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NONEXISTENCE OF SYNCHRONOUS ORBITS AND CLASS COEXISTENCE IN MATRIX POPULATION MODELS*

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Abstract. Existence of synchronous orbits in a general class of matrix population models is considered. Our results show that a matrix population model does not possess a synchronous orbit if the associated directed graph is primitive. Furthermore, it is also shown that if there are no synchronous orbits, then all classes coexist. To illustrate these results, the density dependent Leslie matrix model is analyzed.

Key words. synchronous phenomena, periodic insects, permanence, Leslie matrix models, discrete dynamical systems

AMS subject classifications. 39A11, 92D25

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1. Introduction.

In this paper, we consider the dynamics of structured populations that are modeled by the following difference equation:

$$\mathbf{x}(t+1) = A_{\mathbf{x}(t)}\mathbf{x}(t), \quad t \in \mathbb{Z}_+, \tag{1}$$

where $\mathbb{Z}_+ = \{0, 1, 2, \ldots, \}$, $\mathbf{x}(t) = (x_1(t), x_2(t), \ldots, x_n(t))^\top$, and $A_\mathbf{x} = (a_{ij}(\mathbf{x}))$ is an $n \times n$ matrix function of $\mathbf{x}$. This equation is a general framework for matrix population models in which a population is divided into n classes (e.g., by chronological age, developmental stage, or habitat position) and the density (or number) of individuals in the ith class is denoted by x_i. Therefore, our interest concentrates on solutions in the nonnegative cone $\mathbb{R}^n_+ := \{\mathbf{x} \in \mathbb{R}^n : x_1 \geq 0, x_2 \geq 0, \ldots, x_n \geq 0\}$.

The following equation is a specific example of (1):

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \\ x_3(t+1) \\ \vdots \\ x_n(t+1) \end{pmatrix} = \begin{pmatrix} f_1(\mathbf{x}(t)) & f_2(\mathbf{x}(t)) & \cdots & f_{n-1}(\mathbf{x}(t)) & f_n(\mathbf{x}(t)) \\ p_1(\mathbf{x}(t)) & 0 & \cdots & 0 & 0 \\ 0 & p_2(\mathbf{x}(t)) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & p_{n-1}(\mathbf{x}(t)) & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \\ x_3(t) \\ \vdots \\ x_n(t) \end{pmatrix}.$$

This equation is the (density dependent) Leslie matrix model for the dynamics of an age-structured population. The variables x_i, $i = 1, 2, \ldots, n$, denote the densities (or numbers) of individuals of age i. The functions $f_i(\mathbf{x})$, $i = 1, 2, \ldots, n$, denote the numbers of offspring produced by one individual of age i, and $p_i(\mathbf{x})$, $i = 1, 2, \ldots, n-1$, denote the probabilities of surviving the ith age-class in one unit of time. This model assumes that the length of life cycle is fixed at n. In addition to the Leslie matrix model, we can find many examples of matrix population models in the literature

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[5, 7]. For example, we can find matrix population models incorporating stage or spatial structure (e.g., see [20, 22]).

One of the interesting topics in the study of matrix population models is synchronization. A typical example of synchronous phenomena is found in a density dependent Leslie matrix model with a single reproductive age-class (e.g., see [1, 4, 8, 9, 10, 12, 19, 24]). More precisely, in the Leslie matrix model with $f_1 = \cdots = f_{n-1} = 0$, we can find an orbit $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ such that each $\mathbf{x}(t)$ consists of a single nonzero entry whose position moves to the right in a unit of time (e.g., $\mathbf{x}(0) = (+, 0, 0, \ldots, 0)^\top, \mathbf{x}(1) = (0, +, 0, \ldots, 0)^\top, \ldots$). This kind of behavior is called single year class (SYC) dynamics (e.g., see Davydova, Diekmann, and van Gils [12]) since all but one year class are missing. Recently, the concept of SYC dynamics was extended, and the term "multiple year class (MYC) dynamics" was introduced by Mjølhus, Wikan, and Solberg [19]. Synchronous phenomena are also observed in natural insect populations (e.g., see [14, 17, 18, 21]). Periodical cicadas, inhabiting the eastern United States, are typical examples. Their nymphs remain underground for precisely 17 years (or, in the south, 13 years) before emerging from the ground synchronously and in tremendous numbers. Mature nymphs become adults, mate, lay their eggs, and die within the few weeks (see [17]). Therefore, the lengths of their life cycles are fixed (17 or 13 years), and all individuals in each population have the same age; i.e., all but one year class are missing (this phenomenon corresponds to SYC dynamics). In order to explain this synchronization, the Leslie matrix model with $f_1 = \cdots = f_{n-1} = 0$ has been studied.

Although it is known that the structure of the Leslie matrix with a single reproductive age-class can give rise to synchronous phenomena, it is unknown whether this is the only structure leading to synchronous phenomena. For example, some insect undoubtedly has two or more reproductive age-classes, but it is not clear whether the additional reproductive age-classes dissipate synchronous phenomena. In order to clarify this relationship between the structure of the life cycle and the phenomenon of synchronization, we will investigate a structure that eliminates synchronous phenomena from a general class of matrix population models.

Synchronous phenomena are characterized by an orbit on the boundary of the nonnegative cone $\mathrm{bd}\mathbb{R}^n_+ := \{\mathbf{x} \in \mathbb{R}^n_+ : x_1 x_2 \cdots x_n = 0\}$. Hence, following Cushing [8], we define a synchronous orbit as follows.

DEFINITION 1.1 (synchronous orbits). *An orbit* $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ *of system* (1) *is said to be synchronous if* $\mathbf{x}(t) \in \mathrm{bd}\mathbb{R}^n_+$ *for all* $t \geq 0$. *A synchronous orbit is said to be nontrivial if* $\mathbf{x}(0) \neq 0$.

Notice that a synchronous orbit does not have to be periodic. It is clear that an SYC dynamics pattern does not appear as long as there are no nontrivial synchronous orbits. Moreover, we see that a nontrivial synchronous orbit always includes some missing classes.

In this paper, we will show that, under certain assumptions, the primitivity of the matrix $A_{\mathbf{x}}$ determines the existence of nontrivial synchronous orbits. It is worth mentioning that Cull and Vogt [6] have addressed the primitivity of a density independent Leslie matrix model to study its periodic behavior of age distributions, i.e., the periodicity of $\mathbf{x}(t)/\sum_{i=1}^n x_i(t)$. As in the study by Cull and Vogt [6], the theory of nonnegative matrices is very useful in our study, although we are concerned not with the periodicity of age distributions but with the existence of synchronous orbits. Since our system involves nonlinear terms, unlike the system of Cull and Vogt [6], we will obtain a result on class coexistence with bounded population densities due to the nonlinearity. That is, we will show that, under certain assumptions, nonexistence of nontrivial synchronous orbits ensures coexistence of all classes in the sense of *c-permanence*, which is defined as follows. (The definition of *p-permanence* is introduced below to distinguish population survival from class coexistence.)

DEFINITION 1.2 (c-permanence). *System* (1) *is said to be c-permanent if there exist positive constants* $\delta > 0$ *and* $D > 0$ *such that*

$$\delta \leq \liminf_{t\to\infty} x_i(t) \leq \limsup_{t\to\infty} x_i(t) \leq D, \quad i = 1, 2, \ldots, n,$$

for all solutions $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ *with* $\mathbf{x}(0) \in \mathbb{R}^n_+\backslash\{(0, 0, \ldots, 0)\}$.

The remainder of this paper is organized as follows. In section 2, we introduce some notation and assumptions. That section also includes a new result on the boundedness of solutions, which will be used to prove permanence of a specific matrix population model in section 5. In section 3, we review a known result on permanence for population survival (i.e., p-permanence), which is used to consider c-permanence in the subsequent sections. In section 4, we consider existence of nontrivial synchronous orbits and class coexistence. That section includes the main results of this paper. In section 5, we apply our results to the density dependent Leslie matrix model, which is introduced above, to illustrate our main results. The final section discusses future problems.

2. Preliminaries. In this section, we introduce some notation, assumptions, and preliminary results.

For vectors $\mathbf{x} = (x_1, x_2, \ldots, x_n)^\top$ and $\mathbf{y} = (y_1, y_2, \ldots, y_n)^\top$, we write $\mathbf{x} \geq \mathbf{y}$ if $x_i \geq y_i$ for all i, and $\mathbf{x} > \mathbf{y}$ if $\mathbf{x} \geq \mathbf{y}$ and $\mathbf{x} \neq \mathbf{y}$. A vector $\mathbf{x}$ is called *nonnegative* if $\mathbf{x} \geq 0$, where 0 denotes the zero vector. A matrix $A = (a_{ij})$ is called *nonnegative* if $a_{ij} \geq 0$ for all i, j. Some important properties of nonnegative matrices are listed in the appendix, which also includes the definitions of *irreducibility* and *primitivity* of matrices and their characteristics. These properties of nonnegative matrices are extensively used in this paper. For matrices $A = (a_{ij})$ and $B = (b_{ij})$, we write $\text{sign}(A) = \text{sign}(B)$ if a_{ij} and b_{ij} have the same sign $-, 0$, or $+$; i.e., the sign pattern of A is identical with that of B. We also write $\text{sign}(\mathbf{x}) = \text{sign}(\mathbf{y})$ for vectors $\mathbf{x}$ and $\mathbf{y}$ if they have the same sign pattern. The set consisting of only the origin is denoted by O.

Throughout this paper, we always assume that system (1) satisfies the following conditions (H1)–(H4):

(H1) each $a_{ij}(\mathbf{x})$ is continuous,
(H2) $A_\mathbf{x}\mathbf{x} \geq 0$ for all $\mathbf{x} \geq 0$,
(H3) $A_\mathbf{x}\mathbf{x} > 0$ for all $\mathbf{x} > 0$,
(H4) system (1) is *dissipative*; i.e., there exists a positive constant $D > 0$ such that $\limsup_{t\to\infty} \sum_{i=1}^n x_i(t) \leq D$ for all solutions $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ with $\mathbf{x}(0) \geq 0$.

Assumption (H1) ensures that the map $f(\mathbf{x}) := A_\mathbf{x}\mathbf{x}$, which is the right-hand side of (1), is continuous. Assumption (H2) implies that all solutions of (1) with $\mathbf{x}(0) \geq 0$ are always nonnegative. Hence, the nonnegative cone $\mathbb{R}^n_+$ is forward invariant; i.e., $f(\mathbb{R}^n_+) \subset \mathbb{R}^n_+$. Notice that (H2) holds if $A_\mathbf{x}$ is nonnegative for all $\mathbf{x} \geq 0$. Assumption (H3) implies that no points $\mathbf{x} > 0$ are mapped to the origin. Therefore, assumption (H3) ensures that $\mathbb{R}^n_+\backslash O$ is forward invariant; i.e., $f(\mathbb{R}^n_+\backslash O) \subset \mathbb{R}^n_+\backslash O$. We can show that (H3) holds if $A_\mathbf{x}$ is nonnegative and irreducible for all $\mathbf{x} \geq 0$ as follows. Since $A_\mathbf{x}$ is nonnegative for all $\mathbf{x} > 0$, $A_\mathbf{x}\mathbf{x} \geq 0$ holds for all $\mathbf{x} > 0$. Suppose that $A_\mathbf{y}\mathbf{y} = 0$ for some $\mathbf{y} > 0$ with $y_k > 0$. The irreducibility of $A_\mathbf{y}$ ensures that $a_{ik}(\mathbf{y}) > 0$ for some i. Otherwise, there are no paths from the vertices P_k to the other vertices in the directed graph of $A_{\mathbf{y}}$. This implies that $A_{\mathbf{y}}$ is not strongly connected and hence not irreducible (see Definition A.3 and Theorem A.4 of the appendix). Therefore, $A_{\mathbf{x}}\mathbf{x} > 0$ holds for all $\mathbf{x} > 0$. Assumption (H4) implies that the total population density does not explode. We can find many matrix population models that satisfy assumptions (H1)–(H4) (e.g., see [5, 7]).

In comparison with (H1)–(H3), it is not always easy to check whether system (1) satisfies (H4). In the rest of this section, we obtain a sufficient condition for the dissipativity of system (1). To obtain the sufficient condition in Theorem 2.2, we need the following lemma on dynamical systems.

LEMMA 2.1 (Hutson [15, Lemma 2.1]). *Let (X, d) be a metric space, and let $f : X \to X$ be a continuous function. Let $\gamma^+(\mathbf{x}) = \{\mathbf{x}, f(\mathbf{x}), f^2(\mathbf{x}), \dots\}$ be a semi-orbit of the discrete dynamical system $f : X \to X$. 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 $\gamma^+(\mathbf{x}) \cap N \neq \emptyset$ for every $\mathbf{x} \in Y$. Then $M = \gamma^+(\overline{N})$ is a compact absorbing set for Y; i.e., M is a forward invariant compact subset of Y and $\gamma^+(\mathbf{x}) \cap M \neq \emptyset$ for every $\mathbf{x} \in Y$.*

By using this lemma, under assumptions (H1)–(H3), we can obtain the following theorem of dissipativity.

THEOREM 2.2. *Assume that* (H1)–(H3) *hold. Suppose that there exist positive constants $K > 0$ and $\lambda_\infty > 0$ such that the inequalities $\sum_{i=1}^n a_{ij}(\mathbf{x}) \leq \lambda_\infty$, $j = 1, 2, \dots, n$, hold for all $\mathbf{x} \in \mathbb{R}^n_+$ with $\sum_{i=1}^n x_i \geq K$. Then system* (1) *is dissipative if $\lambda_\infty < 1$.*

Proof. Let $\{\mathbf{x}(t)\}_{t \in \mathbb{Z}_+}$ be a solution of (1) with $\mathbf{x}(0) \in \mathbb{R}^n_+$. Suppose that $\sum_{i=1}^n x_i(t) \geq K$ for all $t \geq 0$. Then, from (1), we have

$$\begin{aligned} \sum_{i=1}^n x_i(t) &= \sum_{i=1}^n \sum_{j=1}^n a_{ij}(\mathbf{x}(t-1)) x_j(t-1) \\ &\leq \lambda_\infty \sum_{i=1}^n x_i(t-1) \\ &\vdots \\ &\leq \lambda_\infty^t \sum_{i=1}^n x_i(0). \end{aligned}$$

Since $\lambda_\infty < 1$, we have $\mathbf{x}(t) \to 0$ as $t \to \infty$. This is a contradiction. Hence, for every $\mathbf{x}(0) \in \mathbb{R}^n_+$ there exists a $T \geq 0$ such that $\sum_{i=1}^n x_i(T) < K$.

Let $X = Y = \mathbb{R}^n_+$ and $N = \{\mathbf{x} \in \mathbb{R}^n_+ : \sum_{i=1}^n x_i < K\}$. Then it is clear that Y is a forward invariant open subset of X, and N is an open set with a compact closure $\overline{N} \subset Y$. By the above argument, we see that $\gamma^+(\mathbf{x}) \cap N \neq \emptyset$ for every $\mathbf{x} \in Y$. Therefore, Lemma 2.1 implies that $\gamma^+(\overline{N})$ is a compact absorbing set for Y, that is, every solution eventually enters the compact set $\gamma^+(\overline{N})$ and remains there. This implies that system (1) is dissipative. ∎

Remark. It is straightforward to see that this theorem improves a result by Cushing [7] (cf. Theorem 1.2.2 of [7]). In Theorem 1.2.1 of [7], we can find a sufficient condition that ensures global extinction, i.e., $\lim_{t\to\infty} \mathbf{x}(t) = 0$ for all $\mathbf{x}(0) \in \mathbb{R}^n_+$. In this case, the system is certainly dissipative.

3. P-permanence. In this section, we introduce a known result on the *p-permanence* of system (1), which is defined as follows.

Definition 3.1 (p-permanence). *System* (1) *is said to be p-permanent if there exist positive constants* $\delta > 0$ *and* $D > 0$ *such that*

$$\delta \leq \liminf_{t\to\infty} \sum_{i=1}^{n} x_i(t) \leq \limsup_{t\to\infty} \sum_{i=1}^{n} x_i(t) \leq D$$

for all solutions $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ *with* $\mathbf{x}(0) \in \mathbb{R}^n_+ \backslash O$.

A result on p-permanence shall be used to consider class coexistence, i.e., c-permanence, in sections 4 and 5. We see that if system (1) is p-permanent, then the total population density $\sum_{i=1}^n x_i(t)$ is eventually bounded within some positive interval. Therefore, p-permanence is a mathematical term corresponding to population survival.

The recent study by Kon, Saito, and Takeuchi [16] provides a sufficient condition for the p-permanence of system (1) as follows.

Theorem 3.2 (see [16]). *Assume that* (H1)–(H4) *hold. Suppose that the matrix* $A_{\mathbf{x}}$ *at the origin, which is denoted by* A_0*, is irreducible. Then system* (1) *is p-permanent if the dominant eigenvalue* λ_0 *of* A_0 *satisfies* $\lambda_0 > 1$.

Remark. Since A_0 corresponds to the Jacobian matrix of (1) evaluated at the origin, $\lambda_0 > 1$ implies that the origin is unstable. Moreover, $\lambda_0 < 1$ implies that the origin is stable, i.e., that system (1) is not p-permanent. Therefore, the magnitude of λ_0 determines whether or not system (1) is p-permanent except in the critical case $\lambda_0 = 1$.

4. Synchronous orbits and class coexistence. In this main section, we consider the existence of synchronous orbits and the possibility of class coexistence, i.e., c-permanence.

The following theorem provides a necessary and sufficient condition for the existence of a nontrivial synchronous orbit.

Theorem 4.1. *Assume that* (H1)–(H4) *hold. Suppose that* A_0 *is irreducible and* $\mathrm{sign}(A_{\mathbf{x}}) = \mathrm{sign}(A_0)$ *holds for all* $\mathbf{x} \in \mathrm{bd}\mathbb{R}^n_+$. *Then system* (1) *has a nontrivial synchronous orbit if and only if* A_0 *is imprimitive.*

Proof. Suppose that A_0 is imprimitive with index of imprimitivity $h > 1$. Then, by Theorem A.7 of the appendix, A_0^h can be rearranged into quasi-diagonal form by renumbering the indices of rows and columns. So, without loss of generality, we can assume

$$A_0^h = \mathrm{diag}\{B_1, B_2, \dots, B_h\},$$

where $B_1, B_2, \dots, B_h$ are primitive matrices. Hence, we can choose a $\mathbf{z} \in \mathrm{bd}\mathbb{R}^n_+ \backslash O$ such that $A_0^{kh}\mathbf{z} \in \mathrm{bd}\mathbb{R}^n_+ \backslash O$ for all $k \in \mathbb{Z}_+$ (e.g., if B_1 is an $n_1 \times n_1$ matrix, then choose $\mathbf{z} = (z_1, z_2, \dots, z_n)^\top$ with $z_i > 0$ for $i = 1, \dots, n_1$ and $z_i = 0$ for $i = n_1 + 1, \dots, n$). Since A_0 is irreducible and nonnegative, once $A_0^T\mathbf{z} \in \mathrm{int}\mathbb{R}^n_+ := \mathbb{R}^n_+ \backslash \mathrm{bd}\mathbb{R}^n_+$ holds for some $T \geq 0$, $A_0^t\mathbf{z} \in \mathrm{int}\mathbb{R}^n_+$ holds for all $t \geq T$. Otherwise, A_0 has a row with only zero entries, so that A_0 is reducible. Therefore, for the $\mathbf{z} \in \mathrm{bd}\mathbb{R}^n_+ \backslash O$ chosen above, $A_0^t\mathbf{z} \in \mathrm{bd}\mathbb{R}^n_+ \backslash O$ holds for all $t \geq 0$.

It is clear that if $\mathrm{sign}(A) = \mathrm{sign}(B)$ and $\mathrm{sign}(\mathbf{x}) = \mathrm{sign}(\mathbf{y})$ hold for some nonnegative matrices A, B and some nonnegative vectors $\mathbf{x}, \mathbf{y} \in \mathbb{R}^n_+$, then $\mathrm{sign}(A\mathbf{x}) = \mathrm{sign}(B\mathbf{y})$ holds. Therefore, if we let $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ be a solution of system (1) with $\mathbf{x}(0) = \mathbf{z}$, then $\mathrm{sign}(A_{\mathbf{x}(0)}\mathbf{x}(0)) = \mathrm{sign}(A_0\mathbf{z})$ holds, and inductively $\mathrm{sign}(A_{\mathbf{x}(t)}) = \mathrm{sign}(A_0)$ and $\mathrm{sign}(A_{\mathbf{x}(t-1)}\mathbf{x}(t-1)) = \mathrm{sign}(A_0^t\mathbf{z})$ hold for all $t \geq 0$. This implies that $\mathbf{x}(t) \in \mathrm{bd}\mathbb{R}^n_+ \backslash O$ for all $t \in \mathbb{Z}_+$, and then $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ is a nontrivial synchronous orbit.

Suppose that A_0 is primitive. Then, by Theorem A.6 of the appendix, there exists an integer $k \geq 1$ such that $A_0^k > 0$. Suppose that there exists a solution $\{\mathbf{x}(t)\}_{t\in\mathbb{Z}_+}$ such that $\mathbf{x}(t) \in \mathrm{bd}\mathbb{R}_+^n \backslash O$ for all $t \geq 0$. Then we have $A_{\mathbf{x}(k-1)}A_{\mathbf{x}(k-2)}\cdots A_{\mathbf{x}(0)} > 0$. This is a contradiction. Therefore, there are no nontrivial synchronous orbits. □

This theorem ensures that if A_0 is primitive, then there are no orbits remaining in $\mathrm{bd}\mathbb{R}_+^n$; that is, every orbit starting in $\mathrm{bd}\mathbb{R}_+^n$ leaves there and enters the interior of $\mathbb{R}_+^n$ after finite iterations. In the rest of this section, we consider whether or not an interior orbit approaches $\mathrm{bd}\mathbb{R}_+^n$ and show that primitivity implies c-permanence. The following lemma is used below to consider such a problem.

LEMMA 4.2. *Let (X, d) be a compact metric space, and let f and $\gamma^+(\mathbf{x})$ be the same as in Lemma* 2.1. *Let Y be a compact subset of X. Suppose that $\gamma^+(\mathbf{x}) \cap (X\backslash Y) \neq \emptyset$ for every $\mathbf{x} \in X$ and that $X\backslash Y$ is forward invariant. Then there exists a compact absorbing set M for X with $d(M, Y) > 0$.*

Proof. Define $U_t = \{\mathbf{x} \in X : f^t(\mathbf{x}) \in X\backslash Y\}$. Let $\mathbf{x} \in U_t$. Then $f^t(\mathbf{x}) \in X\backslash Y$. By the continuity of f, there exists an open neighborhood $V(\mathbf{x})$ of $\mathbf{x}$ such that $f^t(V(\mathbf{x})) \subset X\backslash Y$. Hence, $V(\mathbf{x}) \subset U_t$. This implies that U_t is open. Since $\gamma^+(\mathbf{x})\cap(X\backslash Y) \neq \emptyset$ for every $\mathbf{x} \in X$, the family of open sets U_t forms an open cover for X. Then, by the compactness of X, there exists a finite subcover $\{U_{t_1}, U_{t_2}, \ldots, U_{t_m}\}$. The forward invariance of $X\backslash Y$ implies $U_t \subset U_{t+1}$. Hence, $X \subset U_T$ holds for $T = \max\{t_1, t_2, \ldots, t_m\}$; i.e., $f^T(X) \subset X\backslash Y$.

Since f is continuous and X is compact, $f^T(X)$ is compact. Let $N = f^T(X)$. Then $\gamma^+(N) = \bigcup_{t=0}^{T-1} f^t(N)$ holds and is compact. Since $\gamma^+(N)$ and Y are compact and $\gamma^+(N) \cap Y = \emptyset$, $d(\gamma^+(N), Y) > 0$ holds. Therefore, we see that $\gamma^+(N)$ is a compact absorbing set for X with $d(\gamma^+(N), Y) > 0$. □

By using this lemma, we can show that if A_0 is primitive, i.e., there are no nontrivial synchronous orbits, then there are no interior orbits converging to $\mathrm{bd}\mathbb{R}_+^n$, as follows.

THEOREM 4.3. *Assume that* (H1)–(H4) *hold. Suppose that $A_\mathbf{x}$ is irreducible for all $\mathbf{x} \in \mathbb{R}_+^n$, $\mathrm{sign}(A_\mathbf{x}) = \mathrm{sign}(A_0)$ holds for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}_+^n$, and system* (1) *is p-permanent. Then system* (1) *is c-permanent if and only if A_0 is primitive.*

Proof. By Theorem 4.1, the ($\Rightarrow$) part is clear since an imprimitive A_0 leads to a nontrivial synchronous orbit.

Suppose that A_0 is primitive. Since system (1) is p-permanent, by using Lemma 2.1, we can construct a compact absorbing set X for $\mathbb{R}_+^n\backslash O$ such that $X \cap O = \emptyset$. Let $Y = \mathrm{bd}\mathbb{R}_+^n \cap X$. By Theorem 4.1, for every $\mathbf{x}(0) \in Y$ there exists a $T \geq 0$ such that $\mathbf{x}(T) \in X\backslash Y$. Furthermore, since $A_{\mathbf{x}(t)}$ is irreducible for all $t \geq 0$, $\mathbf{x}(t) \in X\backslash Y$ holds for all $t \geq T$. Otherwise, $A_{\mathbf{x}(t)}$ has a row with only zero entries, and thus $A_{\mathbf{x}(t)}$ is reducible. This fact implies that $X\backslash Y$ is forward invariant. Hence, Lemma 4.2 shows that there exists a compact absorbing set M for X with $d(M, Y) > 0$. This completes the proof. □

Remark. Notice that $A_\mathbf{x}$ is assumed to be irreducible not only at $\mathbf{x} = 0$ but also at $\mathbf{x} \in \mathbb{R}_+^n$. If $A_\mathbf{x}$ is assumed to be irreducible only at $\mathbf{x} = 0$, then we can construct a matrix function $A_\mathbf{x}$ such that (1) has a periodic orbit that visits alternately an interior point and a boundary point. For instance, consider the following example:

$$A_\mathbf{x} = \begin{pmatrix} 0 & 16\sigma(x_1, x_2)\exp(-x_1 - x_2) \\ 0.5 & 0.5\sigma(x_1, x_2) \end{pmatrix},$$

where $\sigma(x_1, x_2)$ is the continuous function defined by

$$\sigma(x_1, x_2) = \begin{cases} -x_1x_2 + 1, & 0 \leq x_1x_2 < 1, \\ 0, & x_1x_2 \geq 1. \end{cases}$$

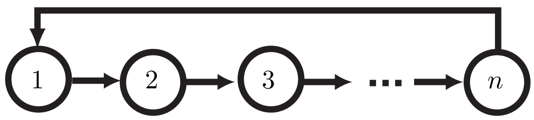

FIG. 1. *The graph of $A_{\mathbf{x}}$ for a semelparous population. This graph has a loop $\{1, 2, \ldots, n, 1\}$, whose length is n. Since there are only loops whose lengths are multiples of n, the greatest common divisor of the lengths are equal to n. Hence, this graph is imprimitive with index of imprimitivity n.*

Note that A_0 is irreducible (and primitive), but $A_{\mathbf{x}}$ is reducible if $x_1 x_2 \geq 1$. Moreover, $\operatorname{sign}(A_{\mathbf{x}}) = \operatorname{sign}(A_0)$ holds for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}^2_+$. We see that $\{(6\ln 2, (3/2)\ln 2), (0, 3\ln 2)\}$ is a periodic orbit of this example.

5. Applications. In this section, we apply the results obtained in the preceding sections to the (density dependent) Leslie matrix model, which was introduced in section 1.

For the functions $f_i(\mathbf{x})$, $i = 1, 2, \ldots, n$, and $p_i(\mathbf{x})$, $i = 1, 2, \ldots, n-1$, we assume the following:

(A1) All $f_i(\mathbf{x})$ and $p_i(\mathbf{x})$ are continuous. $f_1(\mathbf{x}), f_2(\mathbf{x}), \ldots, f_{n-1}(\mathbf{x})$ are nonnegative, and $f_n(\mathbf{x})$ and $p_1(\mathbf{x}), p_2(\mathbf{x}), \ldots, p_{n-1}(\mathbf{x})$ are positive for all $\mathbf{x} \in \mathbb{R}^n_+$.

In order to emphasize that the irreducibility of $A_{\mathbf{x}}$ is determined solely by its sign pattern, in (A1) we do not assume that the functions $p_i(\mathbf{x})$ are less than one. However, from a biological point of view, they must be less than one since they are survival probabilities. In the example studied below, we assume the specific functions $p_i(\mathbf{x})$ that satisfy $0 < p_i(\mathbf{x}) < 1$ for all $\mathbf{x} \in \mathbb{R}^n_+$. It is clear that (A1) ensures that (H1) and (H2) hold. Since $f_n(\mathbf{x})$ and $p_1(\mathbf{x})$, $p_2(\mathbf{x})$, $\ldots$, $p_{n-1}(\mathbf{x})$ are positive for every $\mathbf{x} \geq 0$, the graph $G(A_{\mathbf{x}})$ of $A_{\mathbf{x}}$ has a loop along which we can run through every vertex of the graph (see Figure 1), so that $G(A_{\mathbf{x}})$ is strongly connected (see Theorem A.6 of the appendix). This implies that $A_{\mathbf{x}}$ is irreducible for every $\mathbf{x} \geq 0$. Therefore, (A1) also ensures that (H3) holds. It is clear that dissipativity of the Leslie matrix model is dependent on the forms of the functions f_i and p_i. In fact, if they are all constants, the system becomes linear and hence can exhibit exponential growth. As a nonlinear example, consider the functions $f_i(\mathbf{x})$ and $p_i(\mathbf{x})$:

$$
\begin{aligned}
f_i(\mathbf{x}) &= \frac{\phi_i}{1 + (\sum_{i=1}^n \mu_{ij} x_j)^{\alpha_i}}, \qquad i = 1, 2, \ldots, n, \\
p_i(\mathbf{x}) &= \frac{\sigma_i}{1 + (\sum_{i=1}^n \nu_{ij} x_j)^{\beta_i}}, \qquad i = 1, 2, \ldots, n-1,
\end{aligned} \tag{2}
$$

where the parameters satisfy ϕ_1, ϕ_2, $\ldots$, $\phi_{n-1} \geq 0$, $\phi_n > 0$, $0 < \sigma_i < 1$, $\mu_{ij} > 0$, $\nu_{ij} \geq 0$, $\alpha_i > 0$, $\beta_i > 0$ for all i, j. Note that this specific example satisfies the condition (A1) and that $p_1(\mathbf{x}), p_2(\mathbf{x}), \ldots, p_{n-1}(\mathbf{x}) < 1$ hold for all $\mathbf{x} \in \mathbb{R}^n_+$. In this specific case, we can choose $K > 0$ and $0 < \lambda_\infty < 1$ such that

$$
\begin{aligned}
f_1(\mathbf{x}) + p_1(\mathbf{x}) &\leq \lambda_\infty \\
&\vdots \\
f_{n-1}(\mathbf{x}) + p_{n-1}(\mathbf{x}) &\leq \lambda_\infty \\
f_n(\mathbf{x}) &\leq \lambda_\infty
\end{aligned}
$$

hold for all $\mathbf{x} \in \mathbb{R}^n_+$ with $\sum_{i=1}^n x_i \geq K$. Therefore, Theorem 2.2 ensures that the Leslie matrix model with such functions is dissipative; i.e., the assumption (H4) holds.

Let us consider p-permanence of the Leslie matrix model. As shown in Theorem 3.2, the magnitude of the dominant eigenvalue of A_0 plays a crucial role for p-permanence of system (1). The dominant eigenvalue λ_0 of A_0 usually has a strong relationship with the so-called *inherent net reproductive number* $\mathcal{R}_0$, which is defined to be the expected number of offspring per individual per lifetime evaluated by the constant matrix A_0 (see Theorem 1.1.3 of Cushing [7] and Theorem 3 and section 3.1 of Cushing and Yicang [11]). The inherent net reproductive number $\mathcal{R}_0$ of the Leslie matrix is given by

$$\mathcal{R}_0 = \sum_{i=1}^{n} f_i(0) \prod_{j=1}^{i} p_{j-1}(0),$$

where for notational convenience $p_0(0)$ is defined to be 1. For the Leslie matrix model, it is known that $\mathcal{R}_0 > 1$ (resp., $\mathcal{R}_0 < 1$) if and only if $\lambda_0 > 1$ (resp., $\lambda_0 < 1$) (see Cushing [7] and Cushing and Yicang [11]). Therefore, Theorem 3.2 implies that the Leslie matrix model is p-permanent if it is dissipative and $\mathcal{R}_0 > 1$.

Let us consider primitivity of $A_{\mathbf{x}}$ under the assumption (A1). As mentioned above, under the assumption (A1), $A_{\mathbf{x}}$ is irreducible for every $\mathbf{x} \geq 0$. The graph of $A_{\mathbf{x}}$ with $f_1(\mathbf{x}) = f_2(\mathbf{x}) = \cdots = f_{n-1}(\mathbf{x}) = 0$ is depicted in Figure 1. A population with this life cycle is called *semelparous.* In a semelparous population, individuals can reproduce only once in their lives. By Theorem A.5 of the appendix, we see that the index of imprimitivity of $A_{\mathbf{x}}$ for a semelparous population is equal to n, the order of the matrix $A_{\mathbf{x}}$; that is, $A_{\mathbf{x}}$ is not primitive for all $\mathbf{x} \geq 0$. Therefore, Theorem 4.1 ensures that a semelparous population has a nontrivial synchronous orbit. On the other hand, consider the case where $f_1(\mathbf{x}) = f_2(\mathbf{x}) = \cdots = f_{n-1}(\mathbf{x}) = 0$ does not hold. By Theorem A.5, we see that if there are two consecutive fertile age-classes such that $f_i(\mathbf{x}) > 0$ for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}^n_+$, then $A_{\mathbf{x}}$ is primitive for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}^n_+$. Hence, if $f_1(\mathbf{x}), f_2(\mathbf{x}), \ldots, f_n(\mathbf{x}) > 0$ for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}^n_+$, i.e., all age-classes are fertile, then $A_{\mathbf{x}}$ is clearly primitive for all $\mathbf{x} \in \mathrm{bd}\mathbb{R}^n_+$. In such a primitive case, Theorem 4.3 ensures that all age-classes coexist if system (1) is p-permanent.

Figure 2 considers the dynamics of the Leslie matrix model with four age-classes. We use the functions f_i and p_i defined by (2). Figure 2(a) shows the population dynamics of the fourth age-class in an imprimitive Leslie matrix model. From this figure, we see that the orbit converges to a nontrivial synchronous orbit, where all but one year class are missing. If individuals in the third age-class are also fertile, then the orbit stays in the interior of the nonnegative cone. So, we see that all classes coexists as ensured by Theorem 4.3 (see Figures 2(b) and (c)).

6. Discussion. In this paper, we have considered the existence of nontrivial synchronous orbits in a general class of matrix population models. In Theorem 4.1, we showed that the primitivity of the matrix $A_{\mathbf{x}}$ on the boundary $\mathrm{bd}\mathbb{R}^n_+$ is essential for this existence. Furthermore, in Theorem 4.3, we showed that if there are no nontrivial synchronous orbits, then all classes coexist in the sense of c-permanence. By using the specific Leslie matrix model, we confirmed these results in section 5.

Since Theorem 4.1 ensures only existence of a nontrivial synchronous orbit, that orbit's stability is unknown. However, in our example in Figure 2(a), the nontrivial synchronous orbit seems to be stable. It is a future problem to consider the relationship between stability of synchronous orbits and structure of matrix population

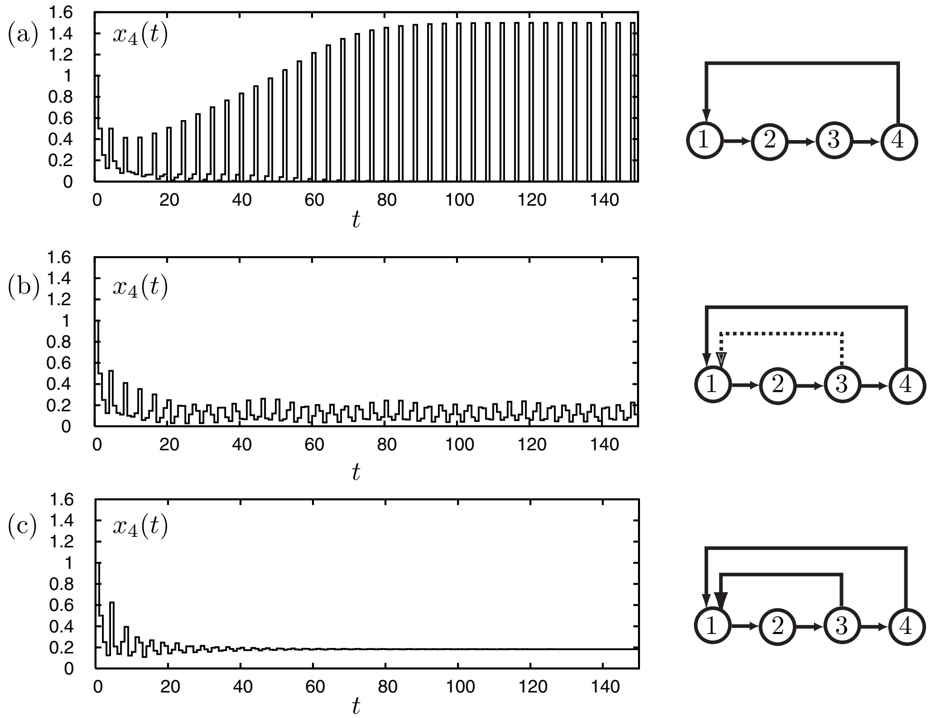

Fig. 2. *The population dynamics of the Leslie matrix model with four age-classes. The left figures show temporal fluctuations of the fourth age-class density. The parameters are* $\phi_1 = 0$, $\phi_2 = 0$, $\phi_4 = 20$, $\sigma_1 = \sigma_2 = \sigma_3 = 0.5$, $\mu_{ij} = \nu_{ij} = \alpha_i = \beta_i = 1$ *for all* i, j, *and the initial condition satisfies* $x_1(0) = x_2(0) = x_3(0) = x_4(0) = 1$. *The parameter* ϕ_3 *is chosen as follows:* (a) $\phi_3 = 0$, (b) $\phi_3 = 1$, (c) $\phi_3 = 5$.

models (see [4, 9, 10, 12, 19, 24] for stability of synchronous orbits in semelparous populations).

In the definition of c-permanence (Definition 1.2), all nonzero orbits are required to be attracted by some compact set in the interior of the nonnegative cone, $\mathrm{int}\mathbb{R}^n_+$. However, we often observe the case where all positive orbits are attracted by some compact set in $\mathrm{int}\mathbb{R}^n_+$ even if the system has a nontrivial synchronous orbit; i.e., the system is not c-permanent. For example, in the Leslie matrix model for a semelparous population, we can find this type of class coexistence. Therefore, it is an important future problem to study class coexistence involving synchronous orbits.

Appendix. In this section, we list some useful theorems of nonnegative matrices. There are several books which discuss the properties of such matrices (e.g., see [2, 3, 5, 13, 23]).

One of the most important properties of nonnegative matrices is irreducibility, which is defined as follows.

Definition A.1 (irreducibility). *A square matrix A is said to be irreducible if it can be rearranged into the following form by renumbering the indices of rows and columns:*

$$\begin{pmatrix} B & 0 \\ C & D \end{pmatrix},$$

where B and D are square matrices and 0 *denotes the matrix with only zero entries. Otherwise A is called irreducible.*

An irreducible nonnegative matrix can have multiple eigenvalues whose magnitudes are equal to the magnitude of the dominant eigenvalue λ. By the number of such eigenvalues, irreducible nonnegative matrices are classified as follows.

Definition A.2. *Let A be an irreducible nonnegative matrix that has h eigenvalues $\lambda_1, \lambda_2, \ldots, \lambda_h$, whose magnitudes are equal to the magnitude of the dominant eigenvalue $\lambda = \lambda_1$. A is called primitive if $h = 1$, and imprimitive if $h > 1$. h is called the index of imprimitivity of A.*

The theory of nonnegative matrices has a strong relationship with a graph theory.

Definition A.3. *The associated directed graph, $G(A)$, of an $n \times n$ matrix A consists of n vertices $P_1, P_2, \ldots, P_n$, where an edge leads from P_j to P_i if $a_{ij} \neq 0$. A directed graph G is said to be strongly connected if for any ordered pair (P_i, P_j) of vertices of G there exists a path which leads from P_i to P_j. Let $P = \{P_{i_0}, P_{i_1}, \ldots, P_{i_\ell}\}$ be a path in a graph G. Then ℓ is the length of P. P is a loop if $P_{i_0} = P_{i_\ell}$.*

Irreducibility and the index of imprimitivity are characterized by directed graphs as follows.

Theorem A.4 (e.g., see Theorem 2.2.7 of [3]). *A matrix A is irreducible if and only if $G(A)$ is strongly connected.*

Theorem A.5 (e.g., see Theorem 2.2.30 of [3]). *Let A be an irreducible nonnegative matrix. The index of imprimitivity of A is equal to the greatest common divisor of the lengths of loops in $G(A)$.*

Remark. This theorem shows that indices of imprimitivity h (like irreducibility) depend only on the pattern of a matrix; i.e., every irreducible nonnegative matrix that has positive entries in exactly the same positions has the same index of imprimitivity.

The following two theorems are utilized in obtaining Theorem 4.1.

Theorem A.6 (e.g., see Theorem 13.8 of [13]). *A nonnegative square matrix A is primitive if and only if there exists an integer $k \geq 1$ such $A^k > 0$.*

Theorem A.7 (e.g., see Corollary 13.2 of [13]). *If A is an imprimitive matrix with index of imprimitivity h, then A^h can be rearranged into the following quasi-diagonal form by renumbering the indices of rows and columns:*

$$\operatorname{diag}\{A_1, A_2, \ldots, A_h\} = \begin{pmatrix} A_1 & 0 & \ldots & 0 \\ 0 & A_2 & \ldots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \ldots & A_h \end{pmatrix}, \tag{3}$$

where $A_1, A_2, \ldots, A_h$ are primitive matrices with the same dominant eigenvalue and 0 *denotes the matrix with only zero entries.*

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