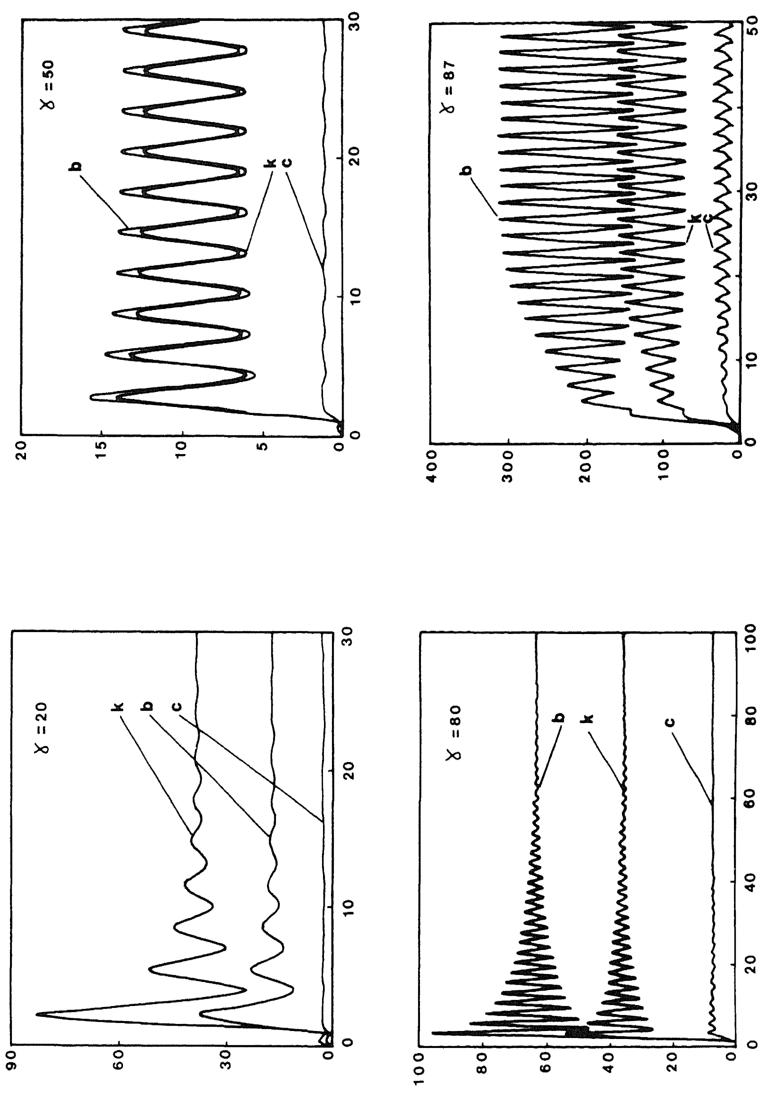

FIG. 6. Numerical solutions for parameters corresponding to various points on a horizontal line $q = \alpha\rho = 90$ in the parameter space of Figure 1(d).

In the first series (Figure 4) we took $\nu = 1$, $T_3 = 1$, $\alpha = 2$, $\rho = 60$ and varied γ. This corresponds to a horizontal transect at $q = \alpha\rho = 120$ in the parameter space of Figure 1(c), and we see, indeed, the transitions from stability to oscillations and then back to stability.

Figure 5 corresponds to a diagonal transect $q = 30 + \gamma$ in the parameter space of Figure 1(c): we took $\nu = 1$, $T_3 = 1$, $\alpha = 2$, and $\gamma = 2\rho - 30$. The results suggest that the periodic solution remains stable and that further bifurcations leading to more complicated dynamical behavior do not occur. However, we have done far too little numerical work to warrant this conclusion, and the repertoire of dynamical behavior in the "unstable" region of parameter space is not yet known.

In the third series (Figure 6) we took $\nu = 1$, $T_3 = 0.975$, $\alpha = 2$, and $\rho = 45$ and varied γ. This again corresponds to a horizontal transect, but now in the parameter space of Figure 1(d) at $q = \alpha\rho = 90$, where we expect to see a repeated transition from stability to oscillations. The results are clearly in agreement with this expectation.

A distinctive feature found in all numerical studies [except the one shown in Figure 6(d)] is that the oscillations of b and k reach their maxima and minima almost simultaneously and that, as a consequence, the quantity c remains almost constant.

5. CONCLUDING REMARKS

The infinitesimally short "vulnerable" age interval in the Gurtin-Levine model is both the reason for its tractability and the source of difficulties and confusion in choosing a concrete survival function. If constructing a practical model of cannibalism in any specific situation, we would almost certainly drop this assumption, include a short (but finite) stage through which individuals are vulnerable, and model feeding in a realistic manner. However, if we want "strategic" models capable of elucidating the dynamic consequences of cannibalism on very young individuals (or eggs), we do not want to complicate the mathematics with an extra stage. This work has the aim of establishing a consistent framework within which models with *both* a mechanistic description of feeding *and* an infinitesimally short vulnerable stage may be studied.

Our analytical results on periodic solutions are based on the local Hopf bifurcation theorem and therefore only yield information for parameter values near the stability boundary. Gurtin and Levine [8] consider special kernels, which allow them to reduce the problem to a three-dimensional system of ordinary differential equations, and subsequently they prove the existence of periodic solutions without such restrictions on parameters. The implicitly defined survival function, which we derived in this paper, fits into their Model C, but unfortunately their assumption (5.2)(b) is *not* satisfied.

So the global (with respect to parameters) existence and stability of periodic solutions remains an open problem, although some preliminary conclusions can be drawn from the numerical work presented in Figures 4–6.

Several possibly important aspects of cannibalism are not included in our model. We have neglected the positive effects of the consumed young for the growth, health, and/or fecundity of the cannibals. Since we use age and not size to distinguish the individuals from each other, we are not able to incorporate density-dependent individual growth rates as in Botsford [1], Diekmann et al. [3], Gurney and Nisbet [6], and Nisbet and Gurney [12]. In fact we have neglected all other types of density dependence and thus studied the effects of cannibalism in isolation; but the subtle ways in which nonlinearities can interact to produce multiple stable steady states could be interesting and important (Botsford [1], Frauenthal [4]).

Periodic rates of recruitment are propagated through the population age density as traveling waves. Near the Hopf bifurcation these look like

$$n(t,a) \approx e^{-\nu a}\{C_1 + C_2 \cos\omega(t-a)\},$$

where C_1 and C_2 are constants. We found that the frequency ω can be rather high when cannibalism is practiced by immature individuals. Such short-term fluctuations will be strongly damped in the adult population, since this is obtained from $n(t,a)$ by integration over the relevant age interval. We refer to Fujii [5] for related observations.

APPENDIX I. THE INTERCHANGEABILITY OF LINEARIZATION AND THE LIMIT $\epsilon \downarrow 0$

Consider the model defined by (2.8), (2.3), (2.5), and (2.6). It turns out that the calculations can be made much more explicitly if we make the reasonable assumption that for some $\delta > 0$ the support of C is contained in $[0,\delta)$ whereas the supports of B and K are contained in $[\delta,\infty)$. Moreover, we normalize C so that $\int_0^\delta C(a)\,da = \theta = 1$. The steady-state equations are now

$$\begin{aligned}
1 &= \gamma e^{-k\Phi(c)},\\
k &= \rho b e^{-k\Phi(c)},\\
c &= b\int_0^\infty C(a)Q(a)\,e^{-\int_0^a \nu(\sigma)\,d\sigma}e^{-k\Phi(c)\int_0^a C(\sigma)\,d\sigma}\,da.
\end{aligned}$$

By partial integration we can transform the third equation into

$$\begin{aligned}
c\Phi(c) = \frac{b}{k}\Bigg\{ & Q(0) - Q(\delta)\,e^{-\int_0^\delta \nu(\sigma)\,d\sigma}e^{-k\Phi(c)}\\
& + \int_0^\delta \frac{d}{da}\left(Q(a)\,e^{-\int_0^a \nu(\sigma)\,d\sigma}\right)e^{-k\Phi(c)\int_0^a C(\sigma)\,d\sigma}\,da\Bigg\}.
\end{aligned}$$

Upon substitution of $k\Phi(c)=\ln\gamma$ and $b/k=\gamma/\rho$, the right-hand side is independent of b, k, and c, and we arrive, as before, at the conclusion that there exists a unique solution c^* precisely when the righthand side belongs to the range of the monotone function $c\Phi(c)$. Given c^*, we find $k^*=(\ln\gamma)/\Phi(c^*)$ and $b^*=(\gamma\ln\gamma)/\rho\Phi(c^*)$.

By straightforward but tedious calculations it can be shown that the linearized problem has a solution of the form $e^{\lambda t}$ times a fixed vector if and only if one of the eigenvalues of the matrix

$$\begin{pmatrix} \bar{g}(\lambda) & -\dfrac{\gamma\ln\gamma}{\rho}\bar{g}(\lambda)\bar{C}(-\lambda) & -b^*k^*\Phi'(c^*)\bar{g}(\lambda)\bar{C}(-\lambda) \\ \dfrac{\rho}{\gamma}\bar{h}(\lambda) & -\ln\gamma\,\bar{h}(\lambda)\bar{C}(-\lambda) & -(k^*)^2\Phi'(c^*)\bar{h}(\lambda)\bar{C}(-\lambda) \\ \bar{\zeta}(\lambda) & -\dfrac{\gamma\ln\gamma}{\rho}\eta(\lambda) & -b^*k^*\Phi'(c^*)\eta(\lambda) \end{pmatrix}$$

equals one. Here

$$\zeta(a):=C(a)Q(a)e^{-\int_0^a\nu(\sigma)\,d\sigma}e^{-(\ln\gamma)\int_0^aC(\sigma)\,d\sigma}$$
$$\eta(\lambda):=\int_0^\infty\zeta(a)e^{-\lambda a}\int_0^a e^{\lambda\sigma}C(\sigma)\,d\sigma\,da.$$

If we now let $C(a)=(1/\epsilon)h(a/\epsilon)$, it easily follows that both the steady-state equation and this matrix converge as $\epsilon\downarrow 0$ to their respective counterparts, which are derived by first taking the limit $\epsilon\downarrow 0$ in the dynamical model equations. In particular one finds that the condition that one of the eigenvalues of the limiting matrix

$$\begin{pmatrix} \bar{g}(\lambda) & -\dfrac{\gamma\ln\gamma}{\rho}\bar{g}(\lambda) & -b^*k^*\Phi'(c^*)\bar{g}(\lambda) \\ \dfrac{\rho}{\gamma}\bar{h}(\lambda) & -\ln\gamma\,\bar{h}(\lambda) & -(k^*)^2\Phi'(c^*)\bar{h}(\lambda) \\ \dfrac{\gamma-1}{\gamma\ln\gamma} & \dfrac{\ln\gamma-\gamma+1}{\rho\ln\gamma} & \left(\dfrac{Q(0)b^*}{\gamma}-c^*\right)\dfrac{\Phi'(c^*)}{\Phi(c^*)} \end{pmatrix}$$

should equal one, is precisely the characteristic equation (3.11).

Standard perturbation arguments now imply that the roots of the characteristic equation depend continuously on ϵ. Hence, if all roots lie in the left half plane for $\epsilon=0$, the same has to be true for $\epsilon>0$ sufficiently small, and if some root lies in the right half plane for $\epsilon=0$, it remains there if ϵ is slightly increased. Of course the precise location of the stability boundary in parameter space depends on ϵ, but in a continuous manner.

We conclude that our results indeed describe the stability of the steady state for small positive ϵ.

APPENDIX II. A STILL MORE GENERAL MODEL

If the interaction of aggressor and victim depends in a general way on the ages of both, we may take for the age-specific death rate

$$\mu(t,a)=\nu(a)+\int_0^\infty D(a,a')\Phi(c(t,a'))n(t,a')\,da'$$

with

$$c(t,a')=\int_0^\infty D(a,a')E(a,a')n(t,a)\,da$$

Here D is the attack rate, E the handling time, c an effective number and Φ a functional response factor (which does not depend on a' explicitly). The reasonable factorization assumption

$$D(a,a')=C(a)K(a'),$$
$$E(a,a')=Q(a)M(a')$$

leads to some (but not much) simplification. (Note that, given D and E, the factors are unique up to a multiplicative constant only.) However, if we assume

$$K(a')M(a')=\text{constant},$$

we are back to the model introduced in Section 2, since then c becomes independent of a'. Since K and M describe how, respectively, the attack rate and the handling time depend on the age of the aggressor, this assumption seems not too unreasonable

APPENDIX III. THE DIRECTION OF HOPF BIFURCATION

In [2] a formula is derived for the direction of Hopf bifurcation (for systems of Volterra convolution equations) which is explicit apart from the inversion of two $N\times N$ matrices, where N is the dimension of the system. Here we restrict ourselves to the simplest case, viz. $N=1$.

We consider the equation

$$b(t)=\int_0^\infty g(a)f(b(t-a))\,da,$$

where the kernel g is normalized to have integral one, and where both g and the nonlinear function f depend on parameters (which, however, are suppressed in the notation). Linearization around a steady state b^* leads to the characteristic equation

$$1=f'(b^*)\bar{g}(\lambda),$$

and the condition for Hopf bifurcation is

$$\begin{aligned}\operatorname{Im}\bar{g}(i\omega)&=0,\\ f'(b^*)&=[\operatorname{Re}\bar{g}(i\omega)]^{-1}.\end{aligned}$$

Given parameter values and ω such that these conditions are satisfied, we define

$$c_1=-\frac{1}{2[f'(b^*)]^2\bar{g}'(i\omega)}\left\{f'''(b^*)+2\frac{[f''(b^*)]^2}{1-f'(b^*)}+\frac{[f''(b^*)]^2\bar{g}(2i\omega)}{1-f'(b^*)\bar{g}(2i\omega)}\right\}.$$

THEOREM

Consider a path in parameter space along which a root of the characteristic equation crosses the imaginary axis at ω from left to right. If $\operatorname{Re} c_1<0$, *the bifurcating periodic solution exists supercritically, whereas it exists subcritically if* $\operatorname{Re} c_1>0$.

So determining the direction of bifurcation amounts to determining the sign of $\operatorname{Re} c_1$.

Now let

$$f(b)=\gamma b e^{-(\rho/\gamma)b\Phi(c)},$$

where c is the function of b defined by

$$\alpha c\Phi(c)=\frac{\gamma}{\rho}\left(1-e^{-(\rho/\gamma)b\Phi(c)}\right)$$

and

$$\Phi(c)=\frac{1}{1+c}.$$

Moreover, we take $g(a)=e^{-(a-1)}$ for $a\geqslant 1$ and $g(a)=0$ for $a<1$. Let ω be such that $\sin\omega=-\omega\cos\omega$, then $\operatorname{Im}\bar{g}(i\omega)=0$. With $b^*=(\alpha\gamma\ln\gamma)/(\alpha\rho$

$-\gamma+1)$ we find, after long and tedious calculations,

$$f'(b^*)=\frac{1}{\cos\omega}$$

$$f''(b^*)=\frac{\omega^2}{\gamma\ln\gamma}\,\frac{(\alpha\rho-\gamma+1)^2}{\alpha(\alpha\rho-\gamma+1+\ln\gamma)}$$

$$f'''(b^*)=\frac{\alpha\rho-\gamma+1}{\alpha\gamma^2\ln^2\gamma}\left(\frac{\cos\omega-1}{\cos\omega}\right)^2\left(1-\frac{\cos\omega-1}{(\alpha\rho-\gamma+1)\cos\omega}\right)$$
$$\times\left(\frac{3(1+\cos\omega)}{\alpha\cos^2\omega}+\frac{(\alpha\rho-\gamma+1)(1+2\cos\omega)}{\alpha\cos\omega}\right)$$

and, up to a positive factor,

$$\operatorname{Re}c_1=\frac{1}{f'(b^*)}\left\{f'''(b^*)+\frac{2[f''(b^*)]^2}{1-f'(b^*)}+[f''(b^*)]^2Q\right\},$$

where

$$Q=\frac{-f'(b^*)-1+2(1+2\omega^2)\cos^2\omega-\dfrac{2\omega^2}{2+\omega^2}\sin^2\omega}{[f'(b^*)+1]^2+4\omega^2-4f'(b^*)(1+2\omega^2)\cos^2\omega}.$$

At any point of the stability boundary, γ and $\alpha\rho=q$ have a specific value, but we may choose ρ arbitrary. Numerically it is found that in all points $\operatorname{Re}c_1$ is a negative (and decreasing) function of ρ. So we conclude that the bifurcating periodic solution exists supercritically and is stable.

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