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UNIFORM PERSISTENCE IN NONAUTONOMOUS DELAY DIFFERENTIAL KOLMOGOROV-TYPE POPULATION MODELS

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Dedicated to Paul Waltman on the occasion of his 60th birthday

ABSTRACT. In this paper we establish sufficient conditions for uniform persistence in nonautonomous Kolmogorov-type delayed population models. The method involves the construction of a set of proper autonomous ordinary differential systems whose solutions can serve as lower or upper bounds for the delayed system in certain regions. The results are new even for nonautonomous ordinary differential systems.

1. Introduction. A basic and important ecological question associated with the study of mathematical population interaction models is the long term coexistence of the involved populations. Mathematically, this is equivalent to the so-called persistence of the populations. Roughly speaking, we say a population $x(t)$ is persistent if

$$\liminf_{t\to+\infty} x(t) > 0, \tag{1.1}$$

and we say a system is persistent if all its populations are persistent. Most of the existing persistence results are established for autonomous systems of ordinary differential equations which make use of the dynamics in Euclidean spaces. Recently, the persistence theory of nonautonomous and infinite dimensional systems has also received some attention. An excellent survey of such activities is given by Hutson and Schmitt [**16**]. Detailed persistence theory for systems of autonomous ordinary differential equations can be found in Butler et al. [**2**] and [**3**]. A general persistence theory for autonomous infinite dimensional systems is documented in [**14**]. See also [**19**].

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In this paper we consider the persistence aspect of general nonautonomous delay differential Kolmogorov-type population interaction models of the form

$$x'(t) = x(t)f(t, x_t, y_t),$$
$$y'(t) = y(t)g(t, x_t, y_t), \tag{1.2}$$

where f and g are continuously differentiable with respect to (t, x_t, y_t). Here $x_t(\theta) = x(t+\theta)$, $y_t(\theta) = y(t+\theta)$, $\theta \in [-\tau, 0]$, $\tau < +\infty$. When there exists no delay, standard assumptions for (1.2) to be competition or predator-prey models are well documented in [**10**].

Persistence results for autonomous delay differential population models are documented in Burton and Hutson [**1**] for Lotka-Volterra type systems with infinite delay, and in Cao et al. [**4**] for two species Kolmogorov-type systems with a single discrete delay, and in Wang and Ma [**21**] for Lotka-Volterra type systems with discrete delays. The results in the first two papers exploit the dynamical system properties of the solution maps of the considered systems, while Wang and Ma's results make use of the autonomous Lotka-Volterra structure and discrete delay properties.

Since system (1.2) is nonautonomous, the general theory of Hale and Waltman [**14**] no longer applies and construction of persistence functionals becomes daunting. To overcome these difficulties we construct a set of proper autonomous ordinary differential systems whose solutions can serve as lower or upper bounds for the delayed system (1.2) in certain regions. Such comparison arguments may be extended to higher dimensional systems (multi-species interaction models). Our results are new even for nonautonomous ordinary differential systems. They are also sharp in the sense that when they are applied to the well-known autonomous Lotka-Volterra type ordinary differential systems, the conditions become both necessary and sufficient.

In the next section, we describe our models and definitions in detail and consider the persistence question for a single species model. In Section 3, we obtain persistence results for competition interaction population models. Section 4 is the main part of this paper, where we present persistence results for system (1.2) when it is used to model predator-prey interactions. The paper is ended with a brief discussion section.

2. Models and preliminaries. We view $x(t)$ and $y(t)$ in system (1.2) as population densities at time t for species x and y, respectively. We therefore consider (1.2) with initial conditions

$$\begin{aligned} x(\theta) &= \varphi_1(\theta) \geq 0, \qquad \theta \in [-\tau, 0], \\ y(\theta) &= \varphi_2(\theta) \geq 0, \qquad \theta \in [-\tau, 0], \end{aligned} \tag{2.1}$$

where φ_1 and φ_2 are continuous. Existence, uniqueness and continuous dependence of solutions are assured by Theorems 2.2.1–2.2.3 in Hale [**13**]. Moreover, it is easy to show that solutions are nonnegative in their maximum interval of existence, and if $\varphi_1(0) > 0$ and/or $\varphi_2(0) > 0$, then $x(t) > 0$ and/or $y(t) > 0$ in the maximum interval of existence.

In the following, we place proper assumptions on functions f and g to make it consistent with models of competition and predator-prey interactions (see [**10**]). We denote $C^+ = C([-\tau, 0], R^+)$ the set of continuous functions that map $[-\tau, 0]$ into $R^+ = \{x : x \geq 0\}$ with norm

$$||\phi|| = \max\{\phi(\theta) : \theta \in [-\tau, 0]\}, \qquad \phi \in C^+.$$

Competition assumptions. The following assumptions on f and g render (1.2) a competition model.

(C1$_f$): There exist positive constants $\delta_1 = \delta_1(f)$, $\delta_2 = \delta_2(f)$, $K_1 = K_1(f)$, $K_2 = K_2(f)$, with $K_1 < K_2$ such that for all $t \geq 0$,

$$f(t, x_t, 0) > \delta_1, \qquad \text{for } x(t+\theta) \in [0, K_1], \qquad \theta \in [-\tau, 0], \tag{2.2}$$

and

$$f(t, x_t, 0) < -\delta_2, \qquad \text{for } x(t+\theta) \in [K_2, \infty), \qquad \theta \in [-\tau, 0]. \tag{2.3}$$

(C2$_f$): $f(t, x_t, 0) \geq f(t, x_t, y_t)$ for all $t \geq 0$, x_t, $y_t \in C^+$, and there exist positive constants $\delta_3 = \delta_3(f)$ and $k = k(f)$ such that for all $t \geq 0$, $x_t \in C^+$

$$f(t, x_t, y_t) < -\delta_3, \qquad \text{for } y(t+\theta) \in [k, \infty), \qquad \theta \in [-\tau, 0]. \tag{2.4}$$

Also, for each pair (x_0, y_0), $x_0 > 0$, $y_0 > 0$, there exists $l(x_0, y_0)$ such that

$$f(t, x_t, y_t) \geq -l(x_0, y_0), \qquad \text{for } ||x_t|| \leq x_0, \qquad ||y_t|| \leq y_0. \tag{2.5}$$

($C3_f$): There exists a positive constant $M = M(f)$, such that

$$f(t, x_t, y_t) \le M, \qquad \text{for } t \ge 0, \qquad x_t, y_t \in C^+. \tag{2.6}$$

$C1_f$ assumes that the growth rate for small population in the absence of competitors is positive, while there is a self-crowding effect creating a negative growth rate at high population levels, even in the absence of competition. $C2_f$ states that the existence of y is negative to the growth of x and when the population of y is large, the growth rate of x becomes negative. (2.5) assumes that the negative fluctuation effect on the growth rate of x is limited for limited population densities of species x and y, while $C3_f$ assumes that there is an upper bound for the growth rate of x.

In ($C1_f$)–($C3_f$) we replace f by g and denote the resulting assumptions as ($C1_g$)–($C3_g$), respectively. When system (1.2) satisfies ($C1_f$)–($C3_f$) and ($C1_g$)–($C3_g$), we call it a competition system.

Predator-prey assumptions. The following assumptions on f and g make (1.2) a predator-prey model.

(P1): The same as ($C1_f$).

(P2): The same as ($C2_f$).

(P3): The same as ($C3_f$).

(P4): $g(t, x_t, 0) \ge g(t, x_t, y_t)$, $t > 0$, $x_t, y_t \in C^+$.

(P5): There is a continuous function $m(x)$ for $x \ge 0$, with $m(0) < 0$, such that for each $x_0 > 0$, $t \ge 0$, x_t, $y_t \in C^+$, $g(t, x_t, y_t) \le m(x_0)$, when $||x_t|| \le x_0$.

(P4) assumes the existence of self-crowding effect for species y. (P5) says that the growth rate of y is uniformly limited by the prey density x. When prey is absent, predator density y decreases.

Remark 2.1. Clearly, ($C3_f$) implies that for $t \ge 0$, $x(t)$ is bounded by $x(0)e^{Mt}$, as long as $y(t)$ exists. For the competition model, the same conclusion applies to $y(t)$; therefore, $(x(t), y(t))$ exists for all $t \ge 0$. For predator-prey models, (P5) implies that $y(t)$ exists so long as $x(t)$ exists. A standard continuation argument indicates that $(x(t), y(t))$ also exists for all $t \ge 0$.

Definition 2.1. We say the population $x(t)$ in system (1.2) is *uniformly persistent*, if there are positive constants μ_1 and μ_2 (independent of initial conditions), $\mu_1 < \mu_2$, such that for large t we have $x(t) \in [\mu_1, \mu_2]$. The same definition applies to $y(t)$. And we say system (1.2) is uniformly persistent, if both $x(t)$ and $y(t)$ are so.

Equivalently, we say system (1.2) is uniformly persistent if there exists a compact region $D \subset \operatorname{int} R_+^2$ such that every solution of (1.2) with initial conditions satisfying (2.1) and $x(0) > 0$, $y(0) > 0$ will eventually enter and remain in region D. Please note the slight differences of our definition with that of Hale and Waltman [**14**]; here we also require that the system be dissipative. The above definition is used in Wang and Ma [**21**], and in [**1**], where it is called *permanently coexistent*.

Theorem 2.1. *Let* $F(t, x_t) = f(t, x_t, 0)$ *and let* f *satisfy* $(\mathrm{C1}_f)$–$(\mathrm{C3}_f)$. *Then the solution* $x(t)$ *of*

$$x'(t) = F(t, x_t), \qquad x_0 \in C^+, \qquad x(0) > 0$$

is uniformly persistent.

Proof. In other words, we need to show that there are two positive constants (independent of x_0) η_1 and η_2, $\eta_1 < \eta_2$, such that for large t (depending on x_0), $x(t) \in [\eta_1, \eta_2]$. We show first that we can choose $\eta_2 = K_2 e^{M\tau}$. From (2.3) in $(\mathrm{C1}_f)$ we see that for any $t_0 > 0$, there is a $t_1 > t_0$, such that $x(t_1) \le K_2$; otherwise, $x(t)$ tends to zero, contradicting (2.3). If for large t, $x(t) > \eta_2$, then there exist t_1, t_2, $t_2 > t_1 > 0$, such that

$$x(t_1) = K_2, \qquad x(t_2) = \eta_2, \qquad x'(t_2) \ge 0, \qquad x(t) \in [K_2, \eta_2]$$

for $t \in [t_1, t_2]$.

Since $(\mathrm{C3}_f)$, we have for $t \ge t_1$,

$$x(t) \le x(t_1) e^{M(t - t_1)},$$

which implies that $t_2 - t_1 \ge \tau$. However, by (2.3), we thus have

$$f(t_2, x_{t_2}, 0) < -\delta_2 < 0,$$

and hence $x'(t_2) < 0$, a contradiction.

Let $\eta_1 = K_1 \exp(-l(\eta_2 + 1)\tau)$, where $l(x) \equiv l(x, 0)$ as defined in $(\mathrm{C}2_f)$. We show now that for large t, $x(t) > \eta_1$. By (2.2), we see that for any $t_0 > 0$, there is a $t_1 > t_0$ such that $x(t_1) \geq K_1$; otherwise $x(t)$ will tend to infinity, contradicting (2.2). Assume that for $t \geq \bar{t} > \tau$, $x(t) \leq \eta_2 + 1$. If for large t, $x(t) < \eta_1$, then there are t_1 and t_2, $t_2 > t_1 > \bar{t} + \tau$, such that

$$x(t_1) = K_1, \qquad x(t_2) = \eta_1, \qquad x'(t_2) \leq 0, \qquad x(t) \in [\eta_1, K_1],$$

for $t \in [t_1, t_2]$.

Since (2.5), we have for $t \in [t_1, t_2]$,

$$x(t) > x(t_1) e^{-l(\eta_2+1)(t-t_1)}.$$

Hence,

$$t_2 - t_1 \geq \tau,$$

and by (2.2), we must have $x'(t_2) > 0$, a contradiction. □

3. Competition systems. In this section, we assume system (1.2) satisfies $(\mathrm{C}1_f)$–$(\mathrm{C}3_f)$, $(\mathrm{C}1_g)$–$(\mathrm{C}3_g)$. For convenience, we denote $\delta_{1f} = \delta_1(f)$, and similarly for δ_{2f}, K_{1f}, δ_{1g}, δ_{2g}, M_f, M_g, l_f, l_g, etc. We have the following dissipativity result for system (1.2).

Lemma 3.1. *Let $\eta_x = K_{2f} \exp(M_f \tau)$, $\eta_y = K_{2g} \exp(M_g \tau)$, and $(x(t), y(t))$ be a solution of* (1.2) *and* (2.1) *such that* $x(0) > 0$, $y(0) > 0$. *Then*

$$\limsup_{t\to+\infty} x(t) \leq \eta_x, \qquad \limsup_{t\to+\infty} y(t) \leq \eta_y. \tag{3.1}$$

Proof. We need only show that $\limsup_{t\to+\infty} x(t) \leq \eta_x$, since $\limsup_{t\to+\infty} y(t) \leq \eta_y$ can be shown similarly. Indeed, the arguments are very much like the first half of the proof of Theorem 2.1.

If the conclusion is false, then there exist t_1, t_2, $t_2 > t_1 > 0$, such that

$$x(t_1) = K_{2f}, \qquad x(t_2) = \eta_x, \qquad x'(t_2) \geq 0, \qquad x(t) \in [K_{2f}, \eta_x]$$

for $t \in [t_1, t_2]$. From (C3$_f$), we have

$$t_2 - t_1 > \tau.$$

And (2.3) leads to $x'(t_2) < 0$, a contradiction. This proves the lemma. □

Theorem 3.1. *In system* (1.2) *assume* (C1$_f$)–(C3$_f$) *and* (C1$_g$)–(C3$_g$) *hold. Assume further*

(C): *There is a positive constant* δ_0*, such that for all* $t \geq 0$*,*

(i) $f(t, x_t, y_t) > \delta_0$*, for* $||x_t|| \leq \delta_0$*,* $||y_t|| \leq \eta_y + \delta_0$*,*

(ii) $g(t, x_t, y_t) > \delta_0$*, for* $||x_t|| \leq \eta_x + \delta_0$*,* $||y_t|| \leq \delta_0$*, where* η_x *and* η_y *are defined in Lemma* 3.1*.*

Then system (1.2) *is uniformly persistent.*

Proof. We adopt a similar approach as the proof of Theorem 2.1. Let

$$\begin{aligned}\bar{\eta}_x &= \delta_0 \exp\{-l_f(\eta_x + \delta_0, \eta_y + \delta_0)\tau\},\\ \bar{\eta}_y &= \delta_0 \exp\{-l_g(\eta_x + \delta_0, \eta_y + \delta_0)\tau\}.\end{aligned}$$

We prove below that

$$\liminf_{t \to +\infty} x(t) \geq \bar{\eta}_x. \tag{3.2}$$

The proof of $\liminf_{t\to+\infty} y(t) \geq \bar{\eta}_y$ is similar. From Lemma 3.1, we know that there exists $t_0 > 0$, such that for $t \geq t_0$,

$$x(t) < \eta_x + \delta_0, \qquad y(t) < \eta_y + \delta_0. \tag{3.3}$$

If (3.2) is false, then there exist t_1, t_2, $t_2 > t_1 > t_0$, such that

$$x(t_1) = \delta_0, \qquad x(t_2) = \bar{\eta}_x, \qquad x'(t_2) \leq 0, \qquad x(t) \in [\bar{\eta}_x, \delta_0],$$

for $t \in [t_1, t_2]$.

Clearly, (2.5) implies that

$$t_2 - t_1 \geq \tau.$$

However, by (i), we must have

$$x'(t_2) = x(t_2)f(t_2, x_{t_2}, y_{t_2}) > \delta_0 x(t_2) > 0,$$

a contradiction. $\square$

In the following, we apply the above theorem to the nonautonomous Lotka-Volterra type competition system with distributed delays of the form

(3.4)
$$x'(t) = x(t)\left[a(t) - b(t)\int_{-\tau}^{0} x(t+\theta)\,d\mu_1(\theta) - c(t)\int_{-\tau}^{0} y(t+\theta)\,d\mu_2(\theta)\right],$$
$$y'(t) = y(t)\left[k(t) - h(t)\int_{-\tau}^{0} x(t+\theta)\,d\mu_3(\theta) - f(t)\int_{-\tau}^{0} y(t+\theta)\,d\mu_4(\theta)\right],$$

where $0 \le \tau < +\infty$, and μ_i, $i = 1, 2, 3, 4$, are nondecreasing functions satisfying $\mu_i(0^+) - \mu_i(-\tau^-) = 1$. $a(t), b(t), c(t), k(t), h(t)$ and $f(t)$ are bounded positive continuous functions that are also bounded away from zero. For convenience, we assume that

$$\begin{aligned} &a(t) \in [\underline{a}, \bar{a}], \qquad b(t) \in [\underline{b}, \bar{b}], \qquad c(t) \in [\underline{c}, \bar{c}], \\ &k(t) \in [\underline{k}, \bar{k}], \qquad h(t) \in [\underline{h}, \bar{h}], \qquad f(t) \in [\underline{f}, \bar{f}], \end{aligned} \tag{3.5}$$

where $\underline{a}, \underline{b}, \underline{c}, \underline{k}, \underline{h}$ and $\underline{f}$ are positive constants. It is easy to see that assumptions $(\mathrm{C1}_f)$–$(\mathrm{C3}_f)$ and $(\mathrm{C1}_g)$–$(\mathrm{C3}_g)$ are satisfied by system (3.4). For detailed biological interpretation, see Freedman (1980). Applying Theorem 3.1 to (3.4), we have

Theorem 3.2. *Assume that system* (3.4) *satisfies*

$$\underline{a} - \bar{c}\frac{\bar{k}}{\underline{f}}e^{\bar{k}\tau} > 0 \quad \text{and} \quad \bar{k} - \bar{h}\frac{\bar{a}}{\underline{b}}e^{\bar{a}\tau} > 0. \tag{3.6}$$

Then (3.4) *is uniformly persistent.*

Proof. Since all the coefficients are positive and bounded from both below and above, we see that $(\mathrm{C1}_f)$–$(\mathrm{C3}_f)$ and $(\mathrm{C1}_g)$–$(\mathrm{C3}_g)$ are all satisfied.

From (3.6), we see that there exists a constant $\epsilon > 0$, such that

$$\bar{a} - \bar{c}\left(\frac{\bar{k}}{\underline{f}} + \epsilon\right)e^{\bar{k}\tau} > 0, \quad \text{and} \quad \bar{k} - \bar{h}\left(\frac{\bar{a}}{\underline{b}} + \epsilon\right)e^{\bar{a}\tau} > 0.$$

Define

$$K_{2f} \equiv \frac{\bar{a}}{\underline{b}} + \epsilon, \qquad K_{2g} \equiv \frac{\bar{k}}{\underline{f}} + \epsilon.$$

We see that $(\mathrm{C}1_f)$ and $(\mathrm{C}1_g)$ can be satisfied by letting $K_2(f) = K_{2f}$, $K_2(g) = K_{2g}$. Clearly, $M_f = M(f) = \bar{a}$, $M_g = M(g) = \bar{k}$. Hence, we have

$$\eta_x = \left(\frac{\bar{a}}{\underline{b}} + \epsilon\right)e^{\bar{a}\tau}, \qquad \eta_y = \left(\frac{\bar{k}}{\underline{f}} + \epsilon\right)e^{\bar{k}\tau}.$$

It is now easy to see that (i) in Theorem 3.1 reduces to

$$\bar{a} - \bar{c}\left(\frac{\bar{k}}{\underline{f}} + \epsilon\right)e^{\bar{k}\tau} > 0,$$

while (ii) in Theorem 3.1 reduces to

$$\bar{k} - \bar{h}\left(\frac{\bar{a}}{\underline{b}} + \epsilon\right)e^{\bar{a}\tau} > 0.$$

Theorem 3.2 now follows from Theorem 3.1. $\square$

In the autonomous case, that is, when $\bar{a} = \underline{a}$, $\bar{b} = \underline{b}$, $\bar{c} = \underline{c}$, $\bar{k} = \underline{k}$, $\bar{h} = \underline{h}$, and $\bar{f} = \underline{f}$, condition (3.6) reduces to the uniform persistence condition (4.4) in [**4**]. When, in addition, $\tau = 0$, i.e., when (3.4) reduces to autonomous ordinary differential system, our persistence condition (3.6) becomes

$$\frac{b}{h} > \frac{a}{k} > \frac{c}{f},$$

which in fact is both necessary and sufficient for uniform persistence (see [**20**]).

4. Predator-prey systems. We assume throughout this section that system (1.2) satisfies (P1)–(P5). Note that we do not assume that

g is strictly decreasing with respect to y_t, which amounts to the so-called self-crowding effect. If such an effect exists, then boundedness of solutions of (1.2) with (2.1) are easy to obtain. This is the case for the work of Wang and Ma [**21**]. As we have mentioned in section 2, it is easy to show that $x(t)$ is bounded (see also the proof of Lemma 3.1). The next lemma shows that $y(t)$ is also bounded.

Lemma 4.1. *Assume system* (1.2) *satisfies* (P1)–(P5). *Then there is a positive constant* q *such that*

$$\limsup_{t\to+\infty} y(t) \le q,$$

for all solutions of (1.2) *with* (2.1).

Proof. Let $\eta_x = K_{2f}\exp(M_f\tau)$; then a similar argument as the proof of Lemma 3.1 shows that

$$\limsup_{t\to+\infty} x(t) \le \eta_x \tag{4.1}$$

for all solutions of (1.2) with (2.1).

Since ($C2_f$), there exist positive constants δ_3 and k such that for all $t \ge 0$, $x_t \in C^+$,

$$f(t, x_t, y_t) < -\delta_3, \qquad \text{for } y(t+\theta) \ge k,\ \theta \in [-\tau, 0]. \tag{4.2}$$

From (P5), we see that there exists a positive constant p such that $m(p) < 0$

$$g(t, x_t, y_t) \le m(p) < 0, \qquad t \ge 0,\ x_t, y_t \in C^+,\ ||x_t|| \le p. \tag{4.3}$$

Let $\epsilon \in (0, 1)$ be a constant. There exists a constant $T > 0$, such that the solution $x(t)$ of

$$x'(t) = -\delta_3 x(t) \tag{4.4}$$

$$0 \le x(t_0) \le \eta_x + \epsilon, \tag{4.5}$$

satisfies

$$x(t) \le p, \qquad \text{for } t - t_0 \ge T. \tag{4.6}$$

Denote

$$\xi = \xi(\epsilon) = m(\eta_x + \epsilon), \tag{4.7}$$

$$\eta_y = k \exp(\xi(\tau + T)). \tag{4.8}$$

We claim that

$$\limsup_{t \to +\infty} y(t) \le \eta_y. \tag{4.9}$$

Assume in the following that (4.9) is false. Note that for any $t_0 > 0$, there is a $t > t_0$ such that $y(t) < k$. Otherwise, $x(t)$ tends to zero and we must have, from (P5),

$$y'(t) \le y(t)m(p)$$

and, therefore,

$$y(t) \to 0, \qquad \text{as } t \to +\infty,$$

a contradiction. Since (4.1), there is a $t_0 = t_0(\epsilon) > \tau$ such that

$$||x_t|| \le \eta_x + \epsilon, \qquad \text{for } t \ge t_0. \tag{4.10}$$

The preceding arguments indicate that there exist $t_2 > t_1 \ge t_0$ such that

$$y(t_1) = k, \qquad y(t_2) = \eta_y, \qquad y'(t_2) \ge 0, \qquad y(t) \in [k, \eta_y), \ t \in [t_1, t_2]. \tag{4.11}$$

From (P5), we obtain

$$y'(t) \le m(\eta_x + \epsilon) y(t) = \xi y(t), \qquad t \ge t_0. \tag{4.12}$$

Hence, we must have

$$t_2 - t_1 \ge \tau + T. \tag{4.13}$$

However, the solution $x(t)$ of

$$x'(t) = x(t) f(t, x_t, y_t), \qquad ||x_{t_1}|| \le \eta_x + \epsilon, \tag{4.14}$$

satisfies

$$x'(t) \le -\delta_3 x(t)$$

and, hence,

$$x(t) \le x(t_1)e^{-\delta_3(t-t_1)} \le p, \qquad \text{for } t - t_1 \ge T.$$

This implies that

$$||x_{t_2}|| \le p,$$

and, hence,

$$y'(t_2) = y(t_2)g(t_2, x_{t_2}, y_{t_2}) < m(p)\eta_y < 0,$$

a contradiction. This proves the lemma. □

In the following, we denote

$$f(t, x, y) \equiv f(t, \hat{x}, \hat{y}), \tag{4.15}$$

$$g(t, x, y) \equiv g(t, \hat{x}, \hat{y}), \tag{4.16}$$

where we denote $\hat{x}, \hat{y} \in C^+$, $\hat{x}(\theta) = x$, $\hat{y}(\theta) = y$, $\theta \in [-\tau, 0]$; that is, replacing ϕ, ψ in $f(t, \phi, \psi)$, $g(t, \phi, \psi)$ by constants x and y, respectively. Also, we assume that there exist continuously differentiable functions $\underline{f}(x, y)$, $\underline{g}(x, y)$ and $\bar{g}(x, y)$ such that for $t \ge 0$,

$$\underline{f}(x, y) \le f(t, x, y), \tag{4.17}$$

$$\underline{g}(x, y) \le g(t, x, y) \le \bar{g}(x, y). \tag{4.18}$$

Assume further that

(P6) $\underline{f}$ is strictly decreasing with respect to both x and y, $\underline{f}(0, 0) > 0$, and

$$\lim_{x\to+\infty} \underline{f}(x, 0) = \lim_{y\to+\infty} \underline{f}(0, y) = -\infty.$$

(P7) $\underline{g}$ and $\bar{g}$ are increasing with respect to x, but nonincreasing with respect to y. $\bar{g}(0, 0) < 0$.

Let $\epsilon \in (0, 1)$ be a constant. From the proof of Lemma 4.1, we see that there is a $t_0 = t_0(\epsilon, \varphi_1, \varphi_2)$, such that for $t \ge t_0$,

$$x(t) \le \eta_x + \epsilon, \qquad y(t) \le \eta_y + \epsilon,$$

where η_y is defined as in (4.8). Clearly,

$$-\alpha \equiv -\alpha(\epsilon) \equiv \underline{f}(\eta_x + \epsilon, \eta_y + \epsilon) < 0. \tag{4.19}$$

And hence the solution (x_t, y_t) of (1.2) satisfies

$$x'(t) \geq x(t)\underline{f}(\eta_x + \epsilon, \eta_y + \epsilon) = -\alpha x(t), \qquad t \geq t_0 + \tau, \tag{4.20}$$

which implies that

$$x(t) \geq x(t+\theta)e^{\alpha\theta}, \qquad \theta \in [-\tau, 0],\ t \geq t_0 + \tau,$$

or equivalently,

$$x(t+\theta) \leq x(t)e^{-\alpha\theta}, \qquad \theta \in [-\tau, 0],\ t \geq t_0 + \tau. \tag{4.21}$$

Also, we have from (C3$_f$),

$$x'(t) \leq x(t)M,$$

which leads to

$$x(t+\theta) \geq x(t)e^{M\theta}, \qquad \theta \in [-\tau, 0],\ t \geq t_0 + \tau. \tag{4.22}$$

Similarly, we have that for $t \geq t_0 + \tau$,

$$-\beta \equiv -\beta(\epsilon) \equiv \underline{g}(0, \eta_y + \epsilon) \leq y'(t)/y(t) \leq \bar{g}(\eta_x + \epsilon, 0) \equiv \gamma(\epsilon) \equiv \gamma, \tag{4.23}$$

and hence, for $t \geq t_0 + \tau$,

$$e^{\gamma\theta}y(t) \leq y(t+\theta) \leq e^{-\beta\theta}y(t), \qquad \theta \in [-\tau, 0]. \tag{4.24}$$

For convenience, we denote

$$F(x,y) = \underline{f}(e^{\alpha\tau}x, e^{\beta\tau}y), \tag{4.25}$$

$$\overline{G}(x,y) = \bar{g}(e^{\alpha\tau}x, e^{-\gamma\tau}y), \qquad \underline{G}(x,y) = \underline{g}(e^{-M\tau}x, e^{\beta\tau}y). \tag{4.26}$$

In the following, we need to compare solutions of (1.2) with those of the following two nondelayed autonomous predator-prey systems

$$\begin{aligned} u'(t) &= u(t)F(u(t), v(t)), \qquad u(0) > 0, \\ v'(t) &= v(t)\overline{G}(u(t), v(t)), \qquad v(0) > 0 \end{aligned} \tag{4.27}$$

and

$$\begin{aligned} u'(t) &= u(t)F(u(t), v(t)), \qquad u(0) > 0, \\ v'(t) &= v(t)\underline{G}(u(t), v(t)), \qquad v(0) > 0. \end{aligned} \tag{4.28}$$

Further, we let $x^* > 0$ be the unique solution of

$$F(x, 0) = 0. \tag{4.29}$$

We now state and prove the main result of this section.

Theorem 4.1. *Assume system* (1.2) *satisfies* (P1)–(P7), *and*

$$\underline{G}(x^*, 0) > 0. \tag{P8}$$

Then (1.2) *is uniformly persistent.*

Proof. From the definition of uniform persistence, we need only show that there is a $\delta > 0$, independent of initial data, such that

$$\min\{\liminf_{t\to+\infty} x(t), \liminf_{t\to+\infty} y(t)\} > \delta. \tag{4.30}$$

Denote $x_1 > 0$ the unique solution of

$$\overline{G}(x, 0) = 0. \tag{4.31}$$

We claim that there is an $\bar{x} \geq \min\{x^*, x_1\}$, and a sequence $\{t_i\}_{i=1}^{\infty}$, $t_i = t_i(\varphi_1, \varphi_2) > \tau$, $t_i \to +\infty$ as $i \to +\infty$, such that $x(t_i) = \bar{x}$. Otherwise, we have for all large t, $y'(t) < 0$, and hence we must have $\lim_{t\to+\infty} y(t) = 0$, which leads to

$$\limsup_{t\to+\infty} x(t) \geq x^*,$$

and (P8) thus implies for all large t, $y'(t) > 0$, a contradiction.

Recalling that we have assumed that for $t \geq t_0 = t_0(\epsilon, \varphi_1, \varphi_2)$,

$$x(t) \leq \eta_x + \epsilon, \qquad y(t) \leq \eta_y + \epsilon.$$

We assume below that $\epsilon < 1$.

We have two cases to consider:

(i) there is a $t_1 \geq t_0 + \tau$, such that

$$x(t_1) = \bar{x}, \qquad F(x(t_1), y(t_1)) \leq 0; \tag{4.32}$$

(ii) there is a $t_1 \geq t_0 + \tau$ such that

$$x(t_1) = \bar{x}, \qquad F(x(t_1), y(t_1)) > 0.$$

We define

$$\hat{x} = \frac{1}{2} \min\{x^*, x_1\}.$$

We denote

$$\bar{u}(t) = u(t, \hat{x}, \eta), \qquad \bar{v}(t) = v(t, \hat{x}, \eta), \tag{4.33}$$

the solution of (4.27) with initial value $(\hat{x}, \eta)$, where $\eta \geq \max\{\eta_x + 1, \eta_y + 1\}$ satisfying $F(0, \eta) < 0$. Then, from a standard phase plane analysis of system (4.27), we know that there is a $\tau_1 > 0$ such that

$$\begin{aligned} &\bar{u}'(\tau_1) = 0 \quad \text{and} \quad \bar{u}'(t) < 0 \quad \text{for } t \in [0, \tau_1), \\ &\text{and} \quad \bar{v}'(t) < 0 \quad \text{for } t \in [0, \tau_1]. \end{aligned}$$

Denote

$$\underline{u}(t) = \underline{u}(t, \bar{u}(\tau_1), \bar{v}(\tau_1)), \qquad \underline{v}(t) = \underline{v}(t, \bar{u}(\tau_1), \bar{v}(\tau_1)), \tag{4.34}$$

the solution of (4.28) with initial value $(\bar{u}(\tau_1), \bar{v}(\tau_1))$. Then there is a $\tau_2 > 0$, such that $\underline{v}'(\tau_2) = 0$. Denote

$$\begin{aligned} \Gamma_1 &= \{(\bar{u}(t), \bar{v}(t)) : 0 \leq t \leq \tau_1\}, \\ \Gamma_2 &= \{(\underline{u}(t), \underline{v}(t)) : 0 \leq t \leq \tau_2\}, \\ \Gamma_3 &= \{(x, \underline{v}(\tau_2)) : \underline{u}(\tau_2) \leq x \leq \eta\}, \\ \Gamma_4 &= \{(\eta, y) : \underline{v}(\tau_2) \leq y \leq \eta\}, \\ \Gamma_5 &= \{(x, \eta) : \hat{x} \leq x \leq \eta\}. \end{aligned}$$

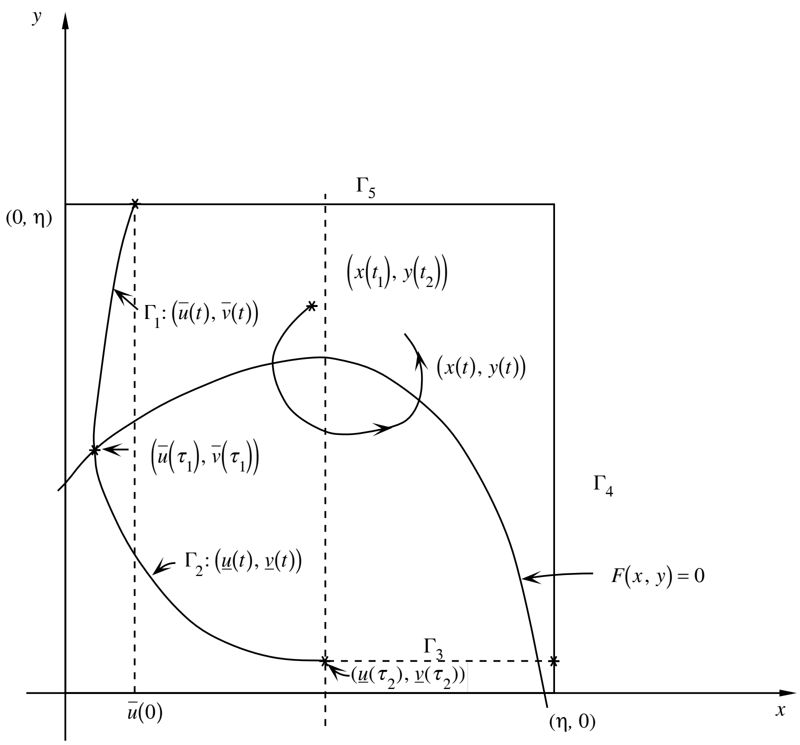

FIGURE 1. Illustration of the proof of Theorem 4.1.

Then $\cup_{i=1}^{5}\Gamma_i$ constitutes the boundary of a closed bounded region $\Omega = \Omega(\hat{x})$ in the $x - y$ plane. *We claim that for* $t \geq t_1 = t_1(\epsilon, \varphi_1, \varphi_2)$, $(x(t), y(t)) \in \Omega$. Note that Ω is independent of initial value (φ_1, φ_2).

We consider first case (i). Observe that for $t \geq t_1$, $(x(t), y(t))$ can never leave Ω through Γ_1. Since if $(x(t), y(t)) = (\bar{u}(\bar{t}), \bar{v}(\bar{t})) \in \Gamma_1$, then $0 > x'(t) \geq \bar{u}'(\bar{t})$, $y'(t) \leq \bar{v}'(\bar{t}) < 0$, which implies that $dy/dx > du/dv$. Similarly, we see that $(x(t), y(t))$ cannot leave Ω through Γ_2. And it is obvious that $(x(t), y(t))$ cannot cross Γ_3, Γ_4 and Γ_5. This proves the claim for case (i).

Consider now case (ii). Clearly, we can replace $\hat{x}$ in (4.33) by a sufficiently small $\bar{u}(0)$ and construct a new region $\Omega(\bar{u}(0))$ accordingly to envelope $(x(t_1), y(t_1))$. However, as our notation suggests, the region

$\Omega(\bar{u}(0))$ now depends on $(x(t_1), y(t_1))$.

Observe that since (P6), there is a constant $\rho_0 > 0$, such that if

$$\max\{x(t), y(t)\} < \rho_0,$$

then $x'(t) > 0$. By choosing sufficiently small constant ρ_1, we claim that for any solution $(x(t), y(t))$ of (1.2), there must be a $t^* > 0$, such that

$$\min\{x(t^*), y(t^*)\} > \rho_1.$$

This is because for sufficiently small constant $\rho > 0$, $y(t)$ cannot always stay in

$$\Omega_1 = \{(x, y) : 0 \le y \le \rho\}.$$

Since otherwise $\liminf_{t\to+\infty} x(t)$ will be larger than or very close to the value x^* and hence forces $y'(t) > 0$ for large t, because of (P8). Also, we knew earlier that $x(t)$ cannot always stay in

$$\Omega_2 = \{(x, y) : 0 \le x \le \rho\}$$

for sufficiently small ρ. Moreover, for $\rho < \rho_0$, $(x(t), y(t))$ can only travel from Ω_2 to Ω_1 and not the other way around. We stress here that ρ_1 is independent of (φ_1, φ_2).

Finally, we conclude that we can choose sufficiently small $\bar{u}(0)$, $0 < \bar{u}(0) < \hat{x}$, such that

$$\{(\rho_1, y) : \rho_1 \le y \le \eta\} \cup \{(x, \rho_1) : \rho_1 \le x \le \eta\} \subset \Omega(\bar{u}(0)).$$

For this $\Omega(\bar{u}(0))$ (independent of (φ_1, φ_2)), we have that for any solution $(x(t), y(t))$ of (1.2) with $x(0) > 0$, $y(0) > 0$, there is a $t^* = t^*(\varphi_1, \varphi_2)$, such that

$$(x(t), y(t)) \in \Omega, \qquad \text{for } t \ge t^*.$$

This proves the theorem. $\square$

Clearly, when applying the above theorem, one can take $\epsilon = 0$ in selecting α, β, γ in $F, \underline{G}, \overline{G}$.

In the rest of this section we apply the proof of Theorem 4.1 to the nonautonomous Lotka-Volterra Michaelis-Menten type predator-prey system

(4.35)

$$x'(t) = x(t)\Big[a(t) - b(t)\int_{-\tau_1}^{0} x(t+\theta)\,d\mu_1(\theta) - \frac{c(t)\int_{-\tau_2}^{0} y(t+\theta)\,d\mu_2(\theta)}{1+n(t)\int_{-\tau_3}^{0} x(t+\theta)\,d\mu_5(\theta)}\Big],$$

$$y'(t) = y(t)\Big[-k(t) + \frac{h(t)\int_{-\tau_4}^{0} x(t+\theta)\,d\mu_3(\theta)}{1+n(t)\int_{-\tau_5}^{0} x(t+\theta)\,d\mu_6(\theta)} - f(t)\int_{-\tau_6}^{0} y(t+\theta)\,d\mu_4(\theta)\Big];$$

again all the coefficients are positive continuous functions bounded both above and away from zero, and $\tau_i \geq 0$, $\mu_i(\theta)$ are nondecreasing, $\mu_i(0^+) - \mu_i(-\tau^-) = 1$, $i = 1, 2, \ldots, 6$. We assume, in addition to (3.5),

$$n(t) \in [\underline{n}, \bar{n}]. \tag{4.36}$$

When all coefficients are constants and $\tau_i = 0$, $i = 1, 2, \ldots, 6$, (4.35) reduces to the well-known Lotka-Volterra Michaelis-Menten type predator-prey system (see (4.41) below) which is described in [**10**].

Theorem 4.2. *In* (4.35)*, let* α *be defined by* (4.19) *with* $\epsilon = 0$ *and* $x^* = \underline{a}\bar{b}^{-1}e^{-\alpha\tau_1}$. *If*

$$\underline{h}e^{-\bar{a}\tau_4}x^* > \bar{k}(1 + \bar{n}e^{-\bar{a}\tau_5}x^*) \tag{4.37}$$

then (4.35) *is uniformly persistent.*

Proof. Clearly (4.35) satisfies (P1)–(P5). We have

$$\underline{f}(x,y) = \underline{a} - \bar{b}x - \frac{\bar{c}y}{1+\underline{n}x},$$

$$\underline{g}(x,y) = -\bar{k} + \frac{\underline{h}x}{1+\bar{n}x} - \bar{f}y,$$

$$\bar{g}(x,y) = -\underline{k} + \frac{\bar{h}x}{1+\underline{n}x} - \underline{f}y.$$

It is easy to see that (P6) and (P7) are satisfied. We have $M = \bar{a}$.

It is not difficult to see that we can define

$$\begin{aligned} F(x,y) &= \underline{a} - \bar{b}e^{\alpha\tau_1}x, \\ \overline{G}(x,y) &= -\underline{k} + \frac{\bar{h}e^{\alpha\tau_4}x}{1+\underline{n}e^{\alpha\tau_5}x} - \bar{f}e^{-\gamma\tau_6}y, \\ \underline{G}(x,y) &= -\bar{k} + \frac{\underline{h}e^{-\bar{a}\tau_4}x}{1+\bar{n}e^{-\bar{a}\tau_5}x} - \underline{f}e^{\beta\tau_6}y, \end{aligned}$$

and almost repeat the proof of Theorem 4.1 to show that if x^* is the solution of

$$F(x,0) = 0$$

and

$$\underline{G}(x^*,0) > 0,$$

then (4.35) is uniformly persistent. This is equivalent to

$$x^* = \underline{a}\bar{b}^{-1}e^{-\alpha\tau_1},$$

and

$$\underline{h}e^{-\bar{a}\tau_4}x^* > \bar{k}(1+\bar{n}e^{-\bar{a}\tau_5}x^*).$$

This completes the proof. $\square$

In particular, if we have $\tau_1 = 0$, then condition (4.37) reduces to

$$\underline{h}e^{-\bar{a}\tau_4}\underline{a}\bar{b}^{-1} > \bar{k}(1+\bar{n}e^{-\bar{a}\tau_5}\underline{a}\bar{b}^{-1}), \tag{4.38}$$

which is an inequality explicitly in terms of bounds of coefficients.

When, in addition, $\tau_4 = \tau_5 = 0$, then (4.37) becomes

$$\underline{ha}\bar{b}^{-1} > \bar{k}(1+\bar{n}\underline{a}\bar{b}^{-1}). \tag{4.39}$$

Note that condition (4.39) does not depend on $\tau_2, \tau_3, \tau_6, c$, and f!

When (4.35) is autonomous (i.e., $\underline{a} = \bar{a} = a$, $\underline{b} = \bar{b} = b$, $\underline{k} = \bar{k} = k$, $\underline{n} = \bar{n} = n$, $\underline{h} = \bar{h} = h$, $\underline{c} = \bar{c} = c$, $\underline{f} = \bar{f} = f$), (4.39) reduces to

$$ah > k(b + na), \tag{4.40}$$

which is exactly the necessary and sufficient condition for the uniform persistence of

$$\begin{aligned} x'(t) &= x(t)\left(a - bx(t) - \frac{cy(t)}{1 + nx(t)}\right), \\ y'(t) &= y(t)\left(-k + \frac{hx(t)}{1 + nx(t)} - fy(t)\right). \end{aligned} \tag{4.41}$$

5. Discussion. In this paper, we considered the uniform persistence aspect of general nonautonomous two species interaction systems with time delays. Our approach is very different from standard ones. In fact, standard methods such as dynamical systems theory of Hale and Waltman [**14**] cannot be applied to nonautonomous systems, and so does the Liapunov functional approach developed by Burton and Hutson [**1**], which was used (with some difference) in Wang and Ma [**21**] as well. Our approach basically is some kind of comparison argument. In predator-prey systems, we construct two relevant ordinary differential systems (which are also predator-prey models) whose solutions can serve as bounds for that of the delayed system.

Our results are complementary to existing results for autonomous delayed systems. They are not as sharp as should be in some special cases. For example, when reduced to Lotka-Volterra autonomous systems with discrete delays, our results for predator-prey models depend on lengths of delays while the result of Wang and Ma [**21**] does not. Of course, our results are much more general. We do not even assume self crowding effect among predators, another key assumption in Wang and Ma's [**21**] result. However, when applied to autonomous Lotka-Volterra systems without delays, our conditions are necessary and sufficient.

We would like to point out here that the monotonicity assumptions made in (P6) and (P7) can be weakened. This can be seen from the proof of Theorem 4.1.

Finally, we would like to see some kind of generalization of our approach to higher dimensional systems. So far, we find this is quite difficult.

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