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

Tran Thi Loan and Trinh Tuan Anh
Department of Mathematics, Hanoi University of Pedagogy I
Hanoi, Vietnam
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Abstract. We consider a model of a predator-prey population with the action of a parasite in the almost periodic case. We establish a uniform persistence criterion for the model.

1. Introduction

Consider the following system of nonautonomous ordinary differential equations:

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

where $X = S + I$; $B, D, P_1, P_2, \Gamma : R \times [0, +\infty) \to R$ are uniformly almost periodic in the first variable; and $\beta_0, \beta_1, c : R \to (0, +\infty)$ are almost periodic bounded below by positive constants.

The system (1.1) was proposed by Freedman [1] to model the interactions between a prey population X and a predator population Y with the action of a parasite. Due to the action of the parasite, the prey population X is divided

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into two classes: the susceptible class S and the infective class I. The predators are assumed to be all infected.

The case of functions $B, D, P_1, P_2, \Gamma, \beta_1, \beta_2, c$ not depending on t-variable was considered in [1]. The periodic case was studied in [5]. Our concern in this paper is with the more general case in which the model is depending on time t almost periodically. Such a generalization seems to be a natural one 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 further assumptions on the functions of the system (1.1) are given below, which are based on those in [1].

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) $B(t,0) = 0$, $B(t,.)$ is increasing for each $t \in R$, and there exists $\alpha > 0$ such that $\liminf\limits_{X\to 0^+} \dfrac{B(t,X)}{X} \geq \alpha$ for all $t \in R$.

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 $D(t,.)$ is increasing for $t \in R$.

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 rates corresponding to each prey class are proportional to the relative densities of that class, i.e., $\dfrac{S}{X}D(t,X)$ and $\dfrac{I}{X}D(t,X)$ 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 Eqs. (1.1)):

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

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 $R \times [0,+\infty)$; $\lim\limits_{T\to+\infty} \dfrac{1}{T}\displaystyle\int_0^T g(t,0)dt > 0$ and there exists $\alpha > 0$ such that $\mathcal{D}_X g(t,X) \leq -\alpha$ for all $(t,X) \in R \times [0,+\infty)$, where $\mathcal{D}_X$ denotes any Dini partial derivative in X.

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) $P_i(t,0) = 0$ $(i = 1,2)$ and the function $P_2(t,.) - P_1(t,.)$ is increasing for each $t \in R$, and there exists $\gamma > 0$ such that $\limsup\limits_{X\to 0^+} \dfrac{P_2(t,X)}{X} < \gamma$ for all $t \in R$.

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

(H_5) $\inf_{t\in R} \Gamma(t, 0) > 0$ and $\Gamma(t, .) > 0$ is increasing for each $t \in R$.

Let us denote by R^3_+ the set $\{(S, I, Y) \in R^3 : S \geq 0, I \geq 0, Y \geq 0\}$, $\mathcal{H}(t, S, I, Y)$ $(\mathcal{H} : R \times R^3_+ \to R^3)$ the right hand side of (1.1). The following hypothesis is needed for technical mathematical reason, in fact, this condition ensures that the theory of skew-product semi-flows is applicable.

(H_6) The vector function $\mathcal{H}$ is locally Lipschitz in (S, I, Y) uniformly in t.

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 the system (1.1), the reader is referred to [1].

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* $(S(t_0), I(t_0), Y(t_0)) \in \text{int}(R^3_+)$ - *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.*

The system is called dissipative if there exists a positive constant M *such that* $\limsup_{t\to+\infty} |S(t)| \leq M$, $\limsup_{t\to+\infty} |I(t)| \leq M$, $\limsup_{t\to+\infty} |Y(t)| \leq M$.

If the system is uniformly persistent and dissipative, we say that it is permanent.

Permanence theory has developed into a mathematically fascinating area for its significance in the differential equation models in population dynamics. It formalizes the concepts of nonextinction (uniform persistence) and nonexplosion (dissipativity) for the considered species.

For a survey of permanence theory, the reader is referred to Hutson and Schmitt [3], Waltman [7].

Our purpose is to give a sufficient condition for permanence of the system (1.1). The approach in this paper is based on analyzing the skew-product semi-flows associated with (1.1). The reader is referred to Sell [4] for background on skew-product flows. For the theory of almost periodic functions, see Yoshizawa [8].

The paper is organized as follows: In Sec. 2 we study behavior of solutions of the system (1.1) in the absence of preys and in the absence of predators respectively. The skew product semi-flow is introduced here. We also recall a well-known result on persistence in semi-flows. Sec. 3 contains our main result on permanence of (1.1).

2. Preliminaries

2.1. Asymptotic Behavior of Solutions of the System (1.1) on the Boundary of R^3_+

Let us denote by $\operatorname{int}\mathbb{R}^3_+$, ∂R^3_+ the interior and the boundary of R^3_+, respectively; $\mathcal{A}_+$ the set of all almost periodic functions from R into R which are bounded below by a positive constant.

Let $F(t,x)$ $(F: R\times\Omega \to R^n, \Omega\subset R^d)$ be uniformly almost periodic in t. We recall Bochner's criterion for the almost periodicity: *$F(t,x)$ is almost periodic in t uniformly for $x\in\Omega$ if and only if for every sequence of numbers $\{\tau_m\}_{m=1}^{\infty}$, there exists a subsequence $\{\tau_{m_k}\}_{k=1}^{\infty}$ such that the sequence of translates $\{F(\tau_{m_k}+t,x)\}_{k=1}^{\infty}$ converges uniformly on $R\times K$, where K is any compact subset of Ω.*

Denote by F_τ the τ-translation of F; that is, $F_\tau(t,x)=F(t+\tau,x)$, $H(F)$ the hull of F; that is, the closure (in the compact open topology) of the set $\{F_\tau : \tau\in R\}$. We have $H(F)$ is compact, and $F^*(t,x)$ is uniformly almost periodic in t for all $F^*\in H(F)$.

Define $\mathcal{G}=(B,D,P_1,P_2,\Gamma,c,\beta_0,\beta_1)$. For each $\mathcal{G}^*=(B^*,D^*,P_1^*,P_2^*,\Gamma^*,c^*$ $\beta_0^*,\beta_1^*)\in H(\mathcal{G})$, let us consider

$$\begin{aligned}
\dot S &= B^*(t,X) - \frac{SD^*(t,X)}{X} - [\beta_0^*(t)+\beta_1^*(t)Y]S - \frac{SP_1^*(t,X)Y}{X},\\
\dot I &= [\beta_0^*(t)+\beta_1^*(t)Y]S - \frac{ID^*(t,X)}{X} - \frac{IP_2^*(t,X)Y}{X},\\
\dot Y &= Y\left[-\Gamma^*(t,Y) + c^*(t)\frac{SP_1^*(t,X)+IP_2^*(t,X)}{X}\right].
\end{aligned}\tag{2.1}$$

It is easy to see that the system (2.1) satisfies (H_1)–(H_6). By (H_6), the Cauchy problem for (2.1) with the nonnegative initial values has a unique solution. It is easy to see that R^3_+ is positively invariant with respect to (2.1). The boundedness of solutions of (2.1) is shown by the following lemma.

Lemma 2.1. *For the system* (2.1), *there exists a positive number L such that the set $\mathcal{B}=\{(S,I,Y)\in R^3_+ : c_M(S+I)+Y\le L\}$, where $c_M=\sup_{t\in R} c(t)$, is strongly attractive with respect to R^3_+.*

Proof. By (H_3) there exists $K>0$ such that $g(t,K)\le -1$ for all $t\in R$. Put

$$L=c_MK + c_M \sup_{(t,X)\in R\times R^3_+}\{B(t,X)-D(t,X)\}/\inf_{t\in R}\Gamma(t,0).$$

It is easy to see that

$$c_M=\sup_{t\in R} c^*(t),\ \ g^*(t,K)\le -1\ \text{ for all } t\in R,$$

$$L=c_MK+c_M\sup_{(t,X)\in R\times R^3_+}\{B^*(t,X)-D^*(t,X)\}/\inf_{t\in R}\Gamma^*(t,0),$$

where $g^*(t,X) = [B^*(t,X) - D^*(t,X)]/X$.

Let $(S(t), I(t), Y(t))$ be any solution to (2.1) with $(S,I,Y)(t_0) \in R_+^3$ for some $t_0 \in R$. We have

$$\begin{aligned}\frac{d}{dt}[c_M X(t) + Y(t)] &\le c_M [B^*(t,X(t)) - D^*(t,X(t))] - \Gamma^*(t,Y(t))Y(t)\\ &\le c_M [B^*(t,X(t)) - D^*(t,X(t))] - \Gamma^*(t,0)Y(t).\end{aligned} \tag{2.2}$$

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, (2.2) implies that $\frac{d}{dt}[c_M X(t) + Y(t)] < 0$ whenever $c_M X(t) + Y(t) > L$. This proves the lemma.

By Lemma 2.1, the solution $(S(t), I(t), Y(t))$ of (2.1) with initial values $S(t_0) = S_0 \ge 0$, $I(t_0) = I_0 \ge 0$, $Y(t_0) = Y_0 \ge 0$ can be continued for all $t \ge t_0$.

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:

$$\begin{aligned}\dot{S} &= B^*(t,X) - \frac{SD^*(t,X)}{X} - \beta_0^*(t)S,\\ \dot{I} &= \beta_0^*(t)S - \frac{ID^*(t,X)}{X}.\end{aligned} \tag{2.3}$$

Adding the two above equations we get the equation

$$\dot{X} = Xg^*(t,X), \tag{2.4}$$

where $g^*(t,X) = [B^*(t,X) - D^*(t,X)]/X$.

In order to analyze the asymptotic behavior of solutions of the equation (2.4) we use the following lemma in [6].

Lemma 2.2. *Let $\Phi : R \times [0,+\infty) \to R$ be uniformly almost periodic in the first variable and satisfy:*

(i) $\displaystyle\lim_{T\to+\infty} \frac{1}{T}\int_0^T \Phi(t,0)dt > 0$ *and*

(ii) *there exists $\alpha > 0$ such that $\mathcal{D}_X\Phi(t,X) \le -\alpha$ for all $(t,X) \in R \times [0,+\infty)$, where $\mathcal{D}_X$ denotes any Dini partial derivative in X.*

Then the following problem

$$\dot{X} = X\,\Phi(t,X), \quad X(.) \in \mathcal{A}_+, \tag{2.5}$$

($\mathcal{A}_+$ is the set of all almost periodic functions from R into R which are bounded below by a positive constant) has a unique solution $X^*(\,.\,)$. Moreover, if $X(t)$ is any solution of the equation in (2.5) with $X(t_0) > 0$ for some $t_0 \in R$ then $\lim_{t\to+\infty} |X(t) - X^*(t)| = 0$.

By Lemma 2.2, the problem (2.4) with $X(.) \in \mathcal{A}_+$ has a unique solution, say $\widehat{X}^*(.)$.

For the system (2.3), we have the following result.

Theorem 2.3. *System (2.3) has a unique almost periodic solution* $(\widehat{S}^*(t), \widehat{I}^*(t))$ *whose components are bounded below by positive constants.*

Moreover, $\widehat{S}^*(t) + \widehat{I}^*(t) = \widehat{X}^*(t)$, *where* $\widehat{X}^*(.)$ *is the unique solution in* $\mathcal{A}_+$ *of (2.4), and* $\lim_{t\to\infty} |S(t) - \widehat{S}^*(t)| = 0$, $\lim_{t\to+\infty} |I(t) - \widehat{I}^*(t)| = 0$ *for all solutions* $(S(t), I(t))$ *of (2.3) with the initial conditions satisfying* $(S(t_0), I(t_0)) \in R^2_+ \setminus \{(0,0)\}$.

The following lemma is needed for proving Theorem 2.3.

Lemma 2.4. *Let* $a(t)$ *and* $b(t)$ *be almost periodic functions such that* $a(.) \in \mathcal{A}_+$ *and* $\lim_{T\to\infty} \frac{1}{T}\int_0^T b(t)dt > 0$. *Then the equation*

$$\dot{X} = a(t) - b(t)X \tag{2.6}$$

has a unique solution $X^0(.) \in \mathcal{A}_+$. *Moreover, we have* $\lim_{t\to\infty} |X^0(t) - X(t)| = 0$ *for any solution* $X(t)$ *of (2.4) with the initial value satisfying* $X(t_0) = X_0 > 0$.

Proof. It is easy to see that $(0, +\infty)$ is invariant. Let us consider (2.6) for $X \in (0, +\infty)$. By the change of variable $\overline{X} = 1/X$ in (2.6) we get an equation which has the form of the equation in (2.5). The lemma follows by using Lemma 2.2.

Proof of Theorem 2.3.

(i) *Existence.* Since $\widehat{X}^*(t)$ is a solution to the equation (2.3), we have

$$\frac{d}{dt}\ln X^*(t) = B^*(t, \widehat{X}^*(t)) - D^*(t, \widehat{X}^*(t)).$$

Since $\widehat{X}^*(.)$ is bounded above and below by positive constants, we get

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T \left[B^*(t, \widehat{X}^*(t)) - D^*(t, \widehat{X}^*(t))\right] dt = 0.$$

By (H_1), there exists $\varepsilon > 0$ such that $B^*(t, \widehat{X}^*(t)) > \varepsilon$ for all $t \in R$. Thus,

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T D^*(t, \widehat{X}^*(t))dt > 0.$$

By Lemma 2.4, the problem

$$\dot{\overline{S}} = B^*(t, \widehat{X}^*(t)w) - \left[\frac{D^*(t, \widehat{X}^*(t))}{\widehat{X}^*(t)} + \beta^0_+(t)\right]\overline{S}, \quad \overline{S}(.) \in \mathcal{A}_+\,, \tag{2.7}$$

has a unique solution, say $\widehat{S}^*(.)$, and the problem

$$\dot{\overline{I}} = \beta^*_0(t)\widehat{S}^*(t) - \frac{D(t, \widehat{X}^*(t))}{\widehat{X}^*(t)}\overline{I}, \quad \overline{I}(.) \in \mathcal{A}_+, \tag{2.8}$$

has a unique solution, say $\widehat{I}^*(.)$. We now consider

$$\dot{\overline{X}} = B^*(t, \widehat{X}^*(t)) - \frac{D^*(t, \widehat{X}^*(t))}{\widehat{X}^*(t)} \overline{X}, \quad \overline{X}(.) \in \mathcal{A}_+. \tag{2.9}$$

It is not hard to see that $\widehat{X}^*(.)$ and $\widehat{S}^*(.) + \widehat{I}^*(.)$ are two solutions to (2.9). By the uniqueness in Lemma 2.4 it implies $\widehat{X}^*(t) = \widehat{S}^*(t) + \widehat{I}^*(t)$.

(ii) *Attractivity and uniqueness.* Suppose that $(S(t), I(t))$ is any solution to (2.3) with 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 (2.4), we have, by Lemma 2.2, that $\lim_{t \to +\infty} |X(t) - \widehat{X}^*(t)| = 0$. From (2.3) we get

$$\frac{d}{dt}\big[\widehat{S}^* - S\big](t) = -u(t)\big[\widehat{X}^*(t) - S(t)\big] + v(t), \tag{2.10}$$

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

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

Clearly $u_L = \inf_{t \in R}\{u(t)\} > 0$. By ($H_3$), there exists $k > 0$ such that $\sup_{t \in R} g^*(t, k) < 0$. 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 $\lim_{t \to +\infty} |X(t) - \widehat{X}^*(t)| = 0$, we have $v(t) \to 0$ as $t \to +\infty$.

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

Indeed, there are two exhaustive possibilities: (a) there exists $t_1 \geq t_0$ such that $\frac{d}{dt}[\widehat{S}^*(t) - S(t)] \neq 0$ for $t \geq t_1$, and (b) there exists a sequence $\{s_n\}_{n=1}^{\infty}$ in $[t_0, +\infty)$ such that for $n \geq 1$, $s_n < s_{n+1}$, $\frac{d}{dt}(\widehat{S}^* - S)(s_n) = 0$ and $s_n \to +\infty$ as $n \to \infty$.

If (a) holds, then $\lim_{t \to +\infty}(\widehat{S}^* - S)(t)$ exists. If $\lim_{t \to +\infty}(\widehat{S}^* - S)(t) \neq 0$, then since $u(t) \geq u_L > 0$ and $v(t) \to 0$ as $t \to +\infty$, (2.10) implies the existence of numbers $\alpha > 0$ and $t_2 > t_1$ such that $\left|\frac{d}{dt}(\widehat{S}^* - S)(t)\right| \geq \alpha$ for all $t \geq t_2$. This contradicts the boundedness of $(\widehat{S}^* - S)(t)$ on $[t_0, +\infty)$. Therefore, if (a) holds then $\lim_{t \to +\infty} |\widehat{S}^*(t) - S(t)| = 0$.

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

$$|\widehat{S}^*(\tau_n) - S(\tau_n)| = \max_{s_n \leq t \leq s_{n+1}} |\widehat{S}^*(t) - S(t)|. \tag{2.11}$$

Since $\frac{d}{dt}(\widehat{S}^* - S)(s_n) = 0$ for $n \geq 1$, it follows that $\frac{d}{dt}(\widehat{S}^* - S)(\tau_n) = 0$ for $n \geq 1$. Therefore, by (2.10), $\widehat{S}^*(\tau_n) - S(\tau_n) = v(\tau_n)/u(\tau_n)$. Since $u(\tau_n) \geq u_L > 0$ and $v(t) \to 0$ as $t \to +\infty$, we have

$$\lim_{n \to +\infty} (\widehat{S}^*(\tau_n) - S(\tau_n)) = 0. \tag{2.12}$$

Since $\tau_n \to +\infty$ as $n \to \infty$, (2.11) and (2.12) imply that $\widehat{S}^*(t) - S(t) \to 0$ as $t \to +\infty$.

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

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

The theorem is proved.

Let us denote by $\bar{X}(t)$ the unique positive almost periodic solution of (1.2), and $(\widehat{S}(t), \widehat{I}(t))$ the unique almost periodic solution of

$$\begin{aligned} \dot{S} &= B(t,X) - \frac{SD(t,X)}{X} - \beta_0(t)S, \\ \dot{I} &= \beta_0(t)S - \frac{ID(t,X)}{X}. \end{aligned} \tag{2.13}$$

Lemma 2.5. *Let $\{\tau_n\} \subset R$ be a sequence such that B_{τ_n}, D_{τ_n}, $\beta_{0\tau_n}$ converge to B^*, D^*, β_0^*, respectively in the compact open topology as $n \to \infty$. Then $\widehat{S}_{\tau_n}$, $\widehat{I}_{\tau_n}$ converge to $\widehat{S}^*$, $\widehat{I}^*$, respectively, in the compact open topology as $n \to \infty$.*

Proof. Since $(\widehat{S}(t), \widehat{I}(t))$ is almost periodic, there exists a subsequence $\{\tau_{n_k}\}$ of $\{\tau_n\}$ such that $(\widehat{S}_{\tau_{n_k}}(t), \widehat{I}_{\tau_{n_k}}(t))$ converges to some almost periodic function $(S^0(t), I^0(t))$ uniformly on R as $k \to +\infty$. Consider

$$\begin{aligned} \dot{S} &= B_{\tau_{n_k}}(t,X) - \frac{SD_{\tau_{n_k}}(t,X)}{X} - \beta_{0\tau_{n_k}}(t)S, \\ \dot{I} &= \beta_{0\tau_{n_k}}(t)S - \frac{ID_{\tau_{n_k}}(t,X)}{X}. \end{aligned} \tag{2.14}$$

Since the right hand side of (2.14) converges to the right hand side of (2.3) uniformly on any compact subset of $R \times R_+^3$, $(S^0(t), I^0(t))$ is a solution of (2.3). The uniqueness in Theorem 2.3 implies that $\widehat{S}^*(t) = S^0(t)$ and $\widehat{I}^*(t) = I^0(t)$ for all $t \in R$. Since $\{(\widehat{S}_{\tau_n}, \widehat{I}_{\tau_n})\}$ is relatively compact, the lemma is proved.

2.2. The Skew-Product Semi-Flow

Let

$$\dot{x} = f(t,x), \tag{2.15}$$

$(f : R \times R_+^3 \to R^3)$, be induced from (1.1) by making the change of variables

$$x_1(t) = \frac{1}{\widehat{S}(t)} S(t), \quad x_2(t) = \frac{1}{\widehat{I}(t)} I(t), \quad x_3(t) = Y(t), \tag{2.16}$$

where $(\widehat{S}(t), \widehat{I}(t))$ is the solution of (2.13) as in Theorem 2.3.

It is clear that $(0,0,0)$ and $(1,1,0)$ are stationary solutions of (2.15).

Since $\widehat{S}(.), \widehat{I}(.) \in A_+$, we have the following remark:

Remark 2.1. System (1.1) is persistent (uniformly persistent, permanent) if and only if System (2.15) is persistent (uniformly persistent, permanent).

For $f^* \in H(f)$, let us consider the following equation

$$\dot{x} = f^*(t,x). \tag{2.17}$$

Since $f^* \in H(f)$, there is a sequence $\{t_n\} \subset R$ such that $f_{t_n} \to f^*$ as $n \to \infty$. Since $\mathcal{G} = (B, D, P_1, P_2, \Gamma, c, \beta_0, \beta_1)$ are uniformly almost periodic, there exists a subsequence $\{\tau_{n_k}\}$ such that $\mathcal{G}_{\tau_{n_k}} \to \mathcal{G}^* = (B^*, D^*, P_1^*, P_2^*, \Gamma^*, c^*, \beta_0^*, \beta_1^*)$ as $k \to \infty$. By Lemma 2.5, $(\widehat{S}_{\tau_{n_k}}, \widehat{I}_{\tau_{n_k}}) \to (\widehat{S}^*, \widehat{I}^*)$ as $k \to \infty$. Therefore, by making the change of variables

$$x_1(t) = \frac{1}{\widehat{S}^*(t)} S(t), \ \ x_2(t) = \frac{1}{\widehat{I}^*(t)} I(t), \ \ x_3(t) = Y(t) \tag{2.18}$$

in (2.1) we get (2.17). Thus we have the following remark.

Remark 2.2. For each $f^* \in H(f)$ there exists a unique $\mathcal{G}^* \in H$ ($\mathcal{G}$ being such that f^* is obtained by making the change of variables (2.18)).

We will obtain conditions for permanence of the system (2.11) via analyzing the skew-product semi-flow corresponding to (2.11). In the following we introduce this semi-flow.

Let us set $\mathcal{X} = H(f) \times R_+^3$ (with the product topology).

Denote by $x(f^*, x_0, t)$ the solution of the system (2.1) such that $x(0) = x_0$. It is clear that this solution can be continued for all $t \geq 0$. Define the map $\Pi : \mathcal{X} \times R_+ \to \mathcal{X}$ by setting

$$\Pi((f^*, x_0), t) = (f_t^*, x(f^*, x_0, t)). \tag{2.19}$$

It is clear that Π is a semi-flow on $\mathcal{X}$.

2.3. Permanence for a Semi-Flow

For the sake of easy accessibility, we now recall some definitions and well-known results on persistence for semi-flows.

Let $\mathcal{E}$ be a complete metric space (with metric d) which is the closure of an open set $\mathcal{E}^0$; that is, $\mathcal{E} = \mathcal{E}^0 \cup \partial\mathcal{E}^0$, where $\partial\mathcal{E}^0$ (assumed to be nonempty) is the boundary of $\mathcal{E}^0$. Let Φ be a semi-flow or semi-dynamical system on $\mathcal{E}$, i.e., a continuous mapping $\Phi : R_+ \times \mathcal{E} \to \mathcal{E}$ with the following properties:

$$\Phi_t \Phi_s = \Phi_{t+s}, \ t, s \geq 0; \ \ \Phi_0 u = u \text{ for all } u \in \mathcal{E}, \tag{2.20}$$

where Φ_t denotes the mapping from $\mathcal{E}$ into $\mathcal{E}$ given by $\Phi_t(u) = \Phi(t, u)$. A set $U \subset \mathcal{E}$ is said to be forward (or positive) invariant if $\Phi_t U \subset U$ and invariant if $\Phi_t U = U$, for all $t \in R_+$.

We assume that Φ_t satisfies

$$\Phi_t : \mathcal{E}^0 \to \mathcal{E}^0, \ \ \Phi_t : \partial\mathcal{E}^0 \to \partial\mathcal{E}^0, \tag{2.21}$$

i.e., $\mathcal{E}^0$ and $\partial\mathcal{E}^0$ are forward invariant. Denote by Φ_t^∂ the restriction of Φ_t, on $\partial\mathcal{E}$. The positive orbit $\gamma^+(u)$ through u is defined by $\gamma^+(u) = \bigcup\limits_{t \geq 0} \Phi_t u$. The ω-limit set of the orbit through u is defined as

$$\omega(u) = \{v \in \mathcal{E} : \exists\{t_n\} \subset [0, +\infty) \text{ such that } \lim_{t\to\infty} t_n = +\infty, \ \lim_{n\to\infty} \Phi_{t_n} u \to v\}.$$

An orbit through u is a continuous mapping $\phi : R \to \mathcal{E}$ such that $\phi(0) = u$ and $\Phi_t\phi(\tau) = \phi(t+\tau)$, $t \in R_+$, $\tau \in R$. The range of ϕ is denoted by $\gamma(x)$. Note that the orbit through u may not exist, and even when it exists, it may not be unique. It is easy to see that through each point u of an invariant set U there is at least one orbit $\gamma(u) \subset U$.

For an orbit $\gamma(u)$, the α-limit set is defined as

$$\alpha_\gamma(u) = \{v \in \mathcal{E} : \exists\{t_n\} \subset (-\infty, 0] \text{ such that } \lim_{t\to\infty} t_n = -\infty,\ \lim_{n\to\infty} \Phi_{t_n} u \to v\}.$$

Let U be compact and invariant. The stable set and unstable set of U are respectively defined as follows

$$W^s(U) = \{u \in \mathcal{E} : \omega(u) \neq \emptyset, \omega(u) \subset U\},$$

$$W^u(U) = \{u \in \mathcal{E} : \text{there exists an orbit } \gamma(u) \text{ such that } \alpha_\gamma(u) \neq \emptyset,\ \alpha_\gamma(u) \subset U\}.$$

A nonempty invariant subset of $\mathcal{E}$ is called an isolated invariant set if it is a maximal invariant set of a neighborhood of itself.

Let U, V be isolated invariant sets (not necessarily distinct). U is said to be chained to V, write $U \to V$, if there exists an element $u \notin U \cup V$ such that $u \in W^u(U) \cap W^s(V)$. A finite sequence $U_1, U_2, ..., U_k$ of isolated invariant sets will be called a chain if $U_1 \to U_2 \to \cdots \to U_k$ ($U_1 \to U_1$ if $k = 1$). The chain is called a cycle if $U_1 = U_k$.

The particular invariant sets of interest are $\omega(\partial\mathcal{E}^0) = \bigcup_{u\in\partial\mathcal{E}^0} \omega(u)$. $\omega(\partial\mathcal{E}^0)$ is said to be isolated if it has a finite covering $U = \bigcup_{i=1}^k U_i$ by pairwise disjoint, compact sets $U_1, U_2, ..., U_k$ that are isolated invariant for Φ_t. U then is called an isolated covering. $\omega(\partial\mathcal{E}^0)$ is said to be acyclic if there exist some isolated covering $U = \bigcup_{i=1}^k U_i$ such that no subset of the U_i's forms a cycle; the covering then is called acyclic.

The semi-flow Φ_t is said to be dissipative if there is a bounded set U such that $\lim_{t\to+\infty} d(\Phi_t u, U) = 0$ for all $u \in \mathcal{E}$.

The semi-flow Φ_t is said to be persistent (with respect to $\partial\mathcal{E}^0$) if for any $u \in \mathcal{E}^0$ we have $\lim_{t\to+\infty} d(\Phi_t u, \partial\mathcal{E}^0) > 0$, where $d(\Phi_t u, \partial\mathcal{E}^0)$ is the distance from $\Phi_t u$ to $\partial\mathcal{E}^0$.

If there is an $\varepsilon > 0$ such that, for any $u \in \mathcal{E}^0$, $\lim_{t\to+\infty} d(\Phi_t u, \partial\mathcal{E}^0) \geq \varepsilon$, then Φ_t is called uniformly persistent.

Theorem 2.5. (see [2]) *Suppose that Φ_t satisfies (2.21) and we have the following:*

(i) *There is a $t_0 \geq 0$ such that Φ_t is compact for $t > t_0$,*

(ii) *Φ_t is dissipative in $\mathcal{E}$,*

(iii) *$\omega(\partial\mathcal{E}^0)$ is isolated and has acyclic covering $U = \bigcup_{i=1}^k U_i$.*

Then Φ_t is uniformly persistent if and only if for each U_i

$$W^s(U_i) \cap \mathcal{E}^0 = \emptyset. \tag{2.22}$$

3. Persistence for System (1.1)

Let us denote by E_1 the Y-axis or x_3-axis, E_2 the positive cone of the SI-plane or x_1x_2-plane. Put $E = E_1 \cup E_2$. It is easy to see that solutions of (1.1) (or (2.15)) through points in $\partial R^3_+ \setminus E$ all move directly into the interior of R^3_+. Thus (1.1) (or (2.15)) is uniformly persistent with respect to ∂R^3_+ if and only if it is uniformly persistent with respect to E.

We now go back to consider the semi-flow Π defined by (2.19). Write $\Pi_t(f^*, x) = \Pi((f^*, x), t)$. We set $\partial\mathcal{X}^0 = H(f) \times E$, $\mathcal{X}^0 = \mathcal{X} \setminus \partial X^0$. It is clear that

$$\Pi_t(\mathcal{X}_0) \subset \mathcal{X}^0, \ \Pi_t(\partial\mathcal{X}^0) \subset \partial\mathcal{X}^0,$$

$$\omega(\partial\mathcal{X}^0) = [H(f) \times \{O(0,0,0)\}] \cup [H(f) \times \{Q(1,1,0)\}].$$

Moreover, (2.15) is uniformly persistent with respect to E if and only if Π_t is uniformly persistent with respect to $\partial\mathcal{X}^0$.

Lemma 3.1. *$H(f) \times \{O(0,0,0)\}$ is isolated invariant with respect to Π_t. Moreover, there is no $(f^*, x_0) \in \chi^0$ such that $\Pi_t(f^*, x_0) \to H(f) \times \{O\}$ as $t \to +\infty$.*

Proof. We will show that there exists a neighborhood V of the set $H(f) \times \{O\}$ such that $H(f) \times \{O\}$ is a maximal invariant set in this neighborhood.

Put $\widehat{S}_M = \sup_{t\in R} \widehat{S}(t)$, $\widehat{I}_M = \sup_{t\in R} \widehat{I}(t)$.

Let $g^* \in H(g)$. By (H_3), $\lim\limits_{T\to+\infty} \frac{1}{T}\int_0^T g^*(t,0)dt = \lim\limits_{T\to+\infty} \frac{1}{T}\int_0^T g(t,0)dt > 0$. Since $g^*(t,X)$ is uniformly almost periodic in t, $g^*(t,X)$ is uniformly continuous on any set of the form $R \times K$, where K is a compact subset of $[0,+\infty)$. Thus, there exists $\varepsilon_1 > 0$ such that

$$\varepsilon_1 \le \widehat{S}_M + \widehat{I}_M,$$
$$\lim_{T\to\infty} \frac{1}{T}\int_0^T g^*(t,\varepsilon_1)dt = \lim_{T\to\infty} \frac{1}{T}\int_0^T g(t,\varepsilon_1)dt > r > 0. \tag{3.1}$$

By (H_4), there exists $\varepsilon_2 > 0$ ($\varepsilon_2 \le \varepsilon_1$) such that $P_2^*(t,X) \le \gamma X$ for all $X \in [0,\varepsilon_2]$, $t \in R$, $P_2^* \in H(P)$.

Put $\varepsilon_3 = \dfrac{r}{2\gamma}$, $K = [0, \dfrac{\varepsilon_2}{4\widehat{S}_M}] \times [0, \dfrac{\varepsilon_2}{4\widehat{I}_M}] \times [0, \varepsilon_3]$, $V = H(f) \times K$.

We will prove that $H(f) \times \{O\}$ is a maximal invariant set in V.

Suppose that it is false, i.e., there exists an orbit $\gamma(f^*, x_0)$ such that $\gamma(f^*, x_0) \subset V \setminus H(f) \times \{O\}$. Thus, the following problem

$$\dot{x} = f^*(t,x), \ \ x(0) = x_0$$

has a solution $x(t)$ defined on R which satisfies $x(t) \in K$ for all $t \in R$. Consider the system (2.1) which is corresponding to f^* (see Remark 2.2). Let $(\widehat{S}^*(t), \widehat{I}^*(t))$ be the positive almost periodic solution of (2.3). Since $(\widehat{S}^*, \widehat{I}^*) \in H(\widehat{S}, \widehat{I})$, $\sup_{t\in R} \widehat{S}^*(t) = \widehat{S}_M$, $\sup_{t\in R} \widehat{I}^*(t) = \widehat{I}_M$. This implies that $S(t) = x_1(t)\widehat{S}^*(t)$, $I(t) = x_2(t)\widehat{I}^*(t)$, $Y(t) = x_3(t)$ is a solution of (2.1) and $(S, I, Y)(t) \in [0, \varepsilon_2/4] \times [0, \varepsilon_3]$ for all $t \in R$.

By Theorem 2.3, $Y(0) > 0$. Thus, $X(0) = S(0) + I(0) > 0$. Since $0 < Y(t) \le \varepsilon_3$, it follows from (2.1) that

$$\begin{aligned} \dot{X} &\ge B^*(t,X) - D^*(t,X) - P_2^*(t,X)Y(t) \\ &\ge B^*(t,X) - D^*(t,X) \\ &\ge \varepsilon_3 \gamma X = X\Big[g^*(t,\varepsilon_2) - \frac{r}{2}\Big]. \end{aligned}$$

Thus, $X(t) \ge X(0)e^{\int_0^t [g^*(s,\varepsilon_2)-r/2]ds}$ for all $t \ge 0$.
Since $\lim\limits_{T\to+\infty} \int_0^T \frac{1}{T}[g^*(s,\varepsilon_2)-r/2]ds \ge r/2 > 0$ (by (3.1)), $\lim_{t\to+\infty} X(t) = +\infty$. This contradiction implies that $H(f) \times \{O\}$ is a maximal invariant set in the neighborhood V.

We now prove the second assertion. Suppose that it is false, i.e., there exists $(f^*, x_0) \in \mathcal{X}^0$ such that $\Pi_t(f^*, x_0) \to H(f) \times \{O\}$ as $t \to +\infty$. Thus, there exists $t_0 \ge 0$ such that $\Pi_t(f^*, x_0) \in V$ for all $t \ge t_0$. By the same argument given before, we get $X(t) \ge X(t_0)e^{\int_{t_0}^t [g^*(t,\varepsilon_2)-r/2]ds}$ for all $t \ge t_0$. Thus, $\lim_{t\to+\infty} X(t) = +\infty$. This is a contradiction and the lemma is proved.

Lemma 3.2. *Let*

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T \Big[- \Gamma(t,0) + c(t)\frac{P_1(t,\widehat{X}(t))\widehat{S}(t) + P_2(t,\widehat{X}(t))\widehat{I}(t)}{\widehat{X}(t)}\Big] dt > 0 \tag{3.2}$$

hold. Then $H(f) \times \{(1,1,0)\}$ is isolated invariant. Moreover, there is no point $(f^*, x_0) \in \mathcal{X}^0$ such that $\Pi_t(f^*, x_0) \to H(f) \times \{(1,1,0)\}$ as $t \to +\infty$.

Proof. Let $f^* \in H(f)$. Consider the system (2.1) which is corresponding to f^* (see Remark 2.2). It is easy to see that

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T \Big[-\Gamma^*(t,0) + c^*(t)\frac{P_1^*(t,\widehat{X}^*(t))\widehat{S}^*(t) + P_2^*(t,\widehat{X}^*(t))\widehat{I}^*(t)}{\widehat{X}^*(t)}\Big] dt > 0. \tag{3.3}$$

For sufficiently small $\varepsilon > 0$, let us set

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

By (3.3), there exists a positive number ε_0 such that

$$\lim_{T\to\infty} \frac{1}{T}\int_0^T b^*(t,\epsilon_0)dt > 0. \tag{3.4}$$

It suffices to show that there is no solution of (2.1) which satisfies $S(t_0)+I(t_0) > 0, Y(t_0) > 0$ and $|S(t)-\widehat{S}(t)| < \epsilon_0$, $|I(t)-\widehat{I}(t)| < \epsilon_0$, $|Y(t)| < \epsilon_0$ for all $t \ge t_0$. To this end, we suppose that it is false. From (2.1), we get $\frac{d}{dt}Y(t) \ge Y(t)b^*(t,\varepsilon_0)$. Thus, for $t \ge t_0$,

$$Y(t) \ge Y(t_0)\exp\{\int_{t_0}^t b^*(s,\epsilon_0)ds\}.$$

Thus, it follows from (3.4) that $\lim_{t\to+\infty} Y(t) = +\infty$, which contradicts $Y(t) \le \varepsilon_0$ for all $t \ge t_0$. The lemma is proved.

The following is our main result:

Theorem 3.3. *Let* (3.2) *hold. Then* (1.1) *is permanent.*

Proof. By Lemma 2.1, it suffices to show (1.1) is uniformly persistent. In fact, it suffices to prove that Π_t is uniformly persistent with respect to $\partial\mathcal{X}^0$.

We have

$$\omega(\partial\mathcal{X}^0) = \left[H(f)\times\{O(0,0,0)\}\right] \cup \left[H(f)\times\{Q(1,1,0)\}\right].$$

By Lemmas 3.1 and 3.2, $H(f)\times\{O\}$ and $H(f)\times\{Q\}$ are isolated invariant. Moreover, $H(f)\times\{O\}\to H(f)\times\{Q\}$. Thus, the theorem follows by Theorem 2.5 and Lemmas 3.1 and 3.2.

Corollary 3.4. *Let* (3.2) *hold. Then* (1.1) *has a solution* $(\widetilde{X},\widetilde{I},\widetilde{Y})(t)$ *which is defined on* R *and whose components are bounded above and below by positive constants.*

Proof. It suffices to show that (2.15) has a solution $\widetilde{x}(t)$ which is defined on R and whose components are bounded above and below by positive constants. By (3.2), Π_t is permanent with respect to $\partial\mathcal{X}^0$. As we mention before Lemma 3.1, Π_t is permanent with respect to $H(f)\times\partial R^3_+$. Let (f^*,x_0) be any point in $\mathcal{X}^0$. Consider the ω-limit set $\omega(f^*,x_0)$. We have that $\emptyset\ne\omega(f^*,x_0)\subset H(f)\times\mathrm{int}(R^3_+)$, and it is closed and invariant. We define a projection $\mathcal{P}$ from $\mathcal{X}$ onto R^3_+ as follows: $\mathcal{P}(f^*,x)=x$. Then $\mathcal{P}(\omega(\hat{f},\hat{x}_0))$ is closed bounded and is contained in $\mathrm{int}R^3_+$. Let $(\hat{f},\hat{x}_0)\in\omega(f^*,x_0)$. Then there exists an orbit $\gamma(\hat{f},\hat{x}_0)\subset\omega(f^*,x_0)$ through $(\hat{f},\hat{x}_0)$. Let $\mathcal{P}(\Pi_t,(\hat{f},\hat{x}_0)) = x(t)(t\in R)$. We have that $x(t)$ is a solution defined on R of the equation

$$\dot{x} = \hat{f}(t,x).$$

Since $x(t)\in\mathcal{P}(\omega(f^*,x_0))$, it follows that there exist positive numbers δ,Δ such that

$$\delta \le x_i(t) \le \Delta\ \ (i=1,2,3), \tag{3.5}$$

for all $t\in R$. Since $H(f)=H(\hat{f})$, there exists a sequence $\{\tau_n\}\subset R$ such that $\hat{f}_{\tau_n}\to f$ as $n\to\infty$. By (3.5), without loss of generality, we assume that $x_{\tau_n}(0)\to\eta\in[\delta,\Delta]$. Let $\tilde{x}(t)$ be the solution of (2.15) with $\tilde{x}(0)=\eta$. Since the right hand side of

$$\dot{x} = \hat{f}_{\tau_n}(t,x) \tag{3.6}$$

converges to the right hand side of (2.15) and $x_{\tau_n}(t)$ is a solution of (3.6), we have that x_{τ_n} converges to $\tilde{x}(t)$ uniformly on any compact subset of R as $n\to\infty$. Thus, $\delta\le\tilde{x}_i(t)\le\Delta$, $(i=1,2,3)$, for all $t\in R$. The corollary is proved.

The following is an extinction result for the predator.

Theorem 3.5. *Let*

$$\lim_{T\to\infty}\frac{1}{T}\int_0^T\big\{-\Gamma(t,0)+c(t)\big[P_1(t,\widehat{X}(t))+P_2(t,\widehat{X}(t))\big]\big\}dt<0 \tag{3.7}$$

hold, where $\widehat{X}(t)$ *is the positive almost periodic solution to* (1.2). *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. For sufficiently small $\varepsilon>0$, let us set

$$b(t,\epsilon):=-\Gamma(t,0)+c(t)\big[P_1(t,\widehat{X}(t)+\epsilon)+P_2(t,\widehat{X}(t)+\epsilon)\big].$$

By (3.7), there exists a positive number $\epsilon_0>0$ such that

$$\lim_{T\to\infty}\frac{1}{T}\int_0^T b(t,\epsilon_0)dt<0. \tag{3.8}$$

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 $\dot{X}(t)\le B(t,X(t))-D(t,X(t))=Xg(t,X)$, for $t\ge t_0$. Since $\lim_{t\to+\infty}|X(t)-\widehat{X}(t)|=0$ for any solution of (1.2) with the initial value $X(t_0)=X_0>0$ (Lemma 2.2), it follows from the standard comparison theorem that there exists a $t_1\ge t_0$ such that $X(t)\le\widehat{X}(t)+\epsilon_0$ 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 $t\ge t_1$. Thus, by (3.8) we have $\lim_{t\to+\infty}Y(t)=0$.

The theorem is proved.

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