Uniform Persistence in Functional Differential Equations

H. I. FREEDMAN*

Applied Mathematics Institute, Department of Mathematics, University of Alberta, Edmonton, Alberta, Canada T6G 2G1

AND

SHIGUI RUAN[†]

The Fields Institute for Research in Mathematical Sciences, 185 Columbia Street West, Waterloo, Ontario, Canada N2L 5Z5

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In this paper, we investigate the question of uniform persistence for retarded functional differential equations. By utilizing Liapunov-like functions, Razumikhin techniques, and differential inequalities, we are able to establish criteria for uniform persistence analogous to those obtained by others for ordinary differential equations, difference equations, and reaction-diffusion equations. We apply these criteria to some well known biological models with delay. Our results indicate that the conditions which guarantee the existence of an interior equilibrium are enough to ensure uniform persistence. Moreover, these conditions are equivalent to uniform persistence for the cases without delay as well.

1. Introduction

In recent years the concept of persistence has played an important role in mathematical ecology. Biologically, when a system of interacting species is persistent in a suitable sense, it means that all the species survive in the long term. Mathematically, persistence of a system means that strictly positive solutions do not have any omega limit points on the boundary of the nonnegative cone.

Various definitions of persistence have been developed in order to analyze mathematical models. (Weak) persistence was considered by Freedman and Waltman [20] and Gard and Hallam [26], and was defined as strong flow-invariance by Gard [25] and Fernandes and

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[†] Research partially supported by a University of Alberta Ph.D. scholarship. Present address: Department of Mathematics, Dalhousie University, Halifax, Nova Scotia, Canada.

Zanolin [12]. Persistence was defined and discussed by Freedman and Waltman [21, 22]. Uniform persistence was first introduced by Schuster et al. [51]. A dissipative and uniformly persistent system was called cooperative by Hofbauer [33], and permanent by Hofbauer and Sigmund [35] and Hutson [37, 38]. The latter is now often used in the literature. Even through permanence and uniform persistence are equivalent for most purposes, Yang and Ruan [56] have shown that a uniformly persistent system is not necessarily dissipative. The connections of various definitions of persistence have been discussed by Butler et al. [5], and recently by Freedman and Moson [17] who also introduced the concept of weakly weak persistence.

Most of the applications of persistence have been to ordinary differential equations (cf. Gard and Hallam [26], Fernandes and Zanolin [14], and the references cited therein), and to difference equations (cf. Hutson and Moran [39]). Dunbar et al [11], Hutson and Moran [40], and Cantrell et al. [7] investigated persistence for reaction-diffusion models. Burton and Hutson [2] obtained some very interesting results on persistence of autonomous functional differential equations with infinite delay. Criteria for one or more forms of persistence to hold in general dynamical systems were given by Butler and Waltman [6], Fonda [15], Freedman et al. [19], Garay [24], Hofbauer [34] and Hofbauer and So [36], among others. Also, Freedman and So [18] dealt with discrete dynamical systems and Hale and Waltman [31] developed persistence criteria for infinite-dimensional systems. For more details and more references on this subject, we refer the reader to the recent survey paper of Hutson and Schmitt [41].

Recently, Freedman and Wu [23] discussed persistence in a delayed system by using the monotone dynamical systems theory developed by Smith [53]. By constructing suitable persistence functionals, Wang and Ma [54] obtained uniform persistence conditions for Lotka-Volterra predator-prey systems with a finite number of discrete delays. Their results suggested that delays are "harmless" for uniform persistence. Similar phenomena were observed by Zanolin [58] in delayed Kolmogorov competing species systems. By utilizing the results in Hale and Waltman [31], Cao et al. [8] studied uniform persistence for Kolmogorov-type predatorprey and competition models with per capita net growth rates that are dependent on time-delayed population densities. Kuang and Tang [44] also established sufficient conditions for uniform persistence in nonautonomous Kolmogorov-type delayed population models. See also Cao and Gard [9], Kuang and Tang [45] and Ruan [49]. However, all together there are very few general results on persistence in delay equations which have a significant background in biology (cf. Cushing [10], Gopalsamy [27], MacDonald [48], etc.).

The methods of Liapunov-like functions and differential inequalities are standard techniques in studying stability, flow-invariance, and the existence of periodic solutions (cf. Fernandes and Zanolin [12, 13] and the references cited therein), and have been proposed as techniques in the investigation of persistence (cf. see Hofbauer [33], Hutson [37], etc.). The Razumikhin technique is an important method which is utilized in studying the stability of functional differential equations (see Haddock and Terjéki [28] and Hale [29]). By this technique, one only needs to choose a Liapunov function (instead of a Liapunov functional) and to verify the nonpositivity of the derivative function for some initial data (instead of all initial data) under certain restrictions in order to have stability.

In the present paper, motivated by the work of Fernandes and Zanolin [13, 14] for nonautonomous ordinary differential equations, we investigate retarded functional differential equations. Liapunov-like functions, the Razumikhin technique, and differential inequalities are used to derive uniform persistence criteria for the retarded functional differential equation (RFDE). Our uniform persistence theorems are analogous to that for ordinary differential equations (Hofbauer [33], Hutson [37], and Fernandes and Zanolin [14]), difference equations (Hutson and Moran [39]) and reaction-diffusion equations (Hutson and Moran [40]). Some well known examples are analyzed to illustrate the obtained results. Our result in the first example indicates that the conditions which guarantee the existence of an interior equilibrium are enough to ensure uniform persistence. In Examples 2 and 3, the criteria we obtained are equivalent to uniform persistence for the cases without delay.

2. Preliminaries

Suppose $r \ge 0$ is a given real number, $R = (-\infty, \infty)$, $C = C([-r, 0], R^n)$ is the Banach space of continuous functions mapping the interval [-r, 0] into R^n with the topology of uniform convergence. For an element $\varphi \in C$, designate the norm of φ by $\|\varphi\| = \sup_{-r \le \varphi \le 0} |\varphi(\theta)|$. If $t_0 \in R$, $A \ge 0$ and $x \in C([t_0 - r, t_0 + A], R^n)$, then for any $t \in [t_0, t_0 + A]$ let $x_t \in C$ be defined by $x_t(\theta) = x(t + \theta)$, $-r \le \theta \le 0$. If $f: R \times C \to R^n$ is a given function, we have a RFDE

$$\dot{x}(t) = f(t, x_t). \tag{2.1}$$

For given $(t_0, \varphi) \in R \times C$, by $x_i(t_0, \varphi)$ we denote a solution of RFDE (2.1) with initial value φ at t_0 , i.e. $x_{i_0}(t_0, \varphi) = \varphi$. We assume that solutions of RFDE (2.1) globally exist and are unique and continuous.

Let $(X, \|\cdot\|)$ be the metric space with $\varphi \in X$ if $\varphi \in C$, $\|\varphi\|$ exists and each component $\varphi_i(s) \ge 0$ for $-r \le s \le 0$. Then X is a subset of C which

contains the only biologically meaningful elements. In the following we also use d to denote $\|\cdot\|$ sometimes.

Let $N \subseteq X$ be closed relative to X and suppose that N is a *flow-invariant* set with respect to RFDE (2.1); that is, if $x_t(t_0, \varphi)$ is any (noncontinuable) solution of (2.1) through $(t_0, \varphi) \in R \times N$, then $x_t(t_0, \varphi) \in N$ for all $t \in I_x = [t_0, t_x)$, where I_x is the right maximal interval of existence. For given $M \subseteq N$, we denote by $\inf_N M$, $\inf_N M$ and $\operatorname{cl}_N M$ respectively the interior, boundary (frontier), and closure of M relative to N.

DEFINITION 2.1. Given a set $M \subset N$ with $\operatorname{int}_N M \neq \emptyset$, we say RFDE (2.1) is *persistent* relative to M if for each $(t_0, \varphi) \in R \times \operatorname{int}_N M$ and $x_t(t_0, \varphi)$ the solution of (2.1), we have $x_t(t_0, \varphi) \in \operatorname{int}_N M$ for each $t \in [t_0, t_x)$, such that

$$\lim_{t \to t_{\bar{k}}} \inf d(x_t(t_0, \varphi), \operatorname{fr}_N M) > 0.$$

If there is a $\delta > 0$ such that

$$\lim_{t \to t_{\bar{x}}} \inf d(x_t(t_0, \varphi), \operatorname{fr}_N M) > \delta$$

for any $x_t(t_0, \varphi) \in \text{int}_N M$, $t \in [t_0, t_x)$, we say system (2.1) is uniformly persistent relative to M.

The concept of uniform persistence essentially involves two conditions: flow-invariance of $\operatorname{int}_N M$ and repulsivity of $\operatorname{fr}_N M$ with respect to the solutions of (2.1) with values in $\operatorname{int}_N M$. Flow-invariance was studied by Gard [25] and Fernandes and Zanolin [12, 13] (and the references cited therein) for ODE, and by Seifert [52] for RFDE. Now we suppose that $\emptyset \neq G \subset N$ is a set open relatively to N and $S \subset N$, $S \cap G = \emptyset$. We shall find conditions for the repulsivity of S with respect to the solutions of (2.1) lying in S. Define $S^* = S \cap \operatorname{fr}_N G$.

DEFINITION 2.2. Let $Z \subset N \setminus G$, we say Z is uniformly repelling with respect to G if there exist an open neighbourhood \mathscr{A} of Z and $t_1 \in [t_0, t_x)$, such that for any solution $x_t(t_0, \varphi)$ of (2.1) with $x_t(t_0, \varphi) \in G$ for all $t \in [t_0, t_x)$, we have $x_t(t_0, \varphi) \notin \mathscr{A}$ for all $t \in [t_1, t_x)$. In the particular case that $Z = \{u\}$, with $u \notin G$, the point u is said to be uniformly repulsive with respect to G.

Following Fernandes and Zanolin [14], we have the following

PROPOSITION 2.3. If S^* is compact and each point $u \in S^*$ is uniformly repulsive with respect to G, then S is uniformly repelling. If S is

compact and uniformly repelling with respect to G, then there is $\delta > 0$ such that

$$\lim_{t \to t_1^-} \inf_{t \to t_1^-} d(x_t(t_0, \varphi), S) > \delta$$

for each $x_t(t_0, \varphi)$ solution of (2.1) with $x_t(t_0, \varphi) \in G$, $t \in [t_0, t_1)$.

Choosing $G = \operatorname{int}_N M$ and $S = \operatorname{fr}_N M$ in Proposition 2.3, we get the following.

PROPOSITION 2.4. Let $M \subset N$, such that $\operatorname{int}_N M \neq \emptyset$ and $\operatorname{fr}_N M$ is compact. Suppose that $\operatorname{int}_N M$ is flow-invariant with respect to the RFDE (2.1) and each point of $\operatorname{fr}_N(\operatorname{int}_N M)$ is uniformly repulsive with respect to $\operatorname{int}_N M$. Then the RFDE (2.1) is uniformly persistent.

If $V: R \times R^n \to R$ is a continuous function, then the derivative of V along the solutions of (2.1) is defined as

$$\dot{V}(t, \varphi(0)) = \lim_{h \to 0^+} \inf_{0^+} \frac{1}{h} \left[V(t+h, x_{t+h}(t_0, \varphi)) - V(t, \varphi(0)) \right].$$

In the following, we suppose that $t_0 \ge 0$ and consider $t \in J = [t_0, b)$, $b \le \infty$.

A special case of (2.1) is the autonomous RFDE

$$\dot{x} = f(x_t). \tag{2.2}$$

Similarly we can define a space X for (2.2). If a map $\pi: X \times J \to X$ satisfies for all $u \in X$ that

- (i) $\pi(u, 0) = u$,
- (ii) $\pi(\pi(u, s), t) = \pi(u, t+s)$ for $t, s \in J$,
- (iii) π is continuous,

then (π, X, J) is a semidynamical system (see Saperstone [50] and Hale [30]). For convenience we often write $\pi(u, t) = u_t$, where u is a unique solution of (2.2). The semi-orbit through u is denoted by

$$\gamma^+(u) = \{u_t \colon t \in J\},\,$$

and for a subset $M \subset X$,

$$\gamma^+(M) = \bigcup_{u \in M} \gamma^+(u).$$

The omega limit set of u is defined to be

$$\omega(u) = \bigcap_{s \geqslant 0} \operatorname{cl} \bigcup_{t \geqslant s} u_t,$$

and for a set $M \subset X$, the omega limit set is defined as

$$\omega(M) = \bigcup_{u \in M} \omega(u).$$

It is known that if $\gamma^+(u)$ is relatively compact, then $\omega(u)$ is nonempty, connected, compact, and invariant (see Hale [30]).

3. MAIN RESULTS

THEOREM 3.1. Assume that $f: J \times C \to R^n$ is completely continuous, $u \in \operatorname{fr}_N G$, and there is an open neighbourhood $X_1 \subset X$ of u and two continuous functions V(t, x) and g(t, z) with $V: J \times R^n \to R$ locally Lipschitzian in x and $g: J \times (-\infty, 0) \to R$ such that

- (i) $K = \{ \psi \in X_1 \cap \operatorname{fr}_N G : \lim \sup_{t \to b^-, \varphi \to \psi} V(t, \varphi(0)) = 0 \}$ is compact and $u \in K \subset X_1$;
 - (ii) $\lim_{t\to b^-} V(t, \varphi(0)) = 0$ uniformly for $\varphi \in G$ and $d(\varphi, K) \to 0$;
 - (iii) $\limsup_{t\to\sigma^-, \omega\to\psi} V(t, \varphi(0)) < 0 \text{ for all } (\sigma, \psi) \in J \times (G \cap X_1);$
- (iv) $\dot{V}_{(2.1)}(t, \varphi(0)) \leq g(t, V(t, \varphi(0)))$ if $V(t + \theta, \varphi(\theta)) \leq V(t, \varphi(0))$, $\theta \in [-r, 0]$ for all $(t, \varphi) \in J \times (G \cap X_1)$;
- (v) for every k > 0, there exist $\eta_k > 0$ and $\delta > 0$ such that for each $t_0 \le \sigma < b$, the problem

$$\dot{z} = g(t, z), \qquad z(\sigma) = -k \tag{3.1}$$

has a maximial solution z(t) on $[t_0, t_z)$ with

$$\sup_{t \geqslant \sigma} z(t) < -\eta_k \quad and \quad \liminf_{t \to t_-^-} z(t) < -\delta.$$

Then u is uniformly repulsive with respect to G.

Proof. For $\rho > 0$, denote

$$B[K, \rho] = \{ \psi \in X : \exists \varphi \in K, \|\psi - \varphi\| \leq \rho \}.$$

Let ε_1 be fixed such that $0 < \varepsilon_1 < \delta$. Since $K \subset X_1$ is compact, there is a $\rho_0 > 0$ such that $B[K, \rho_0] \subset X_1$. Condition (ii) implies that there are β_1 and ρ_1 with $t_0 \le \beta_1 < b$, $0 < \rho_1 \le \rho_0$ such that

$$\inf\{V(t,\varphi(0))\colon t\in [\beta_1,b),\,\varphi\in G\cap B[K,\rho_1]\}\geqslant -\varepsilon_1. \tag{3.2}$$

Claim I. There is β_2 with $\beta_1 \le \beta_2 < b$ such that

$$\sup\{V(t,\varphi(0)): t \in [\beta_2,b), \varphi \in G \cap \text{fr } B[K,\rho_1]\} = -\varepsilon_2 < 0.$$

Indeed, condition (iii) implies that there is a β_2 such that $-\varepsilon_2 \leq 0$. If $\varepsilon_2 = 0$, then we can find a sequence $(t_n, \varphi_n) \in [\beta_1, b) \times (G \cap \operatorname{fr} B[K, \rho_1])$ with $t_n \to b$, such that $V(t_n, \varphi_n(0)) \to 0$. Without loss of generality, we assume that $\varphi_n \to \psi \in \operatorname{cl}_N G \cap \operatorname{fr} B[K, \rho_1] \subset \operatorname{cl}_N G \cap X_1$. Since $\psi \notin K$, by condition (i), we have $\psi \in G$, which contradicts condition (iii). Hence Claim I is proved.

According to condition (v), let $\eta_{\epsilon_2} > 0$ be chosen. Condition (ii) again implies that there are β_3 and ρ with $\beta_3 \le \beta_2 < b$, $0 < \rho < \rho_1$ such that

$$\inf\{V(t,\varphi(0)): t \in [\beta_3,b), \varphi \in G \cap B[K,\rho]\} = -\varepsilon_3 > -\eta_{\varepsilon_2}. \tag{3.3}$$

Define $\mathscr{A} = B(K, \rho) = \{ \psi \in X : \exists \varphi \in K, \| \psi - \varphi \| < \rho \}$, an open neighbourhood of u. Since $cl \mathscr{A} = B[K, \rho] \subset X$ is a closed set and f is completely continuous, if $t_x < b$, then by the continuation of solutions (see Hale [29], Theorem 3.2 in Chapter 2), there is $t_1 \ge t_0$ such that $x_t(t_0, \varphi) \notin \mathscr{A}$ for $t \in [t_1, t_x)$. Hence we assume $t_x = b$ and set $\gamma = \max\{t_0, \beta_3\}$, $x(t) = x_t(t_0, \varphi)$.

If $x(t) \notin B[K, \rho_1]$ for all $t \in [\gamma, b)$, then for $t_1 = \gamma$, $x(t) \notin \mathscr{A}$ for all $t \in [t_1, b)$ and we prove the theorem. Now suppose that there is $\gamma_1 \ge \gamma$ such that $x(\gamma_1) \in B[K, \rho_1]$.

Claim II. There is $\gamma_2 > \gamma_1$ such that $x(\gamma_2) \notin B[K, \rho_1]$.

In fact, suppose by contradiction that $x(t) \in B[K, \rho_1]$ for all $t \in [\gamma_1, b)$, define a function

$$v(t) = V(t, x(t)).$$

For all $t \in [\gamma_1, b)$, condition (iii) implies

$$v(t) < 0, \tag{3.4}$$

inequality (3.2) implies

$$v(t) \geqslant -\varepsilon_1,\tag{3.5}$$

and by condition (iv) we have

$$\dot{v}(t) \leqslant g(t, v(t)) \tag{3.6}$$

if $v(\xi) \le v(t)$ for $t - \tau \le \xi \le t$. Let $z(t) = z(t, \gamma_1, z^0)$ be the maximal solution of

$$\dot{z} = g(t, z), \qquad z(\gamma_1) = v(\gamma_1)$$

on $[\gamma_1, t_z)$ according to condition (v). Since $v(\gamma_1) = z(\gamma_1, \gamma_1, z^0) = z^0$, $v(\xi) \le z(\xi, \gamma_1, z^0) \le z(\gamma_1, \gamma_1, v(\gamma_1)) = v(\gamma_1)$ for $\xi \in [\gamma_1 - r, \gamma_1]$, we have

$$\dot{v}(\gamma_1) \leqslant g(\gamma_1, v(\gamma_1)) = \dot{z}(\gamma_1, \gamma_1, z^0),$$

which means that at $t = \gamma_1$, the derivative of $v(t) - z(t, \gamma_1, z^0)$ is negative, but

$$v(\gamma_1)-z(\gamma_1,\,\gamma_1,\,z^0)=0.$$

Hence, by continuity, there exists l > 0 sufficiently small such that

$$v(t) \le z(t, \gamma_1, z^0)$$
 for $\gamma_1 \le t \le \gamma_1 + l$.

We claim that

$$v(t) \le z(t)$$
 for all $\gamma_1 \le t < t_z$.

Suppose that there is $t_1 > \gamma_1 + l$ such that

$$v(t) > z(t, \gamma_1, z^0)$$
 for $t \ge t_1$.

Let $z_m(t)$ be any solution of

$$\dot{z} = g(t, z) + \frac{1}{m}, \qquad z(\gamma_1) = z^0 = v(\gamma_1), \qquad m = 1, 2,$$

We know that the maximal solution z(t) can be expressed as (see Lakshmikantham and Leela [46])

$$z(t) = \lim_{m \to \infty} z_m(t).$$

Then there is a sufficiently large m > 0 such that

$$v(t) > z_m(t)$$
 for some $t \ge t_1$.

Since $z_m(t)$ is nondecreasing and $v(\gamma_1) \le z_m(\gamma_1)$, by continuity, there is $t_2 \in [\gamma_1, t_1]$ such that $v(t_2) = z_m(t_2)$, $v(t) \le z_m(t) \le z_m(t_2) = v(t_2)$ for all $t \in [\gamma_1, t_2]$, and moreover

$$\dot{v}(t_2) \geqslant \dot{z}_m(t_2) = g(t_2, z_m(t_2)) + \frac{1}{m} = g(t_2, v(t_2)) + \frac{1}{m}.$$

On the other hand, since $v(t_2) = z_m(t_2) \ge z_m(\gamma_1) \ge v(\gamma_1)$, i.e. $v(\xi) \le v(t_2)$ for $t_2 - r \le \xi \le t_2$, by condition (iv) we have

$$\dot{v}(t_2) \leqslant g(t_2, v(t_2)),$$

a contradiction. Therefore

$$v(t) \leqslant z(t, \gamma_1, z^0) = z(t)$$
 for $\gamma_1 \leqslant t < t_z$.

By (3.2) and (3.5) it follows that

$$\lim_{t \to t_{\bar{z}}} \inf z(t) = \lim_{t \to t_{\bar{z}}} \inf v(t) \ge -\varepsilon_1 > -\delta,$$

which contradicts condition (v). Claim II is proved.

Thus $x(\gamma_2) \notin B[K, \rho_1]$ for some $\gamma_2 > \gamma_1$. If $x(t) \notin B(K, \rho_1)$ for all $t \ge \gamma_2$, then for $t_1 = \gamma_2$, $x(t) \notin \mathcal{A}$ for all $t \ge t_1$ and we prove the theorem. So, suppose there is $\bar{t} > \gamma_2$ such that $x(\bar{t}) \in B(K, \rho_1)$; define

$$\bar{\gamma} = \sup\{t \in [\gamma_2, \bar{t}] : x(t) \notin B[K, \rho_1]\},$$

then $\gamma_2 < \bar{\gamma} < \bar{t}$, $x(\bar{\gamma}) \in G \cap \text{fr } B[K, \rho_1]$, and $x(t) \in B[K, \rho_1]$ for $t \in [\bar{\gamma}, \bar{t}]$. Similarly, v(t) satisfies (3.4), (3.5), (3.6), and, by Claim I, $v(\bar{\gamma}) \le -\varepsilon_2$.

Let $\bar{z}(t)$ be the maximal solution of

$$\dot{z} = g(t, z), \qquad z(\bar{\gamma}) = -\varepsilon_2$$

on $[\bar{\gamma}, t_{\bar{z}})$ according to condition (v), then $\bar{z}(t) < -\eta_{\epsilon_2}$ for all $t \in [\bar{\gamma}, t_{\bar{z}})$. Again by the comparison technique used above, we have $v(t) \leq \bar{z}(t)$ for $t \geq \bar{\gamma}$. Now by the continuity of v(t) we have $\bar{t} < t_{\bar{z}}$. Hence $v(t) \leq \bar{z}(t)$ for all $t \in [\bar{\gamma}, \bar{t}]$ and $v(\bar{t}) < -\eta_{\epsilon}^2$.

Finally by (3.3) we get $x(\bar{t}) \notin \mathcal{A}$. Since \bar{t} is arbitrary we have proved that

$$x(t) \notin \mathcal{A}$$
 for all $t \ge t_1 = \gamma_2$.

This completes the proof.

Remark 3.2. The assumptions in Theorem 3.1 also guarantee that the point u is not reachable through G; that is, there is no solution of RFDE (2.1) with $\varphi \in G$ such that $x_{t_1}(t_0, \varphi) = u$ for some $t_1 \in I_x$ and $x_t(t_0, \varphi) \in G$ for all $t \in [t_0, t_1)$.

COROLLARY 3.3. In Theorem 3.1 if

$$g(t, z) = -\rho(t) q(|z|)$$
 (3.7)

with $q:(0, +\infty) \to (0, +\infty)$ and $\rho: J \to R$ continuous functions such that

$$\lim_{\mu \to 0} \int_{\mu}^{\mu_0} \frac{1}{q(\xi)} d\xi = +\infty \qquad (\mu_0 > 0)$$
 (3.8)

and

$$\int_{t_0}^{b} \rho(s) \, ds = +\infty, \qquad \int_{s_1}^{s_2} \rho(s) \, ds > -m = constant \tag{3.9}$$

for all $s_1, s_2 \in J$ with $s_1 < s_2$, then the conclusion of Theorem 3.1 holds.

Proof. Let z(t) be a maximal solution of (3.1) with (3.7) and let $t_z \le b$ be such that z(t) < 0 for all $t \in [\sigma, t_z)$, with t_z maximal. From (3.7) and (3.9), for $t \in [\sigma, t_z)$ and $k = |z(\sigma)|$ we have

$$\int_{|z(t)|}^{k} \frac{1}{q(\xi)} d\xi = -\int_{t}^{\sigma} \frac{z'(y)}{q(|z(y)|)} dy = -\int_{\sigma}^{t} \rho(s) ds < m,$$

that is,

$$\int_{|z(t)|}^{\mu_0} \frac{1}{q(\xi)} d\xi \le -\int_{\sigma}^{t} \rho(s) ds + \left| \int_{k}^{\mu_0} \frac{1}{q(\xi)} d\xi \right|. \tag{3.10}$$

Define

$$\Phi(\mu) = \int_{\mu}^{\mu_0} \frac{1}{q(\xi)} d\xi.$$

Observe that $\Phi: \mathbb{R}^+ \to (-L, +\infty)$ is decreasing and

$$\lim_{\mu \to 0^+} \inf \Phi(\mu) = +\infty$$

by condition (3.8), where $L = \int_{\mu_0}^{\infty} (1/q(\xi)) d\xi$. Now the second inequality in (3.9) implies that

$$\Phi(|z(t)|) \leq m + \left| \int_{k}^{\mu_0} \frac{1}{q(\xi)} d\xi \right|.$$

Hence there is $\eta_k = \Phi^{-1}(m + |\int_k^{\mu_0} (1/q(\xi)) d\xi|) > 0$, such that

$$z(t) < -\eta_k < 0$$
 for all $t \in [\sigma, t_z^-)$. (3.11)

If $t_z < b$, then $\lim_{t \to t_z^-} z(t) = -\infty$. If $t_z = b$, taking limits as $t \to b^-$ in both sides of (3.10) and using the first equality in (3.9), we get

$$\lim_{t \to b^{-}} \int_{\mu_{0}}^{|z(t)|} \frac{1}{q(\xi)} d\xi = +\infty,$$

and by (3.11), we have $L = +\infty$ and

$$\lim_{t\to h^{-}}|z(t)|=+\infty.$$

Hence assumption (v) follows.

Suppose that V can be chosen independent of t, i.e., V = V(x): $R^n \to R$, set $V_0 = \{ \varphi \in X \colon V(\varphi(0)) = 0 \}$.

THEOREM 3.4. Assume that $f: J \times C \to \mathbb{R}^n$ is completely continuous, fr_N M is a compact set, and, for each $u \in \operatorname{fr}_N(\operatorname{int}_N M)$, there is a differentiable function $V: \mathbb{R}^n \to \mathbb{R}$ such that

(i) V(u(0)) = 0 for $u \in \text{fr}_N M$ and $V(\varphi(0)) < 0$ for $\varphi \in \text{int}_N M$.

Assume that there exist a continuous function $g: J \times (-\infty, 0) \to R$ and an open neighbourhood X_2 of $V_0 \cap \operatorname{fr}_N(\operatorname{int}_N M)$, such that

- (ii) $\dot{V}_{(2.1)}(\varphi(0)) \leq g(t, V(\varphi(0)))$ if $V(\varphi(\theta)) \leq V(\varphi(0))$, $\theta \in [-r, 0]$ for all $(t, \varphi) \in J \times (X_2 \cap \text{int}_N M)$;
 - (iii) condition (v) of Theorem 3.1 holds.

Then the RFDE (2.1) is uniformly persistent.

Proof. Define the open set $G = \operatorname{int}_N M$, the closed sets $S = \operatorname{fr}_N M$ and $S^* = \operatorname{fr}_N G$. First we note that G is flow-invariant for the RFDE (2.1). Indeed, by Remark 3.2, no point of S^* is reachable through G. Since, for each $u \in S^*$, the set $V_0 \cap \operatorname{fr}_N G \subset X$ is compact, Theorem 3.1 ensures that each point $u \in S^*$ is uniformly repulsive with respect to $\operatorname{int}_N M$. Thus Proposition 2.2 implies the conclusion.

In Theorem 3.4, we suppose that $fr_N M$, a subset of C, is compact. Here we introduce the following definition.

DEFINITION 3.5. A system of the RFDE (2.1) is dissipative (or equivalently uniformly ultimately bounded) if for any solution $x_t(t_0, \varphi)$ of (2.1) there is a constant B such that, for any $(t_0, \varphi) \in R \times C$, there is a constant $T(t_0, \varphi) > 0$ such that $|x_t(t_0, \varphi)| \leq B$ for $t \geq t_0 + T(t_0, \varphi)$.

Remark 3.6. The above definition of dissipativeness is equivalent to bounded dissipativeness in Hale [30].

Suppose that $x_i(t_0, \varphi)$ inherits the nonnegative property; that is, if $\varphi \in X$, then any solution $x_i(t_0, \varphi)$ defined for $t \ge 0$ satisfies $x_i^i(t_0, \varphi) \ge 0$ for $0 \le t < \infty$ and i = 1, 2, ..., n if $\varphi_i(s) \ge 0$. Let B be defined as in Definition 3.5, define $X_0 = \{\varphi \in X : \|\varphi\| \le B\}$, and let $N = \{\psi : \exists t \ge 0, \exists \varphi \in X_0, \ \psi = x_i(t_0, \varphi)\}$. Similar to Lemmas 3.4, 3.5 and 3.6 of Burton and Hutson [2], we know that N is flow-invariant and is compact in the $\|\cdot\|$ norm.

Let S be a closed subset of N consisting of those φ such that $\varphi_j(0) = 0$ for at least one j. For the sake of biological relevance, assume that RFDE (2.1) is such that S and $M = N \setminus S$ are flow-invariant. Since $S = \operatorname{fr}_N M$ is a closed subset of compact set N, it is compact. Hence we have the following result.

THEOREM 3.7. Suppose that $f: J \times C \to R^n$ is completely continuous and system (2.1) is dissipative. Let $P: R^n \to R$ be a differentiable function satisfying

(i) $P(\varphi(0)) = 0$ for $\varphi \in \text{fr}_N M$, $P(\varphi(0)) > 0$ for $\varphi \in \text{int}_N M$.

Assume further that there exist a continuous function $\rho: J \to R$ and a neighborhood X_3 of $\operatorname{fr}_N M$ such that for every $\varphi \in X_3 \cap \operatorname{int}_N M$ and $t \in J$,

- (ii) $\dot{P}_{(2,1)}(\varphi(0)) \geqslant P(\varphi(0)) \rho(t)$ if $P(x(\xi)) \geqslant P(x(t))$ for $t r \leqslant \xi \leqslant t$;
- (iii) $\int_{t_0}^{b} \rho(t) dt = +\infty$ and $\int_{t_1}^{t_2} \rho(s) ds > -m$ for every $t_0 \le t_1 < t_2 < b$.

Then the RFDE (2.1) is uniformly persitent.

Proof. Setting

$$V(\varphi(0)) = -P(\varphi(0)),$$

$$g(t, z) = -\rho(t) |z|,$$

then by Corollary 3.3 and Theorem 3.5 the theorem follows.

Remark 2.8. Varieties of Theorem 3.7 have been proved by Hofbauer [33] and Hutson [37] for autonomous ODE, by Fernades and Zanolin [14] for nonautonomous ODE, by Hutson and Moran [39] for difference equations, by Hutson and Moran [40] for reaction—diffusion equations, and by Burton and Hutson [2] for autonomous equations with infinite delay.

Remark 3.9. If $f: J \times C \to R^n$ is T-periodic in the time variable, then the hypothesis on the function $\rho(t)$ in Theorem 3.7 is satisfied provided that

$$\langle \rho \rangle = \frac{1}{T} \int_0^T \rho(s) \, ds > 0.$$

Under minor modifications, the above results hold for the autonomous retarded functional differential equation (2.2). Especially, as in Hutson [37], Burton and Hutson [2], and Fonda [15], the differential inequalities in Theorems 3.1 and 3.4 only need to hold in $\omega(u)$ and in the omega limit set of $u \in S$, and in Theorem 3.7 assumption (ii) only needs to be true for $\varphi \in \omega(S)$, the omega limit set of the boundary S. In fact, we have the following.

THEOREM 3.10. Suppose that $f: C \to \mathbb{R}^n$ is completely continuous and system (2.2) is dissipative. Let $P: \mathbb{R}^n \to \mathbb{R}$ be a differentiable function satisfying

(i) $P(\varphi(0)) = 0$ for $\varphi \in S$, $P(\varphi(0)) > 0$ for $\varphi \in \text{int}_N M$.

Assume further that there exists a continuous function $\rho: J \to R$ such that for every $\varphi \in \omega(S)$

- (ii) $\dot{P}_{(2,2)}(\varphi(0)) \geqslant P(\varphi(0)) \rho(t)$ if $P(x(\xi)) \geqslant P(x(t))$ for $t r \leqslant \xi \leqslant t$;
- (iii) $\int_{t_0}^{b} \rho(t) dt = +\infty$ and $\int_{t_1}^{t_2} \rho(s) ds > -m$ for every $t_0 \le t_1 < t_2 < b$.

Then RFDE (2.2) is uniformly persistent.

Remark 3.11. As in the classical Razumikhin-type theorems in stability theory (see Hale [29] and Haddock and Terjéki [28]), we do not require that the differential inequalities in the above persistence theorems hold for all initial values, but for some initial values under the restriction $P(x(\xi)) \ge P(x(t))$ for $t - r \le \xi \le t$. This kind of condition is usually called Razumikhin condition (see Haddock and Terjéki [28]).

If $P(\cdot)$ is a Liapunov-like functional, as in Burton and Hutson [2], we have the following.

THEOREM 3.12. Suppose that $f: C \to \mathbb{R}^n$ is completely continuous and system (2.2) is dissipative. Let $P: C \to \mathbb{R}$ be a differentiable functional satisfying

- (i) $P(\varphi(0)) = 0$ for $\varphi \in S$, $P(\varphi(0)) > 0$ for $\varphi \in \text{int}_N M$;
- (ii) $\psi(u) = \dot{P}(u)/P(u) > 0$ for $u \in \omega(S)$.

Then the autonomous RFDE(2.2) is uniformly persistent.

4. APPLICATIONS

1. Consider the predator-prey model with delay proposed by Leung [47] (see also Kuang [42])

$$\dot{x} = x(t)[a - bx(t) - cy(t)]$$

$$\dot{y} = \alpha y(t)[x(t - \tau) - \beta],$$
(4.1)

where a, b, c, α, β , and τ are positive constants. The initial population sizes are provided in the form

$$x(s) = \varphi(s) \ge 0,$$
 $s \in [-\tau, 0],$ $y(0) = y_0 \ge 0.$

It is known that if

$$a - b\beta > 0 \tag{4.2}$$

then system (4.1) has a unique equilibrium $E^* = (x^*, y^*)$ where

$$x^* = \beta, \qquad y^* = \frac{a - b\beta}{c}.$$

In [46], Leung showed that, under (4.2) and other conditions, there exist periodic solutions, hence coexistence could occur. We shall see that actually (4.2) implies uniform persistence of system (4.1).

Let

$$x(t) = X(t) + x^*, y(t) = Y(t) + y^*.$$

System (4.1) can be transformed into

$$\dot{X} = (X(t) + x^*)[-bX(t) - cY(t)]$$

$$\dot{Y} = \alpha(Y(t) + y^*)X(t - \tau)$$
(4.3)

Choose a Liapunov function as follows

$$V(X(t), Y(t)) = X(t) - x^* \ln\left(1 + \frac{X(t)}{x^*}\right) + \frac{c}{\alpha q} \left[Y(t) - y^* \ln\left(1 + \frac{Y(t)}{y^*}\right)\right],$$

where q > 1 is a given constant. If X(t) = Y(t) = 0, then V = 0, and V is positive definite for bounded $X(t) > \beta$, $Y(t) > (a - b\beta)/c$. We have

$$\begin{split} \dot{V}_{(4.3)}(X(t), \ Y(t)) &= \frac{X(t)}{X(t) + x^*} \cdot \dot{X} + \frac{c}{\alpha q} \frac{Y(t)}{Y(t) + y^*} \cdot \dot{Y} \\ &= -bX^2(t) - cX(t) \ Y(t) + \frac{c}{q} X(t - \tau) \ Y(t) \\ &\leq -bX^2(t) \end{split}$$

if $|X(t-\tau)| \le q|X(t)|$ and $|X(t)| \ge \beta$, $|Y(t)| \ge (a-b\beta)/c$ (see Hale [29, Chapter 5]). Thus by the classical Liapunov-Razumikhin theorem for boundedness (see Hale [29], Theorem 4.3 in Chapter 5), system (4.3) and hence system (4.1) is dissipative.

THEOREM 4.1. If (4.2) holds, then system (4.1) is uniformly persistent.

Proof. System (4.1) has two boundary equilibria, $E_0 = (0, 0)$ and $E_1 = (a/b, 0)$. For $(x, y) \in \omega(S)$, the omega limit set of the boundary S, if y = 0, from the first equation of (4.1) it follows that $\pi(x, t) = x_t \to (a/b)$ as $t \to \infty$. If x(0) = 0 then $\pi(x, t) \equiv 0$ and $\pi(y, t) = y_t \to 0$ as $t \to \infty$. Thus the omega limit set of S is the union of $E_0 = (0, 0)$ and $E_1 = (a/b, 0)$.

Now choose $P(x, y) = x^{\alpha_1}y^{\alpha_2}$, where α_1 and α_2 are positive undetermined constants. Defining

$$\rho(t) = \alpha_1 [a - bx(t) - cy(t)] + \alpha_2 \alpha [x(t) - \beta],$$

we have

$$\dot{P}(x, y) = P(x, y) \cdot \left\{ \alpha_1 [a - bx(t) - cy(t)] + \alpha_2 \alpha [x(t - \tau) - \beta] \right\}$$

$$\geqslant P(x, y) \rho(t)$$

if $x(\xi) \geqslant x(t)$ for $t - \tau \leqslant \xi \leqslant t$. The choice $\alpha_1 = 1$ ensures that $\rho(t) > 0$ at E_0 . If (4.2) holds, the second term in $\rho(t)$ is positive at E_1 . Hence there is always a choice of α_2 to ensure $\rho(t) > 0$. The result follows from Theorem 3.10.

2. For the Lotka-Volterra competition model with delay

$$\dot{x} = x(t)(r_1 - a_1 x(t - \tau) - b_1 y(t - \tau))$$

$$\dot{y}(t) = y(t)(r_2 - a_2 x(t - \tau) - b_2 y(t - \tau))$$
(4.4)

under initial conditions

$$x(s) = \varphi_1(s) \ge 0,$$
 $s \in [-\tau, 0],$ $\varphi_1(0) > 0$
 $y(s) = \varphi_2(s) \ge 0,$ $s \in [-\tau, 0],$ $\varphi_2(0) > 0,$

where r_i , a_i , b_i (i = 1, 2) and τ are positive constants, both $\varphi_1(s)$ and $\varphi_2(s)$ are continuous on $[-\tau, 0]$. System (4.4) has three boundary equilibria $E_0 = (0, 0)$, $E_1 = (r_1/a_1, 0)$ and $E_2 = (0, r_2/b_2)$.

THEOREM 4.2. If

$$r_2 a_1 - r_1 a_2 > 0, (4.5)$$

$$r_1b_2 - r_2b_1 > 0,$$
 (4.6)

then system (4.4) is uniformly persistent.

Proof. It is not difficult to prove that system (4.3) is dissipative. Now for $u \in \omega(S)$, if $u_1(0) = 0$, then $\pi(u_1, t) = 0$ and $\pi(u_2, t) \to r_2/b_2$ as $t \to \infty$. If $u_2(0) = 0$, then $\pi(u_2, t) = 0$ and $\pi(u_1, t) \to r_1/a_1$ as $t \to \infty$. Thus the omega limit set of S is the union of E_0 , E_1 and E_2 .

Choosing $P(u) = u_1^{\alpha_1} u_2^{\alpha_2}$, where $u = (u_1, u_2)$, α_1 and α_2 are positive undetermined constants, we have

$$\psi(u) = \frac{\dot{P}(u)}{P(u)} = \alpha_1 [r_1 - a_1 u_1(\theta) - b_1 u_2(\theta)] + \alpha_2 [r_2 - a_2 u_1(\theta) - b_2 u_2(\theta)].$$

For any positive α_1 and α_2 , ψ is always positive at E_0 . If (4.5) holds, the second term of ψ is positive at E_1 ; if (4.6) holds the first term of ψ is positive at E_2 , hence we can choose α_1 and α_2 to ensure $\psi > 0$. By Theorem 3.12, system (4.4) is uniformly persistent.

Remark 4.3 It is well known that (4.5) and (4.6) are persistence conditions for system (4.4) without delay (see Hallam [32]). Recently, Cao, et al. [8] showed that

$$r_2 a_1 - r_1 a_2 e^{r_1 \tau} > 0, (4.7)$$

$$r_1 b_2 - r_2 b_1 e^{r_2 \tau} > 0 (4.8)$$

are sufficient for uniform persistence in system (4.4). Obviously (4.5) and (4.6) are sharper than (4.7) and (4.8).

3. Now consider the following delayed Gause-type predator-prey model with Michaelis-Menten functional response

$$\dot{x} = x(t) \left[\gamma - ax(t) - \frac{by(t)}{1 + cx(t)} \right]$$

$$\dot{y} = y(t) \left[-v + \frac{dx(t - \tau)}{1 + cx(t - \tau)} \right],$$
(4.9)

where a, b, γ, ν , and τ are positive constants, $x(t) = \varphi(t) \ge 0$ on $[-\tau, 0]$, $y(0) = y_0 \ge 0$. Zhao et al. [59] showed that system (4.9) is dissipative and has a Hopf bifurcation under certain restrictions on the parameters. Here we have the following result.

THEOREM 4.4 If

$$\frac{d\gamma}{a+c\gamma} > v,\tag{4.10}$$

then system (4.9) is uniformly persistent.

Proof. Similar to the proof of Theorem 4.1, we know that the omega limit set of the boundary $S = \text{fr}_N M$ is the union of the boundary equilibria $E_0 = (0, 0)$ and $E_1 = (\gamma/a, 0)$. We choose $P(x(t), y(t)) = x(t)^{\alpha_1} y(t)^{\alpha_2}$, where α_1 and α_2 are undetermined positive constants, then

$$\dot{P}(x(t), y(t)) = P(x(t), y(t)) \left[\alpha_1 \left(\gamma - ax(t) - \frac{by(t)}{1 + cx(t)} \right) + \alpha_2 \left(-v + \frac{dx(t - \tau)}{1 + cx(t - \tau)} \right) \right]$$

$$\geqslant P(x(t), y(t)) \rho(t)$$

if $x(\xi) \ge x(t)$ for $t - \tau \le \xi \le t$, where

$$\rho(t) = \alpha_1 \left(\gamma - ax(t) - \frac{by(t)}{1 + cx(t)} \right) + \alpha_2 \left(-\nu + \frac{dx(t)}{1 + cx(t)} \right).$$

The choice $\alpha_1 = 1$ ensures that $\rho(t)$ is positive at E_0 . If (4.10) holds, the second term of $\rho(t)$ is positive at E_1 . Hence there is always a choice of α_2 such that $\rho(t) > 0$. The result again follows from Theorem 3.10.

Note that condition (4.10) is equivalent to the uniform persistent criterion for system (4.9) without delay; that is the delay in system (4.9) is also "harmless" for uniform persistence.

5. DISCUSSION

By using Liapunov-like functions, Razumikhin technique, and differential inequalities, we have obtained criteria for the uniform persistence of retarded functional differential equations. These criteria are quite general in their applicability to ecological systems. The conditions for uniform persistence do not require any special assumptions on the interaction terms and the conclusions are very precise in specific cases.

The examples described in Section 4 show that for some models uniform persistence criteria are exactly the conditions used previously to establish the existence of an interior equilibrium. Similar results were obtained by Cantrell et al. [7] for reaction—diffusion systems. It is well known (see Butler et al. [5] and Hutson [38]) that uniform persistence actually implies the presence of an interior equilibrium. Generally, however, possessing an interior equilibrium is neither necessary nor sufficient for persistence. We see that in a rather wide range of problems the conditions which guarantee the existence of an interior equilibrium are in fact enough to ensure uniform persistence.

For the Lotka-Volterra competition model with delay and the delayed Gause-type predator-prey model, our results indicate that the criteria for uniform persistence in the delay models are equivalent to criteria for uniform persistence in the ODE cases. Hence, as shown by Wang and Ma [52], the delay is "harmless" for uniform persistence.

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REFERENCES

- 1. T. A. Burton, "Stability and Periodic Solutions of Ordinary and Functional Differential Equations," Academic Press, Orlando, 1985.
- T. A. Burton and V. Hutson, Repellers in systems with infinite delay, J. Math. Anal. Appl. 137 (1989), 240-263.
- 3. T. A. Burton and V. Hutson, Permanence for non-autonomous predator-prey systems, Differential Integral Equations 4 (1991), 1269-1280.
- 4. S. BUSENBERG, K. COOKE, AND H. THIEME, Demographic change and persistence of HIV/AIDS in heterogeneous population, SIAM J. Appl. Math. 51 (1991), 1030-1052.
- G. J. BUTLER, H. I. FREEDMAN AND P. WALTMAN, Uniformly persistent systems, Proc. Amer. Math. Soc. 96 (1986), 425-430.
- 6. G. J. BUTLER AND P. WALTMAN, Persistence in dynamical systems, J. Differential Equations 63 (1986), 255-263.
- 7. R. S. CANTRELL, C. COSNER, AND V. HUTSON, Permanence in ecological systems with spatial heterogeneity, *Proc. Roy. Soc. Edinburgh* 123A (1993), 533-559.
- 8. Y. CAO, J.-P. FAN, AND T. C. GARD, Uniform persistence for population interaction models with delay, *Appl. Anal.* 51 (1993), 197-210.
- 9. Y. CAO AND T. C. GARD, Uniform persistence for population models with time delay using multiple Liapunov functions, J. Differential Integral Equations 6 (1993), 883-898.
- J. M. Cushing, "Integrodifferential Equations and Delay Models in Population Dynamics," Springer-Verlag, Berlin, 1977.
- 11. S. Dunbar, K. Rybakowski, and K. Schmitt, Persistence in models of predator-prey populations with diffusion, *J. Differential Equations* 65 (1986), 117-138.
- 12. M. FERNANDES AND F. ZANOLIN, Remarks on strongly flow invariant sets, J. Math. Anal. Appl. 128 (1987), 176-188.
- 13. M. Fernandes and F. Zanolin, Repelling conditions for boundary sets using Liapunov-like functions. I. Flow-invariance, terminal value problems and weak persistence, *Rend. Sem. Mat. Univ. Padova* 80 (1988), 95-116.
- M. FERNANDES AND F. ZANOLIN, Repelling conditions for boundary sets using Liapunovlike functions. II. Persistence and periodic solutions, J. Differential Equations 86 (1990), 33-58.
- A. FONDA, Uniformly persistence semi-dynamical systems, Proc. Amer. Math. Soc. 104 (1988), 111-116.
- 16. H. I. FREEDMAN AND K. GOPALSAMY, Nonoccurence of stability switching in systems with discrete delays, Canad. Math. Bull. 31 (1988), 52-58.
- 17. H. I. Freedman and P. Moson, Persistence definitions and their connections, *Proc. Amer. Math. Soc.* 109 (1990), 1025-1033.
- 18. H. I. Freedman and J. So, Persistence in discrete semidynamical systems, SIAM J. Math. Soc. 20 (1989), 930–938.
- 19. H. I. Freedman, S. Ruan and M. Tang, Generalized Ura-Kimura theorems and uniform persistence, J. Dynamics Differential Equations, in press.
- 20. H. I. Freedman and P. Waltman, Mathematical analysis of some three-species food-chain models, *Math. Biosci.* 33 (1977), 257–276.
- 21 H. I. FREEDMAN AND P. WALTMAN, Persistence in three interacting predator-prey populations, *Math. Biosci.* 68 (1984), 213-231.
- 22. H. I. Freedman and P. Waltman, Persistence in a model of three competitive populations, *Math. Biosci.* 73 (1985), 89-101.
- H. I. FREEDMAN AND J. WU, Persistence and global asymptotical stability of single species dispersal models with stage structure, Quart. Appl. Math. Appl. 49 (1991), 351-371.

- B. M. GARAY, Uniform persistence and chain recurrence, J. Math. Anal. Appl. 139 (1989), 372-381.
- 25. T. C. GARD, Strongly flow-invariant sets, Appl. Anal. 10 (1980), 285-293.
- T. C. GARD AND T. G. HALLAM, Persistence of food webs. I. Lotka-Volterra food chains, Bull. Math. Biol. 41 (1979), 877-891.
- K. GOPALSAMY, Delayed responses and stability in two-species systems, J. Austral. Math. Soc. Ser. B 25 (1984), 473-500.
- 28. J. R. HADDOCK AND J. TERJÉKI, Liapunov-Razumikhin functions and an invariance principle for functional differential equations, *J. Differential Equations* 48 (1983), 95-122.
- J. K. Hale, "Theory of Functional Differential Equations," Springer-Verlag, New York, 1977.
- 30. J. K. Hale, "Asymptotic Behavior of Dissipative Systems," Amer. Math. Soc., Providence, 1988
- 31. J. K. HALE AND P. WALTMAN, Persistence in infinite dimensional systems, SIAM J. Math. Anal. 20 (1989), 388-395.
- 32. T. G. Hallam, Persistence in Lotka-Volterra models of food chains and competition, in "Modeling and Differential Equations in Biology" (T. A. Burton, Ed.), pp. 1-11, Dekker, New York, 1980
- 33. J. HOFBAUER, A general cooperation theorem for hypercycles, *Monatsh. Math.* 91 (1981), 233-240.
- 34. J. HOFBAUER, A unified approach to persistence, Acta. Appl. Math. 14 (1989), 11-22.
- 35. J. HOFBAUER AND K. SIGMUND, "Dynamical Systems and the Theory of Evoluation," Cambridge Univ. Press, Cambridge 1988.
- J. HOFBAUER AND J. So, Uniform persistence and repellers for maps, Proc. Amer. Math. Soc. 107 (1989), 1137-1142.
- 37. V. Hutson, A theorem on average Liapunov functions, *Monatsh. Math.* 98 (1984), 267-275.
- 38. V. Hutson, The existence of an equilibrium for permanent systems, *Rocky Moutain J. Math.* 20 (1990), 1033-1040.
- 39. V. Hutson and W. Moran, Persistence of species obeying difference equations, *Math. Biosci.* 15 (1982), 203-213.
- V. Hutson and W. Moran, Repellers in reaction-diffusion systems, Rocky Moutain J. Math. 17 (1987), 301-314.
- 41. V. HUTSON AND K. SCHMITT, Permanence and the dynamics of biological systems, *Math. Biosci.* 111 (1992), 1-71.
- 42. Y. Kuang, Periodic solutions in a class of delayed predator-prey systems, *Trans. Amer. Math. Soc.*, to appear.
- 43. Y. Kuang and H. L. Smith, Global stability in diffusive-delay Lotka-Volterra systems, Differential and Integral Equations 4 (1991), 117-128.
- 44. Y. Kuang and B. Tang, Uniform persistence in nonautonomous delay differential Kolmogorov-type population models, *Rocky Mountain J. Math.* 24 (1994), 165–186.
- 45. Y. Kuang and B. Tang, Uniform persistence in some population models with distributed delay, preprints.
- V. LAKSHMIKANTHAM AND S. LEELA "Differential and Integral Inequalities," Vol. II, Academic Press, New York, 1969.
- 47. A. LEUNG, Periodic solutions for a prey-predator differential delay equation, J. Differential Equations 26 (1977), 391-403.
- 48. N. MACDONALD, "Time Lags in Biological Models," Springer-Verlag, Berlin, 1978.
- 49. S. Ruan, The effect of delays on stability and persistence in plankton models, *Nonlin. Anal. Th. Meth. Appl.*, to appear.

- S. H. SAPERSTONE, "Semidynamical Systems in Infinite Dynamical Systems," Springer-Verlag, New York, 1981.
- 51. P. SCHUSTER, K. SIGMUND AND R. WOLFF, Dynamical systems under constant organization. 3. Cooperative and competitive behavior of hypercycles, *J. Differential Equations* 32 (1979), 357-368.
- 52. G. Seifert, Positively invariance closed sets for systems of delay differential equations, J. Differential Equations 22 (1976), 292-304.
- 53. H. L. SMITH, Monotone semiflows generated by functional differential equations, J. Differential Equations 66 (1987), 420-442.
- 54. W. Wang and Z. Ma, Harmless delays for uniform persistence, J. Math. Anal. Appl. 158 (1991), 256-268.
- G. S. K. Wolkowicz, Invasion of a persistent system, Rocky Mountain J. Math. 20 (1990), 1217-1234.
- 56. F. YANG AND S. RUAN, A generalization of the Butler-McGehee lemma and its applications in persistence theory, Fields Institute Research Report F192-DS03.
- 57. T. YOSHIZANA, "Stability by Liapunov's Second Method," The Math. Soc. Japan, Tokyo, 1966.
- 58. F. Zanolin, Permanence and positive periodic solutions for Kolmogorov competing species systems, *Results in Math.* 21 (1992), 224–250.
- 59. T. Zhao, Y. Kuang, and H. L. Smith, Global existence of periodic solutions in a class of delayed Gause-type predator-prey systems, to appear.