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# The effects of dispersal on population dynamics [1]

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**Abstract** In this paper,we consider the effect of dispersal on the permanence and extinction of single and multiple endangered species that live in changing patches environment. Different from the former studies,our discussion include the more important situation in conservation biology that species live in a weak patchy environment in the sense that species will become extinct in some of the isolated patches. For single population model,we show that the identical species can persist for some dispersal rates,and can also vanish for another set of restriction on dispersal rates,though the endangered single species will vanish in some isolated patches without the contribution from other patches. Furthermore we consider the existence,uniqueness and global stability of the positive periodic solution. For prey-predator system,we can make both prey and predator species to be permanent by choosing the dispersal rates appropriately even if the prey species has negative intrinsic growth rate in some patches. Particularly, for a prey-predator system, we provide a sufficient and necessary condition to guarantee the prey and predator species to be permanent.

**Key words.** Logistic equation,Lotka-Volterra system, diffusion, permanence,extinction, periodic solution, stability.

## 1 Introduction

Since the poineering theoretical work by Skellem [9],many works have focused on the effect of spatial factors which play a crucial rule in persistence and stability of population [1-13]. Most of the previous papers deal with autonomous population systems and indicate that a dispersal process in an ecological system is often considered to have a stabilizing influence on the system [12],but is also probably destabilizing the system[8].

Recently, some authors have also studied the influence of dispersal on the time dependent population models (see [13]). The authors always assume that the intrinsic growth rates are all continuous and bounded above and below by positive constants(this means that every species lived in a suitable environment). They obtained some sufficient conditions that guarantee permanence of every species and global stability of a unique positive periodic solution.

However,the actual living environment of endangered species is not always like this. Because of the ecological effects of the human activities and industry,e.g. the location of manufacturing industries, the pollution of the atmosphere,of river,of soil,etc., more and more habitats were broken into patches and some of the patches were polluted. In some of these patches,even in every patches the species will go extinct without the contribution from other patches,and hence the species live in a weak patchy environment. The living environments of some endangered and rare species such as giant panda [29-31] and alligator sinensis [34] are some convincing examples.

In order to protect the endangered and rare species,we have to consider the effects of habitat fragmentation and diffusion on the permanence and extinction of single and multiple species living in weak environments. The present paper consider the following interesting problem:to what extent does dispersal lead to the permanence or extinction of endangered single and multiple species which could not persist within some isolated patches.

Let $C$ denotes the space of all bounded continuous functions $f : R \to R$,$C_+^0$ is the set of nonnegative $f \in C$ and $C_+$ is the set of all $f \in C$ such that $f$ is bounded below by a positive constant. Given $f \in C$,we denote

$$f^M = \sup_{t\geq 0} f(t), \quad f^L = \inf_{t\geq 0} f(t)$$

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and define the lower average $A_L(f)$ and upper average $A_M(f)$ of $f$ by

$$A_L(f) = \lim_{r\to\infty} \inf_{t-s\geq r} (t-s)^{-1} \int_s^t f(\tau)d\tau$$

and

$$A_M(f) = \lim_{r\to\infty} \sup_{t-s\geq r} (t-s)^{-1} \int_s^t f(\tau)d\tau$$

respectively. If $f \in C$ is $\omega-$periodic,then the average $A_\omega(f)$ of $f$ must be equal to $A_L(f)$ and $A_M(f)$,that is

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

**Definition.** The system of differential equations

$$\dot{x} = F(t, x), \quad x \in R^n$$

is said to be permanent if there exists a compact set $K$ in the interior of $R_+^n = \{(x_1, x_2, \cdots, x_n) \in R^n \mid x_i \geq 0, i = 1, 2, \cdots, n\}$, such that all solutions starting in the interior of $R_+^n$ ultimately enter $K$.

## 2 The effect of habitat fragmentation on single species

In this section, we consider the system as composed of patches connected by discrete and linear diffusions, each patch is assumed to be occupied by a single species as follows

$$\dot{x}_i = x_i[b_i(t) - a_i(t)x_i] + \sum_{j=1}^n D_{ij}(t)(x_j - x_i), \quad (i = 1, 2, \cdots, n) \tag{2.1}$$

where $x_i (i = 1, 2, \cdots, n)$ denotes the species $x$ in patch $i$. $b_i(t) \in C, a_i(t), D_{ij}(t) \in C_+ (i \neq j)$ and $D_{ii}(t) \equiv 0$. $b_i(t)$ is the intrinsic growth rate for species $x$ in patch i; $a_i(t)$ represents the self-inhibition coefficient; and $D_{ij}(t)$ is the dispersal coefficient of species $x$ from patch $j$ to patch $i$.

If $a_i(t), b_i(t)$ are continuous and bounded above and below by positive constants,Wang and Chen [13] showed that the system is permanent for any continuous,nonnegative and bounded dispersal rates $D_{ij}(t)$.

However,in the process that the endangered species be going to extinction,its birth rate is less than the death rate. In this place,we will indicate that human can rescue the endangered species from extinction by controlling dispersal rates.

**Theorem 2.1**[5]. Given any $\xi_i > 0 (i = 1, 2, \cdots, n)$, the initial value problem

$$\begin{aligned} \dot{x}_i &= x_i[b_i(t) - a_i(t)x_i] + \sum_{j=1}^n D_{ij}(t)(x_j - x_i) \\ x_i(0) &= \xi_i, i = 1, 2, \cdots, n \end{aligned} \tag{2.2}$$

has a unique solution $x(t) = (x_1(t), x_2(t), \cdots, x_n(t))$ which exists for all $t \geq 0$. Moreover, there exists $M > 0, \tau > 0$, such that

$$0 < x_i(t) \leq M \quad for \quad t \geq \tau, \tag{2.3}$$

the region $D = \{(x_1, x_2, \cdots, x_n) \mid 0 < x_i \leq M, i = 1, 2, \cdots, n\}$ being positively invariant with respect to (2.1).

A consequence of Theorem 2.1 is that for $\xi_i > 0 (i = 1, 2, \cdots, n)$ the solution of (2.2) is ultimately bounded above. We will show that this solution is also ultimately bounded below away from zero provided that one of the following conditions is satisfied.

(H2.1) There exists $i_0 (1 \leq i_0 \leq n)$, such that $A_L(\theta) > 0$,where $\theta(t) = b_{i_0}(t) - \sum_{j=1}^n D_{i_0 j}(t)$.

(H2.2) $A_L(\phi) > 0$,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 2.2**[5]. Suppose that (H2.1) or (H2.2) holds, then there exists $\delta_i, 0 < \delta_i < M$ and $\tau \geq 0$, such that the solution of (2.2) satisfies

$$x_i(t) \geq \delta_i, \quad t \geq \tau, i = 1, 2, \cdots, n \tag{2.4}$$

where $\delta_i (i = 1, 2, \cdots, n)$ depend on the various assumptions (H2.1) and (H2.2).

Theorem 2.1 and 2.2 have established that under the one of the assumptions (H2.1) or (H2.2),there exist positive constants $m$ and $M$,the solution of (2.1) with positive initial values ultimately enter the rectangular region $\Omega = \{(x_1, x_2, \cdots, x_n) \mid m \leq x_i \leq M, i = 1, 2, \cdots, n\}$, therefore the population is permanent.

**Remark 2.1.** According to the proof of Theorem 2.2, if species $x$ is permanent in a fixed patch $i$, then species $x$ is also permanent in other patches for any dispersal rates $D_{ji}(t)(i, j = 1, 2, \cdots, n)$.

Next we will consider the extinction of system (2.1). Denote

$$\psi(t) = \max_{1 \leq i \leq n} \{b_i(t) - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t)\}$$

**Theorem 2.3**[5]. Suppose that $\int_0^{+\infty} \psi(t)dt = -\infty$ , then the solution of (2.1) satisfies

$$x_i(t) \to 0 \quad i = 1, 2, \cdots, n, t \to +\infty$$

Next we assume that the functions $b_i(t), a_i(t), D_{ij}(t), (i, j = 1, 2, \cdots, n)$ in system (2.1) are all periodic functions with common period $\omega$,and consider the positive periodic solution of (2.1).

**Theorem 2.4**[4]. Suppose that the assumption (H2.1) or (H2.2) holds, then system (2.1) has at least one positive $\omega$-periodic solution which is globally asymptotically stable.

## 3 Permanence in dispersal prey-predator system

We introduce an exotic predator species $y$ into some patches which were occupied by native species $x$. Assume that species $x$ and $y$ obey following Lotka-Volterra dispersal model

$$\begin{aligned} \dot{x}_i &= x_i[b_i(t) - a_i(t)x_i - c_i(t)y_i] + \sum_{j=1}^{n} D_{ij}(t)(x_j - x_i) \\ \dot{y}_i &= y_i[-d_i(t) + e_i(t)x_i - f_i(t)y_i] + \sum_{j=1}^{n} \lambda_{ij}(t)(y_j - y_i) \\ i &= 1, 2, \cdots, n. \end{aligned} \tag{3.1}$$

where $y_i$ is the density of species $y$ in patch $i$; the coefficients $d_i(t), e_i(t), c_i(t)$ are all nonnegative and bounded continuous functions.$f_i(t), \lambda_{ij}(t) \in C_+ (i \neq j)$ and $\lambda_{ii}(t) \equiv 0$.

**Theorem 3.1**[5].(A).Suppose that following assumption (H3.1) or (H3.2) be satisfied,

(H3.1) There exists $i_0 (1 \leq i_0 \leq n)$ such that $A_L(\theta_1) > 0$,where $\theta_1(t) = b_{i_0}(t) - c_{i_0}(t)N_y - \sum_{j=1}^{n} D_{i_0 j}(t)$,

(H3.2) $A_L(\gamma_1) > 0$,where $\gamma_1(t) = \min_{1 \leq i \leq n} \{b_i(t) - c_i(t)N_y - \sum_{j=1}^{n} D_{ij}(t) + \sum_{j=1}^{n} D_{ji}(t)\}$.

where $N_y$ is the upper bound of $y_i(t)$. Then prey species is permanent.

(B).Suppose further that following assumption (H3.3) or (H3.4) be satisfied,

(H3.3) There exists $i_0 (1 \leq i_0 \leq n)$ such that $A_L(\theta_2) > 0$,where $\theta_2(t) = e_{i_0}(t)\zeta_{x i_0} - d_{i_0}(t) - \sum_{j=1}^{n} \lambda_{i_0 j}(t)$,

(H3.4) $A_L(\gamma_2) > 0$,where $\gamma_2(t) = \min_{1 \leq i \leq n} \{e_i(t)\zeta_{xi} - d_i(t) - \sum_{j=1}^{n} \lambda_{ij}(t) + \sum_{j=1}^{n} \lambda_{ji}(t)\}$.

where $\zeta_{xi}$ is the lower bound of $x_i(t)$.Then predator species is permanent.

**Example 3.1.** Consider the following periodic and patchy predator-prey system

$$\begin{aligned}
\dot{x}_1 &= x_1(12 + \tfrac{1}{4}\sin t - 3x_1 - y_1) + D_{12}(t)(x_2 - x_1)\\
\dot{x}_2 &= x_2(-1 + \tfrac{1}{4}\sin t - x_2 - y_2) + D_{21}(t)(x_1 - x_2)\\
\dot{y}_1 &= y_1(-1 + \sin t + x_1 - y_1) + \lambda_{12}(t)(y_2 - y_1)\\
\dot{y}_1 &= y_2(-1 + \sin t + x_2 - y_2) + \lambda_{21}(t)(y_1 - y_2).
\end{aligned} \tag{3.2}$$

Where $D_{12}(t), D_{21}(t), \lambda_{12}(t)$and $\lambda_{21}(t)$ are all positive continuous and periodic functions with common period $2\pi$.

Note that if the patches are isolated from each other($D_{12}(t) = D_{21}(t) = \lambda_{12}(t) = \lambda_{21}(t) = 0$),it is clear that species $x$ and $y$ will go extinct in patch 2.

Given any positive solution $(x_1(t), x_2(t), y_1(t), y_2(t))$ of (3.2),we have

$$\begin{aligned}
\dot{x}_1 &\le x_1(12 + \tfrac{1}{4}\sin t - 3x_1) + D_{12}(t)(x_2 - x_1)\\
\dot{x}_2 &\le x_2(-1 + \tfrac{1}{4}\sin t - x_2) + D_{21}(t)(x_1 - x_2).
\end{aligned}$$

From the proof of Theorem 3.1,there exists $\tau_1 > 0$,such that

$$0 < x_i(t) \le 25/6, 0 < y_i(t) \le 53/12 (i = 1, 2) \quad for \quad t \ge \tau_1. \tag{3.3}$$

Consequently,

$$\begin{aligned}
\dot{x}_1 &\ge x_1(\tfrac{91}{12} + \tfrac{1}{4}\sin t - 3x_1) + D_{12}(t)(x_2 - x_1)\\
\dot{x}_2 &\ge x_2(-\tfrac{65}{12} + \tfrac{1}{4}\sin t - x_2) + D_{21}(t)(x_1 - x_2)
\end{aligned}$$

for $t \ge \tau_1$. Furthermore,

$$\dot{x}_1 \ge x_1(\frac{22}{3} - D_{12}^M - 3x_1)$$

there exists $\tau_2 (\tau_2 \ge \tau_1)$, such that

$$x_1(t) > \frac{\frac{22}{3} - D_{12}^M}{3} - \epsilon \quad for \quad t \ge \tau_2$$

provided $D_{12}^M < 22/3$,where $\epsilon$ be any positive number. Particularly,we can choose $D_{12}^M \le 1, \epsilon = 1/9$,such that $x_1(t) > 2 = \zeta_{x1}$ for $t \ge \tau_2$.

According to the proof of Theorem 2.2,there exist positive constants $\zeta_{x2}$ and $\tau_3(\tau_3 \ge \tau_2)$,such that $x_2(t) > \zeta_{x2}$ for $t \ge \tau_3$.

Finally,

$$\dot{y}_1 \ge y_1(1 + \sin t + x_1 - y_1) + \lambda_{12}(t)(y_2 - y_1)$$

for $t \ge \tau_3$. By Theorem 2.2,there exist positive constants $\zeta_{y1}, \zeta_{y2}$ and $\tau_4(\tau_4 \ge \tau_3)$ such that

$$y_i(t) \ge \zeta_{yi} \quad for \quad t \ge \tau_4, i = 1, 2$$

provided $A_{2\pi}(\lambda_{12}) < 1$.

To sum up,under the assumptions

$$D_{12}^M \le 1 \quad and \quad A_{2\pi}(\lambda_{12}) < 1 \tag{3.4}$$

the species $x$ and $y$ are permanent.

According to above discussion,we know that people can avoid the local extinction of the endangered species $x$ and $y$ in patch 2 by controlling the dispersal rates.

Next we study the following system

$$\begin{aligned}
\dot{x}_1 &= x_1[b_1(t) - a_1(t)x_1 - c_1(t)y] + D_{12}(t)x_2 - D_{21}(t)x_1\\
\dot{x}_2 &= x_2[b_2(t) - a_2(t)x_2] + D_{21}(t)x_1 - D_{12}(t)x_2\\
\dot{y} &= y[-d(t) + e(t)x_1 - f(t)y - q(t)y(t - \tau)].
\end{aligned} \tag{3.5}$$

$\tau$ is a positive constant. For (3.5) we make the following assumptions

$(H3.5)$ $\quad A_\omega[b_1(t) - D_{21}(t)] > 0.$

**Theorem 3.1.**[6] Under the assumption (H3.5), system (3.5) is permanent if and only if

$$(H3.6) \qquad A_\omega[-d(t) + e(t)x_1^*(t)] > 0.$$

where $(x_1^*(t), x_2^*(t))$ be the positive periodic solution of the system

$$\begin{aligned} \dot{x}_1 &= x_1[b_1(t) - a_1(t)x_1] + D_{12}(t)x_2 - D_{21}(t)x_1 \\ \dot{x}_2 &= x_2[b_2(t) - a_2(t)x_2] + D_{21}(t)x_1 - D_{12}(t)x_2. \end{aligned}$$

# References


[1] L.J.S. Allen, Persistence,extinction,and critical patch number for island populations, J. Math. Biol., 24(1987), 617-625.

[2] E.Beretta and Y.Takeuchi,Global stability of single-species diffusion Volterra models with continuous time delays, Bull.Math.Biol.,49(1987),431-448.

[3] F.Cao and L.Chen, Asymptotic behavior of nonautonomous diffusive Lotka-Volterra model,Syst.Sci.& Math.Sci.,11(1998),107-111.

[4] J. Cui and L. Chen,The effect of diffusion on the time varying Logistic population growth, Computers Math.Applic.,36(1998),1-9.

[5] J. Cui and L. Chen, Permanent and extinction in logistic and Lotka-Volterra systems with diffusion, J. Math. Anal. Appl., 258(2001), 512-535.

[6] J. Cui ,The effect of dispersal on permanence in a predator-prey population growth model, Computers Math.Applic.,44(2002),1085-1097.

[7] H.I.Freedman and P.Waltman, Mathematical models of population interaction with dispersal. I.Stability of two habitats with and without a predator, SIAM J. Math. ,32(1977), 631-648.

[8] S. Levin and L.A.Segel, Hypothesis to explain the origin of planktonic patchness, Nature, 259(1976), 659.

[9] J.D.Skellam,Random dispersal in theoretical population,Biometrika, 38(1951),196-216.

[10] Y.Takeuchi, Global Dynamical Properties of Lotka-Volterra Systems, World Scientific, Singapore, 1996.

[11] Y.Takeuchi, Cooperative system theory and global stability of diffusion models, Acta Appl. Math., 14(1989), 49-57.

[12] Y.Takeuchi,Diffusion-mediated persistence in two-species competition Lotka-Volterra model,Math.Biosci., 95(1989), 65-83.

[13] W.Wang and L.Chen, Global stability of a population Dispersal in a Two-patch Environment,Dynamic Systems and Applications, 6(1997), 207-216.

[14] Y.Xun, State, disturbance and devolopment of Chinese Giant Pandas, Chinese Wildlife, (1990), 9-11.

[15] Y. Zhou, Analysis on decline of wild Alligator Sinensis population, Sichuan Journal of Zoology, 16(1997), 137-139.