

An alternative formulation for a delayed logistic equation [☆]

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Abstract

We derive an alternative expression for a delayed logistic equation, assuming that the rate of change of the population depends on three components: growth, death, and intraspecific competition, with the delay in the growth component. In our formulation, we incorporate the delay in the growth term in a manner consistent with the rate of instantaneous decline in the population given by the model. We provide a complete global analysis, showing that, unlike the dynamics of the classical logistic delay differential equation (DDE) model, no sustained oscillations are possible. Just as for the classical logistic ordinary differential equation (ODE) growth model, all solutions approach a globally asymptotically stable equilibrium. However, unlike both the logistic ODE and DDE growth models, the value of this equilibrium depends on all of the parameters, including the delay, and there is a threshold that determines whether the population survives or dies out. In particular, if the delay is too long, the population dies out. When the population survives, i.e., the attracting equilibrium has a positive value, we explore how this value depends on the parameters. When this value is positive, solutions of our DDE model seem to be well approximated by solutions of the logistic ODE growth model with this carrying capacity and an appropriate choice for the intrinsic growth rate that is independent of the initial conditions.

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0. Introduction

The classical logistic equation was introduced by Verhulst (1838), to describe population growth in a limited environment, and “rediscovered” in the 1920s by Pearl and Reed (1920). Subsequently, many researchers interested in population dynamics studied these equations, trying to identify the parameters for various populations. For example, this was done for human populations in the USA by Pearl and Reed (1930) and Pearl et al. (1940), and

in Canada by MacLean and Willard Turner (1937). To read about how this equation fits into the history of population ecology, see Kingsland (1982). The logistic equation also plays an important role in models involving more than one interacting population, since it is often assumed that the growth rate of one or more of the populations satisfy the logistic equation in the absence of the other populations. See for example the classical models for predator–prey interactions or for competition between species in any textbook on mathematical models in biology (e.g., Edelstein-Keshet, 1988).

Hutchinson (1948) pointed out that the logistic equation would be inappropriate for the description of population growth in the case where there is a lag in some of the processes involved. Although a short remark in a much longer paper about circular causal systems in ecology, the formulation for the delayed logistic equation he proposed has been the object of much attention from the mathematical community. Known as the *delayed logistic equation*, *Hutchinson’s equation*, or under a change of variables,

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Wright's equation, it is one of the first examples of a delay differential equation (DDE) that has been thoroughly examined (see for example Cushing, 1977; MacDonald, 1978; Nisbet and Gurney, 1982; Gopalsamy, 1992 and Kuang, 1993 and the references within). Its study coincides with the development of the theory of delay differential equation (DDE), and it is one of the first examples of the potential for the nature of the solutions of a DDE to be very different, when compared to its ordinary differential equation (ODE) counterpart. Indeed, while the solutions of the logistic ODE all converge monotonically to a positive equilibrium, with value equal to the parameter interpreted as the carrying capacity of the environment, the solutions of this “classical” logistic DDE oscillate about this carrying capacity. These oscillatory solutions are either damped, eventually converging to the carrying capacity, or sustained, i.e., nontrivial periodic solutions.

While the quest for the mathematical understanding of the solutions to this classical logistic DDE has proved fundamental in the development of the theory of DDEs, it was thought by some that this oscillatory behavior limited its usefulness in the field of ecology where intrinsically oscillating populations seem to be infrequently observed. Hutchinson, in fact, argued that this lack of observed oscillatory behavior in nature is likely the consequence of natural selection, with oscillating populations prone to extinction if some catastrophic event takes place when the population is at a minimum. To quote Hutchinson (1948),

In spite of some glaring exceptions, it seems probable that an internally oscillating population is less likely to survive indefinitely than a stable one. If this be so, the time lags will be reduced to minimal values.

There are, however, many examples of processes in the biological world that involve significant delays. The most obvious ones include the time between fertilization and birth in the case of sexual reproduction, the time between initiation of cellular division and effective division in the case of mitosis, and the time required for digestion in the case of consumption of nutrient and its conversion to viable biomass. Should these time lags be ignored in a logistic-type framework, because the models seem to lead to oscillations that are not observed?

The mathematical community was quick to pick up on the exciting new problems stemming from the inclusion of time delays in the logistic equation. However, Hutchinson's reservations about the use of delays in such population models made a lasting impression on the ecological community. As well, Nisbet and Gurney (1982) criticized the classical logistic DDE model because its derivation was not based on clearly defined birth and death processes. Since its introduction, an assortment of other models for single population growth involving delays have been derived and investigated. See Ruan (2006) for an excellent survey describing many of these models, including as well, a discussion of models involving distributed delays in the

form of integro-differential equations. We will restrict our discussion here to logistic-type models involving constant (or discrete) time lags.

In this paper, we provide a derivation for an alternative form of a logistic DDE model in which the rate of change in the population involves a growth rate that depends on the population density at an earlier time, but the rate of decline in the population is assumed to be instantaneous. An important aspect of our derivation, is that we take the actual dynamics of the rate of decline of the population given by the model into consideration when determining how to incorporate the delay in the growth term. Although we do not derive our model from an age-structured model, it has the form suggested by such derivations. However, it is also appropriate when the delay modelled is the time taken for conversion of nutrient consumed to viable biomass. Our model reduces to the logistic ODE model when the delay is set to zero and to a discrete delayed exponential model when one of the parameters is set to zero. (As one would expect, the reciprocal of this parameter is related to the carrying capacity of the environment.)

We compare the dynamics of this alternative form of the logistic DDE with the dynamics of both the classical logistic ODE and DDE, and discuss how both the form and the dynamics of our model compare with other related models. The dynamics of our model are unusual in that convergence is to an equilibrium with value depending on the delay. As might be expected, if the delay is too long, this model predicts that the population dies out. A threshold giving the interface between extinction and survival is determined in terms of parameters in the model.

This paper is organized as follows. In Section 1, we review the main results concerning the dynamics of the classical logistic ODE and DDE equations and describe some other closely related models. In Section 2, we provide a derivation of an alternative logistic DDE. We discuss the global dynamics of this model in Section 3 and indicate how the asymptotic outcome depends on the parameters in the model. However, we leave the technical aspects of the analysis including the proofs to appendices. We also prove that a more general model of similar form has similar dynamics. Finally, we comment on our findings in a Discussion (Section 4) where we compare our model and its dynamics with other related models in the literature and discuss the significance of these results with respect to including delays in population models.

1. Classical logistic type models and other closely related models

1.1. The classical logistic ODE

The classical nondelayed logistic ODE model is given by

$$N'(t) = rN(t) \left(1 - \frac{N(t)}{K} \right). \quad (1)$$

The parameter r denotes the intrinsic growth rate, and K denotes the carrying capacity of the environment. An extensive and captivating review of the history of the logistic equation is given in [Kingsland \(1982\)](#). The analysis of (1) can be found in most undergraduate textbooks on ODEs. Equation (1) is easily solved as either a separable or a Bernoulli equation, with solution given by

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}}, \quad (2)$$

where $N_0 := N(0)$, the initial population size. Recall that all autonomous scalar first-order ODEs have monotone solutions. From either the equation itself or from the given solution, it is easy to see that $N(t)$ increases monotonically to K , if $N_0 < K$, decreases monotonically to K if $N_0 > K$, or remains equal to K for all time if $N_0 = K$.

Typical solutions for a fixed r and K , but a variety of initial conditions look just like those depicted later, in [Fig. 2](#), although the solutions for that figure were found by solving the equation given by our alternative formulation of a logistic DDE.

1.2. The classical logistic DDE

[Hutchinson \(1948\)](#) remarked that for (1) to make sense, the biological mechanisms under consideration must operate so rapidly that the time lag between the instant where a given value N is reached and the instant when the effective reproductive rate $1 - N/K$ is updated, is negligible. Arguing that oscillations have been observed in some *Daphnia* populations, he proposed the following equation:

$$N'(t) = rN(t) \left(1 - \frac{N(t-\tau)}{K} \right). \quad (3)$$

It was derived from (1) by simply assuming that the net per capita rate of change N'/N might depend on the state of the system τ time units in the past.

Another derivation of (3) was given by [Cunningham \(1954\)](#). He assumed that a population whose per capita rate of change would normally be constant (i.e., $N'/N = A$), is subject to additional effects that decrease the rate of growth A . If these effects are functions of the state of the population at the time $t - \tau$ (the previous generation, for example), then one has the equation

$$N'(t) = [A - BN(t-\tau)]N(t).$$

Note that this equation can be obtained from (3) by setting $A = r$ and $B = r/K$.

We will refer to (3) as the classical logistic DDE.

1.3. Equivalent forms of the classical logistic DDE

As already mentioned, the classical logistic DDE is intimately linked with the development of the theory of DDEs. One of reasons for this, is that it is easy to transform (3) into an equation that has a very simple form. For example, (3) has been studied using a change of

variables that considers time in units of τt and transforming it into an equation with time lag equal to one. In particular, [Kakutani and Markus \(1958\)](#) obtained a simplified form of (3) by also transforming the state variable,

$$y(t) = \frac{r\tau}{K} N(\tau t).$$

This gives the equation

$$y'(t) = \{r\tau - y(t-1)\}y(t).$$

[Wright \(1955\)](#) used the state variable

$$y(t) = \frac{N(\tau t)}{K} - 1,$$

instead, obtaining the equation

$$y'(t) = -r\tau\{1 + y(t)\}y(t-1).$$

Letting $a = r\tau$ leads to the classical Wright's equation,

$$y'(t) = -ay(t-1)\{1 + y(t)\}. \quad (4)$$

Historically, it is the form (4) given by Wright that has been the object of most work. Part of the reason lies perhaps, in the fact that, as remarked by Wright himself, this equation appears in many different contexts.

1.4. Dynamics of the classical logistic DDE

In this section we summarize results concerning the basic dynamics of (3). This summary is not meant to be comprehensive, but will be helpful when we compare the dynamics of (3) with the behavior of the model that we propose. Although most of the results here were originally formulated in the context of Wright's equation (4), since our focus here is on the delayed logistic equation, for consistency we use the notation in (3).

In order for the DDE equation to be well-posed, a suitable initial function must be supplied, defined on an interval with length equal to the time lag. In this case, this is done by assuming

(H1) on the interval $[-\tau, 0]$, there is a function $\phi \in C([-\tau, 0], \mathbb{R}_+ \setminus \{0\})$ such that $N(t) = \phi(t)$ for all $t \in [-\tau, 0]$.

The following result summarizes the local behavior of solutions of (3). The proof of (i) and (ii) is quite standard and can be found in [Ruan \(2006\)](#). The proof of (iii) can be found in [Kaplan and Yorke \(1975\)](#).

Theorem 1.1. Consider (3) and assume the initial data satisfies (H1).

- (i) If $r\tau \in (0, \pi/2)$, then K is a locally asymptotically stable equilibrium.
- (ii) At $r\tau = \pi/2$ there is a supercritical Hopf bifurcation of the equilibrium K , giving rise to an asymptotically stable periodic orbit that exists for each choice of $r\tau > \pi/2$.

- (iii) If $r\tau > \pi/2$, then K is unstable, and there is an annulus A in the $(N(t), N(t-\tau))$ -plane whose boundary is a pair of orbits of slowly oscillating periodic solutions. The annulus A is an asymptotically stable invariant set.

Wright (1955) proved that if $0 < r\tau < \frac{37}{24}$, the equilibrium point K attracts all solutions with positive initial data and conjectured that this holds for $0 < r\tau < \pi/2$. The conjecture remains an open problem.

1.5. Other closely related models

For a very nice recent survey of differential delay equations modelling single species growth, we once again refer the reader to Ruan (2006). Here, we only discuss several models that are very closely related to the model that we will derive in the next section.

Kaplan and Yorke (1975) considered a general equation of the form

$$y'(t) = f(y(t-1)),$$

where $f(0) = 0$, $f : \mathbb{R} \rightarrow \mathbb{R}$ is continuously differentiable and $f'(y) < 0$ for all $y \in \mathbb{R}$. To write (3) in this form, use the change of variable

$$y(t) = \ln\left(\frac{N(\tau t)}{K}\right) \quad (5)$$

and the function $f(v) = r\tau(1 - e^v)$.

Walther (1995) considered the more general equation

$$y'(t) = -\mu y(t) + f(y(t-1)) \quad (6)$$

and carried out the most complete study to date of the nature of the attractor. He assumed the parameter μ to be nonnegative and the function f to be differentiable and satisfy $f(0) = 0$, $f'(\xi) < 0$ for all ξ , and $\xi f(\xi) < 0$ for $\xi \neq 0$. Using the change of variables (5) with the function $f(v) = r\tau(1 - e^v)$, and $\mu = 0$, puts (3) in this form.

Note that even though (6) is a very general model, the model that will be derived in the next section is not of this form.

Seifert (1987) considered the Volterra logistic DDE

$$N'(t) = N(t)\{a - bN(t) - N(t-1)\}. \quad (7)$$

Eq. (7) reduces to Wright's equation (4) if $b = 0$. If $b > 1$, any solution of (7) with positive initial data satisfies $\lim_{t \rightarrow \infty} N(t) = a/(b+1)$. For $b < 1$, for certain parameter combinations (a, b) , a Hopf bifurcation yields nonconstant periodic solutions near $N(t) = a/(b+1)$.

Another form, studied by Györi (1989), is the equation with n delays defined for $t \geq 0$ by

$$N'(t) = N(t) \left(a - \sum_{j=1}^n b_j N(t - \tau_j) \right).$$

This equation is meant to describe a situation where several of the processes affecting the population occur with (different) time delays. As for (3) or (7), this equation has

periodic solutions. In this case, oscillatory solutions occur for $\tau = \max_i \tau_i > \pi/2$.

Beddington and May (1975) analysed the DDE:

$$N'(t) = -dN(t) + bN(t-\tau) \left[1 - \frac{N(t-\tau)}{K} \right] \frac{N(t-\tau)}{N(t-\tau) + X_0},$$

that includes an Allee effect, which they described as an approximation to a fully age-structured model first discussed in Oster and Takahashi (1974) and Auslander et al. (1974). This model approaches

$$N'(t) = bN(t-\tau) \left[1 - \frac{N(t-\tau)}{K} \right]$$

if one lets $d \rightarrow 0$ and $X_0 \rightarrow 0$.

In Blythe et al. (1982) a formal derivation from the equations for an age-structured population is given to obtain a model of the general form

$$N'(t) = R(N(t-\tau)) - D(N(t)). \quad (8)$$

They then consider special cases, in particular,

$$N'(t) = PN(t-\tau)e^{-N(t-\tau)} - mN(t)$$

and

$$N'(t) = \frac{PN(t-\tau)}{1 - cN(t-\tau)^d} - mN(t),$$

but they do not explain how the function $R(N(t-\tau))$ was chosen, in either case. The model we derive in the next section is of the form (8). In our derivation, we assume that it is those individuals who were around at time $t-\tau$ who must survive to grow at time t . Under this assumption, we motivate how to choose the function $R(N(t-\tau))$ so that it is consistent with the function $D(N(t))$.

Rodríguez (1998) comes closest to our approach. He talks about the preadult survival rate and solves an ODE, similar to the one we solve to obtain a model of the form

$$N'(t) = N(t-\tau)f(N(t-\tau))s(N(t-\tau)f(N(t-\tau))) - mN(t). \quad (9)$$

The function s is meant to model the probability that a newborn reaches maturity. He assumes that the function f decreases exponentially. He points out that f has no mechanistic justification in the case of competition for food in adults, but might model the crowding effect in adults. Thus, the ODE that he solves is not related to the rate of decline in (9). Once he obtains the model, he carries out simulations that indicate that for large delays the system has limit cycles, but does no local or global analysis.

2. Derivation of an alternative model of delayed logistic growth

In this section we derive an alternative logistic DDE. We assume that growth rate of the population is not proportional to the current population size, but rather depends on the population size some fixed τ time units in the past. However, the rate of decline of the population

depends on the current population. We incorporate the delay in the growth rate in a manner consistent with the rate of decline of the population given by the actual DDE itself.

We begin by assuming that the rate of change of the population depends on three components: growth, death, and intraspecific competition (crowding or direct interference). By the decline rate we mean the death and the intraspecific competition rates together. We assume that the decline rate is instantaneous and that the death rate is given by a linear term whereas the intraspecific competition rate is given by the quadratic term.

With this in mind, we rewrite the classical logistic ODE model (1), using the following notation:

$$N'(t) = \gamma N(t) - \mu N(t) - \kappa N^2(t), \quad (10)$$

where γ , μ , and κ are nonnegative constants. To obtain (1), set

$$r = \gamma - \mu \quad \text{and} \quad K = (\gamma - \mu)/\kappa. \quad (11)$$

In (1), the decline rate is given by $\mu N(t) + \kappa N^2(t)$ and the growth rate is given by $\gamma N(t)$. Both are assumed to depend on the present population size. We continue to assume that the decline rate is instantaneous, but we now assume that the growth rate is proportional to the number of individuals in the population $t - \tau$ time units in the past, that manage to survive until time t .

To obtain an equation that describes how many individuals alive at time $t - \tau$ are still alive at time t , we solve the following first order ODE for $N(t)$ as a function of $N(t - \tau)$:

$$N'(t) = -\mu N(t) - \kappa N^2(t).$$

Using the technique of separation of variables and integrating both sides from $t - \tau$ to t , it follows that

$$\int_{N(t-\tau)}^{N(t)} \frac{1}{\mu N + \kappa N^2} dN = - \int_{t-\tau}^t dt,$$

and hence

$$N(t) = \frac{\mu N(t - \tau)}{\mu e^{\mu\tau} + \kappa(e^{\mu\tau} - 1)N(t - \tau)}. \quad (12)$$

Since we assume that growth in the population at time t is proportional to those individuals alive at time $t - \tau$ who survive until time t , we replace $N(t)$ in the monomial with coefficient γ in (10) by (12), to obtain our *alternative logistic DDE model* with fixed (or discrete) time delay, τ :

$$N'(t) = \frac{\gamma \mu N(t - \tau)}{\mu e^{\mu\tau} + \kappa(e^{\mu\tau} - 1)N(t - \tau)} - \mu N(t) - \kappa N^2(t). \quad (13)$$

If $\tau = 0$, (13) reduces to (1). It is interesting to note that if $\kappa = 0$, then (10) is actually a model of exponential growth, and as expected, setting $\kappa = 0$ in (13), we obtain the discrete delayed exponential model

$$N'(t) = \gamma N(t - \tau)e^{-\mu\tau} - \mu N(t). \quad (14)$$

As is customary, one has to provide initial data over an interval of length τ . Considering the assumption under

which this model has been derived, it only makes sense to consider initial data that is positive over the entire interval. Under this assumption, solutions of both (13) and (14) remain positive. Since (14) is a linear first order scalar DDE, it is easily determined that (e.g., see Kuang, 1993), if $\tau > (1/\mu) \ln(\gamma/\mu)$ then all solutions of (14) approach zero asymptotically and hence the population dies out, whereas if this inequality is reversed, then all solutions blow up.

We show later that solutions of (13) remain bounded and, as in the logistic ODE model, do not oscillate. However, solutions converge to a positive value if $0 \leq \tau < \frac{1}{\mu} \ln(\frac{\gamma}{\mu})$ or the population dies out if this inequality is reversed.

3. Dynamics of the alternative logistic DDE

In this section, we state our results for model (13) as well as for a more general model of similar form. Proofs are postponed to the appendices.

Proposition 3.1. *Let $X := C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$. Then for any given $\phi \in X$, there is a unique solution of (13) satisfying $N(s) = \phi(s)$, $s \in [- \tau, 0]$, and the solution remains positive and bounded, and hence is well-defined.*

It is easy to check that a threshold

$$\tau_H := \frac{1}{\mu} \ln\left(\frac{\gamma}{\mu}\right), \quad (15)$$

exists, and if

$$\mu e^{\mu\tau} \geq \gamma \quad \text{or equivalently } \tau \geq \tau_H,$$

then Eq. (13) admits only the trivial equilibrium $N = 0$, but if

$$\mu e^{\mu\tau} < \gamma \quad \text{or equivalently } \tau < \tau_H,$$

besides the trivial equilibrium, Eq. (13) admits a unique positive equilibrium,

$$\bar{N} = \frac{\sqrt{\mu^2 + 4\alpha\gamma\mu} - \mu(1 + 2\alpha)}{2\alpha\kappa}, \quad (16)$$

where $\alpha = e^{\mu\tau} - 1$. We call this value the *delayed carrying capacity*.

The following theorem characterizes the global behavior of solutions to Eq. (13).

Theorem 3.2. *Consider Eq. (13).*

- (i) *For initial data $\phi \in C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$ such that $\phi(t) < \bar{N}$ for all $t \in [- \tau, 0]$, $N(t) < \bar{N}$ for all $t \geq 0$ and when $\phi(t) > \bar{N}$ for all $t \in [- \tau, 0]$, then $N(t) > \bar{N}$ for all $t \geq 0$.*
- (ii) *If $\tau > \tau_H$ holds then the trivial solution $N(t) = 0$ of (13) is globally asymptotically stable with respect to nonnegative initial data.*
- (iii) *If $0 \leq \tau < \tau_H$ holds then the positive equilibrium \bar{N} of (13) is globally asymptotically stable with respect to positive initial data.*

In fact, using basically the same proof, given in the appendix, the following result concerning a more general model can be proved.

Theorem 3.3. Consider $N'(t) = R(N(t - \tau)) - D(N(t))$, where $R: \mathbb{R}_+ \rightarrow \mathbb{R}_+$, $D: \mathbb{R}_+ \rightarrow \mathbb{R}_+$, $R(0) = D(0) = 0$, and R and D are both continuously differentiable functions. If $(d/dy)R(y) > 0$ and all solutions are bounded, then we have generic convergence to equilibrium, and hence there are no sustained oscillations.

In addition, assume that $R(y) = yr(y)$ and $D(y) = yd(y)$, where $r(y) > 0$ and $d(y) > 0$ for all $y \geq 0$, both $r(y)$ and $d(y)$ are continuously differentiable, $(d/dy)yr(y) > 0$, and $r(y) - d(y)$ is a strictly decreasing function of y for $y > 0$.

- (i) There is at most one positive equilibrium.
- (ii) For initial data $\phi \in C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$ such that $\phi(t) < \bar{N}$ for all $t \in [- \tau, 0]$, $N(t) < \bar{N}$ for all $t \geq 0$, and when $\phi(t) > \bar{N}$ for all $t \in [- \tau, 0]$, then $N(t) > \bar{N}$ for all $t \geq 0$.
- (iii) If $N = 0$ is the only equilibrium point, then it is globally attractive with respect to all solutions with nonnegative initial data.
- (iv) If there is a positive equilibrium point, then it is the only positive equilibrium and it is globally attractive with respect to all solutions with positive initial data.

By Theorem 3.2, the behavior of solutions to (13) is determined by the relative values of τ and τ_H , where τ_H depends on μ and γ . Solutions approach \bar{N} asymptotically if $0 < \tau < \tau_H$, but die out if $\tau > \tau_H$ and in this case, neither sustained oscillations nor damped oscillations about \bar{N} are possible. This behavior is different from the behavior of the classical delayed logistic equation (3), where the population never dies out and the value of the nontrivial equilibrium does not depend on parameters other than K . It is therefore important to study the dependence of \bar{N} , when it exists, on the parameters of the system.

First, notice that $\lim_{\tau \rightarrow 0^+} \bar{N} = (\gamma - \mu)/\kappa$, which corresponds to the carrying capacity K for the classical logistic DDE (3) using the transformation given by (11).

Fig. 1 illustrates the effect of varying τ on the solutions of (13). The delay τ is allowed to vary between 0 and 1.4 in steps of 0.1. All other parameters are fixed: $\gamma = 1$, $\mu = \frac{1}{2}$ and $\kappa = 0.005$. The top curve corresponds to the case $\tau = 0$, i.e., the ODE case. In this case the classical carrying capacity is $K = (\gamma - \mu)/\kappa = 100$. Then, since

$$\frac{\partial \bar{N}}{\partial \tau} = -\frac{\mu^2 e^{\mu\tau} (\sqrt{\mu} - \sqrt{\mu + 4\gamma e^{\mu\tau}} - 4\gamma)^2}{4\sqrt{\mu(\mu + 4\gamma e^{\mu\tau} - 4\gamma)}(e^{\mu\tau} - 1)^2 \kappa} < 0,$$

the value of the equilibrium \bar{N} decreases as τ increases. Each dash-dotted solutions tend to \bar{N} (which is globally asymptotically stable in each case). As τ is further increased, \bar{N} becomes negative and the only biologically relevant equilibrium is zero, towards which the dotted solution curve tends (albeit very slowly).

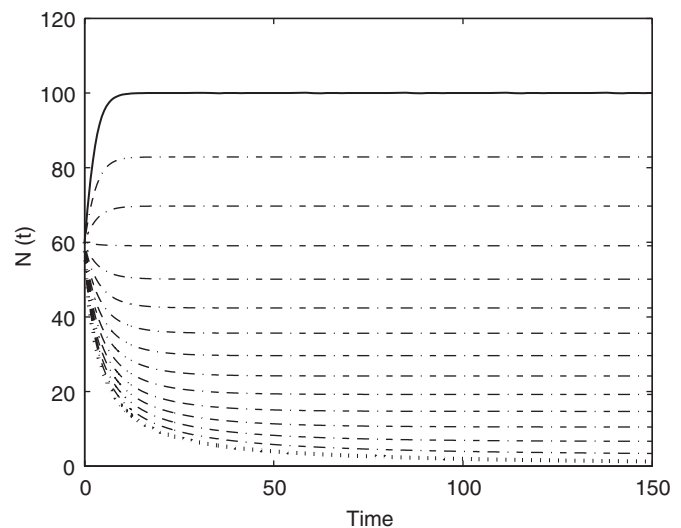


Fig. 1. This figure illustrates how the value of the positive equilibrium \bar{N} decreases as the time lag τ increases from 0 to 1.4. $N(t)$ versus time is shown for increasing values of τ (by steps of 0.1), with $\gamma = 1$, $\mu = 0.5$ and $\kappa = 0.005$. For these values the threshold $\tau_H = 2 \ln(2) \simeq 1.39$. The top curve (solid), illustrates the ODE case ($\tau = 0$). The bottom curve (dotted), illustrates $\tau = 1.4 > \tau_H$, and so this solution approaches zero as do all solutions for which $\tau > \tau_H$. The dash-dotted curves correspond to $0 < \tau < \tau_H$, where $\bar{N} > 0$ is globally asymptotically stable.

It is clear that \bar{N} is monotonically increasing in γ . Finally, the delayed carrying capacity is a monotone decreasing function of μ , as shown in Appendix C.

4. Discussion

Although the original motivation of Hutchinson (1948) for introducing time delay in the classical logistic ODE, to obtain what we have been calling the classical logistic DDE (3), was to try to account for oscillations observed in *Daphnia* populations, on the grounds that “fertility of the pathogenetic female is influenced in part by past population densities,” he also suspected that internally oscillating populations had a disadvantage and were less likely to survive. He thus concluded, since the model he proposed had significant oscillations if time lags were large, that time lags in nature “will be reduced to minimal values.”

Hutchinson’s model (3) has been criticized for several reasons, as described in the Introduction. We criticize this model further. If one considers the total rate of change given by this model, its terms should also be interpretable. In fact, Hutchinson’s aim was to model the effect of delay on the fertility rate, but instead, in (3), it is the rate of decline, not the growth rate that involves the delay. As well, the rate of change involves a cross term of the form $N(t)N(t - \tau)$ that is difficult to justify, since there can be no direct interaction between populations at time t and at time $t - \tau$. As well, the dynamics predicted by the model are suspect. One would expect that if a delay in a population is too long, that population would not be able to avoid

extinction. However, the only effect of increasing the delay in model (3), is to replace the positive equilibrium by a globally attracting positive periodic orbit. Of course, the amplitude of the periodic orbit gets larger as the delay gets larger, and so the solution spends a substantial amount of time at very small population levels. Thus, the model does predict that for large enough delays, stochastic effects, not included in the model, would likely result in the extinction of the population. However, it would be more satisfying if the model predicted that large enough delays actually resulted in the stability of the extinction equilibrium, $N = 0$, since in the case that the delay is too long, the rate of growth would not be able to keep up with the rate of decline. It would then also make sense that in the case of more moderate delays, the equilibrium population level should decrease as the delay is increased and in fact should depend on other species specific parameters.

In this paper we derived what we have been calling an alternative logistic DDE under clearly indicated assumptions to model the delay in growth due to such processes as digestion and/or cell division. Instead of assuming that the *net per capita rate of change* depends on the population τ time units in the past, as Hutchinson did, we derive a logistic-like model considering the *total rate of change* of the population, and ensuring that the delayed growth rate is consistent with the rate of decline given by the model. Although we did not derive our model using the equations for an age-structured population, the model we obtained is of the general form (8), suggested by such derivations. However, we also motivate how to choose the growth term so that it depends on the delay in a manner that is consistent with the term modelling the decline in the population. Eq. (13) takes into account that if the present population growth depends on the population level τ time units in the past, then growth at time t can only depend on those individuals present at time $t - \tau$ that survive to time t . Our model reduces to the classical logistic ODE model when the time delay is ignored, i.e., $\tau = 0$.

We were able to carry out a complete global analysis of our alternative logistic DDE model (13). In Theorem 3.2 we state that a threshold $\tau_H = (1/\mu) \ln(\gamma/\mu)$ exists, and if $0 \leq \tau < \tau_H$ solutions with positive initial data converge to the delayed carrying capacity, $\tilde{N} > 0$, but if $\tau > \tau_H$, they converge to the trivial equilibrium $N = 0$ and the population dies out. Hence, no sustained oscillations are possible. The parameters μ , γ and τ also influence the value of \tilde{N} . This equilibrium value increases as γ increases, but decreases as τ and/or μ increase. Thus, even though the delay in our model does not produce oscillations, delays are *harmful* in that the longer the delay, the lower the value of the delayed carrying capacity, and sufficiently long delays result in the extinction of the population.

Usually one thinks of the carrying capacity of the environment as the total capacity of a population that the environment can support. So you might ask, why should this depend on the length of the delay, τ ? Think of two identical populations, except for the fact that one takes a

longer time to digest or have its cells divide. Why would the carrying capacity be lower for the population with the longer delay? In the case of digestion we distinguish between viable biomass and nonviable biomass. Once nutrient is absorbed, by conservation of mass the total mass of the organism increases. However, only once the nutrient is digested does the viable biomass increase, that part of the mass that will allow increased growth and/or consumption. For example, once nutrient is completely digested by an organism, the organism might develop more receptors for absorbing nutrient. In the case of cell division, if cells take longer to divide, then they must get either bigger or more dense before dividing, due to more stored nutrient. For example, if $N(t)$ is the number of cells in the population, and τ is the time between the beginning of the G_2 phase and the end of cytokinesis, then the larger τ , the more growth of the cells before division. Since cells are either growing or dividing (multiplying), a longer delay results in a smaller number of (potentially larger) cells. Our model predicts that the delayed carrying capacity is also a decreasing function of μ and κ , but an increasing function of γ .

In part (iii) of Theorem 3.2, it was shown that, for initial data that remains less than \tilde{N} for all $t \in [-\tau, 0]$, $N(t)$ remains smaller than \tilde{N} for all $t \geq 0$ and when the initial data remains larger than \tilde{N} for all $t \in [-\tau, 0]$, then, $N(t)$ remains larger than \tilde{N} for all $t \geq 0$, and so, in these cases, there are no overshoots or undershoots of the positive equilibrium value \tilde{N} . This is illustrated in Fig. 2.

This graph should look familiar, since it looks exactly like the graph that would be expected if one solves the classical logistic ODE model for a fixed K and r and various initial conditions. Although the graph in Fig. 2 was produced by numerically solving (13) with $\gamma = 1$, $\mu = 0.5$,

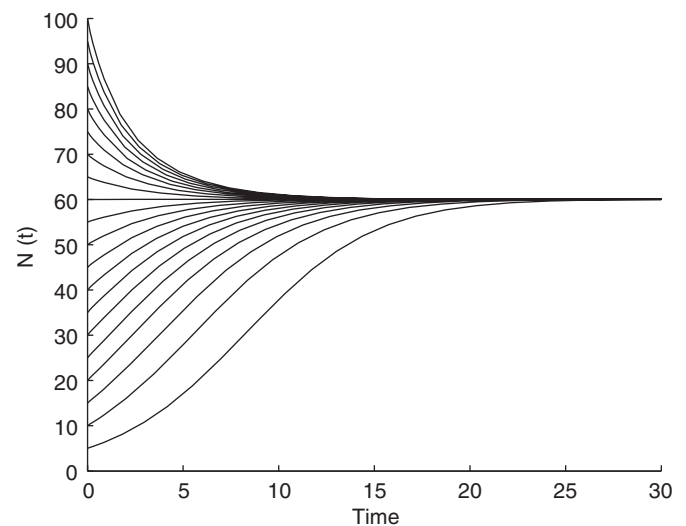


Fig. 2. $N(t)$ versus time, for constant initial data $\phi(s) \equiv \phi$ on $[-\tau, 0]$ increased from 5 to 100 by steps of 5. Parameter values are $\gamma = 1$, $\mu = 0.5$, $\kappa = 0.005$, and $\tau = 0.29$, resulting in $\tilde{N} \simeq 60$. This graph is almost indistinguishable from the graph that would be found by solving (1) using $K = 60$ and $r = 0.3$.

and $\tau = 0.29$, if instead we chose $K = \bar{N}$ and $r = 0.3$ and solved (1), the graph would actually be virtually indistinguishable to the eye. In fact, for $r = 0.294$ and $K = \bar{N}$, if one finds the explicit solution of (1) using (2), and uses this as an approximation of the solution for (13), the left- and right-hand side of (13) agree to at least three decimal places for $t \in [0, 40]$.

When discrete delay is included in a chemostat model using ideas based on the net per capita rate of change, the way that Hutchinson derived the classical logistic DDE model, for sufficiently large delay the solutions also exhibit sustained oscillations (see for example MacDonald, 1978). However, when reasoning similar to the way that the alternative logistic DDE model is derived is used, one obtains the model studied in Wolkowicz and Xia (1997), where it is proved that no sustained oscillations are possible. The population either dies out, if the delay is too long and/or the level of nutrient is not adequate, or it approaches a positive steady state with size dependent on the length of the delay.

Therefore, if the per capita growth rate approach is used to derive the chemostat or logistic DDE models, a term of the form $N(t)N(t - \tau)$, that is difficult to justify, occurs and sustained oscillations are possible. However, with delay included in either model, in the growth rate term in a manner consistent with the decline rate given by the equation, again both models give similar predictions and no sustained oscillations are possible. It seems that by clarifying the role of the various effects acting on the population, we have provided convincing evidence that a simple delayed growth response to account for the delay in such processes as digestion or cell division is *not alone* responsible for sustained oscillations in the growth of single species. If such oscillations occur, then they must be the consequence of delayed dependence on other processes, or of a more complex dependence on past population density, e.g., a model involving different mortality rates for juveniles and adults. For example, our alternative model would probably not be appropriate for populations that lay eggs, and a more complicated model like the models suggested by Rodríguez, or even a model involving difference equations might be more appropriate. Such models are not of logistic type, in that they do not revert to the classical logistic ODE when the delay is set to zero.

In the introduction we asked whether delays should be ignored in a logistic-like framework, because they would lead to oscillations that are not observed. Our model includes delays, but does not lead to oscillations. We could now ask whether it makes a difference if we include delays in models of multi-species interactions when one or more of the populations satisfies a logistic-like equation in the absence of the other species. Many such multi-species models have been studied neglecting the delay. The analysis given here suggests that the answer might be that in the case that the delay is in such processes as digestion or cell division, or even more generally if the rate of change can be modelled by a DDE of the form given in Theorem 3.3, it

does not make a significant difference to the dynamics if, for the sake of mathematical tractability, one uses the ODE and neglects explicitly modelling the delay, but instead adjusts the carrying capacity and intrinsic growth rate appropriately, as described in the example illustrated in Fig. 2. This is the subject of future research. It could also be asked whether similar results occur if distributed delay is used instead of discrete delay. This is also the subject of our ongoing research.

Appendix A. Proof of Proposition 3.1

Proof. By the method of steps (Bellman and Cooke, 1963), we can show that for each $\phi \in X = C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$, there is a unique solution of (13) through ϕ . Denote this solution by $N(\phi, t)$ ($N(t)$ for short). Suppose $N(t)$ admits negative values. Then there is $t_1 > 0$ such that $N(t) > 0$ for $t \in [- \tau, t_1]$, $N(t_1) = 0$ and $N'(t_1) \leq 0$. However,

$$\begin{aligned} N'(t_1) &= -\gamma N(t_1) - \kappa N(t_1)^2 + \frac{\gamma \mu N(t_1 - \tau)}{\mu e^{\mu \tau} + (e^{\mu \tau} - 1) \kappa N(t_1 - \tau)} \\ &= \frac{\gamma \mu N(t_1 - \tau)}{\mu e^{\mu \tau} + (e^{\mu \tau} - 1) \kappa N(t_1 - \tau)} \\ &> 0, \end{aligned}$$

a contradiction. Therefore $N(t)$ remains positive for all $t \geq 0$. We next show that $N(t)$ is bounded. Let M_1 be the unique positive number that satisfies $-\mu M_1 - \kappa M_1^2 + \gamma \mu / ((e^{\mu \tau} - 1) \kappa) = 0$ and let $M_2 = \max_{s \in [- \tau, 0]} \phi(s)$. Then we claim that $N(t) \leq M$ for all $t \geq 0$, where $M = \max(M_1, M_2)$. Note that $N(t) \leq M_2 \leq M$ for $t \in [- \tau, 0]$. Suppose $t_1 > 0$ is the first time at which $N(t_1) = M$. Then

$$\begin{aligned} N'(t_1) &= -\mu N(t_1) - \kappa N(t_1)^2 + \frac{\gamma \mu N(t_1 - \tau)}{\mu e^{\mu \tau} + (e^{\mu \tau} - 1) \kappa N(t_1 - \tau)} \\ &< -\mu M_1 - \kappa M_1^2 + \frac{\gamma \mu}{(e^{\mu \tau} - 1) \kappa} = 0. \end{aligned}$$

This implies that when $N(t)$ reaches M , it will be decreasing. Therefore, $N(t) \leq M$ for $t \geq 0$. The proof is complete. \square

Appendix B. Proof of Theorem 3.2

To prove Theorem 3.2, we first prove the following threshold result concerning the local asymptotic stability of equilibria of Eq. (13).

Lemma B.1.

- (i) If $\tau > \tau_H$ holds, then the equilibrium point, $N = 0$, is locally asymptotically stable. If $0 \leq \tau < \tau_H$ holds, $N = 0$ is unstable.
- (ii) If $0 \leq \tau < \tau_H$ holds, then the equilibrium point, $N = \bar{N} > 0$, is locally asymptotically stable.

Proof. (i) Linearizing Eq. (13) about 0 we obtain

$$N'(t) = -\mu N(t) + \gamma e^{-\mu\tau} N(t - \tau). \quad (\text{B.1})$$

Now (i) follows immediately from the well-known Hayes theorem (Bellman and Cooke, 1963).

(ii) Let $y(t) = N(t) - \bar{N}$. Linearizing (13) about \bar{N} , we obtain

$$y'(t) = -py(t) + qy(t - \tau), \quad (\text{B.2})$$

where

$$p = \mu + 2\kappa\bar{N}, \quad q = \frac{\gamma\mu^2 e^{\mu\tau}}{[\mu e^{\mu\tau} + \kappa\bar{N}(e^{\mu\tau} - 1)]^2}.$$

It suffices to show that the trivial solution $y = 0$ of (B.2) is asymptotically stable. Since \bar{N} is the positive equilibrium of (13), it follows that

$$q = \frac{e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N})^2.$$

Noting that $\alpha = e^{\mu\tau} - 1$, condition $0 \leq \tau < \tau_H$ implies that $\gamma > \mu e^{\mu\tau} = \mu(1 + \alpha)$ and so

$$\begin{aligned} 1 + \sqrt{1 + \frac{4\alpha\gamma}{\mu}} &> 1 + \sqrt{1 + \frac{4\alpha\mu(1 + \alpha)}{\mu}} \\ &= 1 + \sqrt{1 + 4\alpha(1 + \alpha)} = 2(1 + \alpha). \end{aligned}$$

Therefore,

$$\gamma \left(1 + \sqrt{1 + \frac{4\alpha\gamma}{\mu}} \right) > 2\gamma(1 + \alpha),$$

which implies that

$$\begin{aligned} \gamma &> \frac{2\gamma(1 + \alpha)}{1 + \sqrt{1 + (4\alpha\gamma/\mu)}} \\ &= \frac{2\gamma(1 + \alpha)(-1 + \sqrt{1 + (4\alpha\gamma/\mu)})}{(1 + \sqrt{1 + (4\alpha\gamma/\mu)})(-1 + \sqrt{1 + (4\alpha\gamma/\mu)})} \\ &= \frac{(1 + \alpha)\mu}{2\alpha} \left(-1 + \sqrt{1 + \frac{4\alpha\gamma}{\mu}} \right). \end{aligned} \quad (\text{B.3})$$

Subtracting $\mu(1 + \alpha)$ from both sides of (B.3), and using (16) we obtain

$$\begin{aligned} \gamma - \mu(1 + \alpha) &> \frac{(1 + \alpha)}{2\alpha} \left[-(2\alpha + 1)\mu + \sqrt{\mu^2 + 4\alpha\gamma\mu} \right] \\ &= (1 + \alpha)\kappa\bar{N}, \end{aligned}$$

and so

$$\gamma - \mu e^{\mu\tau} > e^{\mu\tau}\kappa\bar{N},$$

from which it follows immediately that

$$\gamma - \mu e^{\mu\tau} - e^{\mu\tau}\kappa\bar{N} > 0.$$

Multiplying by μ/γ and then adding $\kappa\bar{N}$ to both sides, we obtain

$$\frac{\gamma - \mu e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N}) > \kappa\bar{N}.$$

This, together with the obvious fact that $0 < \frac{\gamma - \mu e^{\mu\tau}}{\gamma} < 1$, yields

$$\frac{\gamma - \mu e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N})^2 > \left[\frac{\gamma - \mu e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N}) \right]^2 > (\kappa\bar{N})^2.$$

Thus,

$$(\mu + \kappa\bar{N})^2 > (\kappa\bar{N})^2 + \frac{\mu e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N})^2.$$

This implies that

$$p = \mu + 2\kappa\bar{N} > \frac{e^{\mu\tau}}{\gamma}(\mu + \kappa\bar{N})^2 = q,$$

and so we have shown that $q < p$, in the linear equation (B.2). Therefore, by Hayes' theorem, it follows that \bar{N} is locally asymptotically stable. \square

We are now in a position to prove Theorem 3.2.

Proof (Theorem 3.2). Denote the right-hand side of Eq. (13) by $g(N(t), N(t - \tau))$. Clearly

$$\frac{\partial g}{\partial y}(x, y) > 0.$$

This implies that the scalar delay differential equation (13) generates an eventually strongly monotone semiflow on the space $X = C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$ with the usual pointwise ordering (see Smith, 1995) and hence is strongly order preserving.

(i) First we establish this using a direct and elementary approach. Assume that the initial data $\phi \in C([- \tau, 0], \mathbb{R}_+ \setminus \{0\})$ with $\phi(t) < \bar{N}$ for all $t \in [- \tau, 0]$. Suppose there exists a first time \bar{t} such that $N(\bar{t}) = \bar{N}$. Then $N'(\bar{t}) \geq 0$. But since $N(\bar{t} - \tau) < \bar{N}$, directly from the equation it follows that $N'(\bar{t}) < 0$, since $\gamma r(y)$ is an increasing function of y . Thus, no such \bar{t} exists and the result follows. If instead, $\phi(t) > \bar{N}$, for all $t \in [- \tau, 0]$, the result follows using a similar proof. (Using a less elementary approach, monotone dynamical systems theory, (see Hirsch and Smith, 2004; Smith, 1995), this follows immediately, since in (i) we established that (13) generates an eventually strongly monotone semiflow on the space X).

(ii) When $\tau > \tau_H$, there is only a single nonnegative equilibrium $N = 0$ in the space X and so assertion (i) follows from Theorem 2.3.1 of Smith (1995).

(iii) On the other hand, if $0 < \tau < \tau_H$ holds, there are two equilibrium points in X , namely, 0 and $\bar{N} > 0$. By Proposition 4.1 of Hirsch and Smith (2004) and Theorem 2.3.2 of Smith (1995), it follows that solutions of (13) all converge to one of these equilibria.

Next we show that if $0 \leq \tau < \tau_H$, no solutions with positive initial data converge to the equilibrium $N = 0$, and hence all solutions must converge to the positive equilibrium \bar{N} . Suppose $N(t)$ converges to 0. Then clearly, there exists $T \geq 0$ such that $N(t) < \bar{N}$ for all $t > T$. Now $N'(t)$ is of

the form

$$\begin{aligned} N'(t) &= N(t-\tau)r(N(t-\tau)) - N(t)d(N(t)) \\ &= R(N(t-\tau)) - D(N(t)), \end{aligned}$$

where the function $r(y) = \gamma\mu/(\mu e^{\mu\tau} + \kappa(e^{\mu\tau} - 1)y)$ is a decreasing function of y , and the function $d(y) = \mu + \kappa y$ is a strictly increasing function of y , so that $r(y) - d(y)$ is decreasing in y , but $R(y) = yr(y)$ is strictly increasing in y . Observe therefore, that since $\bar{N} > 0$ is an equilibrium, $r(\bar{N}) - d(\bar{N}) = 0$. If $N(t-\tau) \geq N(t)$ but $N(t) < \bar{N}$, then since $yr(y)$ is increasing, but $r(y) - d(y)$ is strictly decreasing, it follows that $N'(t) = N(t-\tau)r(N(t-\tau)) - N(t)d(N(t)) \geq N(t)r(N(t)) - N(t)d(N(t)) = N(t)[r(N(t)) - d(N(t))] > N(t)[r(\bar{N}) - d(\bar{N})] > 0$. Hence,

$$\text{if } 0 < N(t) < \bar{N} \text{ and } N(t-\tau) \geq N(t) \text{ then } N'(t) > 0. \quad (\text{B.4})$$

Therefore, solutions cannot decrease monotonely to 0.

To rule out the possible nonmonotone convergence to 0, define

$$m := \min_{t \in [T-\tau, T]} N(t).$$

We show that $N(t) \geq m$ for all $t > T$. From (B.4), either $N(T) > m$ or $N(T) = m$ and $N'(T) > 0$. If a first \bar{t} exists, so that $N(t)$ eventually decreases to $N(\bar{t}) = m$, with $\bar{N} > N(t) > m$ for $t \in (T, \bar{t})$, then $N'(\bar{t}) \leq 0$. But since $N(\bar{t} - \tau) \geq m$, from (B.4), we obtain the contradiction that $N'(\bar{t}) > 0$, and so $N(t)$ cannot converge to 0 and so must converge to \bar{N} . \square

The same proof can also be used to prove Theorem 3.3, with only minor modifications. Part (i) of Theorem 3.3 follows immediately, since $r(y) - d(y)$ is strictly decreasing.

Appendix C. \bar{N} is a decreasing function of μ

Note that

$$\bar{N} = \frac{\mu - 2\mu e^{\mu\tau} + \sqrt{\mu^2 + 4\gamma\mu(e^{\mu\tau} - 1)}}{2\kappa(e^{\mu\tau} - 1)}.$$

Then

$$\frac{\partial \bar{N}}{\partial \mu} = \frac{L}{2\kappa(e^{\mu\tau} - 1)^2 \sqrt{\mu^2 + 4\gamma\mu(e^{\mu\tau} - 1)}},$$

where

$$L := \sqrt{\mu^2 + 4\gamma\mu(e^{\mu\tau} - 1)}L_1 + L_2,$$

with $L_1 := 3e^{\mu\tau} - 2e^{2\mu\tau} + \mu\tau e^{\mu\tau} - 1$ and $L_2 := \mu e^{\mu\tau} - 2\gamma\mu\tau e^{2\mu\tau} + 2\gamma e^{2\mu\tau} - 4\gamma e^{\mu\tau} - \mu + 2\gamma\mu\tau e^{\mu\tau} + 2\gamma - \mu^2\tau e^{\mu\tau}$. Let $L_1(x) = 3e^x - 2e^{2x} + xe^x - 1$. Then it is easy to verify that $L_1'(x) < 0$ when $x > 0$. Therefore, $L_1 \leq 0$. Note also that $\bar{N} > 0$ since $\gamma > \mu e^{\mu\tau}$, hence $\mu^2 + 4\gamma\mu(e^{\mu\tau} - 1) > \mu^2 + 4\mu e^{\mu\tau}\mu$

$(e^{\mu\tau} - 1) = \mu^2(2e^{\mu\tau} - 1)^2$. Therefore,

$$\begin{aligned} L &= \sqrt{\mu^2 + 4\gamma\mu(e^{\mu\tau} - 1)}L_1 + L_2 \\ &\leq \mu(2e^{\mu\tau} - 1)L_1 + L_2 \\ &= -2(e^{\mu\tau} - 1)[(e^{\mu\tau} - 1)(2\mu e^{\mu\tau} - \gamma) + (\gamma - \mu)\mu\tau e^{\mu\tau}] \\ &=: -2(e^{\mu\tau} - 1)h(\gamma). \end{aligned}$$

Note that since $h'(\gamma) = \mu\tau e^{\mu\tau} - (e^{\mu\tau} - 1) > 0$, and $h(\mu e^{\mu\tau}) > 0$, it follows that $h(\gamma) > 0$ when $\gamma > \mu e^{\mu\tau}$. Therefore, we have $L \leq 0$ and so

$$\frac{\partial \bar{N}}{\partial \mu} \leq 0.$$

Thus, \bar{N} decreases as μ increases.

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