

Harmless Delays for Uniform Persistence

WANG WENDI*

*Department of Mathematics, Southwest Normal University,
Chongqing, China*

AND

MA ZHIEN[†]

*Department of Mathematics, Xi'an Jiaotong University,
Xi'an, China*

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This paper studies a two-dimensional predator-prey system with a finite number of discrete delays. Our purpose is to demonstrate that the time delays are harmless for uniform persistence of the solutions of the system. The results are obtained by constructing suitable persistence functionals. © 1991 Academic Press, Inc.

1. INTRODUCTION

A number of models in ecology can be formulated as systems of differential equations with time delays. One of the most important problems for this type of systems is to analyze the effect of time delays on the stability of the systems. This has been done in many papers. Reference [1] has shown that if a time delay is incorporated into the resource limitation of the logistic equation, then it has destabilizing effect on the stability of the system. In papers [2-4], criteria are established which when satisfied will imply an equilibrium is stable for all delays. Papers [6-8] have shown that for some systems the stability switches can happen many times and the systems will eventually become unstable when time delays increase. Paper [5] has shown that for certain values of the delay, there occurs an unstable equilibrium with periodic oscillations.

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In this paper we consider a predator–prey system of Lotka–Volterra type with a finite number of discrete delays. Our purpose is to show that there will be no change in uniform persistence of the system when the delays vary. Our results are obtained by considering the orbits of the system in the coordinate plane instead of the space of continuous functions, although delay differential equations often have some good properties in the space of continuous functions.

2. ANALYSIS OF UNIFORM PERSISTENCE

Consider the predator–prey system

$$\begin{aligned} \dot{x}(t) &= x(t) \left[r_1 - \sum_{j=1}^m a_{1j}x(t - \tau_{1j}) - \sum_{j=1}^m b_{1j}y(t - \rho_{1j}) \right] \\ \dot{y}(t) &= y(t) \left[r_2 + \sum_{j=1}^m a_{2j}x(t - \tau_{2j}) - \sum_{j=1}^m b_{2j}y(t - \rho_{2j}) \right] \end{aligned} \tag{2.1}$$

with initial conditions

$$\begin{aligned} x(s) &= \varphi(s) \geq 0, s \in [-\tau, 0]; & 0 < \varphi(0) \\ y(s) &= \psi(s) \geq 0, s \in [-\tau, 0]; & 0 < \psi(0), \end{aligned} \tag{2.2}$$

where r_1 and r_2 are real constants with $r_1 > 0$; $a_{ij}, b_{ij}, \tau_{ij}, \rho_{ij} (i = 1, 2; j = 1, 2, \dots, m)$ are non-negative constants. Not all of a_{1j} and not all of $b_{2j} (j = 1, 2, \dots, m)$ are zero; Both $\varphi(s)$ and $\psi(s)$ are continuous on the interval $[-\tau, 0]$ in which

$$\tau = \max\{\tau_{ij}, \rho_{ij} : i = 1, 2, j = 1, 2, \dots, m\}.$$

If all of the delays τ_{ij} and ρ_{ij} are zero, then the system (2.1) will simplify to an autonomous system of the form

$$\begin{aligned} \dot{x}(t) &= x(t) \left[r_1 - \sum_{j=1}^m a_{1j}x - \sum_{j=1}^m b_{1j}y \right] \\ \dot{y}(t) &= y(t) \left[r_2 + \sum_{j=1}^m a_{2j}x - \sum_{j=1}^m b_{2j}y \right]. \end{aligned} \tag{2.3}$$

It is well known that system (2.3) is uniformly persistent if the conditions

$$r_1 \sum_{j=1}^m a_{2j} + r_2 \sum_{j=1}^m a_{1j} > 0 \tag{2.4}$$

$$r_1 \sum_{j=1}^m b_{2j} - r_2 \sum_{j=1}^m b_{1j} > 0 \tag{2.5}$$

are satisfied. In fact, under these conditions the positive equilibrium of (2.3) is globally asymptotically stable [9]. Furthermore, it is not persistent if either of the inequalities

$$r_1 \sum_{j=1}^m a_{2j} + r_2 \sum_{j=1}^m a_{1j} < 0 \tag{2.6}$$

$$r_1 \sum_{j=1}^m b_{2j} - r_2 \sum_{j=1}^m b_{1j} < 0 \tag{2.7}$$

holds.

In this section we show that the conditions which guarantee the uniform persistence of system (2.3) will also ensure the uniform persistence of the system (2.1) for all values of the delays.

Let $z(t) = (x(t), y(t))^T$ denote the solution of system (2.1) corresponding to the initial conditions (2.2), where T represents the transpose of a vector.

DEFINITION 2.1. System (2.1) is said to be uniformly persistent if there exists a compact region $D \subset \text{int } R_+^2$ such that every solution $z(t)$ of (2.1) with the initial conditions (2.2) eventually enters and remains in the region D . The system is said to be not persistent if there exists a solution $z(t)$ such that the distance $d(z(t), \partial R_+^2)$ of $z(t)$ from the boundary of R_+^2 tends to zero as t approaches infinity.

LEMMA 2.1. Every solution $z(t)$ of system (2.1) with initial conditions (2.2) exists in the interval $[0, +\infty)$ and remains positive for all $t \geq 0$.

Proof. It is true because

$$x(t) = x(0) \exp \left\{ \int_0^t \left[r_1 - \sum_{j=1}^m a_{1j} x(s - \tau_{1j}) - \sum_{j=1}^m b_{1j} y(s - \rho_{1j}) \right] ds \right\}$$

$$y(t) = y(0) \exp \left\{ \int_0^t \left[r_2 + \sum_{j=1}^m a_{2j} x(s - \tau_{2j}) - \sum_{j=1}^m b_{2j} y(s - \rho_{2j}) \right] ds \right\}$$

and $x(0) > 0, y(0) > 0$.

LEMMA 2.2. Every solution $z(t)$ of system (2, 1) with initial conditions (2.2) is bounded for all $t \geq 0$ and all of these solutions are ultimately bounded.

Proof. Because a_{1j} and b_{2j} ($j = 1, 2, \dots, m$) in system (2.1) are non-negative, not all of a_{1j} are zero, and not all of b_{2j} are zero we assume $a_{11} > 0$ and $b_{21} > 0$ without loss of generality. By Lemma 2.1 we have

$$\dot{x}(t) < x(t) [r_1 - a_{11} x(t - \tau_{11})]. \tag{2.8}$$

Taking $M^* = (1 + r_1)/a_{11}$. Then for any $t^* \geq 0$, if $x(t) \geq M^*$ for all $t \geq t^*$, (2.8) implies that $\dot{x}(t) < -x(t)$ for all $t \geq t^* + \tau$. This will lead to a contradiction. Hence there must exist a $t_1 \geq t^*$ such that $x(t_1) < M^*$. If $x(t) \leq M^*$ for all $t \geq t_1$, then $x(t)$ is bounded. If not, suppose $x(\bar{t}_1) > M^*$, where $\bar{t}_1 > t_1$. Then from the above discussion there exists t_1^* and t_1^{**} such that $x(t_1^*) = x(t_1^{**}) = M^*$ and $x(t) > M^*$ for all $t_1^* < t < t_1^{**}$, where $t_1 \leq t_1^* < \bar{t}_1 < t_1^{**}$. Now suppose $x(t)$ with $t_1^* \leq t \leq t_1^{**}$ attains its maximum at \bar{t}_2 , $t_1^* < \bar{t}_2 < t_1^{**}$. Then since $\dot{x}(\bar{t}_2) = 0$, (2.1) implies

$$r_1 - \sum_{j=1}^m a_{1j}x(t_2 - \tau_{1j}) - \sum_{j=1}^m b_{1j}y(t_2 - \rho_{1j}) = 0.$$

This leads to

$$x(t_2 - \tau_{11}) < r_1/a_{11} < M^*.$$

From Lemma 2.1 we have $\dot{x}(t)/x(t) < r_1$. Then an integration from $t_2 - \tau_{11}$ to t_2 on both sides of the inequality yields

$$x(t_2) < x(t_2 - \tau_{11}) \exp(r_1 \tau_{11}) < M^* \exp(r_1 \tau_{11}) \equiv M.$$

Since M is independent of the interval $[t_1^*, t_1^{**}]$, we have $x(t) < M$ for all $t \geq t_1$. Therefore $x(t)$ is also bounded. Furthermore, $M > M^*$ implies that in any case $x(t) < M$ for all $t \geq t_1$ holds

Using the inequality

$$\dot{y}(t) < y(t) \left(r_2 + \sum_{j=1}^m a_{2j}M - \sum_{j=1}^m b_{2j}y(t - \rho_{2j}) \right) \quad \text{for } t \geq t_1 + \tau$$

and by a procedure similar to the discussion above, we can determine a constant $N > 0$ and a $t_2 \geq t_1 + \tau$ such that $y(t) < N$ for all $t \geq t_2$. Consequently $y(t)$ is bounded and

$$0 < x(t) < M; \quad 0 < y(t) < N \quad \text{for } t \geq t_2. \tag{2.9}$$

This completes the proof.

Our main result is the following

THEOREM 2.1. *If conditions (2.4) and (2.5) are satisfied, then system (2.1) is uniformly persistent.*

If either (2.6) or (2.7) is satisfied, then the system is not persistent.

Proof. Part 1: In this part we show that the system is uniformly persistent if conditions (2.4) and (2.5) are satisfied.

Construct a continuous functional

$$\begin{aligned}
 V_1(t) = V_1(t, x, y) = & (x, t) \sum_{j=1}^m a_{2j} (y(t)) \sum_{j=1}^m a_{1j} \\
 & \times \exp \left(- \sum_{j,k=1}^m a_{2j} b_{1k} \int_{t-\rho_{1k}}^t y(s) ds - \sum_{j,k=1}^m a_{2j} a_{1k} \int_t^{\tau_{1k}} x(s) ds \right. \\
 & \left. + \sum_{j,k=1}^m a_{1j} a_{2k} \int_{t-\tau_{2k}}^t x(s) ds - \sum_{j,k=1}^m a_{1j} b_{2k} \int_{t-\rho_{2k}}^t y(s) ds \right) \quad (2.10)
 \end{aligned}$$

Calculating the derivative of V_1 with respect to t along the solution of system (2.1) we have

$$\dot{V}_1(t) = V_1(t) \left(r_1 \sum_{j=1}^m a_{2j} + r_2 \sum_{j=1}^m a_{1j} - \sum_{j,k=1}^m (a_{2j} b_{1k} + a_{1j} b_{2k}) y(t) \right).$$

Put

$$\eta_1 = r_1 \sum_{j=1}^m a_{2j} + r_2 \sum_{j=1}^m a_{1j}.$$

Then $\eta_1 > 0$ by assumption. Choose $0 < h_1 < N$ small enough such that if $0 < y(t) \leq h_1$ we have

$$\dot{V}_1(t) > (\eta_1/2) V_1(t). \quad (2.11)$$

Now construct another continuous functional

$$\begin{aligned}
 V_2(t) = & (x(t)) \sum_{j=1}^m b_{2j} (y(t)) - \sum_{j=1}^m b_{1j} \exp \left(- \sum_{j,k=1}^m b_{2j} a_{1k} \int_{t-\tau_{1k}}^t x(s) ds \right. \\
 & - \sum_{j,k=1}^m b_{2j} b_{1k} \int_{t-\rho_{1k}}^t y(s) ds - \sum_{j,k=1}^m b_{1j} a_{2k} \int_{t-\tau_{2k}}^t x(s) ds \\
 & \left. + \sum_{j,k=1}^m b_{1j} b_{2k} \int_{t-\rho_{2k}}^t y(s) ds \right). \quad (2.12)
 \end{aligned}$$

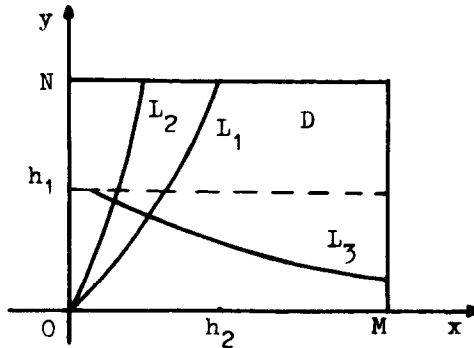


FIG. 1. The region D constructed in the proof of Theorem 2.1.

By similar arguments as above, there exists an $h_2, 0 < h_2 < M$, such that if $0 < x(t) \leq h_2$ we have

$$\dot{V}_2(t) > \eta_2 V_2(t)/2, \tag{2.13}$$

where

$$\eta_2 = r_1 \sum_{j=1}^m b_{2j} - r_2 \sum_{j=1}^m b_{1j} > 0.$$

Set

$$\begin{aligned} M_1 &= \exp\left(\sum_{j,k=1}^m a_{1j} a_{2k} M \tau\right) \\ N_1 &= \exp\left(\sum_{j,k=1}^m b_{1j} b_{2k} N \tau\right) \\ m_1 &= \exp\left(-\sum_{j,k=1}^m (a_{2j} a_{1k} M \tau + a_{2j} b_{1k} N \tau + a_{1j} b_{2k} N \tau)\right) \\ n_1 &= \exp\left(-\sum_{j,k=1}^m (b_{2j} a_{1k} M \tau + b_{2j} b_{1k} N \tau + b_{1j} a_{2k} M \tau)\right) \end{aligned}$$

Consider an orbit $z(t) = (x(t), y(t))^T$ of system (2.1) with initial conditions (2.2). By Lemmas 2.1 and 2.2 there exists a $t_0 > \tau$ such that

$$0 < x(t) < M; \quad 0 < y(t) < N \quad \text{for all } t \geq t_0 - \tau. \tag{2.14}$$

Then it follows from (2.10), (2.12), and (2.14) that

$$m_1(x(t))^{\alpha_1}(y(t))^{\beta_1} \leq V_1(t) \leq (x(t))^{\alpha_1}(y(t))^{\beta_1} M_1 \tag{2.15}$$

$$n_1(x(t))^{\alpha_2}(y(t))^{-\beta_2} \leq V_2(t) \leq (x(t))^{\alpha_2}(y(t))^{-\beta_2} N_1, \tag{2.16}$$

where

$$\begin{aligned} \alpha_1 &= \sum_{j=1}^m a_{2j}; & \alpha_2 &= \sum_{j=1}^m b_{2j} \\ \beta_1 &= \sum_{j=1}^m a_{1j}; & \beta_2 &= \sum_{j=1}^m b_{1j} \end{aligned}$$

and $t \geq t_0$. Now we construct a region D as the following. First, define curve L_1 by

$$L_1: x^{\alpha_2} y^{-\beta_2} = h_2^{\alpha_2} N^{-\beta_2} \quad \text{for } 0 < y \leq N.$$

Choose $C_1 > 0$ small enough so that $C_1 < n_1 h_2^{x_2} N^{-\beta_2}$ and define curve L_2 by

$$L_2: x^{x_2} y^{-\beta_2} = C_1/N_1 \quad \text{for } 0 < y \leq N.$$

Suppose that the intersection point of curve L_2 with $y = h_1$ is (\bar{x}, h_1) . Select such a C_2 that

$$0 < C_2 < m_1 \bar{x}^{x_1} h_1^{\beta_1}$$

and then define L_3 by

$$L_3: x^{x_1} y^{\beta_1} = C_2/M_1 \quad \text{for } 0 < x \leq M.$$

Let D denote the region enclosed by L_2 , L_3 , $x = M$, and $y = N$. In the following we prove that the orbit $z(t)$ eventually enters and remains in the region D . The proof is divided into four steps.

(1) We first show that if there is a $t_0^* > t_0$ such that $z(t_0^*)$ lies in the right side of curve L_1 , then the orbit $z(t)$ will remain in the right side of curve L_2 for all $t \geq t_0^*$. In fact, if $z(t)$ meets L_2 at t_2 , $t_2 > t_0^*$, then there exists a t_1 , $t_0^* < t_1 < t_2$, such that $z(t)$ meets L_1 at $t = t_1$ and lies between L_1 and L_2 for all $t_1 < t < t_2$. By the inequality (2.13) we have

$$V_2(t_1) < V_2(t_2). \tag{2.17}$$

On the other hand

$$\begin{aligned} V_2(t_2) &\leq (x(t_2))^{x_2} (y(t_2))^{-\beta_2} N_1 = C_1 < n_1 h_2^{x_2} N^{-\beta_2} \\ &= n_1 (x(t_1))^{x_2} (y(t_1))^{-\beta_2} \leq V_2(t_1). \end{aligned}$$

This is in contradiction to the inequality (2.17).

(2) In this step we show that if there is a $t_3 > t_0$ such that $y(t_3) > h_1$ and $z(t)$ lies in the right side of curve L_2 for all $t \geq t_3$ $z(t)$ cannot meet L_3 for all $t \geq t_3$. In fact, if $z(t)$ meets L_3 at t_5 , then there exists a t_4 , $t_3 < t_4 < t_5$, such that $y(t_4) = h_1$ and $y(t) < h_1$ for $t_4 < t < t_5$. By (2.11) we have

$$V_1(t_4) < V_1(t_5) \leq (x(t_5))^{x_1} (y(t_5))^{\beta_1} M_1 = C_2. \tag{2.18}$$

But since $z(t)$ lies in the right side of L_2 and $y(t_4) = h_1$, we have

$$V_1(t_4) \geq m_1 (x(t_4))^{x_1} (y(t_4))^{\beta_1} > m_1 \bar{x}^{x_1} h_1^{\beta_1} > C_2.$$

This contradicts (2.18).

(3) In this step we show that if there is a $t_6 > t_0$ such that $y(t_6) \leq h_1$, then there exists a $t_7 > t_6$ such that $y(t_7) > h_1$. Assuming the contrary we

have $y(t) \leq h_1$ for all $t \geq t_6$. Then (2.11) implies that $V_1(t)$ tends to infinity as t tends to infinity. But this is impossible since (2.14) and (2.15) imply that $V_1(t)$ is bounded.

(4) In this step we show that if there is a $t'_0 > t_0$ such that $z(t'_0)$ lies in the left side of the curve L_1 and $y(t'_0) > h_1$, then there exists a $t'_1 > t_0$ such that $x(t'_1) > h_2$.

Define curve L'_1 by

$$L'_1: x^{\alpha_2} y^{-\beta_2} = (x(t'_0))^{\alpha_2} (y(t'_0))^{-\beta_2} \quad \text{for } 0 < y \leq N.$$

Select C'_1 small enough so that

$$0 < C'_1 < n_1 (x(t'_0))^{\alpha_2} (y(t'_0))^{-\beta_2}$$

and define curve L'_2 by

$$L'_2: x^{\alpha_2} y^{-\beta_2} = C'_1 / N_1 \quad \text{for } 0 < y \leq N.$$

Suppose that L'_2 intersects $y = h_1$ at point (\bar{x}', h_1) . Choose C'_2 so that

$$0 < C'_2 < m_1 (\bar{x}')^{\alpha_1} h_1^{\beta_1}.$$

Then define curve L'_3 by

$$L'_3: x^{\alpha_1} y^{\beta_1} = C'_2 / M_1 \quad \text{for } 0 < x \leq M$$

Repeating the procedure of steps (1) and (2) we know that $z(t)$ can meet neither L'_2 nor L'_3 . This implies that there exists an $\varepsilon > 0$ such that $y(t) \geq \varepsilon$ for all $t \geq t'_0$. It follows from (2.16) that $V_2(t)$ is bounded for $t \geq t'_0$.

If $0 < x(t) \leq h_2$ for all $t \geq t'_0$, then (2.13) implies that $V_2(t)$ tends to infinity as t tends to infinity. This contradiction yields the existence of t'_1 satisfying $t'_1 > t_0$ and $x(t'_1) > h_2$.

In summary, if for some $t > t_0$ $z(t)$ lies in the right side of curve L_1 and above the line $y = h_1$, then (2.14) and steps (3) and (4) imply that $z(t)$ will remain in the region D as t increases. This is what we need. Furthermore, if $z(t_1)$ lies below the line $y = h_1$ for some $t_1 > t_0$ step (3) implies that there is a $t_2 > t_1$ such that $z(t_2)$ lies above $y = h_1$. It follows from step (4) that there is a $t_3 \geq t_2$ such that $z(t_4)$ lies in the right side of curve L_1 . Since step (1) implies that $z(t)$ lies in the right side of curve L_2 for all $t \geq t_4$ and step (3) implies that there is a $t_5 \geq t_4$ such that $y(t_5) > h_1$. It follows from step (2) that $z(t)$ will remain in the region D for all $t \geq t_5$. Finally, if $z(t)$ lies in the left of curve L_1 and above the line $y = h_1$, by similar arguments we can conclude $z(t)$ eventually enters and remains in the region D . Since any orbit of system (2.1) corresponding to the initial conditions (2.2) has this property, we can conclude that system (2.1) is uniformly persistent. This completes the proof.

Part 2: Suppose that (2.6) holds. It is easy to get

$$\dot{V}_1(t) < \eta_1 V_1(t),$$

where $\eta_1 < 0$. It follows that $V_1(t)$ tends to zero as t tends to infinity. Then (2.15) implies

$$\lim_{t \rightarrow \infty} (x(t))^{\alpha_1} (y(t))^{\beta_1} = 0.$$

Consequently

$$\lim_{t \rightarrow \infty} d(z(t), \partial R_+^2) = 0.$$

If (2.7) holds then by a similar method we can conclude that system (2.1) is not persistent. This completes the proof.

COROLLARY. *The system*

$$\dot{x}(t) = x(t) \left(r - \sum_{j=1}^m a_j x(t - \tau_j) \right)$$

is uniformly persistent if a_j and $\tau_j (j = 1, 2, \dots, m)$ are non-negative constants, r is a positive constant and not all of $a_j (j = 1, 2, \dots, m)$ are zero.

Remark. Using this corollary we know that the system

$$\dot{N}(t) = N(t)(a - bN(t) - N(t - 1))$$

is uniformly persistent under the assumption that a and b are positive constants. Therefore, for $b < 1$ it is impossible that there exists a sequence $t_k \rightarrow +\infty$ as $k \rightarrow +\infty$ such that $N(t_k) \rightarrow 0$ as $k \rightarrow +\infty$. Hence, one of the open questions suggested by [10] has been solved.

Now we introduce the notation $\langle f \rangle_t$ for any bounded continuous function f by defining $\langle f \rangle_t = \int_0^t f(s) ds/t$.

If (2.4) and (2.5) hold, system (2.1) is uniformly persistent. In this situation, there is a unique positive equilibrium (x^*, y^*) in the system where

$$x^* = \left(r_1 \sum_{j=1}^m b_{2j} - r_2 \sum_{j=1}^m b_{1j} \right) / \sum_{j,k=1}^m (a_{1j} b_{2k} + a_{2j} b_{1k})$$

$$y^* = \left(r_2 \sum_{j=1}^m a_{1j} + r_1 \sum_{j=1}^m a_{2j} \right) / \sum_{j,k=1}^m (a_{1j} b_{2k} + a_{2j} b_{1k}).$$

THEOREM 2.2. *Let (2.4) and (2.5) hold. Then any solution $(x(t), y(t))^T$ of system (2.1) corresponding to the initial conditions (2.2) satisfies*

$$\lim_{t \rightarrow \infty} \langle x \rangle_t = x^*; \quad \lim_{t \rightarrow \infty} \langle y \rangle_t = y^*.$$

Proof. From system (2.1) we have

$$\begin{aligned} \dot{x}/x &= r_1 - \sum_{j=1}^m a_{1j}x(t - \tau_{1j}) - \sum_{j=1}^m b_{1j}y(t - \rho_{1j}) \\ \dot{y}/y &= r_2 + \sum_{j=1}^m a_{2j}x(t - \tau_{2j}) - \sum_{j=1}^m b_{2j}y(t - \rho_{2j}). \end{aligned}$$

Integrating both sides of the equations from 0 to t and deviding the equations by t we get

$$\begin{aligned} \ln(x(t)/x(0))/t &= r_1 - \sum_{j=1}^m a_{1j} \int_0^t x(t - \tau_{1j}) dt/t - \sum_{j=1}^m b_{1j} \int_0^t y(t - \rho_{1j}) dt/t \\ \ln(t(t)/y(0))/t &= r_2 + \sum_{j=1}^m a_{2j} \int_0^t x(t - \tau_{2j}) dt/t - \sum_{j=1}^m b_{2j} \int_0^t y(t - \rho_{2j}) dt/t. \end{aligned}$$

It follows that

$$\begin{aligned} \langle x \rangle_t &= \left(r_1 \sum_{j=1}^m b_{2j} - r_2 \sum_{j=1}^m b_{1j} + \sum_{j=1}^m b_{2j}P(t) - \sum_{j=1}^m b_{1j}Q(t) \right) / H \\ \langle y \rangle_t &= \left(r_2 \sum_{j=1}^m a_{1j} + r_1 \sum_{j=1}^m a_{2j} + \sum_{j=1}^m a_{1j}Q(t) + \sum_{j=1}^m a_{2j}P(t) \right) / H, \end{aligned}$$

where

$$\begin{aligned} P(t) &= -\ln(x(t)/x(0))/t + \left(\sum_{j=1}^m \left(-\int_{-\tau_{1j}}^0 x(s) ds - \int_{-\rho_{1j}}^0 y(s) ds \right. \right. \\ &\quad \left. \left. + \int_{t-\tau_{1j}}^t x(s) ds + \int_{t-\rho_{1j}}^t y(s) ds \right) \right) / t \\ Q(t) &= -\ln(y(t)/y(0))/t + \left(\sum_{j=1}^m \left(\int_{-\tau_{2j}}^0 x(s) ds - \int_{-\rho_{2j}}^0 y(s) ds \right. \right. \\ &\quad \left. \left. + \int_{t-\rho_{2j}}^t y(s) ds - \int_{t-\tau_{2j}}^t x(s) ds \right) \right) / t \\ H &= \sum_{j,k=1}^m (a_{1j}b_{2k} + a_{2j}b_{1k}). \end{aligned}$$

By (2.9) both $x(t)$ and $y(t)$ are bounded from above. From Theorem 2.1 they have positive bound from below. Therefore,

$$\lim_{t \rightarrow \infty} P(t) = 0; \quad \lim_{t \rightarrow \infty} Q(t) = 0.$$

Consequently $\langle x \rangle_t$ tends to x^* and $\langle y \rangle_t$ tends to y^* as t tends to infinity. This completes the proof of Theorem 2.2.

EXAMPLE. Consider the system

$$\begin{aligned} \dot{x}(t) &= x(t)(16 - x(t) - 4x(t - \tau) - y(t)) \\ \dot{y}(t) &= y(t)(-2 + x(t) - y(t)). \end{aligned} \quad (2.19)$$

It is uniformly persistent since both (2.4) and (2.5) are satisfied. In the following we show that the stability of the positive equilibrium of the system will be changed and positive periodic solutions occur as the delay increases.

The positive equilibrium of system (2.19) is $(\frac{4}{3}, 1)$. The linearization of the system with respect to this equilibrium is

$$\begin{aligned} \dot{x}(t) &= -3x(t) - 12x(t - \tau) - 3y(t) \\ \dot{y}(t) &= x(t) - y(t). \end{aligned} \quad (2.20)$$

The characteristic equation of (2.20) is

$$\lambda^2 + 4\lambda + 6 + 12(\lambda + 1)e^{-\lambda\tau} = 0. \quad (2.21)$$

Substituting $\lambda = \alpha + i\beta$ ($\beta \geq 0$) into the equation and separating its real and imaginary parts we obtain

$$\begin{aligned} \alpha^2 - \beta^2 + 4\alpha + 6 + 12e^{-\alpha\tau}[(\alpha + 1)\cos\beta\tau + \beta\sin\beta\tau] &= 0 \\ 2\alpha\beta + 4\beta + 12e^{-\alpha\tau}[\beta\cos\beta\tau - (\alpha + 1)\sin\beta\tau] &= 0. \end{aligned} \quad (2.22)$$

Setting $\alpha = 0$ in (2.22) and solving $\cos\beta\tau$, $\sin\beta\tau$ we get

$$\begin{aligned} \cos\beta\tau &= -(3\beta^2 + 6)/(12\beta^2 + 12) \\ \sin\beta\tau &= (\beta^3 - 2\beta)/(12\beta^2 + 12). \end{aligned} \quad (2.23)$$

An application of identity $\cos^2\beta\tau + \sin^2\beta\tau = 1$ yields

$$u^2 - 140u - 108 = 0, \quad (2.24)$$

where $u = \beta^2$. From the above procedure we see that $\lambda = i\beta$ is a root of (2.21) if and only if β satisfies (2.24) and β , τ satisfy (2.23). It is obvious

that (2.24) has a unique positive root $u = u_0$. Set $\beta_0 = \sqrt{u_0}$. Substituting it into (2.23) and solving τ from (2.23) we know that there is a unique solution τ_0 with $\pi/2 < \beta_0 \tau_0 < \pi$ in (2.23). Furthermore, a tedious calculation yields $\dot{\alpha}(\tau_0) > 0$. Since the two roots of Eq. (2.21) have negative real parts at $\tau = 0$, it follows that the equilibrium $(\frac{4}{3}, 1)$ of system (2.19) is asymptotically stable if $0 < \tau < \tau_0$, is unstable if $\tau > \tau_0$. Consequently, the theory of Hopf bifurcation implies that system (2.19) has a non-constant periodic solution for certain τ near τ_0 [11].

3. DISCUSSION

In this paper we have considered the two-dimensional system with arbitrarily finite number of time delays. We have shown that system (2.1) is uniformly persistent irrespective of the size of the delays.

The literature on ecological models with time delays is quite large. But most of the works are concerned with the stability of positive equilibria and the existence of positive periodic solutions of the models. Very few studies focus upon the persistence of the systems. In this paper we have analyzed the effect of the time delays on the uniform persistence of the system. Theorem 2.1 and the example indicate that although the asymptotic behavior of the system may be complex as the delays increase, for example, locally asymptotic stability of positive equilibrium may be lost and positive periodic solutions exist, the system remains uniformly persistent; i.e., the time delays are harmless for the uniform persistence. Theorem 2.2 may be compared with the result for the system without time delays, i.e., system (2.3). Conditions (2.4) and (2.5) imply that the solution $(x(t), y(t))^T$ of system (2.3) with positive initial values tends to (x^*, y^*) as t tends to infinity. For system (2.1) in which the time delays occur, the analogue of that result is obtained of the solution is replaced by temporal average $(\langle x \rangle_t, \langle y \rangle_t)$ of the solution of system (2.1). Finally, it is worthwhile to mention that there are arbitrarily many delays in system (2.1). In this situation, the analysis for local stability of equilibria is often difficult and the conditions for no stability switching are severe.

We expect a similar technique to work in higher-dimensional systems and the systems with distributed delays. We leave this investigation for future work.

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