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Persistence and Global Stability in a Population Model

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A difference equation modelling the dynamics of a population undergoing a density-dependent harvesting is considered. A sufficient condition is established for all positive solutions of the corresponding discrete dynamic system to converge eventually to the positive equilibrium. Elementary methods of differential calculus are used. The result of this article provides a generalization of a result known for a simpler special model with no harvesting. © 1998 Academic Press

1. INTRODUCTION

This article is concerned with the dynamics of a logistically growing population subjected to a density-dependent harvesting modelled by the following autonomous differential equation with a piecewise constant argument:

$$\frac{1}{N(t)}\frac{dN(t)}{dt} = r\{1 - aN(t) - bN([t])\}, \qquad t \neq 0, 1, 2, \ldots, t \in (0, \infty). \tag{1.1}$$

It is assumed in (1.1) that $N(t)$ denotes the biomass (or population density) of a single species where r, a, b denote positive numbers and $[t]$ denotes the integer part of $t \in (0, \infty)$. Equation (1.1) in its present form is not convenient for further study and we shall obtain an equivalent difference

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equation. For $t \in [n, n+1)$, $n = 0, 1, 2, \ldots,$ one can rewrite Eq. (1.1) as follows:

$$\frac{dN(t)}{dt} = rN(t)\{(1 - bN(n)) - aN(t)\},$$
$$t \in [n, n+1), n = 0, 1, 2, \ldots . \quad (1.2)$$

It follows from (1.2) that

$$N(t) = N(n)\exp\left\{r\int_n^t (1 - aN(s) - bN(n))\,ds\right\}, \qquad n \le t < n+1. \quad (1.3)$$

It is found from (1.3) that

$$N(n) > 0 \Rightarrow N(t) > 0 \qquad \text{for } t \in [n, n+1), n = 0, 1, 2, \ldots .$$

Allowing $t \to n+1$, in (1.3), we note that $N(n+1) > 0$ and by an inductive procedure it can be shown that $N(t) > 0$ for $t \in [0, \infty)$, if $N(0) > 0$. Eq. (1.1) can be integrated on intervals of the form $[n, n+1)$; first we rewrite (1.1) as follows:

$$\frac{d}{dt}\left\{\frac{1}{N(t)}\exp\{r[1 - bN(n)]t\}\right\} = ar\exp\{r[1 - bN(n)]t\},$$
$$t \in [n, n+1). \quad (1.4)$$

Integrating both sides of (1.4) with respect to t on $[n, t)$, one obtains

$$N(t) = \frac{N(n)\exp\{r[1 - bN(n)](t-n)\}}{1 + aN(n)\big((\exp\{r[1 - bN(n)](t-n)\} - 1)/(1 - bN(n))\big)},$$
$$n \le t < n+1. \quad (1.5)$$

We let $t \to n+1$ in (1.5) and obtain

$$N(n+1) = \frac{N(n)\exp\{r[1 - bN(n)]\}}{1 + aN(n)\big((\exp\{r[1 - bN(n)]\} - 1)/(1 - bN(n))\big)},$$
$$n = 0, 1, 2, \ldots . \quad (1.6)$$

It is now possible to obtain $N(1), N(2), N(3), \ldots$ from (1.6) which together with (1.5) provides a solution of (1.1). Such a solution process does not, however, reveal the rich dynamical characteristics and the asymptotic behaviour of the dynamical system (1.1) for a variety of parameter values of r, a, b. It is the purpose of this article to study in detail the discrete dynamical system (1.6). First we rescale the dependent variable N by setting

$$bN(n) \equiv x(n)$$

so that (1.6) simplifies to

$$x(n+1) = \frac{x(n)\exp\{r[1 - x(n)]\}}{1 + \alpha x(n)\big((\exp\{r[1 - x(n)]\} - 1)/(1 - x(n))\big)}, \qquad n = 0, 1, 2, \dots, \tag{1.7}$$

where $\alpha = a/b$; note that $b \neq 0$ since $b = 0$ results in the trivial dynamics of (1.1) leading to those of the elementary logistic equation. The equilibria of (1.7) are the roots of

$$x = \frac{x \exp[r(1 - x)]}{1 + \alpha x\big((\exp[r(1 - x)] - 1)/(1 - x)\big)} \tag{1.8}$$

and (1.8) simplifies to

$$x[x(1 + \alpha) - 1]\left(\frac{\exp[r(1 - x)] - 1}{1 - x}\right) = 0, \qquad r \in (0, \infty). \tag{1.9}$$

Thus the nonnegative equilibria are given by x_o^* and x^* where

$$x_o^* = 0 \qquad \text{and} \qquad x^* = \frac{1}{1 + \alpha}. \tag{1.10}$$

In the following we establish the persistence of the species under the type of harvesting considered and also obtain conditions for the global asymptotic stability of the positive equilibrium of the discrete dynamic system (1.7).

Equation (1.1) is a differential equation with a piecewise constant argument. We refer to the monographs of Wiener [19] and Carvalho and Cooke [2] for a discussion of differential equations with piecewise constant arguments. We remark that the initial condition needed for the solution of (1.1) is a number and hence (1.1) is not in the category of delay differential equations. For an extensive discussing of the stability of delay differential equations (including piecewise constant arguments) modelling the dynamics of interacting populations, we refer to the monograph of Gopalsamy [7].

2. PERSISTENCE AND LINEAR STABILITY

One of the important problems in the study of the dynamics of populations subjected to harvesting pressures is related to the persistence of the population. By persistence of a population governed by (1.7), we mean the following:

$$x(0) > 0 \Rightarrow \liminf_{n \to \infty} x(n) > 0.$$

Thus if persistence holds then the population is not driven to eventual extinction by harvesting or intraspecific competition. In this section we show first that the population governed by (1.7) persists and then discuss the linear stability of the positive equilibrium. For convenience of notation, we reformulate Eq. (1.7) as follows:

$$x(n+1) = f_\alpha(r, x(n)), \qquad n = 0, 1, 2, \dots, \tag{2.1}$$

where

$$f_\alpha(r, x) = \frac{x \exp[r(1-x)]}{F_\alpha(r, x)}, \qquad x \in [0, \infty), \tag{2.2}$$

$$F_\alpha(r, x) = 1 + \alpha x \left(\frac{\exp[r(1-x)] - 1}{1 - x} \right), \qquad x \in [0, \infty). \tag{2.3}$$

We have from (2.2) and (2.3) that

$$F_\alpha(r, x) f_\alpha(r, x) = x \exp[r(1-x)]. \tag{2.4}$$

Differentiating both sides of (2.4) with respect to x where $(d/dx) f_\alpha(r, x) = f'_\alpha(r, x)$,

$$F_\alpha(r, x) f'_\alpha(r, x) + F'_\alpha(r, x) f_\alpha(r, x) = (1 - rx) \exp[r(1-x)]. \tag{2.5}$$

If we let $x = 0$ in (2.5), then we have

$$F_\alpha(r, 0) f'_\alpha(r, 0) + F'_\alpha(r, 0) f_\alpha(r, 0) = e^r,$$

which with (2.2) and (2.3) leads to

$$f'_\alpha(r, 0) = e^r, \qquad \alpha \in [0, \infty). \tag{2.6}$$

We let $x = x^* = 1/(1 + \alpha)$ in (2.5) and obtain

$$F_\alpha(r, x^*) f'_\alpha(r, x^*) + F'_\alpha(r, x^*) f_\alpha(r, x^*) = (1 - rx^*) \exp[r(1-x)],$$

which again with (2.2) and (2.3) leads to

$$f'_\alpha(r, x^*) = \frac{\exp[-r\alpha/(1+\alpha)]\,(1+\alpha) - 1}{\alpha}. \tag{2.7}$$

The value of $f'_\alpha(r, x^*)$ obtained in (2.7) will be used later in this section to discuss the linear stability of the equilibrium x^*. We now establish the persistence of the population governed by (2.1)–(2.3).

THEOREM 2.1. *Let* $r \in (0,\infty)$ *and* $\alpha \in [0,\infty)$. *Let* $x(n)$ *denote any solution of* (2.1)–(2.3). *If* $x(0) > 0$ *then*

$$\liminf_{n\to\infty} x(n) > 0. \tag{2.8}$$

Proof. It is sufficient to show that there exists ϵ such that if $x(j) \in (0, \epsilon)$ for some positive integer j, then $x(j+k) > \epsilon$ for a positive integer k. Figure 1 will enable us to clarify the idea behind the proof.

We know that $f'_\alpha(r,0) > 1$ and, by the continuity of $f'_\alpha(r,\cdot)$, it follows that there exists $\epsilon_0 > 0$ such that $f'_\alpha(r,x) > 1$ for $x \in (0, \epsilon_0)$. Let $m(\alpha, r) = \sup_{x>0} f_\alpha(r,x)$ and let ϵ_1 be the smallest positive number such that $f_\alpha(r, \epsilon_1) = f_\alpha(r, m)$. As $f_\alpha(r,x)$ is continuous with respect to x on $[0,\infty)$ and furthermore $f(x) \to 0$ as $x \to \infty$, $m(\alpha, r)$ is finite for any positive number of α and r. It follows that $f_\alpha(r,x) > \epsilon_1$ for $x \in [\epsilon_1, m]$ (it is possible for $\epsilon_1 = m$). Now choose $\epsilon = \min\{\epsilon_0, \epsilon_1\}$.

Suppose now that $x(j) < \epsilon$. Then we have by using the mean value theorem of differential calculus,

$$x(j+1) = f_\alpha(r, x(j)) = x(j) f'_\alpha(r, \xi_j), \qquad \xi_j \in (0, x(j)); \tag{2.9}$$

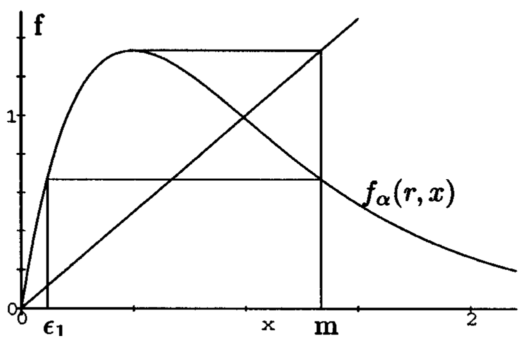


FIGURE 1.

if $x(j+1) > \epsilon$ we are finished; otherwise, we can repeat the above procedure and obtain

$$x(j+2) = x(j+1) f'_\alpha(x, \xi_{j+1}), \qquad \xi_{j+1} \in (0, x(j+1)). \quad (2.10)$$

Continuing this procedure,

$$x(j+k) = x(j) \left\{ \prod_{i=j}^{j+k-1} f'_\alpha(r, \xi_i) \right\}, \qquad \xi_i \in (0, x(j+i)). \quad (2.11)$$

Since $f'_\alpha(r, \xi_i) > 1$, it will follow that there exists a k for which $x(j+k) > \epsilon$ and once $x(j+k) > \epsilon$ then $x(n) > \epsilon$ for $n \geq j+k$. The persistence in the sense of (2.8) follows and this completes the proof.

We now proceed to examine the linear stability of the positive equilibrium of (2.1) given by $x^* = 1/(1+\alpha)$. It is well known (see, for instance, Sandefur [16] or Hale and Kọcak [9]) that the positive equilibrium of (2.1) is linearly stable if $|f'_\alpha(r, x^*)| < 1$ or, equivalently, when $\alpha > 0$,

$$\left| \frac{(1+\alpha)\exp[-r\alpha/(1+\alpha)] - 1}{\alpha} \right| < 1;$$

we note that the above inequality can be simplified to the form

$$\frac{1-\alpha}{1+\alpha} < \exp(-r\alpha/1+\alpha) < 1 \quad (2.12)$$

It is easily seen from (2.12) that if $\alpha \geq 1$, then the inequality (2.12) holds for all $r \in (0, \infty)$. Hence let us consider in the following $\alpha \in [0, 1)$. For this case (2.12) holds if and only if

$$r < \left(\frac{1+\alpha}{\alpha} \right) \ln \left(\frac{1+\alpha}{1-\alpha} \right), \qquad \alpha \in [0, 1). \quad (2.13)$$

It is known from the linear variational system corresponding to $x^* = 1/(1+\alpha)$ given by

$$y(n+1) = f'_\alpha(r, x^*) y(n) \quad (2.14)$$

that the convergence of $y(n)$ to 0 as $n \to \infty$ is monotonic (nonoscillatory) if

$$0 < f'_\alpha(r, x^*) < 1 \quad (2.15)$$

and oscillatory if

$$-1 < f'_\alpha(r, x^*) < 0. \quad (2.16)$$

We note from the nature of $f'_\alpha(r, x^*)$ that when x^* is linearly stable, the eventual convergence of solutions to x^* is monotonic if

$$r < \left(\frac{1+\alpha}{\alpha}\right)\ln(1+\alpha) \tag{2.17}$$

and damped oscillatory if

$$\left(\frac{1+\alpha}{\alpha}\right)\ln(1+\alpha) < r < \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right). \tag{2.18}$$

Some of these observations are illustrated in the plane of the parameters α and r in Fig. 2.

3. GLOBAL STABILITY

Derivation of necessary and sufficient conditions for the global asymptotic stability of positive equilibria of discrete dynamical systems modelling single-species dynamics is quite involved in most cases. For a number of special cases of systems having globally asymptotically stable equilibria, we refer to Cull [4], and Kocic and Ladas [11], and Agarwal [1]. While a necessary condition for global asymptotically stability is easily obtained

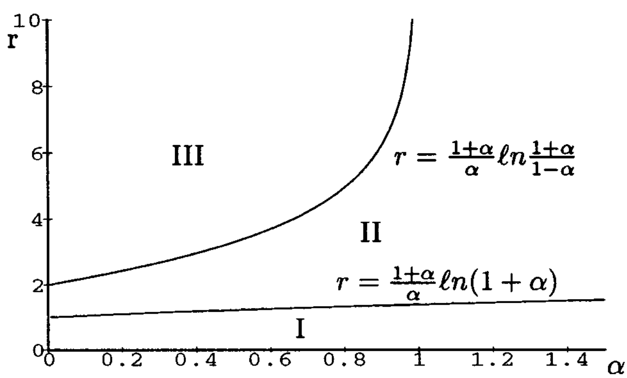


FIG. 2. Regions of linear stability and instability of x^*. I: monotonic damping; II: damped oscillation; III: unstable.

from a linear variational system, establishing that the necessary condition is also sufficient for the global asymptotic stability is usually difficult.

In this section we establish sufficient conditions for all positive solutions of

$$x(n+1) = \frac{x(n)\exp\{r[1-x(n)]\}}{1+\alpha x(n)\{(\exp\{r[1-x(n)]\}-1)/(1-x(n))\}},$$
$$n = 0,1,2,\ldots,\ \alpha \in (0,\infty),\ r \in (0,\infty), \quad (3.1)$$

to converge to the positive equilibrium $x^* = 1/(1+\alpha)$. The result will be established in two portions, corresponding to $\alpha \in [1,\infty)$ and $\alpha \in (0,1)$ respectively.

THEOREM 3.1. *Suppose that* $\alpha \in [1,\infty)$, $r \in (0,\infty)$. *Then the positive equilibrium* $x^* = 1/(1+\alpha)$ *of* (3.1) *is globally asymptotically stable.*

Proof. We consider a Lyapunov function $V(n)$ defined by

$$V(n) = [x(n) - x^*]^2, \qquad n = 0,1,2,\ldots. \quad (3.2)$$

We calculate the change $\Delta V(n)$ in $V(n)$ along the solutions of (3.1):

$$\begin{aligned} \Delta V(n) &= V(n+1) - V(n) = V(x)(n+1) - V(x)(n) \\ &= [x(n+1) - x^*]^2 - [x(n) - x^*]^2 \\ &= [x(n+1) + x(n) - 2x^*][x(n+1) - x(n)]. \end{aligned} \quad (3.3)$$

It is found from (3.1) that

$$\begin{aligned} x(n+1) - x(n) &= \frac{x(n)\exp\{r[1-x(n)]\}}{F_\alpha(r,x(n))} - x(n) \\ &= \frac{x(n)}{F_\alpha(r,x(n))}\left[\frac{\exp\{r[1-x(n)]\}-1}{1-x(n)}\right] \\ &\quad \times (1+\alpha)[x^* - x(n)], \end{aligned} \quad (3.4)$$

where $F_\alpha(r, x(n))$ is defined by (2.3). Again we derive from (3.1)

$$
\begin{aligned}
&x(n+1) + x(n) - 2x^* \\
&\quad = \frac{x(n)\exp\{r[1-x(n)]\}}{F_\alpha(r, x(n))} + x(n) - 2x^* \\
&\quad = \frac{1}{F_\alpha(r, x(n))}\Bigg[x(n)\exp\{r[1-x(n)]\} + [x(n) - 2x^*] \\
&\qquad\qquad \times \left\{1 + \alpha x(n)\left(\frac{\exp\{r[1-x(n)]\} - 1}{1 - x(n)}\right)\right\}\Bigg] \\
&\quad = \frac{1}{F_\alpha(r, x(n))}\Bigg[x(n)\big(\exp\{r[1-x(n)]\} - 1\big) + 2[x(n) - x^*] \\
&\qquad\qquad + [x(n) - 2x^*]\,\alpha x(n)\frac{\exp\{r[1-x(n)]\} - 1}{1 - x(n)}\Bigg] \\
&\quad = \frac{x(n)}{F_\alpha(r, x(n))}\,\frac{\exp\{r[1-x(n)]\} - 1}{1 - x(n)}(1+\alpha)[x^* - x(n)] \\
&\qquad \times \left[\frac{1-\alpha}{1+\alpha} - \frac{2}{(1+\alpha)x(n)}\left(\frac{1 - x(n)}{\exp\{r[1-x(n)]\} - 1}\right)\right]. \qquad (3.5)
\end{aligned}
$$

Now combining (3.4) and (3.5), we obtain

$$
\begin{aligned}
\Delta V(n) &= [x(n+1) - x(n)][x(n+1) + x(n) - 2x^*] \\
&= \left(\frac{x(n)}{F_\alpha(r, x(n))}\,\frac{\exp\{r[1-x(n)]\} - 1}{1 - x(n)}(1+\alpha)[x^* - x(n)]\right)^2 \\
&\qquad \times \left[\frac{1-\alpha}{1+\alpha} - \frac{2}{(1+\alpha)x(n)}\left(\frac{1 - x(n)}{\exp\{r[1-x(n)]\} - 1}\right)\right] \\
&\le 0 \qquad \text{for } \alpha \ge 1. \qquad (3.6)
\end{aligned}
$$

We have from (3.6) that for $\alpha \ge 1$, $\Delta V(n) \le 0$; also we know from the definition of V that $V(n)$ is nonnegative; it follows from (3.6) that $V(n)$ is nonincreasing for $n = 0, 1, 2, 3 \dots$.

It is known from LaSalle's invariance principle [12] that positive solutions of (3.1) approach, as $n \to \infty$, the largest invariant set M contained in the set $\{x \in (0, \infty) | \Delta V(n) = 0\}$ and such a set consists of the points 0 and

x^*. By the persistence result of Theorem 2.1, we know that 0 cannot be approached. It follows that $x(0) > 0 \Rightarrow x(n) \to x^*$ as $n \to \infty$. Combining this with the local stability results in the previous section, we get the conclusion of the theorem.

The next result is concerned with the case $\alpha \in (0,1)$; note that $\alpha = a/b$ and hence this case corresponds to that of the negative feedback due to harvesting dominating the intraspecific self-regulating negative feedback of the logistic growth.

THEOREM 3.2. *Suppose* $\alpha \in (0,1)$ *and* $r \in (0,\infty)$. *If*

$$r \le \frac{1}{\alpha}\ln(1 + 2\alpha) + \ln\left(\frac{1+\alpha}{1-\alpha}\right), \tag{3.7}$$

then the positive equilibrium $x^* = 1/(1+\alpha)$ *of* (3.1) *is globally asymptotically stable*.

Proof. We note that the local stability of x^* under condition (3.7) is valid from the previous section and the relation

$$\frac{1}{\alpha}\ln(1 + 2\alpha) + \ln\left(\frac{1+\alpha}{1-\alpha}\right) \le \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right), \qquad 0 < \alpha < 1. \tag{3.8}$$

The validity of (3.8) can be seen from the following. Let ρ and φ be as follows:

$$\rho(\alpha) = \frac{1}{\alpha}\ln(1 + 2\alpha) + \ln\left(\frac{1+\alpha}{1-\alpha}\right),$$
$$\varphi(\alpha) = \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right).$$

It can be found that

$$\lim_{\alpha\to 0^+} \rho(\alpha) = \lim_{\alpha\to 0^+} \varphi(a) = 2,$$
$$\lim_{\alpha\to 1^-} \rho(\alpha) = \lim_{\alpha\to 1^-} \varphi(\alpha) = +\infty.$$

We have also

$$\varphi(\alpha) - \rho(\alpha) = \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right) - \frac{1}{\alpha}\ln(1+2\alpha) - \ln\left(\frac{1+\alpha}{1-\alpha}\right)$$
$$= \frac{1}{\alpha}\left[\ln\left(\frac{1+\alpha}{1-\alpha}\right) - \ln(1+2\alpha)\right]$$
$$\geq 0 \qquad \left(\text{since } \frac{1+\alpha}{1-\alpha} > 1+2\alpha \text{ and } \alpha \in (0,1)\right),$$

from which the relation (3.8) follows. In order to prove the global asymptotic stability of x^*, we only need to prove the global attractivity of x^*.

We consider again the Lyapunov function $V(n) = V(x)(n)$ defined by

$$V(x)(n) = [x(n) - x^*]^2 \tag{3.9}$$

and obtain from (3.1) and (3.9) the following:

$$\Delta V(n) = V(x)(n+1) - V(x)(n)$$
$$= [x(n+1) - x^*]^2 - [x(n) - x^*]^2$$
$$= [x(n+1) + x(n) - 2x^*][x(n+1) - x(n)], \tag{3.10}$$

$$x(n+1) - x(n) = \frac{x(n)}{F_\alpha(r, x(n))}\left[\frac{\exp\{r[1 - x(n)]\} - 1}{1 - x(n)}\right] \times (1+\alpha)[x^* - x(n)], \tag{3.11}$$

$$x(n+1) + x(n) - 2x^* = \frac{x(n)\exp\{r[1 - x(n)]\}}{F_\alpha(r, x(n))} + [x(n) - 2x^*]. \tag{3.12}$$

It follows from (3.10)–(3.12) that

$$\Delta V(x)(n) = \left\{\frac{x(n)}{F_\alpha(r, x(n))}\left(\frac{\exp\{r[1 - x(n)]\} - 1}{1 - x(n)}\right) \times (1+\alpha)[x^* - x(n)]\right\} \times \left\{\frac{x(n)\exp\{r[1 - x(n)]\}}{F_\alpha(r, x(n))} + [x(n) - 2x^*]\right\} \leq 0 \quad \text{if } x(n) \geq 2x^*. \tag{3.13}$$

From (3.13), we note that we have to investigate the sign of $\Delta V(x)(n)$ for $x(n) \in (0, 2x^*)$. Proceeding further on from (3.12), one can simplify (3.12) to obtain

$$
\begin{aligned}
&x(n+1) + x(n) - 2x^* \\
&\quad = \frac{x(n)}{F_\alpha(r, x(n))} \frac{[1 - (1+\alpha)x(n)]}{1 - x(n)} \\
&\qquad \times \left[\frac{1-\alpha}{1+\alpha} \exp\{r[1 - x(n)]\} - \frac{2 - (1+\alpha)x(n)}{(1+\alpha)x(n)} \right] \qquad (3.14)
\end{aligned}
$$

so that $\Delta V(x)(n)$ is given by

$$
\begin{aligned}
\Delta V(x)(n) = &\left(\frac{x^2(n)}{F_\alpha^2(r, x(n))} \frac{\exp\{r[1 - x(n)]\}^{-1}}{1 - x(n)} [1 - (1+\alpha)x(n)]^2 \right) \\
&\times \left(\frac{1}{1 - x(n)} \left[\frac{1-\alpha}{1+\alpha} \exp\{r[1 - x(n)]\} \right.\right. \\
&\qquad \left.\left. - \frac{2 - (1+\alpha)x(n)}{(1+\alpha)x(n)} \right] \right). \qquad (3.15)
\end{aligned}
$$

It is found from (3.15) that the sign of $\Delta V(x)(n)$ for $x(n) \in (0, 2x^*)$ is determined by that of $W(x)(n)$ where

$$
\begin{aligned}
W(x)(n) = &\frac{1}{1 - x(n)} \left[\frac{1-\alpha}{1+\alpha} \exp\{r[1 - x(n)]\} \right. \\
&\left. - \frac{2 - (1+\alpha)x(n)}{(1+\alpha)x(n)} \right], \qquad x(n) \in (0, 2x^*). \qquad (3.16)
\end{aligned}
$$

We examine the sign of $W(x)(n)$ for $x(n) \in (0, 2x^*)$ in several stages.

(i) $x(n) \in (0, x^*)$. On this interval the sign of $W(x)(n)$ is governed by that of

$$
\begin{aligned}
P(x) &= \frac{1-\alpha}{1+\alpha} \exp[r(1-x)] - \frac{1 - (1+\alpha)x}{(1+\alpha)x} \\
&= \left(\frac{1-\alpha}{1+\alpha} \right) \left\{ \exp[r(1-x)] - \left(\frac{1+\alpha}{1-\alpha} \right) \right. \\
&\qquad \left. \times \left(\frac{2 - (1+\alpha)x}{2 - (1+\alpha)x + 2\alpha} \right) \left(\frac{2}{x} - 1 \right) \right\}. \qquad (3.17)
\end{aligned}
$$

This $P(x) \leq 0$ is equivalent to

$$r \leq \left\{ \left(\frac{1}{1-x} \right) \ln \left[\left(\frac{1+\alpha}{1-\alpha} \right) \left(\frac{2-(1+\alpha)x}{2-(1+\alpha)x+2\alpha} \right) \right] \right\} + \left(\frac{1}{1-x} \right) \ln \left(\frac{2}{x} - 1 \right), \qquad x \in \left(0, \frac{1}{1+\alpha} \right]. \tag{3.18}$$

As $x \in (0, 1/(1+\alpha)]$, the first term on the right-hand side of (3.18) is greater than

$$\ln \left\{ \left(\frac{1+\alpha}{1-\alpha} \right) \left(\frac{1}{1+2\alpha} \right) \right\}. \tag{3.19}$$

We let

$$h(x) = \left(\frac{1}{1-x} \right) \ln \left(\frac{2}{x} - 1 \right), \tag{3.20}$$

and note that

$$\lim_{x \to 0^+} h(x) = \infty, \qquad \lim_{x \to 1^-} h(x) = 2. \tag{3.21}$$

By Taylor expansion,

$$\begin{aligned} h(x) &= \left(\frac{1}{1-x} \right) \{ \ln(2-x) - \ln x \} \\ &= \left(\frac{1}{1-x} \right) \{ \ln[1+(1-x)] - \ln[1-(1-x)] \} \\ &= 2 \sum_{k=1}^{\infty} \frac{(1-x)^{k-1}}{k!}. \end{aligned} \tag{3.22}$$

Since $0 < 1 - x < 1$ for $0 < x < 1/(1+\alpha)$, we obtain that

$$h'(x) = -2 \sum_{k=2}^{\infty} \frac{(k-1)(1-x)^{k-2}}{k!} < 0. \tag{3.23}$$

Using the decreasing nature of h,

$$h(x) > h\left(\frac{1}{1+\alpha} \right) = \left(\frac{1+\alpha}{\alpha} \right) \ln(1+2\alpha), \qquad x \in \left(\frac{1}{1+\alpha}, 1 \right).$$

Thus we have verified that

$$\ln\left\{\left(\frac{1+\alpha}{1-\alpha}\right)\left(\frac{1}{1+2\alpha}\right)\right\}+\left(\frac{1+\alpha}{\alpha}\right)\ln(1+2\alpha)$$
$$\leq\left(\frac{1}{1-x}\right)\left\{\ln\left[\left(\frac{1+\alpha}{1-\alpha}\right)\left(\frac{2-(1+\alpha)x}{2-(1+\alpha)x+2\alpha}\right)\right]\right.$$
$$\left.+\ln\left(\frac{2}{x}-1\right)\right\},\qquad 0<x<\frac{1}{1+\alpha}.$$

Hence if

$$r<\frac{1}{\alpha}\ln(1+2\alpha)+\ln\left(\frac{1+\alpha}{1-\alpha}\right),$$

then $P(x)\leq 0$ for $x\in(0,x^*)$.

(ii) $x(n)\in(x^*,1)$. Again we note that the sign of $W(x)(n)$ is governed by that of $P(x)$ for $x\in(1/(1+\alpha),1)$; we rewrite $P(x)$ as follows:

$$P(x)=\frac{1-\alpha}{1+\alpha}\frac{[2-(1+\alpha)x]}{(1+\alpha)x}$$
$$\times\left[\frac{(1+\alpha)x}{2-(1+\alpha)x}\exp[r(1-x)]-\frac{1+\alpha}{1-\alpha}\right] \tag{3.24}$$

and examine the sign of $q(x)$ where (note that $1<(1+\alpha)x<2$ since $\alpha\in(0,1)$)

$$q(x)=\frac{(1+\alpha)x}{2-(1+\alpha)x}\exp[r(1-x)]-\frac{1+\alpha}{1-\alpha},\qquad x\in\left[\frac{1}{1+\alpha},1\right]; \tag{3.25}$$

it follows from (3.25) and our hypothesis on r that

$$q\left(\frac{1}{1+\alpha}\right)=\exp\left(\frac{r\alpha}{1+\alpha}\right)-\frac{1+\alpha}{1-\alpha}$$
$$=\frac{1+\alpha}{1-\alpha}\left[\frac{1-\alpha}{1+\alpha}\exp\left(\frac{r\alpha}{1+\alpha}\right)-1\right]<0, \tag{3.26}$$
$$q(1)=\frac{1+\alpha}{1-\alpha}-\frac{1+\alpha}{1-\alpha}=0.$$

We will now show that $q(x) < 0$ for $x \in (1/(1+\alpha), 1)$; we consider two cases corresponding to

$$r \in (0, 2(1+\alpha)] \qquad \text{and} \qquad r \in \left(2(1+\alpha), \frac{1+\alpha}{\alpha}\ln\left(\frac{1+\alpha}{1-\alpha}\right)\right).$$

Suppose that $r \in (0, 2(1+\alpha))$; it is found from the definition of q that

$$\begin{aligned} q'(x) &= \frac{(1+\alpha)\exp[r(1-x)]}{[2-(1+\alpha)x]^2}\left[2 - 2rx + r(1+\alpha)x^2\right] \\ &> 0 \qquad \text{for } x \in \left(\frac{1}{1+\alpha}, 1\right) \text{ and } r \in (0, 2(1+\alpha)), \end{aligned} \tag{3.27}$$

$$\begin{aligned} q'(x) &= \frac{(1+\alpha)\exp[2(1-x)]}{[2-(1+\alpha)x]^2}[(1+\alpha)x - 1]^2 \\ &> 0 \qquad \text{for } x \in \left(\frac{1}{1+\alpha}, 1\right), \ r = 2(1+\alpha). \end{aligned} \tag{3.28}$$

It follows from (3.24)–(3.28) that $q(x) < 0$ and hence $P(x) < 0$ for $x \in (1/(1+\alpha), 1)$ and $r \in (0, 2(1+\alpha))$.

We proceed to consider the sign of $P(x)$ for

$$x \in \left(\frac{1}{1+\alpha}, 1\right) \qquad \text{and} \qquad r \in \left(2(1+\alpha), \frac{1+\alpha}{\alpha}\ln\left(\frac{1+\alpha}{1-\alpha}\right)\right).$$

Note that

$$P\left(\frac{1}{1+\alpha}\right) = \frac{1-\alpha}{1+\alpha}\exp\left(\frac{r\alpha}{1+\alpha}\right) - 1 < 0, \qquad P(1) = 0, \tag{3.29}$$

our strategy is to show that P cannot have local maxima on $(1/(1+\alpha), 1)$ which with (3.29) will show that $P(x) < 0$ for $x \in (1/(1+\alpha), 1)$. We derive from the definition of P in (3.24) that

$$\begin{aligned} P'(x) &= \frac{1-\alpha}{1+\alpha}\exp[r(1-x)](-r) + \frac{2}{(1+\alpha)x^2} \\ P''(x) &= \frac{1-\alpha}{1+\alpha}\exp[r(1-x)]r^2 - \frac{4}{(1+\alpha)x^3}. \end{aligned} \tag{3.30}$$

If $\bar{x}$ provides a local extremum of P on $(1/(1+\alpha), 1)$, then we deduce from (3.30) that

$$\begin{aligned}
P''(\bar{x}) &= \frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r^2 - \frac{4}{(1+\alpha)\bar{x}^3} \\
&= \frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r^2 - \frac{2}{\bar{x}}\left\{\frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r\right\} \\
&= \frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r\left[r - \frac{2}{\bar{x}}\right] \\
&> \frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r[r - 2(1+\alpha)] \qquad \text{since } \bar{x} > \frac{1}{1+\alpha} \\
&> \frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})]r(1+\alpha)\left[\frac{1}{\alpha}\ln\frac{1+\alpha}{1-\alpha} - 2\right] > 0. \qquad (3.31)
\end{aligned}$$

Hence any local extremum of P (if one exists) corresponds to a local minimum only. If $P(x) > 0$ for some $x \in (1/(1+\alpha), 1)$, then since $P(1/(1+\alpha)) < 0$, $P(1) = 0$ will imply that $P(x)$ will have to have a local maximum; since local maxima are not possible for P, we conclude that $P(x) \le 0$ for $x \in (1/(1+\alpha), 1)$. Our investigation of the sign of $W(x)(n)$ for $x(n) \in (1/(1+\alpha), 1)$ is now complete and we have

$$W(x)(n) \le 0 \qquad \text{for } x \in \left(\frac{1}{1+\alpha}, 1\right) \text{ and } 0 < r < \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right).$$

(iii) $x(n) = 1$. It is found from the definition of $W(x)(n)$ that W is not defined when $x(n) = 1$; however, W has removable singularity at $x(n) = 1$ and hence we examine the limiting value of W as $x(n) \to 1$. For convenience we write

$$W(x) = \frac{1}{(1-x)}\left[\frac{1-\alpha}{1+\alpha}\exp[r(1-x)] - \frac{2-(1+\alpha)x}{(1+\alpha)x}\right].$$

By L'Hopital's rule one can determine that

$$\begin{aligned}
\lim_{x\to 1} W(x) &= \frac{1-\alpha}{1+\alpha}\left[r - \frac{2}{1-\alpha}\right] \\
&\le \frac{1-\alpha}{1+\alpha}\left[\frac{1+\alpha}{\alpha}\ln\left(\frac{1+\alpha}{1-\alpha}\right) - \frac{2}{1-\alpha}\right] \\
&\le 0.
\end{aligned}$$

(iv) $x(n) \in (1, 2x^*)$. We note from (3.16) that

$$\Delta V(x)(n) \leq 0 \qquad \text{for } x(n) \in (1, 2x^*)$$

if and only if $P(x)$ defined in (3.24) satisfies $P(x) > 0$ for $x \in (1, 2x^*)$. We note that

$$P(1) = 0, \qquad P(2x^*) = P\left(\frac{1}{1+\alpha}\right) = \frac{1-\alpha}{1+\alpha}\exp\left(-r\frac{1-\alpha}{1+\alpha}\right) > 0.$$

Also we have

$$P'(1) = \frac{1-\alpha}{1+\alpha}\left(\frac{2}{1-\alpha} - r\right) > 0.$$

If $P(x) < 0$ for some $x \in (1, 2x^*)$, then $P(\mathrm{x})$ must have at least one local maximum point on $(1, 2x^*)$ and this is due to the fact that $P'(1) > 0$, $P(1) = 0$, $P(2x^*) > 0$. Let $\bar{x}$ be a local extremum point of P; then $P'(\bar{x}) = 0$ and

$$\begin{aligned} P''(\bar{x}) &= r^2\left(\frac{1-\alpha}{1+\alpha}\right)\exp[r(1-\bar{x})] - \frac{4}{(1+\alpha)\bar{x}^3} \\ &= r^2\left(\frac{1-\alpha}{1+\alpha}\right)\exp[r(1-\bar{x})] - \left(\frac{1-\alpha}{1+\alpha}\right)\frac{2r}{\bar{x}}\exp[r(1-\bar{x})] \\ &= \frac{r(1-\alpha)}{1+\alpha}\exp[r(1-\bar{x})]\left(r - \frac{2}{\bar{x}}\right) \\ &> r\frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})](r-2). \end{aligned}$$

If $r > 2$, we have $P''(\bar{x}) > 0$, which means that $P(x)$ has no local maximum and hence $P(x) > 0$ when $r > 2$ and $x \in (1, 2/(1+\alpha))$. Hence $P(x) > 0$ on $(1, 2x^*)$.

Next consider the case $r \leq 2$. If a local minimum exists let the minimum be at $\bar{x}$. Then $P'(\bar{x}) = 0$ and hence from (3.30)

$$P'(\bar{x}) = 0 \quad \Rightarrow \quad r\frac{1-\alpha}{1+\alpha}\exp[r(1-\bar{x})] = \frac{2}{(1+\alpha)\bar{x}^2}.$$

Then for $x > 1$, we have from the definition of $P(x)$ in (3.17)

$$\begin{aligned} P(\bar{x}) &= \frac{2}{r(1+\alpha)\bar{x}^2} - \frac{2}{(1+\alpha)\bar{x}} + 1 \\ &\geq \frac{1}{(1+\alpha)\bar{x}^2} - \frac{2}{(1+\alpha)\bar{x}} + 1 \\ &= \frac{1}{1+\alpha}\left(\frac{1}{\bar{x}^2} - \frac{2}{\bar{x}} + 1 + \alpha\right) \\ &> \frac{1}{1+\alpha}\left(\frac{1}{\bar{x}^2} - \frac{2}{\bar{x}} + 1\right) \\ &= \frac{1}{1+\alpha}\left(\frac{1}{\bar{x}} - 1\right)^2 > 0. \end{aligned}$$

It follows that $P(x) > 0$ for $x \in (1, 2x^*)$.

From (i)–(iv), we conclude that

$$\Delta V(n) \leq 0 \qquad \text{for } x(n) \in (0, 2x^*).$$

We have already verified that $\Delta V(n) \leq 0$ for $x(n) \in [x^*, \infty)$. One can now argue as in the case of the proof of Theorem 2.1 and derive that

$$\lim_{n \to \infty} x(n) = x^* = \frac{1}{1+\alpha}.$$

This completes the proof of Theorem 3.2.

The following corollary is concerned with the asymptotic behaviour of positive solutions of (1.2) and is a consequence of Theorems 3.1 and 3.2.

COROLLARY 3.3. *Let r, a, b be positive numbers. Assume that any one of the following two conditions hold*:

(i) $a \geq b$;

(ii) $0 < a < b$ *and*

$$0 < r < \frac{b}{a}\ln\left(1 + \frac{2b}{a}\right) + \ln\left(\frac{a+b}{a-b}\right).$$

Then all positive solutions of (1.2) *satisfy*

$$\lim_{t \to \infty} N(t) = \frac{1}{a+b}.$$

Proof. We have from (1.6) that any solution of (1.2) is given by

$$N(n+t) = \frac{N(n)\exp\{r[1-bN(n)]t\}}{1 + aN(n)\big((\exp\{r[1-bN(n)]t\} - 1)/(1-bN(n))\big)},$$
$$0 \le t \le 1,\ n = 0, 1, 2, \dots .$$

We note from Theorems 3.1 and 3.2 that when the condition of Corollary 3.3 holds, then

$$\lim_{n\to\infty} bN(n) = x^* = \frac{1}{1+\alpha}, \qquad \text{where } \alpha = \frac{a}{b}.$$

We have from the above that

$$\begin{aligned}
\lim_{\tau\to\infty} N(\tau) &= \lim_{n\to\infty} N(n+t) \\
&= \lim_{n\to\infty} \frac{N(n)\exp\{r[1-bN(n)]t\}}{1 + aN(n)\big((\exp\{r[1-bN(n)]t\} - 1)/(1-bN(n))\big)} \\
&= \frac{1}{b}\left(\frac{1}{1+\alpha}\right) = \frac{1}{b}\left(\frac{1}{1+a/b}\right) \\
&= \frac{1}{a+b}.
\end{aligned}$$

and the proof is completed.

A result similar to that of Corollary 3.3, but concerned with an equation containing a more general class of delays, has been established by Cooke and Huang [3] under the assumption $a > b$. A condition of this type means that the stabilizing undelayed negative feedback dominates other negative feedbacks with delays (for more details of this type of conditions, we refer to Gopalsamy [7]).

4. A FEW COMMENTS

We have established that all positive solutions of the discrete dynamic system (1.7) converge to the positive equilibrium if $\alpha \ge 1$; if $\alpha \in (0, 1)$, then a sufficient condition for such a convergence is given by the requirement of (3.7). From the proof of Theorem 3.2 we see that the condition (3.7) is not necessary. If

$$r = \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right), \qquad \alpha \in (0,1), \tag{4.1}$$

then the linear stability criterion is not applicable since in such a case we have

$$f'_\alpha(r, x^*) = -1. \tag{4.2}$$

It is, however, known (for instance, see Sandefur [16]) that when (4.2) holds, if

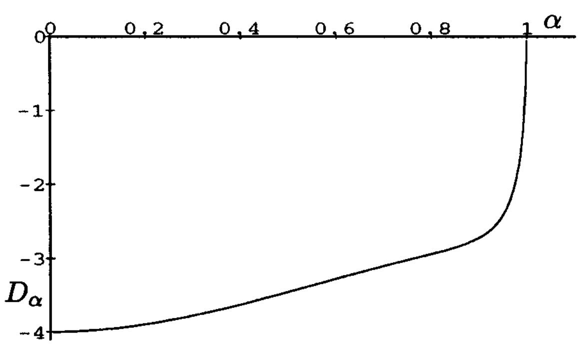
$$\begin{aligned} D_\alpha(x^*) &= -2f'''_\alpha(r, x^*) - 3[f''_\alpha(r, x^*)]^2 < 0, \\ r &= \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right), \end{aligned} \tag{4.3}$$

then x^* is locally stable. Calculation of the derivatives involved in (4.3) is tedious; we have used the Maple symbolic program to calculate $D_\alpha(x^*)$ of (4.3) for the case where r satisfies the equality in (4.3). The resulting function $D_\alpha(x^*)$ of the parameter $\alpha \in (0, 1)$ is plotted using Maple's plotting procedure and the graph is displayed in Fig. 3.

From the graph it is found that $D_\alpha(x^*) < 0$ for $\alpha \in (0, 1)$ and hence we conclude that x^* of (2.1)–(2.3) is asymptotically stable provided

$$r \le \left(\frac{1+\alpha}{\alpha}\right)\ln\left(\frac{1+\alpha}{1-\alpha}\right). \tag{4.4}$$

If (4.4) is violated then x^* is not linearly stable. One can see from (2.7) that $f'_\alpha(r, x^*) < -1$ is sufficient for instability of x^*. Thus (4.4) provides a necessary condition for the asymptotic stability of x^* when $\alpha \in (0, 1)$. The authors believe that (2.13) is sufficient for the global asymptotic stability of x^*; however, they have not been able to prove this.



Graph of $D_\alpha(x^*)$ for $\alpha \in (0, 1)$

FIGURE 3.

When $\alpha = 0$, the system (2.1)–(2.3) reduces to the simpler dynamic system

$$x(n+1) = x(n)\exp\{r[1 - x(n)]\}, \qquad n = 0, 1, 2, \dots . \tag{4.5}$$

Several authors (see May [13], May and Oster [14], Fisher and Goh [6], Seifert [17, 18], Norris and Soewono [15], Guckenheimer, Oster, and Ipaktchi [8], and Dohtani [5]) have investigated the stability and oscillatory characteristics of (4.5). It is known that if $0 < r \leq 2$, then all positive solutions of (4.5) converge to the positive equilibrium of (4.5). One can obtain this special result from our investigation by evaluating the following limit:

$$\lim_{\alpha \to 0} \left(\frac{1+\alpha}{\alpha} \right) \ln\left(\frac{1+\alpha}{1-\alpha} \right) = 2. \tag{4.6}$$

The global asymptotic stability of x^* implies that the dynamics of the system has no persistent periodic solutions or other types of complex solutions of the "chaotic type." In fact, when the requirement in (4.1) is violated, period-doubling bifurcations and complex dynamics of the system (1.7) emerge and it has not been the intention of the authors to consider this in this article. We conclude with the remark that there exists vast literature concerned with singular perturbations of delay differential equations and their connection with certain associated difference equations with a continuous argument (for a survey see Ivanov and Sharkovsky [10] and the references therein). We remark that the discrete dynamic system (1.7) is not derived from the differential equation (1.1) through any regular or singular perturbation.

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