Predator-Prey Dynamics with Delay when Prey Dispersing in n-Patch Environment

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Abstract

A model with time delay is considered for a predator-prey system. Here, a single species disperses between n patches of a heterogeneous environment with barriers between patches while a predator does not involve a barrier between patches. It is shown that the system is permanent under some appropriate conditions, and sufficient conditions are established for the global asymptotic stability of the positive equilibrium of the system.

Keywords: Permanence; globally asymptotically stable; predator-prey dynamics; equilibrium; positive solution.

1 Introduction

Much interest has been growing in the study of mathematical models of biological populations dispersing among patches in a heterogeneous environment, which has been the subject of several recent papers (see e.g. [1]–[7], [9, 10, 16, 17, 19, 20] and references cited therein). Particularly, the single population dispersing among patches has been studied in [1], [3]–[9], and the predator-prey interactions in a patchy environment have been dealt with in [2], [5]–[7], [10, 17, 18]. Some of them, [1, 4, 5, 17, 21, 22] deal with the question of global stability of the equilibrium solution.

This paper is concerned with a model of a single species that disperses among the n patches of a heterogeneous environment with barriers between patches, and with a predator against the species for which the dispersal between patches does not involve a barrier, and due to gestation the time delay is considered. Such models are often found in nature and we can find their examples in [11, 12].

The work in this paper can be regarded as a continuation of the work in [4, 5, 24]. In particular the model we choose to study here is based upon those developed in [5, 24]. Freedman and Takeuchi [5] considered the system of $n+1$ autonomous ordinary differential equations as a model of the predator-prey system living in a patchy environment and the question of global stability for the single-species (prey) subsystem. They deal with the extinction and persistence of the predator. Wa and Ma [24] considered the asymptotic behavior of solutions of a predator-prey system incorporating time delay, in which the prey disperses between just two patches of a heterogeneous environment. Then how about the result for the model which deals with a single species that disperses between n patches?

In this study, we analyze such a system with n patches, each is permitted to have a different level of difficulty in its "escaper" barrier. Furthermore, once the population has left its present patch it may not successfully reach a new one of the environment (predation, harvesting, or for other reasons). In the analysis, we regard the probabilities of a successful transition between patches as a given condition, and show that the equilibrium is permanent under some appropriate conditions, and that the delay does not affect the permanence of the populations. Moreover, sufficient conditions are established for the global asymptotic stability of the positive equilibrium of the system.

The paper is organized as follows. In the next section, our model is described in detail. Section 3 deals with the question of the existence of positive equilibrium. In Section 4, we obtain sufficient conditions, under which the populations are permanent, and other sufficient conditions are established to ensure the absolute global asymptotic stability of the positive equilibrium of the system. A special case is considered in Section 5. Lastly, Section 6 gives a discussion of our results.

2 Modelling equations

We consider the following predator-prey system with diffusion and time delay in an n-patch environment:

$$\begin{cases} \dot{x}_i = x_i f_i(x_i, y) - \varepsilon_i h_i(x_i) + \displaystyle\sum_{j=1,\ j\neq i}^{n} p_{ji}\varepsilon_j h_j(x_j), \quad i = 1, 2, \dots, n \\ \dot{y} = y\left(-s(y) + \displaystyle\sum_{i=1}^{n} c_i P_i(x_i(t-\tau))\right), \end{cases} \tag{2.1}$$

with $x(\theta) = \phi(\theta) \geq 0$, $\theta \in [-\tau, 0]$, $y(0) \geq 0$. Here the dot denotes the differentiation with respect to time, $x_i(t)$ $(i = 1, \dots, n)$ represents the prey population in the ith patch at a given time $t \geq -\tau$, while $y(t)$ stands for the total predator population for n patches. The barriers of patches are assumed to be effective only as far as the prey population is concerned; thus the predator population has no barriers between patches. The function $f_i(x, y)$ is the specific growth rate of the prey relating to the predator biomass y, the function $h_i(x_i)$ is the desire to disperse out of the ith patch, p_{ji} is the probability of successful transition from jth patch to ith patch, where i is different from j, and $P_i(x_i)$ is the predator functional response of the predator population on the prey in the ith patch. $s(y)$ is the density-dependent death rate of the predator in the absence of its food (the prey).

The quantity $\tau \geq 0$ stands for a constant delay due to gestation. Moreover the inverse barrier strength ε_j is nonnegative, whereas the conversion ratio of prey into predator c_i positive. Fig. 2.1 displays the circumstances that the prey population, who leaves the jth patch, reachs other patches at time t. The hatched part in the jth patch is the total of the prey population leaving the patch at time t.

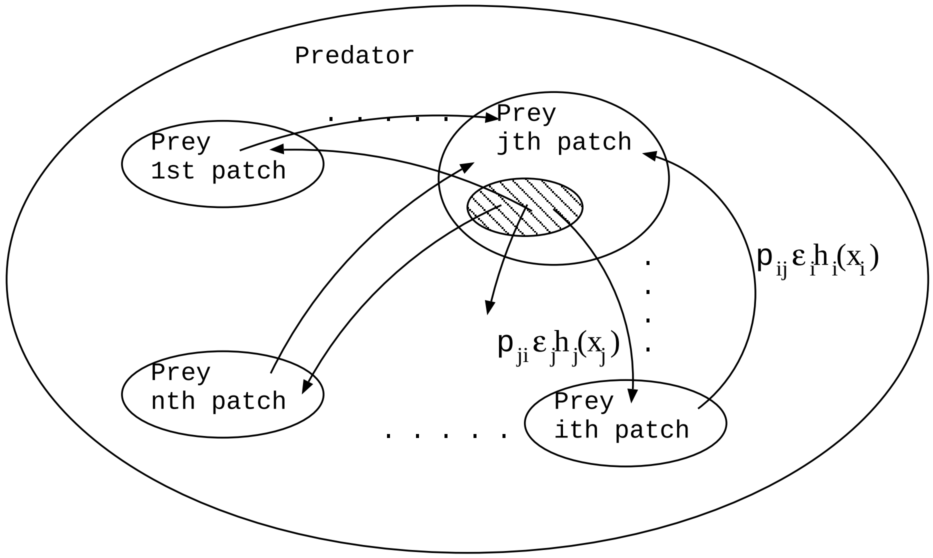

Figure 2.1: The n-patch configuration

Set

$$\mathbb{R}^n_+ = \{x = (x_1, \dots, x_n) : x_i \geq 0, i = 1, \dots, n\};$$

and let

$$C^+ \equiv C([-\tau, 0], \mathbb{R}^{n+1}_+),$$

denote the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into $\mathbb{R}^{n+1}_+$. C^+ is chosen as the initial function space for system (2.1).

The system (2.1) brings the following assumptions, all of which are usual in modelling the target phenomena.

(H1) f_i, P_i and h_i are continuously differentiable for all i ;

(H2) $f_i(0, 0) > 0$; $\partial f_i / \partial x_i < 0$ in *int* $\mathbb{R}^{n+1}_+$; there is a $k_i > 0$ such that $f_i(k_i, 0) = 0$, $i = 1, \dots, n$;

(H3) $\partial f_i / \partial y < 0$ in *int* $\mathbb{R}^{n+1}_+$, $i = 1, \dots, n$;

(H4) $P_i(0) = 0$; $P'_i(x) > 0$ for positive x $(i = 1, \dots, n)$;

(H5) $s(0) = 0$, $s'(y) > 0$ for $y > 0$, $s(y) \to +\infty$ as $y \to +\infty$;

(H6) $h_i(0) = 0$, $\eta \geq h'_i(x_i) \geq h'_i(0) > 0$;

(H7) $0 \le p_{ji} \le 1, \ \sum_{i=1,\ i\neq j}^{n} p_{ji} \le 1.$

Note that in **(H6)** the requirement $h_i'(x) \ge h_i'(0) > 0$ is a technical condition required in the proofs. The quantity η is a bound on the growth rate of $h_i(x_i)$ for all i. Without loss of generality, we assume that $h_i'(0) = 1$.

For notational simplicity, define $p_{ii} = -1$, $i = 1, \ldots, n$ and we rewrite the system (2.1) as

$$\begin{cases} \dot{x}_i &= x_i f_i(x_i, y) + \sum_{j=1}^{n} p_{ji}\varepsilon_j h_j(x_j), \quad i = 1, 2, \ldots, n \\ \dot{y} &= y\left(-s(y) + \sum_{i=1}^{n} c_i P_i(x_i(t-\tau))\right). \end{cases} \tag{2.2}$$

Lastly, assume that

$$\varepsilon_i = \alpha_i \varepsilon, \quad \alpha_i > 0, \quad p_{ji} \neq 0, \quad i, j = 1, \ldots, n,$$

then the system (2.2) becomes

$$\begin{cases} \dot{x}_i &= x_i f_i(x_i, y) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j), \quad i = 1, 2, \ldots, n \\ \dot{y} &= y\left(-s(y) + \sum_{i=1}^{n} c_i P_i(x_i(t-\tau))\right), \end{cases} \tag{2.3}$$

Hereafter we suppose that all the above assumptions are satisfied throughout the paper.

Since $y(t) \equiv 0$ satisfies the second equation of (2.3), when we denote by $(\xi_1, \xi_2, \ldots, \xi_n)$ the solution of the simultaneous equations

$$x_i f_i(x_i, 0) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j) = 0 \quad (i = 1, \ldots, n)$$

with respect to x_i $(i = 1, 2, \ldots, n)$, the constant solution

$$x_i(t) \equiv \xi_i \ (i = 1, 2, \ldots, n), \quad y(t) \equiv 0$$

fulfils (2.3). Therefore, we introduce the quantity

$$d = -s(0) + \sum_{i=1}^{n} c_i P_i(\xi_i). \tag{2.4}$$

As d depends on ε, we often write d as $d(\varepsilon)$, too.

Furthermore, let us introduce

$$\psi(x_1,\dots,x_n)=\begin{cases} s^{-1}\left(\sum_{i=1}^{n} c_iP_i(x_i)\right) & \text{if } \sum_{i=1}^{n} c_iP_i(x_i)>s(0),\\ 0 & \text{otherwise,}\end{cases}$$

where s^{-1} denotes the inverse function of $s(y)$, $y\in[0,+\infty)$, then ψ is readily proved to be nonnegative and continuous on $\mathbb{R}^n_+$ and to satisfy

$$\partial\psi/\partial x_i>0 \quad i=1,\dots,n, \text{ when } \psi(x_1,\dots,x_n)>0.$$

Next we will give the definition of notions which are fundamental in this paper.

Definition 2.1 *([16], P273) We say a population $x(t)$ is permanent if there exist two positive constants m and M, $m<M$, such that, for sufficiently large t, the bound $m\le x(t)\le M$ holds. We say a system of populations is permanent if all of its components are permanent.*

Definition 2.2 *([16], P149) The equilibrium $E(x_1,\dots,x_n,y)$ of system (2.1) (equivalently of (2.3)), if it exists, is said to be globally asymptotically stable (G.A.S.), if, for a fixed τ, all positive solutions of system (2.1) tend to E as $t\to+\infty$.*

We say $E(x_1,\dots,x_n,y)$ is absolutely globally asymptotically stable (A.G.A.S.) if it is globally asymptotically stable for all $\tau>0$.

For the discussion of the following sections, now we concern a general n-dimensional cooperative system

$$\dot{x}=F(x), \tag{2.5}$$

where F belongs to C^1-class on a domain $\mathbb{R}^n_+$ and has Jacobian matrix $DF(x)$ with nonnegative off-diagonal elements, *i.e.*, for all $i\ne j$, $i,j=1,\dots,n$, $\partial F_i/\partial x_j\ge 0$, for all $x\in\mathbb{R}^n_+$. Denote the solution of (2.5) as $x(t)$ whose initial value is $x(0)$. The reference [13, 19, 20] gives the following.

Lemma 2.1 ***(i)*** *Suppose that $x(t)$ is the positive solution of (2.5), then $x(t)$ is strictly increasing (decreasing) and converges to an equilibrium of (2.5) provided that $F(x(0))>0$ ($F(x(0))<0$) and it is bounded.*

(ii) *Suppose that $x(t)$ is the positive solution of (2.5) existing on $[0,+\infty)$. Then if $\dot{m}(t)\le F(m(t))$, $t\ge 0$, and $m(0)\le x(0)$, we have $m(t)\le x(t)$ for $t\ge 0$. Furthermore, if $\dot{m}(t)\ge F(m(t))$, $t\ge 0$ and $m(0)\ge x(0)$, we have $m(t)\ge x(t)$, $t\ge 0$.*

3 Positive Equilibria

The origin $E_0(0,\dots,0)$ is clearly an equilibrium of (2.3). When $\varepsilon = 0$, there may be an equilibrium in the positive subspace, *i.e.,* of the form $\hat{E}(\xi_1,\dots,\xi_n,0)$, where $\xi_i > 0, i = 1,\dots,n$. Let P denote the $n\times n$ matrix (p_{ji}). By [4], we know that $\hat{E}$ also exists for sufficiently small ε, and they show that if $\det P = 0$, $\hat{E}$ exists for all $\varepsilon > 0$. Hereafter, we deal with the positive equilibrium of the system (2.1).

We fix y as a nonnegative λ and consider the subcommunity equations consisting of n preys:

$$\dot{x}_i = x_i f_i(x_i,\lambda) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j) \quad (i = 1,\dots,n). \tag{3.1}$$

Let $(x_1^*(\lambda),\dots,x_n^*(\lambda))$ be the positive equilibrium of (3.1).

We will study the global stability of the positive equilibrium, when it exists, of system (3.1) and denote this equilibrium by $E_{(\lambda)}(x_1^*(\lambda),\dots,x_n^*(\lambda))$ throughout this section. We assume that $E_{(\lambda)}$ is unique if it exists.

Lemma 3.1 *Suppose that λ satisfies $f_i(0,\lambda) > 0$ $(i = 1,\dots,n)$, and the two conditions*

(i) $0 \le \varepsilon \le \min(f_i(0,\lambda)/\alpha_i)$ $(i = 1,\dots,n)$,

(ii) $\lim_{x_i\to\infty} f_i(x_i,y) = -\infty$

hold. Then the system (3.1) has a G.A.S. positive equilibrium $E_{(\lambda)}$.

One can adopt the technique of Theorems 3.1 and 4.1 in [5] to prove this lemma, since the system (3.1) is similar to that given by Eq. (3.4) of [5].

Lemma 3.2 *Suppose the assumptions of Lemma 3.1 are satisfied, then every component of the equilibrium $E_{(\lambda)}$ of system (3.1) is continuous and strictly decreasing with respect to λ defined on the set $D = \{\lambda \ge 0 : f_i(0,\lambda) > 0\ (i = 1,\dots,n)\}$.*

Proof. Let λ_1 and λ_2 be in D and ordered as $\lambda_1 < \lambda_2$. Suppose that $(u_1(t),\dots,u_n(t))$ is the solution of the system (3.1) initiating at $(x_1^*(\lambda_2),\dots,x_n^*(\lambda_2))$.

Now we rewrite the subcommunity equations (3.1) as

$$\dot{x}_i = F_i(x_1,\dots,x_n;\lambda), \quad i = 1,\dots,n. \tag{3.2}$$

The assumption **(H3)** implies the inequality

$$F_i(u_1(0),\dots,u_n(0);\lambda_1) > F_i(x_1^*(\lambda_2),\dots,x_n^*(\lambda_2);\lambda_2) = 0 \quad (i = 1,\dots,n),$$

which asserts that $(u_1(t),\dots,u_n(t))$ is strictly increasing and converges to $(x_1^*(\lambda_1),\dots,x_n^*(\lambda_1))$ by applying Lemma 2.1. Consequently the order $x_i^*(\lambda_1) > x_i^*(\lambda_2)$ holds for all $i = 1,\dots,n$. Therefore $(x_1^*(\lambda),\dots,x_n^*(\lambda))$ is strictly decreasing.

Next we will show the continuity. Let

$$\boldsymbol{x}^*(\lambda) = E_{(\lambda)}(x_1^*(\lambda), \dots, x_n^*(\lambda))$$

be a positive equilibrium of the system (3.1). For a function defined by

$$\varphi_i(a, x^*) = a x_i^* f_i(a x_i^*, \lambda) - \varepsilon \alpha_i h_i(a x_i^*) + \varepsilon \sum_{j=1,\ j\neq i}^{n} p_{ji} \alpha_j h_j(a \hat{x}_j),$$

we have

$$\frac{\partial \varphi_i}{\partial a}(0, x^*) = x_i^* f_i(0, \lambda) - x_i^* \varepsilon \alpha_i + \varepsilon \sum_{j=1,\ j\neq i} p_{ji} \alpha_j x_j^*.$$

Since $0 \le \varepsilon \le \min_{1\le i\le n} (f_i(0, \lambda)/\alpha_i)$, we obtain

$$\frac{\partial \varphi_i}{\partial a}(0, x^*) > 0 \quad \text{for} \quad i = 1, \dots, n.$$

Hence, there exists a positive a_0 which gives $\varphi(a, \hat{x}(\lambda)) > 0$ for $0 < a < a_0,\ i = 1, \dots, n$.

Since $\partial f_i/\partial x_i < 0$ and h_i' is bounded, the equation $\lim_{x_i\to\infty} f_i(x_i, y) = -\infty$ yields that there exists a positive b_0 which derives

$$\varphi_i(b, x^*) < 0 \quad \text{for} \quad b > b_0 \quad (i = 1, \dots, n).$$

Henceforth we obtain

$$F_i(a_0 x_1^*(\lambda), \dots, a_0 x_n^*(\lambda), \lambda) > 0, \qquad F_i(b_0 x_1^*(\lambda), \dots, b_0 x_n^*(\lambda), \lambda) < 0$$

and

$$a_0 x_i^*(\lambda) < x_i^*(\lambda_2) < x_i^*(\lambda_1) < b_0 x_i^*(\lambda)$$

for $i = 1, \dots, n$ and $\lambda_1 \le \lambda \le \lambda_2$. Let $\hat{a}_i = a_0 x_i^*(\lambda)$ and $\hat{b}_i = b_0 x_i^*(\lambda)$ $(i = 1, \dots, n)$, and introduce a point-set E of $\mathbb{R}_+^n$ as

$$E = \{(x_1, \dots, x_n) : \hat{a}_i < x_i < \hat{b}_i, i = 1, \dots, n, \}.$$

Then it is easily verified that E is a positive invariant of the system (3.1).

Let $\boldsymbol{x}(t; x_0, \lambda)$ be the positive solution of (3.1) initiating at $\boldsymbol{x}_0$. Since (3.1) is autonomous, it is easily shown that $(x_1^*(\lambda^*), \dots, x_n^*(\lambda^*))$ is uniform attractor of the positive solutions of (3.1), where $\lambda = \lambda^*$. Consequently, for any $\beta > 0$, there is a $T > 0$ such that any solution $\boldsymbol{x}(t; x_0, \lambda^*)$ of (3.1) starting with $\boldsymbol{x}_0 \in E$ lies in the β-neighbourhood of $(x_1^*(\lambda^*), \dots, x_n^*(\lambda^*))$ for $t > T$.

Furthermore, one can choose a positive δ such that $\boldsymbol{x}(T, x_0, \lambda)$ lies in the (2β)-neighbourhood of $(x_1^*(\lambda^*), \dots, x_n^*(\lambda^*))$ when $|\lambda - \lambda^*| < \delta$, for the solutions depend on the parameter λ continouously. As a result, $(x_1^*(\lambda), \dots, x_n^*(\lambda))$ lies in (2β)-neighbourhood for $|\lambda - \lambda^*| < \delta$. This proves that the $x_i^*(\lambda)$ $(i = 1, \dots, n)$ are continuous with respect to λ. ∎

Lemma 3.3 *Suppose the assumption (ii) of Lemma 3.1 are satisfied and the following conditions hold.*

(1) $-s(0)+\sum_{i=1}^{n} c_i P_i(x_i^*(0))>0$;

(2) there exists a positive λ^* *satisfying*

$$\min_{1\le i\le n} f_i(0,\lambda^*)>0 \quad \textit{and} \quad \lim_{\lambda\to\lambda^*-0}\{-s(\lambda)+\sum_{i=1}^{n} c_i P_i(x_i(\lambda^*))\}<0.$$

Then there exists a unique positive equilibrium $(e_1,\dots,e_{n+1})$ *of system (2.3) with* $0\le\varepsilon\le\min_{1\le i\le n}(f_i(0,\lambda^*)/\alpha_i)$ *in the region* $0<y\le\lambda^*$.

Proof. As is described at the beginning of this section, the positive equilibrium of the system (2.1) can be determined by the following system of equations:

$$H_i(x_1,\dots,x_n,y)=0 \quad (i=1,\dots,n), \quad \text{and} \quad y=\psi(x_1,\dots,x_n), \tag{3.3}$$

where $H_i(x_1,\dots,x_n,y)=x_i f_i(x_i,\lambda)+\varepsilon\sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j)$. Since $f_i(0,y)>0$ for $0<y\le\lambda^*$ $(i=1,\dots,n)$, Eq. (3.3) has a unique solution $(x_1^*(y),\dots, x_n^*(y))$ when $0<y\le\lambda^*$ and $0\le\varepsilon\le\min_{1\le i\le n}(f_i(0,\lambda^*)/\alpha_i)$. Due to Lemma 3.2 $x_i^*(y)$ is strictly decreasing with respect to y for every i. Therefore the function $G(y)=y-\psi(x_1^*(y),\dots,x_n^*(y))$ is strictly increasing. The inequalities $G(0)<0$ and $\lim_{\lambda\to\lambda^*-0}G(\lambda)>0$ imply the unique existence of the positive solution for $G(y)=0$ not exceeding λ^*. ∎

4 Criteria for Stability

The main purpose of this section is to show under which conditions the system is permanent and the positive equilibrium of system (2.1) is globally asymptotically stable.

Theorem 4.1 *Let the equilibrium* $\tilde{E}$ *of the system (2.3) exists uniquely, and* $E_{(0)}(x_1^*(0),\dots,x_n^*(0))$ *is G.A.S. in the x-space. Then the negativeness of* $d=d(\varepsilon)$ *defined by (2.4) implies the limits* $\lim_{t\to+\infty}x_i(t)=x_i^*(0)$ $(i=1,\dots,n)$ *and* $\lim_{t\to+\infty}y(t)=0$.

Proof. Consider the system

$$\dot{x}_i\le x_i f_i(x_i,0)+\varepsilon\sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j), \quad i=1,\dots,n, \tag{4.1}$$

and compare this with

$$\dot{v}_i=v_i f_i(v_i,0)+\varepsilon\sum_{j=1}^{n} p_{ji}\alpha_j h_j(v_j), \quad i=1,\dots,n. \tag{4.2}$$

Since the solutions of system (4.2) tend to $E_{(0)}$ as $t \to \infty$ by the hypothesis, there exists a positive T giving the inequality

$$x_i(t) \le x_i^*(0) + \delta \quad \text{for} \quad t \ge T.$$

Choose $\delta > 0$ so small that the inequality $-s(0) + \sum_{i=1}^{n} c_i P_i(x_i^*(0) + \delta) < 0$ holds. Then we have $\dot{y} < y[-s(0) + \sum_{i=1}^{n} c_i P_i(x_i(t-\tau))] < 0$ for $t \ge T + \tau$. This completes the proof. ∎

Theorem 4.2 *Suppose $d(\varepsilon) > 0$. Then the system (2.1) exhibits permanence.*

Proof. At first, we show the positive solutions of system (2.1) are eventually bounded. Since the solutions are positive and we assume **(H3)**, we have

$$\begin{aligned}\dot{x}_i &= x_i f_i(x_i, y) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j) \\ &< x_i f_i(x_i, 0) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j). \quad i = 1, \dots, n.\end{aligned}$$

Comparing this system with

$$\dot{x}_i = x_i f_i(x_i, 0) + \varepsilon \sum_{j=1}^{n} p_{ji}\alpha_j h_j(x_j), \quad i = 1, \dots, n,$$

we can find $(b_1, \dots, b_n)$ with positive b_i $(i = 1, \dots, n)$ which gives upper bound of any positive solution $(x_1(t), \dots, x_n(t), y(t))$ of system (2.1) as $x_i(t) < b_i$ $(i = 1, \dots, n)$ for sufficiently large t. This can be seen though the proof of Lemma 3.2 by letting, for example, $b_i = b_0 x_i^*(0)$.

Henceforth the first n components of positive solutions of system (2.1) are eventually bounded, and thus, the sum of $c_i P_i(x_i(t-\tau))$, $(i = 1, \dots, n)$, is eventually bounded as well. By **(H5)**, there exists $k > 0$ such that $y(t) < k$ for all sufficiently large t. Therefore the positive solutions of system (2.1) are eventually bounded.

Secondly, we show uniformly persistence of the system. Let

$$\begin{aligned} C_1 &= \{\zeta = (0, \dots, 0, \zeta_{n+1}) \in C^+\}; \\ C_2 &= \{\zeta = (\zeta_1, \dots, \zeta_n, 0) \in C^+\}. \end{aligned}$$

And let $C^* = C_1 \cup C_2$, by Theorem 4.1 in [8], and adopting the technique of Theorem 1 in [24], we can know C^* is a uniform repeller. Therefore, there exists a δ_1 such that for any positive solution $(u_1(t), \dots, u_n(t), v(t))$ of system (2.1), $v(t) > \delta_1$ for all sufficiently large t and $\{u_1(t), \dots, u_n(t), v(t)\}$ lies outside of the region

$$\{(x_1, \dots, x_n, y) \in \mathbb{R}_{n+1}^+ : 0 \le x_i \le \delta_1, i = 1, \dots, n\},$$

when t is sufficiently large.

Without loss of generality, we can assume that there exists an integer m_1 $(1 \le m_1 < n)$ satisfying

$$\begin{array}{l} 0 \le x_i \le \delta_i, \quad i = 1, \dots, m_1 \\ \delta_j \le x_j \le b_j, \quad j = m_1 + 1, \dots, n, \\ 0 < y < k, \end{array}$$

with positive δ_i $(i = 1, \dots, n)$.

Then we have

$$\begin{aligned} \dot{x}_i &= x_i f_i(x_i, y) - \varepsilon \alpha_i h_i(x_i) + \varepsilon \sum_{j \ne i} p_{ji} \alpha_j h_j(x_j) \\ &\ge x_i f_i(x_i, y) - \varepsilon \alpha_i h_i(x_i) + \varepsilon \sum_{j=m_1+1}^{n} p_{ji} \alpha_j h_j(\delta_j), \end{aligned}$$

for $i = 1, \dots, m_1$.

Since there exist δ_i^* and $\bar{\delta}_i$ satisfying both conditions

$$h_i(x_i) < \frac{1}{2\alpha_i} \sum_{j=m_1+1}^{n} p_{ji} \alpha_j h_j(\delta_j) \quad \text{for} \quad 0 \le x_i \le \delta_i^*, i = 1, \dots, m_1,$$

and

$$f_i(x_i, y) > 0 \quad \text{for} \quad 0 < y \le \bar{\delta}_i, \quad 0 \le x_i \le \bar{\delta}_i, \; i = 1, \dots, m_1,$$

by putting

$$\tilde{\delta}_i = \min(\bar{\delta}_i, \delta_i^*),$$

we obtain

$$\dot{x}_i > \frac{\varepsilon}{2} \sum_{j=m_1+1}^{n} p_{ji} \alpha_j h_j(\varepsilon_j), \quad \text{if} \quad 0 \le x_i \le \tilde{\delta}_i.$$

Therefore the positive solution $(u_1(t), \dots, u_n(t), v(t))$ can not enter into the region

$$\begin{array}{ll} \{x \in \mathbb{R}^+_{n+1}, & 0 \le x_i \le \delta_i, (i = 1, \dots, m_1), \\ & \delta_j \le x_j \le b_j, (j = m_1 + 1, \dots, n), \\ & 0 < y \le k\}, \end{array}$$

when t is sufficiently large, for any m_1 $(1 \le m_1 < n)$.

The above discussion leads to the

$$u_i(t) > \delta_i, \quad \text{for all large } t \quad \text{and} \quad i = 1, \dots, n,$$

which completes the proof. ∎

Theorem 4.3 *Provided that we have the following conditions*

(a) $d(\varepsilon) > 0$,

(b) $f_i(0, h) > 0$, *for* $i = 1, \dots, n$, $0 \le \varepsilon \le \min_{1 \le i \le n} (f_i(0, h)/\alpha_i)$, *where* $h = \psi(x_1^*(0), \dots, x_n^*(0))$,

(c) $\lim_{x_i \to +\infty} f_i(x_i, y) = -\infty$,

then the system (2.1) has a unique positive equilibrium $(e_1, \dots, e_{n+1})$.

The proof can be obtained by the technique of Theorem 2 in [24].

And Theorem 3 and Corollary 4 in [24] readily yield the following two results of this section.

Theorem 4.4 *Under the assumptions of Theorem 4.3, the positive equilibrium* $(e_1, \dots, e_{n+1})$ *is absolutely globally asymptotically stable, provided that*

$$\sigma(\sigma(y)) < y \quad \text{for} \quad e_{n+1} < y < h, \tag{4.3}$$

where $\sigma(y) = \psi(x_1^*(y), \dots, x_n^*(y))$.

Corollary 4.1 *Suppose the assumptions of Theorem 4.4 are satisfied except that the condition on* σ *is replaced with*

$$-1 < \sigma'(x) \le 0 \quad \text{for all } x \in (0, h].$$

Then the statement of Theorem 4.4 remains valid.

5 The special case of linear $h_i(x_i)$

In this section, we deal with the special case that the $h_i(x_i)$ are linear. Then the system (2.1) can be converted to

$$\begin{aligned} \dot{x}_i &= x_i f_i(x_i, y) + \varepsilon \sum_{j=1}^{n} p_{ji} \beta_j x_j, \\ \dot{y} &= y \left(-s(y) + \sum_{i=1}^{n} c_i P_i(x_i(t - \tau)) \right). \end{aligned} \tag{5.1}$$

We show that the theorems of the previous section are valid without the requirement of the assumption for ε and the assumption (ii) in Lemma 3.1.

When $y(t) = \lambda$, the function φ_i in the proof of Lemma 3.2 can be simplified as

$$\varphi_i(a, \hat{x}) = a\hat{x}_i f_i(a\hat{x}_i, \lambda) + a\varepsilon \sum_{j=1} p_{ji} \beta_j \hat{x}_j = a\hat{x}_i (f_i(a\hat{x}_i, \lambda) - f_i(\hat{x}_i, \lambda)).$$

Since $\partial f_i/\partial x_i$ is negative, and $f_i(x_i, \lambda)$ is a decreasing function of x_i, we can get

$$\varphi_i(a, \hat{x}) < 0 \quad \text{for} \quad 0 < a < 1.$$

On the other hand, we have

$$\varphi_i(a, \hat{x}) > 0 \quad \text{for} \quad a > 1.$$

Therefore we can assert

$$F_i(a\hat{x}_1, \ldots, a\hat{x}_n, \lambda) < 0 \;\text{ for }\; 0 < a < 1 \quad \text{and} \quad F_i(a\hat{x}_1, \ldots, a\hat{x}_n, \lambda) > 0 \;\text{ for }\; a > 1,$$

where F_i is defined by (3.2).

Due to Theorem 4.4 in [4], the equality $\det P = 0$ implies that the system (3.1) has an equilibrium, which is shown to be A.G.A.S. by Theorem 6.1 in [5]. Therefore, applying similar techniques in the proofs of the theorems of the present paper, we can obtain the following.

Theorem 5.1 *If* $\det P = 0$*,* $d(\varepsilon) > 0$ *and the condition (4.3) hold, then the system (2.1) with linear* $h_i(x_i)$ $(i = 1, \ldots, n)$ *has a unique A.G.A.S. equilibrium for all* $\varepsilon \geq 0$*.*

Remark 5.1 In the case of linear $h_i(x_i)$, the assumption of the uniqueness of $E_{(\lambda)}$ in Section 3 can be relaxed, for Theorem 6.2 of [5] guarantees the uniquness as an automatic consequence of the linearity.

Remark 5.2 Consider the case that when any member of the prey leaves a given patch, it successfully reach a new patch in the environment. As described in [11], the case is observed in the mite dispersal on strawberry patches. Then the condition $\det P = 0$ is always satisfied, since $\sum_{i=1, i\neq j}^{n} p_{ji} = 1$. Hence the assumptions of Theorem 5.1 can be simplified.

6 Concluding remarks

We have analyzed a predator-prey system with time delay and dispersal among n patches in a heterogeneous environment. The barriers are considered only for the prey, but not for the predator, between patches. Furthermore, we have assumed that there is a positive probability that any member of the prey, who leaves a given patch, may not reach safely any other patch in the environment. Criteria for permanence and extinction are presented. Conditions, under which the positive steady state is absolutely globally asymptotically stable, are obtained by the continuity and monotonicity of the subsystem of the preys. Furthermore we have obtained criteria for the equilibrium to be absolutely globally asymptotically stable in the case that the dispersal is linear.

Theorem 4.2 may be regarded as an extension of similar results in [5] and [24]. In the former they show the persistence of the system without delay term, which means that each component $N(t)$ of the system satisfies $\liminf_{t\to\infty} N(t) > 0$, when $N(0) > 0$. The latter considered a model in a two-patch environment and with time delays. Since we deal with the delay in the system, the system (2.1) is obviously more general than either in [24] or in [5].

Mathematically, we can further assume that there are barriers against predator dispersal among patches. We leave this to future studies.

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