

# Global Stability in a Nonlinear Difference-Delay Equation Model of Flour Beetle Population Growth

YANG KUANG\*

Department of Mathematics, Arizona State University, Tempe, AZ 85287-1804,  
USA

J. M. CUSHING†

USA Department of Mathematics, University of Arizona, Tucson, AZ 85721, USA

This paper presents some sufficient conditions for the positive equilibrium in a recent model of flour beetle population growth due to B. Dennis et al. (1994) to be globally asymptotically stable.

AMS Nos.: 39A11, 92B05.

KEYWORDS: difference-system, difference-delay equation, equilibrium, global stability  
(Received March 3, 1995; in final form June 2, 1995)

## 1. INTRODUCTION

The following larval-pupal-adult (LPA) model of flour beetle (*Tribolium*) population growth is proposed and studied by B. Dennis et al. (1994):

$$L_{t+1} = bA_t \exp(-c_{ea}A_t - c_{el}L_t), \quad (1.1)$$

$$P_{t+1} = (1 - \mu_l) L_t, \quad (1.2)$$

$$A_{t+1} = P_t \exp(-c_{pa}A_t) + (1 - \mu_a)A_t. \quad (1.3)$$

Here  $L_t$ ,  $P_t$ , and  $A_t$  are the number of feeding larvae, pupae, and non-feeding larvae, and adults, respectively, at time  $t$ ; the unit of time is taken to be the feeding larval maturation period so that after one unit of time, a larva either dies or survives and pupates. This unit of time is also the time spent as a non-feeding larva, pupa and callow (young adult).  $b$  is a positive constant describing the number of eggs laid per adult per unit of time. System (1.1)—(1.3) models a class of flour beetles of the genus *Tribolium* that are cannibalistic (Park et al. 1965). For these flour beetles, adults may feed on eggs, larvae, pupae and callows, while larvae may eat eggs, pupae, and callows. Neither larvae nor adults eat mature adults and larvae do not feed on larvae. In the above model, the cannibalism of larvae and callows by adults and of pupae and callows by larvae is assumed negligible since it typically occurs at much reduced rates. The constants  $\mu_l$  and  $\mu_a$  are the larval and adult probability of

\*Research partially supported by NSF Grant DMS-9306239

†Research partially supported by NFS Grant DMS-9306271

dying from causes other than cannibalism, respectively.  $\exp(-c_{ea}A_t)$  and  $\exp(-c_{el}L_t)$  represent the probabilities that an egg is not eaten in the presence of  $A_t$  adults and  $L_t$  larvae, and  $\exp(-c_{pa}A_t)$  is the survival probability of a pupa in the presence of  $A_t$  adults. The nonnegative constants  $c_{ea}$ ,  $c_{el}$ , and  $c_{pa}$  are called the "cannibalism coefficients." It is assumed here that the only significant source of pupal mortality is adult cannibalism.

Following B. Dennis et al. (1994), we consider here the simplified case when larval cannibalism of eggs is not present, i.e.,  $c_{el} = 0$ . In this case, we can see that system (1.1)–(1.3) is equivalent to the following difference-delay equation

$$A_{t+1} = (1 - \mu_a)A_t + b(1 - \mu_l)A_{t-2} \exp(-c_{ea}A_{t-2} - c_{pa}A_t), \quad t \geq 2. \quad (1.4)$$

When  $A_0$ ,  $P_0$ , and  $L_0$  are given, we have

$$\begin{aligned} A_1 &= P_0 \exp(-c_{pa}A_0) + (1 - \mu_a)A_0, \\ A_2 &= (1 - \mu_l)L_0 \exp(-c_{pa}A_1) + (1 - \mu_a)A_1. \end{aligned}$$

We assume that  $A_0$ ,  $P_0$ , and  $L_0$  are nonnegative. A complete analytical description of the local stability region was given in this case by B. Dennis et al. (1994). Our objective here is to derive some sufficient conditions for the global stability of the positive equilibrium (which, when it exists, is unique).

We would like to mention that global stability results for general difference-delay equations are rare. Some of the recent results can be found in Kocic and Ladas (1993). The following theorem is a trivial extension of a result due to Hautus and Bolis (1979), which is stated as Theorem 2.6.2 in Kocic and Ladas (1993). This result will be used in our subsequent analysis.

**Theorem 1.1** (Hautus and Bolis (1979)). *Consider the difference equation*

$$x_{t+1} = F(x_t, x_{t-1}, \dots, x_{t-k}), \quad t \geq 0, \quad (1.5)$$

where  $F \in C(D, R)$ ,  $D \subset R^{k+1}$ , is increasing in each of its arguments (when restricted to the region  $D$ ). Let  $x^*$  be an equilibrium of (1.5) and  $I$  an interval such that  $x^* \in I$  and  $I^{k+1} = \{(u_1, \dots, u_{k+1}): u_i \in I, i = 1, 2, \dots, k+1\} \subset D$ . Moreover, assume that for  $u \neq x^*$ ,

$$(u - x^*)[F(u, u, \dots, u) - u] < 0. \quad (1.6)$$

Then with initial data  $x_0, x_{-1}, \dots, x_{-k} \in I$ , we have  $x_t \in I$  for  $t \geq 0$  and

$$\lim_{t \rightarrow \infty} x_t = x^*.$$

## 2. MAIN RESULT

The main objective of this paper is to obtain sufficient conditions for the global stability of the positive equilibrium (which is unique, when it exists). Our method

here is to apply the general result, namely, Theorem 1.1. In order to do so, we need some preparations. For convenience, we define

$$\alpha = 1 - \mu_a, \quad \beta = b(1 - \mu_l), \quad c_1 = c_{ea}, \quad c_2 = c_{pa}, \quad x_t = A_{t+2} \quad \text{for } t \geq -2.$$

Then (1.4) becomes

$$x_{t+1} = \alpha x_t + \beta x_{t-2} \exp(-c_1 x_{t-2} - c_2 x_t), \quad t \geq 0, \tag{2.1}$$

where

$$\begin{aligned} x_{-2} &= A_0 \\ x_{-1} &= A_1 = P_0 e^{-c_{pa} A_0} + (1 - \mu_a) A_0 \\ x_0 &= A_2 = (1 - \mu_l) L_0^{-c_{pa} A_1} + (1 - \mu_a) A_1. \end{aligned}$$

Note that if  $0 \leq (L_0, P_0, A_0) \neq 0$ , then  $x_0 > 0$ . It should be pointed out here that we are only interested in nonnegative solutions of (2.1). We assume below that  $x_{-2}, x_{-1}, x_0$  are nonnegative. We also assume that  $c_1 + c_2 > 0, 1 > \alpha > 0$ , and  $\beta > 0$ . Moreover, since we are interested in nontrivial solutions, we assume  $0 \leq (L_0, P_0, A_0) \neq 0$ , which implies  $x_0 > 0$ .

A simple computation reveals that when  $\alpha + \beta \leq 1$ , Eq. (2.1) has only one nonnegative equilibrium, namely,  $x_t \equiv 0$ . When  $\alpha + \beta > 1$ , Eq. (2.1) has two equilibria, they are  $x_t \equiv 0$  and  $x_t \equiv x^*( > 0)$ , where

$$x^* = \frac{1}{c_1 + c_2} \ln \frac{\beta}{1 - \alpha}.$$

The linearized equation of Eq. (2.1) about an equilibrium  $\bar{x}$  is

$$y_{t+1} = [\alpha - \beta c_2 \bar{x} e^{-(c_1 + c_2) \bar{x}}] y_t + \beta(1 - c_1 \bar{x}) e^{-(c_1 + c_2) \bar{x}} y_{t-2}, \quad t \geq 0. \tag{2.2}$$

For the trivial equilibrium  $x = 0$ , Eq. (2.2) reduces to

$$y_{t+1} = \alpha y_t + \beta y_{t-2}, \tag{2.3}$$

which is asymptotically stable if and only if  $\alpha + \beta < 1$ .

The linearized equation about the positive equilibrium  $x^*$  takes the form

$$y_{t+1} = -A y_t - B y_{t-2}, \quad t \leq 0, \tag{2.4}$$

where

$$A = \frac{c_2(1 - \alpha)}{c_1 + c_2} \left( \ln \frac{\beta}{1 - \alpha} \right) - \alpha$$

and

$$B = (1 - \alpha) \left[ \frac{c_1}{c_1 + c_2} \left( \ln \frac{\beta}{1 - \alpha} \right) - 1 \right].$$

By employing the well known Schur-Cohn criterion (Theorem 1.3.3 in [3]), we can obtain that Eq. (2.4) is asymptotically stable if and only if

$$|A + B| < 1, \quad |A - 3B| < 3, \quad \text{and} \quad B(B - A) < 1. \quad (2.5)$$

The following result is straightforward.

**Lemma 2.1** *Assume that  $x_s > 0$  for some  $s \geq 0$ ; then for  $t > s$ ,  $x_t > 0$ .*

**Proof** This is obvious from (2.1). In fact,

$$x_t \geq \alpha^{t-s} x_s > 0, \quad t \geq s. \quad (2.6)$$

The following theorem states that when  $\alpha + \beta \leq 1$ , the trivial equilibrium  $x_t \equiv 0$  of (2.1) is globally asymptotically stable with respect to nonnegative solutions. Recall that the local stability analysis yields asymptotical stability only when  $\alpha + \beta < 1$ .

**Theorem 2.1** *If  $\alpha + \beta \leq 1$ , then  $\lim_{t \rightarrow +\infty} x_t = 0$ .*

**Proof** Since  $x_0 > 0$ , we see from Lemma 2.1 that  $x_t > 0$  for  $t > 0$ . Let

$$\bar{x}_t = \max\{x_t, x_{t-1}, x_{t-2}\}.$$

Then for  $t > 2$ ,

$$x_{t+1} \leq \alpha \bar{x}_t + \beta \bar{x}_t \exp(-c_1 x_{t-2} - c_2 x_t).$$

Since  $c_1 \geq 0$ ,  $c_2 \geq 0$  and  $c_1 + c_2 > 0$ , and  $x_{t-2} > 0$ ,  $x_t > 0$ , we have

$$x_{t+1} < \alpha \bar{x}_t + \beta \bar{x}_t \leq \bar{x}_t.$$

This implies that  $\bar{x}_t$  is nonincreasing. Let

$$\bar{x} = \lim_{t \rightarrow +\infty} \bar{x}_t. \quad (2.7)$$

Assume that  $\bar{x} > 0$ . Since  $\alpha + \beta \exp[-(c_1 + c_2)\alpha^2 \bar{x}] < 1$ , there is an  $\epsilon > 0$  such that

$$\alpha(\bar{x} + \epsilon) + \beta(\bar{x} + \epsilon) \exp[-(c_1 + c_2)\alpha^2 \bar{x}] < \bar{x} - \epsilon.$$

From (2.7), there is a  $T > 0$  such that if  $t > T$ , then  $x_t < \bar{x} + \epsilon$ . Note that (2.6) implies that

$$x_t \geq \max\{x_t, \alpha x_{t-1}, \alpha^2 x_{t-2}\},$$

we see that for  $t > T + 2$ ,  $x_t \geq \alpha^2 \bar{x}_t \geq \alpha^2 \bar{x}$ . Hence we have for  $t > T + 2$ ,

$$x_{t+1} < \alpha(\bar{x} + \epsilon) + \beta(\bar{x} + \epsilon) \exp[-(c_1 + c_2)\alpha^2 \bar{x}] < \bar{x} - \epsilon,$$

which implies that  $\lim_{t \rightarrow +\infty} \bar{x}_t \leq \bar{x} - \epsilon$ , a contradiction to (2.7). This shows that  $\bar{x} = 0$ , and hence  $\lim_{t \rightarrow +\infty} x_t = 0$ . ■

We are now ready to state our main result, which presents sufficient conditions for  $x_t \equiv x^*$  in (2.1) to be globally asymptotically stable with respect to positive solutions. It can be shown that these conditions imply (2.5).

**Theorem 2.2** *Assume that  $\alpha + \beta > 1$  and*

$$\beta < \min\{e(1 - \alpha), e\alpha c_1/c_2\}. \tag{2.8}$$

*If  $\max\{x_{-2}, x_{-1}, x_0\} > 0$ , then  $\lim_{t \rightarrow +\infty} x_t = x^*$ .*

In order to prove this result, we need two simple lemmas. First of all, we would like to obtain some result on the estimate of the eventual upper bound of solutions of Eq. (2.1).

**Lemma 2.2** *If  $\alpha + \beta > 1$ , then  $\limsup_{t \rightarrow +\infty} x_t \leq \beta[c_1 e(1 - \alpha)]^{-1}$ .*

**Proof** Clearly, for  $t \geq 0$ , we have

$$x_{t+1} \leq \alpha x_t + \beta x_{t-2} e^{-c_1 x_{t-2}}.$$

It is easy to show that  $x e^{-c_1 x} \leq (c_1 e)^{-1}$ . Hence

$$x_{t+1} \leq \alpha x_t + \beta(c_1 e)^{-1}.$$

This implies that

$$x_{t+1} \leq \alpha^{t+1} x_0 + \frac{\beta(c_1 e)^{-1}}{1 - \alpha} (1 - \alpha^{t+1}).$$

Since  $0 < \alpha < 1$ , we thus have

$$\limsup_{t \rightarrow +\infty} x_t \leq \frac{\beta}{c_1 e(1 - \alpha)}. \quad \blacksquare$$

In the following we define

$$F(x_t, x_{t-1}, x_{t-2}) = \alpha x_t + \beta x_{t-2} \exp(-c_1 x_{t-2} - c_2 x_t), \tag{2.9}$$

and

$$g(u) = F(u, u, u) - u = \alpha u + \beta u e^{-(c_1+c_2)u} - u. \quad (2.10)$$

Clearly  $g(u) = 0$  if and only if  $u = 0$  or  $x^*$ . Also,  $g(+\infty) < 0$ . Hence, for  $u > 0$ ,  $u \neq x^*$ , we have

$$(u - x^*)[F(u, u, u) - u] < 0.$$

This proves the following lemma.

**Lemma 2.3** *Let  $F$  be defined by (2.9); then for  $u > 0$ ,  $u \neq x^*$ .*

$$(u - x^*)[F(u, u, u) - u] < 0.$$

We are now ready to prove Theorem 2.2.

**Proof of Theorem 2.2** Let  $F$  be defined by (2.9); then

$$\begin{aligned} \frac{\partial F}{\partial x_t} &= \alpha - c_2 \beta x_{t-2} \exp(-c_1 x_{t-2} - c_2 x_t), \\ \frac{\partial F}{\partial x_{t-1}} &= 0, \\ \frac{\partial F}{\partial x_{t-2}} &= \beta(1 - c_1 x_{t-2}) \exp(-c_1 x_{t-2} - c_2 x_t) \end{aligned}$$

Since  $\beta < e(1 - \alpha)$ , and by Lemma 2.2,  $\limsup_{t \rightarrow +\infty} x_t \leq \beta[c_1 e(1 - \alpha)]^{-1}$ , we see that there is a  $T > 2$  such that, for  $t > T$ ,

$$x_{t-2} < c_1^{-1}.$$

In the following, we denote  $I = (0, c_1^{-1})$  and  $D = I^3$ ; then  $x^* \in I$  and  $\partial F / \partial x_{t-i} \geq 0$  for  $i = 1, 2$ . Note that for  $x_{t-2} \geq 0$ ,

$$x_{t-2} \exp(-c_1 x_{t-2} - c_2 x_t) \leq x_{t-2} \exp(-c_1 x_{t-2}) \leq (e c_1)^{-1}.$$

Hence, for  $x_t \geq 0$ ,  $x_{t-2} \geq 0$ ,

$$\frac{\partial F}{\partial x_t} \geq \alpha - \frac{c_2 \beta}{c_1 e} \geq 0.$$

This shows that  $F$  is increasing in each of its arguments when restricted to  $D$ . Lemma 2.3 asserts that condition (1.6) of Theorem 1.1 is also met. Since Eq. (2.1) is autonomous and by Lemma 2.2, for the set of initial data such that

$\max\{x_{-2}, x_{-1}, x_0\} > 0$ , there is a  $t_0 = t_0(x_{-2}, x_{-1}, x_0) > 0$ , such that for  $t \geq t_0$ , this solution satisfies

$$0 < x_{t-2} < c_1^{-1}.$$

If we denote  $\hat{x}_0 = x_{t_0}$ ,  $\hat{x}_{-1} = x_{t_0-1}$ ,  $\hat{x}_{-2} = x_{t_0-2}$ , and the solution with initial data  $x_0 = \hat{x}_0$ ,  $x_{-1} = \hat{x}_{-1}$  and  $x_{-2} = \hat{x}_{-2}$  as  $\hat{x}_t$ , then by Theorem 1.1, we have  $\lim_{t \rightarrow +\infty} \hat{x}_t = x^*$ . However,  $\hat{x}_t = \hat{x}_{t+t_0}$ . Therefore,  $\lim_{t \rightarrow +\infty} x_t = x^*$ . This proves the theorem. ■

In terms of the original model parameters the global stability conditions of Theorem 2.2 are equivalent to the following constraints on  $b$

$$\frac{\mu_a}{1 - \mu_i} < b < \min \left\{ e \frac{\mu_a}{1 - \mu_i}, e \frac{c_{ea}}{c_{pa}} \frac{1 - \mu_a}{1 - \mu_i} \right\}. \tag{2.11}$$

The first inequality is required for the existence of the positive equilibrium (2.2), which in the original parameters is given by the formula

$$x^* = \frac{1}{c_{ea} + c_{pa}} \ln \left( b \frac{1 - \mu_i}{\mu_a} \right).$$

This situation can be viewed as a bifurcation phenomenon in which this unique positive equilibrium emerges from the trivial (extinction) equilibrium  $x^* = 0$  as  $b$  is increased through the critical value  $\mu_a/(1 - \mu_i)$ . The result implied by Theorem 2.2 and Condition (2.11) is that the bifurcating positive equilibrium is *globally* stable at least for values of  $b$  not too much larger than the critical value. (The inequality (2.11) implicitly requires a constraint on the adult death rate, namely,  $\mu_a < ec_{ea}/(ec_{ea} + c_{pa})$ .) In Dennis et al. (1995) the region of local linearized stability of the positive equilibrium is computed and drawn in the  $(\mu_a, b)$  plane (see Fig. 1). The triangular set described by (2.11) represents a subregion in which *global* equilibrium stability is guaranteed to occur.

**References**

[1] B. Dennis, R.A. Desharnais, J.M. Cushing, and R.F. Costantino, Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments, *Ecol. Mongr.*, **65**, No. 3 (1995), 261–281.  
 [2] M.L.J. Hautus and T.S. Bolis, Solution to problem E2721, *The American Mathematical Monthly* **86** (1979), 865–866.  
 [3] V.L. Kocic and G. Ladas, *Global behavior of nonlinear difference equations of higher order with applications*, Kluwer Academic Publishers, Dordrecht, 1993.  
 [4] T. Park, D.B. Mertz, W. Grodzinski, and T. Prus, Cannibalistic predation in populations of flour beetles, *Physiological Zoology* **38** (1965), 289–321.