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Persistence in a Model of Predator-Prey Population Dynamics with the Action of a Parasite in Periodic Environment*

Trinh Tuan Anh and Tran Van Nhung

Department of Mathematics, Hanoi National University, 334 Nguyen Trai Str. Thanh Xuan, Hanoi, Vietnam

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Abstract. We consider a model of a predator-prey population with the action of a parasite in the periodic case. We establish a uniform persistence criteria for the model. This is a generalization of a result by Freedman [1] from the autonomous case to the periodic one.

1. Introduction

In [1], Freedman considered a mathematical model of a predator-prey population in which each member of prey may or may not be infected by a parasite, but the predators are all infected. That model was described by a system of three autonomous ordinary differential equations and conditions for persistence of all populations were given (see [1]). Our concern in this paper is with the more general case in which the model is depending on time t periodically. Such a generalization seems to be natural considering the oscillations to which any ecological parameter might quite naturally be exposed (for example, those due to seasonal effects of weather, food supply, mating habits, hunting or harvesting seasons, etc.).

The model considered in this paper is described by the following system of non-autonomous ordinary differential equations:

$$\begin{aligned}
\dot{S} &= B(t,X) - \frac{SD(t,X)}{X} - [\beta_0(t) + \beta_1(t)Y]S - \frac{SP_1(t,X)Y}{X},\\
\dot{I} &= [\beta_0(t) + \beta_1(t)Y]S - \frac{ID(t,X)}{X} - \frac{IP_2(t,X)Y}{X}, \qquad (1.1)\\
\dot{Y} &= Y\left[-\Gamma(t,Y) + c(t)\frac{SP_1(t,X) + IP_2(t,X)}{X}\right],
\end{aligned}$$

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where S, I, $X = S+I$, Y are the susceptible, infective, total prey and predator population densities, respectively; $B, D, P_1, P_2, \Gamma : R \times [0, +\infty) \to R$ are continuous, T-periodic in the first variable ($T > 0$) and continuously differentiable in the second variable; and $\beta_0, \beta_1, c : R \to (0, +\infty)$ are continuous and T-periodic.

The case of functions $B, D, P_1, P_2, \Gamma, \beta_0, \beta_1, c$ not depending on t-variable was considered in [1]. Further assumptions on the functions of the system (1.1) are given below, which are based on those in [1]. In the following, we denote by $B'_X, D'_X, P'_{1X}, P'_{2X}, \Gamma'_Y$ the partial derivatives of the functions B, D, P_1, P_2, Γ, respectively, with respect to the second variable.

The function $B(t, X)$ is the birth rate of the prey population at time t and is assumed to be independent of parasite infection. Further, it is assumed that the birth rate increases with increasing population. Hence,

(H$_1$) $B(t, 0) = 0$ and $B'_X(t, X) > 0$ for $t \in [0, T]$ and $X \in [0, +\infty)$.

The function $D(t, X)$ represents the "natural" death rate of the prey population at time t, that is, death due to any occurrence other than predation. It is also assumed that the death rate increases with increasing population. Hence,

(H$_2$) $D(t, 0) = 0$ and $D'_X(t, X) \geq 0$ for $t \in [0, T]$ and $X \in [0, +\infty)$.

In the system (1.1) all prey members are born into the susceptible class and may be subjected to parasitism immediately after birth. The natural death rate corresponding to each prey class are proportional to the relative densities of that class, i.e., $(S/X)D(t, X)$ and $(I/X)D(t, X)$ are the natural death rates of the susceptible and infective prey populations, respectively.

If there are no predators and parasites, the prey population can be described by the following equation (see Eq. (1.1)):

$$X = Xg(t, X), \tag{1.2}$$

where $g(t, X) = [B(t, X) - D(t, X)]/X$ is the specific growth rate of the prey population at time t. Due to limited resources at time t, the specific growth rate is decreasing with increasing population. Eventually, it becomes negative since food supply can support only a finite population. Therefore,

(H$_3$) $g(t, X)$ is continuous on $R \times [0, +\infty)$; $g(t, 0) > 0$ and $g(t, .)$ is strictly decreasing for any fixed $t \in [0, T]$; and furthermore, there exists a T-periodic function $k(t) > 0$ such that $K := \sup_{t \in [0,T]} k(t) < +\infty$, $g(t, k(t)) < 0$ for all $t \in [0, T]$.

The function $P_i(t, X)$ $(i = 1, 2)$ is the predator functional response of the susceptible and infective populations, respectively. It is assumed that owing to the action of the parasites, the infected prey has an increasingly higher functional response than the uninfected prey. Hence,

(H$_4$) $P_i(t, 0) = 0$, $P'_{2X}(t, X) > P'_{1X}(t, X) > 0$ for all $(t, X) \in [0, T] \times [0, +\infty)$.

The function $\Gamma(t, Y)$ is the density dependent death rate of the predator in the absence of prey, which should be increasing with increasing population. Hence,

(H$_5$) $\Gamma(t, 0) > 0$ and $\Gamma'_Y(t, Y) > 0$ for $t \in [0, T]$ and $Y \in [0, +\infty)$.

The following hypothesis is needed for a technical mathematical reason.

(H_6) All functions in System (1.1) are so sufficiently smooth that the Cauchy problem for (1.1) with the non-negative initial values has a unique solution which is continuable for all positive time.

The function $c(t)$ represents the proportion of prey that is converted to predator biomass. The function $\beta_0(t)$ represents the infection rate of susceptible prey in the absence of predators, the function $\beta_1(t)$ is the rate per unit predator of prey infection due to parasitic reproduction in the predator population. In the system (1.1), we assume that all predators are infected. Hence, susceptible prey infected by parasites are removed from the susceptible class at a specific rate of $\beta_0(t) + \beta_1(t)Y$, and an equivalent number of prey are added to the infected class.

For the ecological significance of system (1.1), the reader is referred to [1].

Persistence in mathematical models of population dynamics corresponds to the survival of populations and thus it represents an important qualitative property for such models.

We say that (1.1) is persistent if $\liminf_{t\to+\infty} d((S(t), I(t), Y(t)), \partial R^3_+) > 0$ for any solution to (1.1) with initial conditions $(S(t_0), I(t_0), Y(t_0)) \in \operatorname{int}(R^3_+)$—the interior of $R^3_+ = \{(S, I, Y) : S \geq 0, I \geq 0, Y \geq 0\}$, where $d((S(t), I(t), Y(t)), \partial R^3_+)$ is the Euclidean distance from $(S(t), I(t), Y(t))$ to ∂R^3_+—the boundary of R^3_+.

If, in addition, $\liminf_{t\to+\infty} d((S(t), I(t), Y(t)), \partial R^3_+) \geq \delta > 0$ where δ does not depend on positive initial conditions, then (1.1) is said to be uniformly persistent.

For a survey of permanence theory (i.e., uniform persistence and dissipativity), the reader is referred to [4].

In the next section, we discuss an equivalence of persistence between periodic differential equations and discrete semidynamical systems corresponding to them, and recall some well-known results on persistence in discrete semidynamical systems. In Sec. 3, we prove a persistence criteria for system (1.1).

2. Preliminaries

2.1. Persistence in Periodic Differential Equations

We consider the following equation:

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

where $f : R \times R^d_+ \to R^d$ $(d \geq 1)$ is continuous and T-periodic in t-variable; and $R^d_+ := \{(x_1, \ldots, x_d) : x_i \geq 0,\ i = 1, 2, ..., d\}$. We assume that

(i) the Cauchy problem for (2.1) with the initial condition $x(t_0) = x_0 \in R^d_+$; $(t_0 \in R)$ has a solution which is unique and continuable for all $t \geq t_0$;

(ii) system (2.1) is dissipative, i.e., there exists a compact neighborhood $\mathcal{A}$ of the origin such that, for each solution $x(t)$ to (2.1) with $x(t_0) \in R^d_+$ for some $t_0 \in R$, there exists $t_1 > t_0$ such that $x(t) \in \mathcal{A}$ for all $t \geq t_1$.

By (i), we may introduce for any $t \geq t_0$ the Cauchy operator $G(t, t_0)$; it is defined on R^d_+ and maps the initial datum x_0 into the solution $x(t)$ at time t. Straightforward properties of G are: G is continuous and t-differentiable for $t \geq t_0$; $G(t, s)G(s, t_0) = G(t, t_0),\ t \geq s \geq t_0$; $G(t + T, t_0 + T) = G(t, t_0),\ t \geq t_0$; $G(t, t_0)R^d_+ \subset R^d_+$ for $t \geq t_0$; and $G(t_0, t_0) = Id$ (the identity).

Let $H(\tau) = G(T+\tau, \tau)$ $(\tau \in R)$. We have the discrete semidynamical system:

$$\mathbb{N} \times R_+^d \ni (n, x) \mapsto H^n(\tau)x \in R_+^d. \tag{2.2τ}$$

Definition.

(i) *System (2.1) is said to be persistent (with respect to* ∂R_+^d*) if* $\liminf_{t\to+\infty} d(x(t), \partial R_+^d) > 0$*, for any solution* $x(t)$ *to (2.1) with initial conditions* $x(t_0) \in \mathrm{int}(R_+^d)$*. It is uniformly persistent if* $\liminf_{t\to+\infty} d(x(t), \partial R_+^d) \geq \epsilon$ *for some positive* ϵ *not depending on positive initial condition* $x(t_0) = (x_{01}, ..., x_{0d})$.

(ii) $H(\tau)$ (or (2.2τ)) is said to be persistent (with respect to ∂R_+^d) if $\liminf_{n\to+\infty} d(H^n(\tau)x, \partial R_+^d) > 0$ for all $x \in \mathrm{int}(R_+^d)$. It is uniformly persistent if there exists $\epsilon > 0$ such that $\liminf_{n\to+\infty} d(H^n(\tau)x, \partial R_+^d) \geq \epsilon$ for all $x \in \mathrm{int}(R_+^d)$.

We shall prove the following:

Theorem 2.1.

(i) *System (2.1) is persistent if and only if, for each* $\tau \in [0, T]$*,* $H(\tau)$ *is persistent.*

(ii) *System (2.1) is uniformly persistent if and only if, for each* $\tau \in [0, T]$*,* $H(\tau)$ *is uniformly persistent.*

Before proving Theorem 2.1, we prove the following lemma:

Lemma 2.2. *The function* $\delta(\tau) = \inf_{x\in\mathrm{int}(R_+^d)}\{\liminf_{n\to+\infty} d(H^n(\tau)x, \partial R_+^d)\}$ *is continuous on* $[0, T]$.

Proof. Let $M > 0$ be such that $M^2 = \Sigma_{i=1}^d \sup_{t\in[0,T], x\in\mathcal{A}} |f_i(t, x)|$. We shall prove that $|\delta(\tau) - \delta(\tau')| \leq M|\tau - \tau'|$ for $\tau, \tau' \in [0, T]$. It suffices to show that, for any $x^1 \in \mathrm{int}(R_+^d)$, there exists $x^2 \in \mathrm{int}(R_+^d)$, such that

$$|\liminf_{n\to+\infty} d(H^n(\tau)x^1, \partial R_+^d) - \liminf_{n\to+\infty} d(H^n(\tau')x^2, \partial R_+^d)| \leq M|\tau - \tau'|. \tag{2.3}$$

Let $x(t)$ be the solution to (2.1) with $x(\tau) = x^1$. Put $x^2 = x(T+\tau')$ and $x^3 = x(T+\tau)$. Let $t_1 \geq \tau$ be such that $x(t) \in \mathcal{A}$ for all $t \geq t_1$. We have that

$$\begin{aligned}\liminf_{n\to+\infty} d(H^n(\tau)x^3, \partial R_+^d) &= \liminf_{n\to+\infty} d(H^{n+1}(\tau)x^1, \partial R_+^d) \\ &= \liminf_{n\to+\infty} d(H^n(\tau)x^1, \partial R_+^d).\end{aligned} \tag{2.4}$$

Let $n_0 \in \mathbb{N}$ be such that $n_0T + \tau \geq t_1$ and $n_0T + \tau' \geq t_1$. Since $x(t) \in \mathcal{A}$ for all $t \geq t_1$, it follows that, for $n \geq n_0$,

$$\begin{aligned}|d(H^n(\tau)x^3, \partial R_+^d) - d(H^n(\tau')x^2, \partial R_+^d)| &\leq \|H^n(\tau)x^3 - H^n(\tau')x^2\| \\ &= \|x((n+1)T+\tau) - x((n+1)T+\tau')\| \leq M|\tau - \tau'|.\end{aligned} \tag{2.5}$$

We claim that

$$|\xi - \xi'| \leq M|\tau - \tau'|, \tag{2.6}$$

where $\xi = \liminf_{n\to+\infty} d(H^n(\tau)x^3, \partial R_+^d)$, $\xi' = \liminf_{n\to+\infty} d(H^n(\tau')x^2, \partial R_+^d)$.

Suppose the claim is false. Then there exist two sequences $\{n_k\}$ and $\{n'_k\}$ of $\{n\}$ such that

$$\xi = \lim_{k\to+\infty} d(H^{n_k}(\tau)x^3, \partial R^d_+),$$
$$\xi' = \lim_{k\to+\infty} d(H^{n'_k}(\tau')x^2, \partial R^d_+),$$
$$|\xi - \xi'| > M|\tau - \tau'|.$$

Without loss of generality we may assume $\xi > \xi'$. By going to a subsequence if necessary, we may assume that $\lim_{k\to+\infty} d(H^{n'_k}(\tau)x^3, \partial R^d_+) = \xi_1$. Clearly, $\xi_1 \geq \xi > \xi'$. Thus, it follows from (2.5) that $\xi_1 - \xi' \leq M|\tau - \tau'|$, which contradicts $\xi_1 - \xi' \geq \xi - \xi' > M|\tau - \tau'|$. Thus, the claim is proved, and (2.3) follows from (2.4) and (2.6). The lemma is proved. ∎

Proof of Theorem 2.1. Proof of Part (i). Necessity. It is obvious.

Sufficiency. Suppose it is false. Then there exists a solution $x(t)$ to (2.1) with $x(t_0) \in \mathrm{int}(R^d_+)$ (for some $t_0 \in R$), and a sequence $\{t_n\}_{n=1}^{\infty} \subset [t_0, +\infty) \uparrow +\infty$ such that $\lim_{n\to+\infty} d(x(t_n), \partial R^d_+) = 0$. Let $\tau_n = t_n - [t_n/T]T$ for $n \geq 1$, where $[t_n/T] = \sup\{k \in Z : k \leq t_n/T\}$. Then $\tau_n \in [0, T]$ for all $n \geq 1$. By going to a subsequence if necessary, we may assume $\tau_n \to \tau_0 \in [0, T]$ as $n \to \infty$. Let $\bar{t}_n := \tau_0 + [t_n/T]T$. Then $\bar{t}_n \to +\infty$ as $n \to +\infty$. Let $\bar{t} > t_0$ be such that $x(t) \in A$ for all $t \geq \bar{t}$, and n_0 be such that $\bar{t}_n > \bar{t}$ and $t_n > \bar{t}$ for all $n \geq n_0$. Thus, for $n \geq n_0$, we have

$$|d(x(t_n), \partial R^d_+) - d(x(\bar{t}_n), \partial R^d_+)| \leq \|x(t_n) - x(\bar{t}_n)\| \leq M|t_n - \bar{t}_n|$$
$$= M|\tau_n - \tau_0|,$$

and it follows that $|d(x(t_n), \partial R^d_+) - d(x(\bar{t}_n), \partial R^d_+)| \to 0$ as $n \to +\infty$. Hence, $\lim_{n\to+\infty} d(x(\bar{t}_n), \partial R^d_+) = 0$, and so $\liminf_{n\to+\infty} d(H^n(\tau_0)x(\bar{t}_1 + T), \partial R^d_+) \leq 0$, (here, we take $\bar{t}_1 + T$ to make sure that $\bar{t}_1 + T \geq t_0$), which contradicts $\liminf_{n\to+\infty} d(H^n(\tau_0)x(\bar{t}_1 + T), \partial R^d_+) > 0$. Therefore, system (2.1) is persistent.

Proof of Part (ii). Necessity. It is obvious.

Sufficiency. By Lemma 2.2, $\delta(\tau)$ is continuous. Since $\delta(\tau) > 0$ on $[0, T]$, it follows that $\delta_0 := \inf_{\tau\in[0,T]} \delta(\tau) > 0$. We claim that $\liminf_{n\to+\infty} d(x(t), \partial R^d_+) \geq \delta_0$ for any solution to (2.1) with $x(t_0) \in \mathrm{int}(R^d_+)$ for some $t_0 \in R$, which implies the uniform persistence of the system (2.1).

Suppose it is false. Then there exists a solution $x(t)$ with $x(t_0) \in \mathrm{int}(R^d_+)$ for some $t_0 \in R$ such that $\lim_{t\to+\infty} d(x(t), \partial R^d_+) = \gamma < \delta_0$. Thus, there exists a sequence $\{t_n\}_{n=1}^{\infty} \subset (t_0, +\infty) \uparrow +\infty$ such that $\lim_{t\to+\infty} d(x(t_n), \partial R^d_+) = \gamma$. Put $\tau_n = t_n - [t_n/T]T$. Clearly, $\tau_n \in [0, T]$. By going to a subsequence if necessary, we can assume that $\tau_n \to \tau_0 \in [0, T]$. Put $\bar{t}_n = \tau_0 + [t_n/T]T$, then $\bar{t}_n \uparrow +\infty$ as $n \to +\infty$. By the same argument given in the proof of part (i), we have $\lim_{n\to+\infty} d(x(\bar{t}_n), \partial R^d_+) = \gamma$. Thus, $\delta_0 \leq \liminf_{n\to+\infty} d(H^n(\tau_0)x(\bar{t}_1 + T), \partial R^d_+) \leq \gamma < \delta_0$. This contradiction implies the claim. Thus, the theorem is proved. ∎

2.2. Persistence for Maps

For the sake of convenience, we now recall some definitions and well-known results on persistence for maps.

Let V be a metric space with metric d and let W be a closed subset of V. Let $F : V \to V$ be continuous such that $F(W) \subset W$ and $F(V\backslash W) \subset V\backslash W$. We denote by $F|_W$ the restriction of F on W. Denote Z the set of integers and Z^+ the set of non-negative integers. Recall that a sequence $\{u_n\}_{n\in Z^+}$ ($\{u_{-n}\}_{n\in Z^+}$, respectively) of points in V is said to be a positive (negative) orbit through $u \in V$ if $u_0 = u$ and $Fu_n = u_{n+1}$ ($Fu_{-n-1} = u_{-n}$) for all $n \in Z^+$; a sequence $\{u_n\}_{n\in Z}$ with $u_0 = u$ and $Fu_n = u_{n+1}$ for all $n \in Z$ is called an orbit through u. A positive (respectively, negative) orbit is said to be compact if the sequence, when considered as a subset of V, is precompact. Denote by $\Lambda^+(\{u_n\}_{n\in Z^+})$ or $\Lambda^+(u)$ (respectively, $\Lambda^-(\{u_{-n}\}_{n\in Z^+})$) the omega limit set (the alpha limit set) of the positive (negative) orbit through u (see [2]). F is said to be dissipative if the set $\Omega(F) = \cup\{\Lambda^+(u) : u \in V\}$ is precompact.

Let $M \subset V$. M is positively invariant (respectively, invariant) (under F) if $F(M) \subset M$ (respectively, $f(M) = M$).

A non-empty, closed invariant subset M is an isolated invariant set if it is the maximal (under the order of inclusion) invariant set in some neighborhood of itself.

Let M be an isolated invariant set. A compact positive orbit $\{u_n\}_{n\in Z^+}$ is said to be in the stable set of M (under F) (in notation, $\{u_n\}_{n\in Z^+} \in W(M)$) if $\Lambda^+(\{u_n\}_{n\in Z^+}) \subset M$; a compact negative orbit $\{u_{-n}\}_{n\in Z^+}$ is said to be in the unstable set of M (in notation, $\{u_{-n}\}_{n\in Z^+} \in W^-(M)$) if $\Lambda^-(\{u_{-n}\}_{n\in Z^+}) \subset M$.

For two isolated sets M_1 and M_2 we say that M_1 is chained to M_2, in notation $M_1 \to M_2$, if there exists an orbit $\{u_n\}_{n\in Z}$ with $u_k \notin M_1 \cup M_2$ for some $k \in Z$ such that $\{u_{-n}\}_{n\in Z_+} \in W^-(M_1)$ and $\{u_n\}_{n\in Z_+} \in W^+(M_2)$. A finite sequence $M_1, ..., M_k$ of isolated invariant sets will be called a chain if $M_1 \to M_2 \to \cdots \to M_k$ ($M_1 \to M_1$ if $k = 1$). The chain is a cycle if $M_k = M_1$. A covering $\Pi = \{M_1, ..., M_k\}$ of $\overline{\Omega}(F|_W) :=$ the closure of $\Omega(F|_W)$ is called an isolated covering of $F|_W$ if $M_1, ..., M_k$ are pairwise disjoint, compact, and isolated invariants (under F); the isolated covering Π is called an acyclic covering if no subsets of Π form a cycle for $F|_W$ in W

The following theorem is a special case of Theorem 4.2 in [3].

Theorem 2.3. *Suppose*

(i) *F is dissipative;*
(ii) *$F|W$ has an acyclic covering $\Pi = \{M_1, ..., M_k\}$.*

Then F is uniformly persistent with respect to W (i.e. there exists $\epsilon > 0$ such that $\liminf_{n\to+\infty} d(F^n u, W) \geq \epsilon$ for all $u \in V\backslash W$) if and only if the following condition holds:

(H) There is no positive orbit $\{u_n\}_{n\in Z_+}$ in $V\backslash W$ such that $\{u_n\}_{n\in Z_+} \in W^+(M_i)$ for some $i \in \{1, 2, ..., k\}$.

Theorem 2.4. [4, Theorem 6.3] *Suppose $V = R^d_+$, $W = \partial R^d_+$ and F is uniformly persistent and dissipative. Then F has a fixed point in* $\text{int}(R^d_+)$.

3. Persistence for System (1.1)

We now consider system (1.1). First, it is easy to see that the Y-axis is invariant and solutions initiating on the Y-axis approach the origin $O(0, 0, 0)$ as $t \to +\infty$, representing starvation of the predator in the absence of any prey. Also, the SI-plane is invariant and the subsystem in this plane represents the prey population in the absence of predators:

$$\dot{S} = B(t, X) - \frac{SD(t, X)}{X} - \beta_0(t)S,$$
$$\dot{I} = \beta_0(t)S - \frac{ID(t, X)}{X}. \tag{3.1}$$

Adding the two above equations, we obtain Eq. (1.2) in the first section. For Eq. (1.2), the following lemma follows directly from Corollary 2 in [5].

Lemma 3.1. *Equation (1.2) has a unique strictly positive, T-periodic solution $\hat{X}(t)$. Moreover, if $X(t)$ is any solution to (1.2) with $X(t_0) > 0$ for some $t_0 \in R$, then* $\lim_{t\to+\infty} |X(t) - \hat{X}(t)| = 0$.

For system (3.1), we have the following result.

Theorem 3.2. *System (3.1) has a unique T-periodic solution $(\hat{S}(t), \hat{I}(t))$ which satisfies that $\hat{S}(t) > 0$, $\hat{I}(t) > 0$ for all $t \in [0, T]$. Moreover, $\hat{S}(t) + \hat{I}(t) = \hat{X}(t)$, where $\hat{X}(t)$ is the positive T-periodic solution to (1.2), and $(\hat{S}(t), \hat{I}(t))$ is asymptotically globally stable with respect to $R^2_+ \setminus \{(0, 0)\}$.*

The following lemma is needed for proving Theorem 3.2.

Lemma 3.3. *Let $a(t)$ and $b(t)$ be continuous, strictly positive, and T-periodic functions. Then the equation*

$$\dot{X} = a(t) - b(t)X, \tag{3.2}$$

has a unique T-periodic solution $X^0(t)$. Moreover, that solution is strictly positive and asymptotically globally stable.

Proof. The solution of (3.2) satisfying $X(0) = X_0 \in R$ is

$$X(t) = [X_0 + \int_0^t b(s)e^{\int_0^s a(\tau)d\tau} ds]e^{-\int_0^s a(s)ds}.$$

Clearly, $X(t)$ is T-periodic if and only if $X(T) = X_0$, thus if and only if

$$X_0 = [1 - e^{-\int_0^T a(s)ds}]^{-1} e^{-\int_0^T a(s)ds} \int_0^T b(s)e^{\int_0^s a(\tau)d\tau} ds.$$

Therefore, (3.2) has a unique T-periodic solution, say $X^0(t)$. It is easy to see that $X^0(t)$ is strictly positive and asymptotically globally stable. The lemma is proved. ■

Proof of Theorem 3.2. Existence. By Lemma 3.3, the equation

$$\dot{\bar{S}} = B(t, \hat{X}(t)) - \left[\frac{D(t, \hat{X}(t))}{\hat{X}(t)} + \beta_0(t)\right]\bar{S}, \tag{3.3}$$

has a unique positive T-periodic solution, say $\hat{S}(t)$, and the equation

$$\dot{\bar{I}} = \beta_0(t)\hat{S}(t) - \frac{D(t, \hat{X}(t))}{\hat{X}(t)}\bar{I}, \tag{3.4}$$

has a unique positive T-periodic solution, say $\hat{I}(t)$. We now consider

$$\dot{\bar{X}} = B(t, \hat{X}(t)) - \frac{D(t, \hat{X}(t))}{\hat{X}(t)} \bar{X}. \tag{3.5}$$

It is not hard to see that $\hat{X}(t)$ and $\hat{S}(t) + \hat{I}(t)$ are positive T-periodic solutions to (3.5). The uniqueness in Lemma 3.3 implies $\hat{X}(t) = \hat{S}(t) + \hat{I}(t)$ for all $t \in [0, T]$.

Attractivity and Uniqueness. Suppose that $(S(t), I(t))$ is any solution to (3.1) with its initial conditions satisfying $S(t_0) \geq 0$, $I(t_0) \geq 0$, and $S(t_0) + I(t_0) > 0$ for some $t_0 \in R$. Since $X(t) = S(t) + I(t)$ is a solution to (1.2), we have, by Lemma 3.1, that $\lim_{t\to+\infty} |X(t) - \hat{X}(t)| = 0$. From (1.1) and (3.3), we obtain

$$\frac{d}{dt}[\hat{S} - S](t) = -u(t)[\hat{S}(t) - S(t)] + v(t), \tag{3.6}$$

where $u(t) = \dfrac{D(t, \hat{X}(t))}{\hat{X}(t)} + \beta_0(t)$, and

$$v(t) = B(t, \hat{X}(t)) - B(t, X(t)) + \left[\frac{D(t, X(t))}{X(t)} - \frac{D(t, \hat{X}(t))}{\hat{X}(t)}\right] S(t).$$

Clearly, $u_L = \inf_{t\in R}\{u(t)\} > 0$. It is not hard to see that $S(t) \leq X(t) \leq \max\{K, X(t_0)\}$ for all $t \geq t_0$. Thus, since $\lim_{t\to+\infty} |X(t) - \hat{X}(t)| = 0$, we have $v(t) \to 0$ as $t \to +\infty$.

We claim that $\lim_{t\to+\infty} |\hat{S}(t) - S(t)| = 0$.

Indeed, there are two exhaustive possibilities:

(a) there exists $t_1 \geq t_0$ such that $d/dt[\hat{S}(t) - S(t)] \neq 0$ for $t \geq t_1$, and
(b) there exists a sequence $\{s_n\}_{n=1}^{\infty}$ in $[t_0, +\infty)$ such that for $n \geq 1$, $s_n < s_{n+1}$, $d/dt(\hat{S} - S)(s_n) = 0$ and $s_n \to +\infty$ as $n \to \infty$.

If (a) holds, then $\lim_{t\to+\infty}(\hat{S} - S)(t)$ exists. If $\lim_{t\to+\infty}(\hat{S} - S)(t) \neq 0$, then since $u(t) \geq u_L > 0$ and $v(t) \to 0$ as $t \to +\infty$, (3.6) implies the existence of numbers $\alpha > 0$ and $t_2 > t_1$ such that $|d/dt(\hat{S}-S)(t)| \geq \alpha$ for all $t \geq t_2$. This contradicts the boundedness of $(\hat{S} - S)(t)$ on $[t_0, +\infty)$. Therefore, if (a) holds, then $\lim_{t\to+\infty} |\hat{S}(t) - S(t)| = 0$.

If (b) holds, let $\tau_n \in [s_n, s_{n+1}]$ be chosen for each $n \geq 1$ such that

$$|\hat{S}(\tau_n) - S(\tau_n)| = \max_{s_n \leq t \leq s_{n+1}} |\hat{S}(t) - S(t)|. \tag{3.7}$$

Since $d/dt(\hat{S} - S)(s_n) = 0$ for $n \geq 1$, it follows that $d/dt(\hat{S} - S)(\tau_n) = 0$ for $n \geq 1$. Therefore, by (3.6), $\hat{S}(\tau_n) - S(\tau_n) = v(\tau_n)/u(\tau_n)$. Since $u(\tau_n) \geq u_L > 0$ and $v(t) \to 0$ as $t \to +\infty$, we have

$$\lim_{n\to+\infty} (\hat{S}(\tau_n) - S(\tau_n)) = 0. \tag{3.8}$$

Since $\tau_n \to +\infty$ as $n \to \infty$, (3.7) and (3.8) imply that $\hat{S}(t) - S(t) \to 0$ as $t \to +\infty$.

Since (a) and (b) are exhaustive, the claim is proved.

Thus, since $\hat{X}(t) - X(t) \to 0$ as $t \to +\infty$ and $X(t) = S(t) + I(t)$, we have that $\hat{I}(t) - I(t) \to 0$ as $t \to +\infty$. The attractivity is proved. The uniqueness is the consequence of the attractivity.

Stability. Making the change of variable $(X, I) = (S + I, I)$ in (3.1), we obtain

$$\dot{X} = B(t, X) - D(t, X),$$
$$\dot{I} = \beta_0(t)(X - I) - \frac{ID(t, X)}{X}. \tag{3.9}$$

Thus, $(\hat{X}(t), \hat{I}(t))$ is a T-periodic solution to (3.9). Since the stability of (3.1) is equivalent to the stability of (3.9), it suffices to show that $(\hat{X}(t), \hat{I}(t))$ is a stable solution to (3.9). For (3.9), the variational system at the solution $(\hat{X}(t), \hat{I}(t))$ is

$$\dot{Z}_1 = \Big[B'_X(t, \hat{X}(t)) - D'_X(t, \hat{X}(t))\Big] Z_1,$$
$$\dot{Z}_2 = \left[\beta_0(t) - \frac{\hat{I}(t)D'_X(t, \hat{X}(t))}{\hat{X}(t)} + \frac{\hat{I}(t)D(t, \hat{X}(t))}{\hat{X}^2(t)}\right] Z_1 - \left[\beta_0(t) + \frac{D(t, \hat{X}(t))}{\hat{X}(t)}\right] Z_2. \tag{3.10}$$

Let $Z(t)$ be the matrix solution to (3.10) with $Z(0) = Id$ — the identity matrix. Then some elements of $Z(t)$ are

$$Z_{11}(t) = \exp\left\{\int_0^t \Big[B'_X(\tau, \hat{X}(\tau)) - D'_X(\tau, \hat{X}(\tau))\Big] d\tau\right\},$$
$$Z_{22}(t) = \exp\left\{-\int_0^t \left[\beta_0(\tau) + \frac{D(\tau, \hat{X}(\tau))}{\hat{X}(\tau)}\right] d\tau\right\}, \quad Z_{12}(t) = 0. \tag{3.11}$$

Thus, $Z(T)$ has two eigenvalues $\lambda_1 = Z_{11}(T)$, $\lambda_2 = Z_{22}(T)$. Clearly, $|\lambda_2| < 1$. Since Eq. (1.2) is scalar, Lemma 3.1 implies that $\hat{X}(t)$ is an asymptotically stable solution to (1.2). Thus, $0 < |\lambda_1| < 1$. Now, the stability of $(\hat{X}(t), \hat{I}(t))$ follows by standard linearization arguments. The theorem is proved. ■

The boundedness of solutions to (1.1) is shown by the following lemma.

Lemma 3.4. *The set* $\mathcal{A} = \{(S, I, Y) \in R^3_+ : c_M(S + I) + Y \le L\}$, *where* $c_M = \max_{0 \le t \le T} c(t)$ *and* $L = c_M K + c_M \max_{0 \le t \le T; 0 \le X \le K}\{B(t, X) - D(t, X)\}/ \min_{0 \le t \le T} \Gamma(t, 0)$, *is strongly attractive with respect to* R^3_+.

Proof. Let $(S(t), I(t), Y(t))$ be any solution to (1.1) with $(S, I, Y)(t_0) \in R^3_+$ for some $t_0 \in R$. We have

$$\frac{d}{dt}\big[c_M X(t) + Y(t)\big] \le c_M\big[B(t, X(t)) - D(t, X(t))\big] - \Gamma(t, Y(t))Y(t)$$
$$\le c_M\big[B(t, X(t)) - D(t, X(t))\big] - \Gamma(t, 0)Y(t). \tag{3.12}$$

If $c_M X(t) + Y(t) > L$ for some $t \ge t_0$, then either $X(t) \ge K$ or $X(t) < K$ and $Y(t) > L - c_M K$. Thus, (3.12) implies that $d/dt[c_M X(t) + Y(t)] < 0$ whenever $c_M X(t) + Y(t) > L$. This proves the lemma. ■

The following is an extinction result for the predator.

Theorem 3.5. *Let*

$$\int_0^T \Big\{ -\Gamma(t,0) + c(t)\big[P_1(t,\hat{X}(t)) + P_2(t,\hat{X}(t))\big]\Big\} dt < 0, \tag{3.13}$$

where $\hat{X}(t)$ *is the positive* T*-periodic solution to (1.2), hold, then* $\lim_{t\to+\infty} Y(t) = 0$ *for any solution* $(S(t), I(t), Y(t))$ *with* $(S(t_0), I(t_0), Y(t_0)) \in R^3_+$ *for some* $t_0 \in R$.

Proof. Let us set $b(t,\epsilon) := -\Gamma(t,0) + c(t)[P_1(t,\hat{X}(t)+\epsilon) + P_2(t,\hat{X}(t)+\epsilon)]$. By (3.13), there exists a positive number $\epsilon_0 > 0$ such that $\int_0^T b(t,\epsilon_0)dt < 0$. Suppose that $(S(t), I(t), Y(t))$ is any solution to (1.1) with $(S(t_0), I(t_0), Y(t_0)) \in R^3_+$ for some $t_0 \in R$. We have $\dot{X}(t) \le B(t, X(t)) - D(t, X(t))$, for $t \ge t_0$. Thus, by Lemma 3.1 and the standard comparison theorem, there exists a $t_1 \ge t_0$ such that $X(t) \le \hat{X}(t) + \epsilon_0$ for all $t \ge t_1$. Therefore, $\dot{Y}(t) \le Y(t)b(t,\epsilon_0)$, for $t \ge t_1$. This implies that $Y(t) \le Y(t_1)\exp\{\int_{t_1}^t b(s,\epsilon_0)ds\}$, for $t \ge t_1$. Since $b(t,\epsilon_0)$ is T-periodic, $\lim_{t\to+\infty} Y(t) = 0$. The theorem is proved. ∎

For system (1.1), we also denote by $G(t,t_0)$ the Cauchy operator, $(t \ge t_0)$, and put $H(\tau) = G(\tau, T+\tau)$, for $\tau \in [0,T]$. Let us set $R_+ = [0,+\infty)$, $E_1 = \{(0,0,Y) : Y \in R_+\}$, $E_2 = \{(S,I,0) : S \in R_+, I \in R_+\}$, and $E = E_1 \cup E_2$.

Remark. It is clear that solutions through points in $\partial R^3_+ \setminus E$ all move directly into the interior of R^3_+ from outside R^3_+. Thus, in order to prove $H(\tau)$ is uniformly persistent, it suffices to show that $H(\tau)$ is uniformly persistent with respect to E.

Our main result is the following:

Theorem 3.6. *Let*

$$\int_0^T \left[-\Gamma(t,0) + c(t)\frac{P_1(t,\hat{X}(t))\hat{S}(t) + P_2(t,\hat{X}(t))\hat{I}(t)}{\hat{X}(t)} \right] dt > 0 \tag{3.14}$$

hold. Then system (1.1) is uniformly persistent.

Before proving Theorem 3.6, we need some lemmas. By Theorem 3.2, system (1.1) has only two T-periodic solutions in E, which are $(\hat{S}(t), \hat{I}(t), 0)$ and $(0,0,0)$.

Lemma 3.7. *The characteristic multipliers of the linear variational system corresponding to the trivial solution* $(0,0,0)$ *to (1.1) have moduli different from 1.*

Proof. Making the change of variable $(X, I, Y) = (S+I, I, Y)$ in (1.1), we obtain

$$\begin{aligned}
\dot{X} &= B(t,X) - D(t,X) - \frac{(X-I)P_1(t,X)Y + IP_2(t,X)Y}{X},\\
\dot{I} &= [\beta_0(t) + \beta_1(t)Y](X-I) - \frac{ID(t,X)}{X} - \frac{IP_2(t,X)Y}{X},\\
\dot{Y} &= Y\left[-\Gamma(t,Y) + c(t)\frac{(X-I)P_1(t,X) + IP_2(t,X)}{X}\right].
\end{aligned} \tag{3.15}$$

Since the stability character of (1.1) is equivalent to that of (3.15), we consider (3.15) instead of (1.1). The change of variable makes the trivial solution (0, 0, 0) to (1.1) into the trivial solution (0, 0, 0) to (3.15). For (3.15), the variational system at the trivial solution is

$$\begin{aligned} \dot{Z}_1 &= [B'_X(t,0) - D'_X(t,0)]Z_1, \\ \dot{Z}_2 &= \beta_0(t)Z_1 - [\beta_0(t) + D'_X(t,0)]Z_2, \\ \dot{Z}_3 &= -\Gamma(t,0)Z_3. \end{aligned} \tag{3.16}$$

Let $Z(t)$ be the matrix solution to (3.17) with $Z(0) = Id$. Some elements of $Z(t)$ are

$$\begin{aligned} Z_{11}(t) &= \exp\left\{ \int_0^t [B'_X(\tau,0) - D'_X(\tau,0)]d\tau \right\}, \\ Z_{22}(t) &= \exp\left\{ -\int_0^t [\beta_0(\tau) + D'_X(\tau,0)]d\tau \right\}, \\ Z_{33}(t) &= \exp\left\{ -\int_0^t \Gamma(\tau,0)d\tau \right\}, \\ Z_{12}(t) &= Z_{13}(t) = Z_{23}(t) = 0. \end{aligned} \tag{3.17}$$

Thus, $Z(T)$ has three eigenvalues $\lambda_1 = Z_{11}(T)$, $\lambda_2 = Z_{22}(T)$, $\lambda_3 = Z_{33}(T)$. Clearly, $|\lambda_2| < 1$ and $|\lambda_3| < 1$. Since $B'_X(t,0) - D'_X(t,0) = g(t,0) > 0$, $|\lambda_1| > 1$. Thus, the lemma is proved. ■

Lemma 3.8. *Let the inequality (3.14) hold. Then the characteristic multipliers of the linear variational system corresponding to the solution $(\hat{S}(t), \hat{I}(t), 0)$ have moduli different from 1.*

Proof. By the same argument given in the proof of Lemma 3.7, it is enough to consider system (3.15) with its T-periodic solution $(\hat{X}(t), \hat{I}(t), 0)$. For (3.15), the variational system at the solution $(\hat{X}(t), \hat{I}(t), 0)$ is

$$\begin{aligned} \dot{Z}_1 &= [B'_X(t,\hat{X}(t)) - D_X(t,\hat{X}(t))]Z_1 - \frac{\hat{S}(t)P_1(t,\hat{X}(t)) + \hat{I}(t)P_2(t,\hat{X}(t))}{\hat{X}(t)} Z_3, \\ \dot{Z}_2 &= \left[\beta_0(t) - \frac{\hat{I}(t)D'_X(t,\hat{X}(t))}{\hat{X}(t)} + \frac{\hat{I}(t)D(t,\hat{X}(t))}{\hat{X}(t)} \right] Z_1 \\ &\quad - \left[\beta_0(t) + \frac{D(t,\hat{X}(t))}{\hat{X}(t)} \right] Z_2 - \frac{\hat{I}(t)P_2(t,\hat{X}(t))}{\hat{X}(t)} Z_3, \\ \dot{Z}_3 &= \left[-\Gamma(t,0) + c(t)\frac{\hat{S}(t)P_1(t,\hat{X}(t)) + \hat{I}(t)P_2(t,\hat{X}(t))}{\hat{X}(t)} \right] Z_3. \end{aligned} \tag{3.18}$$

Let $Z(t)$ be the matrix solution to (3.18) with $Z(0) = Id$. Some elements of $Z(t)$ are

$$Z_{11}(t) = \exp\left\{\int_0^t \left[B'_X(\tau, \hat{X}(\tau)) - D'_X(\tau, \hat{X}(\tau))\right]d\tau\right\},$$

$$Z_{22}(t) = \exp\left\{-\int_0^t \left[\beta_0(\tau) + \frac{D(t, \hat{X}(\tau))}{\hat{X}(\tau)}\right]d\tau\right\}, \; Z_{31}(t) = Z_{32}(t) = Z_{12}(t) = 0$$

$$Z_{33}(t) = \exp\left\{\int_0^t \left[-\Gamma(\tau, 0) + c(\tau)\frac{(\hat{X}(\tau) - \hat{I}(\tau))P_1(\tau, \hat{X}(\tau)) + \hat{I}(\tau)P_2(\tau, \hat{X}(\tau))}{\hat{X}(\tau)}\right]d\tau\right\}. \tag{3.19}$$

Thus, $Z(T)$ has three eigenvalues $\lambda_1 = Z_{11}(T)$, $\lambda_2 = Z_{22}(T)$, $\lambda_3 = Z_{33}(T)$. Clearly $|\lambda_2| < 1$. By the same argument given in the proof of Theorem 3.2, we obatin $|\lambda_1| < 1$. By (3.14), $|\lambda_3| > 1$. Thus, the lemma is proved. ■

Proof of Theorem 3.6. By Theorem 2.1 and Remark before Theorem 3.6, it is enough to prove that $H(\tau)$ is uniformly persistent with respect to E for all $\tau \in [0, T]$. Let us fix $\tau \in [0, T]$. It is not hard to see that $H(\tau)E \subset E$ and $H(\tau)(R^3_+\backslash E) \subset R^3_+\backslash E$. We shall use Theorem 2.3 to prove the uniform persistence for $H(\tau)$. Lemma 3.4 implies that $H(\tau)$ satisfies the hypothesis (i) in Theorem 2.3 with $V = R^3_+$ and $W = E$. By Theorem 3.2, $\Omega(H(\tau)|_E) = \{O, Q_\tau\}$, where O is the origin and $Q_\tau = (\hat{S}(\tau), \hat{I}(\tau), 0)$. It follows from Lemmas 3.7 and 3.8 that $\{O\}$ and $\{Q_\tau\}$ are isolated invariant sets under $H(\tau)$. Thus, $\Pi = \{\{O\}, \{Q_\tau\}\}$ is an isolated covering of $H(\tau)|_E$. Furthermore, by Theorem 3.2, Π is acyclic. We shall prove that $H(\tau)$ satisfies the hypothesis (H) in Theorem 2.3 for the acyclic covering Π.

Suppose that it is false. Then at least one of the two following alternatives is met:

(a) there exists $\{H^n(\tau)u\}_{n=0}^{\infty} \subset \text{int}(R^3_+)$ such that $\lim_{n\to+\infty} \|H^n(\tau)u\| = 0$;
(b) there exists $\{H^n(\tau)u\}_{n=0}^{\infty} \subset \text{int}(R^3_+)$ such that $\lim_{n\to+\infty} \|H^n(\tau)u - Q_\tau\| = 0$.

If (a) holds, then by the Arzela–Ascoli theorem, the sequence of continuous functions $\{(S, I, Y)(t + \tau + nT)\}_{n=0}^{\infty}$ on $[0, T]$ converges uniformly to $(0, 0, 0)$ as $n \to \infty$, where $(S, I, Y)(t)$ is the solution to (1.1) with $(S, I, Y)(\tau) = u$. This implies that $\lim_{t\to+\infty}(S, I, Y)(t) = (0, 0, 0)$. Let $\epsilon > 0$ be such that

$$\inf_{t\in[0,T]} g(t, 0) - \epsilon \sup_{(t,X)\in[0,T]\times[0,K]} \frac{P_2(t, X)}{X} > 0.$$

$(H_3), (H_4), (1.1)$ imply that $\dot{X}(t) \geq B(t, X(t)) - D(t, X(t)) - \epsilon P_2(t, X(t)) > 0$, whenever $Y(t) < \epsilon$, $I(t) < K$ and $S(t) < K$. This contradicts the fact that $\lim_{t\to+\infty}(S, I, Y)(t) = (0, 0, 0)$. Thus, (a) cannot happen.

If (b) holds, then by the same argument given above, we obtain

$$\lim_{t\to+\infty} |S(t) - \hat{S}(t)| = \lim_{t\to+\infty} |I(t) - \hat{I}(t)| = \lim_{t\to+\infty} |Y(t)| = 0,$$

where $(S, I, Y)(t)$ is the solution to (1.1) with $(S, I, Y)(\tau) = u$. Let us set

$$b(t, \epsilon) = -\Gamma(t, \epsilon) + c(t)\frac{(S(t) - \epsilon)P_1(t, \hat{X}(t) - 2\epsilon) + (\hat{I}(t) - \epsilon)P_2(t, \hat{X}(t) - 2\epsilon)}{\hat{X}(t) + 2\epsilon}.$$

By (3.15), there exists a positive number ϵ_0 such that $\int_0^T b(t, \epsilon_0)dt > 0$. Let $t_1 \geq \tau$ be such that $|S(t) - \hat{S}(t)| < \epsilon_0$, $|I(t) - \hat{I}(t)| < \epsilon_0$ and $|Y(t)| < \epsilon_0$ for all $t \geq t_1$. Then (1.1) implies that, for $t \geq t_1$, $(d/dt)Y(t) \geq Y(t)b(t, \epsilon_0)$. Thus, for $t \geq t_1$,

$$Y(t) \geq Y(t_1) \exp\left\{\int_{t_1}^{t} b(s, \epsilon_0)ds\right\}.$$

Since $b(t, \epsilon_0)$ is T-periodic, it follows that $\lim_{t\to+\infty} Y(t) = +\infty$, which contradicts $\lim_{t\to+\infty} Y(t) = 0$. Thus, (b) cannot happen.

Since (a) and (b) are exhaustive, $H(\tau)$ satisfies (H) in Theorem 2.3. The theorem is proved. ■

Corollary 3.9. *Let (3.14) hold. Then (1.1) has at least one T-periodic solution whose components are strictly positive.*

Proof. Since $H(0)$ is uniformly persistent and dissipative, by Theorem 2.4, $H(0)$ has at least one fixed point, say P, in $\text{int}(R^3_+)$. Clearly $(S(t), I(t), Y(t)) = G(t, 0)P$ is a T-periodic solution to (1.1) which is in $\text{int}(R^3_+)$. The corollary is proved. ■

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