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PERMANENCE OF 2-HOST 1-PARASITOID SYSTEMS

Ryusuke Kon[1] and Yasuhiro Takeuchi[1]

[1] Department of Systems Engineering, Faculty of Engineering
Shizuoka University, Johoku 3-5-1, Hamamatsu, Shizuoka 432-8561, Japan

Abstract. In this paper, permanence of a host-parasitoid system, which is composed of two hosts and one parasitoid, is considered. Sufficient conditions for permanence of the system are obtained by using average Liapunov functions. One of the sufficient conditions shows that even if two hosts cannot coexist by themselves, they can coexist with a help of a parasitoid in a sense of permanence .
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1 Introduction

In population ecology, it is important to consider coexistence of species. Concerning with an interaction between hosts and parasitoids, which is a popular interaction in insect populations (Hassell [4], [5]), Comins and Hassell [2] considered the following host-parasitoid model:

$$\begin{cases} H_1(t+1) &=& \lambda_1 H_1(t)\exp[-\sum_{j=1}^{2}\mu_{1j}H_j(t)]\exp[-a_1P(t)] \\ H_2(t+1) &=& \lambda_2 H_2(t)\exp[-\sum_{j=1}^{2}\mu_{2j}H_j(t)]\exp[-a_2P(t)] \\ P(t+1) &=& \sum_{j=1}^{2} b_jH_j(t)(1-\exp[-a_jP(t)]), \end{cases} \tag{1}$$

$$(H_1(t), H_2(t), P(t)) \in \mathbf{R}_+^3 := \{(H_1, H_2, P) \in \mathbf{R}^3 : H_1 \geq 0, H_2 \geq 0, P \geq 0\}$$
$$t \in \mathbf{Z}_+ := \{0, 1, 2, \ldots\},$$

where $\lambda_i > 1, \mu_{ij} > 0, a_i > 0, b_i > 0$ $(i, j = 1, 2)$. This system is composed of two hosts, H_1 and H_2, and one parasitoid, P, whose population densities at generation t are denoted by $H_1(t)$, $H_2(t)$ and $P(t)$, respectively. By investigating stability of a positive equilibrium point of system (1), Comins and Hassell [2] considered whether two hosts competing with each other can coexist with a help of the parasitoid. Since the species in discrete-time systems often coexist without a stable equilibrium point, in this paper we consider permanence (see Definition 1), which ensures coexistence of species irrespective of population dynamics. To emphasize an influence of a parasitoid on the possibility of coexistence of the competing hosts, we assume that one of the hosts is dominant in system (1) in the absence of the parasitoid (see Definition 5), that is, two hosts are assumed not to be able to coexist without the parasitoid.

This paper is organized as follows. In Section 2, we give the definitions of permanence and dominance, some notations and lemmas used in the successive sections. In Section 3, we obtain sufficient conditions for permanence by constructing average Liapunov functions. The final section includes discussions and future problems.

2 Preliminaries

Let $x := (H_1, H_2, P)$ and $x(t) := (H_1(t), H_2(t), P(t))$. The interior of $\mathbf{R}^3_+ = \{x \in \mathbf{R}^3 : H_1 \geq 0, H_2 \geq 0, P \geq 0\}$ is denoted by $\mathrm{int}\mathbf{R}^3_+$. The boundary of $\mathbf{R}^3_+$, $\mathbf{R}^3_+ \backslash \mathrm{int}\mathbf{R}^3_+$, is denoted by $\mathrm{bd}\mathbf{R}^3_+$

The definition of permanence is given as follows:

Definition 1 *System* (1) *is said to be permanent, if there exist* $\delta > 0$ *and* $D > 0$ *such that*

$$\begin{aligned} \delta &\leq \liminf_{t\to\infty} H_i(t) \leq \limsup_{t\to\infty} H_i(t) \leq D \quad i = 1, 2 \\ \delta &\leq \liminf_{t\to\infty} P(t) \leq \limsup_{t\to\infty} P(t) \leq D \end{aligned}$$

for all $x(0) \in \mathrm{int}\mathbf{R}^3_+$.

¿From this definition, the species in a permanent system can coexist in the sense that once the population densities of all the species in the system are positive, then the population densities are bounded away from zero (extinction) and infinity (explosion) for all the time after some generations.

The existence of a supremum limit of population densities, D, is assured by the following lemma:

Lemma 2 (Yakubu [12], Corollary 1) *Let* $\{x(t)\}_{t\in\mathbf{Z}_+}$ *be a solution of system* (1). *The solution of system* (1) *is (ultimately) uniformly bounded, that is, there exists a compact set* $X := \{x \in \mathbf{R}^3_+ : H_1 \leq D, H_2 \leq D, P \leq D\}$ *such that for all* $x(0) \in \mathbf{R}^3_+$ *there exists* $T = T(x(0)) > 0$ *satisfying* $x(t) \in X$ *for all* $t \geq T$.

¿From this lemma, it is enough to focus on the dynamics in X to consider permanence of (1). We divide $X \cap \mathrm{bd}\mathbf{R}^3_+$ into three faces as follows:

$$\begin{aligned} S_i &:= \{x \in X : H_i = 0\} \quad i = 1, 2 \\ S_3 &:= \{x \in X : P = 0\}. \end{aligned}$$

The following lemmas give a method for proving the existence of a positive infimum limit of population densities, δ, with average Liapunov functions:

Lemma 3 (Hutson [7], Theorem 2.2) *Let (X, d) be a metric space. Consider the system $f : X \to X$, where f is continuous. 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 $P : X \to \mathbf{R}_+$, which is called an average Liapunov function, satisfying 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 S is repellor, that is, there is a compact forward invariant set M with $d(M, S) > 0$ such that every orbit $\{x(t)\}_{t \in \mathbf{Z}_+}$ in $X \backslash S$ is ultimately in M.

Lemma 4 (Hutson [7], Corollary 2.3) *The conclusion of Lemma 3 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 $\Omega(S) = \cup_{x \in S} \Omega(x)$ and $\Omega(x) = \{y \in X : \lim_{t_k \to \infty} f^{t_k}(x) = y$ for some $t_k \to \infty\}$.

System (1) in the absence of the parasitoid ($P(t) = 0$ in (1)) is given as follows:

$$\begin{cases} H_1(t+1) &= \lambda_1 H_1(t) \exp[-\sum_{j=1}^{2} \mu_{1j} H_j(t)] \\ H_2(t+1) &= \lambda_2 H_2(t) \exp[-\sum_{j=1}^{2} \mu_{2j} H_j(t)]. \end{cases} \tag{2}$$

The dynamics of (2) has been investigated in several papers (for example, Hofbauer *et al.* [6], Franke and Yakubu [3] and Lu and Wang [11]).

We define the dominance as follows:

Definition 5 *In system (2), the host H_k is dominant if N_i $(i \neq k)$ is a proper subset of N_k, where*

$$N_l := \{(H_1, H_2) \in \mathbf{R}_+^2 : \lambda_l \exp[-\sum_{j=1}^{2} \mu_{lj} H_j] \geq 1\}.$$

¿From this definition, host H_i is dominant if

$$\frac{\ln \lambda_i}{\mu_{ii}} \geq \frac{\ln \lambda_j}{\mu_{ji}} \quad \text{and} \quad \frac{\ln \lambda_i}{\mu_{ij}} \geq \frac{\ln \lambda_j}{\mu_{jj}}$$

with at least one strict inequality, where $i, j \in \{1, 2\}$ and $i \neq j$. System (2) has the following dynamical properties about the dominance:

Lemma 6 (Franke and Yakubu [3], Theorem 3.1) *Let $\{(H_1(t), H_2(t))\}_{t \in \mathbf{Z}_+}$ be a solution of system (2). If in system (2) the host H_i is dominant, then $\lim_{t \to \infty} H_j(t) = 0$ $(i, j \in \{1, 2\}; i \neq j)$ for all $(H_1(0), H_2(0)) \in \mathrm{int}\mathbf{R}_+^2$.*

3 Sufficient conditions for permanence

Define the following continuous functions $P_i : X \to \mathbf{R}_+$ $(i = 1, 2, 3)$ by setting

$$P_i(x) = H_i \quad (i = 1, 2) \quad \text{and} \quad P_3(x) = P.$$

Note that X is the compact set defined in Lemma 2. Put

$$\sigma_i(x) = \sup_{t\geq 0} \liminf_{y\to x, y\in X\backslash S_i} \frac{P_i(f^t(y))}{P_i(y)} \quad \text{for } i = 1, 2, 3,$$

where f is defined as the right-hand side of system (1). By using Eq.(1) and the notations $\overline{H}_i(t) = \sum_{k=0}^{t-1} H_i(k)/t$ $(i = 1, 2)$ and $\overline{P}(t) = \sum_{k=0}^{t-1} P(k)/t$, we have:

$$\begin{aligned}
\sigma_i(x) &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\backslash S_i} \frac{I_i(t)}{I_i(t-1)} \cdots \frac{I_i(1)}{I_i(0)} \\
&= \sup_{t\geq 0} \liminf_{y\to x, y\in X\backslash S_i} \prod_{k=0}^{t-1} \frac{I_i(k) \exp[\ln \lambda_i - \sum_{j=1}^{2} \mu_{ij} I_j(k) - a_i Q(k)]}{I_i(k)} \\
&= \sup_{t\geq 0} \left(\exp \left[\ln \lambda_i - \sum_{j\neq i} \mu_{ij} \overline{H}_j(t) - a_i \overline{P}(t) \right] \right)^t, \quad x \in S_i \ (i = 1, 2) \\
\sigma_3(x) &= \sup_{t\geq 0} \liminf_{y\to x, y\in X\backslash S_3} \frac{Q(t)}{Q(t-1)} \cdots \frac{Q(1)}{Q(0)} \\
&= \sup_{t\geq 0} \liminf_{y\to x, y\in X\backslash S_3} \prod_{k=0}^{t-1} \sum_{i=1}^{2} \left(b_i I_i(k) \frac{1 - \exp[-a_i Q(k)]}{Q(k)} \right) \\
&= \sup_{t\geq 0} \prod_{k=0}^{t-1} \sum_{i=1}^{2} a_i b_i H_i(k), \quad x \in S_3,
\end{aligned}$$

where $(H_1(t), H_2(t), P(t)) = f^t(x)$ for $x \in S_i$ and $(I_1(t), I_2(t), Q(t)) = f^t(y)$ for $y \in X\backslash S_i$, and the continuity of f is used. The $\sigma_i(x)$ is clearly positive for all $x \in S_i$ $(i = 1, 2)$, and the $\sigma_3(x)$ is also positive for all $x \in S_3\backslash S_i$ $(i = 1, 2)$.

By using the above average Liapunov functions with Lemma 4, we have the following theorem, which gives a sufficient condition for permanence of system (1):

Theorem 7 *Let $\{x(t)\}_{t\in \mathbf{Z}_+}$ be a solution of system* (1). *If for $i, j \in \{1, 2\}$ $(i \neq j)$,*

(a) $\sigma_j(x(0)) > 1$ *for all* $x(0) \in \Omega(S_j)$,

(b) $\sigma_3(x(0)) > 1$ *for all* $x(0) \in \Omega(S_3\backslash S_j)$ *and*

(c) $\sigma_i(x(0)) > 1$ *for all* $x(0) \in \Omega(S_i\backslash(S_j \cup S_3))$,

then system (1) *is permanent.*

Proof. We give the proof only for $i = 1, j = 2$. The case for $i = 2, j = 1$ can be proved similarly. ¿From Lemma 4 with the condition (a) and the fact that $\sigma_2(x(0)) > 0$ for all $x(0) \in S_2$, we see that the face S_2 is repellor for the orbits in $X \backslash S_2$, that is, there exists a $\delta_2 > 0$ such that for all $x(0) \in X \backslash S_2$ there exists a $T_2 = T_2(x(0)) > 0$ satisfying $x(t) \in M_2 := \{x \in X : H_2 \geq \delta_2\}$ for all $t \geq T_2$. Moreover Lemma 4 with the condition (b) and the fact that $\sigma_3(x(0)) > 0$ for all $x(0) \in S_3 \backslash S_2$ imply that there exists a $\delta_3 > 0$ such that for all $x(0) \in M_2 \backslash S_3$ there exists a $T_3 = T_3(x(0)) > 0$ satisfying $x(t) \in M_3 := \{x \in M_2 : P \geq \delta_3\}$ for all $t \geq T_3$. Finally, Lemma 4 with the condition (c) and the fact that $\sigma_1(x(0)) > 0$ for all $x(0) \in S_1$ means that the face S_1 is repellor for the orbit in $M_3 \backslash S_1$, that is, there exists a $\delta_1 > 0$ such that for all $x(0) \in M_3 \backslash S_1$ there exists a $T_1 = T_1(x(0)) > 0$ satisfying $x(t) \in M_1 := \{x \in M_3 : H_1 \geq \delta_1\}$ for all $t \geq T_1$. This completes the proof.

q.e.d

The sufficient conditions for permanence of (1) in Theorem 7 are difficult to check, so that in the rest of this section, we attempt to obtain the sufficient conditions checked easily.

¿From the condition in Theorem 7, we see that it is important to know the dynamics of system (1) on S_1, S_2 and S_3. If one of the hosts is dominant in system (2), then Lemma 6 gives the behavior of the orbits on intS_3. Hereafter we investigate the dynamics of system (1) on S_i $(i = 1, 2)$, of which dynamics is given as follows:

$$\left\{ \begin{array}{lcl} H_i(t+1) & = & \lambda_i H_i(t) \exp[-\mu_{ii} H_i(t)] \exp[-a_i P(t)] \\ P(t+1) & = & b_i H_i(t)(1 - \exp[-a_i P(t)]). \end{array} \right. \tag{3}$$

This system is a Nicholson-Bailey model with density dependence in a host population (Hassell [4], [5]) and a local stability analysis was carried out by Beddington *et al.* [1]. Permanence of system (3) was investigated by Kon and Takeuchi [10] and obtained:

Lemma 8 (Kon and Takeuchi [10], Theorem 3) *If the following conditions hold, then system* (3) *is permanent:*

$$\left\{ \begin{array}{ll} (a_i b_i \ln \lambda_i)/\mu_{ii} > 1 & \text{if} \quad 0 < \ln \lambda_i \leq 2 \\ a_i b_i \exp[(\xi_i \ln \lambda_i)/\mu_{ii} + \zeta_i] > 1 & \text{if} \quad 2 < \ln \lambda_i, \end{array} \right.$$

where

$$\begin{array}{rcl} \eta_i & = & \lambda_i(\lambda_i/(\mu_{ii} e)) \exp[-\lambda_i/e] \\ & = & \exp[2 \ln \lambda_i - \ln \mu_{ii} - 1 - \exp[\ln \lambda_i - 1]] \\ \xi_i & = & \dfrac{(\ln \lambda_i - \ln \mu_{ii} - 1) - \ln \eta_i}{\exp[\ln \lambda_i - \ln \mu_{ii} - 1] - \eta_i} \\ \zeta_i & = & \ln \eta_i - \xi_i \eta_i. \end{array}$$

Lemma 9 *Let* $\{(H_i(t), P(t))\}_{t \in \mathbf{Z}_+}$ *be a solution of system* (3). *There exists a* $\delta > 0$ *such that for all* $(H_i(0), P(0)) \in \mathbf{R}^2_+$ *with* $H_i(0) > 0$ *there exists a* $T = T(H_i(0), P(0)) > 0$ *satisfying* $H_i(t) \geq \delta$ *for all* $t \geq T$.

The proof of this lemma is deduced directly from that of Theorem 2 in Kon and Takeuchi [10].

Lemma 10 (Kon and Takeuchi [10], Lemma 4) *Let* $\{(H_i(t), P(t))\}_{t\in\mathbf{Z}_+}$ *be a solution of system* (3). *Suppose that there are real numbers* $h_m > 0$ *and* h_M, *and a sequence* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $h_m \le H_i(t_k) \le h_M$, $0 \le P(t_k) \le h_M$. *Then there is a subsequence* $\{t_j\}$ *with* $t_j \to \infty$ *of* $\{t_k\}$ *such that*

$$\ln \lambda_i = \mu_{ii} \lim_{j\to\infty} \overline{H}_i(t_j) + a_i \lim_{j\to\infty} \overline{P}(t_j).$$

The proof of this lemma is deduced directly from that of Lemma 2.4 in Hofbauer *et al.* [6].

By using Lemmas 8, 9 and 10 with Theorem 7, we have the following theorem:

Theorem 11 *Let* $\{x(t)\}_{t\in\mathbf{Z}_+}$ *be a solution of system* (1). *For* $i, j \in \{1, 2\}$ $(i \ne j)$, *suppose that* $(\ln \lambda_i)/a_i > (\ln \lambda_j)/a_j$. *If*

(a) *for all* $x(0) \in S_j\backslash(S_i \cap S_j)$ *there exists a* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $\lim_{k\to\infty} \overline{H}_i(t_k) > \widehat{H}_i$,

(b) *the host* H_j *is dominant in system* (2) *and the condition in Lemma 8 for system* (3) *composed of* H_j *and* P *holds and*

(c) *for all* $x(0) \in S_i\backslash(S_j \cup S_3)$ *there exists a* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $\lim_{k\to\infty} \overline{H}_j(t_k) < \widehat{H}_j$,

then system (1) *is permanent. Here*

$$\widehat{H}_i := \frac{\dfrac{\ln \lambda_i}{a_i} - \dfrac{\ln \lambda_j}{a_j}}{\dfrac{\mu_{ii}}{a_i} - \dfrac{\mu_{ji}}{a_j}} > 0.$$

Proof. We give the proof only for $i = 1$ and $j = 2$. The other case can be shown similarly. We can see that $\Omega(S_1 \cap S_2) = \{(0,0,0)\}$. Hence for $x(0) \in \Omega(S_1 \cap S_2)$ we have $\sigma_2(x(0)) = \sup_{t\ge 0} \lambda_2^t > 1$. ¿From Lemma 9, we have $\Omega(S_2\backslash(S_1 \cap S_2)) \subset S_2\backslash(S_1 \cap S_2)$. ¿From Lemma 10, for all $x(0) \in S_2\backslash(S_1 \cap S_2)$ there exists $\{t_j\}$ with $t_j \to \infty$ such that

$$\ln \lambda_1 = \mu_{11} \lim_{j\to\infty} \overline{H}_1(t_j) + a_1 \lim_{j\to\infty} \overline{P}(t_j).$$

It follows that for any $x(0) \in S_2 \backslash (S_1 \cap S_2)$ by (a)

$$\begin{aligned}
\sigma_2(x(0)) &= \sup_{t\geq 0} \left(\exp[\ln\lambda_2 - \mu_{21}\overline{H}_1(t) - a_2\overline{P}(t)]\right)^t \\
&= \sup_{t\geq 0} \left(\exp\left[a_2\left\{\left(\frac{\ln\lambda_2}{a_2} - \frac{\ln\lambda_1}{a_1}\right)\right.\right.\right. \\
&\quad \left.\left.\left. - \left(\frac{\mu_{21}}{a_2} - \frac{\mu_{11}}{a_1}\right)\overline{H}_1(t) + \frac{\ln\lambda_1}{a_1} - \frac{\mu_{11}}{a_1}\overline{H}_1(t) - \overline{P}(t)\right\}\right]\right)^t \\
&\geq \sup_{j\geq 0} \left(\exp\left[a_2\left\{\left(\frac{\mu_{11}}{a_1} - \frac{\mu_{21}}{a_2}\right)\left(\overline{H}_1(t_j) - \widehat{H}_1\right)\right.\right.\right. \\
&\quad \left.\left.\left. + \frac{1}{a_1}\left(\ln\lambda_1 - \mu_{11}\overline{H}_1(t_j) - a_1\overline{P}(t_j)\right)\right\}\right]\right)^{t_j} \\
&> 1.
\end{aligned}$$

Note that if the host H_2 is dominant in system (2) and $(\ln\lambda_1)/a_1 > (\ln\lambda_2)/a_2$, then $\mu_{11}/a_1 - \mu_{21}/a_2 > 0$. Therefore the condition (a) in Theorem 7 holds.

The (a) in Theorem 7 implies that S_2 is repellor. It follows with the dominance of the host H_2 that $\Omega(S_3 \backslash S_2) \subset (S_3 \cap S_1) \backslash S_2$. As shown in the proof of Theorem 3 in Kon and Takeuchi [10], we have $\sigma_3(x(0)) > 1$ for all $x(0) \in (S_3 \cap S_1) \backslash S_2$.

Finally we have to show that $\sigma_1(x(0)) > 1$ for all $x(0) \in \Omega(S_1 \backslash (S_2 \cup S_3))$. Since system (3) composed of H_2 and P is permanent by (b), we have $\Omega(S_1 \backslash (S_2 \cup S_3)) \subset S_1 \backslash (S_2 \cup S_3)$. ¿From Lemma 10, for any $x(0) \in S_1 \backslash (S_2 \cup S_3)$ there exists a $t_j \to \infty$ such that

$$\ln\lambda_2 = \mu_{22} \lim_{j\to\infty} \overline{H}_2(t_j) + a_2 \lim_{j\to\infty} \overline{P}(t_j).$$

Then for any $x(0) \in S_1 \backslash (S_2 \cup S_3)$ by (c)

$$\begin{aligned}
\sigma_1(x(0)) &= \sup_{t\geq 0} \left(\exp[\ln\lambda_1 - \mu_{12}\overline{H}_2(t) - a_1\overline{P}(t)]\right)^t \\
&= \sup_{t\geq 0} \left(\exp\left[a_1\left\{\left(\frac{\ln\lambda_1}{a_1} - \frac{\ln\lambda_2}{a_2}\right)\right.\right.\right. \\
&\quad \left.\left.\left. - \left(\frac{\mu_{12}}{a_1} - \frac{\mu_{22}}{a_2}\right)\overline{H}_2(t) + \frac{\ln\lambda_2}{a_2} - \frac{\mu_{22}}{a_2}\overline{H}_2(t) - \overline{P}(t)\right\}\right]\right)^t \\
&\geq \sup_{j\geq 0} \left(\exp\left[a_1\left\{\left(\frac{\mu_{12}}{a_1} - \frac{\mu_{22}}{a_2}\right)\left(\widehat{H}_2 - \overline{H}_2(t_j)\right)\right.\right.\right. \\
&\quad \left.\left.\left. + \frac{1}{a_2}\left(\ln\lambda_2 - \mu_{22}\overline{H}_2(t_j) - a_2\overline{P}(t_j)\right)\right\}\right]\right)^{t_j} \\
&> 1.
\end{aligned}$$

Note that if the host H_2 is dominant in system (2) and $(\ln\lambda_1)/a_1 > (\ln\lambda_2)/a_2$, then $\mu_{12}/a_1 - \mu_{22}/a_2 > 0$. This completes the proof.

q.e.d

Note that the $\widehat{H}_i$ indicates the H_i coordinate of the intersection of the null clines for H_1 and H_2 on the face $H_j = 0$. That is, the $\widehat{H}_i$ is given as a root of the following:

$$\begin{cases} \lambda_i \exp[-\mu_{ii}\widehat{H}_i]\exp[-a_i P] = 0 \\ \lambda_j \exp[-\mu_{ji}\widehat{H}_i]\exp[-a_j P] = 0. \end{cases}$$

To estimate the average population densities $\overline{H}_i(t)$, we have the following lemmas:

Lemma 12 *Let* $\{(H_i(t), P(t))\}_{t\in\mathbf{Z}_+}$ *be a solution of system* (3) *with* $P(0) > 0$ *and* $H_i(0) > 0$. *Suppose that there are real numbers* $h_m > 0$ *and* h_M, *and a sequence* $\{t_k\}$ *with* $t_k \to \infty$ *such that* $h_m \leq P(t_k) \leq h_M$. *Then there is a subsequence* $\{t_j\}$ *with* $t_j \to \infty$ *of* $\{t_k\}$ *such that*

$$\lim_{j\to\infty} \overline{H}_i(t_j) \geq \frac{1}{a_i b_i}.$$

Proof. ¿From the second equation of (3), we have

$$\frac{P(t+1)}{P(t)} = b_i H_i(t)\frac{1-\exp[-a_i P(t)]}{P(t)}.$$

Since $\mathrm{int}\mathbf{R}^2_+$ is invariant under system (3), then $H_i(0) > 0$ and $P(0) > 0$ imply that $P(t) > 0$ for all $t \in \mathbf{Z}_+$. Hence

$$\begin{aligned} \frac{P(t)}{P(t-1)}\cdots\frac{P(1)}{P(0)} &= b_i^t \prod_{k=0}^{t-1} H_i(k)\frac{1-\exp[-a_i P(k)]}{P(k)} \\ \frac{\ln P(t) - \ln P(0)}{t} &= \ln b_i + \ln\left(\prod_{k=0}^{t-1} H_i(k)\right)^{1/t} + \frac{1}{t}\sum_{k=0}^{t-1}\ln\frac{1-\exp[-a_i P(k)]}{P(k)} \\ &\leq \ln b_i + \ln \overline{H}_i(t) + \frac{1}{t}\sum_{k=0}^{t-1}\ln a_i. \end{aligned}$$

Since there exists $\{t_k\}$ such that $P(t_k)$ is bounded, there exists a subsequence $\{t_j\}$ with $t_j \to \infty$ of $\{t_k\}$ such that

$$1 \leq a_i b_i \lim_{j\to\infty} \overline{H}_i(t_j).$$

q.e.d

Lemma 13 *Let* $\{x_i(t)\}_{t\in\mathbf{Z}_+} := \{H_i(t), P(t)\}_{t\in\mathbf{Z}_+}$ *be a solution of system* (3). *If* $(a_i b_i \ln\lambda_i)/\mu_{ii} < 1$, *then* $\lim_{t\to\infty} P(t) = 0$ *for any* $x_i(0) \in \mathbf{R}^2_+$.

Note that system (3) has a positive equilibrium point if and only if $(a_i b_i \ln \lambda_i)/\mu_{ii} > 1$ (see Kon and Takeuchi [9]). Lemma 13 is proved by using the following lemma with Lemmas 9 and 10:

Lemma 14 *Let (X,d), $f : X \to X$, S, $X \backslash S$ be as the same as Lemma 3. Suppose that there is a continuous function $P : X \to \mathbf{R}_+$ which satisfies the following conditions:*

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

(b) $\inf_{t \geq 0} \limsup_{y \to x, y \in X \backslash S} \dfrac{P(f^t(y))}{P(y)} < 1 \quad (x \in S)$

(c) $\inf_{t \geq 0} \dfrac{P(f^t(x))}{P(x)} < 1 \quad (x \in X \backslash S)$

Then all orbits in X converge to S as $t \to \infty$, that is, $\Omega(X) \subset S$.

Proof. This lemma is proved similarly as Hutson [7] proved Lemma 3 (see also Hofbauer *et al.*[6], Theorem 2.7, and Hutson and Schmitt [8], Theorem 2.18). For $x \in X$ and $t \geq 0$ define

$$\alpha(t,x) = \begin{cases} \dfrac{P(f^t(x))}{P(x)} & (x \in X \backslash S) \\ \limsup_{y \to x, y \in X \backslash S} \dfrac{P(f^t(y))}{P(y)} & (x \in S) \end{cases}$$

and note that $\alpha(t, \cdot)$ is upper semicontinuous. For $h > 0$, $t \geq 0$ set $U(h,t) = \{x : \alpha(t,x) < 1 - h\}$. ¿From the semicontinuity each $U(h,t)$ is open, and clearly $U(h_1,t) \supset U(h_2,t)$ if $h_1 < h_2$. ¿From the conditions (b) and (c), $X \subset \bigcup_{h>0,t>0} U(h,t)$, and since X is compact, there is an $\overline{h} > 0$ and $\tau_1, \ldots, \tau_n \geq 0$ such that $X \subset \bigcup_{i=1}^{n} U(\overline{h}, \tau_i)$. Then for any $x \in X \backslash S$ there is a t_1 with $0 \leq t_1 \leq \overline{t} = \max\{\tau_1, \ldots, \tau_n\}$ such that

$$\begin{aligned} \alpha(t_1, x) &< 1 - \overline{h} \\ P(f^{t_1}(x)) &< P(x)(1 - \overline{h}). \end{aligned}$$

Since $X \backslash S$ is forward invariant, $f^{t_1}(x) \in X \backslash S$. Then there exists a t_2 with $0 \leq t_2 \leq \overline{t}$ such that

$$\begin{aligned} \alpha(t_2, f^{t_1}(x)) &< 1 - \overline{h} \\ P(f^{t_2+t_1}(x)) &< P(f^{t_1}(x))(1 - \overline{h}) \\ &< P(x)(1 - \overline{h})^2. \end{aligned}$$

By iterations, we have a sequence $t_j \to \infty$ with $0 \leq t_j \leq \overline{t}$ such that $\lim_{j \to \infty} P(f^{\sum_{i=1}^{j} t_i})(x) = 0$. Finally, since

$$P(f^{t + \sum_{i=1}^{j} t_i}(x)) \leq \overline{\alpha} P(f^{\sum_{i=1}^{j} t_i}(x))$$

holds for all t with $0 \leq t \leq t_{j+1}$, where

$$\overline{\alpha} = \sup\{\alpha(t,x) : 0 \leq t \leq \overline{t}, x \in X\},$$

we conclude that $\lim_{t\to\infty} P(f^t(x)) = 0$ and $\Omega(X) = S$.

q.e.d

Let us prove Lemma 13.

Proof of Lemma 13. We check the conditions in Lemma 14, ¿From Lemma 2, the solution of system (3) is uniformly bounded, that is, there exists a compact subset X_i such that for all $x_i(0) \in \mathbf{R}^2_+$ there exists $T = T(x_i(0)) > 0$ satisfying

$$x_i(t) \in X_i$$

for all $t \geq T$. Define S_H and $P_H : X_i \to \mathbf{R}^2_+$ as follows:

$$S_H = \{x_i \in X_i : P = 0\},$$

$$P_H(x_i) = P$$

where $x_i := (H_i, P)$. Put for $x_i \in S_H$

$$\sigma_H(x_i) = \inf_{t\geq 0} \limsup_{y_i \to x_i, y_i \in X_i \setminus S_H} \frac{P_H(f_H^t(y_i))}{P_H(y_i)},$$

where f_H is defined as the right-hand side of system (3). As we calculated σ_3, we have

$$\begin{aligned} \sigma_H(x_i(0)) &= \inf_{t\geq 0} \prod_{k=0}^{t-1} a_i b_i H_i(k) \\ &\leq \inf_{t\geq 0} \left(a_i b_i \overline{H}_i(t)\right)^t. \end{aligned} \tag{4}$$

¿From Lemmas 9 and 10, for all $x_i(0) \in S_H$ we have a $\{t_j\}$ with $t_j \to \infty$ such that

$$\ln \lambda_i = \mu_{ii} \lim_{j\to\infty} \overline{H}_i(t_j).$$

It follows with Eq. (4) that $\sigma_H(x_i(0)) < 1$ for all $x_i(0) \in S_H$.

For $x_i(0) \in X_i \setminus S_H$ we have

$$\begin{aligned} \inf_{t\geq 0} \frac{P_H(f^t(x_i(0)))}{P_H(x_i(0))} &= \inf_{t\geq 0} \prod_{k=0}^{t-1} \frac{b_i H_i(k)(1-\exp[-a_i P(k)])}{P(k)} \\ &\leq \inf_{t\geq 0} \prod_{k=0}^{t-1} a_i b_i H_i(k) \\ &\leq \inf_{t\geq 0} \left(a_i b_i \overline{H}_i(t)\right)^t \end{aligned}$$

¿From Lemmas 9 and 10, for all $x(0) \in X_i \backslash S_H$ we have a sequence $\{t_j\}$ with $t_j \to \infty$ such that

$$\begin{aligned} \ln \lambda_i &= \mu_{ii} \lim_{j\to\infty} \overline{H}_i(t_j) + a_i \lim_{j\to\infty} \overline{P}(t_j) \\ &\geq \mu_{ii} \lim_{j\to\infty} \overline{H}_i(t_j), \end{aligned}$$

which implies $\inf_{t\geq 0} \left(a_i b_i \overline{H}_i(t)\right)^t < 1$. This completes the proof.

q.e.d

By using Lemmas 12 and 13, we have the following theorem, which gives a sufficient condition for permanence of system (1). The conditions can be easily checked.

Theorem 15 *Suppose that* $(\ln \lambda_i)/a_i > (\ln \lambda_j)/a_j$. *Assume that*

(a)

$$\begin{cases} (a_i b_i \ln \lambda_i)/\mu_{ii} < 1 & \textit{or} \\ (a_i b_i \ln \lambda_i)/\mu_{ii} \geq 1 & \textit{and} \quad 1/(a_i b_i) > \widehat{H}_i, \end{cases}$$

(b)

$$\frac{\ln \lambda_i}{\mu_{ii}} < \frac{\ln \lambda_j}{\mu_{ji}} \quad \textit{and} \quad \frac{\ln \lambda_i}{\mu_{ij}} = \frac{\ln \lambda_j}{\mu_{jj}},$$

and the condition in Lemma 8 for system (3) *composed of* H_j *and* P *holds, where* $i, j \in \{1,2\}$ *and* $i \neq j$.

Then (1) *is permanent.*

Proof. Consider the case $i = 1$ and $j = 2$. If $(a_1 b_1 \ln \lambda_1)/\mu_{11} < 1$, then Lemmas 9, 10 and 13 show that for all $x(0) \in S_2 \backslash (S_1 \cap S_2)$ there exists a $\{t_j\}$ with $t_j \to \infty$ such that

$$\lim_{j\to\infty} \overline{H}_1(t_j) = \frac{\ln \lambda_1}{\mu_{11}} > \widehat{H}_1.$$

If $(a_1 b_1 \ln \lambda_1)/\mu_{11} \geq 1$, there are two possibilities for orbits $\{x(t)\}_{t\in \mathbf{Z}_+}$ with $x(0) \in S_2 \backslash (S_1 \cap S_2)$. The one is a possibility that $\lim_{t\to\infty} P(t) = 0$. In this case, there exists a $\{t_j\}$ with $t_j \to \infty$ satisfying the above inequality. The other is a possibility that there exist an $\{t_k\}$ with $t_k \to \infty$ and an $h_m > 0$ such that $P(t_k) \geq h_m$. Then Lemmas 9 and 12 show that there exists a subsequence $\{t_j\}$ with $t_j \to \infty$ of $\{t_k\}$ such that

$$\lim_{j\to\infty} \overline{H}_1(t_j) \geq \frac{1}{a_1 b_1} > \widehat{H}_1.$$

Hence the condition (a) in Theorem 11 holds.

¿From Lemma 8, it is clear that the condition (b) in Theorem 11 holds.

Finally, since system (3) composed of H_2 and P is permanent, there exists a $\delta > 0$ such that for all $x(0) \in S_1 \backslash (S_2 \cup S_3)$ there exists a $T = T(x(0)) > 0$ satisfying $P(t) \geq \delta$ for all $t > T$. It follows with Lemma 10 that there exists $\{t_j\}$ with $t_j \to \infty$ such that

$$\ln \lambda_2 \geq \mu_{22} \lim_{j\to\infty} \overline{H}_2(t_j) + a_2\delta.$$

Then

$$\lim_{j\to\infty} \overline{H}_2(t_j) \leq \frac{\ln \lambda_2 - a_2\delta}{\mu_{22}} < \widehat{H}_2.$$

Hence the condition (c) in Theorem 11 holds.

q.e.d.

The parameters satisfying the conditions in the theorem are shown in Fig.1.

4 Discussion

We considered a host-parasitoid system composed of two hosts and one parasitoid, and obtained some sufficient conditions for its permanence. The sufficient condition obtained in Theorem 15 is checked easily whether given parameters satisfy it. The conditions in Theorem 15 roughly imply that under the dominance of the host j, it is sufficient for permanence of System (1) that the dominated host H_i can coexist with the parasitoid P and the dominant host H_j suffers relatively more parasitism than the dominated host H_i does.

Yakubu [12] investigated host dominance in multihost systems with parasitoid. The result in Yakubu [12] gives the following theorem for (1):

Theorem 16 *Let $\{(H_1(t), H_2(t), P(t))\}_{t\in\mathbf{Z}_+}$ be a solution of System* (1). *If there exists a positive constant c satisfying*

$$\left\{\lambda_j \exp[-\sum_{k=1}^{2} \mu_{jk} H_k] \exp[-a_j P]\right\}^c < \lambda_i \exp[-\sum_{k=1}^{2} \mu_{ik} H_k] \exp[-a_i P]$$

for each $(H_1, H_2, P) \in \mathbf{R}^3_+$, *then* $\lim_{t\to\infty} H_j(t) = 0$ *for all* $(H_1(0), H_2(0), P(0)) \in \mathrm{int}\mathbf{R}^3_+$.

By the theorem with $c = \ln \lambda_i / \ln \lambda_j$, we have

Corollary 17 *Let $\{(H_1(t), H_2(t), P(t))\}_{t\in\mathbf{Z}_+}$ be a solution of System* (1). *If the following conditions hold:*

$$\frac{\ln \lambda_i}{\mu_{ii}} > \frac{\ln \lambda_j}{\mu_{ji}}, \quad \frac{\ln \lambda_i}{\mu_{ij}} > \frac{\ln \lambda_j}{\mu_{jj}} \quad \text{and} \quad \frac{\ln \lambda_i}{a_i} > \frac{\ln \lambda_j}{a_j},$$

then $\lim_{t\to\infty} H_j(t) = 0$ *for all* $(H_1(0), H_2(0), P(0)) \in \mathrm{int}\mathbf{R}^3_+$.

The conditions in the corollary and in Theorem 15 are certainly disjoint.

Comins and Hassell [2] investigated an effect of a parasitoid on a possibility that two hosts competing with each other can coexist. They showed that two hosts which cannot coexist by themselves can coexist with a help of a parasitoid in a sense of local stability of an equilibrium point. Theorem 15 shows that this conclusion obtained by Comins and Hassell [2] is also true in a sense of permanence. However, by comparing the conditions for dominance (Definition 5) and the condition (b) in Theorem 15, we see that the later is a special case of the former. That is, Theorem 15 does not ensure for all two-host systems with a dominant host to make permanent by the introduction of a parasitoid. It is a future problem to show it. Moreover, it is also a future problem to consider permanence of 2-host 1-parasitoid systems without the assumption about the dominance of the host.

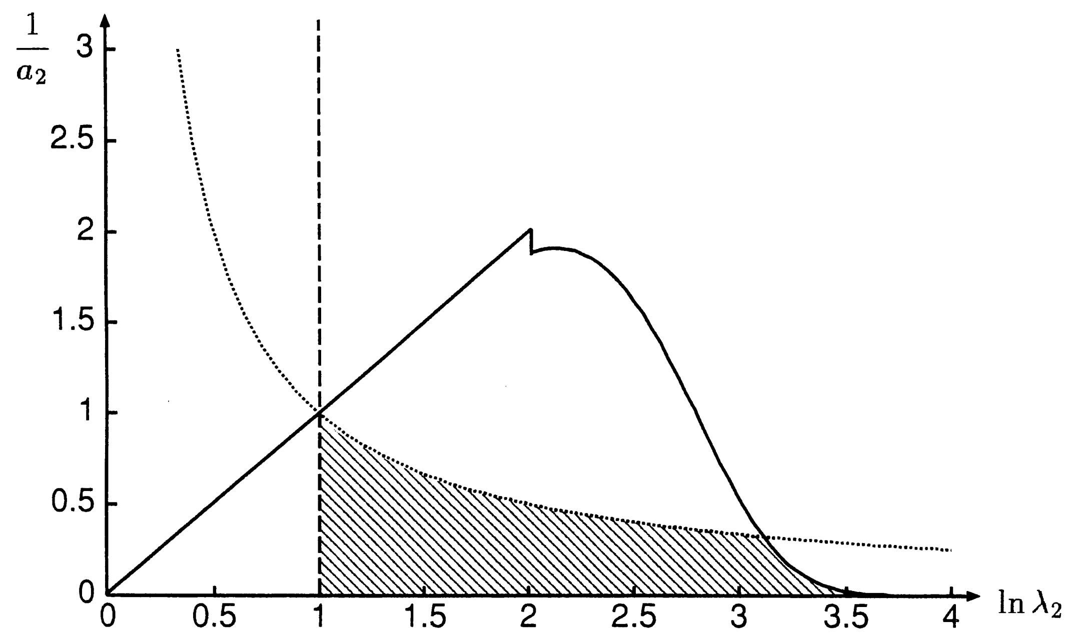

Figure 1: The parameter space $\ln \lambda_2 - 1/a_2$. The parameters are set as follows: $\ln \lambda_1 = 1$, $a_1 = 1$, $b_1 = 0.5$, $b_2 = 1$, $\mu_{11} = 1$, $\mu_{12} = 1/\ln \lambda_2$, $\mu_{21} = 1$, $\mu_{22} = 1$. In this case, the sufficient conditions in Theorem 15 become $1 > \ln \lambda_2 / a_2$ (dotted line), $1 < \ln \lambda_2$ (broken line), $\ln \lambda_2 / \mu_{12} = 1$, $a_2 \ln \lambda_2 > 1$ (if $0 < \ln \lambda_2 \leq 2$) and $a_2 \exp[\xi_2 \ln \lambda_2 + \zeta_2] > 1$ (if $2 < \ln \lambda_2$) (solid line). The hatched area satisfies these conditions.

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