WHERE TO PUT DELAYS IN POPULATION MODELS, IN PARTICULAR IN THE NEUTRAL CASE

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ABSTRACT. Hutchinson’s model or the delayed logistic equation explains oscillations in populations by delayed response to exhaustion of nutrients. The exploration of periodic solutions and global behavior of nonlinear delay equations has started from this model. Another delay model for oscillations in populations is the blowfly equation which has been thought to be better suited to explain experiments. Also delay differential equations of neutral type have been proposed as population models. The Gurtin-MacCamy system of a partial differential equation with boundary condition models populations structured by age with birth and death rates depending on age and on total population size. If written as a renewal equation then piecewise constant coefficients, even with delta peaks, are admissible. It is shown that these “realistic caricatures” of age structure models are equivalent to delay equations, in general of neutral type. In the standard retarded case (as opposed to the neutral case) the resulting systems have the form of the blowfly equation. Hence the latter seems indeed better justified than the delayed logistic equation. In the case of neutral equations the age structure approach presented here is a rigorous derivation of such population models. Also in the retarded case the view on oscillations is drastically changed since Hutchinson’s model and the blowfly model have distinct stability properties.

1 Introduction  Deterministic biological models in continuous time assume the form of ordinary differential equations, reaction diffusion equations, Volterra integral equations and, in particular, delay equations. Similar to reaction diffusion equations or damped wave equations, delay equations define infinite-dimensional dynamical systems with compactifying flows. On the other hand, they share many properties with

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ordinary differential equations, in particular with respect to oscillatory behavior. Whereas in technology a retarded argument typically corresponds to a well-defined physical delay, e.g., the time a signal takes between the station and the receiver, delays in biology mostly represent hidden compartments such as unknown steps in reaction chains, unknown transport processes, the time to regrow resources or maturation intervals. That is why in many models based on delay equations the interpretation of the delay is somewhat vague.

The densities of some animal species and the prevalence of some infectious diseases show regular cycles over many years with periods ranging from two years as in measles infections in some human populations to seventeen years in some North American cicadas. Such oscillations have been explained using mathematical models in several ways which all, if implicitly, involve another species or type. The most common explanation is based on prey-predator interaction. This view started with Volterra, Kolmogorov, and continues with MacArthur, Rosenzweig, and Holling. Another explanation uses periodic forcing by the annual cycle and subharmonic bifurcation, e.g., Nisbet and Gurney [24]. This argument has also been applied to infectious diseases where the roles of interacting “species” are played by the susceptible and the infectious individuals. Finally, there is the idea of the eminent ecologist G.E. Hutchinson [14], [15] that oscillations result from delayed response to diminishing resources due to a hatching period or juvenile state, as further explained in [20]. In this approach the role of the second species is played by the juveniles (e.g., larvae) or the underlying resources.

First we follow the argument of Hutchinson [14]. The standard model for the dynamics of a simple (single) population in terms of its density is the Verhulst equation \( \dot{u} = au(1 - u/K) \) which is based on the idea that the population grows exponentially at low densities and saturates towards the carrying capacity \( K \) at high densities. According to the Verhulst law population change is proportional to the population size \( u \) and also to the remaining resources \( K - u \). Hutchinson argued that the population adapts only with a delay to the remaining resources (“... all the vacant space \( K - u \) might be filled well before reproduction stops”) and that the Verhulst equation should rather be replaced by

\[
(1) \quad \dot{u}(t) = au(t) \left( 1 - \frac{u(t - \tau)}{K} \right)
\]

with some delay \( \tau > 0 \). He suggested that models of this form may explain sustained oscillations in simple populations. Indeed, solutions
of equation (1) near the stationary state \( u = K \) become oscillatory if \( a\tau > 1/e \) and they approach nonconstant periodic solutions if \( a\tau > \pi/2 \).

At about the same time as Hutchinson, E.M. Wright [31] studied the equation \( \dot{x}(t) = -\gamma x(t - \tau)(1 + x(t)) \) which had occurred in number theory. Equation (1) and Wright’s equation are equivalent via the transformation \( u = K(1 + x) \). The latter equation can be carried into the form \( \dot{y}(t) = -\gamma f(y(t - \tau)) \) with \( f(y) = e^y - 1 \). This equation has been generalized by incorporating a non-delayed feedback in [18] and [12]

\[
(2) \quad \dot{y}(t) = -\beta y(t) - \gamma f(y(t - \tau)).
\]

In equation (2) we always use the normalization \( f'(0) = 1 \). In another parametrization the equation reads \( \epsilon \dot{z}(t) = g(z(t - \tau)) - z(t) \). For \( \epsilon \to 0 \) this equation can be seen as continuous approximation to a difference equation [19]. For given \( \gamma > \beta \geq 0 \) the equation (2) exhibits stable periodic oscillations for sufficiently large values of \( \tau \), see [16], [25], [26], [19], [30] for global attractors, and the monographs [13], [5], [17].

The idea of introducing an ad hoc carrying capacity as in the Verhulst equation and in (1) can be questioned. It certainly leads to difficulties when one considers several species jointly. On the other hand, birth rates \( b(u) \) and death rates \( \mu(u) \) can be measured as functions of population density \( u \), and hence a model \( \dot{u} = bu - \mu u \) can be based on data. In the case of multi-species models the rates \( b \) and \( \mu \) will depend on the densities of all species considered. Typically the function \( b(u) \) is decreasing and \( \mu(u) \) is increasing, with \( b(0) > \mu(0) \) and \( b(u) < \mu(u) \) for large \( u \). Then the equation \( b(u) = \mu(u) \) has a single positive solution \( \bar{u} \) which can be interpreted \textit{a posteriori} as the carrying capacity. In the case of the Verhulst equation, the nonlinearity can be split into a birth and a death term in many ways, e.g., \( b(u) = a, \mu(u) = au/K \).

The classical experiments by Nicholson [22], [23] on oscillatory behavior in blowfly populations were the subject of numerous theoretical studies based on age-structure models as well as on time-lag models, e.g., by Gurney, Blythe and Nisbet [9], May [20], Maynard Smith [21], Perez, Malta and Coutinho [27] showing some limitations of the delayed logistic model. The main objection is that it is not based on clearly defined birth and death rates and hence cannot be fitted to data without difficulty, in particular it cannot explain two bursts of reproductive activity per adult population cycle.

Some authors [24], [27], [11], [4] have argued that a delay should enter the birth term \( b(u) \) rather than the death term and that the model
with delay should read

\[ \dot{u}(t) = b(u(t - \tau))u(t - \tau) - \mu(u(t))u(t). \]

Maynard Smith [21] distinguished three effects causing delayed feedback: development time, discrete breeding seasons and delayed response by limiting factors. The second effect would rather cause periodic forcing and perhaps subharmonic bifurcations. Maynard Smith connected the third effect to Hutchinson’s equation, with a slight shift in the argument, speaking of delayed response by the limiting factor instead of delayed response of the population. With respect to the first effect he suggested that with constant food supply (for blowflies) the number of eggs is proportional to the surplus food. He arrived at equation (3) with \( \mu = \text{const} \) and \( b(u) = (1-u)/u \), positive constants omitted. Then \( (b(u)u)' < 0 \) which property is an essential condition for oscillatory behavior. May [20] tried to interpret Hutchinson’s equation in terms of the blowfly data.

Other authors, e.g., [17], have proposed refined versions of equation (1) which take the delayed derivative of the function \( u \) into account. Then one arrives at neutral delay equations of the form

\[ \dot{u}(t) = au(t) \left( 1 - \frac{u(t - \tau) + r\dot{u}(t - \tau)}{K} \right). \]

A delay equation is called neutral, if the (highest) derivative enters at more than one value of the time variable, see [13], Chapter 9. To justify the delay in the derivative in terms of measurable ecological quantities seems a challenging problem.

The aim of the present note is to derive population models in the form of delay equations and neutral delay equations from basic principles, i.e., from undisputed structured population models in the form of partial differential equations or Volterra integral equations. Our derivation will show that models of the form (3) can be justified, as well as some related neutral equations. One the other hand, this approach does not open an alley towards Hutchinson’s equation.

### 2 Structured population models

Our starting point is the standard Sharpe-Lotka or McKendrick model for a population structured by
age, in the form of a generalized Gurtin-MacCamy system \([10]\),

\[
\begin{align*}
    u_t + u_a + \mu(a, w) &= 0 \\
    u(t, 0) &= \int_0^\infty b(a, w)u(t, a)da \\
    w(t) &= \int_0^\infty \rho(a)u(t, a)da
\end{align*}
\]  
(5)

with initial data \(u(0, a) = u_0(a)\). Here \(a\) is chronological age, the function \(u(t, a)\) is the age distribution at time \(t\). The function \(w\) is a weighted average of the total population with weight function \(\rho(a) \geq 0\). The birth rate \(b(a, w)\) and the death rate \(\mu(a, w)\) depend on age and on the average \(w\). If \(\rho(a) \equiv 1\) then \(w\) is the total population size and the system is the Gurtin-MacCamy model. If \(b(a)\) and \(\mu(a)\) do not depend on \(w\) (formally \(\rho(a) \equiv 0\)) then the system reduces to the classical Sharpe-Lotka-McKendrick model.

For the model (5) we assume that there is a critical age \(\tau > 0\) which separates adults with ages \(a > \tau\) from juveniles with \(a < \tau\). Further we assume that for any fixed value of the average \(w\), the rates \(b(a, w)\) and \(\mu(a, w)\) are constant in the intervals \(a < \tau\) and \(a > \tau\), with a possible jump or delta peak at \(a = \tau\). Hence we assume that the functions \(b\) and \(\mu\) have the form

\[
\begin{align*}
    b(a, w) &= b_0(w) + (b_1(w) - b_0(w))H_\tau(a) + b_2(w)\delta_\tau(a) \\
    \mu(a, w) &= \mu_0(w) + (\mu_1(w) - \mu_0(w))H_\tau(a) + \mu_2(w)\delta_\tau(a)
\end{align*}
\]  
(6)

where \(H_\tau(a)\) is the Heaviside function with jump at \(a = \tau\) and \(\delta_\tau(a)\) is the delta function with peak at \(a = \tau\). Since the peaks and jumps of the two functions occur at the same position, we must specify how they are applied. We define “birth comes before death” in accordance with biological reality, say, for fish or insect populations which die after having produced offspring. This principle “birth before death” can be rigorously defined in terms of the corresponding renewal equations \([3]\). The coefficients (6) are realistic caricatures of parameter functions for populations with a distinguished juvenile class and/or a preferred age interval for reproduction \([3]\).

Also we assume that the weight function \(\rho(a)\) is a step function with a (possible) step at \(a = \tau\),

\[
\rho(a) = \rho_0 + (\rho_1 - \rho_0)H_\tau(a).
\]  
(7)
Next we introduce the total juvenile $U(t)$ and the total adult population $V(t)$ as the integrals over the age classes

\begin{align*}
U(t) &= \int_{0}^{t_{-}} u(t, a) da, \\
V(t) &= \int_{t_{+}}^{\infty} u(t, a) da.
\end{align*}

Then the function $w$ is given by

\begin{equation}
(9) \quad w(t) = p_{0} U(t) + p_{1} V(t).
\end{equation}

In [3] it has been shown that the two functions $U(t)$ and $V(t)$ satisfy a system of delay differential equations. Hence certain classes of population models in the form of delay equations can be derived from the renewal equations of Gurtin and MacCamy. More precisely, in [3] the following has been shown for general initial data $u(0, a) = u_{0}(a)$: For $0 < t < \tau$ the functions $U(t)$ and $V(t)$ satisfy a non-autonomous system of ordinary differential equations (without delays) with coefficients depending on $u_{0}(a)$, i.e., depending on the history of the problem (5). For $t > \tau$ the functions $U(t)$ and $V(t)$ satisfy a system of autonomous neutral delay differential equations. For special initial data $u_{0}(a)$, resulting from a solution $u(t, a)$ of (5) that has existed already for a time interval of length no less then $\tau$, the autonomous delay equations hold right away for $t \geq 0$.

Here we consider a situation which is most relevant for realistic applications: juveniles do not reproduce and their mortality does not depend on age, i.e., $b_{0} \equiv 0$ and $\mu_{0} = \text{const}$. For the transient non-autonomous system we refer to [3]. We present the (neutral) delay system

\begin{align*}
(10) \quad \dot{U}(t) &= b_{1}(w(t)) V(t) - \mu_{0} U(t) + (b_{2}(w(t)) - 1) \\
&\times \left[ b_{1}(w(t - \tau)) V(t - \tau) + b_{2}(w(t - \tau)) e^{\mu_{2}(w(t - \tau))} \right] \\
&\times \left\{ \dot{V}(t - \tau) + \mu_{1}(w(t - \tau)) V(t - \tau) \right\} e^{-\mu_{0} \tau} \\
(11) \quad \dot{V}(t) &= b_{1}(w(t - \tau)) V(t - \tau) + b_{2}(w(t - \tau)) e^{\mu_{2}(w(t - \tau))} \\
&\times \left\{ \dot{V}(t - \tau) + \mu_{1}(w(t - \tau)) V(t - \tau) \right\} e^{-\mu_{0} \tau - \mu_{2}(w(t))} - \mu_{1}(w(t)) V(t)
\end{align*}

whereby the function $w$ is given by the equation (9).

The equation (11) for $V$ depends on the variable $U$ only via the function $w$. Hence, if we assume that the functional $w$ depends only
on the adult population $V$, then the system separates, one can first solve the equation for $V$ and then that for $U$. Therefore we assume $\rho_0 = 0, \rho_1 = 1$ and obtain $w = V$, and the equation (11) for $V$ does not depend on $U$ at all. The function $V$ satisfies a scalar nonlinear neutral delay equation which is (11) with $w$ replaced by $V$. If, for simplicity, we assume that there is no peak in the mortality, $\mu_2 \equiv 0$ (such peak could describe additional mortality related to reproduction, as, e.g., in salmon), then this equation has the form

$$\dot{V}(t) = g(V(t - \tau))V(t - \tau) + h(V(t - \tau))\dot{V}(t - \tau) - \mu_1(V(t))V(t)$$

where the coefficient functions $g(V)$ and $h(V)$ are

$$g(V) = [b_1(V) + b_2(V)\mu_1(V)]e^{-\mu_0\tau}$$

$$h(V) = b_2(V)e^{-\mu_0\tau}.$$  

Equation (12) is a basic delay equation model for a single adult population. The delay represents the hidden compartment of the juvenile phase. The exponential $e^{-\mu_0\tau}$ reflects mortality in the juvenile phase. The equation for juveniles is rather complicated even for $\mu_2 \equiv 0$. Equation (12) contains various special cases as we shall show in the next two sections.

For the proof of equations (10)–(11) we refer to [3]. The proof is somewhat technical although the idea is simple. Split the evolution of the Gurtin-MacCamy system into an evolution for $0 \leq t < \tau$ and another one for $t > \tau$. Also split the integrals for the birth law and the functional $w$ at $a = \tau$. Then in each of these systems the coefficients are constant in $a$ and the function $u$ can be integrated over $a$ to produce a system for $U$ and $V$ and various boundary and transition terms. The main difficulty is to inspect these terms and to recognize them either as functions of $U$, $V$, $\dot{V}$ or express them in terms of the initial data.

### 3 Standard retarded population model

Assume that there is no peak in the birth rate, $b_2(V) \equiv 0$. Then the birth rate is a step function with respect to chronological age which is zero for $a < \tau$ and which is positive for $a > \tau$ and furthermore depends on $V$. In equation (13) we find $h \equiv 0$, the system (10)–(11) becomes

$$\dot{U}(t) = b_1(V(t))V(t) - b_1(V(t - \tau))V(t - \tau)e^{-\mu_0\tau} - \mu_0 U(t)$$

$$\dot{V}(t) = b_1(V(t - \tau))V(t - \tau)e^{-\mu_0\tau} - \mu_1(V(t))V(t).$$
In the special case $b_1 = \text{const.}, \mu_1(V) = \text{const.V}$, equations (14)–(15) define a system that has been introduced by Aiello and Freedman [1] and has been extended recently to incorporate diffusion and prey-predator interaction [6], [7].

The simpler system (14)–(15) shows even better than the general system (10)–(11) that the choice of appropriate initial data poses a problem. While any nonnegative initial function $V(t), -\tau \leq t \leq 0$, produces a nonnegative solution $V(t)$ for $t \geq 0$, nonnegative initial data $U, V$ do not necessarily lead to a nonnegative solution $U, V$ for $t \geq 0$, since in (14) the removal term may be greater than the birth term. In other words, only a certain cone in a function space of initial data is feasible. For a thorough discussion of this problem see [3]. This difficulty is not so obvious (although it is present) if one studies the equation (15) for adults alone.

The same positivity problem arises whenever in a model for juveniles and adults there is a term of the form $A(t) - A(t-\tau)e^{-\mu t}$ in the equation for juveniles and a corresponding term $A(t-\tau)e^{-\mu t}$ for adults, examples are the models in [6], [7], [8].

In (15) we incorporate the exponential factor into the birth rate. Then we get

$$\dot{V}(t) = b_1(V(t-\tau))V(t-\tau) - \mu_1(V(t))V(t).$$

Equation (16) is the blowfly equation (3) in different notation. Hence (3) should be seen as a model for the total adult population. On comparing the blowfly equation (3) to the equation (15) the blowfly equation can be interpreted as follows. The function $\mu(V)$ in (3) is nothing else than the mortality of adults $\mu_1(V)$ depending on the total adult population. The birth rate $b(V)$ is the fertility of adults $b_1(V)$ multiplied by a discount factor $\exp\{-\mu_0\tau\}$ taking juvenile death into account. Hence the equation (3) is thoroughly justified in terms of structured population theory.

In the original work of Perez et al. [27] the rate $\mu$ is constant and $b(V)$ is a piecewise linear function, $b(V) = V_0 - \alpha V$ for $V \in [0, V_0/\alpha]$, $b(V) = 0$ for $V > V_0/\alpha$. The equation has been designed to simulate the oscillatory dynamics in Nicholson’s experiments. Gurney et al. [9] have chosen $\mu$ as constant and $b(V) = pe^{-V/V_0}$ with constant $p$ (with $V_0$ representing the population size at which the population as a whole achieves maximum reproduction success). This model gives a richer pattern of oscillatory dynamics, e.g., double-humped peaks per population cycle. Hence the observed oscillations can be explained as arising from
the interaction of a delay with a “humped” birth term \( b(V)V \). Notice
that the birth rate \( b(V) \) chosen in [9] is strictly decreasing. This equation
has been studied in several papers [28], also with diffusion in space [29].

4 Neutral delay equations \( \) Equation (12) shows the following:
(i) The equation is of neutral type if and only if the function \( b_2 \) does
not vanish. In other words, within the chosen framework of an age-
structure model the neutral term results from a sharp peak in the birth
rate. Thereby the size of the peak may depend on the total size of the
adult population. (ii) If there is a peak in the birth rate, \( b_2 \neq 0 \), then
there is necessarily also a contribution from \( b_2 \) to the simple delay term,
unless the product \( b_2 \mu_1 \) vanishes identically.

We underline that we do not arrive at a neutral equation of a type
described by (4) with a delayed death term but rather at a neutral
extension of the blow-up equation (3).

Now we use the functions \( b_1, \mu_1, b_2 \) explicitly and incorporate the
term containing \( \mu_0 \) into the rates \( b_1, b_2 \) (which mathematically amounts
to putting \( \mu_0 = 0 \)). Then we get from (12)

\[
\dot{V}(t) = b_1(V(t-\tau))V(t-\tau) + b_2(V(t-\tau))\dot{V}(t-\tau)
+ \mu_1(V(t-\tau))V(t-\tau) - \mu_1(V(t))V(t)
\]

as a standard model with peak fertility at the beginning of the adult
phase. If \( b_1 \) vanishes then fertility is concentrated at the peak and indi-
viduals of ages \( a > \tau \) do not reproduce. Then the system is essentially
a model for discrete generations. Hence the case \( b_1 \neq 0 \) seems more
interesting with respect to delay equations.

The theory of nonlinear neutral delay equations is quite involved and
it is difficult to pose a correct initial value problem in terms of the
state variables \( V \) and \( \dot{V} \). In the present case we can borrow concepts
from epidemic modelling like prevalence and incidence. Following [3]
we introduce a new variable \( Z \) by \( Z = \dot{V} + \mu_1(V)V \) and get an equivalent
form of (17) with variables \( \dot{V} \) and \( Z \)

\[
\dot{V}(t) = Z(t) - \mu_1(V(t))V(t)
\]

\[
Z(t) = b_1(V(t-\tau))V(t-\tau) + b_2(V(t-\tau))Z(t-\tau).
\]

The variable \( V \) is the total adult population size (prevalence) and \( Z \)
describes the number of individuals entering the adult population (inci-
dence). The first equation in (18) is an ordinary differential equation.
The term $-\mu_1(V)V$ describes density dependent mortality. The second equation is a discrete mapping $(V, Z) \rightarrow Z$ taking the duration of the juvenile stage into account. As a dynamical system and also from a computational point of view (18) is more convenient than (17). Also preservation of positivity is much simpler. Indeed, when non-negative initial data for $V(0)$ and $Z(s), -\tau \leq s \leq 0$ are given, then the solution is obviously non-negative for $t \geq 0$. For a detailed discussion of the positivity problem see [3].

We propose (18) as a natural extension of the blowfly equation for the case of a peak fertility.

5 Stability of stationary solutions

We perform a linear stability analysis for the models in question. Our starting point is equation (2). We linearize at the stationary solution of biological interest (which here is the zero solution) and get the linear delay equation (recall $f'(0) = 1$)

$$\dot{v}(t) = -\gamma v(t - \tau) - \beta v(t).$$

Consider the equation

$$\lambda + \alpha \lambda e^{-\lambda \tau} + \beta + \gamma e^{-\lambda \tau} = 0.$$ 

The special case is the characteristic equation of (19). This equation has been discussed in the literature (Hayes theorem), see [2], [13], [12], and [21], [11] for graphic discussions in terms of immediate and delayed feedback control. Here we refer to [17], pp 67ff, in particular Theorem 2.1. For $|\alpha| < 1$ (for $\alpha = 0$ in particular) stability can be discussed in terms of the quantities $\beta + \gamma$ and $\beta - \gamma$. If $\beta + \gamma$ and $\beta - \gamma$ are both positive or both negative then the stability properties for $\tau > 0$ are the same as for $\tau = 0$. If $\beta - \gamma > 0$ and $\beta + \gamma < 0$ then the zero solution is unstable for all $\tau \geq 0$. If $\beta - \gamma < 0$ and $\beta + \gamma > 0$ then there is a critical value $\tau_0 > 0$ such that the zero solution is stable for $\tau < \tau_0$ and unstable for $\tau > \tau_0$ whereby at $\tau = \tau_0$ a pair of complex conjugate roots crosses the imaginary axis.

For Hutchinson’s equation (1) the positive stationary solution is $u = K$. Linearizing at this solution gives $\dot{v} = -au(t - \tau)$ and the characteristic equation $\lambda + ae^{-\lambda \tau} = 0$. All roots have negative real parts as long as $a\tau < \pi/2$. If $\tau$ increases from 0 to large values then at $\tau = \pi/(2a)$ a first pair of conjugate complex roots crosses the imaginary axis. It is known that equation (1) has a non-constant periodic solution whenever $\tau \geq \pi/(2a)$. 

Hutchinson’s equation (1) shows oscillatory behavior for a sufficiently large delay $\tau$, whatever the actual values of the exponent of growth $a$ and of the carrying capacity $K$ are.

Equations of the form (2) show similar behavior if the equation is of delayed negative feedback type, i.e., if the function $f$ satisfies $f(x)x > 0$ for $x \neq 0$ and $f'(0) = 1$, and $0 < \beta < \gamma$ (immediate control is weaker than delayed control). Then there is a critical value for $\tau_0$ above which non-constant periodic solutions exist [12]. There may be secondary bifurcations if $\tau$ is further increased. There may be more complicated behavior if $f$ is a steep hump function and the delay is very large. Hence we can say that equations of the Hutchinson form typically show periodic behavior once the delay is large.

Now consider the blowfly equation (16). We assume that $b_1(V)$ and $\mu_1(V)$ are positive functions as $b, \mu$ in the introduction, i.e., $b_1$ decreasing to zero, $\mu_1$ increasing to infinity, with $b_1(0) > \mu_1(0)$. Then there is a unique stationary solution $\overline{V}$. We linearize at $\overline{V}$ and get the linear equation (19) with coefficients

\[ (21) \quad \gamma = -(b_1(V)V)'_{V=\overline{V}}, \quad \beta = (\mu_1(V)V)'_{V=\overline{V}} > 0. \]

Hence

\[ \beta + \gamma = -(b_1'(V) - \mu_1'(V))V > 0 \]

\[ (22) \quad \beta - \gamma = [(b_1(V) + \mu_1(V))V]'_{V=\overline{V}} \]

\[ = (b_1'(V) - \mu_1'(V))V + 2(\mu_1(V)V)'_{V=\overline{V}}. \]

Hence a necessary condition for a Hopf bifurcation for some $\tau > 0$ is $(b_1(V)V)' < 0$ at $V = \overline{V}$. But this inequality is not sufficient. In order to have $\beta - \gamma < 0$, the negative quantity $(b_1(V)V)'$ must compensate the positive quantity $(\mu_1(V)V)'$. Hence we see:

For the blowfly equation (16) a necessary and sufficient condition for a Hopf bifurcation from the non-trivial stationary solution for some $\tau > 0$ is that the sum $(b_1(V) + \mu_1(V))V$ has negative derivative at the stationary solution $\overline{V}$.

Non-trivial stationary solutions of the Gurtin-MacCamy system (5) can be described in terms of the survival function

\[ p(a, w) = \exp \left\{ - \int_0^a \mu(s, w) \, ds \right\} \]
and the age distribution \( u(a) = p(a, w)u_0 \). The value \( w \) can be determined from the equation

\[
\int_0^\infty b(a, w)p(a, w) \, da = 1
\]

and then \( u_0 \) from \( w = \int_0^\infty \rho(a)p(a, w) \, da \). If the function \( b(a, w) \) is strictly decreasing to zero as a function of \( w \) and \( \mu(a, w) \) is strictly increasing to infinity then there is at most one non-trivial stationary solution. There is a stationary solution if furthermore \( \int_0^\infty b(a, 0)p(a, 0) \, da > 1 \).

As we have seen, the neutral equation (17) can be seen as a caricature of the Gurtin-MacCamy model, with \( w = V \). Hence there is a correspondence between stationary states of the Gurtin-MacCamy model (5) and the neutral equation (17). Define the function

\[
F(V) = b_1(V) - \mu_1(V)(1 - b_2(V)).
\]

It would seem natural to study the function \( b_1/(1 - b_2) - \mu_1 \), but the function \( F \) is better suited for the stability analysis. Assume, in agreement with what has been said about the birth and death rates before, that \( b_1(V) \) and \( b_2(V) \) are strictly decreasing to zero and \( \mu_1 \) is strictly increasing to infinity. Then the function \( F \) is strictly decreasing.

Nontrivial constant solutions \( V \) of equation (17) are solutions of the equation \( F(V) = 0 \). In view of our assumptions the function \( F \) is strictly decreasing and there is at most one non-zero solution. There is a solution \( \ numerator \) if \( F(0) = b_1(0) - \mu_1(0)(1 - b_2(0)) > 0 \). The same result can be obtained from the system (18). In particular, if \( b_2(0) > 1 \) then there is no stationary solution at all, in this case typical time-dependent solutions are ever increasing.

Linearizing either (17) or (18) at \( \overline{V} \) (or \( \overline{\nu}, \overline{Z} \)), respectively, with the corresponding value of \( Z \) gives \( \dot{\overline{\nu}} = -\alpha \overline{\nu}(t - \tau) - \beta \overline{\nu}(t) - \gamma \overline{\nu}(t - \tau) \) and then the characteristic equation (20) with coefficients

\[
\alpha = -b_2(\overline{V}),
\]

\[
\beta = [\mu_1(V)V]'_{V=\overline{V}},
\]

\[
\gamma = -[b_1(V)V + b_2(V)\mu_1(V)V]'_{V=\overline{V}}.
\]

We have \( 0 \leq b_2(\overline{V}) < 1 \) in view of \( F(\overline{V}) = 0 \), hence \( -1 < \alpha \leq 0 \).
Furthermore

\[ \beta + \gamma = -F'(\overline{V})\overline{V}, \]

(26)

\[ \beta - \gamma = [(b_1(V) + (b_2(V) + 1)\mu_1(V))]' \]

\[ = F'(\overline{V})\overline{V} + 2(\mu_1(V)\overline{V})'_{\overline{V}=\overline{V}}. \]

We have \( F'(\overline{V}) < 0 \), hence \( \beta + \gamma > 0 \). In view of the biological interpretation \( \mu_1(V)\overline{V} \) is increasing. Now there are two cases.

Case 1: \( \beta - \gamma > 0 \).

The delay does not affect the stability properties. For \( \tau = 0 \) we have \( \lambda = -(\beta + \gamma)/(1 + \alpha) < 0 \). Hence the stationary state is stable for all values of \( \tau \). In this case \( (\mu_1(V)\overline{V})' \) is so large that \( \beta - \gamma \) is positive although \( F'(\overline{V}) \) is negative.

Case 2: \( \beta - \gamma < 0 \).

Then there is a critical value \( \tau_0 \) of the delay \( \tau \) such that the stationary state is stable for \( \tau < \tau_0 \) and unstable for \( \tau > \tau_0 \) whereby at \( \tau = \tau_0 \) a pair of conjugate complex roots pass through the imaginary axis.

For the neutral equation (17) or the population model (18) transition to stable oscillations for increasing delay \( \tau \) occurs only under certain conditions. A necessary and sufficient condition for such oscillations to occur for some \( \tau > 0 \) is that the expression

\[ (b_1(V) + (b_2(V) + 1)\mu_1(V))V \]

has negative derivative at \( V = \overline{V} \).

Hence we expect oscillations when at the equilibrium the birth rate is strongly decreasing. For \( b_2 = 0 \) we recover the condition for the blowfly equation.
REFERENCES


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