Dynamics of a neutral delay equation for an insect population with long larval and short adult phases

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Abstract

We present a global study on the stability of the equilibria in a nonlinear autonomous neutral delay differential population model formulated by Bocharov and Hadeler. This model may be suitable for describing the intriguing dynamics of an insect population with long larval and short adult phases such as the periodical cicada. We circumvent the usual difficulties associated with the study of the stability of a nonlinear neutral delay differential model by transforming it to an appropriate non-neutral nonautonomous delay differential equation with unbounded delay. In the case that no juveniles give birth, we establish the positivity and boundedness of solutions by ad hoc methods and global stability of the extinction and positive equilibria by the method of iteration. We also show that if the time adjusted instantaneous birth rate at the time of maturation is greater than 1, then the population will grow without bound, regardless of the population death process.

Short Title: Dynamics of a neutral delay equation

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1 Introduction

Some insect species have a very long larval stage of many years and, by comparison, an extremely short adult stage of just a few weeks or less which is essentially devoted entirely to mating. One of the most striking examples is probably the three species of seventeen-year periodical cicada, namely Magicicada cassini, M. septendecim and M. septendecula which

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appear in different parts of the northern and eastern USA and have the longest juvenile
development of any insect ([16]). The well known “Brood X” last emerged in 2004 and
affected the eastern seaboard west through Indiana and south to Tennessee. The nymphs
of these cicadas live underground, where they have very limited mobility and feed on plant root
xylem fluids. Adult periodical cicadas live only four to six weeks and concentrate almost
entirely on reproduction. When an adult male has used up his sperm, he dies. The female
will lay several hundred eggs in slits in the bark of young twigs, and then die. After six to
eight weeks the eggs hatch and the nymphs burrow into the ground where they remain for the
next seventeen years. Nymph mortality can be very high especially in the first two years ([6]).
Prior to entering the ground they risk predation by ants and spiders. Once underground
they are safe from most predators but are still at some risk from ground dwellers such as
mole. Intense competition for space can be a problem, and the very long developmental
period poses numerous additional hazards to nymphs which can include destruction of forests,
urbanisation and forest fires. There are other species of cicadas which follow a thirteen year
cycle, and large numbers of species have a two to five year life cycle. Newly emerged adult
cicadas are easy to catch and are subject to intense predation, and this may in fact be
one reason for the evolution of very long juvenile developmental periods and synchronised
emergences of vast numbers. This has the effect of satiating predators so that large numbers
of adult cicadas can survive to reproduce. Adopting a life cycle duration of a large prime
number of years is itself believed to be a predator-avoidance strategy because it minimises
the chances of synchronising with the life cycles of birds and other predators.

Another example of the type of insect we have in mind in this paper is the marine midge
*Pontomyia* which as an adult lives for only a couple of hours, but has a larval duration of
around one month ([15]). During their very short adult lives the males must find mates and
the females besides mating must find a suitable place to deposit fertilized eggs.

Though the cicadas and the marine midges differ substantially in the actual durations
of their respective larval and adult phases, the two species have one thing in common: their
adult phase is extremely short by comparison with the larval phase. Cicadas and marine
midges both suggest the need for a type of mathematical model that models the dynamics
of the entire life cycle using a continuous time model in which the egg laying is an event
that only happens at a certain exact age. The egg laying event is in some sense an impulsive
one for each individual because it occurs when that particular individual reaches a certain
age. It need not occur at the same instant in time for all individuals in the population,
even in the case of a periodical cicada species due to synchronised emergences, or even in non-periodical species since emergences tend to occur at a particular
time of year (typically late Spring).

Standard approaches to the study of age structured populations usually start from an
equation of the form

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u(t,a),$$  \hspace{1cm} (1.1)

where $t$ is time, $a$ is age and $u(t,a)$ is density of individuals of age $a$. If this equation is
supplemented with
\[ u(0, a) = u_0(a), \quad u(t, 0) = N(t) \]
where \( N(t) \) is the birth rate, then we get the explicit solution
\[
u(t, a) = \begin{cases} 
  u_0(a - t) \exp \left( - \int_{a-t}^{a} \mu(s) \, ds \right) & a > t, \\
  N(t - a) \exp \left( - \int_{0}^{a} \mu(s) \, ds \right) & a < t.
\end{cases}
\] (1.2)

For the birth rate \( N(t) \), or \( u(t, 0) \), we might assume a relation of the following kind:
\[
u(t, 0) = \int_{0}^{\infty} b(a) u(t, a) \, da. \] (1.3)

This assumes that any individual of positive age \( a > 0 \) might produce offspring, but it is more likely to happen at certain ages than others. In this case we obtain a renewal equation for \( N(t) \):
\[
  N(t) = \int_{0}^{t} b(a) p(a) N(t - a) \, da + R(t),
\]
where \( p(a) \) is the probability of survival to age \( a \) and is given by
\[
p(a) = \exp \left( - \int_{0}^{a} \mu(s) \, ds \right),
\]
and
\[
  R(t) = \int_{0}^{\infty} b(\xi + t) u_0(\xi) \exp \left( - \int_{\xi}^{\xi+t} \mu(s) \, ds \right) \, d\xi.
\]

When the birth law is of the form \( u(t, 0) = b(u_m(t)) \) rather than (1.3), a common and useful approach is to reformulate (1.1) as a delay equation for the variable \( u_m(t) \). The simplest approach is to introduce the variables (2.1) below, with \( u_m(t) \) obeying an equation of the form (2.2) below. The implication of \( u(t, 0) = b(u_m(t)) \) is that the birth rate is a function of the total number of adults. A delay equation of the following form can be obtained for \( t > \tau \):
\[
  \frac{du_m}{dt} = \exp \left( - \int_{0}^{\tau} \mu(s) \, ds \right) b(u_m(t - \tau)) - d(u_m(t)), \] (1.4)
and another equation for an initial transient period \( t \in (0, \tau) \), namely
\[
  \frac{du_m}{dt} = u_0(\tau - t) \exp \left( - \int_{\tau-t}^{\tau} \mu(s) \, ds \right) - d(u_m(t)).
\]

It is common to ignore the equation that governs the initial transient and to work with (1.4) as if it were valid for all times \( t > 0 \) and in many situations this is reasonable. In the present
paper our approach is in a sense a combination of the two abovementioned approaches to dealing with the birth rate. It uses an expression of the form (1.3) for the birth rate, yet ends up with delay differential equations for the variables $u_m$ and $u_i$. However, the delay equations we obtain are not like (1.4), they are neutral delay equations and this represents a significant complication. Moreover there is one equation for $t > \tau$ and a separate one for $t \in (0, \tau)$ but, as will become clear, if the implications of this are taken care of correctly it gives the whole model system a structure which enables considerable analytic progress to be made.

### 2 Model derivation

Let $t$ and $a$ denote time and age and let $u(t, a)$ be the density of individuals of age $a$ at time $t$. It will be assumed that individuals take time $\tau$ to mature, so that the total numbers of mature and immature members $u_m$ and $u_i$ are given respectively by

$$u_m(t) = \int_{\tau}^{\infty} u(t, a) \, da, \quad u_i(t) = \int_{0}^{\tau} u(t, a) \, da. \quad (2.1)$$

We will assume that the total number of adults $u_m$ obeys an equation of the form

$$\frac{du_m(t)}{dt} = u(t, \tau) - d(u_m(t)). \quad (2.2)$$

The term $u(t, \tau)$ is the maturation rate, being the rate at which individuals pass through maturation age $\tau$, and $d(u_m)$ is the adult mortality function which at this stage satisfies only

$$d(0) = 0, \quad d(u_m) \text{ strictly increasing in } u_m. \quad (2.3)$$

It will be assumed that the juveniles (larvae/nymphs) have a constant linear death rate $\mu$ and therefore that the juvenile population is governed by

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu u, \quad 0 < a < \tau \quad (2.4)$$

subject to

$$u(t, 0) = \int_{0}^{\infty} b(a) u(t, a) \, da, \quad (2.5)$$

where $b(a) \geq 0$ is the birth rate function, and the initial condition

$$u(0, a) = u_0(a) \geq 0, \quad a \geq 0. \quad (2.6)$$

The birth rate $N(t)$ will be an important quantity. It is given by

$$N(t) = u(t, 0).$$
What we propose to do is achieve a neutral delay equation for the total number of adults, \( u_m(t) \). Following Bocharov and Hadeler [2] we shall choose

\[
  b(a) = b_0 + (b_1 - b_0)H(a - \tau) + b_2 \delta(a - \tau)
\]  

(2.7)

where \( H(a) \) is the Heaviside function and \( \delta(a) \) the Dirac delta function. This choice for \( b(a) \) implies that individuals of age less than \( \tau \) produce \( b_0 \) eggs per unit time, those of age greater than \( \tau \) produce \( b_1 \) eggs per unit time, and additionally each individual lays \( b_2 \) eggs on reaching maturation age \( \tau \) (the \( b_2 \) eggs all being laid at exactly that instant). We are of course at liberty to take \( b_0 = b_1 = 0 \) so that all eggs are laid on reaching maturation age, and this is what we consider to be an entirely sensible approximation in the case of an insect which has a very brief adult duration and relatively speaking a very long larval one as we discussed in the introduction with cicadas in mind. Keeping \( b_0 \) and \( b_1 \) allows for the possibility of births occurring at ages other than \( \tau \); we might think of these constants as small, especially \( b_0 \) which is the birth rate for ages less than \( \tau \). In fact we shall take \( b_0 = 0 \) for most of this paper which is entirely sensible for the species we mostly have in mind.

In the case of (2.7),

\[
  u(t,0) = \int_{0}^{\infty} (b_0 + (b_1 - b_0)H(a - \tau) + b_2 \delta(a - \tau))u(t,a) \, da
\]

\[
= b_2u(t,\tau) + b_0 \int_{0}^{\tau} u(t,a) \, da + b_1 \int_{\tau}^{\infty} u(t,a) \, da
\]

giving

\[
u(t,0) = b_2u(t,\tau) + b_0u_i(t) + b_1u_m(t).
\]  

(2.8)

Note in particular that if \( b_0 = b_1 = 0 \) then \( u(t,0) = b_2u(t,\tau) \) which means that the birth rate equals \( b_2 \) times the maturation rate, so that each individual lays exactly \( b_2 \) eggs at the instant of reaching age \( \tau \). We want to find \( u(t,\tau) \) in terms of the variables \( u_i \) and \( u_m \). Now, the solution of (2.4) subject to (2.6) and \( u(t,0) = N(t) \) is

\[
u(t,a) = \begin{cases}  
  u_0(a-t) \exp(-\mu t), & t < a \\
  N(t-a) \exp(-\mu a), & t > a.
\end{cases}
\]  

(2.9)

Expression (2.9) furnishes \( u(t,\tau) \), but with the consequence that when \( t < \tau \) the evolution equations for \( u_i \) and \( u_m \) are different from those for \( t > \tau \) as explained earlier.

For \( t > \tau \),

\[
u(t,\tau) = N(t-\tau)e^{-\mu \tau}
\]

\[
= u(t-\tau,0)e^{-\mu \tau}
\]

\[
= (b_2u(t-\tau,\tau) + b_0u_i(t-\tau) + b_1u_m(t-\tau))e^{-\mu \tau}
\]

by (2.8). But, from (2.2),

\[
u(t-\tau,\tau) = u'_m(t-\tau) + d(u_m(t-\tau)).
\]
Thus
\[ u(t, \tau) = (b_2u'_m(t - \tau) + b_2d(u_m(t - \tau)) + b_0u_i(t - \tau) + b_1u_m(t - \tau))e^{-\mu \tau} \]

and so the equation for the adult population becomes the neutral delay equation
\[ u'_m(t) = (b_2u'_m(t - \tau) + b_2d(u_m(t - \tau)) + b_0u_i(t - \tau) + b_1u_m(t - \tau))e^{-\mu \tau} - d(u_m(t)), \quad t \geq \tau. \]

For \( t \leq \tau \), \( u(t, \tau) = u_0(\tau - t)e^{-\mu t} \) and so in this case \( u_m(t) \) is governed by the nonautonomous equation
\[ u'_m(t) = u_0(\tau - t)e^{-\mu t} - d(u_m(t)), \quad t \leq \tau \]

which involves the initial data for (2.4). Equation (2.11) is solved subject to
\[ u_m(0) = \int_{\tau}^{\infty} u_0(a) \, da. \]

We may derive similar equations for the total immature population \( u_i(t) \). Differentiating the expression for \( u_i(t) \) in (2.1) and using (2.4) gives
\[ u'_i(t) = u(t, 0) - u(t, \tau) - \mu u_i(t) \]
\[ = (b_2 - 1)u(t, \tau) + b_0u_i(t) + b_1u_m(t) - \mu u_i(t) \]

so that for \( t > \tau \),
\[ u'_i(t) = (b_2 - 1)\{b_2u'_m(t - \tau) + b_2d(u_m(t - \tau)) + b_0u_i(t - \tau) + b_1u_m(t - \tau)\}e^{-\mu \tau} \]
\[ + b_0u_i(t) + b_1u_m(t) - \mu u_i(t) \]

and for \( t \leq \tau \),
\[ u'_i(t) = (b_2 - 1)u_0(\tau - t)e^{-\mu t} + b_0u_i(t) + b_1u_m(t) - \mu u_i(t). \]

In the remainder of this paper we shall consider in detail the case when \( b_0 = 0 \). In other words, we assume that individuals below age \( \tau \) do not produce offspring. The total adult population \( u_m(t) \) obeys equation (2.11) for \( 0 < t \leq \tau \), and the neutral delay equation (2.10), with \( b_0 = 0 \), for times \( t > \tau \).

### 2.1 Positivity

Given non-negative initial data \( u_0(a) \) for (2.4), this section will show that the adult population \( u_m(t) \) remains non-negative. Note that, in view of the term \( u'_m(t-\tau) \) in the right hand side of (2.10), such a result is far from obvious.

**Theorem 1** Assume that \( d(0) = 0 \), that \( b(a) \) is given by (2.7) with \( b_0 = 0 \) and that \( u_0(a) \geq 0 \) for all \( a \geq 0 \). Then the solution \( u_m(t) \) of (2.11), (2.10) satisfies \( u_m(t) \geq 0 \) for all \( t > 0 \). Furthermore if \( u_0(a) \neq 0 \) on \( (\tau, \infty) \) then \( u_m(t) > 0 \) for all \( t > 0 \).
**Proof.** On the interval \( t \in (0, \tau] \), \( u_m(t) \) satisfies (2.11) and so

\[
u'_m(t) \geq -d(u_m(t)), \quad 0 < t \leq \tau.
\]

The initial value for \( u_m \) is \( u_m(0) = \int_0^\infty u_0(a) \, da \geq 0 \). Also, since \( d(0) = 0 \) by Taylor expansions it follows that \( d(u_m(t)) \) has a factor of \( u_m(t) \) and so from standard arguments it follows that \( u_m(t) \geq 0 \) for \( 0 < t \leq \tau \).

Next we prove non-negativity of \( u_m(t) \) for times \( t \in (\tau, 2\tau] \). For such times, \( t - \tau \leq \tau \) so that, from (2.11),

\[
u'_m(t - \tau) + d(u_m(t - \tau)) = u_0(2\tau - t)e^{-\mu(t-\tau)}
\]

and so, from (2.10),

\[
u'_m(t) = (b_2u_0(2\tau - t)e^{-\mu(t-\tau)} + b_1u_m(t - \tau))e^{-\mu \tau} - d(u_m(t)) \geq -d(u_m(t))
\]

because we have already shown non-negativity of \( u_m(t) \) on the interval \((0, \tau] \). Using \( d(0) = 0 \) and non-negativity of \( u_m(\tau) \), it follows that \( u_m(t) \geq 0 \) for \( t \in (\tau, 2\tau] \).

For \( t \in (2\tau, 3\tau] \), we know from the previous step that \( u_m(t - \tau) \geq 0 \). Thus

\[
u'_m(t) = \begin{cases} b_2(u'_m(t - \tau) + d(u_m(t - \tau))) + b_1u_m(t - \tau) & \geq 0 \\ b_2 \{u'_m(t - \tau) + d(u_m(t - \tau))\} e^{-\mu \tau} - d(u_m(t)) & \geq b_2 e^{-\mu \tau} \{b_2u_m'(t - 2\tau) + b_2d(u_m(t - 2\tau)) + b_1u_m(t - 2\tau)\} e^{-\mu \tau} - d(u_m(t)) \\
\geq b_2^2 e^{-2\mu \tau} \{u'_m(t - 2\tau) + d(u_m(t - 2\tau))\} - d(u_m(t)) \\
= b_2^2 e^{-2\mu \tau} u_0(3\tau - t)e^{-\mu(t-2\tau)} - d(u_m(t)) & \text{since } t - 2\tau \in (0, \tau]
\end{cases}
\]

so that

\[
u'_m(t) \geq -d(u_m(t)) \quad \text{for } t \in (2\tau, 3\tau].
\]

Hence \( u_m(t) \geq 0 \) for \( t \in (2\tau, 3\tau] \). This argument can be continued to include all positive times and so non-negativity of \( u_m(t) \) has been shown.

If \( u_0(a) \neq 0 \) on \((\tau, \infty)\) then \( u_m(0) > 0 \). In this situation, inspection of the details of the above analysis shows that we can draw the conclusion that \( u_m(t) \) is strictly positive for all positive times. \( \square \)

3 Alternative formulations

This section presents some alternative formulations of the model equations for the adult population \( u_m(t) \), given by (2.11) and (2.10). The first of these is an exact reformulation
as a nonautonomous non-neutral equation involving a summation term which is a weighted average of the solution not just at time \( t - \tau \) but at all the previous times \( t - \tau, t - 2\tau, \ldots, t - n\tau \) where \( n \) is such that \( t - n\tau \in (0, \tau] \). This approach dispenses with the term \( u'_m(t - \tau) \) in (2.10), at the expense of introducing, essentially, a distributed delay term where the distribution is discrete involving summation rather than an integral. This exact reformulation is essential for the remainder of the paper and will enable us to prove theorems on the dynamics of the solutions. The second reformulation we shall describe is approximate and involves using the Euler-Maclaurin summation, which if invoked in its simplest form keeping only lowest order terms results in an equation with a discrete delay and a distributed delay involving an integral. These approximate reformulations are not treated in detail in this paper since the exact reformulation as a non-neutral equation can be treated analytically and its dynamics determined. However, the approximate approach is presented briefly as it may provide a useful approach to the treatment of more complicated neutral delay equations that might arise in other contexts.

### 3.1 Exact reformulation as a non-neutral delay equation

The structure of equation (2.10) enables us to apply it recursively (for times \( t > 2\tau \)) without the algebra becoming intractable.

For times \( t \in (\tau, 2\tau] \), the term \( u'_m(t - \tau) \) in the right hand side of (2.10) can be worked out from (2.11). Thus, for \( t \in (\tau, 2\tau] \),

\[
u'_m(t) = b_2 e^{-\mu t} u_0(2\tau - t) + b_1 e^{-\mu \tau} u_m(t - \tau) - d(u_m(t)). \tag{3.1}\]

For times \( t \in (2\tau, 3\tau] \), equation (2.10) is used recursively once to get \( u'_m(t) \) in terms of \( u'_m(t - 2\tau) \), which is then given by (2.11). The result is

\[
u'_m(t) = b_2^2 e^{-\mu t} u_0(3\tau - t) + b_2 b_1 e^{-2\mu \tau} u_m(t - 2\tau) + b_1 e^{-\mu \tau} u_m(t - \tau) - d(u_m(t)). \tag{3.2}\]

This process can be continued. The result is that, for \( n = 1, 2, 3, \ldots \), the evolution of \( u_m(t) \) for times \( t \in (n\tau, (n + 1)\tau] \) is given by

\[
u'_m(t) = b_2^n e^{-\mu t} u_0((n + 1)\tau - t) + b_1 e^{-\mu \tau} \sum_{j=0}^{n-1} b_2^j e^{-j\mu \tau} u_m(t - (j + 1)\tau) - d(u_m(t)), \tag{3.3}\]

a nonautonomous delay differential equation involving, via the first term in its right hand side, the initial data for (2.4). Note that if \( b_2 e^{-\mu \tau} < 1 \) this term approaches zero as \( n \to \infty \). Therefore the nonautonomous term gradually loses its influence as \( t \) gets larger. If we look for the equilibria of the asymptotically autonomous delay equation obtained by letting \( n \) and \( t \) go to infinity in (3.3) we find that the equilibria satisfy

\[b_1 u_m e^{-\mu \tau} = d(u_m)(1 - b_2 e^{-\mu \tau}), \]

and this is consistent with previous analysis.
3.2 Approximate reformulation using Euler-Maclaurin summation

The Euler-Maclaurin summation formula [1], namely

\[ \sum_{k=1}^{n-1} f_k = \int_0^n f(k) \, dk - \frac{1}{2} (f(0) + f(n)) + \sum_{k=1}^{\infty} \frac{B_{2k}}{(2k)!} [f^{(2k-1)}(n) - f^{(2k-1)}(0)], \tag{3.4} \]

where the \( B_n \) are the Bernoulli numbers, can be formally applied to the summation in (3.3). Ignoring terms with derivatives (this point will be discussed below) the result is that, for \( t \in (n\tau, (n+1)\tau] \),

\[ u_m'(t) = b_2 e^{-\mu\tau} u_0((n+1)\tau - t) + b_1 e^{-\mu\tau} \left( \int_0^n b_s e^{-s\mu\tau} u_m(t - \tau - s\tau) \, ds + \frac{1}{2} u_m(t - \tau) \right. \]
\[ \left. - \frac{1}{2} b_2 e^{-n\mu\tau} u_m(t - (n+1)\tau) \right) - d(u_m(t)) \tag{3.5} \]

so that if \( b_2 e^{-\mu\tau} < 1 \) then for large times the evolution equation for \( u_m(t) \) is approximately

\[ u_m'(t) = b_1 e^{-\mu\tau} \left( \int_0^\infty b_s e^{-s\mu\tau} u_m(t - \tau - s\tau) \, ds + \frac{1}{2} u_m(t - \tau) \right) - d(u_m(t)). \tag{3.6} \]

What we have achieved, albeit in an approximate sense, is to replace the original neutral delay differential equation for \( u_m(t) \) by an equation, namely (3.6) above, that does not involve delay in the terms with derivatives but involves both discrete and distributed delay. In the distributed delay part the integration is over times up to \( t - \tau \) rather than \( t \). Note also the kernel of integration has emerged from the analysis as being the function with values \( b_s e^{-s\mu\tau} \). Other (especially older) distributed delay models of population dynamics in the literature often suffered from the criticism that the kernel in the distribution could not be derived and was therefore chosen rather arbitrarily, based solely on what authors intuitively felt was ecologically reasonable.

We mentioned above that in the application of the Euler-Maclaurin summation formula we would ignore terms with derivatives. It is important to point out that by “terms with derivatives”, we do not mean derivatives of the state variable \( u_m(t) \), but derivatives of the function \( s \rightarrow b_s e^{-s\mu\tau} u_m(t - (s+1)\tau) \). A consequence of this is that the approximated equation (3.6) does not predict the equilibria quite right (except for the trivial zero equilibrium). One way to address this deficiency might be to keep some of these “derivative” terms in the Euler Maclaurin formula. If we retain just the one involving the Bernoulli number \( B_2 \), then (3.4) yields

\[ \sum_{j=0}^{n-1} f_j \approx f(0) + \sum_{j=1}^{n-1} f_j = \frac{1}{2} f(0) - \frac{1}{2} f(n) + \int_0^n f(j) \, dj + \frac{1}{12} (f'(n) - f'(0)). \]

With \( f(j) = b_j e^{-j\mu\tau} u_m(t - (j+1)\tau) \), after some algebra we deduce that if \( b_2 e^{-\mu\tau} < 1 \) then,
for large times, $u_m(t)$ is given approximately by

$$u'_m(t) = b_1 e^{-\mu \tau} \left( \frac{1}{2} u_m(t - \tau) + \int_0^{\infty} b_2 e^{-s \mu \tau} u_m(t - (s + 1) \tau) \, ds \right)$$

$$- \frac{1}{12} \left[ -\tau u'_m(t - \tau) + \ln(b_2 e^{-\mu \tau}) u_m(t - \tau) \right] - d(u_m(t)).$$

(3.7)

The above equation is, of course, another neutral delay equation. It may predict the equilibria more accurately but will not be any easier to analyze than the original equation (2.10).

4 Convergence of solutions

We will present some results on the convergence of solutions. For this purpose we will use the alternative formulation of the model describing $u_m(t)$ consisting of equation (3.3). No approximations were used to derive this particular equation. Our first theorem is for the case when $b_1 = 0$.

**Theorem 2** Suppose that $b_1 = b_0 = 0$ and $b_2 e^{-\mu \tau} < 1$. Let $d(u_m)$ be a continuous strictly monotonic increasing function of $u_m$ satisfying $d(0) = 0$. Then the solution of (2.10,2.11) satisfies $u_m(t) \to 0$ as $t \to \infty$.

**Proof.** Equation (3.3) is for $t \in (n\tau, (n + 1)\tau]$ so $t$ and $n$ must go to infinity together. Since $b_1 = 0$ the term with summation is absent. Furthermore, the involvement of $u_0(\cdot)$ is for values of its argument between 0 and $\tau$ only, so $u_0((n + 1)\tau - t)$ can be bounded independently of $n$ and $t$. Let $\epsilon > 0$ be arbitrary, and choose $N$ sufficiently large that

$$b_2 e^{-\mu \tau} \sup_{a \in [0,\tau]} u_0(a) < \epsilon \quad \text{whenever } n \geq N.$$

Then it follows that, for $t > N\tau$,

$$u'_m(t) \leq \epsilon - d(u_m(t)).$$

From a simple comparison argument, and using the stated properties of the function $d$, and also positivity of $u_m$, it follows that

$$0 \leq \limsup_{t \to \infty} u_m(t) \leq d^{-1}(\epsilon).$$

This is true for any $\epsilon > 0$ and therefore $\lim_{t \to \infty} u_m(t) = 0$. The proof is complete. \(\square\)

It is easy to interpret Theorem 2 ecologically. Let us refer back to the expression for $b(a)$, expression (2.7). With $b_1$ and $b_0$ both being zero, expression (2.7) implies that each individual produces exactly $b_2$ offspring when it is of age exactly $\tau$, and produces no offspring at any other age. Each one of those offspring will itself produce $b_2$ offspring $\tau$ time units
later, but only if it is still alive to do so. The assumption about juvenile mortality is that it follows a linear law with rate constant $\mu$. Therefore, the probability of surviving from birth until age $\tau$ is $e^{-\mu \tau}$. So if $b_2 e^{-\mu \tau} < 1$ then the individuals are not replacing themselves.

Our next result admits the case when $b_1 > 0$. The result implicitly assumes $b_2 e^{-\mu \tau} < 1$.

**Theorem 3** Suppose that $b_0 = 0$, $b_1 > 0$ and

$$b_1 u_m e^{-\mu \tau} < d(u_m)(1 - b_2 e^{-\mu \tau}) \quad \text{for all } u_m > 0. \quad (4.1)$$

Let $d(u_m)$ be a continuous strictly monotonic increasing function of $u_m$ satisfying $d(0) = 0$. Then the solution of (2.10,2.11) satisfies $u_m(t) \to 0$ as $t \to \infty$.

**Proof.** Note first that (4.1) forces $b_2 e^{-\mu \tau} < 1$. It is sufficient to prove that non-negative solutions of the alternative formulation (3.3) of the original model (2.10,2.11) tend to zero as $t \to \infty$, and we shall first establish that these solutions are bounded.

Recall that (3.3) is for times $t > \tau$. For times $t \in (0, \tau)$, $u_m(t)$ is determined by (2.11) subject to (2.12). In what follows we will drop the subscript $m$ for convenience. Let $U = \max(\max\{u_0(a) : a \in [0, \tau]\}, \max\{u(t) : t \in [0, \tau]\})$ and choose $p$ sufficiently large that $p > b_2/b_1$. We claim that

$$\limsup_{t \to \infty} u(t) \leq (p + 1)U. \quad (4.2)$$

Suppose the contrary, then since the solution is bounded by $U$ for $t \in [0, \tau]$ there must exist $t_1 > \tau$ such that

$$u(t_1) = (p + 1)U, \quad u(t) < (p + 1)U \quad \text{for all } t < t_1, \text{ and } u'(t_1) \geq 0 \quad (4.3)$$

and an integer $k$ such that $t_1 \in (k\tau, (k + 1)\tau]$. But, from (3.3),

$$u'(t_1) = b_2 k e^{-\mu \tau} u_0((k + 1)\tau - t_1) + b_1 e^{-\mu \tau} \sum_{j=0}^{k-1} b_2^j e^{-j\mu \tau} u(t_1 - (j + 1)\tau) - d(u(t_1))$$

$$\leq b_2^k e^{-k\mu \tau} U - b_1 e^{-\mu \tau} b_2^{k-1} e^{-(k-1)\mu \tau} pU + b_1 e^{-\mu \tau} b_2^{k-1} e^{(k-1)\mu \tau} (p + 1)U$$

$$+ b_1 e^{-\mu \tau} \sum_{j=0}^{k-2} b_2^j e^{-j\mu \tau} (p + 1)U - d((p + 1)U).$$

The second and third terms (taken together) in the right hand side of this inequality are an upper bound for the $j = k - 1$ term in the previous summation. The $j = k - 1$ term has been written separately from the rest of the summation to take advantage of the availability of the bound $U$ on $\{u(t) : t \in [0, \tau]\}$; for the other terms in the summation the higher bound
of $(p+1)U$ has been used. Next, we move the term $b_1e^{-\mu\tau}b_2^{k-1}e^{-(k-1)\mu\tau}(p+1)U$ back into the summation to obtain

$$u'(t_1) \leq b_2^{k-\mu\tau}U - b_1e^{-\mu\tau}b_2^{k-1}e^{-(k-1)\mu\tau}pU$$

$$+ b_1e^{-\mu\tau} \sum_{j=0}^{k-1} b_2^{j}e^{-j\mu\tau}(p+1)U - d((p+1)U)$$

$$\leq b_2^{k-\mu\tau}[b_2 - b_1p]U + b_1e^{-\mu\tau} \sum_{j=0}^{\infty} b_2^{j}e^{-j\mu\tau}(p+1)U - d((p+1)U)$$

$$= b_2^{k-\mu\tau}[b_2 - b_1p]U + \frac{b_1e^{-\mu\tau}(p+1)U}{1 - b_2e^{-\mu\tau}} - d((p+1)U)$$

$$< 0$$

using (4.1). This contradicts (4.3) and therefore $u(t)$ is bounded.

Let $K$ be an upper bound for $u(t)$, and let $\eta > 0$ be arbitrary. As noted earlier, the nonautonomous term in (3.3) goes to zero as $t \to \infty$. Again dropping the subscript $m$, it follows that for $t$ sufficiently large the nonautonomous term is bounded by $\eta$ and therefore

$$u'(t) \leq \eta + \frac{Kb_1e^{-\mu\tau}}{1 - b_2e^{-\mu\tau}} - d(u(t)).$$

From this, we find that

$$\limsup_{t \to \infty} u(t) \leq d^{-1}(\eta + Kb_1e^{-\mu\tau}/(1 - b_2e^{-\mu\tau})).$$

This is true for all $\eta > 0$, and therefore

$$\limsup_{t \to \infty} u(t) \leq d^{-1}(Kb_1e^{-\mu\tau}/(1 - b_2e^{-\mu\tau})) := u_1^*.$$

That $u_1^*$ is well defined follows from (4.1) and the other hypotheses on $d(\cdot)$.

In the subsequent steps of this analysis the nonautonomous term in (3.3) can be rigorously dealt with by introducing a small parameter which is later shrunk to zero as just described, and it is therefore sufficient to study the asymptotically autonomous form of (3.3), which is

$$u'(t) = b_1e^{-\mu\tau} \sum_{j=0}^{n-1} b_2^{j}e^{-j\mu\tau}u(t-(j+1)\tau) - d(u(t)), \quad t \in (n\tau, (n+1)\tau], \quad n = 1, 2, 3, \ldots \quad (4.4)$$

Using Heaviside’s function $H(t)$, (4.4) can be rewritten as

$$u'(t) = b_1e^{-\mu\tau} \sum_{j=0}^{\infty} b_2^{j}e^{-j\mu\tau}H(t-(j+1)\tau)u(t-(j+1)\tau) - d(u(t)). \quad (4.5)$$
Let $\epsilon > 0$. There exists $T > 0$ such that, for all $t \geq T$, $u(t) \leq u_1^* + \epsilon$. Choose an integer $N$ sufficiently large that
$$
\sum_{j=N}^{\infty} b_2^j e^{-j\mu \tau} < \epsilon
$$
which is possible because $b_2 e^{-\mu \tau} < 1$. From (4.5) we find that, for $t > N\tau + T$,
$$
u'(t) = b_1 e^{-\mu \tau} \sum_{j=0}^{\infty} b_2^j e^{-j\mu \tau} H(t - (j + 1)\tau) u(t - (j + 1)\tau) - d(u(t))
$$
$$= b_1 e^{-\mu \tau} \left( \sum_{j=0}^{N-1} b_2^j e^{-j\mu \tau} u(t - (j + 1)\tau) + \sum_{j=N}^{\infty} b_2^j e^{-j\mu \tau} H(t - (j + 1)\tau) u(t - (j + 1)\tau) \right)
$$
$$- d(u(t)) 
\leq b_1 e^{-\mu \tau} \left( u_1^* + \epsilon \right) \sum_{j=0}^{N-1} b_2^j e^{-j\mu \tau} + K\epsilon - d(u(t)) 
\leq b_1 e^{-\mu \tau} \left( \frac{u_1^* + \epsilon}{1 - b_2 e^{-\mu \tau}} + K\epsilon \right) - d(u(t)).
$$

From this, we deduce an $\epsilon$-dependent upper bound for $\limsup_{t \to \infty} u(t)$, and we may then shrink $\epsilon$ to zero to obtain
$$
\limsup_{t \to \infty} u(t) \leq d^{-1} \left( \frac{b_1 e^{-\mu \tau} u_1^*}{1 - b_2 e^{-\mu \tau}} \right) := u_2^*.
$$

By repeating the above procedure, we generate a sequence $u_n^*$, $n = 1, 2, 3, \ldots$ of real numbers with the property that $\limsup_{t \to \infty} u(t) \leq u_n^*$ for each $n$ and
$$
d(u_{n+1}^*) = \frac{b_1 e^{-\mu \tau} u_n^*}{1 - b_2 e^{-\mu \tau}}, \quad n = 1, 2, 3, \ldots.
$$

From (4.1) it follows that $d(u_{n+1}^*) < d(u_n^*)$ and therefore, since $d(\cdot)$ is strictly monotonic increasing, $u_{n+1}^* < u_n^*$. Therefore $u_n^*$ approaches a limit $u^* \geq 0$ as $n \to \infty$, which satisfies $d(u^*) = \frac{b_1 e^{-\mu \tau} u^*}{1 - b_2 e^{-\mu \tau}}$. By (4.1), this limit $u^*$ must be zero, and therefore $\limsup_{t \to \infty} u(t) = 0$. The proof of the theorem is complete.

The next theorem establishes that if a positive steady state exists in ecologically sensible circumstances then it is globally stable. Later, we shall consider the situation when $b_2 e^{-\mu \tau} > 1$.

**Theorem 4** Suppose that $b_0 = 0$, $b_1 > 0$, $b_2 e^{-\mu \tau} > 1$ and that there exists $u_m^* > 0$ such that
\[ b_1 u_m e^{-\mu \tau} > d(u_m)(1 - b_2 e^{-\mu \tau}) \quad \text{when } 0 < u_m < u_m^*; \]
\[ b_1 u_m e^{-\mu \tau} < d(u_m)(1 - b_2 e^{-\mu \tau}) \quad \text{when } u_m > u_m^*. \]
(4.6)
Let \( d(u_m) \) be an increasing differentiable function of \( u_m \) satisfying \( d(0) = 0 \) and \( d(u_m) = o(u_m) \) as \( u_m \to 0 \). Then if \( u_0(a) \in C[0,\infty) \), \( u_0(a) \geq 0 \) and \( u_0(a) \neq 0 \), then the solution of (2.10,2.11) satisfies \( u_m(t) \to u_m^* \) as \( t \to \infty \).

**Proof.** The initial data for the problem is the function \( u_0(a), a \in [0,\infty) \), and the evolution initially proceeds according to (2.11), with (2.12) as initial data. Note that our claim is violated at some time, i.e. suppose that there exists \( t \) such that \( u(t) \) violates our claim. We shall consider (4.8) as an initial value problem starting at time \( t_0 \). Let \( u(t) \) be an increasing differentiable function of \( t \), and what we have just shown implies that \( u(t) \) remains increasing for all subsequent time.

As noted previously, since \( b_2 e^{-\mu t} < 1 \) the asymptotic behavior of solutions of (3.3) is the same as the asymptotic behavior of solutions of

\[
u'(m) = b_1 e^{-\mu t} \sum_{j=0}^{n-1} b_2 e^{-j\mu t} u_m(t - (j + 1)\tau) - d(u_m(t)), \quad t \in (n\tau, (n + 1)\tau), \quad n = 1, 2, 3, \ldots
\]

(4.8)

We shall consider (4.8) as an initial value problem starting at time \( t = \tau \), with the function \( u_m(s), s \in [0, \tau] \) treated as the initial data. From our comments above, we may assume that \( \min_{s \in [0, \tau]} u_m(s) > 0 \).

We claim that a comparison principle holds for (4.8), that is to say, if we take three sets of initial data ordered such that \( u_m(s) \leq u_m(s) \leq \overline{u}_m(s), s \in [0, \tau] \), then the corresponding solutions preserve this ordering, i.e. \( u_m(t) \leq u_m(t) \leq \overline{u}_m(t) \) for all \( t > \tau \). The proof of this is similar to that of Theorem 5.1.1 on page 78 of Smith [14] though our situation is not covered by that result so we present here a short self contained argument. Let \( \delta > 0 \) be small and let \( \overline{u}_m^\delta(t) \) satisfy

\[
\frac{d\overline{u}_m^\delta(t)}{dt} = b_1 e^{-\mu t} \sum_{j=0}^{n-1} b_2 e^{j\mu t} \overline{u}_m^\delta(t -(j + 1)\tau) - d(\overline{u}_m^\delta(t)) + \delta, \quad t \in (n\tau, (n + 1)\tau), \quad n = 1, 2, 3, \ldots
\]

(4.9)

and \( \overline{u}_m^\delta(s) = \overline{u}_m(s) + \delta, s \in [0, \tau] \). We claim that \( u_m(t) < \overline{u}_m^\delta(t) \) for all \( t > \tau \). Shrinking \( \delta \) to 0 then gives \( u_m(t) \leq \overline{u}_m(t) \). Certainly \( u_m(\tau) \leq \overline{u}_m(\tau) = \overline{u}_m^0(\tau) - \delta < \overline{u}_m^\delta(\tau) \), so suppose that our claim is violated at some time, i.e. suppose that there exists \( t^* > \tau \) such that
\( u_m(t^*) = \overline{u}_m(t^*) \) and \( u_m(t) < \overline{u}_m(t) \) for all \( t \in [\tau, t^*) \). Then, for the appropriate \( n \),
\[
\frac{d\overline{u}_m(t^*)}{dt} = b_1 e^{-\mu t} \sum_{j=0}^{n-1} b_2 j^{-\mu} \overline{u}_m(t^* - (j + 1)\tau) - d(\overline{u}_m(t^*)) + \delta
\]
\[
> b_1 e^{-\mu t} \sum_{j=0}^{n-1} b_2 j^{-\mu} u_m(t^* - (j + 1)\tau) - d(u_m(t^*)) = \frac{du_m(t^*)}{dt}.
\]
Let \( F(t) = \overline{u}_m(t) - u_m(t) \), then \( F(t) \) has the following properties: \( F(\tau) > 0 \), \( F(t^*) = 0 \), \( F(t) > 0 \) on \( [\tau, t^*) \) and \( F'(t^*) > 0 \). This is a contradiction. The proof that \( u_m(t) \leq u_m(t) \) is similar.

To show that \( u_m(t) \to u_m^* \) it suffices to show that \( \underline{u}_m(t) \to u_m^* \) and \( \overline{u}_m(t) \to u_m^* \) as \( t \to \infty \), where \( \underline{u}_m(t) \) and \( \overline{u}_m(t) \) are comparison functions that satisfy (4.8) subject to the initial conditions
\[
\underline{u}_m(s) = \epsilon, \quad s \in [0, \tau], \quad \text{where} \quad 0 < \epsilon < \min(u_m^*, \min_{\xi \in [0, \tau]} u_m(\xi)),
\]
\[
\overline{u}_m(s) = K, \quad s \in [0, \tau], \quad \text{where} \quad K > \max(u_m^*, \max_{\xi \in [0, \tau]} u_m(\xi)).
\]
(4.10)

Recall that \( \min_{\xi \in [0, \tau]} u_m(\xi) > 0 \), by (4.7). The need for one further smallness constraint on \( \epsilon \) will become apparent below. We shall show that \( u_m(t) \) is monotone increasing for all \( t \geq \tau \), and this will be achieved via the method of steps, starting with \( t \in (\tau, 2\tau) \). For a time \( t \in (\tau, 2\tau) \), choose \( h > 0 \) sufficiently small that \( t + h \in (\tau, 2\tau] \) and such that \( \underline{u}_m(\tau + h) - \underline{u}_m(\tau) \geq 0 \). The latter is possible because
\[
\underline{u}_m'(\tau) = b_1 e^{-\mu \tau} \underline{u}_m(0) - d(\underline{u}_m(\tau)) = b_1 e^{-\mu \tau} \epsilon - d(\epsilon) > 0
\]
for sufficiently small \( \epsilon \), since \( d(u_m) = o(u_m) \) as \( u_m \to 0 \). Let
\[
w_h(t) = \underline{u}_m(t + h) - \underline{u}_m(t).
\]
Then, for \( t \in (\tau, 2\tau) \),
\[
w_h'(t) = b_1 e^{-\mu t} \underbrace{[\underline{u}_m(t + h - \tau) - \underline{u}_m(t - \tau)]}_{=\epsilon-\epsilon=0} - [d(\underline{u}_m(t + h)) - d(\underline{u}_m(t))]
\]
\[
= -w_h(t)d'(\theta(t, h))
\]
where \( \theta(t, h) \) is some function arising from an application of the mean value theorem. Also, \( w_h(\tau) \geq 0 \). Thus \( w_h(t) \geq 0 \) for all \( t \in (\tau, 2\tau) \). Letting \( h \to 0 \), we deduce that \( w_h(t) \geq 0 \) for \( t \in (\tau, 2\tau) \), and this can be extended to \( t \in (\tau, 2\tau) \) by continuity.

For \( t \in (2\tau, 3\tau) \), we argue that \( \underline{u}_m'(t) \geq 0 \) again by using the function \( w_h(t) \) for sufficiently small \( h > 0 \), as follows, using (4.8) with \( n = 2 \):
\[
w_h(t) = b_2 b_1 e^{-2\mu t} \underbrace{[\underline{u}_m(t + h - 2\tau) - \underline{u}_m(t - 2\tau)]}_{=\epsilon-\epsilon=0} + b_1 e^{-\mu t} \underbrace{[\underline{u}_m(t + h - \tau) - \underline{u}_m(t - \tau)]}_{\geq 0 \text{ because } t-\tau, t+h-\tau \in (\tau, 2\tau)}
\]
\[
\geq -w_h(t)d'(\theta(t, h)).
\]
Also \( w_h(2\tau) \geq 0 \). Therefore \( w_h(t) \geq 0 \) on \((2\tau, 3\tau)\), and hence also \( u'_m(t) \geq 0 \) on \((2\tau, 3\tau)\). This argument can be continued to deal with all intervals \((n\tau, (n + 1)\tau)\) and therefore all times \( t > \tau \), and we conclude that \( u_m(t) \) is monotone increasing for all \( t > \tau \).

The proof that \( \overline{u}_m(t) \) is monotone decreasing is similar, and from the first step in the process it will become apparent that \( K \) has to be such that \( b_1 e^{-\mu \tau} K < d(K) \). However, the theorem hypotheses assure us that this is automatically true for any \( K \) consistent with (4.10).

We have established that \( u_m(t) \) is monotone increasing and bounded above (by \( K \)), and therefore must approach some limit \( \geq \epsilon > 0 \), while \( \overline{u}_m(t) \) is monotone decreasing and is bounded below (by \( \epsilon \)). These functions must approach some strictly positive limit, which must be an equilibrium of (4.8). Thus \( \lim_{t \to \infty} u_m(t) = \lim_{t \to \infty} \overline{u}_m(t) = u^*_m \). Hence also \( \lim_{t \to \infty} u_m(t) = u^*_m \). The proof is complete. \( \square \)

In the next theorem we show that if \( b_2 e^{-\mu \tau} > 1 \) then non-trivial solutions grow without bound as \( t \) increases.

**Theorem 5** Suppose that \( b_0 = 0, b_1 > 0 \) and \( b_2 e^{-\mu \tau} > 1 \). Let \( d(u_m) \) be an increasing differentiable function of \( u_m \) satisfying \( d(0) = 0 \) and \( d(u_m) = o(u_m) \) as \( u_m \to 0 \). Then if \( u_0(a) \in C[0, \infty), u_0(a) \geq 0 \) and \( u_0(a) \neq 0 \), then the solution \( u_m(t) \) of (2.10,2.11) grows without bound as \( t \) increases.

**Proof.** Under the hypotheses, we may again assume without loss of generality that \( u_m(t) \) satisfies (4.7). However, the assumption \( b_2 e^{-\mu \tau} > 1 \) implies that the first term in the right hand side of (3.3) does not tend to zero as \( t \to \infty \). However, we may nevertheless state that

\[
u'_m(t) \geq b_1 e^{-\mu \tau} \sum_{j=0}^{n-1} b_2 e^{-j\mu \tau} u_m(t - (j + 1)\tau) - d(u_m(t)), \quad t \in (n\tau, (n + 1)\tau], \quad n = 1, 2, 3, \ldots,
\]

and therefore, again by comparison arguments, it follows that \( u_m(t) \geq u_m(t) \) for all \( t \geq \tau \), where \( u_m(t) \) is the solution of

\[
u'_m(t) = b_1 e^{-\mu \tau} \sum_{j=0}^{n-1} b_2 e^{-j\mu \tau} u_m(t - (j + 1)\tau) - d(u_m(t)), \quad t \in (n\tau, (n + 1)\tau], \quad n = 1, 2, 3, \ldots,
\]

such that \( u_m(s) = \epsilon \) for all \( s \in [0, \tau] \), where \( \epsilon > 0 \) is a suitably small number. For a suitable \( \epsilon \), it can be shown by the same technique as in the proof of Theorem 4 that \( u_m(t) \) is monotone increasing for all \( t > \tau \). However, this time \( u_m(t) \) cannot approach a limit, because the search for a non-zero limit furnishes a divergent geometric series, since \( b_2 e^{-\mu \tau} > 1 \). Hence \( u_m(t) \) grows without bound as \( t \) increases, and therefore so does \( u_m(t) \). \( \square \)

Numerical simulations, carried out using the SIMULINK facility within MATLAB, were carried out to illustrate some of our results. The results of some of these simulations are shown in Figs. 1 and 2.
Figure 1: Simulation of (2.10) showing $u_m(t)$ plotted against $t$, with $d(u_m) = 3u_m^2$, $\tau = 0.5$, $\mu = 0.7$, $b_0 = 0$, $b_1 = 2$, $b_2 = 1.2$. For these values $b_2 e^{-\mu \tau} = 0.84563 < 1$, and Theorem 4 applies. The solution approaches the steady state $u_m \approx 3.04$.

5 Discussion

Neutral delay differential models arise from applications naturally. For example, as we demonstrated here, they can be reduced from a typical structured population model ([5, 2, 3, 12, 13]). They can also appear in general compartmental systems where transition from one compartment to another takes time ([4]) and in a situation where a growing population demands additional resources ([7, 8, 9, 10, 11]). A main reason for their lack of popularity in the literature is the difficulties encountered in their analysis and simulation.

In this paper, we present a global study on the stability of the equilibria in a nonlinear autonomous neutral delay differential population model recently formulated by Bocharov and Hadeler ([5, 2]) via the reduction of a standard structured population model. This model may be suitable for describing the intriguing dynamics of an insect population with long larval and short adult phases such as periodical cicadas ([6, 16]) and the flightless marine midges ([15]). We circumvent the usual difficulties associated with the study of the stability of a nonlinear neutral delay differential model by transforming it to an appropriate non-neutral nonautonomous delay differential equation of unbounded delay. In the natural case that no juveniles give birth, we show that the biologically meaningful solutions are always positive and bounded provided that the time adjusted instantaneous birth rate at the time of maturation ($b_2 e^{-\mu \tau}$) is less than 1. We also present some sharp results on the global stability of the extinction and positive equilibria obtained by the method of iteration. This
Figure 2: Simulation of (2.10) showing $u_m(t)$ plotted against $t$, with $d(u_m) = 3u_m^2$, $\tau = 0.5$, $\mu = 0.7$, $b_0 = 0$, $b_1 = 2$, $b_2 = 1.46$. For these values $b_2e^{-\mu\tau} = 1.02884 > 1$. Theorem 5 applies and the solution grows without bound.

work illustrates the possibility of a good understanding of a well formulated neutral delay differential model.

A surprising insight gained from our analysis is the fact that if the time adjusted instantaneous birth rate at time of maturation ($b_2e^{-\mu\tau}$) is greater than 1, then the population will grow unboundedly regardless of the population death process. This, of course, will not happen in a well formulated delay differential model without neutral terms.

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References


