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Competitive Exclusion Between Year-Classes in a Semelparous Biennial Population

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Summary. We investigate competitive exclusion between two reproductively isolated year-classes in the Leslie matrix model for a semelparous biennial population. Our results show that competitive exclusion occurs if competition is more severe between than within year-classes. Our criterion is applicable even if the model exhibits complex behavior.

Key words: Leslie matrix, permanence, average Lyapunov function.

7.1 Introduction

A species is said to be semelparous if it reproduces only once during its lifetime. There are numerous examples of semelparous species. Pacific salmon and many insects such as cicadas are typical examples of semelparous species.

If, in addition to semelparity, the individuals reproduce at the same chronological age, then the population can be divided into reproductively isolated year-classes according to the year of birth. For example, consider the 17-year periodical cicada, inhabiting the Eastern United States. The life cycle of this cicada has a fixed length of 17 years and the adults reproduce at the end of their life [18, 19] (see also [20, 22]). Therefore, the 17-year periodical cicada can be divided into 17 reproductively isolated year-classes according to the year of birth. None of the year-classes contributes to the reproduction of the others. We can find many other examples of semelparous species with several reproductively isolated year-classes.

It is known that the existence of reproductively isolated year-classes plays a key role in the synchronous behavior of insect emergence. For example, consider again the 17-year periodical cicada. In a given region, the adults emerge synchronously from the ground every seventeenth year. Thus, in intervening years, we cannot see any adults above the ground. Such synchronous emergence results from elimination of all but one year-class because once a reproductively isolated year-class is eliminated, it cannot reappear spontaneously. On the other hand, if year-classes are not reproductively isolated, then temporally eliminated year-classes can reappear due to the reproduction of the others. There are many other examples of insects whose adults emerge synchronously (see [1, 10]).

We have to note that existence of reproductively isolated year-classes is a necessary but not a sufficient condition for synchronous emergence. Competition between year-classes is regarded as one of the important factors leading to synchronous emergence. Bulmer [1] studied the Leslie matrix model with n year-classes and found a stable solution corresponding to synchronous emergence when competition is more severe between than within year-classes. Davydova et al. [8] concentrated on the case $n = 2$, i.e., the case of biennials, and obtained a mathematical condition for stability of periodic solutions corresponding to synchronous emergence. There are several studies addressing the stability of such interesting solutions (e.g., see [6,7,23]). However, we have few criteria that can properly evaluate the possibility of synchronization even if the model has a complex solution (but see [21]). In this chapter, we concentrate on the biennial case and obtain a criterion for synchronous emergence that is applicable irrespective of the dynamical complexity of the model.

This chapter is organized as follows. In the next section, we introduce the Leslie matrix model for a semelparous population with n reproductively isolated year-classes. Furthermore, by addressing the biennial case, we show some important properties of the Leslie matrix model for a semelparous population. In Section 7.4, we obtain the main results of this paper. Our main results give sufficient conditions both for coexistence and for competitive exclusion between two reproductively isolated year-classes. The final section includes concluding remarks. Some mathematical results that are necessary for proving our main results are given in the Appendix.

7.2 Leslie Matrix Model for a Semelparous Population

Let us consider the following Leslie matrix model for a semelparous population (see [2,3] for the Leslie matrix model):

$$\mathbf{x}(t+1) = A(\mathbf{x}(t))\mathbf{x}(t), \quad t \in \mathbb{Z}_+ := \{0, 1, 2, \dots\}, \tag{7.1}$$

where $\mathbf{x} = (x_0, x_1, \dots, x_{n-1})^\top$ and

$$A(\mathbf{x}) = \begin{pmatrix} 0 & 0 & \cdots & 0 & \phi s_{n-1}\sigma_{n-1}(\mathbf{x}) \\ s_0\sigma_0(\mathbf{x}) & 0 & \cdots & 0 & 0 \\ 0 & s_1\sigma_1(\mathbf{x}) & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-2}\sigma_{n-2}(\mathbf{x}) & 0 \end{pmatrix}.$$

In this model, the population is divided into n age-classes according to the chronological age. The density (or number) of each age-class i is denoted by x_i. The parameter s_i denotes the probability of surviving the ith age-class in the absence of density dependence. The function $\sigma_i(\mathbf{x})$ represents the intensity of density dependence on s_i. The parameter ϕ denotes the number of offspring produced by one individual of the last age-class $n-1$. It is assumed that these parameters and functions satisfy

$$s_i \in (0, 1], \quad \phi > 0, \quad \sigma_i : \mathbb{R}^n_+ \to (0, 1],$$

where $\mathbb{R}^n_+$ is the non-negative cone, i.e., $\mathbb{R}^n_+ = \{\mathbf{x} \in \mathbb{R}^n : x_0 \geq 0, x_1 \geq 0, \ldots, x_{n-1} \geq 0\}$. The above assumption for the function σ_i implies that the population density always reduces the survival probability. Note that the function σ_{n-1} can also be regarded as the density dependence function for the fertility ϕ or for both s_{n-1} and ϕ. It is clear that this model assumes that the individuals can reproduce only once at the end of their life.

For mathematical reasons, we focus on the case where the functions σ_i are defined by

$$\sigma_i(\mathbf{x}) = \exp\left[-\sum_{j=0}^{n-1} a_{ij}x_j\right].$$

Then the survival probability decreases as the population density increases. This implies that there exists competition between year-classes. The intensity of competition is determined by the positive constants $a_{ij} > 0$, $i, j \in \{0, 1, \ldots, n-1\}$. As a_{ij} increases, the survival probability of the year-class i is strongly reduced by the year-class j. Under this assumption on σ_i, our model is identical to the model studied by Bulmer [1].

If $n = 2$, the Leslie matrix model is reduced to

$$\begin{cases} x_0(t+1) = \phi s_1 x_1(t)\exp[-a_{10}x_0(t) - a_{11}x_1(t)] \\ x_1(t+1) = s_0 x_0(t)\exp[-a_{00}x_0(t) - a_{01}x_1(t)] \end{cases}. \tag{7.2}$$

If $a_{10} = \alpha a_{11}$ and $a_{00} = \alpha a_{01}$ for some $\alpha > 0$, then this model is reduced to the model studied by Davydova et al. [8]. Let $f : \mathbb{R}^2_+ \to \mathbb{R}^2_+$ be the right-hand side of (7.2). Define S_0 and S_1 as follows:

$$S_0 = \{\mathbf{x} \in \mathbb{R}^2_+ : x_0 = 0\}, \quad S_1 = \{\mathbf{x} \in \mathbb{R}^2_+ : x_1 = 0\}.$$

The sets S_0 and S_1 correspond to the x_1- and x_0-axes, respectively. We can recognize from (7.2) that if $\mathbf{x} \in S_0$ (resp. $\mathbf{x} \in S_1$), then $f(\mathbf{x}) \in S_1$ (resp. $f(\mathbf{x}) \in S_0$). Moreover, if $\mathbf{x} \in \mathbb{R}^2_+ \backslash (S_0 \cup S_1)$, then $f(\mathbf{x}) \in \mathbb{R}^2_+ \backslash (S_0 \cup S_1)$. Therefore, both $\mathbb{R}^2_+ \backslash (S_0 \cup S_1)$ and $S_0 \cup S_1$ are forward invariant. The interesting feature of (7.2) is that $f(S_0) \subset S_1$ and $f(S_1) \subset S_0$. This implies that every orbit $\{\mathbf{x}(t)\}_{t \in \mathbb{Z}_+}$ with $\mathbf{x}(0) \in S_0 \cup S_1$ visits S_0 and S_1 alternately. This kind of orbit is called a synchronous orbit (e.g., see [4, 15]). A synchronous orbit corresponds to the periodical emergence of insects since along a synchronous orbit we observe the adults only every other year.

By the linearization of (7.2) at the trivial fixed point $\mathbf{0}$, we have

$$\begin{cases} x_0(t+1) = \phi s_1 x_1(t) \\ x_1(t+1) = s_0 x_0(t) \end{cases}.$$

This linear system is stable if every eigenvalue λ of the non-negative matrix

$$\begin{pmatrix} 0 & \phi s_1 \\ s_0 & 0 \end{pmatrix}$$

satisfies $|\lambda| < 1$ and unstable if $|\lambda| > 1$. Define $\mathcal{R}_0 := \phi s_0 s_1$. We can show that $|\lambda| > 1$ if $\mathcal{R}_0 > 1$ and $|\lambda| < 1$ if $\mathcal{R}_0 < 1$. Hence, the trivial fixed point (7.2) is locally stable if $\mathcal{R}_0 < 1$ and unstable if $\mathcal{R}_0 > 1$. The number $\mathcal{R}_0$ is called the basic reproduction ratio and it is identical to the number of offspring per individual per lifetime.

7.3 Preliminary Results

In this section, we list some preliminary results. These results are necessary to show our main results, which appear in Section 7.4.

First, we consider the boundedness of solutions. The following lemma shows that all solutions of (7.2) are attracted by some bounded set.

Proposition 1 (Lemma 4.1 [16]) *Let* $C = [0, \mathcal{R}_0/(a_{00}e)] \times [0, \mathcal{R}_0/(a_{11}e)]$. *Then the compact set* $B = C \cup f(C)$ *is an absorbing set for* $\mathbb{R}^2_+$, *i.e.,* $f(B) \subset B$ *and for every* $\mathbf{x} \in \mathbb{R}^2_+$ *there exists a* $T > 0$ *such that* $f^T(\mathbf{x}) \in B$ *holds.*

The following lemma shows that if the basic reproduction ratio $\mathcal{R}_0$ is less than one or equal to one, then the population goes extinct irrespective of the initial population densities.

Proposition 2 (Lemma 4.2 [16]) *If* $\mathcal{R}_0 \leq 1$ *holds, then*

$$\lim_{t\to\infty} (x_0(t), x_1(t)) = (0, 0)$$

holds for all $(x_0(0), x_1(0)) \in \mathbb{R}^2_+$.

If $\mathcal{R}_0 > 1$, then we can show that the population can survive in the sense of permanence, which is defined as follows.

Definition 1 *System* (7.2) *is said to be permanent if there exist positive constants* $\delta > 0$ *and* $D > 0$ *such that*

$$\delta \leq \liminf_{t\to\infty}(x_0(t) + x_1(t)) \leq \limsup_{t\to\infty}(x_0(t) + x_1(t)) \leq D$$

holds for all $(x_0(0), x_1(0)) \in \mathbb{R}^2_+$ *with* $x_0(0) + x_1(0) > 0$.

In fact, by using the above two propositions with Theorem 3 [17], we can obtain the following proposition.

Proposition 3 (Theorem 4.4 [16]) *System* (7.2) *is permanent if and only if* $\mathcal{R}_0 > 1$ *holds.*

7.4 Main Results

Since the population cannot persist under the assumption $\mathcal{R}_0 \le 1$ (see Proposition 2), we concentrate on the case $\mathcal{R}_0 > 1$.

Let $\gamma_+(\mathbf{x}) = \{\mathbf{x}, f(\mathbf{x}), f^2(\mathbf{x}), \dots\}$. Proposition 3 ensures that if $\mathcal{R}_0 > 1$, then there exists a compact set $M \subset \mathbb{R}^2_+$ such that $M \cap \{\mathbf{0}\} = \emptyset$ and $\gamma_+(\mathbf{x}) \cap M \neq \emptyset$ for every $\mathbf{x} \in \mathbb{R}^2_+ \backslash \{\mathbf{0}\}$. In this case, by using Lemma 2.1 of [13], we can construct a forward invariant compact set $X \subset \mathbb{R}^2_+$ such that $X \cap \{\mathbf{0}\} \neq \emptyset$ and $\gamma_+(\mathbf{x}) \cap X \neq \emptyset$ for every $\mathbf{x} \in \mathbb{R}^2_+ \backslash \{\mathbf{0}\}$. Therefore, for understanding the ultimate behavior of $\gamma_+(\mathbf{x})$, it is enough to investigate $\gamma_+(\mathbf{x})$ with $\mathbf{x} \in X$. So, in this section, we investigate the dynamics in X. In particular, we investigate the attractivity of S defined by $S = \{\mathbf{x} \in X : x_0 x_1 = 0\}$, i.e., $S = (S_0 \cup S_1) \cap X$. Since the compact set X does not contain the trivial fixed point, the attractivity of S does not imply extinction of the population, but extinction of one of the two year-classes. If S is attractive, then all orbits starting in a neighborhood of S converge to S visiting the neighborhoods of S_0 and S_1 alternately. It is clear that if S is a repellor, then two year-classes coexist.

The following lemma will be used below to consider the attractivity of S.

Lemma 1 *Suppose that $\mathcal{R}_0 > 1$ holds. Then for every $(0, x_1(0)) \in S_0$ with $x_1(0) > 0$ there exists a sequence $t_j \to \infty$ such that*

$$\ln \mathcal{R}_0 = a_{00} \lim_{j\to\infty} \frac{1}{t_j} \sum_{i=0}^{t_j-1} \widetilde{x}_0(2i) + a_{11} \lim_{j\to\infty} \frac{1}{t_j} \sum_{i=0}^{t_j-1} x_1(2i), \tag{7.3}$$

and for every $(x_0(0), 0) \in S_1$ with $x_0(0) > 0$ there exists a sequence $t_j \to \infty$ such that

$$\ln \mathcal{R}_0 = a_{00} \lim_{j\to\infty} \frac{1}{t_j} \sum_{i=0}^{t_j-1} x_0(2i) + a_{11} \lim_{j\to\infty} \frac{1}{t_j} \sum_{i=0}^{t_j-1} \widetilde{x}_1(2i),$$

where $\widetilde{x}_0(t) = \phi s_1 x_1(t) e^{-a_{11}x_1(t)}$ and $\widetilde{x}_1(t) = s_0 x_0(t) e^{-a_{00}x_0(t)}$.

Proof Let $(0, x_1(0)) \in S_0$ with $x_1(0) > 0$. Then it follows from (7.2) that

$$\frac{x_1(t+2)}{x_1(t)} = \mathcal{R}_0 \exp[-a_{00}\widetilde{x}_0(t) - a_{11}x_1(t)]$$

holds for every even number $t \ge 0$. Note that $x_0(t) = 0$ for all even numbers $t \ge 0$. Consequently, we have

$$\frac{1}{t} \sum_{i=0}^{t-1} \ln \frac{x_1(2i+2)}{x_1(2i)} = \frac{1}{t} \sum_{i=0}^{t-1} (\ln \mathcal{R}_0 - a_{00}\widetilde{x}_0(2i) - a_{11}x_1(2i)).$$

The sum on the left-hand side tends to 0 as $t \to \infty$ since (7.2) is permanent (i.e., $x_1(2i)$ is bounded away from 0 and ∞). We choose a subsequence $t_j \to \infty$ such that both $\lim_{j\to\infty} \sum_{i=0}^{t_j-1} \widetilde{x}_0(2i)/t_j$ and $\lim_{j\to\infty} \sum_{i=0}^{t_j-1} x_1(2i)/t_j$ converge (this is possible since they are bounded). Then we obtain (7.3). The case $(x_0(0), 0) \in S_1$ with $x_0(0) > 0$ can be proved similarly. □

By using this lemma, we can prove the following two theorems.

Theorem 1 *Suppose that $\mathcal{R}_0 > 1$ holds. If $a_{00} < a_{10}$ and $a_{11} < a_{01}$ hold, then S is an attractor of the system $f : X \to X$, i.e., there exists a neighborhood U of S such that $\omega(\mathbf{x}) \subset S$ for every $\mathbf{x} \in U$.*

Proof We shall prove this theorem by using the average Lyapunov function $P : X \to \mathbb{R}_+$ defined by $P(\mathbf{x}) = x_1 x_2$. This continuous function satisfies $P(\mathbf{x}) = 0$ if and only if $\mathbf{x} \in S$. The theory of average Lyapunov functions ensures that S is an attractor if for all $\mathbf{x} \in S$, $\inf_{t\geq 0} \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) < 1$, where $\psi : X \to \mathbb{R}_+$ is a continuous function with $P(f(\mathbf{x})) \leq \psi(\mathbf{x})P(\mathbf{x})$ (see Appendix).

Define $\psi : X \to \mathbb{R}_+$ by $\psi(\mathbf{x}) = \mathcal{R}_0 \exp[-(a_{00} + a_{10})x_0 - (a_{01} + a_{11})x_1]$. Then $P(f(\mathbf{x}))/P(\mathbf{x}) = \psi(\mathbf{x})$ holds. Let $\Lambda(\mathbf{x}, t) = \sum_{i=0}^{2t-1} \ln \psi(f^i(\mathbf{x}))/2t$. Then we have

$$\Lambda(\mathbf{x}(0), t) = \ln \mathcal{R}_0 - (a_{00} + a_{10})\frac{1}{2t}\sum_{i=0}^{2t-1} x_0(i) - (a_{01} + a_{11})\frac{1}{2t}\sum_{i=0}^{2t-1} x_1(i),$$

where $(x_0(t), x_1(t)) = f^t(\mathbf{x}(0))$. Let $\mathbf{x}(0) \in S_0 \cap S$. Then $x_0(2t) = x_1(2t+1) = 0$ for all $t \in \mathbb{Z}_+$. Hence, we have

$$\Lambda(\mathbf{x}(0), t) = \ln \mathcal{R}_0 - \frac{a_{00} + a_{10}}{2}\frac{1}{t}\sum_{i=0}^{t-1} \tilde{x}_0(2i) - \frac{a_{01} + a_{11}}{2}\frac{1}{t}\sum_{i=0}^{t-1} x_1(2i).$$

Note that $x_0(2i+1) = \phi s_1 x_1(2i) e^{-a_{11}x_1(2i)} = \tilde{x}_0(2i)$. Since X is compact and $X \cap \{\mathbf{0}\} \neq \emptyset$, there exists a positive $\Delta > 0$ such that

$$\ln \mathcal{R}_0 - \frac{a_{00} + a_{10}}{2}x_0 - \frac{a_{01} + a_{11}}{2}x_1 \leq \ln \mathcal{R}_0 - a_{00}x_0 - a_{11}x_1 - \Delta$$

for all $\mathbf{x} \in X$. Therefore, by using Lemma 1, we can show that there exists a subsequence $t_j \to \infty$ such that

$$\lim_{j\to\infty} \Lambda(\mathbf{x}(0), t_j) < 0.$$

This implies that $\inf_{t\geq 1} \prod_{i=0}^{2t-1} \psi(f^i(\mathbf{x})) < 1$ for all $\mathbf{x} \in S_0 \cap S$. The case $\mathbf{x}(0) \in S_1 \cap S$ can be checked similarly. □

Theorem 2 *Suppose that $\mathcal{R}_0 > 1$ holds. If $a_{00} > a_{10}$ and $a_{11} > a_{01}$ hold, then S is a repellor of the system $f : X \to X$, i.e., there exists a neighborhood U of S such that for all $\mathbf{x} \notin S$ there exists $T = T(\mathbf{x}) > 0$ satisfying $f^T(\mathbf{x}) \notin U$ for all $t \geq T$.*

Proof We again use $P(\mathbf{x}) = x_0 x_1$ as an average Lyapunov function. The theory of average Lyapunov functions ensures that S is a repellor if for all $\mathbf{x} \in S$,

$$\sup_{t\geq 0} \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) > 1,$$

where $\psi : X \to \mathbb{R}_+$ is a continuous function with $P(f(\mathbf{x})) \geq \psi(\mathbf{x})P(\mathbf{x})$ (see [12] and Appendix). We again use the function ψ defined in Theorem 1 since $P(f(\mathbf{x}))/P(\mathbf{x}) = \psi(\mathbf{x})$ holds. Let $\mathbf{x}(0) \in S_0 \cap S$. Then by a similar argument as that above, we obtain

$$\Lambda(\mathbf{x}(0), t) = \ln \mathcal{R}_0 - \frac{a_{00} + a_{10}}{2} \frac{1}{t} \sum_{i=0}^{t-1} \widetilde{x}_0(2i) - \frac{a_{01} + a_{11}}{2} \frac{1}{t} \sum_{i=0}^{t-1} x_1(2i),$$

where $(x_0(t), x_1(0)) = f^t(\mathbf{x}(0))$. Note that $x_0(2i+1) = \phi s_1 x_1(2i) e^{-a_{11}x_1(2i)} = \widetilde{x}_0(2i)$. By using Lemma 1, we can show that there exists a subsequence $t_j \to \infty$ such that

$$\lim_{j \to \infty} \Lambda(\mathbf{x}(0), t_j) > 0.$$

This implies that $\sup_{t \geq 1} \prod_{i=0}^{2t-1} \psi(f^i(\mathbf{x})) > 1$ for all $\mathbf{x} \in S_0 \cap S$. The case $\mathbf{x}(0) \in S_1 \cap S$ can be checked similarly. □

Fig. 7.1 and 7.2 illustrate the above two theorems. In these figures, $x_1(t)$ is plotted against t and the solid and dotted lines connect $(x_1(t), t)$ to $(x_1(t+2), t+2)$ with even t and odd t, respectively. These lines represent the population dynamics of two different year-classes. In Fig. 7.1, the condition of Theorem 1 holds. Hence, two year-classes do not coexist and one of the two year-classes goes extinct. The orbits in Fig. 7.1 (a), (b) and (c) converge to the 2-periodic, 4-periodic and chaotic orbits on $S_0 \cup S_1$, respectively. In Fig. 7.2, the condition of Theorem 2 holds. Hence, two year-classes coexist. In Fig. 7.2 (a), two year-classes coexist at a stable fixed point. In Fig. 7.2 (b), two year-classes coexist with chaotic oscillation. Although the population densities oscillate with large amplitude, Theorem 2 ensures that any orbits do not approach the boundary of $\mathbb{R}^2_+$.

7.5 Concluding Remarks

In this paper, we have investigated competitive exclusion between two year-classes. This investigation gave a sufficient condition for competitive exclusion. More precisely, we have showed that competitive exclusion occurs in system (7.2) if the inequalities $a_{00} < a_{10}$ and $a_{11} < a_{01}$ hold. This condition implies that competition is more severe between than within year-classes. Furthermore, we have shown that two-year classes coexist if competition is more severe within than between year-classes, i.e., $a_{00} > a_{10}$ and $a_{11} > a_{01}$. The numerical investigations show that our results properly evaluate the possibility of competitive exclusion even if the system composed of a single year-class exhibits complex behavior (see Fig. 7.1 (b)). However, note that our results do not cover the following two cases: (i) $a_{00} \geq a_{10}$ and $a_{11} \leq a_{01}$ and (ii) $a_{00} \leq a_{10}$ and $a_{11} \geq a_{01}$. It is known that in these cases the competitive exclusion depends also on the remaining parameters ϕ, s_0 and s_1 (see [5,8,16]).

There are a few studies of the higher dimensional case. For example, Mjølhus et al. [21] studied system (7.1) with $\sigma_i(\mathbf{x}) \equiv 1, i = 0, 1, \ldots, n-2$ and $\sigma_{n-1}(\mathbf{x}) = F(x_0 +$

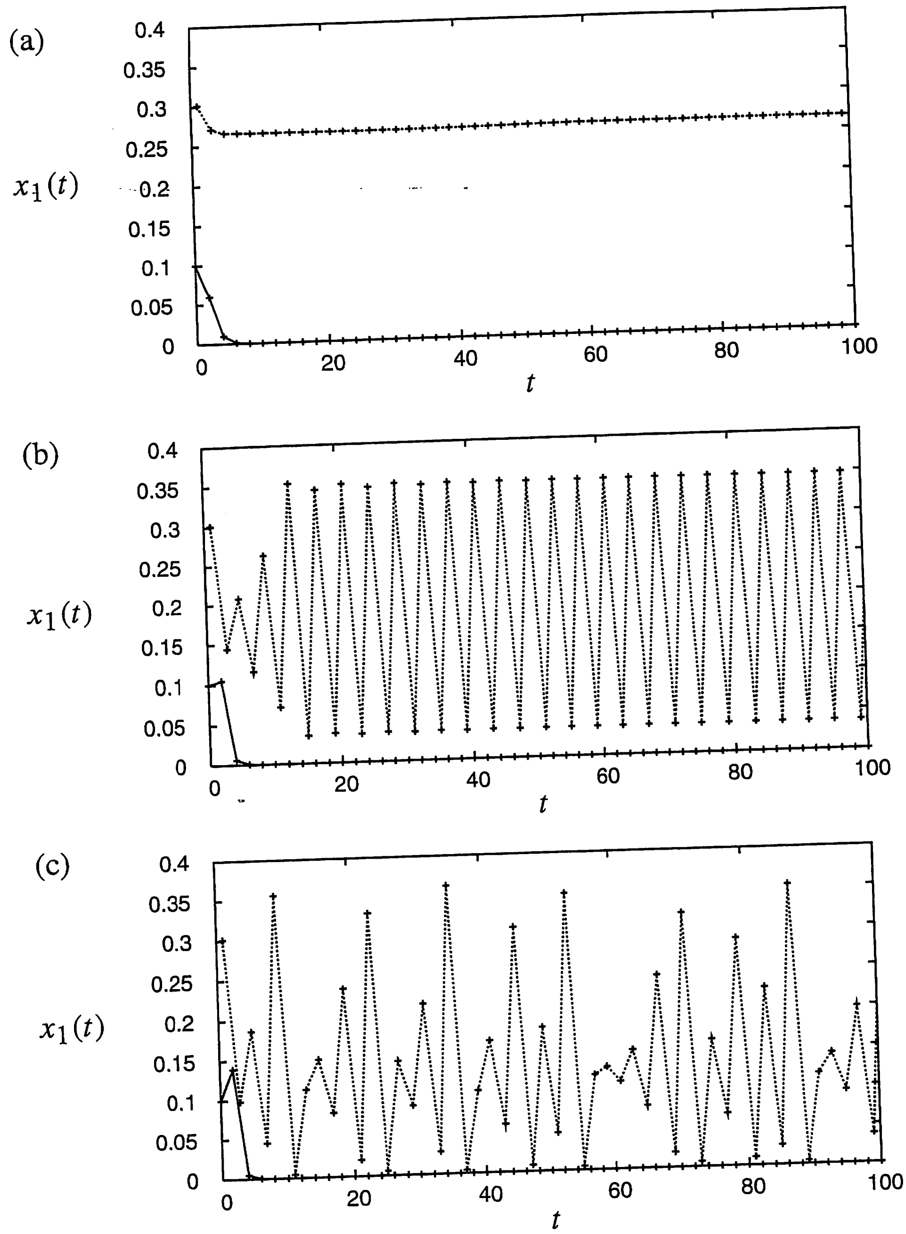

Fig. 7.1. The dynamics of system (7.2) with the initial condition $x_0(0) = 1, x_1(0) = 0.1$. The solid (resp. dotted) line represents $x_1(t)$ at even (resp. odd) years t (i.e., the population densities of two different year-classes). The parameters are $a_{00} = a_{11} = 1, a_{12} = a_{21} = 2, s_0 = 1, s_1 = 0.5$, (a) $\phi = 20$ ($\mathcal{R}_0 = 10$), (b) $\phi = 40$ ($\mathcal{R}_0 = 20$) and (c) $\phi = 60$ ($\mathcal{R}_0 = 30$).

$x_1 + \cdots + x_{n-1}$), where F is a continuous function of the total population density. That is, they assumed that the survival probabilities are constant and the fecundity decreases with the total population density. It is a future problem to relax these assumptions. As reported by Bulmer [1], system (7.1) can have a heteroclinic orbit connecting periodic points on the coordinates if $n \geq 3$ (see [4] for a mathematical proof concerning the existence of heteroclinic orbits in the Leslie matrix model). Hence, it is expected that the higher dimensional Leslie matrix model exhibits various dynamical behavior. It is interesting to challenge the higher dimensional case (see [9]).

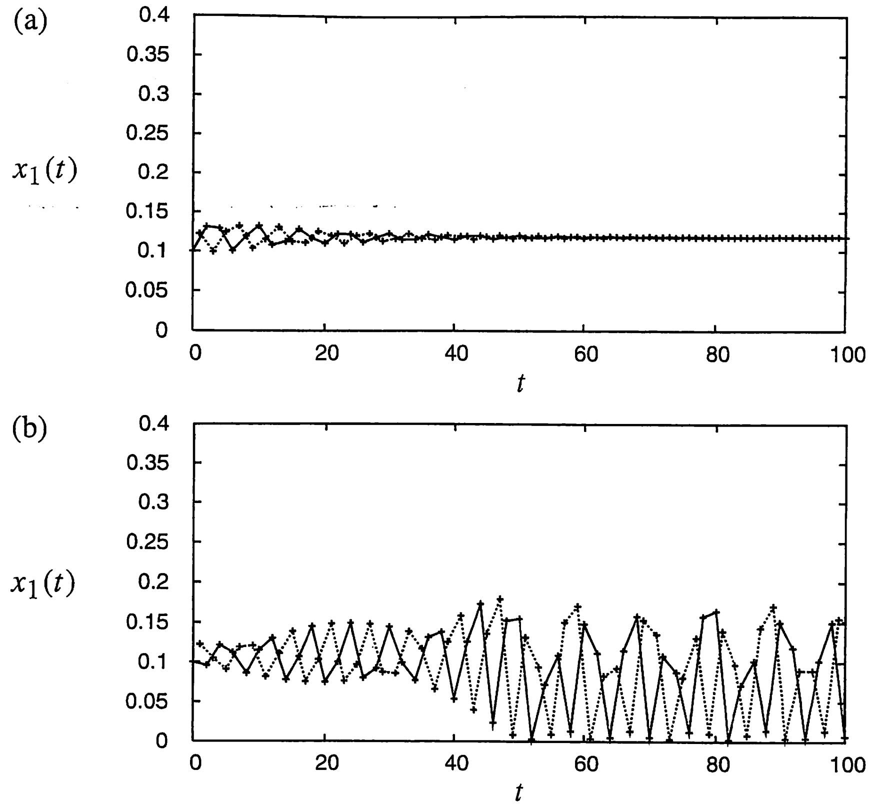

Fig. 7.2. The dynamics of system (7.2) with the initial condition $x_0(0) = 1, x_1(0) = 0.1$. The solid (resp. dotted) line represents $x_1(t)$ at even (resp. odd) years t (i.e., the population densities of two different year-classes). The parameters are $a_{00} = a_{11} = 2, a_{12} = a_{21} = 1, s_0 = 1, s_1 = 0.5$, (a) $\phi = 60$ ($\mathcal{R}_0 = 30$) and (b) $\phi = 80$ ($\mathcal{R}_0 = 40$).

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Appendix

In this appendix, we consider the semi-dynamical system generated by the continuous map $f : X \to X$, where X is a compact metric space.

Let $M \subset X$ be a compact forward invariant set, i.e., $f(M) \subset M$. The set M is said to be a repellor if there exists a neighborhood U of M such that for all $\mathbf{x} \notin M$ there exists $T = T(\mathbf{x}) > 0$ satisfying $f^t(\mathbf{x}) \notin U$ for all $t \geq T$. M is said to be an attractor if there exists a neighborhood U of M such that $\omega(\mathbf{x}) \subset M$ for all $\mathbf{x} \in U$, where $\omega(\mathbf{x})$ is the omega-limit set of $\mathbf{x}$ defined by $\omega(\mathbf{x}) := \{\mathbf{y} \in X : \lim_{j\to\infty} f^{t_j}(\mathbf{x}) = \mathbf{y}$ for some sequence $t_j \to \infty\}$.

The following theorem of average Lyapunov functions is utilized to show that the compact forward invariant set M is a repellor (see also Theorem 2.2 [13] and Theorem 2.17 [14]).

Theorem 3 (Corollary 2.3 [12])*Let $X \backslash M$ be forward invariant. Then M is a repellor if there exists a continuous function $P : X \to \mathbb{R}_+$ such that* (i) $P(\mathbf{x}) = 0$ *if and only if* $\mathbf{x} \in M$, (ii) *for all* $\mathbf{x} \in M$, $\sup_{t \geq 1} \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) > 1$, *where* $\psi : X \to \mathbb{R}_+$ *is a continuous function with* $P(f(\mathbf{x})) \geq \psi(\mathbf{x})P(\mathbf{x})$.

By using the same technique, we can prove the following theorem, which is used to show that the compact forward invariant set M is an attractor (see also Theorem 2.7 [11] and Theorem 2.18 [14])

Theorem 4 *Let $X \backslash M$ be forward invariant. Then M is an attractor if there exists a continuous function $P : X \to \mathbb{R}_+$ such that* (i) $P(\mathbf{x}) = 0$ *if and only if* $\mathbf{x} \in M$, (ii) *for all* $\mathbf{x} \in M$, $\inf_{t \geq 1} \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) < 1$, *where* $\psi : X \to \mathbb{R}_+$ *is a continuous function with* $P(f(\mathbf{x})) \leq \psi(\mathbf{x})P(\mathbf{x})$.

Proof For $p \in (0, 1)$ and $t \geq 1$, define

$$U(p, t) = \left\{ \mathbf{x} \in X : \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) < p \right\}.$$

Then $U(p, t)$ is open. Since $\inf_{t \geq 1} \prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) < 1$ for all $\mathbf{x} \in M$,

$$M \subset \bigcup_{p \in (0,1),\ t \geq 1} U(p, t)$$

holds. Since M is compact, there exist $\overline{p} \in (0, 1)$ and $t_1, \ldots, t_m \geq 1$ such that $M \subset \bigcup_{i=1}^{m} U(\overline{p}, t_i) =: W$. Let $\overline{t} = \max\{t_1, \ldots, t_m\}$.

Let $W_p = \{\mathbf{x} \in X : P(\mathbf{x}) < p\}$. Choose $p \in (0, 1)$ such that $\overline{W_p} \subset W$, where $\overline{W_p}$ is the closure of W_p . Let $\mathbf{x} \in W_p \subset W$. Then there exists $T \in [1, \overline{t}]$ such that $x \in U(\overline{p}, T)$. Furthermore, $P(f^T(\mathbf{x})) < \overline{p}P(\mathbf{x})$ holds. This implies that $f^T(\mathbf{x}) \in W_p$. Therefore, by iteration we obtain a sequence $T_j \to \infty$ with $T_{j+1} - T_j \leq \overline{t}$ such that $f^{T_j}(\mathbf{x}) \in W_p$ and $P(f^{T_j}(\mathbf{x})) \to 0$ as $j \to \infty$. Since $P(f^t(\mathbf{x})) \leq \alpha P(f^{T_j}(\mathbf{x}))$ holds for all t with $T_j \leq t \leq T_{j+1}$, where $\alpha = \max\{\prod_{i=0}^{t-1} \psi(f^i(\mathbf{x})) : 1 \leq t \leq \overline{t}, x \in X\}$, we conclude that $P(f^t(\mathbf{x})) \to 0$ as $t \to \infty$. This completes the proof. □

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