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Permanence of host-parasitoid systems

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Abstract

In this paper, permanence of host-parasitoid systems is investigated. Permanence is the property which assures of coexistence of all the species in a system for a long time. For Lotka-Volterra difference equations the permanence has been investigated by using average Liapunov functions. We construct average Liapunov functions to the simple host-parasitoid system and obtain the sufficient condition for its permanence. Furthermore, we obtain the necessary condition for permanence of this system by using numerical investigations. This necessary condition shows that the host-parasitoid system is not always permanent even if it has a positive equilibrium. This property is different from that of the Lotka-Volterra difference equation for a prey-predator interaction.

1 Introduction

In this paper, we obtain conditions for permanence of host-parasitoid systems. It is important to know conditions for coexistence of species in population ecology. An interaction of a host and a parasitoid is one of the most popular one. The interaction of a host and a parasitoid is modeled by difference equations because of their non-overlapping generations (see Hassell [5]). Such difference equations have very complex solutions even in one dimensional case. It is difficult to predict an asymptotic behavior of such solutions. Conditions for coexistence can be obtained by investigating permanence of systems regardless of complexity of the population dynamics.

The definition of permanence is given as follows:

Definition 1 *Consider the following discrete dynamical system:*

$$x(t+1) = f(x(t)), \quad x(t) \in \mathbf{R}^n_+, \quad t \in \mathbf{Z}_+. \tag{1}$$

System (1) is said to be permanent (with respect to $\partial\mathbf{R}^n_+$) if there is a compact

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set $M \subset \mathbf{R}_+^n$ such that minimum distance between M and $\partial\mathbf{R}_+^n$ is positive, and for every initial value in $\mathrm{int}\mathbf{R}_+^n$ *the orbits enter and remain in M.*

In this paper, we investigate the following host-parasitoid system:

$$\begin{cases} H(t+1) = H(t)\exp\left[\lambda\left(1-\dfrac{H(t)}{K}\right)\right]\exp[-aP(t)] \\ P(t+1) = bH(t)(1-\exp[-aP(t)]), \quad (H(t),P(t)) \in \mathbf{R}_+^2, \end{cases} \tag{2}$$

where $H(t)$ and $P(t)$ are the host and the parasitoid population densities at generation t respectively, λ expresses the potential growth rate of the host ($\exp[\lambda]$ is an intrinsic rate of increase of the host), K is a carrying capacity of the host, a is a parameter that measures the efficiency of the parasitoid and b is a number of parasitoids which emerge from each host. The parameters, λ, K, a and b are positive constants. This is a Nicholson-Bailey model with density dependence in the host population growth. A local stability analysis of a positive equilibrium of system (2) was carried out by Beddington *et al.* [2]. A sufficient condition for persistence, not permanence, of system (2) was obtained by Freedman and So [4]. System (2) without the parasitoid is a Ricker model, of which dynamics was investigated by May and Oster [9].

Now we introduce the non-dimensional quantities by

$$u(t) = \frac{\lambda H(t)}{K}, \quad v(t) = aP(t), \quad r = \exp[\lambda], \quad c = \frac{abK}{\lambda}.$$

By substituting these quantities, system (2) becomes

$$\begin{cases} u(t+1) = ru(t)\exp[-u(t)]\exp[-v(t)] \\ v(t+1) = cu(t)(1-\exp[-v(t)]), \quad (u(t),v(t)) \in \mathbf{R}_+^2. \end{cases} \tag{3}$$

This model contains only two parameters, $r > 1$ and $c > 0$. In the following sections, we investigate the dynamics of this non-dimensionalized system.

2 Sufficient condition for permanence

In this section, we obtain a sufficient condition for permanence of system (3). Before obtaining Theorem 2 below, we introduce some known results and notations which are used to prove Theorem 2.

Lemma 1 *(Kon and Takeuchi [8]) The solution of system (3) is uniformly* *bounded, that is, there exists a compact subset X of $\mathbf{R}_+^2$ such that for every initial value in $\mathbf{R}_+^2$ the orbits enter and remain in X.*

Sufficient conditions for permanence of general discrete dynamical systems (1) are given by the following Theorem 1 and Corollary 1, which are used to obtain a sufficient condition for permanence of system (3).

Theorem 1 *(Hutson [7]) Consider system (1). Assume that X is compact and that S is a compact subset of X with empty interior. Let S and $X \backslash S$ be forward invariant. Suppose that there is a continuous function $P : X \mapsto \mathbf{R}_+$ which satisfies the following conditions:*

(a) $P(x) = 0 \Longleftrightarrow x \in S$,

(b) $\sup_{t \geq 0} \liminf_{y \to x, y \in X \backslash S} \dfrac{P(f^t(y))}{P(y)} > 1 \quad (x \in S)$.

Then there is a compact set $M \subset X$ such that minimum distance between M and S is positive, and for every initial value in $X \backslash S$ the orbits enter and remain in M.

Corollary 1 *(Hutson [7]) The conclusion of Theorem 1 remains true if instead of (b) it is assumed that*

$$\sup_{t \geq 0} \liminf_{y \to x, y \in X \backslash S} \frac{P(f^t(y))}{P(y)} > \begin{cases} 1 \ (x \in \Omega(S)) \\ 0 \ (x \in S), \end{cases}$$

where $\Omega(S)$ is the omega limit set of S.

Now we introduce the following two notations: for a compact set X obtained in Lemma 1,

$$S_1 = \{(u, v) \in X | u = 0\},$$
$$S_2 = \{(u, v) \in X | v = 0\}.$$

Now define the following continuous functions $P_i : X \mapsto \mathbf{R}_+$ $(i = 1, 2)$ by setting

$$P_1(x) = u, \quad P_2(x) = v.$$

Put

$$\sigma_i(x) = \sup_{t \geq 0} \liminf_{y \to x, y \in X \backslash S_i} \frac{P_i(f^t(y))}{P_i(y)} \quad \text{for } i = 1, 2$$

where f is defined as the right-hand side of system (3) By using Eq.(3), we can calculate $\sigma_i(x)$, $(i = 1, 2)$ as follows:

$$\begin{aligned}\sigma_1(x) &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\setminus S_1} \frac{u(t)}{u(t-1)}\cdots\frac{u(1)}{u(0)} \\ &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\setminus S_1} \prod_{i=0}^{t-1} \frac{u(i)\exp[\ln r - u(i) - v(i)]}{u(i)} \\ &= \sup_{t\geq 0} \exp[t\ln r - \sum_{i=0}^{t-1} v(i)], \quad x \in S_1 \\ \sigma_2(x) &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\setminus S_2} \frac{v(t)}{v(t-1)}\cdots\frac{v(1)}{v(0)} \\ &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\setminus S_2} \prod_{i=0}^{t-1} \left(cu(i)\frac{1-\exp[-v(i)]}{v(i)}\right) \\ &= \sup_{t\geq 0} c^t \prod_{i=0}^{t-1} u(i), \quad x \in S_2\end{aligned}$$

where $(u(t), v(t)) = f^t(x)$ for $t \in \mathbf{Z}_+$ and the continuity of f is used.

The following Theorem 2 is the first main result of this paper:

Theorem 2 *System (3) is permanent if the following condition holds:*

$$\sigma_2(x) > 1 \quad \textit{for any } x \in \Omega(S_2\setminus\{(0,0)\}).$$

Proof. From the second equation of (3), $\Omega(S_1) = \{(0,0)\}$. Then

$$\sigma_1(x) = \sup_{t\geq 0} r^t > 1 \quad \text{for any } x \in \Omega(S_1). \tag{4}$$

Since $v(t) = 0$ for any $x \in S_1$ and $t \geq 1$,

$$\begin{aligned}\sigma_1(x) &= \sup_{t\geq 0} \exp[t\ln r - \sum_{i=0}^{t-1} v(i)] \\ &\geq \sup_{t\geq 1} \left(\exp\left[\ln r - \frac{v(0)}{t}\right]\right)^t > 0 \quad \text{for any } x \in S_1.\end{aligned} \tag{5}$$

Hence Corollary 1 with Eq.(4) and (5) shows that there is a compact set $M_1 \subset X$ such that minimum distance between M_1 and S_1 is positive, and for every initial value in $X\setminus S_1$ the orbits enter and remain in M_1.

Consider the behavior of the orbits in M_1. From the assumption of the theorem

$$\sigma_2(x) > 1 \quad \text{for any } x \in \Omega(S_2 \cap M_1). \tag{6}$$

Clearly

$$\sigma_2(x) = \sup_{t\geq 0} c^t \prod_{i=0}^{t-1} u(i) > 0 \quad \text{for any } x \in S_2 \cap M_1. \tag{7}$$

Then Corollary 1 with Eq.(6) and (7) shows that there is a compact set $M_2 \subset M_1$ such that minimum distance between M_2 and $S_2 \cap M_1$ is positive, and for every initial value in $M_1 \backslash S_2$ the orbits enter and remain in M_2. This completes the proof of the theorem.

Theorem 2 gives a sufficient condition for permanence of the host-parasitoid system. But it is not easy to check the condition. In the rest of this section, we obtain a sufficient condition which can be checked easily.

Lemma 2 *(Cull [3]) Let* $\{u(t), v(t)\}_{t\in\mathbf{Z}_+}$ *be a solution of system (3) with* $u(0) > 0$ *and* $v(0) = 0$. *If* $0 < \ln r \leq 2$, *then*

$$\lim_{t\to\infty} u(t) = \ln r.$$

The following Lemma 3 can be easily proved by using the property of the function $g(u) = ru\exp[-u]$, which is the map describing the one dimensional dynamics of system (3) with $v(0) = 0$.

Lemma 3 *Let* $\{u(t), v(t)\}_{t\in\mathbf{Z}_+}$ *be a solution of system (3) with* $u(0) > 0$ *and* $v(0) = 0$. *If* $2 < \ln r$, *then*

$$\eta \leq \liminf_{t\to\infty} u(t) \leq \limsup_{t\to\infty} u(t) \leq r/e,$$

where $\eta = r(r/e)\exp[-r/e] = \exp\{2\ln r - 1 - \exp[\ln r - 1]\}$.

The following Lemma 4 gives the property about an arithmetic mean of the host population density. To know average population densities is very important to obtain a sufficient condition for permanence by using the above Theorem 1 and Corollary 1. The proof of Lemma 4 is deduced directly from that of Lemma 2.4 in Hofbauer *et al.* [6].

Lemma 4 *Let* $\{(u(t), v(t))\}_{t\in\mathbf{Z}_+}$ *be a solution of system (3). Suppose that there are real numbers* $h_m > 0$ *and* h_M, *and a sequence* $t_i \to \infty$ *such that* $h_m \leq u(t_i) \leq h_M$, $0 \leq v(t_i) \leq h_M$. *Then there is a subsequence* $t_j \to \infty$ *of*

$\{t_i\}$ such that

$$\ln r = \lim_{j\to\infty} \frac{\sum_{i=0}^{t_j-1} u(i)}{t_j} + \lim_{j\to\infty} \frac{\sum_{i=0}^{t_j-1} v(i)}{t_j}.$$

The following Theorem 3 is the second main result of this paper.

Theorem 3 *If the following conditions hold, then system (3) is permanent:*

$$\begin{cases} c\ln r > 1 & \text{if} \quad 0 < \ln r \le 2 \\ c\exp[\xi \ln r + \zeta] > 1 & \text{if} \quad 2 < \ln r, \end{cases}$$

where

$$\xi = \frac{(\ln r - 1) - \ln \eta}{\exp[\ln r - 1] - \eta}$$
$$\zeta = \ln r - 1 - \exp[\ln r - 1]\xi.$$

Proof. First consider the case where $0 < \ln r \le 2$. In this case, from Lemma 2

$$\lim_{t\to\infty} u(t) = \ln r \quad \text{for any } x \in S_2 \backslash \{(0,0)\}.$$

Then

$$\sigma_2(x) = \sup_{t\ge 0}(c\ln r)^t > 1 \quad \text{for any } x \in \Omega(S_2\backslash\{(0,0)\}).$$

From Theorem 2, this completes the proof of the first case.

Next consider the case where $2 < \ln r$. In this case, from Lemma 3

$$\Omega(S_2\backslash\{(0,0)\}) \subset \{x \in S_2 | \eta \le u \le r/e\} \equiv M_3.$$

From Lemma 4, for any $x \in M_3$ there is a sequence $t_j \to \infty$ such that

$$\lim_{j\to\infty} \frac{\sum_{i=0}^{t_j-1} u(t_j)}{t_j} = \ln r.$$

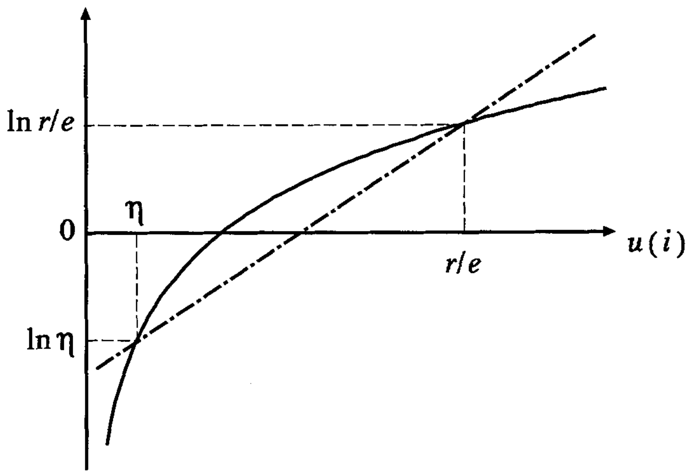

Fig. 1. The graph of $\ln u(i)$ (solid line) and $\xi u(i) + \zeta$ (dot-dashed line).

Then from the assumption of the theorem,

$$\lim_{j\to\infty} c\exp\left[\xi\frac{\sum_{i=0}^{t_j-1} u(t_j)}{t_j} + \zeta\right] > 1 \quad \text{for any } x \in M_3.$$

Hence for any $x \in M_3$

$$\begin{aligned}
\sigma_2(x) &\geq \sup_{j\geq 0}\left(c\left(\prod_{i=0}^{t_j-1} u(i)\right)^{\frac{1}{t_j}}\right)^{t_j} \\
&= \sup_{j\geq 0}\left(c\exp\left[\frac{\sum_{i=0}^{t_j-1}\ln u(i)}{t_j}\right]\right)^{t_j} \\
&\geq \sup_{j\geq 0}\left(c\exp\left[\frac{\sum_{j=0}^{t_j-1}(\xi u(i)+\zeta)}{t_j}\right]\right)^{t_j} \\
&= \sup_{j\geq 0}\left(c\exp\left[\xi\frac{\sum_{j=0}^{t_j-1} u(i)}{t_j} + \zeta\right]\right)^{t_j} \\
&> 1,
\end{aligned}$$

where the convexity of a logarithmic function, that is

$$\ln u(i) \geq \xi u(i) + \zeta \quad \text{for any } u(i) \in [\eta, r/e],$$

is used (see Fig.2). This completes the proof of the theorem.

The sufficient condition for permanence obtained in the above and some known results on system (3) are shown in Fig.2. From Fig.2, we see that the area that system (3) is permanent contains the area that system (3) has an unstable positive equilibrium.

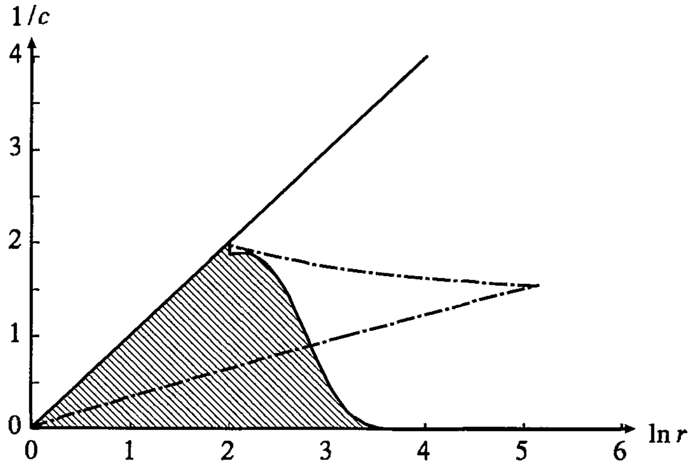

Fig. 2. The parameter space $\ln r - 1/c$. Below the line $\ln r = 1/c$, system (3) has two boundary equilibria which are unstable and a positive equilibrium. In the area enclosed by the dot-dashed lines and the line $\ln r = 1/c$, a positive equilibrium is stable. System (3) is permanent within the hatched area, which is the sufficient condition obtained in Theorem 3.

3 Necessary condition for permanence

In the previous section, we obtained a sufficient condition for permanence of system (3). But as shown in Fig.2, it does not coincide with the necessary and sufficient condition for existence of a positive equilibrium. In the following we, by investigating the stability of 2-cycle on S_2 numerically, show that system (3) is not always permanent when it has a positive equilibrium .

The system restricted on S_2, that is the Ricker model, has a stable 2-cycle $\{u_i\}_{i=1,2}$ if $2 < \ln r < 2.526\cdots$ (see May and Oster [9]). $\{p_i\}_{i=1,2} = \{(u_i, 0)\}_{i=1,2}$ is also a 2-cycle of system (3). The stability of $\{p_i\}_{i=1,2}$ depends on the eigenvalues of the following Jacobian matrix:

$$J = \prod_{i=1}^{2} \begin{pmatrix} r(1-u_i)\exp[-u_i] & -ru_i\exp[-u_i] \\ 0 & cu_i \end{pmatrix}.$$

Then the eigenvalues of J are

$$\prod_{i=1}^{2} r(1-u_i)\exp[-u_i] \quad \text{and} \quad \prod_{i=1}^{2} cu_i.$$

Since $\{u_i\}_{i=1,2}$ is a stable periodic orbit of the Ricker model,

$$\left|\prod_{i=1}^{2} r(1-u_i)\exp[-u_i]\right| < 1.$$

Hence if the following inequality holds, $\{p_i\}_{i=1,2}$ is stable, that is system (3) is not permanent:

$$\frac{1}{c} > \left(\prod_{i=1}^{2} u_i\right)^{\frac{1}{2}}. \tag{8}$$

From numerical investigations, we see that Eq.(8) can hold even if there exists a positive equilibrium, that is $1/c < \ln r$ (see Fig.3). In other words, system (3) is not always permanent even if it has a positive equilibrium.

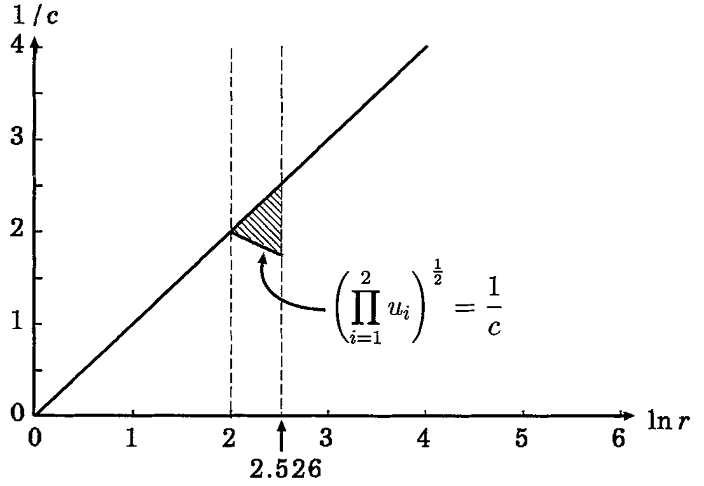

Fig. 3. The parameter space $\ln r - 1/c$. The line $1/c = \ln r$ is the boundary for existence of a positive equilibrium of system (3). System (3) has a positive equilibrium below the line. $\left(\prod_{i=1}^{2} u_i\right)^{1/2}$ are calculated from $\ln r = 2$ to 2.526 numerically. System (3) has a positive equilibrium and a stable 2-cycle on the boundary simultaneously at least in the hatched area.

4 Discussion

In section 2, we obtained a sufficient condition for permanence of the host-parasitoid system. In section 3, we showed that the necessary condition for permanence of the host-parasitoid system does not coincide with one for existence of the positive equilibrium. This property is different from that of the following Lotka-Volterra difference equation:

$$\begin{cases} x(t+1) = x(t)\exp[\ln r - x(t) - y(t)] \\ y(t+1) = y(t)\exp[s(-1+\beta x(t))], \end{cases} \tag{9}$$

where $x(t)$ and $y(t)$ are the population densities of prey and predator, respectively, and r, s and β are the positive constants. System (9) is permanent if and only if there exists a positive equilibrium (see Hofbauer *et al.* [6] and Anderson *et al.* [1]). By comparing system (3) and (9), we see that the dynamics of the host population and the prey population in each system obey the same equation, but parasitism and predation are expressed in the different way. To obtain the necessary and sufficient condition of the host-parasitoid system is a future work.

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