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Persistence and stability for a two-species ratio-dependent predator–prey system with distributed time delay

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Abstract

A two-species ratio-dependent predator–prey model with distributed time delay is investigated. It is shown that the system is persistent under some appropriate conditions, and sufficient conditions are obtained for both the local and global stability of the positive equilibrium of the system. © 2002 Elsevier Science (USA). All rights reserved.

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1. Introduction

An important and ubiquitous problem in predator–prey theory and related topics in mathematical ecology concerns the long term coexistence (or persistence) of species. Standard Lotka–Volterra type models, on which a large body of existing predator–prey theory is built, assume that the per capita rate of predation depends on the prey numbers only. There is growing explicit biological and physiological evidence [1–4] that in many situations, especially when predators have to search,

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share or compete for food, a more suitable, general predator–prey model should be based on the "ratio-dependent" theory. This roughly states that the per capita predator growth rate should be a function of the ratio of prey to predator abundance. Moreover, as the number of predators often changes slowly (relative to prey number), there is often competition among the predators, and the per capita rate of predation should therefore depend on the numbers of both prey and predator, most likely and simply on their ratio [5]. These hypotheses are strongly supported by numerous field and laboratory experiments and observations [2,3,6,7].

A generic ratio-dependent predator–prey model takes the form

$$\begin{cases} \dot{x} = xf(x) - yp(x/y), \\ \dot{y} = -dy + cyq(x/y), \end{cases} \tag{1.1}$$

where x, y respectively denote prey and predator density. The functions $p(s)$ (the predator functional response) and $q(s)$ satisfy standard properties such as being non-negative and increasing, and equal to zero at zero. In particular, the ratio-dependent predator–prey model with Michaelis–Menten type functional response is as follows:

$$\begin{cases} \dot{x} = ax(1 - x/K) - cxy/(my + x), \\ \dot{y} = y(-d + fx/(my + x)). \end{cases} \tag{1.2}$$

From a formal point of view, this model looks very similar to the much better known and applied Michaelis–Menten–Holling predator–prey model

$$\begin{cases} \dot{x} = ax(1 - x/K) - cxy/(b + x), \\ \dot{y} = y(-d + fx/(b + x)). \end{cases} \tag{1.3}$$

Indeed, the only difference between models (1.2) and (1.3) is that the parameter b in (1.3) is replaced by my in (1.2). Such a term (my or b) is proportional to the searching time of the predator, i.e., the time spent by each predator to find one prey. Thus, in the Michaelis–Menten–Holling model, the searching time is assumed to be independent of predator density, while in the ratio-dependent Michaelis–Menten type model, the searching time is proportional to predator density (i.e., predators strongly interfere).

It is generally recognized that some kind of time delay is inevitable in population interactions and tends to be destabilising in the sense that longer delays may destroy the stability of positive equilibria (see [8,9] and references cited therein). Time delay due to gestation is a common example, because generally the consumption of prey by the predator throughout its past history governs the present birth rate of the predator. The effect of this kind of delay on the asymptotic behavior of populations has been studied by a number of authors (see, for example, [10–13]).

In this paper we incorporate a distributed time delay due to for example gestation or extended digestion, into the ratio-dependent predator–prey system. For the two-species ratio-dependent predator–prey model with Michaelis–Menten type functional response, this results in the following delayed system:

$$\begin{cases} \dot{x}(t) = x(t)\left(a - bx(t) - \frac{cy(t)}{my(t)+x(t)}\right), \\ \dot{y}(t) = y(t)\left(-d + f\int_0^{\infty} K(s)\frac{x(t-s)}{my(t-s)+x(t-s)}\,ds\right) \end{cases} \tag{1.4}$$

with initial conditions

$$(x, y) = \Phi(s), \quad s \in (-\infty, 0], \qquad \Phi = (\Phi_1, \Phi_2),$$
$$\Phi_i(s) \geqslant 0, \quad \Phi_i(0) > 0 \quad (i = 1, 2). \tag{1.5}$$

The functions Φ_i $(i = 1, 2)$ are continuous and bounded, a, b, c, d, f, and m are positive constants and we consider kernels $K(t) : [0, \infty) \mapsto [0, \infty)$ for which

$$\sigma := \int_0^{\infty} K(s)s\,ds < \infty \quad \text{and} \quad \int_0^{\infty} K(s)\,ds = 1. \tag{1.6}$$

A special case of (1.4) is considered (along with other, related systems) in [5]. In [5], the Michaelis–Menten type functional response is augmented with a discrete time delay of length τ. This system as considered in [5] can be recovered from (1.4) via the special case $K(s) := \delta(s - \tau)$, where δ is the standard Dirac-delta function. In this case, note that the second condition in (1.6) is clearly satisfied and also that the "mean delay time" σ simply equates to the discrete delay τ. In essence, the following work shows that certain results in [5] can be generalised to a wider class of delays. The methods of proof of our results follow generally those used in [5].

We adopt the following notations and concepts throughout this paper. Let $X = (x, y) \in \mathbf{R}_+^2 = \{(x, y) \in \mathbf{R}^2\colon\ x, y \geqslant 0\}$. The notation $X > 0$ denotes $X \in \operatorname{Int} \mathbf{R}_+^2$. Then we can make the following definition (see, e.g., [1, p. 347]).

Definition 1.1. System (1.4) is said to be uniformly persistent if there exists a compact region $D \subset \operatorname{Int} R_+^2$ such that for every solution $X(t) = (x(t), y(t))$ of system (1.4) with initial conditions (1.5), $\exists T = T(\Phi) \geqslant 0$ such that $X(t) \in D$, $\forall t > T$.

In the next section, we detail necessary and sufficient conditions for the existence of a positive equilibrium of (1.4) and derive a persistence result. In Section 3, a local stability condition, dependent on the "mean delay time" σ as defined in (1.6) above, is formulated. This is extended to a global stability result in Section 4. Note that on setting $K(s) = \delta(s)$, (1.4) is reduced to an instantaneous system, i.e., one without time delay. From (1.6), it follows that in this case, $\sigma = 0$. The results in Sections 3 and 4 are derived in view of corresponding results for the instantaneous system. Finally, a suitable example is given illustrating how the conditions of our theorems relate to each other. Numerical simulations of this and other examples are included to highlight both stability and instability properties.

2. Uniform persistence

It is straight forward to show that system (1.4) has a unique positive equilibrium given by

$$x^* = \frac{amf - c(f-d)}{bmf}, \qquad y^* = \frac{(amf - c(f-d))(f-d)}{bm^2 fd},$$

if and only if

$$0 < f - d < \frac{amf}{c}.$$

In the following, we always assume that such a positive equilibrium exists and denote it by $E^*(x^*, y^*)$. The following lemmas are required for the derivation of a persistence result.

Lemma 2.1. *Solutions of system* (1.4) *corresponding to initial conditions* (1.5) *are defined on* $(0, \infty)$ *and remain positive for all* $t \geqslant 0$.

The proof of Lemma 2.1 follows standard arguments and is similar to that of Lemma 2.1 in [12] and is therefore omitted here.

Lemma 2.2. *Let* $(x(t), y(t))$ *denote any positive solution of system* (1.4) *with initial conditions* (1.5). *Suppose that the kernel* $K(s)$ *satisfies*

$$\int_0^\infty K(s)e^{(f-d)s}\,ds < \infty.$$

Then there exists a $T > 0$ *such that*

$$x(t) \leqslant \frac{a}{b}, \quad y(t) \leqslant M, \quad \text{for } t \geqslant T, \tag{2.1}$$

where

$$\frac{a(f-d)}{bdm}\int_0^\infty K(s)e^{(f-d)s}\,ds < M < \infty.$$

Proof. The method of proof is similar to that of Theorem 2.1 in [5]. From the first equation of (1.4), we obtain

$$\dot{x}(t) \leqslant x(t)\bigl(a - bx(t)\bigr).$$

A standard comparison argument shows that

$$\limsup_{t\to+\infty} x(t) \leqslant \frac{a}{b}.$$

In fact, there exists a $T_1 > 0$, such that if $t \geqslant T_1$, we have $x(t) < a/b$ as we now show. From the first equation in (1.4), it follows directly that $\dot{x}(t) < 0$ at $x(t) = a/b$. Suppose then that $x(t) > a/b$ and $x(t) \to a/b$ as $t \to \infty$. Then, it follows from the first equation in (1.4) that $y(t) \to 0$ as $t \to \infty$. Hence, and from (1.6),

$$\int_0^\infty K(s)\frac{x(t-s)}{my(t-s)+x(t-s)}\,ds \to 1 \quad \text{as } t \to \infty.$$

Therefore there exists a $T > 0$ such that

$$\int_0^\infty K(s)\frac{x(t-s)}{my(t-s)+x(t-s)}\,ds > \frac{d}{f}$$

for all $t > T$. But from the second equation in (1.4), this implies that $\dot{y}(t) > 0$ for all $t > T$ which is a contradiction.

From the second equation of system (1.4), we see that

$$\dot{y}(t) \leqslant y(t)(f-d),$$

which implies that

$$\ln\left(\frac{y(t)}{y(t-s)}\right) \leqslant (f-d)s, \quad \text{for } t > 0,\ s \geqslant 0.$$

Hence, we have

$$y(t-s) \geqslant y(t)e^{-(f-d)s}, \quad \text{for } t > 0,\ s \geqslant 0. \tag{2.2}$$

It follows from (2.2), the second equation of (1.4) and (1.6), that for all $t \geqslant T_1$,

$$\begin{aligned}
\dot{y}(t) &\leqslant y(t)\left[\int_0^\infty K(s)\left(\frac{fa/b}{my(t-s)+a/b} - d\right)ds\right] \\
&\leqslant y(t)\left[\int_0^\infty K(s)\left(\frac{fa/b}{me^{-(f-d)s}y(t)+a/b} - d\right)ds\right] \\
&= y(t)\left[\int_0^\infty K(s)\left(\frac{fe^{(f-d)s}a/b}{my(t)+a/be^{(f-d)s}} - d\right)ds\right] \\
&\leqslant \frac{y(t)}{my(t)+a/b}\left[\frac{a(f-d)}{b}\int_0^\infty K(s)e^{(f-d)s}\,ds - dmy(t)\right].
\end{aligned}$$

A standard comparison argument shows that

$$\limsup_{t\to+\infty} y(t) \leqslant \frac{a(f-d)}{bdm} \int_0^\infty K(s)e^{(f-d)s}\,ds =: M^*.$$

Therefore, given any constant $M > M^*$, there exists a $T(M) \geqslant T_1$ such that $y(t) \leqslant M$ if $t \geqslant T$ and the proof is complete. □

Remark. The upper bounds for corresponding positive solutions obtained in [5] can be recovered by substituting $K(s) = \delta(s-\tau)$ in the bounds obtained here for the more general case.

We now derive our main result in this section.

Theorem 2.1. *Suppose that $a > c/m$ and the hypothesis on the kernel $K(s)$ as given in Lemma* 2.2 *holds. Then system* (1.4), (1.5) *is uniformly persistent.*

Proof. Suppose $(x(t), y(t))$ is a positive solution of system (1.4), (1.5). According to the first equation of system (1.4),

$$\dot{x}(t) > x(t)\left[a - \frac{c}{m} - bx(t)\right], \tag{2.3}$$

which implies that $\liminf_{t\to+\infty} x(t) \geqslant (a - c/m)/b =: m_1 > 0$. Hence, $\exists T_1 > 0$ such that for $t \geqslant T_1$, $x(t) > m_1/2$ and from the second equation in (1.4),

$$\dot{y}(t) \geqslant y(t)\left[-d + f\int_0^\infty K(s)\frac{m_1/2}{my(t-s) + m_1/2}\,ds\right].$$

From this it follows (in a similar manner to the derivation of (2.2) above) that

$$y(t-s) \leqslant y(t)e^{ds}, \quad \text{for } t > 0,\ s \geqslant 0.$$

Hence, for $t \geqslant T_1$, we have

$$\begin{aligned}
\dot{y}(t) &\geqslant y(t)\left[-d + f\int_0^\infty K(s)\frac{m_1/2}{my(t)e^{ds} + m_1/2}\,ds\right] \\
&= y(t)\left[\int_0^\infty K(s)\left(\frac{fm_1e^{-ds}/2}{my(t) + m_1e^{-ds}/2} - d\right)ds\right] \\
&\geqslant y(t)\left[\int_0^\infty K(s)\left(\frac{fm_1e^{-ds}/2}{my(t) + m_1/2} - d\right)ds\right]
\end{aligned}$$

$$\geqslant \frac{y(t)}{my(t)+m_1/2}\left[(f-d)\frac{m_1}{2}\int_0^\infty K(s)e^{-ds}\,ds - mdy(t)\right],$$

which yields

$$\liminf_{t\to+\infty} y(t) \geqslant \frac{m_1}{2md}(f-d)\int_0^\infty K(s)e^{-ds}\,ds =: m_2.$$

Therefore, $\exists T_2 \geqslant T_1$ such that $y(t) > m_2/2$ for all $t > T_2$.

Now, let

$$D := \left\{(x,y)\in \mathbf{R}^2 \,\middle|\, \frac{m_1}{2} \leqslant x \leqslant \frac{a}{b},\ \frac{m_2}{2} \leqslant y \leqslant M\right\}, \tag{2.4}$$

where M is defined in Lemma 2.2. Then D is a compact region in $\mathbf{R}_+^2$ which has positive distance from the coordinate axes. Hence, from Lemma 2.2 and the above calculations, there exists a $T^*(\Phi) \geqslant 0$, such that for all $t > T^*$, every positive solution of system (1.4) with initial conditions (1.5) has $(x(t), y(t)) \in D$. □

Remark. Again the lower bounds for corresponding positive solutions found in [5] can be recovered by substituting $K(s) = \delta(s-\tau)$ in the bounds we achieve here.

Note that persistence does not directly imply stability of the positive equilibrium E^*; other attractors may lie within the region D defined above (limit cycles, for example). In the following sections, we derive conditions which do ensure both the local and global stability of E^*.

3. Local asymptotic stability

Following standard procedures, it can be shown that linearising system (1.4) at $E^*(x^*, x^*)$ yields

$$\begin{cases} \dot N_1(t) = AN_1(t) + BN_2(t), \\ \dot N_2(t) = C\int_0^\infty K(s)N_1(t-s)\,ds + D\int_0^\infty K(s)N_2(t-s)\,ds, \end{cases} \tag{3.1}$$

where $|N_1(t)|, |N_2(t)| \ll 1$ and

$$A = \frac{c(f^2-d^2) - maf^2}{mf^2}, \qquad B = -c\left(\frac{d}{f}\right)^2,$$

$$C = \frac{(f-d)^2}{mf}, \qquad D = -\frac{d(f-d)}{f}.$$

Note that clearly $B < 0$ and $C > 0$ and also, for the range of parameter values considered here, $D < 0$. $N(t) = (N_1(t), N_2(t)) = 0$ is a solution of (3.1) and we have the following stability result; the stability properties referred to are local and full definitions can be found in [9, p. 25]. This lemma follows directly from Theorem 4.2 in [9, Chapter 2].

Lemma 3.1. *If* $N \equiv 0$ *is a uniformly asymptotically stable solution of* (3.1) *then* E^* *is a uniformly asymptotically stable solution of* (1.4).

By considering functions of the form $N(t) = ke^{\lambda t}$, for constant vector k, the characteristic equation associated with (3.1) can be derived as is standard. Thus it can be shown that the local stability of solutions to (3.1) is determined by the sign of the real part of λ, where λ is a root of the equation

$$\lambda^2 - \left(A + D\int_0^\infty K(s)e^{-\lambda s}\,ds\right)\lambda + (AD - BC)\int_0^\infty K(s)e^{-\lambda s}\,ds = 0. \tag{3.2}$$

Let $\lambda = \alpha + i\beta$. Then on substituting into (3.2) and equating real and imaginary parts we obtain

$$\begin{aligned} &\alpha^2 - \beta^2 - \alpha\left[A + D\int_0^\infty K(s)e^{-\alpha s}\cos(\beta s)\,ds\right] \\ &\quad - \beta D\int_0^\infty K(s)e^{-\alpha s}\sin(\beta s)\,ds \\ &\quad + (AD - BC)\int_0^\infty K(s)e^{-\alpha s}\cos(\beta s)\,ds = 0, \end{aligned} \tag{3.3}$$

$$\begin{aligned} &2\alpha\beta - \beta\left[A + D\int_0^\infty K(s)e^{-\alpha s}\cos(\beta s)\,ds\right] \\ &\quad + \alpha D\int_0^\infty K(s)e^{-\alpha s}\sin(\beta s)\,ds \\ &\quad - (AD - BC)\int_0^\infty K(s)e^{-\alpha s}\sin(\beta s)\,ds = 0. \end{aligned} \tag{3.4}$$

We first establish conditions for the stability of the instantaneous equation. Recall that the instantaneous system associated with (1.4) is obtained by setting $K(s) := \delta(s)$ and in this case, $\sigma = 0$ as defined by (1.6).

Lemma 3.2. *Let $K(s) := \delta(s)$. Then the positive steady state E^* of (1.4) is locally asymptotically stable if $A + D < 0$ and unstable if $A + D > 0$.*

Proof. In view of Lemma 3.1 above we may consider the roots of Eq. (3.2). After a little algebra, it can be shown that $AD - BC > 0$. Therefore, with $K(s) := \delta(s)$, it follows from (3.3) and (3.4) that if $A + D < 0$ then for all roots $\lambda = \alpha + i\beta$ of (3.2), $\alpha < 0$. If $A + D > 0$ then there exists at least one root of (3.2) with $\alpha > 0$ and the proof is complete. Note that in the case $A + D = 0$, the roots λ are purely imaginary suggesting centre dynamics close to $N = 0$. □

We now describe the effect on the local asymptotic stability of E^* of introducing a delay in system (1.4). Essentially, we deduce that if the steady state is stable when $\sigma = 0$, then it remains stable provided the mean delay time is sufficiently small. The following proof uses techniques similar those detailed in [9, Chapter 3].

Theorem 3.1. *Suppose $A < D$. Then the positive steady state E^* of system (1.4) is locally asymptotically stable for any kernel $K(s)$ of the form considered here for which $0 \leqslant \sigma < \sigma_L$, where*

$$\sigma_L := \frac{D - A}{AD - BC}.$$

Proof. In view of Lemma 3.1 we may again consider (3.2). If $A < D$, then by Lemma 3.2, E^* is locally asymptotically stable when $\sigma = 0$. Suppose that on increasing σ from zero, E^* becomes unstable, i.e., at least one root of Eq. (3.2) has positive real part. Then there exists a $\sigma > 0$ for which $\lambda = i\beta$, i.e., at least one root of (3.2) has zero real part. In this case, it follows directly from (3.3) that $\beta \neq 0$ and from (3.4) we obtain

$$0 = \beta\left[A + D\int_0^\infty K(s)\cos(\beta s)\,ds\right] + (AD - BC)\int_0^\infty K(s)\sin(\beta s)\,ds.$$

We assume without loss of generality that $\beta > 0$. Therefore, and on using the inequality $\sin(\theta) < \theta$ for $\theta > 0$, we obtain

$$\begin{aligned}0 &< \beta\left[A + D\int_0^\infty K(s)\cos(\beta s)\,ds\right] + (AD - BC)\beta\sigma \\ &\leqslant \beta\big[A - D + (AD - BC)\sigma\big].\end{aligned}$$

Hence, we have a contradiction if σ is sufficiently small, i.e., if

$$\sigma < \frac{D - A}{AD - BC} =: \sigma_L,$$

and the proof is complete. □

Remark. We have been unable to obtain an "instability result" of the type eluded to in [5] and detailed in [9, Chapter 3]: for $A + D > 0$, the instantaneous equation (1.4) has E^* unstable. We have not been able to determine whether E^* remains unstable for all $\sigma > 0$ in this case. This is due to the complex dependence of the roots λ of (3.2) on the quantity σ. For discrete delays, as discussed in [9], this relationship is more easily defined and in particular, calculating the derivative of the roots with respect to the delay is reasonably straight forward. In this work, varying σ may be equivalent to fixing the functional form of K and varying a parameter within this function. For example, $K(s) := \alpha \exp(-\alpha s), \alpha > 0$, is of the form considered here and it is straight forward to show that in this case $\sigma = 1/\alpha$ (more on this later). However, in general, varying σ could be equivalent to varying the functional form of K and therefore σ parameterizes a path in a space of linear functionals.

4. Global asymptotic stability

We now provide conditions under which the positive equilibrium E^* of system (1.4) is globally asymptotically stable. The method of proof is to construct a suitable Lyapunov functional $V(t)$ for system (1.4). Again we will show that corresponding stability results presented in [5] can be derived as a special case of ours, on setting $K(s) = \delta(s - \tau)$. To this end we first rewrite system (1.4). The following procedure mirrors that used in [5] closely. The crucial differences required in order to take account of the general kernel K are highlighted and the intermediate steps are included for completeness. Let $P(u)$ be defined by

$$P(u) = \frac{u}{m + u},$$

then system (1.4) can be rewritten as

$$\begin{cases} \dot{x} = x\left\{-b(x - x^*) + c\left[\frac{y^*}{x^*} P\left(\frac{x^*}{y^*}\right) - \frac{y}{x} P\left(\frac{x}{y}\right)\right]\right\}, \\ \dot{y} = fy \int_0^\infty K(s)\left[P\left(\frac{x(t-s)}{y(t-s)}\right) - P\left(\frac{x^*}{y^*}\right)\right] ds. \end{cases} \tag{4.1}$$

Define

$$u = \frac{x}{y}, \qquad u^* = \frac{x^*}{y^*},$$

then system (4.1) becomes

$$\begin{cases} \dot{x} = x\{-b(x-x^*) + c[\frac{P(u^*)}{u^*} - \frac{P(u)}{u}]\}, \\ \dot{u} = u\{-b(x-x^*) + c[\frac{P(u^*)}{u^*} - \frac{P(u)}{u}] \\ \qquad - f\int_0^\infty K(s)[P(u(t-s)) - P(u^*)]\,ds\}. \end{cases} \tag{4.2}$$

Now let $v_1(t) = x(t) - x^*$, $v_2(t) = u(t) - u^*$ and

$$F(v_2) = P(u) - P(u^*) = \frac{mv_2}{(m+u^*)(m+u)}. \tag{4.3}$$

Note that the positivity of (x, y) ensures that $v_1 > -x^*$ and $v_2 > -u^*$. Finally, notice that

$$\frac{P(u^*)}{u^*} - \frac{P(u)}{u} = \frac{1}{m}F(v_2). \tag{4.4}$$

Therefore, from (4.1)–(4.4), we obtain

$$\begin{cases} \dot{v}_1 = (v_1 + x^*)[-bv_1 + \frac{c}{m}F(v_2)], \\ \dot{v}_2 = (v_2 + u^*)[-bv_1 + \frac{c}{m}F(v_2) - f\int_0^\infty K(s)F(v_2(t-s))\,ds]. \end{cases} \tag{4.5}$$

In the proof of the following lemma, an alternative formulation for $\dot{v}_2$ will be used: it is clear that we may write

$$F\big(v_2(t-s)\big) = F\big(v_2(t)\big) - \int_{t-s}^{t} \dot{F}\big(v_2(\nu)\big)\,d\nu, \tag{4.6}$$

where

$$\dot{F}\big(v_2(t)\big) = \frac{dF(v_2(t))}{dt} = F'(v_2)\frac{dv_2}{dt},$$

with

$$F'(v_2) := \frac{dF(v_2)}{dv_2} = \frac{m}{(m+u)^2}. \tag{4.7}$$

Hence, we may write

$$\begin{aligned} \dot{v}_2 &= (v_2 + u^*)\Bigg[-bv_1 + \frac{c}{m}F(v_2) \\ &\qquad - f\int_0^\infty K(s)\Bigg(F\big(v_2(t)\big) - \int_{t-s}^{t} F'\big(v_2(\nu)\big)\dot{v}_2(\nu)\,d\nu\Bigg)ds\Bigg] \\ &= (v_2 + u^*)\Bigg[-bv_1 - \left(f - \frac{c}{m}\right)F(v_2) \\ &\qquad + f\int_0^\infty K(s)\int_{t-s}^{t} F'\big(v_2(\nu)\big)\dot{v}_2(\nu)\,d\nu\,ds\Bigg]. \end{aligned} \tag{4.8}$$

Let $v(t)=(v_1(t),v_2(t))$ and $v_t=(v_1(t-s),v_2(t-s)),\, t\geqslant 0,\, s\in[0,\infty)$. We can now formulate a result on the global stability of the equilibrium E^* of (1.4) by first defining a functional related to Eq. (4.5) (cf. Lemma 3.1 in [5]).

Lemma 4.1. *There exists a functional* $V: C([0,\infty),\mathbf{R}^2)\to\mathbf{R}_+$ *given by*

$$\begin{aligned} V(v_t) &= \frac{bm}{c}\left[v_1 - x^*\ln\left(\frac{x^*+v_1}{x^*}\right)\right] + \int_{u^*}^{u}\frac{P(\nu)-P(u^*)}{\nu}\,d\nu \\ &\quad + \frac{1}{2}fm\int_0^\infty K(s)\int_{t-s}^{t}\int_r^t\left[bv_1^2(\nu) + \frac{c}{m}F^2\big(v_2(\nu)\big)\right. \\ &\quad \left. + f\int_0^\infty K(\mu)F^2\big(v_2(\nu-\mu)\big)\,d\mu\right]d\nu\,dr\,ds \\ &\quad + \frac{1}{2}mf^2\sigma\int_0^\infty K(s)\int_{t-s}^{t}F^2\big(v_2(r)\big)\,dr\,ds, \end{aligned} \tag{4.9}$$

whose derivative along solution trajectories of system (4.5) *satisfies*

$$\begin{aligned} \dot V(v_t)\big|_{(4.5)} &\leqslant -\left(\frac{b^2m}{c} - \frac{1}{2}fmb\sigma\right)v_1^2 \\ &\quad - \left(\frac{fm-c}{m} - \frac{1}{2}\frac{f}{m}\left[b + \frac{c}{m}\big(1+m^2\big) + f\big(1+m^2\big)\right]\sigma\right) \\ &\quad \times F^2(v_2). \end{aligned} \tag{4.10}$$

Proof. Let us first consider the functional

$$V_1(v) := \frac{bm}{c}\left[v_1 - x^*\ln\left(\frac{v_1+x^*}{x^*}\right)\right] + \int_{u^*}^{u}\frac{P(\nu)-P(u^*)}{\nu}\,d\nu. \tag{4.11}$$

Then along the solutions of (4.5), we have on using (4.8)

$$\begin{aligned} \dot V_1\big|_{(4.5)} &= \frac{bm}{c}\frac{v_1}{v_1+x^*}\dot v_1 + \frac{F(v_2)}{u}\dot v_2 \\ &= -\frac{b^2m}{c}v_1^2 + bF(v_2)v_1 - bF(v_2)v_1 - \left(f - \frac{c}{m}\right)F^2(v_2) \\ &\quad + fF(v_2)\int_0^\infty K(s)\int_{t-s}^{t}F'\big(v_2(\nu)\big)\dot v_2(\nu)\,d\nu\,ds \end{aligned}$$

$$
\begin{aligned}
&= -\frac{b^2 m}{c} v_1^2 - \left(f - \frac{c}{m}\right) F^2(v_2) \\
&\quad + f F(v_2) \int_0^\infty K(s) \int_{t-s}^{t} F'\big(v_2(\nu)\big) u(\nu) \\
&\quad \times \Bigg[-b v_1(\nu) + \frac{c}{m} F\big(v_2(\nu)\big) \\
&\qquad - f \int_0^\infty K(r) F\big(v_2(\nu - r)\big)\, dr \Bigg]\, d\nu\, ds. \qquad (4.12)
\end{aligned}
$$

Using the inequality $kl \leqslant (1/2)(k^2 + l^2)$ for any real numbers k, l, it follows that

$$
\begin{aligned}
&b F\big(v_2(t)\big) u(\nu)\big(-v_1(\nu)\big) \leqslant \frac{b}{2}\Big(F^2\big(v_2(t)\big) + u^2(\nu) v_1^2(\nu)\Big), \\
&\frac{c}{m} F\big(v_2(t)\big) F\big(v_2(\nu)\big) u(\nu) \leqslant \frac{c}{2m}\Big(F^2\big(v_2(t)\big) + u^2(\nu) F^2\big(v_2(\nu)\big)\Big), \\
&F\big(v_2(t)\big) u(\nu) \left(-f \int_0^\infty K(\mu) F\big(v_2(\nu - \mu)\big)\, d\mu \right) \\
&\quad \leqslant \frac{f}{2} \int_0^\infty K(\mu) \Big(F^2\big(v_2(t)\big) + u^2(\nu) F^2\big(v_2(\nu - \mu)\big)\Big)\, d\mu \\
&\quad = \frac{f}{2} F^2\big(v_2(t)\big) + \frac{f}{2} u^2(\nu) \int_0^\infty K(\mu) F^2\big(v_2(\nu - \mu)\big)\, d\mu,
\end{aligned}
$$

where we have used (1.6) in deriving the third inequality. Using these inequalities, it follows that

$$
\begin{aligned}
\dot V_1\big|_{(4.5)} &\leqslant -\frac{b^2 m}{c} v_1^2 - \left(f - \frac{c}{m}\right) F^2(v_2) \\
&\quad + \frac{f}{2}\left(b + \frac{c}{m} + f\right) F^2(v_2) \int_0^\infty K(s) \int_{t-s}^{t} F'\big(v_2(\nu)\big)\, d\nu\, ds \\
&\quad + \frac{f}{2} \int_0^\infty K(s) \int_{t-s}^{t} F'\big(v_2(\nu)\big) u^2(\nu) \Bigg[b v_1^2(\nu) + \frac{c}{m} F^2\big(v_2(\nu)\big) \\
&\quad + f \int_0^\infty K(\mu) F^2\big(v_2(\nu - \mu)\big)\, d\mu \Bigg]\, d\nu\, ds. \qquad (4.13)
\end{aligned}
$$

It follows directly from (4.7) that

$$F'(v_2) < \frac{1}{m} \quad \text{and} \quad F'(v_2)u^2 = \frac{mu^2}{(m+u)^2} < m.$$

Hence, from (4.13) and on using (1.6), we deduce that

$$\begin{aligned} \dot{V}_1\big|_{(4.5)} \leqslant & -\frac{b^2 m}{c} v_1^2 - \left(f - \frac{c}{m}\right) F^2(v_2) + \frac{f}{2}\left(b + \frac{c}{m} + f\right) F^2(v_2) \frac{1}{m}\sigma \\ & + \frac{1}{2} f m \int_0^\infty K(s) \int_{t-s}^t \Big[b v_1^2(\nu) + \frac{c}{m} F^2\big(v_2(\nu)\big) \\ & + f \int_0^\infty K(\mu) F^2\big(v_2(\nu-\mu)\big)\, d\mu \Big]\, d\nu\, ds. \end{aligned} \tag{4.14}$$

Now let

$$\begin{aligned} V_2(v_t) := V_1(v) + \frac{1}{2} f m \int_0^\infty K(s) \int_{t-s}^t \int_r^t \Big[b v_1^2(\nu) + \frac{c}{m} F^2\big(v_2(\nu)\big) \\ + f \int_0^\infty K(\mu) F^2\big(v_2(\nu-\mu)\big)\, d\mu \Big]\, d\nu\, dr\, ds. \end{aligned} \tag{4.15}$$

To calculate the time derivative of V_2, we require the following consequence of the Fundamental Theorem of Calculus. Let $h:\mathbf{R} \to \mathbf{R}$ be an continuous function and define $g:\mathbf{R}^2 \to \mathbf{R}$ by

$$g(t,r) := \int_r^t h(\nu)\, d\nu, \quad t \geqslant r.$$

Then

$$\begin{aligned} \frac{d}{dt} \int_0^\infty K(s) \int_{t-s}^t g(t,r)\, dr\, ds &= \int_0^\infty K(s) \Big[h(t)s - \int_{t-s}^t h(\nu)\, d\nu \Big]\, ds \\ &= h(t)\sigma - \int_0^\infty K(s) \int_{t-s}^t h(\nu)\, d\nu\, ds. \end{aligned}$$

Using this result and on letting

$$h(t) := b v_1^2(t) + \frac{c}{m} F^2\big(v_2(t)\big) + f \int_0^\infty K(\mu) F^2\big(v_2(t-\mu)\big)\, d\mu,$$

it follows from (4.15) that

$$\dot{V}_2\big|_{(4.5)} = \dot{V}_1\big|_{(4.5)} + \frac{1}{2} fm\left[h(t)\sigma - \int_0^{\infty} K(s) \int_{t-s}^{t} h(\nu)\,d\nu\,ds\right]. \tag{4.16}$$

After a little computation, it can be shown from (4.14)–(4.16) that

$$\begin{aligned}\dot{V}_2\big|_{(4.5)} \leqslant{}& \left(-\frac{b^2m}{c} + \frac{1}{2} fmb\sigma\right)v_1^2 - \left(f - \frac{c}{m}\right)F^2(v_2)\\ &+ \frac{f}{2m}\left(b + \frac{c}{m} + f + cm\right)F^2(v_2)\sigma\\ &+ \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(\mu)F^2\big(v_2(t-\mu)\big)\,d\mu.\end{aligned} \tag{4.17}$$

Finally, define the functional $V(v_t)$ by

$$V(v_t) := V_2(v_t) + \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(s) \int_{t-s}^{t} F^2\big(v_2(r)\big)\,dr\,ds. \tag{4.18}$$

Then from (4.17) and (4.18) we have that

$$\begin{aligned}\dot{V}\big|_{(4.5)} ={}& \dot{V}_2\big|_{(4.5)} + \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(s)\big[F^2\big(v_2(t)\big) - F^2\big(v_2(t-s)\big)\big]\,ds\\ \leqslant{}& \left(-\frac{b^2m}{c} + \frac{1}{2} fmb\sigma\right)v_1^2 - \left(f - \frac{c}{m}\right)F^2(v_2)\\ &+ \frac{1}{2}\frac{f}{m}\left(b + \frac{c}{m} + cm + f\right)F^2(v_2)\sigma\\ &+ \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(s)F^2\big(v_2(t-s)\big)\,ds\\ &+ \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(s)F^2\big(v_2(t)\big)\,ds\\ &- \frac{1}{2} f^2 m\sigma \int_0^{\infty} K(s)F^2\big(v_2(t-s)\big)\,ds\\ ={}& -\left(\frac{b^2m}{c} - \frac{1}{2} fmb\sigma\right)v_1^2\end{aligned}$$

$$-\left(\frac{fm-c}{m}-\frac{1}{2}\frac{f}{m}\left[b+\frac{c}{m}\left(1+m^2\right)+f\left(1+m^2\right)\right]\sigma\right)F^2(v_2)$$

and the proof is complete. □

We are now able to state our main result (cf. Theorem 3.2 in [5]).

Theorem 4.1. *Suppose that* $fm > c$. *Then the positive steady state* E^* *of* (1.4) *is globally asymptotically stable in* $\mathbf{R}^2_+$ *for any kernel* $K(s)$ *of the form considered here provided* $0 \leqslant \sigma < \sigma_G$, *where*

$$\sigma_G := \min\left\{\frac{2b}{fc}, \frac{2(fm-c)}{f}\left[b+\frac{c}{m}\left(1+m^2\right)+f\left(1+m^2\right)\right]^{-1}\right\}.$$

Proof. By the equivalence of (1.4) and (4.5) it follows directly that the positive steady state E^* is globally asymptotically stable (in $\mathbf{R}^2_+$) iff the trivial solution $(v_1, v_2) = (0, 0)$ is globally asymptotically stable (for $v_1 > -x^*$, $v_2 > -u^*$). We may therefore focus on the properties of system (4.5).

It was shown in Lemma 4.1 that there exists a functional $V(v_t)$ associated with (4.5). From (4.9), clearly $V(v_t) \geqslant V_1(v(t))$ as defined in (4.11). Let $\omega_1(|v(t)|) := V_1(v(t))$, where $|\cdot|$ denotes the standard norm in $\mathbf{R}^2$. Then $\omega_1(\cdot)$ is a continuous function and clearly, $\omega_1(0) = 0$. After a little computation, it can also be shown that $\omega_1(s) > 0$ for all $s > 0$ and that $\omega_1(s) \to \infty$ as $s \to \infty$. Let

$$\begin{aligned}\omega_2\left(|v(t)|\right) := &\left(\frac{b^2 m}{c}-\frac{1}{2}fmb\sigma\right)v_1^2(t)\\ &+\left(\frac{fm-c}{m}-\frac{1}{2}\frac{f}{m}\left[b+\frac{c}{m}\left(1+m^2\right)+f\left(1+m^2\right)\right]\sigma\right)\\ &\times F^2(v_2(t)).\end{aligned}$$

Then from Lemma 4.1, $\dot{V}(v_t)|_{(4.5)} \leqslant -\omega_2(|v(t)|)$, $\omega_2(\cdot)$ is a continuous function and clearly $\omega_2(0) = 0$. If $fm > c$ and $0 \leqslant \sigma < \sigma_G$ as defined above, it follows that $\omega_2(s) > 0$ for all $s > 0$. Hence, the functional $V(v_t)$ satisfies the conditions of Corollary 5.2 in [9, Chapter 2] and thus we deduce that the trivial solution $(v_1, v_2) = (0, 0)$ of (4.5) is globally asymptotically stable in $v_1 > -x^*$, $v_2 > -u^*$. The result follows by the arguments detailed at the beginning of the proof. □

Remark 1. Again we can recover corresponding results in [5] by setting $K(s) = \delta(s - \tau)$ (and therefore $\sigma = \tau$). Indeed the functional defined in Lemma 3.1 in [5] is a special case of the functional $V(v_t)$ defined here. We note that, in general, the functional $V(v_t)$ is *not* a Lyapunov functional for system (4.5). For this designation, the extra conditions defined here in Theorem 4.1 are required (see [9, p. 28]). This is contrary to the statement in Lemma 3.1 in [5].

Remark 2. If $K(s) := \delta(s)$, then $\sigma = 0$ and Theorem 4.1 yields that E^* is globally asymptotically stable provided $fm > c$. Alternatively, as detailed in [5], in this case, we may consider the functional $V_1(v(t))$ defined by (4.11) directly. It is straight forward to show that with $K(s) := \delta(s)$,

$$\dot{V}_1|_{(4.5)} \leqslant -\frac{mb^2}{c} v_1^2(t) - \left(\frac{fm-c}{m}\right) F^2\big(v_2(t)\big),$$

which is negative definite provided $fm > c$ and again we may appeal to Corollary 5.2 in [9, Chapter 2]. We therefore have the following corollary to Theorem 4.1.

Corollary 4.1. *The positive equilibrium E^* of system* (1.4) *is globally asymptotically stable for any kernel $K(s)$ of type* (1.6) *if the positive equilibrium of the corresponding instantaneous system* (*without time delay*) *is globally asymptotically stable and $K(s)$ is such that σ is sufficiently small, namely $\sigma < \sigma_G$, where σ_G is as defined in Theorem* 4.1.

5. Example

If the instantaneous system related to (1.4) has a globally stable equilibrium, then, in general, it is anticipated that E^* is globally stable for $\sigma < \sigma_1$, say, locally asymptotically stable for $\sigma < \sigma_2$, say, and system (1.4) remains persistent for $\sigma < \sigma_3$, say, where $0 < \sigma \leqslant \sigma_2 \leqslant \sigma_3$. From the results derived in previous sections, it is not easy to determine whether, in general, the sufficient conditions given there ensure the ordering of the values of σ given above, i.e., $0 < \sigma_1 \leqslant \sigma_2 \leqslant \sigma_3$. However, it is straight forward to find specific examples for which this ordering holds as we now demonstrate.

Consider the system

$$\begin{cases} \dot{x} = x(t)\big(a - bx(t) - c\frac{y(t)}{my(t)+x(t)}\big), \\ \dot{y} = y(t)\big(-d + f\int_0^\infty \alpha e^{-\alpha s} \frac{x(t-s)}{my(t-s)+x(t-s)}\, ds\big), \end{cases} \tag{5.1}$$

with $\alpha > 0$. In this case, $K(s) = \alpha e^{-\alpha s}$ and it follows directly that $K(s)$ satisfies (1.6) and that $\sigma = 1/\alpha$. Let $a = 2, b = 0.1, c = 1, d = 2, f = 4$, and $m = 1$. Then it is straight forward to show that system (5.1) has a unique positive equilibrium $E^*(15, 15)$. For this system, the condition for persistence as given in Lemma 2.2 is $\alpha > f - d$. Therefore, system (5.1) is uniformly persistent if $\alpha > 2$, i.e., $\sigma < 1/2$. With the specific choice of parameter values in this example, it can be shown that the conditions of Theorem 3.1 hold. Hence, E^* is locally asymptotically stable if $\sigma < \sigma_L = 1/6$ (i.e., $\alpha > 6$). Finally, again with the parameter values used here, it can be shown that the conditions of Theorem 4.1 hold and therefore E^* is globally asymptotically stable for $\sigma < \sigma_G = 1/20$ (i.e., $\alpha > 20$).

In order to further investigate solution behaviour, we numerically integrated system (5.1). The procedure is as follows. It is possible to rewrite system (5.1) as an instantaneous system (this is not true in general): let

$$z(t) := \int_0^\infty \alpha e^{-\alpha s} \frac{x(t-s)}{my(t-s)+x(t-s)}\, ds,$$

with $\alpha > 0$. Then system (5.1) may be written as

$$\begin{aligned} \dot{x} &= x\left(a - bx - c\frac{y}{my+x}\right), \\ \dot{y} &= y(-d + fz), \\ \dot{z} &= -\alpha z + \alpha \frac{x}{my+x}, \end{aligned} \tag{5.2}$$

where all variables are functions of t and $\dot{z}$ is calculated by first noting that

$$\begin{aligned} z(t) &:= \int_0^\infty \alpha e^{-\alpha s} \frac{x(t-s)}{my(t-s)+x(t-s)}\, ds \\ &= \int_{-\infty}^t \alpha e^{-\alpha(t-s)} \frac{x(s)}{my(s)+x(s)}\, ds, \end{aligned}$$

and using the consequence of the Fundamental Theorem of Calculus mentioned in Section 4 above. System (5.2) has a unique positive steady state given by (x^*, y^*, z^*), where $z^* = y^*/(y^* + x^*)$, and with the parameter values as given above, $(x^*, y^*, z^*) = (15, 15, 1/2)$. All stability and persistence results for system (5.1) apply for system (5.2) and vice versa.

Numerical integration of the local system (5.2) can now be carried out using standard algorithms. We used the "ode45" package in MATLAB. This employs a Runge–Kutta method for which relative and absolute error tolerances can be chosen by the user. In all cases we found that decreasing the tolerance values below the default setting of 1×10^{-3} and 1×10^{-6}, respectively, had no qualitative effect on the generated solution.

As shown in Figs. 1(a) and (b), for α sufficiently small ($\alpha = 0.1$), system (5.2) is not persistent (and E^* is neither globally nor locally stable) with $x \to 0$ and $y \to \infty$ as $t \to \infty$ from all positive initial data.

However, at $\alpha = 1$, system (5.2) is persistent and the steady state E^* is locally stable. In fact, after testing a large range of initial data, it appears that E^* is globally stable in $\mathbf{R}^2_+$ for $\alpha = 1$ and further numerical integrations suggest that it remains so for all values of $\alpha \geqslant 1$ (see Fig. 2). (Recall that this corresponds to $\sigma \leqslant 1$.) These results suggest that the bounds derived in previous sections are somewhat conservative.

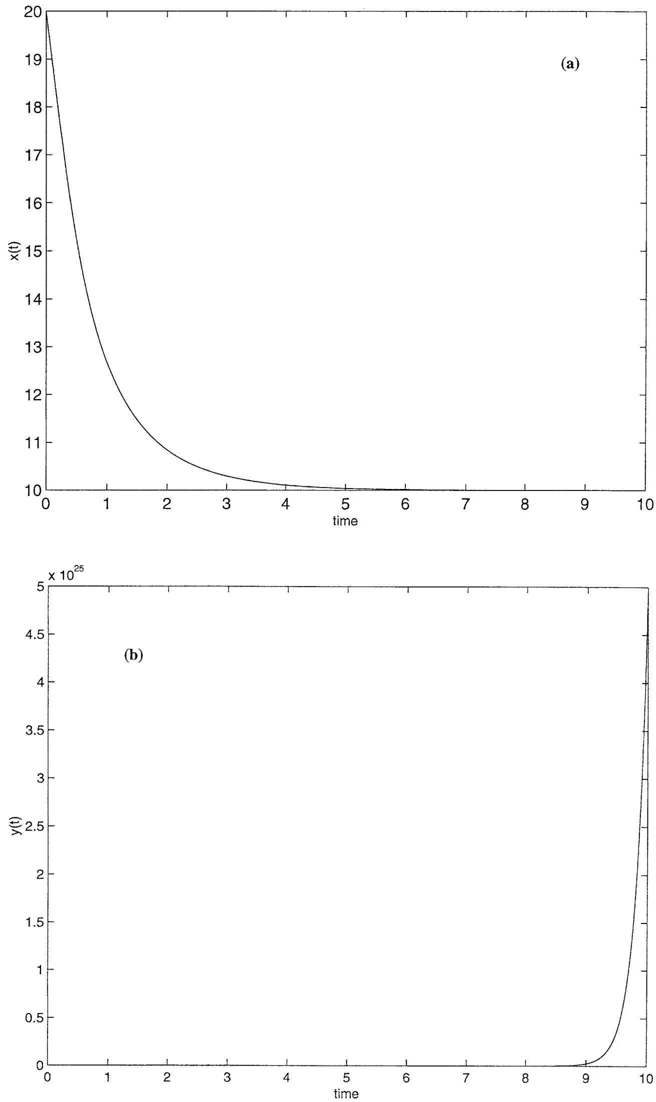

Fig. 1. The temporal evolution of (a) $x(t)$ and (b) $y(t)$ found by numerical integration of system (5.2) with $a = 2, b = 0.1, c = 1, d = 2, f = 4, m = 1$, and $\alpha = 0.1$. Initial data are $(x, y, z) = (20, 20, 2)$.

In Section 3 we were unable to derive an "instability" result, i.e., a result which ensures that instability of E^* for the instantaneous system implies instability of E^* for the distributed system. However, such a result appears to hold at least for the choice of the kernel given above as we now demonstrate.

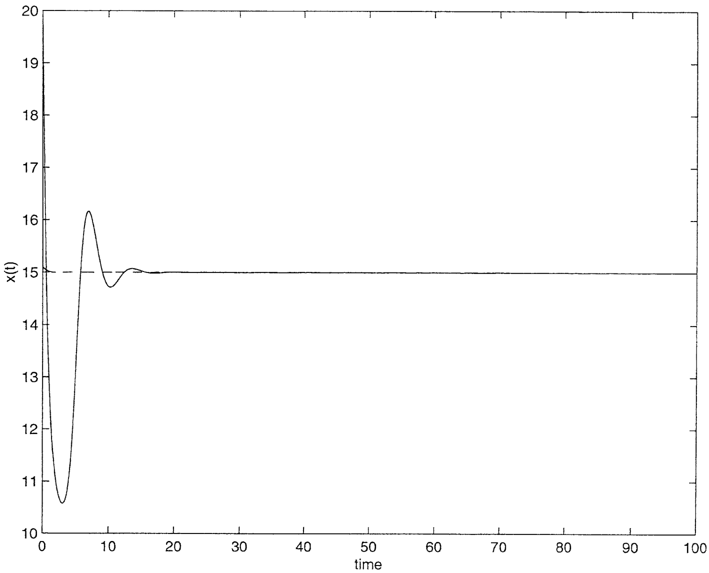

Fig. 2. The temporal evolution of $x(t)$ as found by numerical integration of system (5.2) with $a = 2$, $b = 0.1$, $c = 1$, $d = 2$, $f = 4$, $m = 1$, and $\alpha = 1$. Evolution of $x(t)$ from initial data $(x, y, z) = (20, 20, 2)$ (solid line) and from $(x, y, z) = (15.1, 15.1, 0.5)$ (dashed line) is shown.

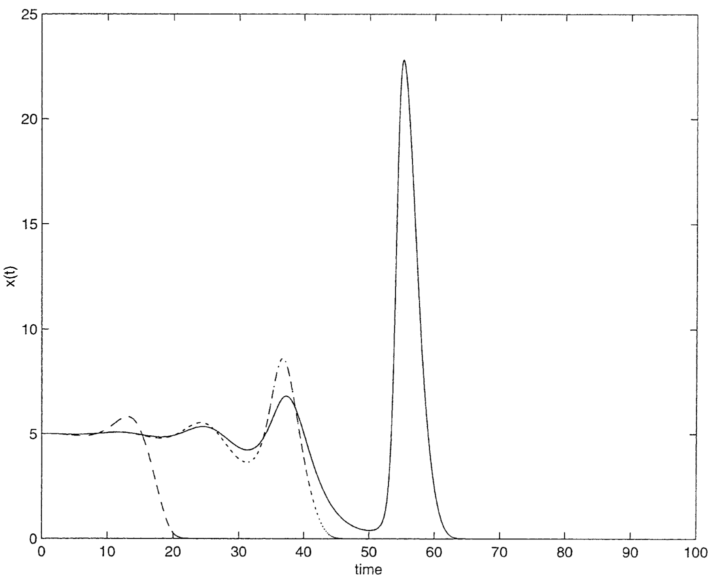

Fig. 3. The temporal evolution of $x(t)$ as found by numerical integration of system (5.2) with $a = 3$, $b = 0.1$, $c = 5$, $d = 1$, $f = 2$, $m = 1$, and $\alpha = 1000$ (solid line), $\alpha = 10$ (dot-dashed line) and $\alpha = 1$ (dashed line). Initial data in all cases are $(x, y, z) = (5.01, 5.01, 0.5)$.

Recall that for any function $g(s)$ with appropriate limiting behaviour at $s = \infty$,

$$\lim_{\alpha \to \infty} \int_0^\infty \alpha e^{-\alpha(t-s)} g(s)\, ds = g(t),$$

i.e., the instantaneous system associated with (5.1) can be recovered in the limit as $\alpha \to \infty$.

If $K(s) = \delta(s)$ and $A + D > 0$, where A and D are as given at the beginning of Section 3, then by Lemma 3.2, E^* is unstable. It is straight forward to show that the values $a = 3, b = 0.1, c = 5, d = 1, f = 2, m = 1$ give $A + D > 0$. Moreover, numerical integration of system (5.2) with these parameter values, provides strong evidence that $E^* = (5, 5, 1/2)$ is unstable for all values $0 < \alpha < \infty$, i.e., for all values of $\sigma > 0$ (see Fig. 3). Notice that decreasing α (increasing σ) has an increasingly destabilising effect.

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