Convex dominates concave : An exclusion principle in discrete-time Kolmogorov systems

Kon, Ryusuke
Faculty of Mathematics, Kyushu University

出版情報：Proceedings of the American Mathematical Society. 134 (10), pp.3025-3034, 2006-10. American Mathematical Society

MHF Preprint Series

Kyushu University
21st Century COE Program
Development of Dynamic Mathematics with High Functionality

Convex dominates concave: an exclusion principle in discrete-time Kolmogorov systems

R. Kon

MHF 2004-27

(Received October 14, 2004)

Faculty of Mathematics
Kyushu University
Fukuoka, JAPAN

CONVEX DOMINATES CONCAVE: AN EXCLUSION PRINCIPLE IN DISCRETE-TIME KOLMOGOROV SYSTEMS

RYUSUKE KON

Abstract. We establish an exclusion principle in discrete-time Kolmogorov systems by using average Liapunov functions. The exclusion principle shows that a weakly dominant species with a convex logarithmic growth rate function eliminates species with concave logarithmic growth rate functions. A general result is applied to specific population models. This application gives an improved exclusion principle for the specific population models.

1. Introduction

In this paper, we consider population dynamics governed by difference equations. One of the most popular types of population models has the following form:

$$x_i(t+1) = x_i(t)g_i(x(t)),\ \ i = 1, \dots , n. \tag{1.1}$$

This type of population models is called Kolmogorov type. The valuable $x_i(t)$ represents a population density of species i at time t and $x(t)$ is a vector of population densities $x(t) = (x_1(t), \dots , x_n(t))^\top$. We focus on the solutions of (1.1) in the nonnegative cone $\mathbb{R}^n_+ := \{x \in \mathbb{R}^n : x_1 \geq 0, \dots , x_n \geq 0\}$. The function g_i is a growth rate of species i, which depends on the vector of population densities $x(t)$. Depending on the property of the functions g_i, System (1.1) can represent several kinds of species interactions, e.g., predator-prey, competitive and cooperative interactions.

From several points of view, the dynamics of System (1.1) has been investigated. For example, in [9, 11, 13, 14, 15], criteria which ensure species coexistence in the sense of *permanence* are studied. In contrast with these studies, Franke and Yakubu [4, 5, 6, 7] obtained several criteria which ensure that some species is dominant in the system, i.e., the species eliminates other species from the system irrespective of the initial population densities. More precisely, dominance is defined as follows:

Definition 1.1. Species k is said to be *dominant* if $\lim_{t\to\infty} x_i(t) = 0$, $i = \{1, \dots , n\}\backslash k$, for every $x(0) \in \mathbb{R}^n_+$ with $x_k(0) > 0$.

We call the criteria which ensure dominance of some species an exclusion principle. From the definition of dominance, it is clear that coexistence of n species in System (1.1) is impossible if there is a dominant species. Therefore, from an exclusion principle, we can derive a necessary condition for coexistence, which is important

Date: February 9, 2004.
1991 *Mathematics Subject Classification.* Primary 92B05; Secondary 39A11.
Key words and phrases. exclusion principle, dominance, average Liapunov functions.
The author is supported by the 21 Century COE Programme "Development of Dynamic Mathematics with High Functionality" of the Ministry of Education, Culture, Sports, Science and Technology of Japan.

in population ecology. Moreover, from the point of view of evolutionary biology, an exclusion principle is important to evaluate the possibility that a successfully invading mutant species replaces a resident species (e.g., see Geritz *et. al.*[8]).

The purpose of this paper is to complement the exclusion principles obtained in the previous works [4, 5, 6, 7]. In the studies of dominance, the following concept of weak dominance is important:

Definition 1.2. Species k is said to be *weakly dominant* if the two subsets D_k^- and $\bigcup_{i\in\{1,\dots,n\}\setminus k} D_i^+$ of $\mathbb{R}_+^n$ are disjoint, where $D_i^+ := \{x \in \mathbb{R}_+^n : g_i(x) \geq 1\}$ and $D_i^- := \{x \in \mathbb{R}_+^n : g_i(x) \leq 1\}$.

From the definition of D_i^+ and D_i^-, the population density of species i is non-decreasing and non-increasing in D_i^+ and D_i^-, respectively. The intersection $D_i^+ \cap D_i^-$ represents a null cline for species i, where the population density of species i remains constant after one unit time. A point $x \in \bigcup_{i=1}^n (D_i^+ \cap D_i^-)$ is a candidate for a positive fixed point, which is a fixed point in the interior of $\mathbb{R}_+^n$. Therefore, if a weakly dominant species exists, System (1.1) does not posses a positive fixed point. This implies that n species cannot coexist at a fixed point. It is known that if all growth rate functions g_i have exponential form, then weak dominance implies dominance (see [1, 5]). However, it is also known that, in general, weak dominance does not always imply dominance. For example, in [4, 5, 6, 7, 17], it is shown, by using specific examples of (1.1) with $n = 2$, that stable periodic solutions can exist in the interior of $\mathbb{R}_+^2$ even if there is a weakly dominant species. Moreover, coexistence with chaotic oscillation is also possible under the assumption of weak dominance (see [16, 17]). These facts lead to an interesting problem of finding an additional condition that ensures that weak dominance implies dominance. After the next preliminary section, we consider this problem and obtain such an additional assumption (Theorem 3.2). In the final section, we apply our result to specific population models, in which each growth rate function g_i is a function of the weighted total population density $\sum_{i=1}^n a_{ij}x_j(t)$.

2. Preliminaries

In this section, we introduce some notations and theorems, which are used in the consequent sections.

Let (X, d) be a metric space with metric d. A map $f : X \to X$ defines a discrete semi-dynamical system $\pi : \mathbb{Z}_+ \times X \to X$ by $\pi(t, x) = f^t(x)$, where $\mathbb{Z}_+ := \{0, 1, 2, \dots\}$ and $f^t(x)$ denotes the t-th iterate of x under f. Throughout this section, we assume that $f : X \to X$ is continuous. Let $\omega(x)$ be an *omega limit set* of x and $\gamma^+(x)$ be a *semi-orbit* through x, i.e., $\omega(x) := \{y \in X : f^{t_j}(x) \to y \text{ for some subsequence } t_j \to \infty\}$ and $\gamma^+(x) := \{y \in X : y = f^t(x) \text{ for } t \in \mathbb{Z}_+\}$. For a subset N of X, we define $\omega(N) := \bigcup_{x\in N} \omega(x)$ and $\gamma^+(N) := \bigcup_{x\in N} \gamma^+(x)$. N is said to be *forward invariant* if $f(N) \subset N$. For subsets N and Y of X, N is said to be *absorbing* for Y if it is forward invariant and $\gamma^+(x) \cap N \neq \emptyset$ for every $x \in Y$.

The following lemma is used to construct a compact absorbing set of System (1.1) in Section 4 (see also Hofbauer *et al.* [9], Lemma 2.1):

Lemma 2.1 (Hutson [12], Lemma 2.1)**.** *Let $Y \subset X$ be open, and let N be open with a compact closure $\overline{N} \subset Y$. Assume that Y is forward invariant and that $\gamma^+(x) \cap N \neq \emptyset$ for every $x \in Y$. Then $M = \gamma^+(\overline{N})$ is a compact absorbing set for Y.*

Now we introduce theorems of average Liapunov functions. In the next section, the following two theorems are used to show that the extinction state of some species is repelling or attracting, respectively.

Theorem 2.2 (Hutson [12], Theorem 2.2)**.** *Assume that X is compact and that S is a compact subset of X with empty interior. Suppose that there is a continuous function $P : X \to \mathbb{R}_+$ which satisfies the following conditions:*

(a) $P(x) = 0 \Longleftrightarrow x \in S$,

(b) $\sup_{T\geq 0} \liminf_{\substack{y\to x \\ y\in X\setminus S}} \dfrac{P(f^T(y))}{P(y)} > 1 \quad (x \in S).$

Then there is a compact absorbing set M for $X\setminus S$ with $d(M, S) > 0$.

Theorem 2.3 (Kon and Takeuchi, [14] Lemma 14)**.** *Let X and S be the same as those in Theorem 2.2. Suppose that there is a continuous function $P : X \to \mathbb{R}_+$ which satisfies the following conditions:*

(a) $P(x) = 0 \Longleftrightarrow x \in S$,

(b) $\inf_{T\geq 0} \limsup_{\substack{y\to x \\ y\in X\setminus S}} \dfrac{P(f^T(y))}{P(y)} < 1 \quad (x \in S),$

(c) $\inf_{T\geq 0} \dfrac{P(f^T(x))}{P(x)} < 1 \quad (x \in X\setminus S).$

Then $\omega(X) \subset S$, i.e., all solutions in X converge to S as $t \to \infty$.

3. Main results

In this section, we obtain the main theorem (Theorem 3.2) of exclusion principles for System (1.1) by using the theorems in the pervious section.

Since System (1.1) represents population dynamics, we only interest in its orbits restricted in the non-negative cone $\mathbb{R}^n_+$. In order to keep orbits starting in $\mathbb{R}^n_+$ remain there and to exclude species extinction in finite time, we introduce the following assumption:

(H): $g_i : \mathbb{R}^n_+ \to \mathbb{R}_+$ is positive and continuous for each $i = 1, \dots , n$.

We see that if the assumption (H) holds, then both $\mathbb{R}^n_+$ and its interior, $\text{int}\mathbb{R}^n_+$, are forward invariant under System (1.1) and the map $f : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ defined by $f = (x_1g_1, \dots , x_ng_n)$ is continuous.

Define $S_i := \{x \in \mathbb{R}^n_+ : x_i = 0\}$, which is the set of the state where species i is extinct. Denote $\bigcap_{i=1}^n S_i$ by O, which is the set consisting only of the origin. From the equation form of System (1.1), it is clear that each S_i is forward invariant. Therefore, every union and every intersection of S_i is also forward invariant.

We define the limit set of time average of solutions as follows (see [10]):

$$\mu(x) := \{y \in \mathbb{R}^n_+ : \lim_{j\to\infty} \frac{1}{t_j} \sum_{t=0}^{t_j-1} x(t) = y \text{ for some sequence } t_j \to \infty\},$$

where $x(t)$ is a solution of System (1.1) with $x(0) = x$. In the following lemma, we obtain the conditions that $\mu(x)$ must satisfy under the assumption that $\ln g_i$ is convex or concave:

Lemma 3.1. *Let $M \subset \mathbb{R}^n_+$ be convex, and let $X \subset \mathbb{R}^n_+$ be compact with $X \subset M \subset \mathbb{R}^n_+$. Assume that* (H) *holds. Suppose that X is forward invariant under* (1.1)*. If $\omega(x) \cap (X\setminus S_i) \neq \emptyset$ for some $x \in X$, then*

(i) $\mu(x) \cap D_i^+ \neq \emptyset$ *if* $\ln g_i$ *is concave on* M,
(ii) $\mu(x) \cap D_i^- \neq \emptyset$ *if* $\ln g_i$ *is convex on* M.

Proof. Let $x(t) = (x_1(t), \ldots, x_n(t))$ be a solution of (1.1) with $x(0) = x$. From (1.1), we have

$$\begin{aligned} \frac{x_i(T)}{x_i(0)} = \frac{x_i(T)}{x_i(T-1)} \frac{x_i(T-1)}{x_i(T-2)} \cdots \frac{x_i(1)}{x_i(0)} &= \prod_{t=0}^{T-1} g_i(x(t)) \\ \frac{\ln x_i(T) - \ln x_i(0)}{T} &= \frac{1}{T} \sum_{t=0}^{T-1} \ln g_i(x(t)). \end{aligned}$$

The assumption $\omega(x) \cap (X \backslash S_i) \neq \emptyset$ implies that there exist a sequence $T_j \to \infty$ and a $\delta > 0$ such that $x_i(T_j) \geq \delta$ for all $j \in \mathbb{Z}_+$. By the compactness of X and the existence of δ, we have

$$0 = \lim_{j \to \infty} \frac{1}{T_j} \sum_{t=0}^{T_j - 1} \ln g_i(x(t)).$$

For the case (i), we can apply Jensen's inequality to the concave function $\ln g_i$ as follows:

$$\frac{1}{T_j} \sum_{t=0}^{T_j - 1} \ln g_i(x(t)) \leq \ln g_i\left(\frac{1}{T_j} \sum_{t=0}^{T_j - 1} x(t)\right).$$

Then there exists a subsequence, again denoted by $T_j \to \infty$, such that

$$0 \leq \ln g_i\left(\lim_{j \to \infty} \frac{1}{T_j} \sum_{t=0}^{T_j - 1} x(t)\right).$$

This implies that $\mu(x) \cap D_i^+ \neq \emptyset$. Similarly, we can prove the case (ii). □

The following theorem is the main theorem of this paper, and it gives testable exclusion principles for specific population models (see the next section).

Theorem 3.2. *Let* M *and* X *be the same as those in Lemma 3.1, and let* $X_i^+ = D_i^+ \cap X$ *and* $X_i^- = D_i^- \cap X$. *Assume that* (H) *holds and* $X \cap O = \emptyset$. *Suppose that the function* $\ln g_k$ *is convex and the functions* $\ln g_i$, $i \in \{1, \ldots, n\} \backslash k$, *are concave on* M. *If* X_k^- *and* $\bigcup_{i \in \{1,\ldots,n\} \backslash k} X_i^+$ *are disjoint, then* $\omega(X \backslash S_k) \subset (\bigcap_{i \in \{1,\ldots,n\} \backslash k} S_i) \backslash S_k$.

Proof. Without loss of generality, we assume $k = 1$. By using Theorem 2.2, we shall show that there exists a compact absorbing set $X' \subset X \backslash S_1$ for $X \backslash S_1$. Define $P_1 : X \to \mathbb{R}_+$ as $P_1(x) = x_1$. It is clear that $P_1(x) = 0$ if and only if $x \in S_1 \cap X$, i.e., the condition (a) of Theorem 2.2 holds. Let us check the condition (b) of Theorem 2.2. For every $x \in S_1 \cap X$ we have

$$\sigma_1(x) = \sup_{T \geq 0} \liminf_{\substack{y \to x \\ y \in X \backslash S_1}} \frac{P_1(f^T(y))}{P_1(y)} = \sup_{T \geq 0} \liminf_{\substack{y \to x \\ y \in X \backslash S_1}} \frac{y_1(T)}{y_1(T-1)} \cdots \frac{y_1(2)}{y_1(1)} \frac{y_1(1)}{y_1(0)},$$

where $y(t) = (y_1(t), \dots, y_n(t))$ is a solution of (1.1) with $y(0) = y$. By using the continuity of f, we have

$$\begin{aligned}\sigma_1(x) &= \sup_{T\geq 0} \prod_{t=0}^{T-1} g_1(x(t)) \\ &= \sup_{T\geq 0} \left(\exp\left[\frac{1}{T}\sum_{t=0}^{T-1} \ln g_1(x(t))\right]\right)^T,\end{aligned}$$

where $x(t)$ is a solution of (1.1) with $x(0) = x$. Since the function $\ln g_1$ is convex on M, Jensen's inequality implies

$$\frac{1}{T}\sum_{t=0}^{T-1} \ln g_1(x(t)) \geq \ln g_1(\frac{1}{T}\sum_{t=0}^{T-1} x(t)).$$

Since $X \cap O = \emptyset$, for every $x \in S_1 \cap X$ there exists an $i \in \{2, \dots, n\}$ such that $\omega(x) \cap (X \backslash S_i) \neq \emptyset$. Then it follows from Lemma 3.1 that for every $x \in S_1 \cap X$ there exists an $i \in \{2, \dots, n\}$ such that $\mu(x) \cap D_i^+ \neq \emptyset$ holds. By the assumption $X_1^- \cap (\bigcup_{i=2}^n X_i^+) = \emptyset$, we see that for every $x \in S_1 \cap X$ there exists a sequence $T_j \to \infty$ such that $\ln g_1(\sum_{t=0}^{T_j-1} x(t)/T_j) > 0$ for a sufficiently large $j \in \mathbb{Z}_+$. This implies that $\sigma_1(x) > 1$ for every $x \in S_1 \cap X$. Hence, by Theorem 2.2, we see that there exists a compact absorbing set $X' \subset X \backslash S_1$ for $X \backslash S_1$

By using Theorem 2.3, we shall show that every solution with the initial condition $x \in X'$ converges to $S' := \bigcap_{i=2}^n S_i \cap X'$, that is, $\omega(X') \subset S'$. Define $P_2 : X' \to \mathbb{R}_+$ as $P_2(x) = \prod_{i=2}^n x_i$ and

$$\sigma_2(x) = \begin{cases} \inf\limits_{T\geq 0} \limsup\limits_{\substack{y\to x\\ y\in X'\backslash S'}} \dfrac{P_2(f^T(y))}{P_2(y)} & \text{if } x \in S' \\ \inf\limits_{T\geq 0} \dfrac{P_2(f^T(x))}{P_2(x)} & \text{if } x \in X'\backslash S'. \end{cases}$$

Then for every $x \in X'$ we have

$$\begin{aligned}\sigma_2(x) &= \inf_{T\geq 0} \prod_{t=0}^{T-1}\prod_{i=2}^{n} g_i(x(t)) \\ &= \inf_{T\geq 0} \left(\exp\left[\sum_{i=2}^n\left(\frac{1}{T}\sum_{t=0}^{T-1} \ln g_i(x(t))\right)\right]\right)^T,\end{aligned}$$

where the continuity of the function f is used and $x(t)$ is a solution of (1.1) with $x(0) = x$. Since the functions $\ln g_i$, $i = 2, \dots, n$, are concave on M, Jensen's inequality implies

$$\frac{1}{T}\sum_{t=0}^{T-1} \ln g_i(x(t)) \leq \ln g_i(\frac{1}{T}\sum_{t=0}^{T-1} x(t)),\ i = 2, \dots, n.$$

Since X' is an invariant set with $d(X', S_1) > 0$, it is clear that $\omega(x) \cap (X' \backslash S_1) \neq \emptyset$ for every $x \in X'$. Then, by Lemma 3.1, we see that $\mu(x) \cap D_1^- \neq \emptyset$ holds for every $x \in X'$. Therefore, the assumption $X_1^- \cap (\bigcup_{i=2}^n X_i^+) = \emptyset$ implies that for every $x \in X'$ there exists a sequence $T_j \to \infty$ such that $\ln g_i(\sum_{t=0}^{T_j-1} x(t)/T_j) < 0$,

$i \in \{2, \dots, n\}$, for a sufficiently large $j \in \mathbb{Z}_+$. This implies that $\sigma_2(x) < 1$ for every $x \in X'$. By Theorem 2.3, we see that $\omega(X') \subset S'$. □

Remark 3.3. If $\ln g_k$ is convex and $\ln g_i$, $i \in \{1, \dots, n\} \backslash k$ are concave on $\mathbb{R}^n_+$, and (1.1) has a compact absorbing set X for $\mathbb{R}^n_+ \backslash O$ satisfying $X \cap O = \emptyset$, then weak dominance of species k implies its dominance.

4. Applications

In this section, we apply our main theorem (Theorem 3.2) to the following system:

$$x_i(t+1) = x_i(t) h_i(\sum_{j=1}^{n} a_{ij} x_j(t)), \quad i = 1, \dots, n, \tag{4.1}$$

where $a_{ij} > 0$, $i, j \in \{1, \dots, n\}$. We assume that each $h_i : \mathbb{R}_+ \to \mathbb{R}_+$ satisfies the following conditions:

(A1): h_i is positive and continuous,

(A2): h_i is strictly decreasing and $h_i(x^*_i) = 1$ at some $x^*_i > 0$.

Note that (A2) implies that $h_i(0) > 1$ for every $i \in \{1, \dots, n\}$. Since the function h_i is a function of the weighted total population density, the null cline $D^+_i \cap D^-_i$ is the simplex $\sum_{j=1}^{n} a_{ij} x_j = x^*_i$. We define $X_{ij} = x^*_i / a_{ij}$.

Under the assumptions, by using Lemma 2.1, we can construct a compact absorbing set X for $\mathbb{R}^n_+ \backslash O$ satisfying $X \cap O = \emptyset$ as follows:

Lemma 4.1. *If* (A1) *and* (A2) *hold, then System* (4.1) *has a compact absorbing set X for $\mathbb{R}^n_+ \backslash O$ satisfying $X \cap O = \emptyset$.*

Proof. By (A1), the non-negative cone $\mathbb{R}^n_+$ is forward invariant. By (A2), there exists an $L > 0$ such that $p \geq L$ implies $h_i(p) < 1$ for all $i \in \{1, \dots, n\}$. Let $N := \{x \in \mathbb{R}^n_+ : (\min_{i,j \in \{1,\dots,n\}} a_{ij})(x_1 + \cdots + x_n) < L\}$. N is an open subset of $\mathbb{R}^n_+$ with a compact closure $\overline{N} \subset \mathbb{R}^n_+$. Let $x(t)$ be a solution of (4.1) with $x(0) \in \mathbb{R}^n_+$. If $x(t) \in \mathbb{R}^n_+ \backslash N$, then $x_i(t+1) < x_i(t)$ holds for all $i \in \{1, \dots, n\}$. Suppose that $x(t) \in \mathbb{R}^n_+ \backslash N$ for all $t \geq 0$. Since h_i is strictly decreasing, there exists a $\delta \in (0,1)$ such that $\max_{i \in \{1,\dots,n\}} h_i(p) \leq \delta$ for all $p \geq L$. Then, by (4.1), we have

$$\begin{aligned} \sum_{i=1}^{n} x_i(t) &= \sum_{i=1}^{n} x_i(t-1) h_i(\sum_{j=1}^{n} a_{ij} x_j(t-1)) \\ &\leq \delta^t \sum_{i=1}^{n} x_i(0). \end{aligned}$$

Hence, $\sum_{i=1}^{n} x_i(t) \to 0$ as $t \to \infty$. This is a contradiction. Therefore, for every $x(0) \in \mathbb{R}^n_+$ there exists a $t \geq 0$ such that $x(t) \in N$, i.e., $\gamma^+(x) \cap N \neq \emptyset$ for every $x \in \mathbb{R}^n_+$. By Lemma 2.1, there exists a compact absorbing set M for $\mathbb{R}^n_+$.

By using Lemma 2.1, we can also construct a compact absorbing set X for $M \backslash O$ satisfying $X \cap O = \emptyset$ as follows. By (A2), there exists an $l > 0$ such that $0 \leq p \leq l$ implies $h_i(p) > 1$ for all $i \in \{1, \dots, n\}$. Then, by the same argument used above, we can show that there exists an open subset V of M with compact closure $\overline{V} \subset M \backslash O$ such that $\gamma^+(x) \cap V \neq \emptyset$ for every $M \backslash O$. Hence $X := \gamma^+(\overline{V})$ is a compact absorbing set for $\mathbb{R}^n_+ \backslash O$ satisfying $X \cap O = \emptyset$. □

Theorem 3.2 with Lemma 4.1 leads the following corollary:

Corollary 4.2. *Consider System* (4.1) *with* (A1) *and* (A2). *Assume that the function* $\ln h_k$ *is convex and the functions* $\ln h_i$, $i \in \{1, \dots, n\}\backslash k$, *are concave on* $\mathbb{R}_+$. *Then species* k *is dominant if* $X_{i1} < X_{k1}, \dots, X_{in} < X_{kn}$ *for all* $i \in \{1, \dots, n\}\backslash k$.

Proof. Each $D_i^+ \cap D_i^-$ is the simplex $a_{i1}x_1 + \cdots + a_{in}x_n = x_i^*$. Then the condition that $X_{i1} < X_{k1}, \dots, X_{in} < X_{kn}$ for all $i \in \{1, \dots, n\}\backslash k$ implies $(\bigcup_{i\in\{1,\dots,n\}\backslash k} D_i^+) \cap D_k^- = \emptyset$. Furthermore, the convexity and concavity of $\ln h_i$ on $\mathbb{R}_+$ imply the convexity and concavity of $\ln g_i(x_1, \dots, x_n) = \ln h_i(\sum_{i=1}^n a_{ij}x_j)$ on $\mathbb{R}_+^n$, respectively. Hence, Theorem 3.2 with Lemma 4.1 completes the proof. □

Remark 4.3. If $a_{i1} = \cdots = a_{in}$ holds for all $i \in \{1, \dots, n\}$, then the condition that $X_{i1} < X_{k1}, \dots, X_{in} < X_{kn}$ for all $i \in \{1, \dots, n\}\backslash k$ is reduced to the condition that $x_i^*/a_{ii} < x_k^*/a_{kk}$ for all $i \in \{1, \dots, n\}\backslash k$. Furthermore, this condition becomes necessary and sufficient for dominance of species k. Indeed, in this case, a segment connecting the fixed points on the x_k- and x_i-axes becomes a continuum of fixed points if $x_i^*/a_{ii} = x_k^*/a_{kk}$, and the fixed point on the x_i-axis attracts some orbits on the interior of the x_k-x_i face if $x_i^*/a_{ii} > x_k^*/a_{kk}$.

The following systems are specific examples of System (4.1):

$$\begin{cases} x_1(t+1) &= x_1(t)\dfrac{\lambda}{(x_1(t) + \alpha x_2(t) + \beta)^\gamma} \\ x_2(t+1) &= x_2(t)\exp\{r - a(bx_1(t) + x_2(t))\}, \end{cases} \tag{4.2}$$

$$\begin{cases} x_1(t+1) &= x_1(t)[\exp\{r_1 - a_1(x_1(t) + x_2(t))\} + s] \\ x_2(t+1) &= x_2(t)\exp\{r_2 - a_2(x_1(t) + x_2(t))\}, \end{cases} \tag{4.3}$$

where the parameters are positive and satisfy $\lambda/\beta^\gamma > 1$ and $0 \le s < 1$. We can find the studies of (4.2) and (4.3) in [5] and [2, 16, 17], respectively. It is clear that both (4.2) and (4.3) satisfy the assumptions (A1) and (A2). It is straightforward to confirm that the following functions $\ln h_1$ and $\ln \overline{h}_1$ are convex and $\ln h_2$ and $\ln \overline{h}_2$ are concave (and convex):

$$\begin{aligned} \ln h_1(p) &= \ln\{\lambda/(p+\beta)^\gamma\}, \quad \ln h_2(p) = r - p, \\ \ln \overline{h}_1(p) &= \ln\{\exp(r_1 - p) + s\}, \quad \ln \overline{h}_2 = r_2 - p. \end{aligned}$$

Hence, the following two corollaries are immediate consequences of Corollary 4.2 and its remark:

Corollary 4.4. *Species* 1 *of* (4.2) *is dominant if*

$$\lambda^{\frac{1}{\gamma}} - \beta > \frac{r}{ab} \text{ and } \frac{\lambda^{\frac{1}{\gamma}} - \beta}{\alpha} > \frac{r}{a}.$$

Corollary 4.5. *Species* 1 *of* (4.3) *is dominant if and only if*

$$\frac{r_1 - \ln(1 - s_1)}{a_1} > \frac{r_2}{a_2}.$$

Note that Corollary 4.4 is identical to Theorem 5.2 of Franke and Yakubu [5], which was obtained by different methods, and Corollary 4.5 improves Theorem 5 of Yakubu [17], in which an exclusion principle was obtained to consider the possibility that the endangered species x_1 could be saved by its planting. It is known that species 2 does not always eliminate species 1 in Systems (4.2) and (4.3) even if species 2 is weakly dominant (see [5] and [17]). This shows that, in general, a weakly dominant speices k with concave $\ln g_k$ does not always eliminate species j with convex $\ln g_j$.

References

[1] Chan, D. M. and Franke, J. E., Multiple extinctions in a discrete competitive system. *Nonlinear Anal. Real World Appl.* **2** (2001), 75-91.

[2] de Feo, O. and Ferriere, R., Bifurcation analysis of population invasion: on-off intermittency and basin riddling, *Internat. J. Bifur. Chaos Appl. Sci. Engrg.* **10** (2000), 443-452.

[3] Elaydi, S. and Yakubu, A.-A., Global stability of cycles: Lotka-Volterra competition model with stocking, *J. Difference Equ. Appl.* **8** (2002) 537–549.

[4] Franke, J. E. and Yakubu, A.-A., Global attractors in competitive systems, *Nonlinear Anal.* **16** (1991), 111-129.

[5] Franke, J. E. and Yakubu, A.-A., Mutual exclusion versus coexistence for discrete competitive systems, *J. Math. Biol.* **30** (1991), 161–168.

[6] Franke, J. E. and Yakubu, A.-A., Geometry of exclusion principles in discrete systems, *J. Math. Anal. Appl.* **168** (1992), 385-400.

[7] Franke, J. E. and Yakubu, A.-A., Species extinction using geometry of level surfaces, *Nonlinear Anal.* **21** (1993), 369-378.

[8] Geritz, S. A. H., Gyllenberg, M., Jacobs, F. J. A. and Parvinen, K., Invasion dynamics and attractor inheritance, *J. Math. Biol.* **44** (2002), 548-560.

[9] Hofbauer, J., Hutson, V. and Jansen, W., Coexistence for systems governed by difference equations of Lotka-Volterra type, *J. Math. Biol.* **25** (1987), 553-570.

[10] Hofbauer, J., A unified approach to persistence, *Acta Appl. Math.* **14** (1989), 11-22.

[11] Hutson, V., Moran, W. and Vickers, G. T., On a Criterion for Survival of Species in models Governed by Difference Equations, *J. Math. Biol.* **18** (1983), 89-90.

[12] Hutson, V., A theorem on average Liapunov functions, *Monatsh. Math.* **98**, (1984) 267-275.

[13] Kon, R. and Takeuchi, Y., Permanence of host-parasitoid systems, *Nonlinear Anal.* **47** (2001), 1383-1393.

[14] Kon, R. and Takeuchi, Y., Permanence of 2-host 1-parasitoid systems, *Dyn. Contin. Discrete Impuls. Syst. Ser. B Appl. Algorithms* **10** (2003), 389-402

[15] Kon, R., Permanence of discrete-time Kolmogorov systems for two species and saturated fixed points, *J. Math. Biol.* **48** (2004), 57-81.

[16] Ranta, E., Kaitala, V., Alaja, S. and Tesar, D., Nonlinear dynamics and the evolution of semeloparous and iteroparous reproductive strategies, *Amer. Natur.* **155** (2000), 294-300.

[17] Yakubu, A.-A., The effects of planting and harvesting on endangered species in discrete competitive systems, *Math. Biosci.* **126** (1995), 369-378.

Faculty of Mathematics, Kyushu University, Hakozaki 6-10-1, Higashiku, Fukuoka 812-8581, Japan

E-mail address: `kon-r@math.kyushu-u.ac.jp`

List of MHF Preprint Series, Kyushu University

21st Century COE Program
Development of Dynamic Mathematics with High Functionality

MHF2004-1 Koji YONEMOTO & Takashi YANAGAWA
Estimating the Lyapunov exponent from chaotic time series with dynamic noise

MHF2004-2 Rui YAMAGUCHI, Eiko TSUCHIYA & Tomoyuki HIGUCHI
State space modeling approach to decompose daily sales of a restaurant into time-dependent multi-factors

MHF2004-3 Kenji KAJIWARA, Tetsu MASUDA, Masatoshi NOUMI, Yasuhiro OHTA & Yasuhiko YAMADA
Cubic pencils and Painlevé Hamiltonians

MHF2004-4 Atsushi KAWAGUCHI, Koji YONEMOTO & Takashi YANAGAWA
Estimating the correlation dimension from a chaotic system with dynamic noise

MHF2004-5 Atsushi KAWAGUCHI, Kentarou KITAMURA, Koji YONEMOTO, Takashi YANAGAWA & Kiyofumi YUMOTO
Detection of auroral breakups using the correlation dimension

MHF2004-6 Ryo IKOTA, Masayasu MIMURA & Tatsuyuki NAKAKI
A methodology for numerical simulations to a singular limit

MHF2004-7 Ryo IKOTA & Eiji YANAGIDA
Stability of stationary interfaces of binary-tree type

MHF2004-8 Yuko ARAKI, Sadanori KONISHI & Seiya IMOTO
Functional discriminant analysis for gene expression data via radial basis expansion

MHF2004-9 Kenji KAJIWARA, Tetsu MASUDA, Masatoshi NOUMI, Yasuhiro OHTA & Yasuhiko YAMADA
Hypergeometric solutions to the q - Painlevé equations

MHF2004-10 Raimundas VIDŪNAS
Expressions for values of the gamma function

MHF2004-11 Raimundas VIDŪNAS
Transformations of Gauss hypergeometric functions

MHF2004-12 Koji NAKAGAWA & Masakazu SUZUKI
Mathematical knowledge browser

MHF2004-13 Ken-ichi MARUNO, Wen-Xiu MA & Masayuki OIKAWA
Generalized Casorati determinant and Positon-Negaton-Type solutions of the Toda lattice equation

MHF2004-14 Nalini JOSHI, Kenji KAJIWARA & Marta MAZZOCCO
Generating function associated with the determinant formula for the solutions of the Painlevé II equation

MHF2004-15 Kouji HASHIMOTO, Ryohei ABE, Mitsuhiro T. NAKAO & Yoshitaka WATANABE
Numerical verification methods of solutions for nonlinear singularly perturbed problem

MHF2004-16 Ken-ichi MARUNO & Gino BIONDINI
Resonance and web structure in discrete soliton systems: the two-dimensional Toda lattice and its fully discrete and ultra-discrete versions

MHF2004-17 Ryuei NISHII & Shinto EGUCHI
Supervised image classification in Markov random field models with Jeffreys divergence

MHF2004-18 Kouji HASHIMOTO, Kenta KOBAYASHI & Mitsuhiro T. NAKAO
Numerical verification methods of solutions for the free boundary problem

MHF2004-19 Hiroki MASUDA
Ergodicity and exponential β-mixing bounds for a strong solution of Lévy-driven stochastic differential equations

MHF2004-20 Setsuo TANIGUCHI
The Brownian sheet and the reflectionless potentials

MHF2004-21 Ryuei NISHII & Shinto EGUCHI
Supervised image classification based on AdaBoost with contextual weak classifiers

MHF2004-22 Hideki KOSAKI
On intersections of domains of unbounded positive operators

MHF2004-23 Masahisa TABATA & Shoichi FUJIMA
Robustness of a characteristic finite element scheme of second order in time increment

MHF2004-24 Ken-ichi MARUNO, Adrian ANKIEWICZ & Nail AKHMEDIEV
Dissipative solitons of the discrete complex cubic-quintic Ginzburg-Landau equation

MHF2004-25 Raimundas VIDŪNAS
Degenerate Gauss hypergeometric functions

MHF2004-26 Ryo IKOTA
The boundedness of propagation speeds of disturbances for reaction-diffusion systems

MHF2004-27 Ryusuke KON
Convex dominates concave: an exclusion principle in discrete-time Kolmogorov systems