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Permanence and global attractivity for Lotka–Volterra difference systems

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Abstract. The permanence and global attractivity for two-species difference systems of Lotka–Volterra type are considered. It is proved that a cooperative system cannot be permanent. For a permanent competitive system, the explicit expression of the permanent set E is obtained and sufficient conditions are given to guarantee the global attractivity of the positive equilibrium of the system.

Key words: Discrete model – Lotka–Volterra type – Permanence – Global attractivity

1. Introduction

The question of whether all species in a multispecies community can be permanent is very important in the theoretical ecology. There have been many mathematical studies for the permanence of models governed by differential equations in the literature (see [6–11] and the references cited therein). It is known that some ecological factors do not affect the conditions of the permanence of species, but others are indeed the reasons of extinction of populations. For differential equation models, for examples, time delays are harmless for the permanence of prey- predator system of Lotka–Volterra type [7] and two species competition model of Lotka–Volterra type [6], but delays destroy the

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permanence of cooperative systems [11] and pery-predator system with functional response [9]. In contrast, studies for the difference population models are mostly related to the local stability of equilibria or the existence of strange attractors. Few papers concern with the collapse of permanence of population models governed by difference systems. In this paper, we consider the following discrete population model

$$\begin{aligned} x_{n+1} &= x_n \exp(r_1 - a_{11}x_n + a_{12}y_n), \\ y_{n+1} &= y_n \exp(r_2 + a_{21}x_n - a_{22}y_n), \end{aligned} \tag{1}$$

where r_i are constants, $A = (a_{ij})_{2\times 2}$ is a contant matrix with $a_{ii} > 0$, $i = 1, 2$ and $a_{ij} \neq 0\,(j \neq i, i = 1, 2)$, x_n represents the density of first species at nth generation, y_n the density of second species at nth generation.

One objective of this paper is to consider the permanence of system (1). System (1) is said to be permanent if there is a compact set E in the interior of R^2_+ such that for each positive initial position, the orbit of system (1) through this initial position eventually enters and remains in E. To facilitate comparisons, let us consider the counterpart of system (1) in the continuous case.

$$\begin{aligned} \frac{dx}{dt} &= x(r_1 - a_{11}x + a_{12}y) \\ \frac{dy}{dt} &= y(r_2 + a_{12}x - a_{22}y) \end{aligned} \tag{2}$$

where r_i and a_{ij} are the same as those in (1). If $a_{11}a_{22} > a_{12}a_{21}$, it is well known that the existence of positive equilibrium in (2) ensures its permanence. If system (1) is a prey-predator sysytem ($a_{12}a_{21} < 0$) or the two species in (1) are competitive ($a_{12} < 0$, $a_{21} < 0$), a theorem in [4] shows that the existence of positive equilibrium in (1) guarantees its permanence. This means that from the point of view of permanence, system (1) has the same qualitative property as its counterpart ODE system. If (1) is cooperative, by adopting the technique of [4] we will show that it can not be permanent in any case. More specifically, we will show that under the condition $a_{11}a_{22} > a_{12}a_{21}$, there is a set in the interior of R^2_+ such that forward orbits of cooperative system (1) starting from this set tend to the union of positive x-axis and y-axis with

$$\liminf_{n\to\infty} x_n = 0 \qquad \limsup_{n\to\infty} x_n = \infty$$

$$\liminf_{n\to\infty} y_n = 0 \qquad \limsup_{n\to\infty} y_n = \infty$$

Hence, sufficiently small statistical fluctuations can lead to extinction of any species. Note that one species is permanent in the absence of the other one, it implies that an invasion of a cooperative species may be deteriorative to the permanence of populations governed by difference equations.

The second purpose of this paper is to obtain permanent region of system (1) in competition case, which is formulated in terms of parameters of the system. In practice, one can choose the parameters according to the formulae so that the numbers of the two species eventually lie in desired region. For example, controlling the parameters such that eventual numbers of the species are greater than those for mating and searching food together. We are also interested in the global attractivity of positive equilibrium of system (1) in competition case. We will show that strong density-dependent coefficients of the two species imply the global attractivity of positive equilibrium of the system.

The organization of this paper is as follows. In next section, we show that system (1) in cooperative case can not be permanent in any case. Section 3 derives explict permanent region for (1) in competition case. In Sect. 4, we establish sufficient conditions for the global attractivity of positive equilibrium of (1) in competition case. A concluding remark follows at Sect. 5.

2. Cooperative system

Let us consider system (1) in cooperative case, i.e.,

$$\begin{aligned} x_{n+1} &= x_n \exp(r_1 - a_{11}x_n + a_{12}y_n), \\ y_{n+1} &= y_n \exp(r_2 + a_{21}x_n - a_{22}y_n), \end{aligned} \tag{3}$$

where $a_{ij} > 0$. If $r_1 = r_2 = r > 0$, $a_{11} = a_{22} = a$ and $a_{12} = a_{21} = b$ with $\exp(r) > a/b > 1$, paper [4] has proved that system (3) can have unbounded orbits. In this section, by using the technique of [4], we can prove following general result for system (3).

Theorem 1. *System* (3) *is not permanent.*

Proof. For convenience, we rewrite system (3) into the following form

$$\begin{aligned} x' &= x \exp(r_1 - a_{11}x + a_{12}y), \\ y' &= y \exp(r_2 + a_{21}x - a_{22}y). \end{aligned} \tag{4}$$

Define continuous function $V(x, y)$ by

$$V(x, y) = x^{\alpha} y^{\beta}.$$

where

$$\alpha = \begin{cases} a_{21} & \text{if } \det(A) = 0 \\ (a_{21} + a_{22})/|\det(A)| & \text{if } \det(A) \neq 0 \end{cases}$$

$$\beta = \begin{cases} a_{11} & \text{if } \det(A) = 0 \\ (a_{11} + a_{12})/|\det(A)| & \text{if } \det(A) \neq 0 \end{cases}$$

Case 1. Suppose $\det(A) = 0$. Along the orbits of (4), we have

$$V(x', y') = V(x, y) \exp(r_1 a_{21} + r_2 a_{11}). \tag{5}$$

If $\Delta = r_1 a_{21} + r_2 a_{11} = 0$, then $V(x, y)$ is invariant along the orbits of (4). In this case, for any given compact set E in the interior of R^2_+, we can take sufficiently large C such that $\{(x, y) | V(x, y) = C\} \cap E = \emptyset$. This implies the nonpermanence of the system.

If $\Delta = r_1 a_{21} + r_2 a_{11} > 0\,(<0)$, then $\exp(\Delta) > 1(<1)$. It follows from (5) that for any given compact set E in the interior of R^2_+, there is a positive orbit of (4) leaving ultimately E and will not return E afterwards. Therefore, system (3) remains not permanent in this case.

Case 2. Suppose $\det(A) < 0$. Along the orbits of (4), we have

$$V(x', y') = V(x, y) \exp(\bar{\Delta} + x + y), \tag{6}$$

where $\bar{\Delta} = (\Delta + r_1 a_{22} + r_2 a_{12})/|\det(A)|$. Since $x > 0$ and $y > 0$, we have, for $\lambda \in (0, 1)$,

$$\lambda x + (1 - \lambda) y \geqq x^{\lambda} y^{1-\lambda}.$$

By taking $\mu = (\alpha + \beta)^{(-1)}$ and $0 < k < \min\{(\alpha\mu)^{(-1)}, (\beta\mu)^{(-1)}\}$, we obtain

$$x + y \geqq k(x^{\alpha} y^{\beta})^{\mu}. \tag{7}$$

As a consequence, (6) leads to

$$V(x', y') \geqq V(x, y) \exp[\bar{\Delta} + k(V(x, y))^{\mu}].$$

Since $k > 0$ and $\mu > 0$, one can take $M > 0$ large enough such that $\varepsilon = \bar{\Delta} + kM^{\mu} > 0$. If we define the region U_M by $U_M = \{(x, y) \in R^2_+ | V(x, y) \geqq M\}$, then (4) maps U_M into $U_{M\exp(\varepsilon)}$. Therefore, all the orbits starting in U_M are unbounded.

Case 3. Suppose $det(A) > 0$. By similar calculations to that in case 2, we have

$$(x')^{\alpha} (y')^{\beta} = x^{\alpha} y^{\beta} \exp(\bar{\Delta} - x - y).$$

Following [4], we consider the regions

$$B_N = \{(x, y) \in R^2_+ | x^\alpha y^\beta \leqq N\},$$

$$B^x_M = \{(x, y) \in R^2_+ | x \geqq M,\ y \geqq x \exp(-Ax)\},$$

$$B^y_M = \{(x, y) \in R^2_+ | y \geqq M,\ x \geqq y \exp(-Ay)\},$$

where $N > 0$ is arbitrarily fixed, $A = \frac{1}{2}\min\{a_{12}, a_{21}\}$ and $M > 0$ is sufficiently large. We claim that (4) maps $B_N \cap B^x_M$ (similarly, $B_N \cap B^y_M$) into $B_N \cap B^y_{M\varepsilon}$ (similarly, $B_N \cap B^x_{M\varepsilon}$) with $\varepsilon > 1$. By iteration, this shows that all orbits starting in $B_N \cap B^x_M$ are unbounded.

Let $(x, y) \in B_N \cap B^x_M$. Then for large M,

$$(x')^\alpha (y')^\beta \leqq x^\alpha y^\beta \exp(\bar{\Delta} - M) \leqq x^\alpha y^\beta \leqq N. \tag{8}$$

Moreover,

$$\begin{aligned} y' &= y \exp(r_2 + a_{21}x - a_{22}y) \\ &\geqq \exp(r_2 + a_{21}x - a_{22}y) \cdot x \exp(-Ax) \\ &= x \exp(r_2 + (a_{21} - A)\, x - a_{22}y) \\ &\geqq x \exp(r_2 + \tfrac{1}{2}\, a_{21}M - a_{22}N^{1/\beta}/M^{\alpha/\beta}) \\ &\geqq x \exp(1/4a_{21}M) \quad (M \text{ large}) \\ &= \varepsilon x \geqq \varepsilon M > M > 1/A. \quad (M \text{ large}) \end{aligned} \tag{9}$$

Since $y \to y \exp(-Ay)$ is monotonically decreasing for $y > 1/A$, we have

$$\begin{aligned} x'/y' \exp(-Ay') &\geqq x \exp(r_1 - a_{11}x + a_{12}y)/(\varepsilon x \exp(-A\varepsilon x)) \\ &= \frac{1}{\varepsilon} \exp[r_1 + (A\varepsilon - a_{11})\, x + a_{12}y] \\ &\geqq \frac{1}{\varepsilon} \exp[r_1 + (A\varepsilon - a_{11})\, M] > 1 \quad (M \text{ large}). \end{aligned} \tag{10}$$

Clearly, (8), (9) and (10) imply $(y', x') \in B_N \cap B^y_{M\varepsilon}$.

This completes the proof of Theorem 1. □

Remark. Suppose $\det(A) > 0$. From the proof, we see that positive orbits of (4) starting from $B^y_M \cup B^x_M$ satisfy

$$\liminf_{n\to\infty} x_n = 0 \qquad \limsup_{n\to\infty} x_n = \infty$$

$$\liminf_{n\to\infty} y_n = 0 \qquad \limsup_{n\to\infty} y_n = \infty$$

Hence, sufficiently small statistical fluctuations can lead to extinction of any species. This means that the two species take the great risk of extinction in practice although they are cooperative and each one can be permanent in the absence of the other one.

3. Competitive system

Let us consider the competitive case, i.e.,

$$\begin{aligned} x_{n+1} &= x_n \exp\{r_1 - a_{11}x_n - a_{12}y_n\}, \\ y_{n+1} &= y_n \exp\{r_2 - a_{21}x_n - a_{22}y_n\}, \end{aligned} \tag{11}$$

where $a_{ij} > 0$ and $r_i > 0$. It is known that if the following conditions hold

$$r_2a_{11} - r_1a_{21} > 0, \qquad r_1a_{22} - r_2a_{12} > 0, \tag{12}$$

then system (11) is permanent. Note that two inequalities in (12) imply

$$a_{11}a_{22} - a_{12}a_{21} > 0. \tag{13}$$

The purpose of Theorem 2 below is to obtain the eventual upper bound and lower bound for positive solutions of (11), and hence to give a suitable set E (in Definition 1) explicitly.

Lemma 1. *Let*

$$M_1(\varepsilon) = (\varepsilon + r_1)\, e^{r_1}/a_{11}, \qquad M_2(\varepsilon) = (\varepsilon + r_2)\, e^{r_2}/a_{22},$$

where $\varepsilon > 0$ *is arbitrarily fixed. Then for each positive solution of system* (11), *there is a* $\bar{N} > 0$ *such that*

$$x_n < M_1(\varepsilon) \qquad y_n < M_2(\varepsilon) \quad \text{for } n > \bar{N} \qquad \square$$

Proof. First, we claim that it is impossible that $x_n \geqq (\varepsilon + r_1)/a_{11}$ for all large n. If not, (11) implies that there exists a $N_1 > 0$ such that

$$x_{n+1} \leqq x_n \exp(r_1 - a_{11}x_n) \leqq x_n \exp(-\varepsilon),$$

for all $n > N_1$. It follows that x_{n+1} tends to zero as n approaches infinity. This is a contradiction to $x_n \geqq (\varepsilon + r_1)/a_{11}$. Therefore, there is a $p_1 \in N$, where N denotes the set of nonnegative integers, such that

$$x_{p_1} < (\varepsilon + r_1)/a_{11}.$$

Then by (11) we have

$$x_{p_1+1} \leqq x_{p_1} e^{r_1} < (\varepsilon + r_1)\, e^{r_1}/a_{11} = M_1(\varepsilon).$$

If $x_{p+1} < (\varepsilon + r_1)/a_{11}$, similar argument leads to $x_{p_1+2} < M_1(\varepsilon)$. If

$$x_{p_1+1} \geqq (\varepsilon + r_1)/a_{11},$$

it is easy to see

$$x_{p_2+2} < x_{p_1+1} e^{-\varepsilon} < M_1(\varepsilon).$$

Thus, in any case, $x_{p_1+2} < M_1(\varepsilon)$. In the same way, we can show that $x_n < M_1(\varepsilon)$ for all $n > p_1$. The second conclusion of Lemma 1 follows similarly. This completes the proof of Lemma 1. □

Theorem 2. *If* (12) *holds, any positive orbit of system* (11) *satisfies*

$$(x_n, y_n) \in E = \{(x, y) | (m_1(\varepsilon), m_2(\varepsilon)) \leqq (x, y) \leqq (M_1(\varepsilon), M_2(\varepsilon))\}$$

for all large n. Here $m_1(\varepsilon)$ *and* $m_2(\varepsilon)$ *are given in* (16).

Proof. Our objective is to show that any positive orbit $z(n) = (x_n, y_n)$ of system (11) eventually enters and remains in E.

Let

$$V_1(x_{n+1}, y_{n+1}) = x_{n+1}^{-a_{21}} y_{n+1}^{a_{11}}.$$

Then calculating $V_1(x_{n+1}, y_{n+1})/V_1(x_n, y_n)$ along the orbit $z(n)$, we have

$$V_1(x_{n+1}, y_{n+1}) = V_1(x_n, y_n) \exp\{r_2 a_{11} - r_1 a_{21} - (a_{11}a_{22} - a_{12}a_{21})\, y_n\}.$$

Let $\varepsilon > 0$ be sufficiently small. Since $a_{11}a_{22} - a_{12}a_{21} > 0$ by the assumption of the theorem, we see that

$$V_1(x_{n+1}, y_{n+1}) \geqq V_1(x_n, y_n)\, e^{\varepsilon}, \tag{14}$$

if

$$y_n < (r_2 a_{11} - r_1 a_{21} - \varepsilon)/(a_{11}a_{22} - a_{12}a_{21}) \triangleq h_1(\varepsilon).$$

Define

$$V_2(x_{n+1}, y_{n+1}) = x_{n+1}^{a_{22}} y_{n+1}^{-a_{12}}.$$

It follows by a similar argument that

$$V_2(x_{n+1}, y_{n+1}) \geqq V_2(x_n, y_n)\, e^{\varepsilon}, \tag{15}$$

if

$$x_n < (r_1 a_{22} - r_2 a_{12} - \varepsilon)/(a_{11}a_{22} - a_{12}a_{21}) \triangleq h_2(\varepsilon).$$

Define curves L_1 and L_2 respectively by

$$L_1\colon x^{-a_{21}} y^{a_{11}} = H_1 \quad (0 < x \leqq M_1(\varepsilon)),$$

where positive constant H_1 satisfies

$$H_1 = M_1^{-a_{21}} (h_1(\varepsilon) \exp(r_2 - a_{22} M_2(\varepsilon) - a_{21} M_1(\varepsilon)))^{a_{11}},$$

$$L_2\colon x^{a_{22}} y^{-a_{12}} = H_2 \qquad (0 < y \leqq M_2(\varepsilon)),$$

in which positive constant H_2 satisfies

$$H_2 = (h_2(\varepsilon)\exp(r_1 - a_{11}M_1(\varepsilon) - a_{12}M_2(\varepsilon)))^{a_{22}}M_2^{-a_{12}}.$$

It is easy to verify that there is a unique intersection point $(m_1(\varepsilon), m_2(\varepsilon))$ of L_1 with L_2 in which

$$\begin{aligned} m_1(\varepsilon) &= (H_2^{a_{11}}H_1^{a_{12}})^{1/(a_{11}a_{22}-a_{12}a_{21})}, \\ m_2(\varepsilon) &= (H_2^{a_{21}}H_1^{a_{22}})^{1/(a_{11}a_{22}-a_{12}a_{21})}. \end{aligned} \tag{16}$$

Let D denote the region enclosed by L_1, L_2, $x = M_1(\varepsilon)$ and $y = M_2(\varepsilon)$.

In the following we will show that the orbit $z(n)$ enters and remains in the region E when n is sufficiently large. Note that $D \subset E$. First, By lemma 1 the orbit lies in the set $\{0 < x < M_1(\varepsilon); 0 < y < M_2(\varepsilon)\}$ when $n \geqq p$. Secondly, we cliam that it is impossible that $y_n < h_1(\varepsilon)$ for all $n > p$. Assuming the contrary we obtain from (14) that

$$V_1(x_{n+1}, y_{n+1}) \to \infty \quad \text{as } n \to \infty.$$

It follow from the definition of V_1 and lemma 1 that $x_n \to 0$ as $n \to \infty$. Then using (15) we obtain $V_2(x_{n+1}, y_{n+1}) \to \infty$ as $n \to \infty$, which implies that $y_n \to 0$ as $n \to \infty$. As a consequence, by (11) we have

$$x_{n+1} > x_n e^{r_1/2},$$

when n is large enough. It follows that $x_n \to \infty$ as $n \to \infty$. We are led to a contradiction. Therefore, there is a $n_1 > p$ such that $y_{n_1} \geqq h_1(\varepsilon)$.

Now we show that the orbit lies above the curve L_1 when $n \geqq n_1$. First, by lemma 1, we have

$$y_{n_1+1} \geqq h_1(\varepsilon)\exp(r_2 - a_{21}M_1(\varepsilon) - a_{22}M_2(\varepsilon)).$$

As a result we have

$$V_1(x_{n_1+1}, y_{n_1+1}) \geqq M_1^{-a_{21}}(h_1(\varepsilon)\exp(r_2 - a_{21}M_1(\varepsilon) - a_{22}M_2(\varepsilon)))^{a_{11}}.$$

Now we claim that

$$V_1(x_{n_1+2}, y_{n_1+2}) \geqq M_1^{-a_{21}}(h_1(\varepsilon)\exp(r_2 - a_{21}M_1(\varepsilon) - a_{22}M_2(\varepsilon)))^{a_{11}}. \tag{17}$$

In fact, in the case where $y_{n_1+1} \geqq h_1(\varepsilon)$, it is obvious since

$$y_{n_1+2} \geqq h_1(\varepsilon)\exp(r_2 - a_{21}M_1(\varepsilon) - a_{22}M_2(\varepsilon)),$$

and $x_{n_1+2} < M_1(\varepsilon)$. In the case that $y_{n_1+1} < h_1(\varepsilon)$, it is true because (14) implies

$$V_1(x_{n_1+2}, y_{n_1+2}) > V_1(x_{n_1+1}, y_{n_1+1})$$

As a result of (17), we conclude $z(n_1 + 2)$ must be above the curve L_1. Finally, by induction we can conclude that $z(n)$ lies above the curve L_1 for all $n \geqq n_1$. Similarly, we can show that there is a $n_2 > p$ such that $z(n)$ lies in the right of the curve L_2 for all $n > n_2$. Consequently, the orbit eventually enters and remains in the region E. The proof of the Theorem 2 is completed. □

Example. Let us consider

$$x_{n+1} = x_n \exp\{0.5 - x_n - 0.5y_n\}$$
$$y_{n+1} = y_n \exp\{0.5 - 0.5x_n - y_n\},$$

By direct calculations, we see that any positive solution of this model satisfies

$$0.030895 \leqq \liminf_{n\to\infty} x_n, \qquad \limsup_{n\to\infty} x_n \leqq 0.824361$$
$$0.030895 \leqq \liminf_{n\to\infty} y_n, \qquad \limsup_{n\to\infty} y_n \leqq 0.824361$$

Here, we obtain an explicit estimate on eventual lower bound and eventual upper bound of the species.

4. Global attractivity

The purpose of this section is to establish sufficient conditions under which the positive equlibrium of (11) is globally attractive. By the transformation of $x_n = r_1\bar{x}_n/a_{11}$ and $y_n = r_2\bar{y}_n/a_{22}$, (11) can be written as

$$\begin{aligned} x_{n+1} &= x_n \exp[r_1(1 - x_n - \mu_1 y_n)], \\ y_{n+1} &= y_n \exp[r_2(1 - \mu_2 x_n - y_n)]. \end{aligned} \tag{18}$$

with $\mu_1 = r_2a_{12}/(r_1a_{22})$ and $\mu_2 = r_1a_{21}/(r_2a_{11})$, where we used x_n, y_n instead of $\bar{x}_n$, $\bar{y}_n$. In the symmetric case, i.e., $r_1 = r_2$ and $\mu_1 = \mu_2$, the existence and local stability of all possible two-cycles are determined and the bifurcations of periodic points of low period are studied in [3]. For the general case, [4] or Theorem 2 shows that system (18) is permanent if $\mu_1 < 1$ and $\mu_2 < 1$. We show below that these permanence conditions, together with small growth rates r_i, ensure that the positive equilibrium is globally attractive.

Theorem 3. *If* $\mu_1 < 1$, $\mu_2 < 1$ *and* $r = \max\{r_1, r_2\}$ *is small enough, system* (18) *has a global attractor*

$$(x^*, y^*) = [(1 - \mu_1)/(1 - \mu_1\mu_2), (1 - \mu_2)/(1 - \mu_1\mu_2)].$$

Proof. By the transformation

$$\bar{x}_n = x_n - x^*, \qquad \bar{y}_n = y_n - y^*,$$

(18) becomes

$$x_{n+1} + x^* = (x_n + x^*)\exp[-r_1(x_n + \mu_1 y_n)],$$

$$y_{n+1} + y^* = (y_n + y^*)\exp[-r_2(\mu_2 x_n + y_n)], \tag{19}$$

here we used x_n, y_n instead of $\bar{x}_n$, $\bar{y}_n$. Clearly, the global attractivity of (x^*, y^*) of system (18) is equivalent to that for (19),

$$(x_n, y_n) \to 0 \quad \text{as } n \to +\infty \tag{20}$$

whenever $(x_0, y_0) > (-x^*, -y^*)$.

Case 1. Suppose $\{x_n\}$ is monotonic for all large n. Since system (18) is permanent, it suffices to consider the solutions $\{(x_n, y_n)\}$ of (19) which are bounded and satisfy $x_n + x^* > 0$, $y_n + y^* > 0$. Suppose $x_n \to c_1$ as $n \to \infty$. By the first equation in (19), we have $y_n \to c_2$. Since $x^* + c_1 > 0$, $y^* + c_2 > 0$ and $\mu_1, \mu_2 < 1$, we obtain $c_1 = c_2 = 0$. Hence (20) holds.

Case 2. Suppose $x_n \geqq 0$ and $y_n \leqq 0$ for all alrge n. Then since $\{x_n\}$ and $\{y_n\}$ are bounded, one can set

$$U_x = \limsup x_n, \qquad V_x = \liminf x_n,$$

$$-U_y = \limsup y_n, \qquad -V_y = \liminf y_n.$$

It is evident that U_x, U_y, V_x and V_y are nonnegative. If x_n (or y_n) is monotonic for large n, repeating the procedure in Case 1 leads to what we desire. If both x_n and y_n are not monotone eventually, there is a subsequence $\{x_{n_k}\}$ such that $x_{n_k+1} \geqq x_{n_k}$ and $x_{n_k+1} \to U_x$ as $n_k \to \infty$. Therefore, by the definitions of U_x, U_y, V_x and V_y, we have, for any $\varepsilon > 0$,

$$-V_y - \varepsilon < y_n < -U_y + \varepsilon, \tag{21}$$

for large n, and

$$U_x - \varepsilon < x_{n_k+1}, \tag{22}$$

for large $n_k + 1$.

Since $x_{n_k+1} \geqq x_{n_k}$, we have from (19) that $-r_1(x_{n_k} + \mu_1 y_{n_k}) \geqq 0$, i.e.,

$$x_{n_k} + \mu_1 y_{n_k} \leqq 0. \tag{23}$$

(21) and (23) lead to

$$x^* + x_{n_k} \leqq x^* - \mu_1 y_{n_k} \leqq x^* + \mu_1(\varepsilon + V_y). \tag{24}$$

Clearly, (19), (21), (22) and (24) imply

$$\begin{aligned}\frac{x^* + U_x - \varepsilon}{x^* + \mu_1(V_y + \varepsilon)} &< \frac{x^* + U_x - \varepsilon}{x^* + x_{n_k}} \\ &\leqq \frac{x^* + x_{n_k+1}}{x^* + x_{n_k}} \\ &= \exp[-r_1(x_{n_k} + \mu_1 y_{n_k})] \\ &< \exp\{-r_1[V_x - \varepsilon + \mu_1(-V_y - \varepsilon)]\}.\end{aligned}$$

Let $\varepsilon \to 0$, we have

$$\frac{x^* + U_x}{x^* + \mu_1 V_y} \leqq \exp[-r_1 V_x + r_1 \mu_1 V_y]. \tag{25}$$

Similarly, by considering a subsequence y_{n_l} of $\{y_n\}$ with $y_{n_l} \geqq y_{n_l+1}$ and $y_{n_l+1} \to -V_y$ as $n_l \to \infty$, we have

$$\frac{y^* - V_y}{y^* - \mu_2 U_x} \geqq \exp[-r_2\mu_2 U_x + r_2 V_y]. \tag{26}$$

Since $\mu_1 < 1$ and $\mu_2 < 1$ and r is small enough, it follows from (24) and (25) in [6] that both (25) and (26) hold if and only if $U_x = U_y = 0$, and therefore, $U_y = V_x = 0$.

Case 3. Suppose $x_n \geqq 0$ (or $x_n \leqq 0$) for all large n, but y_n oscillates about 0, i.e., for any n, there are y_m and y_l with $m > n$, $l > n$ such that $y_m > 0$ and $y_l < 0$.

We only consider the case $x_n \geqq 0$, the other case being similar.

Set

$$U_x = \limsup x_n, \qquad V_x = \liminf x_n,$$
$$U_y = \limsup y_n, \qquad -V_y = \liminf y_n.$$

By a similar procedure as in Case 2, we can obtain four inequalities

$$\frac{x^* + U_x}{x^* + \mu_1 V_y} \leqq \exp[-r_1 V_x + r_1\mu_1 V_y], \tag{27}$$

$$\frac{x^* + V_x}{x^* - \mu_1 U_y} \geqq \exp[-r_1 U_x - r_1\mu_1 U_y], \tag{28}$$

$$\frac{y^* + U_y}{y^* - \mu_2 V_x} \leqq \exp[-r_2\mu_2 V_x + r_2 V_y], \tag{29}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_x} \geqq \exp[-r_2\mu_2 U_x - r_2 U_y]. \tag{30}$$

(i) If $U_x \geqq U_y$, by (27) and (30) we have

$$\frac{x^* + U_x}{x^* + \mu_1 V_y} \leqq \exp[r_1 \mu_1 V_y], \tag{31}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_x} \geqq \exp[-r_2(\mu_2 + 1)\ U_x]. \tag{32}$$

(ii) If $U_x \leqq U_y$, then (29) and (30) lead to

$$y^* + U_x \leqq y^* \exp[r_2 V_y], \tag{33}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_y} \geqq \exp[-r_2(\mu_2 + 1)\ U_y]. \tag{34}$$

Since both (31), (32) and (33), (34) take the form of (25), (26), we can prove $U_x = U_y = V_x = V_y = 0$ as in the Case 2.

Case 4. Suppose that both x_n and y_n oscillate about 0. In this case, let us set

$$U_x = \limsup x_n, \qquad V_x = -\liminf x_n,$$

$$U_y = \limsup y_n, \qquad V_y = -\liminf y_n.$$

Similarly, we can obtain four inequalities

$$\frac{x^* + U_x}{x^* + \mu_1 V_y} \leqq \exp[r_1(V_x + \mu_1 V_y)], \tag{35}$$

$$\frac{y^* + U_y}{y^* + \mu_2 V_x} \leqq \exp[r_2(\mu_2 V_x + V_y)], \tag{36}$$

$$\frac{x^* - V_x}{x^* - \mu_1 U_y} \geqq \exp[-r_1(U_x + \mu_1 U_y)], \tag{37}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_x} \geqq \exp[-r_2(\mu_2 U_x + U_y)]. \tag{38}$$

(i) If $V_x \leqq V_y$ and $U_x \leqq U_y$, by (36) and (38) we have

$$\frac{x^* + U_y}{x^* + \mu_2 V_y} \leqq \exp[r_2(1 + \mu_2)\ V_y], \tag{39}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_y} \geqq \exp[-r_2(1 + \mu_2)\ U_y]. \tag{40}$$

(ii) If $V_x \leqq V_y$ and $U_x \geqq U_y$, by (35) and (38) we have

$$\frac{x^* + U_x}{x^* + \mu_1 V_y} \leqq \exp[r_1(1 + \mu_1)\, V_y], \tag{41}$$

$$\frac{y^* - V_y}{y^* - \mu_2 U_x} \geqq \exp[-r_2(1 + \mu_2)\, U_x]. \tag{42}$$

Since both (39), (40) and (41), (42) take the form of (25) and (26), we can obtain $U_x = U_y = V_x = V_y = 0$ as in the Case 2. This completes the proof of Theorem 3.

5. Concluding remark

We have shown that discrete cooperative difference system (1) cannot be permanent in any case although the counterpart in the continuous case can be permanent for a large range of parameters. Especially, in the case that each species can be permanent and the intra-specific competitions of two species are greater than their cooperative strength ($a_{11}a_{22} > a_{12}a_{21}$), we proved that there is a set of initial values with positive measure such that positive orbits of (1) starting from this set approach x-axis and y-axis , in an oscillating way, as n approaches ∞. This is something similar to that in [12] where the orbits of system of three competing species approach the boundary of R^3_+ in a spiral way. This result indicates that an invasion of a cooperative species may produce negative effect on the original one. For a permanent competitive system (18), it is proved that if the growth rates r_1 and r_2 are small enough, then the positive equilibrium is a global attractor. If system (1) is a prey-predator one, we can write it into the following form

$$\begin{aligned} x_{n+1} &= x_n \exp[r_1(1 - x_n - \mu_1 y_n)], \\ y_{n+1} &= y_n \exp[r_2(\delta + \mu_2 x_n - y_n)], \end{aligned} \tag{43}$$

where r_1, r_2, μ_1 and μ_2 are positive, $\delta = 1$ or -1, or 0.

The method for proving the global attractivity of competitive system (18) seems applicable to prey-predator system (43) in the case of $\mu_1\mu_2 < 1$. Namely, the smallness of r_1 and r_2 implies the global attractivity for the positive equilibrium of (43), provided that the system is permanent.

In general, for a Lotka–Volterra difference system, the permanence and global attractivity are very different. In our case, the region of parameter space where global attractivity holds is a very small subset of that where permanence holds. Namely, we need r_i in (18) to be small to ensure the global attractivity. If $r_i, i = 1, 2$, are large, it may be expected that the dynamical behavior will be complicated, perhaps leading to chaos, although the system is still permanent. In fact, Dohtani's result [2] implies that for permanent system (18), if $r_1(= r_2)$ is large enough ($r_1 \geqq 3.13$), then the system yields chaos in the sense of Diamond [1].

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