

PERMANENCE AND GLOBAL STABILITY FOR DIFFUSION SYSTEMS

Zhengyi LU and Yasuhiro TAKEUCHI

Department of Applied Mathematics, Faculty of Engineering,
Shizuoka University, Hamamatsu 432, JAPAN

ABSTRACT

Based on recently developed cooperative systems theory and an new result for essentially positive matrix, we consider two important ODE systems with discrete diffusion. One is a cooperative Lotka-Volterra diffusion system and another is a logistic system with directed diffusion. Sufficient and necessary conditions are given for the former to be permanent and for the latter to be globally stable.

1 INTRODUCTION

Recently, many authors consider the effect of spatial distributions of species over the range of the habitat in population dynamics[1-8,11-17,19-23,26-31]. It is shown that spatial factors play a fundamental role in persistence and stability of populations, although a complete result has not yet been obtained even in the simplest one-species case. If the population dynamics with the effects of the spatial heterogeneity is modeled by diffusion process, we have two typical equations. One is semilinear parabolic equations, i.e., a reaction-diffusion system where the population is continuously spread out in space[6,8,11,14,15,21-23,26]. The other is a discrete diffusion system where several species are distributed over an interconnected network of multiple

patches and there are population migrations among patches[1-5,7,8,12,13,19,20,27-31].

In this paper, we focus our attention to discrete diffusion systems, namely, a cooperative Lotka-Volterra diffusion system and a logistic directed diffusion system.

For the cooperative Lotka-Volterra diffusion system, based on the homotopy function technique, Beretta[4] and Beretta and Takeuchi[5] provided some sufficient conditions for the existence of a positive globally asymptotically stable equilibrium point. And in[1], Allen introduced a logistic system with directed diffusion. By using comparison theorem, Allen obtained a sufficient condition for the solutions of the system to be bounded in 2-dimensional case.

In this paper, on the basis of the monotonicity for flows of cooperative systems, for the cooperative Lotka-Volterra diffusion system, first, we prove sufficient and necessary conditions ensuring permanence of the system and give a permanent system with two positive equilibrium points to show that permanence does not imply global stability in general. Then, we give sufficient and necessary conditions for the directed diffusion system to be globally stable. The fundamental tools to prove these results are recently developed cooperative system theories[7,24,25,28] and an new result for an essentially positive matrix (Lemma 4).

Section 2 contains some background concepts and fundamental results for a cooperative system and an essentially positive matrix. Section 3 and 4 state our main results: sufficient and necessary conditions for a cooperative Lotka-Volterra diffusion system to be permanent and for a logistic directed diffusion system to be globally stable, respectively. We conclude the paper with some discussions.

In this paper, all matrices are supposed to be non-singular.

2 BACKGROUND CONCEPTS AND RESULTS

To begin with we state some concepts and results concerning a general n -dimensional cooperative system:

$$\dot{x} = F(x) \quad (1)$$

where F is C^1 on a domain $R_+^n = \{x \in R^n | x_i \geq 0, i = 1, \dots, n\}$ and has Jacobian matrix $DF(x)$ with nonnegative off-diagonal elements, i.e. for all $i \neq j$, $i, j = 1, \dots, n$, $(\partial F_i / \partial x_j) \geq 0$, for all $x \in R_+^n$. Denote the solution to (1) as $x(t)$ whose initial value is $x(0)$.

We shall use a key result given by Kamke [10] and Selgrade [24, 25] for system (1), which in our case can be stated as follows :

LEMMA 1. Let R_+^n be invariant for (1). If initial positions are ordered $x(0) \leq y(0)$, then $x(t) \leq y(t)$ for all $t \geq 0$. In addition, if $0 \leq F(x(0))$ then $x(t)$ is non-decreasing for $t \geq 0$; and if $F(x(0)) \leq 0$, then $x(t)$ is nonincreasing for $t \geq 0$. In either case, if the positive orbit of $x(0)$ is bounded then its ω -limit set is precisely one equilibrium point.

To prove global stability for systems in the paper, the following fact which is used in [7] and [28] is very useful.

LEMMA 2. If system (1) possesses a positive equilibrium point x^* satisfying

$$F(\lambda x^*) \begin{cases} > 0 & \text{for } \lambda \in (0, 1), \\ < 0 & \text{for } \lambda \in (1, \infty), \end{cases}$$

then x^* is globally stable.

We also need the permanence concept (see, for example Hofbauer and Sigmund [9]).

Definition 1. System (1) is said to be *permanent* if there exists a compact set K in the interior of the state space R_+^n such that all solutions in the interior of R_+^n enter ultimately K .

Now consider the n -dimensional Lotka-Volterra cooperative system

$$\dot{x}_i = x_i(b_i + \sum_{j=1}^n a_{ij}x_j). \quad (2)$$

Here $b = (b_1, \dots, b_n)^T$ is a positive constant vector and $A = (a_{ij})_{n \times n}$ a constant matrix with $a_{ij} \geq 0$ ($i \neq j, i, j = 1, \dots, n$) and $a_{ii} < 0$ ($i = 1, \dots, n$) (i.e., A is an essentially positive matrix). For system (2), we can find the following important results quoted in [9].

LEMMA 3. For system (2), the following statements are equivalent:

- (i) System (2) admits a positive equilibrium point;
- (ii) The matrix A is VL stable (i.e. there exists a positive diagonal matrix C such that $CA + A^T C$ is negative definite);
- (iii) System (2) is permanent;
- (iv) System (2) is globally stable in the sense that so is the positive equilibrium point;

For convenience, in the following discussions, we use a usual notation $A \in S_w$ to denote that matrix A is VL-stable.

A key to prove the necessary conditions in the main theorems is as follows[19,20].

LEMMA 4. If an essentially positive matrix A does not belong to S_w , then A has a $K(\geq 2)$ -principal minor $A_{(i_1, \dots, i_k)}$ such that the system of linear equations

$$A_{(i_1, \dots, i_k)} \mathbf{y} = \mathbf{1}, \quad (\mathbf{1} = (1, \dots, 1)^T)$$

has a solution $\mathbf{y} > 0$.

3 LOTKA-VOLTERRA SYSTEMS

We consider the following cooperative Lotka-Volterra diffusion systems with two different patches:

$$\begin{aligned}\dot{x}_i &= x_i(b_i + \sum_{j=1}^n a_{ij}x_j) + D_i(y_i - x_i), \\ \dot{y}_i &= y_i(\bar{b}_i + \sum_{j=1}^n \bar{a}_{ij}y_j) + \bar{D}_i(x_i - y_i), \quad i = 1, \dots, n.\end{aligned}\quad (3)$$

where $b_i, \bar{b}_i$ ($i=1, \dots, n$) are positive constants, $a_{ii}, \bar{a}_{ii}$ ($i=1, \dots, n$) negative, $A=(a_{ij})_{n \times n}$, $\bar{A}=(\bar{a}_{ij})_{n \times n}$ essentially positive matrices, $D_i, \bar{D}_i$ ($i=1, \dots, n$) nonnegative diffusion constants and x_i, y_i ($i=1, \dots, n$) describe the densities of species i in the patch X and Y at time t .

Based on Lemmas 1,3 and 4, we can prove our first main result as follows[19].

THEOREM 1. System (3) is permanent iff $A \in S_w$ and $\bar{A} \in S_w$.

From this theorem, we can obtain following corollary[19].

COROLLARY 1. System (3) is globally stable iff $A \in S_w, \bar{A} \in S_w$ and a positive equilibrium point is unique.

A natural problem arising from above results is whether permanence implies global stability, namely, permanence implies the uniqueness of a positive equilibrium point, in general.

The following example of a permanent system with two positive equilibrium points shows that permanence does not imply global stability in general.

Example 1.

$$\begin{aligned}\dot{x}_1 &= x_1(1.3 - 13x_1 + 3.1x_2) + 1.2(y_1 - x_1), \\ \dot{x}_2 &= x_2(1.3 + 53.1x_1 - 13x_2) + 23.1(y_2 - x_2),\end{aligned}$$

$$\begin{aligned}\dot{y}_1 &= y_1(1.3 - 13y_1 + 53.1y_2) + 23.1(x_1 - y_1), \\ \dot{y}_2 &= y_2(1.3 + 3.1y_1 - 13y_2) + 1.2(x_2 - y_2).\end{aligned}\tag{4}$$

System (4) has at least two positive equilibrium points $(x_*, y_*) = (1, 3; 3, 1)$ and $(x^*, y^*) = (2, 7; 7, 2)$. Note that $A, \bar{A} \in S_w$.

Comparing Theorem 1, Corollary 1 and Example 1 for diffusion system (3) with Lemma 3 for isolated patch (2), we know that, since global stability is one kind of permanence, the diffusions will not change the dynamical behaviour of the system in the sense of permanence, but will change it in the sense of global stability.

4 LOGISTIC SYSTEMS

In the preceding section, we have shown sufficient and necessary conditions for a cooperative Lotka-Volterra diffusion system to be permanent. In this section, we consider the following logistic system with directed diffusion terms

$$\dot{x}_i = x_i(a_i - b_i x_i) + \sum_{j=1, j \neq i}^n D_{ij}(x_j^2 - \alpha_{ij} x_i^2).\tag{5}$$

Denote $A = (a_{ij})_{n \times n}$, where $a_{ij} = D_{ij}$ for $j \neq i$, $a_{ii} = -b_i - \sum_{j=1, j \neq i}^n D_{ij} \alpha_{ij}$. We suppose that a_i and b_i are positive constants, the diffusion constants D_{ij} and boundary condition[1] constants α_{ij} are nonnegative. Obviously, matrix A defined as above is an essentially positive one. In Allen[1], for system (5) as $n = 2$, the strong persistence result is shown and some sufficient conditions for the existence of unbounded solutions are also given. In the present section, we obtain the sufficient and necessary conditions for the system to have a globally stable positive equilibrium point, and we show that every solution of the system is unbounded if the conditions are failed to be satisfied. This extends the known result for 2-dimensional system[1] to general n -dimensional one.

THEOREM 2[20]. Consider system (5).

- i) The System possesses a globally stable positive equilibrium point x^* , if $A \in S_w$;
- ii) every solution of the system is unbounded, i.e., $\lim_{t \rightarrow T_x} x(t) = \infty$, if $A \notin S_w$.

Here, $(0, T_x)$ is the maximal interval of existence for $x(t)$.

In the following, we assume, without loss of generality, that the K -th principal minor given in Lemma 4 is the K -th leading one of A , that is, $i_l = l$ for $l = 1, \dots, K$. To prove Theorem 2, we need the following lemma.

LEMMA 5. If $A \notin S_w$, for any positive parameter μ , the following system of linear equations

$$\begin{aligned} a_{11}x_1^2 + a_{12}x_2^2 + \dots + a_{1K}x_K^2 &= \mu, \\ a_{21}x_1^2 + a_{22}x_2^2 + \dots + a_{2K}x_K^2 &= \mu, \\ &\dots \\ a_{K1}x_1^2 + a_{K2}x_2^2 + \dots + a_{KK}x_K^2 &= \mu. \end{aligned} \quad (6)$$

has a positive solution

$$x_1^2 = \frac{\begin{vmatrix} 1 & a_{12} & \dots & a_{1K} \\ 1 & a_{22} & \dots & a_{2K} \\ \vdots & \vdots & \ddots & \vdots \\ 1 & a_{K2} & \dots & a_{KK} \end{vmatrix} \mu}{\det(a_{ij})_{K \times K}}, \dots, x_K^2 = \frac{\begin{vmatrix} a_{11} & a_{12} & \dots & 1 \\ a_{21} & a_{22} & \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ a_{K1} & a_{K2} & \dots & 1 \end{vmatrix} \mu}{\det(a_{ij})_{K \times K}}. \quad (7)$$

Proof. This lemma is a direct consequence of Lemma 4.

Proof of Theorem 2.

Now we write system (5) in the vector form

$$\dot{x} = \text{diag}(a_1, \dots, a_n)x + A(x^2) = G(x),$$

where $x^2 = (x_1^2, \dots, x_n^2)^T$. Since all a_i ($i = 1, \dots, n$) are positive, for sufficiently small positive vector w , we have $G(w) > 0$. Hence, according to Lemma 1, the region $R_+^n + w = \{x \in R_+^n | x_i \geq w_i, i = 1, \dots, n\}$ is positively invariant, and furthermore, we know that all solutions enter ultimately this invariant region. If at least one solution is bounded, then again by Lemma 1, we know that the system possesses a positive equilibrium point x^* . It is easy to check that

$$G_i(\lambda x^*) = a_i x_i^* \lambda (1 - \lambda),$$

then by Lemma 2, x^* is globally stable.

i) When $A \in S_w$, we take a Liapunov function as follows

$$V(x) = \frac{1}{3} \sum_{i=1}^n c_i x_i^3$$

where c_i ($i = 1, \dots, n$) are diagonal elements of a diagonal matrix C such that $CA + A^T C$ is negative definite. Then

$$\dot{V}(x) = (x^2)^T (CA + A^T C)(x^2) + \sum_{i=1}^n c_i a_i x_i^3 < 0,$$

for large enough x . Therefore all solutions are bounded, namely, the system possesses a globally stable positive equilibrium point x^* .

ii) Suppose that $A \notin S_w$. Since the boundedness of at least one solution implies global stability of the system, we only need to check that under condition $A \notin S_w$, the system is not globally stable. Therefore, it is sufficient to show that for any compact set E in R_+^n , there exists an initial $x(0) \notin E$ such that $\Omega(x(0)) \cap E = \emptyset$. Clearly, we can, without loss of generality, suppose that E is the intersection of R_+^n and a given ball with center at the origin 0.

Since $A \notin S_w$, by Lemma 5, we know that there is a minimum $K \geq 2$ such that for any given positive μ , the linear equations (6) have a positive solution (7). Now we take an initial value $x^0 = x(\mu) = (x_1(\mu), \dots, x_n(\mu))$. Here $x_i(\mu)$ ($i = 1, \dots, K$) are

given by (7) for sufficiently large μ and the remaining $x_j(\mu)$ ($j = K + 1, \dots, n$) are sufficiently small such that $G(x(\mu)) > 0$. By Lemma 1, the solution $x(t)$ with the initial value x^0 is increasing for $t \geq 0$. Therefore, either $x(t)$ is unbounded or has an ω -limit set disconnected to E .

This completes the proof of Theorem 2.

5 DISCUSSION

In this paper, based on the specific property of cooperative systems and some results for monotone flow of solutions given by Kamke[10] and Selgrade[24,25], we have obtained the sufficient and necessary conditions for Lotka-Volterra cooperative systems with diffusion to be permanent. Theorem 1 and Example 1 show that if each isolated patch is permanent, then diffusion between patches cannot destroy the permanence, although the diffusion system can have two or more positive equilibrium points.

The global stability of the system is considered and a corollary to guarantee the global stability is obtained. Under the condition of both A and $\bar{A}$ belonging to S_w , the uniqueness of positive equilibrium points ensures global stability.

In Section 4, global asymptotic behavior of a single species dispersing among multiple patches is discussed. Sufficient and necessary conditions for the directed diffusion system to be globally stable are obtained. It is shown that every solution of the system is unbounded if the conditions are failed to be satisfied. This extends a known result for 2-dimensional system[1] to general n -dimensional one.

The key to prove the necessities of both main Theorems 1 and 2 is a result for an essentially positive matrix (Lemma 4) which seems a new one.

It needs to be stated that for a concrete system, the conditions $A \in S_w$ and $\bar{A} \in S_w$ are not difficult to be checked according to Lemma 3. And on the basis of recently developed theory[18] of numerically determining solutions of systems of polynomial

equations, it is also possible to find all positive equilibrium points of system (3) whose number of positive equilibrium points will decide whether it is globally stable or not.

REFERENCES

- [1] Allen L.J.S., Persistence and extinction in single-species reaction-diffusion models, *Bull. Math. Biol.* 45,209-227(1983).
- [2] Allen L.J.S., Persistence and extinction in Lotka-Volterra reaction-diffusion equations, *Math. Biosci.* 65,1-12(1983).
- [3] Allen L.J.S., Persistence, extinction, and critical patch number for island populations. *J. Math. Biol.* 24,617-625(1987).
- [4] Beretta E., A homotopy technique for a linear generalization of Volterra models, *Acta Applicandae Mathematicae* 14,37-47(1989).
- [5] Beretta E. & Takeuchi Y., Global asymptotic stability of Lotka-Volterra diffusion models with continuous time delay, *SIAM J. Appl. Math.* 48,627-651(1988).
- [6] Dunbar S.R., Rybakowski K.P. & Schmitt K., Persistence in model of predator-prey populations with diffusion, *J. Diff. Equations*, 65,117-138(1986).
- [7] Freedman H.I. & Takeuchi, Y., Global stability and predator dynamics in a model of prey dispersal in a patchy environment, *Nonl. Anal. TMA.* 13,993-1002(1989).
- [8] Hastings A., Global stability in Lotka-Volterra systems with diffusion, *J. Math. Biol.* 6,163-168(1978).
- [9] Hofbauer J. & Sigmund K., *The theory of evolution and dynamical systems*, Cambridge Univ. Press (1988).
- [10] Kamke E., *Zur theorie der systeme gewöhnlicher differentialgleichungen*, II, *Acta Math.* 58,57-85(1932).
- [11] Kishimoto K., The diffusive Lotka-Volterra system with three species can have a stable non-constant equilibrium solution, *J. Math. Biol.* 16,103-112(1982).
- [12] Kishimoto K., A stable spatially nonconstant equilibrium of Lotka-Volterra two-patch system with May-Leonard dynamics, in "Biomathematics and Related Computational Problems" (L.M. Ricciardi, Ed.) 331-335, Reidel, Amsterdam(1988).
- [13] Kishimoto K., Coexistence of any number of species in the Lotka-Volterra competitive system over two-patches, *Theor. Pop. Biol.* 38,149-158(1990).
- [14] Kishimoto K., Mimura M. & Yoshida K., Stable spatio-temporal oscillations of diffusive Lotka-Volterra system with three or more species, *J. Math. Biol.* 18,213-221(1983).

- [15] Leung A., Limiting behavior for a prey-predator model with diffusion and crowding effects, *J. Math. Biol.* 6, 87-93 (1978).
- [16] Levin S.A., Dispersion and population interactions. *Am. Nat.* 108, 207-228 (1974).
- [17] Levin S.A., Spatial patterning and the structure of ecological communities. Some mathematical questions in biology (Levin S.A. Ed.) Vol. 7. *Am. Math. Soc.*, Providence, R.I., 1-36 (1976).
- [18] Li T.Y., Sauer T. & Yorke J.A., Numerically determining solutions of systems of polynomial equations, *Bull. Amer. Math. Soc.*, 18, 173-177 (1988).
- [19] Lu Z.Y. & Takeuchi Y., Permanence and global stability for cooperative Lotka-Volterra diffusion systems, *Nonl. Anal. TMA.*, in press.
- [20] Lu Z.Y. & Takeuchi Y., Global asymptotic behavior in single-species discrete diffusion systems, submitted.
- [21] Ludwig D., Aronson D.G. & Weinberger H.F., Spatial patterning of the spruce budworm, *J. Math. Biol.*, 8, 217-258 (1979).
- [22] Redheffer R., Redlinger R. & Walter W., A theorem of LaSalle-Lyapunov type for parabolic systems, *SIAM J. Math. Anal.* 19, 121-132 (1988).
- [23] Rothe F., Convergence to the equilibrium state in the Volterra-Lotka diffusion equations, *J. Math. Biol.* 3, 319-324 (1976).
- [24] Selgrade J.F., Asymptotic behavior of solutions to a single loop positive feedback system, *J. Diff. Equations*, 38, 80-103 (1980).
- [25] Selgrade J.F., On the existence and uniqueness of connecting orbits, *Nonl. Anal. T.M.A.*, 7, 1123-1125 (1983).
- [26] Skellam J.D., Random dispersal in theoretical populations. *Biometrika*, 38, 196-218 (1951).
- [27] Takeuchi Y., Global stability in generalized Lotka-Volterra diffusion systems, *J. Math. Anal. Appl.* 116, 209-221 (1986).
- [28] Takeuchi Y., Cooperative systems theory and global stability of diffusion models, *Acta Applicandae Mathematicae* 14, 49-57 (1989).
- [29] Takeuchi Y., Diffusion-mediated persistence in two-species competition Lotka-Volterra model, *Math. Biosci.* 95, 65-83 (1989).
- [30] Takeuchi Y., Conflict between the need to forage and the need to avoid competition: Persistence of two species model, *Math. Biosci.* 99, 181-194 (1990).
- [31] Takeuchi Y., Diffusion-mediated persistence in three-species competition models with heteroclinic cycles, *Math. Biosci.*, 106, 111-128 (1991).