

PERMANENCE IN LOGISTIC AND LOTKA-VOLTERRA SYSTEMS WITH DISPERSAL AND TIME DELAYS

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ABSTRACT. In this paper, we consider the effect of dispersal on the permanence of single and interacting populations modelled by systems of integro differential equations. Different from former studies, our discussion here includes the important situation when species live in a weak patchy environment; i.e., species in some isolated patches will become extinct without the contribution from other patches. For the single population model considered in this paper, we show that the same species can persist for some dispersal rates and the species will vanish in some isolated patches. Based on the results for a single population model, we derive sufficient conditions for the permanence of two interacting competitive and predator-prey dispersing systems.

1. INTRODUCTION

As discussed by several authors, for many species spatial factors are important in population dynamics. Such theoretical studies of spatial distributions can be traced back at least as far as Skellam [18], and has been extensively considered in many papers; see for example in [1, 2, 8, 9, 10, 11, 12, 14, 15, 16, 17, 24, 21, 22, 23] and references cited therein. Most of the previous papers focused on the coexistence of populations modelled by systems of ordinary differential equations and the stability (local and global) of equilibria. Many existing models deal with a single population dispersing among patches. Some of them deal with competition and predator-prey interactions in patchy environments.

Recently persistence and stability of population dynamical systems involving time delays have been discussed by some authors; see for example [3, 4, 5, 20, 28] and references cited therein. All of these studies assume that the intrinsic growth rates are all positive (this means that populations live in a suitable environment). They obtained some sufficient conditions that guarantee permanence of population or stability of positive equilibria or positive periodic solutions.

However, the actual living environments of some endangered and rare species are not always like this. Because of the ecological effects of the human activities and industry, e.g. the location of manufacturing industries, pollution of the atmosphere,

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rivers, soil, etc., more and more habitats were broken into patches and some of the patches were polluted. In some of these patches the species will go extinct without the contribution from other patches, and hence the species lived in a weak patchy environment. The living environments of some endangered and rare species such as giant panda [27] and alligator sinensis [29] are some convincing examples.

In order to protect endangered and rare species, we should consider theoretically the effect of dispersal on the permanence of single and multiple species living in weak environments. The present paper consider the following interesting problem: How does dispersal lead to the permanence of endangered single and multiple species which could not persist within isolated patches?

The organization of this paper is as follows. In the next section, we introduce notation, give some definitions and state a lemma which will be essential for our proofs. In section 3, a dispersing single species model is given to consider its permanence. We obtain that the dispersal system can be made permanent under different appropriate dispersal conditions, even if the endangered species become extinct in some isolated patches without the contribution from other patches (Theorems 3.2, 3.3). In section 4, by using the main results in section 3, we consider the effect of dispersal on the survival of competitive species. In section 5, we consider the effect of dispersal on the permanence of prey-predator system. We can choose appropriate dispersal rates making the dispersing system permanent even if the prey species has negative intrinsic growth rates in some patches. Finally, the main results obtained in this paper are biologically discussed in section 6.

2. PRELIMINARIES

In this section we introduce some notations and state a lemma which will be useful in the subsequent sections. Let $f(t)$ be a continuous ω -periodic function defined on $\mathbb{R} = (-\infty, +\infty)$, and set

$$A_\omega(f) = \omega^{-1} \int_0^\omega f(t) dt.$$

Let \mathbb{R}_+ be the cone of nonnegative vectors in \mathbb{R}^n . If $x, y \in \mathbb{R}^n$, we write $x \leq y$ if $x_i \leq y_i$ for $i = 1, 2, \dots, n$; similarly $x < y$ if $x_i < y_i$, for $i = 1, 2, \dots, n$. Let $C = C([-\tau, 0], \mathbb{R}^n)$ be the Banach space of continuous functions mapping the interval $[-\tau, 0]$ into \mathbb{R}^n with supremum norm. If $\varphi, \psi \in C$, we write $\varphi \leq \psi$ ($\varphi < \psi$) in case the indicated inequality holds at each point of $[-\tau, 0]$. Denote $C^+ = \{\varphi \in C : \varphi \geq 0, \varphi(0) > 0\}$.

Consider the functional differential equation

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

where $f : C \mapsto \mathbb{R}^n$ and x_t denote the element of C given by $x_t(\theta) = x(t + \theta)$, $-\tau \leq \theta \leq 0$. We assume that $f(t, \varphi)$ is continuously differentiable in φ , $f(t + \omega, \varphi) = f(t, \varphi)$ for all $(t, \varphi) \in \mathbb{R} \times C^+$ and $\omega > 0$. Then by [13], there exists a unique solution of (2.1) through (t_0, φ) for $t_0 \in \mathbb{R}, \varphi \in C^+$. We write $x(t, t_0, \varphi)$ ($x_t(t_0, \varphi)$) for the solution of the initial value problem. By [13], $x(t, t_0, \varphi)$ is continuously differential in φ . In the following the notation $x_{t_0} = \varphi$ will be used as the condition of the initial value of (2.1), by which we mean that we consider the solution $x(t)$ of (2.1) which satisfies $x(t_0 + \theta) = \varphi(\theta)$, $\theta \in [-\tau, 0]$. Consider the hypothesis

(H2.1) If $\varphi, \psi \in C^+$, $\varphi \leq \psi$ and $\varphi_i(0) = \psi_i(0)$ for some i , then $f_i(t, \varphi) \leq f_i(t, \psi)$.

Under the assumption (H2.1), system (2.1) exhibits the following property.

Lemma 2.1 ([19, 25]). *Under assumption (H2.1), we have*

(i) *If $\varphi, \psi \in C^+$ with $\varphi \leq \psi$, then*

$$x(t, t_0, \varphi) \leq x(t, t_0, \psi)$$

for all $t \geq t_0$ for which both are defined.

(ii) *Assume that $y(t)$ is continuously differentiable. If $\dot{y}(t) \leq f(t, y_t)$ and $y_{t_0} \leq \varphi$, we have*

$$y(t) \leq x(t, t_0, \varphi)$$

for all $t \geq t_0$ for which both are defined. If $\dot{y}(t) \geq f(t, y_t)$ and $y_{t_0} \geq \varphi$, we have

$$y(t) \geq x(t, t_0, \varphi)$$

for all $t \geq t_0$ for which both are defined.

Definition. System (2.1) is said to be permanent if there exists a compact set K in the interior of \mathbb{R}_+ , such that all solutions with $x_{t_0} \in C^+$ ultimately enter K .

3. DISPERSING LOGISTIC SYSTEM WITH TIME DELAY

Many authors have studied the stability of positive periodic solution of the following type population dynamical system with time delay

$$\begin{aligned} \dot{x}(t) &= x(t)[b(t) - a(t)x(t) + c(t) \int_{-\tau}^0 x(t+\theta)d\mu(\theta)] \\ x(\theta) &= \varphi(\theta) \geq 0, \theta \in [-\tau, 0], \varphi(0) > 0, \varphi \in C([-\tau, 0], \mathbb{R}_+), \end{aligned} \quad (3.1)$$

where $\mu(\theta)$ is nondecreasing and

$$\int_{-\tau}^0 d\mu(\theta) = \mu(0^+) - \mu(-\tau) = 1, \quad (3.2)$$

the intrinsic growth rate is $b(t)$, the self-inhibition $a(t)$ and the reproduction rate $c(t)$ are continuously ω -periodic functions, and $a(t) > 0$, $b(t) > 0$, $c(t) \geq 0$ for $t \in \mathbb{R}$.

Generally $c(t)$, which weights the effect of the past history on the present population density $x(t)$, will make a superposition of positive and negative effects and here we consider a population x at time t has benefit from the resources accumulated by the population itself in the past (D'Ancona [7]), hence establishing for $c(t)$ in (3.2) a positive sign.

For some particularly endangered species that live in weak environment, the intrinsic growth rate $b(t)$ may become negative for some time t . We have the following extinction result.

Theorem 3.1. *If $b(t) < 0$ and $a(t) - c(t) > 0$, then species x become extinct eventually.*

Proof. Obviously, solutions of system (3.1) are defined on $[0, +\infty)$ and remain positive for $t > 0$. Let $V(x(t)) = \frac{1}{2}x^2(t)$. If $|x(t)| \geq |x(t+\theta)|$, $\theta \in [-\tau, 0]$, then $\dot{V}(x(t)) \leq 2b(t)V(x(t))$. Hence, if $b(t) < 0$, then $V(x(t))$ is a Liapunov function for (3.1), and $x = 0$ is globally asymptotically stable. This means species x become extinct eventually. This completes the proof. \square

To study the effect of dispersal on the permanence of system (3.1), we introduce the following system as composed of multiple heterogeneous patches connected by discrete dispersal.

$$\begin{aligned} \dot{x}_i(t) = & x_i(t)[b_i(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds] \\ & + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)), \quad i = 1, 2, \dots, n, \end{aligned} \quad (3.3)$$

with the initial condition

$$x_i(\theta) = \varphi_i(\theta) \geq 0, \quad -\tau \leq \theta \leq 0, \quad \varphi_i(0) > 0, \quad i = 1, 2, \dots, n, \quad (3.4)$$

where $x_i(t)$ is the density of species x in patch i ; $K_i(s)$ ($i = 1, 2, \dots, n$) denote nonnegative piecewise continuous functions defined on $[-\tau, 0]$ and normalized such that $\int_{-\tau}^0 K_i(s)ds = 1$. We assume $b_i(t), a_i(t), c_i(t)$ and $D_{ij}(t)$ ($i, j = 1, 2, \dots, n$) are continuous ω -periodic functions defined on \mathbb{R} and

$$a_i(t), c_i(t) > 0, D_{ij}(t) \geq 0 \quad \text{and} \quad D_{ii}(t) \equiv 0 \quad \text{for} \quad t \in \mathbb{R}, i, j = 1, 2, \dots, n, \quad (3.5)$$

where $b_i(t)$ is the intrinsic growth rate, $a_i(t)$ represents the intraspecific relationship, $D_{ij}(t)$ is the dispersal coefficient for the species from patch j to patch i ($i \neq j$).

Theorem 3.2. *Suppose that $a_i(t) > c_i(t)$ holds for $i = 1, 2, \dots, n$, then solutions of (3.3) with initial condition (3.4) are uniformly bounded and uniformly ultimately bounded.*

Proof. Similar to the proof in [28], we know that \mathbb{R}_+^n is positively invariant with respect system (3.3). By $a_i(t) > c_i(t)$, there exist p ($1 < p < \min_t \{ \frac{a_1(t)}{c_1(t)}, \frac{a_2(t)}{c_2(t)} \}$) and $H > 1$ such that

$$b_i(t) - (a_i(t) - pc_i(t))H < -1 \quad \text{for} \quad i = 1, 2, \dots, n. \quad (3.6)$$

Define

$$V(t) = V(x_1(t), \dots, x_n(t)) = \max_{1 \leq i \leq n} \{x_i(t)\} = \|x(t)\|.$$

If $V(t + \theta) = \|x(t + \theta)\| \geq H, V(t + \theta) \leq pV(t), \theta \in [-\tau, 0]$, calculating the upper right derivative of $V(t)$ along solutions of (3.3), we have

$$D^+V(t) \leq V(t) \max_i \{b_i(t) - (a_i(t) - pc_i(t))H\} < -H < -1.$$

It follows from the theorem of Lyapunov-Razumikhin type [7, 13, 19, 25, 26] that positive solutions of (3.3) are uniformly ultimately bounded.

Fix $\tilde{H} > H$. Let $x(t) = (x_1(t), \dots, x_n(t))$ denote the solution of (3.1) through (σ, φ) at $t = \sigma$, where $\varphi = (\varphi_1, \dots, \varphi_n) \in C^+$ and $0 \leq \varphi_i(\theta) \leq \tilde{H}$ on $[-\tau, 0]$ for $i = 1, \dots, n$. we claim that $\|x(t)\| \leq \tilde{H}$ for all $t \geq \sigma$. Otherwise, there exists a $\tilde{t} > \sigma$ such that

$$\|x(t)\| \leq \tilde{H} \quad \text{for} \quad \sigma - \tau \leq t < \tilde{t}, \quad (3.7)$$

$$\|x(\tilde{t})\| = \tilde{H}, \quad (3.8)$$

$$D^+V(\tilde{t}) \geq 0. \quad (3.9)$$

Using (3.7) and (3.8), we have from (3.3)

$$D^+V(\tilde{t}) \geq \tilde{H} \max_{1 \leq i \leq n} \{b_i(\tilde{t}) - (a_i(\tilde{t}) - pc_i(\tilde{t}))\tilde{H}\}.$$

It follows from (3.6) that $D^+V(\tilde{t}) < 0$, which contradicts (3.9) and therefore, the uniform boundedness of the positive solutions of (3.3) with (3.4) follows; i.e., positive solutions of (3.3) are uniformly bounded. This completes the proof. \square

For the next theorem we use the following hypotheses:

(H3.1) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_\omega(\bar{\theta}) > 0$, where $\bar{\theta}(t) = b_{i_0}(t) - \sum_{j=1}^n D_{i_0j}(t)$

(H3.2) $A_\omega(\phi) > 0$, where $\phi(t) = \min_{1 \leq i \leq n} \{b_i(t) - \sum_{j=1}^n D_{ij}(t) + \sum_{j=1}^n D_{ji}(t)\}$

Theorem 3.3. *Assume that $a_i(t) > c_i(t)$ ($i = 1, 2, \dots, n$). If one of the assumptions (H3.1) or (H3.2) holds, then there exist positive constants m and M ($m < M$), such that for given $0 < \delta < \iota$, there is a constant $T = T(\delta, \iota) > 0$ such that*

$$m \leq x_i(\sigma, \phi) \leq M, \quad i = 1, \dots, n, \tag{3.10}$$

for $t \geq \sigma + T, \sigma \in \mathbb{R}$ and $\phi \in C^+[\delta, \iota] = \{\phi \in C^+ : \delta \leq \phi(t) \leq \iota\}$.

Proof. Suppose that $a_i(t) < c_i(t)$ ($i = 1, \dots, n$) holds. From Theorem 3.2, the positive solutions of (3.3) with (3.4) are uniformly ultimately bounded. We know that there exists a constant $M > 0$, such that for given $0 < \delta < \iota$, there is a constant $T_1(\delta, \iota) > 0$ such that

$$x_i(\sigma, \phi)(t) \leq M, \quad i = 1, \dots, n, \tag{3.11}$$

for $t \geq \sigma + T_1, \sigma \in \mathbb{R}$ and $\phi \in C^+[\delta, \iota]$. On the other hand,

$$\dot{x}_i(t) \geq x_i(t)[b_i(t) - a_i(t)x_i(t)] + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)), \tag{3.12}$$

$i = 1, 2, \dots, n$. Applying [6, Theorem 2] to the auxiliary system

$$\dot{u}_i(t) = u_i(t)[b_i(t) - a_i(t)u_i(t)] + \sum_{j=1}^n D_{ij}(t)(u_j(t) - u_i(t)), \quad u_i(0) = x_i(0), \tag{3.13}$$

$i = 1, 2, \dots, n$, we obtained that there exist m ($0 < m < M$) and $T_2 \geq 0$, such that positive solutions of (3.13) satisfies

$$u_i(t) \geq m \quad \text{for } i = 1, \dots, n \quad \text{and } t \geq \sigma + T_2,$$

where m dependent on assumptions (H3.1) and (H3.2). Taking $T = \max\{T_1, T_2\}$, by Lemma 2.1, (3.10) holds for $t > \sigma + T$. This completes the proof. \square

Applying the above theorem to a two-patch system, we obtain the following result. Let

(A3.1) $A_\omega(b_1(t) - D_{12}(t)) > 0$

(A3.2) $A_\omega(b_2(t) - D_{21}(t)) > 0$

(A3.3) $b_1(t) + D_{21}(t) - D_{12}(t) \geq b_2(t) + D_{12}(t) - D_{21}(t)$ and $A_\omega(b_2(t) + D_{12}(t) - D_{21}(t)) > 0$

(A3.4) $b_1(t) + D_{21}(t) - D_{12}(t) \leq b_2(t) + D_{12}(t) - D_{21}(t)$ and $A_\omega(b_1(t) + D_{21}(t) - D_{12}(t)) > 0$.

Corollary 3.4. *If $a_i(t) > c_i(t)$ ($i = 1, 2$) and one of the conditions (A3.1)–(A3.4) holds, then the result of Theorem 3.3 holds for $i = 1, 2$.*

4. PERMANENCE IN DISPERSING COMPETITIVE SYSTEM

In this section we consider the competitive Lotka-Volterra dispersal model

$$\begin{aligned} \dot{x}_i(t) &= x_i(t)[b_i(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds - f_i(t)y_i(t)] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)) \\ \dot{y}_i(t) &= y_i(t)[d_i(t) - e_i(t)x_i(t) - q_i(t)y_i(t) + p_i(t) \int_{-\tau}^0 K_i(s)y_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(y_j(t) - y_i(t)) \end{aligned} \quad (4.1)$$

$i = 1, 2, \dots, n$, with initial conditions

$$\begin{aligned} x_i(\theta) &= \varphi_i(\theta) \geq 0, \quad y_i(\theta) = \psi_i(\theta) \geq 0, \\ -\tau \leq \theta \leq 0, \quad \varphi_i(0) &> 0, \quad \psi_i(0) > 0, \quad i = 1, 2, \dots, n, \end{aligned} \quad (4.2)$$

where $y_i(t)$ is the density of species y in patch i ; $K_i(s)$ ($i = 1, 2, \dots, n$) denote nonnegative piecewise continuous functions defined on $[-\tau, 0]$ and normalized such that $\int_{-\tau}^0 K_i(s)ds = 1$. We assume $e_i(t), f_i(t), p_i(t), q_i(t), \lambda_{ij}(t)$ ($i, j = 1, 2, \dots, n$) are continuous ω -periodic functions defined on \mathbb{R} and

$$p_i(t), q_i(t) > 0, \lambda_{ij}(t) \geq 0 \quad \text{and} \quad \lambda_{ii}(t) \equiv 0 \quad (4.3)$$

for $t \in \mathbb{R}$, $i, j = 1, 2, \dots, n$, where $d_i(t)$ is the intrinsic growth rate, $e_i(t)$ represents the intraspecific relationship, $\lambda_{ij}(t)$ is the dispersal coefficient for the species y from patch j to patch i ($i \neq j$).

Theorem 4.1. *Suppose that $a_i(t) > c_i(t)$ and $q_i(t) > p_i(t)$ hold for $t \geq 0$. Let $(x_1(t), \dots, x_n(t), y_1(t), \dots, y_n(t))$ denote any solution of (4.1) with initial conditions (4.2). Then there exist positive constants N_{x_i}, N_{y_i} and τ_1 such that*

$$x_i(t) \leq N_{x_i}, y_i(t) \leq N_{y_i} \quad \text{for } i = 1, \dots, n \text{ and } t \geq \tau_1. \quad (4.4)$$

Proof. Obviously solutions of system (4.1) and (4.2) are defined on $[0, +\infty)$ and remain positive for all $t \geq 0$. It follows from (4.1) and the nonnegativity of the initial values,

$$\begin{aligned} \dot{x}_i(t) &\leq x_i(t)[b_i(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)) \\ \dot{y}_i(t) &\leq y_i(t)[d_i(t) - q_i(t)y_i(t) + p_i(t) \int_{-\tau}^0 K_i(s)y_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(y_j(t) - y_i(t)) \end{aligned}$$

$i = 1, 2, \dots, n$. By Lemma 2.1 and Theorem 3.2, there exist positive constants N_{x_i}, N_{y_i} and τ_1 such that

$$0 < x_i(t) \leq N_{x_i}, 0 < y_i(t) \leq N_{y_i},$$

for $i = 1, \dots, n$ and $t \geq \tau_1$. This completes the proof. \square

For the next theorem, let

(H4.1) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_\omega(\theta_1) > 0$, where $\theta_1(t) = b_{i_0}(t) - f_{i_0}(t)N_{y_{i_0}} - \sum_{j=1}^n D_{i_0j}(t)$

(H4.2) $A_\omega(\phi_1) > 0$, where $\phi_1(t) = \min_{1 \leq i \leq n} \{b_i(t) - f_i(t)N_{y_i} - \sum_{j=1}^n D_{ij}(t) + \sum_{j=1}^n D_{ji}(t)\}$

(H4.3) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_\omega(\theta_2) > 0$, where $\theta_2(t) = d_{i_0}(t) - e_{i_0}(t)N_{x_{i_0}} - \sum_{j=1}^n \lambda_{i_0j}(t)$

(H4.4) $A_\omega(\phi_2) > 0$, where $\phi_2(t) = \min_{1 \leq i \leq n} \{d_i(t) - e_i(t)N_{x_i} - \sum_{j=1}^n \lambda_{ij}(t) + \sum_{j=1}^n \lambda_{ji}(t)\}$.

Theorem 4.2. Assume that $a_i(t) > c_i(t)$ and $q_i(t) > p_i(t)$.

(I) If one of the assumption (H4.1) or (H4.2) holds, then there exist $\zeta_{xi} (0 < \zeta_{xi} < N_{xi})$ and $\tau_2 \geq \tau_1$, such that

$$x_i(t) \geq \zeta_{xi} \quad \text{for } i = 1, 2, \dots, n, \quad t \geq \tau_2 \quad (4.5)$$

(II) If $\lambda_{ij}(t) (i \neq j)$ is positive and one of the assumption (H4.3) or (H4.4) holds, then there exist $\zeta_{yi} (0 < \zeta_{yi} < N_{yi})$ and $\tau_3 \geq \tau_2$, such that

$$y_i(t) \geq \zeta_{yi} \quad \text{for } i = 1, 2, \dots, n, \quad t \geq \tau_3 \quad (4.6)$$

Proof. By Theorem 4.1, there exists $\tau_1 > 0$ such that for $i = 1, \dots, n$,

$$\begin{aligned} \dot{x}_i(t) &\geq x_i(t)[b_i(t) - f_i(t)N_{y_i} - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)) \end{aligned}$$

Let $(u_1(t), \dots, u_n(t))$ be the solution of the initial-value problem

$$\begin{aligned} \dot{u}_i(t) &= u_i(t)[b_i(t) - f_i(t)N_{y_i} - a_i(t)u_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)u_i(t+s)ds] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(u_j(t) - u_i(t)) \\ u_i(s) &= x_i(s), \quad s \in [\tau_1 - \tau, \tau_1], \quad i = 1, \dots, n. \end{aligned}$$

By Theorem 3.3 and Lemma 2.1, there exist $\zeta_{xi} (0 < \zeta_{xi} < N_{xi})$ and $\tau_2 \geq \tau_1$, such that

$$x_i(t) \geq \zeta_{xi} \quad \text{for } i = 1, 2, \dots, n, \quad t \geq \tau_2,$$

provided condition (H4.1) or (H4.2) hold.

We omit the proof of part (II) since it is entirely similar to that of (I). \square

5. PERMANENCE IN DISPERSING PREDATOR-PREY SYSTEM

In this section we consider the dispersing predator-prey model

$$\begin{aligned} \dot{x}_i(t) &= x_i(t)[b_i(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds - f_i(t)y_i(t)] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)) \\ \dot{y}_i(t) &= y_i(t)[-d_i(t) + e_i(t)x_i(t) - q_i(t)y_i(t) + p_i(t) \int_{-\tau}^0 \bar{K}_i(s)y_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(y_j(t) - y_i(t)) \end{aligned} \quad (5.1)$$

$i = 1, 2, \dots, n$, with initial conditions

$$\begin{aligned} x_i(\theta) &= \varphi_i(\theta) \geq 0, \quad y_i(\theta) = \psi_i(\theta) \geq 0, \\ -\tau \leq \theta \leq 0, \quad \varphi_i(0) &> 0, \quad \psi_i(0) > 0, \quad i = 1, 2, \dots, n, \end{aligned} \quad (5.2)$$

where $y_i(t)$ is the density of species y in patch i , $\bar{K}_i(s)$ ($i = 1, 2, \dots, n$) denote nonnegative piecewise continuous functions defined on $[-\tau, 0]$ and normalized such that $\int_{-\tau}^0 \bar{K}_i(s)ds = 1$. All coefficients in system (5.1) are bounded continuous and ω -periodic functions. In addition, $a_i(t)$, $c_i(t)$, $d_i(t)$, $q_i(t)$ and $p_i(t)$ are positive for all $t \in [0, \omega]$ and $D_{ii}(t) \equiv 0$.

Theorem 5.1. *Suppose $a_i(t) > c_i(t)$ and $q_i(t) > p_i(t)$ hold for $t \geq 0$. Let $(x_1(t), \dots, x_n(t), y_1(t), \dots, y_n(t))$ denote any solution of (5.1) with initial conditions (5.2). Then there exist positive constants $\bar{N}_{x_i}, \bar{N}_{y_i}$ and $\bar{\tau}_1$ such that*

$$x_i(t) \leq \bar{N}_{x_i}, y_i(t) \leq \bar{N}_{y_i} \quad \text{for } i = 1, \dots, n \text{ } t \geq \bar{\tau}_1. \quad (5.3)$$

Proof. Obviously, solutions of system (5.1) and (5.2) are defined on $[0, +\infty)$ and remain positive for all $t \geq 0$. It follows from (5.1) and the positivity of the initial values,

$$\dot{x}_i(t) \leq x_i(t)[b_i(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds] + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)).$$

By Theorem 3.3 and Lemma 2.1, there exist positive constants \bar{N}_{x_i} and $\bar{\tau}_1$ such that

$$0 < x_i(t) \leq \bar{N}_{x_i}, \quad i = 1, \dots, n,$$

for $t \geq \bar{\tau}_1$. Moreover, for $t \geq \bar{\tau}_1$ we have

$$\begin{aligned} \dot{y}_i(t) &\leq y_i(t)[e_i(t)\bar{N}_{x_i} - q_i(t)y_i(t) + p_i(t) \int_{-\tau}^0 \bar{K}_i(s)y_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(y_j(t) - y_i(t)). \end{aligned}$$

Let $(v_1(t), \dots, v_n(t))$ be the solution of the initial-value problem

$$\begin{aligned} \dot{v}_i(t) &= v_i(t)[e_i(t)\bar{N}_{xi} - q_i(t)v_i(t) + p_i(t) \int_{-\tau}^0 \bar{K}_i(s)v_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(v_j(t) - v_i(t)) \\ v_i(s) &= y_i(s) > 0, s \in [\bar{\tau}_1 - \tau, \bar{\tau}_1], \quad i = 1, \dots, n. \end{aligned} \quad (5.4)$$

By Theorem 3.3 and Lemma 2.1, there exist positive constants \bar{N}_{yi} and $\bar{\tau}_2 > \bar{\tau}_1$ such that

$$0 < y_i(t) \leq \bar{N}_{yi}, \quad i = 1, \dots, n,$$

for $t \geq \bar{\tau}_2$. This completes the proof. \square

For the next theorem let

(H5.1) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_\omega(\bar{\theta}_1) > 0$, where $\bar{\theta}_1(t) = b_{i_0}(t) - f_{i_0}(t)\bar{N}_{yi_0} - \sum_{j=1}^n D_{i_0j}(t)$

(H5.2) $A_\omega(\bar{\phi}_1) > 0$, where $\bar{\phi}_1(t) = \min_{1 \leq i \leq n} \{b_i(t) - f_i(t)\bar{N}_{yi} - \sum_{j=1}^n D_{ij}(t) + \sum_{j=1}^n D_{ji}(t)\}$.

(H5.3) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_\omega(\bar{\theta}_2) > 0$, where $\bar{\theta}_2(t) = e_{i_0}(t)\bar{\zeta}_{xi_0} - d_{i_0}(t) - \sum_{j=1}^n \lambda_{i_0j}(t)$,

(H5.4) $A_\omega(\bar{\phi}_2) > 0$, where $\bar{\phi}_2(t) = \min_{1 \leq i \leq n} \{e_i(t)\bar{\zeta}_{xi} - d_i(t) - \sum_{j=1}^n \lambda_{ij}(t) + \sum_{j=1}^n \lambda_{ji}(t)\}$.

Theorem 5.2. *Suppose that $a_i(t) > c_i(t)$ and $q_i(t) > p_i(t)$ hold.*

(I) *If one of the assumption (H5.1) or (H5.2) holds, then there exist $\bar{\zeta}_{xi} (0 < \bar{\zeta}_{xi} < \bar{N}_{xi})$ and $\bar{\tau}_3 \geq \bar{\tau}_2$ such that*

$$x_i(t) \geq \bar{\zeta}_{xi} \quad \text{for } i = 1, 2, \dots, n, t \geq \bar{\tau}_3 \quad (5.5)$$

(II) *Suppose further that one of the assumption (H5.3) or (H5.4) holds. Then there exist $\bar{\zeta}_{yi} (0 < \bar{\zeta}_{yi} < \bar{N}_{yi})$ and $\bar{\tau}_4 \geq \bar{\tau}_3$ such that*

$$y_i(t) \geq \bar{\zeta}_{yi} \quad \text{for } i = 1, 2, \dots, n t \geq \bar{\tau}_4 \quad (5.6)$$

Proof. Suppose that condition (H5.1) or (H5.2) holds. By Theorem 5.1, there exists $\bar{\tau}_2$ such that

$$\begin{aligned} \dot{x}_i(t) &\geq x_i(t)[b_i(t) - f_i(t)\bar{N}_{yi}(t) - a_i(t)x_i(t) + c_i(t) \int_{-\tau}^0 K_i(s)x_i(t+s)ds] \\ &\quad + \sum_{j=1}^n D_{ij}(t)(x_j(t) - x_i(t)), \end{aligned}$$

for $t \geq \bar{\tau}_2$. By Theorem 3.3 and Lemma 2.1, there exist $\bar{\zeta}_{xi} (0 < \bar{\zeta}_{xi} < \bar{N}_{xi})$ and $\bar{\tau}_3 \geq \bar{\tau}_2$ such that

$$x_i(t) \geq \bar{\zeta}_{xi} \quad \text{for } i = 1, 2, \dots, n, t \geq \bar{\tau}_3$$

provided condition (H5.1) or (H5.2) holds.

Furthermore, suppose that (H5.3) or (H5.4) be satisfied

$$\begin{aligned} \dot{y}_i(t) &\geq y_i(t)[-d_i(t) + e_i(t)\bar{\zeta}_{xi} - q_i(t)y_i(t) + p_i(t) \int_{-\tau}^0 \bar{K}_i(s)y_i(t+s)ds] \\ &\quad + \sum_{j=1}^n \lambda_{ij}(t)(y_j(t) - y_i(t)) \end{aligned}$$

for $t \geq \bar{\tau}_2$. Similar to the above discussion, there exist $\bar{\zeta}_{yi}(0 < \bar{\zeta}_{yi} < \bar{N}_{yi})$ and $\bar{\tau}_4 \geq \bar{\tau}_3$ such that

$$y_i(t) \geq \bar{\zeta}_{yi} \quad \text{for } i = 1, 2, \dots, n, t \geq \bar{\tau}_4.$$

This completes the proof. \square

6. DISCUSSION

Zhang and Chen [28] showed that in a nonautonomous system composed of two patches connected by random dispersal and occupied by a single species, if the species is able to survive then it continues to do so for any dispersal rate (see [28, Theorem 3.1]).

Different from above consideration, in section 3 of the present paper we focus on the more interesting cases in biology that the species living in a weak environment in the sense that species x in some of the isolated patches will be extinct without the contribution from other patches. By the main results in this section, dispersing species x becomes permanent in every patches depending on the choice of the dispersal rates (see Theorem 3.3). But in [28], the authors assumed that $b_i(t) > 0$. We find that this condition does not hold for a weak patchy environment in the sense that the intrinsic growth rate $b_i(t)$ may become negative on some time intervals.

By using the results obtained in section 3 and Lemma 2.1, we also considered the effect of dispersal on the permanence of competitive and predator-prey systems.

Within the context of the mathematical models used here, the main results of this paper imply that some endangered species can avoid extinction by choosing suitable dispersal rates. Hence dispersal is a major factor on the determination of the permanence or extinction of the endangered species.

REFERENCES

- [1] L. J. S. Allen; *Persistence and extinction in single-species reaction-diffusion models*, Bull. Math. Biol., 45, 209-227 (1983).
- [2] L. J. S. Allen; *Persistence, extinction and critical patch number for island populations*, J. Math. Biol., 24, 617-625 (1987).
- [3] E. Beretta and F. Solimano; *Global stability and periodic orbits for two patch predator-prey diffusion delay models*, Math. Biosci., 85, 153-183 (1987).
- [4] E. Beretta and Y. Takeuchi; *Global stability of single-species diffusion Volterra models with continuous time delays*, Bull. Math. Biol., 49, 431-448 (1987).
- [5] E. Beretta and Y. Takeuchi; *Global asymptotic stability of Lotka-Volterra diffusion models with continuous time delays*, SIAM J. Appl. Math., 48, 627-651 (1988).
- [6] J. Cui and L. Chen; *The effect of diffusion on the time varying logistic population growth*, Computers Math. Applic., 36(3), 1-9 (1998).
- [7] U. D'Ancona; *The struggle for existence*, Leiden, Netherlands: E.J. Brill, 1954.
- [8] H. I. Freedman, B. Rai and P. Waltman; *Mathematical models of population interactions with dispersal II: Differential survival in a change of habitat*, J. Math. Anal. Appl., 115, 140-154 (1986).

- [9] H. I. Freedman and P. Waltman; *Mathematical models of population interactions with dispersal I: Stability of two habitats with and without a predator*, SIAM J. Appl. Math., 32, 631-648 (1977).
- [10] H. I. Freedman and Y. Takeuchi; *Predator survival versus extinction as a function of dispersal in a predator-prey model with patchy environment*, Appl. Anal., 31, 247-266 (1989).
- [11] H. I. Freedman and Y. Takeuchi, *Global stability and predator dynamics in a model of prey dispersal in a patchy environment*, Nonlin. Anal. T.M.A., 13, 993-1002 (1989).
- [12] H. I. Freedman; *Single species migration in two habitats: persistence and extinction*, Math. Model., 8, 778-780 (1987).
- [13] J. K. Hale; *Theory of functional differential equations*, Springer-Verlag, Berlin, 1977.
- [14] A. Hastings; *Dynamics of a single species in a spatially varying environment: The stabilizing role of high dispersal rates*. J. Math. Biol., 16, 49-55 (1982).
- [15] R. D. Holt; *Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution*. Theoret. Pop. Bio. 28, 181-208 (1985).
- [16] Y. Kuang and Y. Takeuchi; *Predator-prey dynamics in models of prey dispersal in two-patch environments*, Math. Biosci., 120, 77-98 (1994).
- [17] S. A. Levin; *Dispersion and population interactions*, Amer. Nat. , 108, 207-228 (1974).
- [18] J. D. Skellern; *Random dispersal in theoretical population*, Biometrika, 38, 196-216 (1951).
- [19] H. L. Smith; *Monotone semiflows generated by functional differential equations*, J. Differential Equations, 66, 420-442 (1987).
- [20] X. Song and L. Chen; *Persistence and global stability for nonautonomous predator-prey system with diffusion and time delay*, Computers Math. Applic., 35 (6), 33-40 (1998).
- [21] Y. Takeuchi; *Cooperative system theory and global stability of diffusion models*, Acta Appl. Math., 14, 49-57 (1989).
- [22] Y. Takeuchi; *Diffusion-mediated persistence in two-species competition Lotka-Volterra model*, Math. Biosci., 95, 65-83 (1989).
- [23] Y. Takeuchi; *Conflict between the need to forage and the need to avoid competition: persistence of two-species model*, Math. Biosci., 99, 181-194 (1990).
- [24] R. R. Vance; *The effect of dispersal on population stability in one-species ,discrete space population growth models*. The American Naturalist, 123, 230-254 (1984).
- [25] W. Wang, P. Fergola and C. Tenneriello; *Global attractivity of periodic solutions of population models*, J. Math. Anal. Appl., 211, 498-511 (1997).
- [26] K. Yang; *Delay differential equations with applications in population dynamics*, Academic Press, INC, 1993.
- [27] Y. Yange et al.; *Giant panda's moving habit in Poping*, Acta Theridogica Sinica, 14(1), 9-14 (1994).
- [28] J. Zhang and L. Chen; *Periodic solutions of Single-Species Nonautonomous Diffusion Models with continuous Time Delays*, Math. Comput. Modelling, 23, 17-27 (1996).
- [29] Y. Zhou; *Analysis on decline of wild Alligator Sinensis population*, Sichuan Journal of Zoology, 16, 137-139 (1997).

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