

**INVASIBILITY OF MISSING YEAR-CLASSES
IN LESLIE MATRIX MODELS
FOR A SEMELPAROUS BIENNIAL POPULATION**

RYUSUKE KON¹

Abstract. Bulmer [Periodical insects, *Amer. Natur.*, **111** (1977), pp.1099–1117] studied the n -dimensional Leslie matrix model for a semelparous population to explain the synchronous emergence of periodical insects, and concluded that all but one year-class are eliminated if competition is more severe between than within year-classes. This conclusion is based on the invasibility condition evaluated at n -cycles of a resident population composed of a single year-class. In this paper, by focusing on the Leslie matrix model for a semelparous biennials population, we show that such an invasibility condition is insufficient since the resident population can exhibit more complex behavior. Furthermore, we report recent results on the invasibility condition that can properly evaluate invasibility of missing-year classes, irrespective of resident population dynamics.

Key words. periodical insect, average Liapunov function, permanence, Kolmogorov type

AMS subject classifications. 39A11, 92D25

1. Introduction. An insect is said to be periodical if the life cycle has a fixed length of n years ($n > 1$) and the adults appear synchronously every n th year [1, 10]. Periodical cicadas are good examples to illustrate this synchronous emergence observed in periodical insects. Periodical cicadas inhabit in the Eastern United States. Their nymphs spend 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 (for more detail see [19, 20, 21, 23]). That is, the life cycles of periodical cicadas have the fixed lengths and the adults appear synchronously. Other examples of periodical insects can be seen in [1, 10].

Although annual insects have the fixed length of life cycle (1-year life cycle) and the adults emerge synchronously every year, their synchronous emergence is strongly governed by abiotic environmental factors. On the contrary, the synchronous emergence of periodical insects is likely to be caused by ecological factors. Therefore, to reveal the ecological mechanism of the synchronous behavior observed in periodical insects is one of the interesting problems in ecology.

Bulmer [1] studied this problem and showed that intra-specific competition is an important factor for the synchronous emergence of periodical insects. Since a periodical insect species have a fixed length of life cycle and the adults reproduce only once at the end of their life, the population is divided into reproductively isolated year-classes according to the year of birth. Because of this isolation, once a year-class is eliminated, it cannot reappear spontaneously. Therefore, the synchronous behavior can result from the elimination of all but one of these reproductively isolated year-classes. By analyzing a mathematical model, Bulmer [1] concluded that all but one year-class are eliminated when competition is more severe between than within year-classes.

¹Faculty of Mathematics, Kyushu University, Fukuoka, Japan

To obtain this conclusion, by using the Leslie matrix model with a single reproductive age-class, Bulmer [1] considered the invasibility of missing year-classes to the resident population composed only of a single year-class. In this analysis, it is assumed that the resident dynamics converges to an n -cycle. However, it is known that the resident dynamics can become more complex (e.g., see [7, 8]). Therefore, the invasibility condition obtained in [1] might not properly evaluate the invasibility of missing year-classes. In this paper, we illustrate this possibility with the Leslie matrix model for a semelparous biennial population (see also [7], Section 9). Furthermore, we report recent results on the invasibility condition that can properly evaluate the invasibility of missing year-classes, irrespective of the resident population dynamics.

This paper is organized as follows. In the next section, we introduce the n -dimensional Leslie matrix model with a single reproductive age-class, and show some important properties of this model. In Section 3, we investigate local stability of the Leslie matrix model with $n = 2$. Then we show that the resident population composed of a single year-class can exhibit complex behavior. Furthermore, we show that the invasibility condition evaluated at n -cycles of the resident population composed of a single year-class does not properly evaluate the invasibility of missing year-classes. In the final section, we report recent results on competitive exclusion between two year-classes.

2. Model. The model studied in [1] is the following Leslie matrix model with a single fertile age-class (see [2, 3]): $\mathbf{x}(t+1) = A(\mathbf{x}(t))\mathbf{x}(t)$, where $\mathbf{x} = (x_0, x_1, \dots, x_{n-1})^\top$ and

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

The variables x_i , $i = 0, 1, \dots, n - 1$ denote the densities (or numbers) of individuals of age i . The parameters $s_i \in (0, 1]$, $i = 0, 1, \dots, n - 1$ denote the probabilities of surviving the i th age-class in one unit of time. The functions $\sigma_i : \mathbb{R}_+^n \rightarrow (0, 1]$, $i = 0, 1, \dots, n - 1$, denote the intensities of density dependence on s_i (\mathbb{R}_+^n is the non-negative cone $\{\mathbf{x} \in \mathbb{R}^n : x_0 \geq 0, x_1 \geq 0, \dots, x_{n-1} \geq 0\}$). Bulmer [1] assumed that $\sigma_i(\mathbf{x}) = \exp[-\sum_{j=0}^{n-1} a_{ij} x_j]$, $i = 0, 1, \dots, n - 1$, where $a_{ij} > 0$ is a competition coefficient. As the parameter a_{ij} becomes larger, the age-class i depresses the survival probability of the age-class j more. The parameter $\phi > 0$ denotes the number of offspring produced by one individual of the last age-class $n - 1$. This model assumes that the length of life cycle is fixed at $n \geq 2$ and only the last age-class can reproduce.

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

$$(2.1) \quad \begin{cases} x_0(t+1) &= \phi s_1 x_1(t) \exp[-a_{10} x_0(t) - a_{11} x_1(t)] \\ x_1(t+1) &= s_0 x_0(t) \exp[-a_{00} x_0(t) - a_{01} x_1(t)]. \end{cases}$$

If $a_{10} = a_{11}$ and $a_{00} = a_{01}$, then this model is identical to the model studied in [7]. Let $f : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+^2$ be the right-hand side of (2.1). 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 (2.1) 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 $\mathbf{x} \in \mathbb{R}_+^2 \setminus (S_0 \cup S_1)$, then $f(\mathbf{x}) \in \mathbb{R}_+^2 \setminus (S_0 \cup S_1)$. Therefore, both $\mathbb{R}_+^2 \setminus (S_0 \cup S_1)$ and $S_0 \cup S_1$ are forward invariant.

The interesting feature of (2.1) 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, 16]) and it is a characteristic orbit possessed by structured population models (see [4, 5, 6, 7, 9, 16, 22, 24] for the studies of synchronous orbits in structured population models). A synchronous orbit corresponds to the periodical emergence of insects since along a synchronous orbit we can observe the adult individuals only every other year. Therefore, in the rest of this paper, we study stability of synchronous orbits.

3. Local dynamics. In this section, we investigate stability of periodic synchronous orbits. It is clear that the origin $\mathbf{0}$ is a fixed point of System (2.1). That is, the orbit starting at $\mathbf{0}$ is a trivial synchronous orbit. Since $f(S_0) \subset S_1$ and $f(S_1) \subset S_0$, the forward invariant set $S_0 \cup S_1$ has no fixed points except the origin. Furthermore, since $f(S_0) \subset S_1$ and $f(S_1) \subset S_0$, the forward invariant set $S_0 \cup S_1$ has no periodic orbits with odd period except the origin. This implies that every non-trivial periodic synchronous orbits must have even period.

Let us consider a $2m$ -cycle of f with a positive integer m . Every $2m$ -cycle of f is an m -cycle of the composition map $f \circ f$, which is given by the right-hand side of the following equation:

$$\begin{cases} x_0(t+2) &= x_0(t)g_0(x_0(t), x_1(t)) \\ x_1(t+2) &= x_1(t)g_1(x_0(t), x_1(t)), \end{cases}$$

where the functions g_0 and g_1 have the following forms:

$$\begin{aligned} g_0(x_0, x_1) &= \mathcal{R}_0 \exp[-a_{10}(\phi s_1 x_1 e^{-a_{10}x_0 - a_{11}x_1}) - a_{11}(s_0 x_0 e^{-a_{00}x_0 - a_{01}x_1})] \\ &\quad \times \exp[-a_{00}x_0 - a_{01}x_1] \\ g_1(x_0, x_1) &= \mathcal{R}_0 \exp[-a_{00}(\phi s_1 x_1 e^{-a_{10}x_0 - a_{11}x_1}) - a_{01}(s_0 x_0 e^{-a_{00}x_0 - a_{01}x_1})] \\ &\quad \times \exp[-a_{10}x_0 - a_{11}x_1]. \end{aligned}$$

Here \mathcal{R}_0 is the basic reproduction ratio defined by $\mathcal{R}_0 = \phi s_0 s_1$.

Let $\{(x_0^{(0)}, 0), (0, x_1^{(0)}), \dots, (x_0^{(m-1)}, 0), (0, x_1^{(m-1)})\}$ be a $2m$ -cycle of f on $S_0 \cup S_1$. Since $f \circ f(S_0) \subset S_0$ and $f \circ f(S_1) \subset S_1$, the $2m$ -cycle satisfies

$$x_0^{(i+1)} = x_0^{(i)} g_0(x_0^{(i)}, 0), \quad i = 0, 1, \dots, m$$

and

$$x_1^{(i+1)} = x_1^{(i)} g_1(0, x_1^{(i)}), \quad i = 0, 1, \dots, m,$$

where $x_0^{(m+1)} = x_0^{(0)}$ and $x_1^{(m+1)} = x_1^{(0)}$. When we need to know the periodic points on $S_0 \cup S_1$, it is enough to solve one of these sets of equations because $x_0^{(i)}$ and $x_1^{(i)}$, $i = 0, 1, \dots, m$, also satisfy

$$x_0^{(i+1)} = s_1 x_1^{(i)} e^{-a_{11}x_1^{(i)}}, \quad x_1^{(i+1)} = \phi s_0 x_0^{(i)} e^{-a_{00}x_0^{(i)}}.$$

The composition map $f \circ f$ is also utilized to know stability of f . For example, in the rest of this section, we utilize the composition map $f \circ f$ to investigate stability of $2m$ -cycles of f on $S_0 \cup S_1$.

It is worth to note that the composition map $f \circ f$ is a special case of difference equations of Kolmogorov type. So, we can use some mathematical techniques developed for such equations (e.g., see [11, 15]).

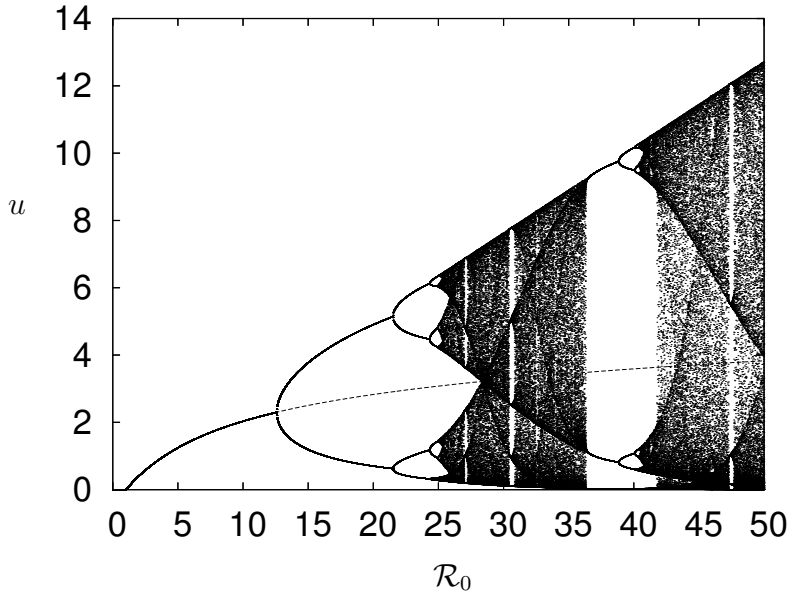


FIG. 3.1. The bifurcation diagram of the single year-class equation (3.1). The dashed line indicates an unstable positive fixed point of (3.1). The parameters are $a_{00} = a_{11} = s_0 = 1$.

3.1. Internal stability. Let us consider the dynamics of the system composed of a single-year class, i.e., the dynamics on $S_0 \cup S_1$. To understand this dynamics, we investigate the dynamics of $f \circ f$ on $S_0 \cup S_1$. Since S_0 is forward invariant under $f \circ f$ and the map f connects the orbits of $f \circ f$ on S_0 to that on S_1 , we concentrate only on the dynamics on S_0 (see [7, 8]). Every orbit of $f \circ f$ on S_0 has the form $\{(u(t), 0)\}_{t \in \mathbb{Z}_+}$ and satisfies

$$(3.1) \quad u(t+1) = u(t)g_0(u(t), 0) = \mathcal{R}_0 \exp[-(a_{11}s_0 e^{-a_{00}u(t)} + a_{00})u(t)]u(t).$$

It is known that this map has at most three positive fixed points as follows (see also [7]):

PROPOSITION 3.1 (Theorem 6.1., Davydova [8]).

- (i) (3.1) has three positive fixed points if the parameters satisfy $\mathcal{R}_0 > e^4$ and $(a_{11}s_0)/a_{00} \in (p_-, p_+)$, where

$$p_{\pm} = e^{x_{\pm}} \left(\frac{\ln \mathcal{R}_0}{x_{\pm}} - 1 \right), \quad x_{\pm} = \frac{\ln \mathcal{R}_0 \pm \sqrt{(\ln \mathcal{R}_0)^2 - 4 \ln \mathcal{R}_0}}{2}.$$

- (ii) (3.1) has two positive fixed points if $\mathcal{R}_0 > e^2$ and $(a_{11}s_0)/a_{00} = p_{\pm}$.

- (iii) In all other cases, (3.1) has a unique positive fixed point.

Remark: If $a_{00} = a_{11}$, then the parameters always satisfy the case (iii).

Fig. 3.1. shows a bifurcation diagram of (3.1). From this figure, we see that the dynamics of a single-year class can be complex (see [7, 8] for more detailed stability analyses of the single year-class equation (3.1)).

3.2. Transversal stability. Let us consider the invasibility of a missing year-class to a resident one. Let $\{(x_0(t), x_1(t))\}_{t \in \mathbb{Z}_+}$ be a $2m$ -cycle of (2.1) with $x_1(0) = 0$

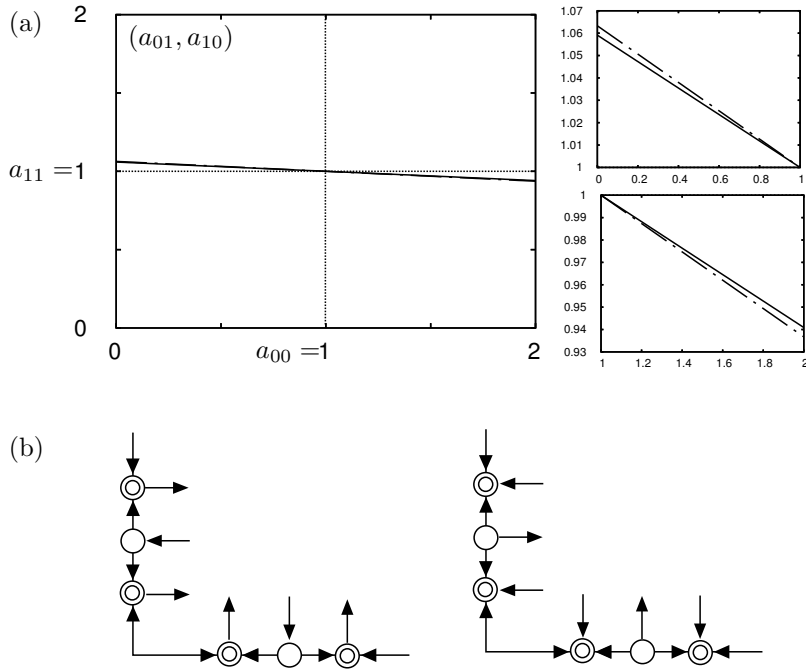


FIG. 3.2. (a) The (a_{01}, a_{10}) parameter plane. The solid and dot-dashed lines represent the boundaries of transversal stability of the 2- and 4-cycles, respectively. The right two figures show the magnified figures of the left one. In these magnified figures, there are two wedges between the solid and dot-dashed lines. The parameters are $a_{00} = a_{11} = s_1 = 1$, $\mathcal{R}_0 = \phi s_0 s_1 = 20$. System (2.1) with these parameters has the 2-cycle $\{(x_0^*, 0), (0, x_1^*)\}$, where $x_0^* = 2.83$, $x_1^* = 0.167$, and the 4-cycle $\{(x_0^{(0)}, 0), (0, x_1^{(0)}), (x_0^{(1)}, 0), (0, x_1^{(1)})\}$, where $x_0^{(0)} = 4.91$, $x_1^{(0)} = 0.0362$, $x_0^{(1)} = 0.699$, $x_1^{(1)} = 0.347$. The solid line is $a_{10} = -0.0591a_{01} + 1.01$, and the dot-dashed line is $a_{10} = -0.0633a_{01} + 1.06$. (b) The schematic (x_0, x_1) phase plane of (2.1). The left and right planes show the case where the parameters belong to the left and right wedges, respectively.

(m is a positive integer). Then the Jacobi matrix evaluated at this $2m$ -cycle is given by $J = J(0)J(1) \cdots J(m-1)$, where

$$J(i) = \begin{pmatrix} g_0(x_0(i), 0) + x_0(i) \left[\frac{\partial}{\partial x_0} g_0(x_0, x_1) \right]_{(x_0, x_1) = (x_0(i), 0)} & c(i) \\ 0 & g_1(x_0(i), 0) \end{pmatrix}$$

with a certain value $c(i)$. Since every $J(i)$ is an upper triangular matrix, the transversal stability of the $2m$ -cycle is determined by the sign of

$$\Lambda = \ln \prod_{i=0}^{m-1} g_1(x_0(i), 0).$$

If $\Lambda < 0$ (resp. $\Lambda > 0$), then the $2m$ -cycle is transversally stable (resp. unstable). Note that g_1 is a positive function. The internal stability of the $2m$ -cycle is determined by the magnitude of the upper left entry of J . Note that this stability is identical to the stability of the associated m -cycle of (3.1).

Fig. 3.2(a) is the (a_{01}, a_{10}) parameter plane with the boundaries of transversal stability of the 2- and 4-cycles. We see that these two boundaries do not coincide and

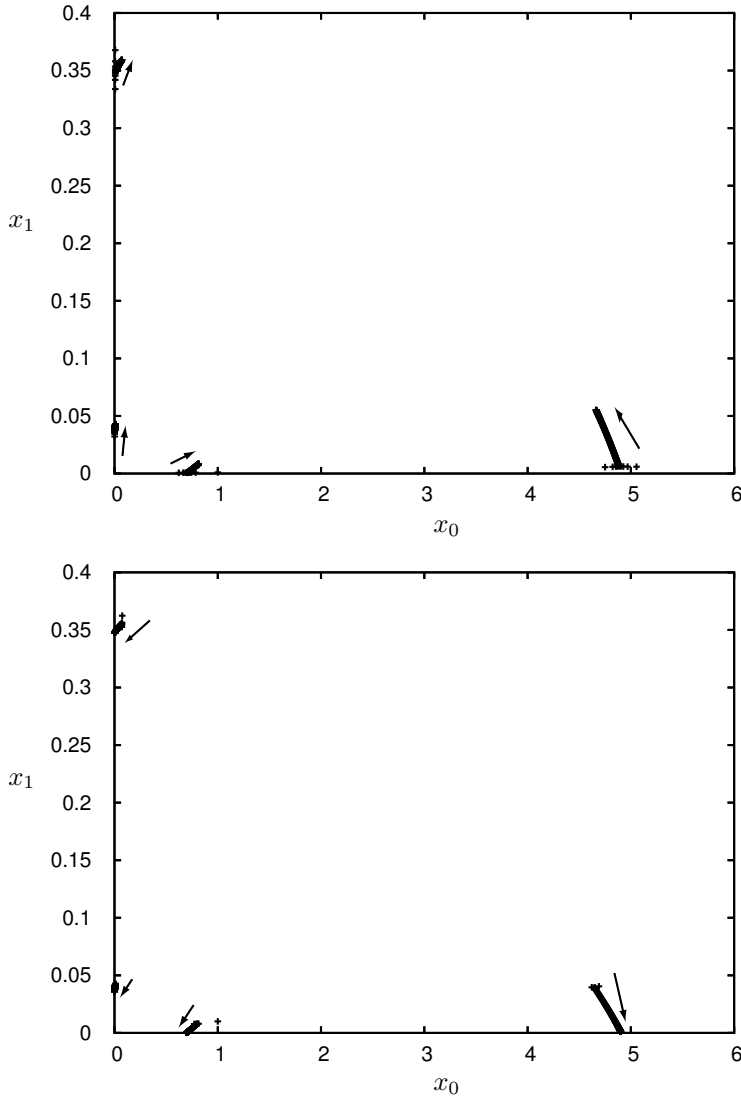


FIG. 3.3. The (x_0, x_1) phase plane of (2.1). The solutions with the initial condition $(x_0(0), x_1(0)) = (1, 0.001)$ are plotted. The parameters are $a_{00} = a_{11} = s_1 = 1$ and $\mathcal{R}_0 = \phi s_0 s_1 = 20$. (a) The solution converges to the 4-cycle in the interior of \mathbb{R}_+^2 , i.e., $\{(0.0708, 0.360), (4.66, 0.0551), (0.00852, 0.0428), (0.814, 0.00827)\}$. The parameter set $a_{01} = 0.5$, $a_{10} = 1.031$ belongs to the left wedge of Fig. 3.2 (a). (b) The solution converges to the 4-cycle on $S_0 \cup S_1$, i.e., $\{(0, 0.347), (4.91, 0), (0, 0.0362), (0.699, 0)\}$. The parameter set $a_{01} = 1.5$, $a_{10} = 0.969$ belongs to the right wedge of Fig. 3.2 (a).

there are two kinds of gaps, i.e., the two wedges between the solid and dot-dashed lines. In these wedges, we have the dynamics schematically illustrated in Fig. 3.2 (b). That is, in the left wedge, the 2-cycle is transversally stable but the 4-cycle is transversally unstable, and in the right wedge, the 2-cycle is transversally unstable but the 4-cycle is transversally stable (see Fig. 3.2 (b)). Since the 2-cycle is internally unstable and the 4-cycle is internally stable, in the left wedge the invasion of the

missing year-class likely to succeed even though the 2-cycle is transversally stable. Furthermore, in the right wedge the invasion likely to fail even though the 2-cycle is transversally unstable. The numerical investigation supports these expectations (see Fig. 3.3). Therefore, when we evaluate the invasibility of a missing year-class, it is not enough to investigate the transversal stability of a 2-cycle of f on $S_0 \cup S_1$ (see also [7], Section 9). Similar remark also holds for the case $n \geq 3$.

4. Global dynamics. In this section, we report recent results on the invasibility condition that can properly evaluate the invasibility of missing year-classes, irrespective of the resident population dynamics. To this end, we show some preliminary results.

The following lemma shows that all solutions of System (2.1) are attracted to some bounded set.

LEMMA 4.1. *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., B is forward invariant under f and for every $\mathbf{x} \in \mathbb{R}_+^2$ there exists a $T > 0$ such that $f^T(\mathbf{x}) \in B$ holds.*

Proof. The following inequalities hold for every $(x_0, x_1) \in \mathbb{R}_+^2$:

$$\begin{aligned} x_0 g_0(x_0, x_1) &\leq \mathcal{R}_0 \exp[-a_{00}x_0]x_0 \leq \mathcal{R}_0/(a_{00}e) \\ x_1 g_1(x_0, x_1) &\leq \mathcal{R}_0 \exp[-a_{11}x_1]x_1 \leq \mathcal{R}_0/(a_{11}e). \end{aligned}$$

From these inequalities we have $f \circ f(\mathbb{R}_+^2) \subset C \subset C \cup f(C) = B$. This implies that for every $\mathbf{x} \in \mathbb{R}_+^2$ there exists $T > 0$ such that $f^T(\mathbf{x}) \in B$ holds.

Since $f(B) = f(C \cup f(C)) = f(C) \cup f \circ f(C) \subset f(C) \cup C = B$, the set B is forward invariant. This completes the proof. \square

If the basic reproduction ratio \mathcal{R}_0 is less than one, then we can show that the population goes extinct as follows.

LEMMA 4.2. *If $\mathcal{R}_0 \leq 1$ holds, then*

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

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

Proof. Let $A(\mathbf{x})$ be the 2×2 matrix function defined by

$$A(\mathbf{x}) = \begin{pmatrix} 0 & \phi s_1 \exp[-a_{10}x_0 - a_{11}x_1] \\ s_0 \exp[-a_{00}x_0 - a_{01}x_1] & 0 \end{pmatrix}.$$

Then for any $\epsilon > 0$ there exists $p(\epsilon) \in (0, 1)$ such that

$$A(\mathbf{x}) \leq \begin{pmatrix} 0 & \phi s_1 p(\epsilon) \\ s_0 p(\epsilon) & 0 \end{pmatrix} =: B_\epsilon$$

holds for all $\mathbf{x} \in \mathbb{R}_+^2$ with $x_0 + x_1 \geq \epsilon$. Since $\mathcal{R}_0 \leq 1$, the dominant eigenvalue of the non-negative matrix B_ϵ is $\phi s_0 s_1 p(\epsilon)^2 = \mathcal{R}_0 p(\epsilon)^2 < 1$. Let $\{\mathbf{x}(t)\}_{t \in \mathbb{Z}_+}$ and $\{\mathbf{y}(t)\}_{t \in \mathbb{Z}_+}$ be solutions of the non-linear system $\mathbf{x}(t+1) = A(\mathbf{x}(t))\mathbf{x}(t)$ and the linear system $\mathbf{y}(t+1) = B_\epsilon \mathbf{y}(t)$, respectively. Since $\mathbf{y}(t) \rightarrow \mathbf{0}$ as $t \rightarrow \infty$, every solution $\{\mathbf{x}(t)\}_{t \in \mathbb{Z}_+}$ eventually satisfies $x_0(t) + x_1(t) < \epsilon$. This implies that every solution $\{\mathbf{x}(t)\}_{t \in \mathbb{Z}_+}$ satisfies $\mathbf{x}(t) \rightarrow \mathbf{0}$ as $t \rightarrow \infty$ since $\bigcup_{t=0}^{\infty} f^t(U_\epsilon)$ with $U_\epsilon = \{\mathbf{x} \in \mathbb{R}_+^2 : x_0 + x_1 < \epsilon\}$ shrinks as $\epsilon \rightarrow 0$. \square

From this lemma, we see that there is no possibility that the population persists if the basic reproduction ratio is less than one. However, if it is greater than one,

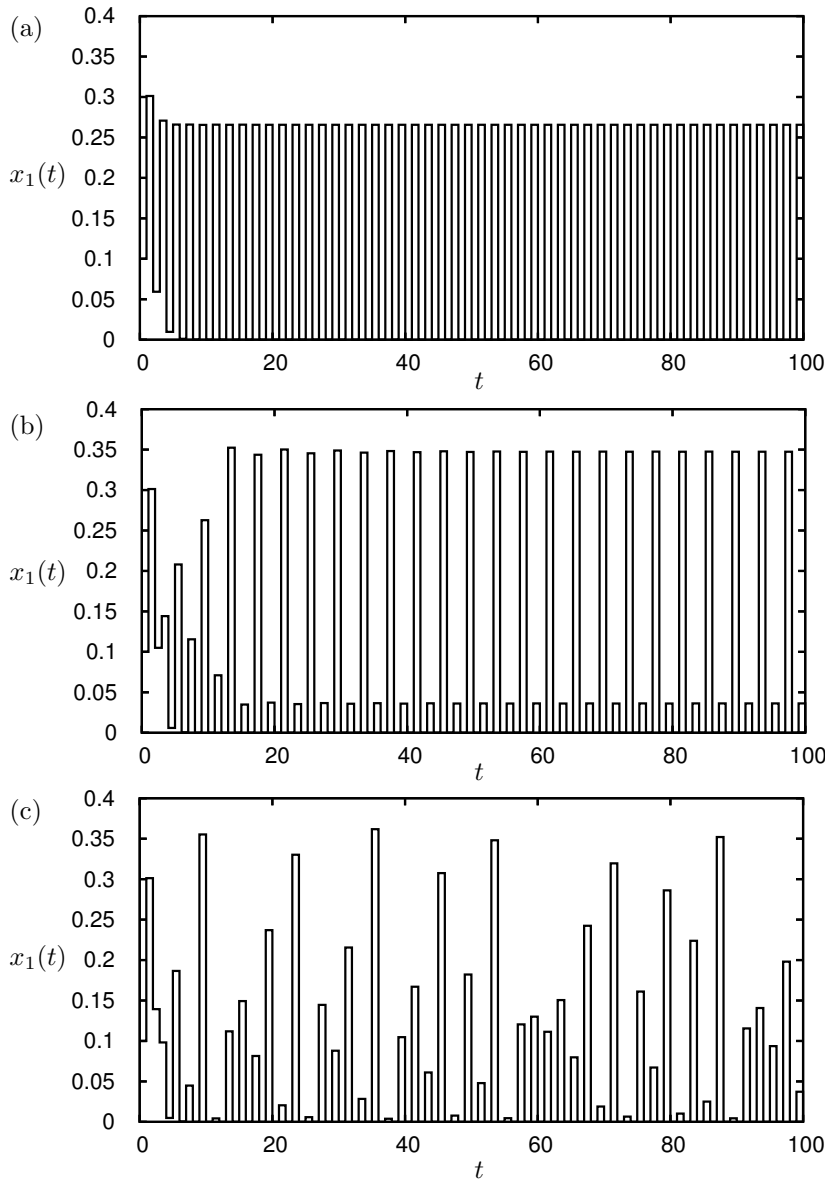


FIG. 4.1. Temporal variations of System (2.1) with the initial condition $x_0(0) = 1$, $x_1(0) = 0.1$. The parameters are $a_{00} = a_{11} = 1$, $a_{12} = a_{21} = 2$, $s_0 = 1$, $s_1 = 0.5$, (a) $\phi = 20$ ($\mathcal{R}_0 = 10$), (b) $\phi = 40$ ($\mathcal{R}_0 = 20$) and (c) $\phi = 60$ ($\mathcal{R}_0 = 30$).

then we can show that the population persists in the sense of permanence, which is defined as follows:

DEFINITION 4.3. System (2.1) is said to be permanent if there exist positive constants $\delta > 0$ and $D > 0$ such that

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

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

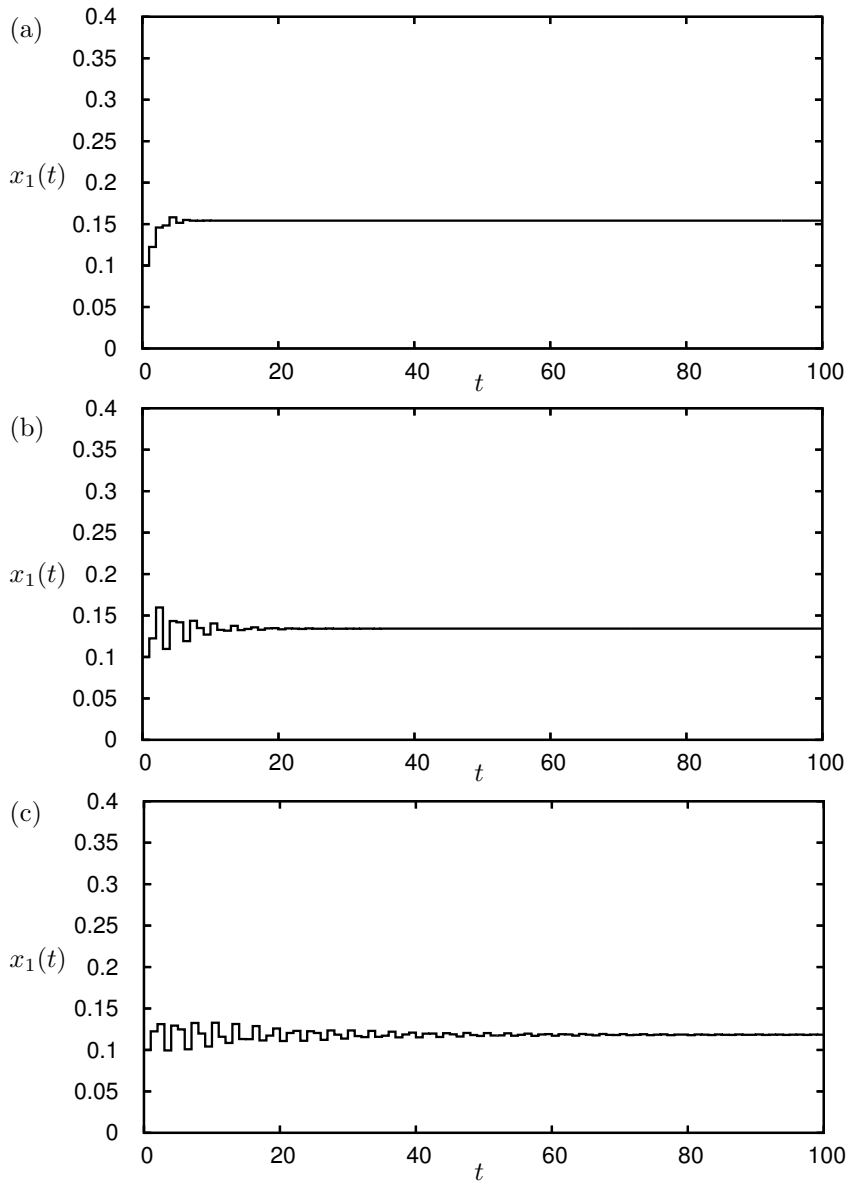


FIG. 4.2. Temporal variations of System (2.1) with the initial condition $x_0(0) = 1$, $x_1(0) = 0.1$. The parameters are $a_{00} = a_{11} = 2$, $a_{12} = a_{21} = 1$, $s_0 = 1$, $s_1 = 0.5$, (a) $\phi = 20$ ($\mathcal{R}_0 = 10$), (b) $\phi = 40$ ($\mathcal{R}_0 = 20$) and (c) $\phi = 60$ ($\mathcal{R}_0 = 30$).

In fact, by using the above two lemmas with Theorem 3 [18], we can obtain the following theorem:

THEOREM 4.4. *System (2.1) is permanent if and only if $\mathcal{R}_0 > 1$ holds.*

Let $\gamma_+(\mathbf{x}) = \{\mathbf{x}, f(\mathbf{x}), f \circ f(\mathbf{x}), \dots\}$. Then this theorem ensures that 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 $\mathbf{x} \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$. Hence, by using Lemma 2.1 of [13], we can construct a forward invariant set $X \subset \mathbb{R}_+^2$ such that $X \cap \{\mathbf{0}\} \neq \emptyset$ and $\gamma_+(\mathbf{x}) \cap X \neq \emptyset$ for every $\mathbf{x} \in \mathbb{R}_+^2 \setminus \{\mathbf{0}\}$. Therefore, for

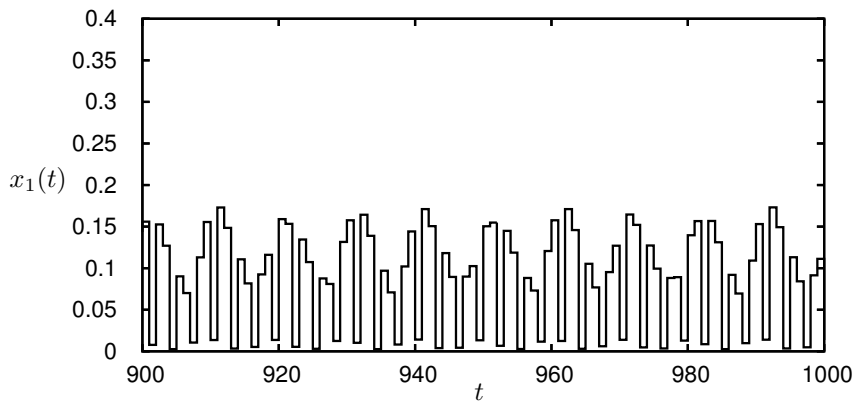


FIG. 4.3. Temporal variations of System (2.1) with the initial condition $x_0(0) = 1$, $x_1(0) = 0.1$. The parameters are $a_{00} = a_{11} = 2$, $a_{12} = a_{21} = 1$, $s_0 = 1$, $s_1 = 0.5$ and $\phi = 80$ ($\mathcal{R}_0 = 40$).

understanding the ultimate behavior of the orbit $\gamma_+(\mathbf{x})$, it is enough to investigate $\gamma_+(\mathbf{x})$ with $\mathbf{x} \in X$. Let $S = \{\mathbf{x} \in X : x_0x_1 = 0\}$. The following theorem provides a sufficient condition under which the missing year-class succeeds to invade the resident population.

THEOREM 4.5. *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 $f : X \rightarrow X$, i.e., there exists a neighborhood U of S such that $\omega(\mathbf{x}) \subset S$ for every $\mathbf{x} \in U$ ($\omega(\mathbf{x})$ is the omega-limit set of \mathbf{x}).*

The inequalities $a_{00} < a_{10}$ and $a_{11} < a_{01}$ imply that competition is more severe between than within year-classes. Fig. 4.1 is a numerical example of this theorem. In this example, one year-class is eliminated. The dynamics of the dominant year-class depends on the parameters. In Fig. 4.1 (a), $x_0(t)$ eventually oscillates with period 2. That is, the orbit converges to the 2-cycle on $S_0 \cup S_1$. In Fig. 4.1 (b), $x_0(t)$ oscillates periodically with period 4 and $x_1(t)$ oscillates chaotically in (c).

The following theorem provides a sufficient condition under which the missing year-class fails to invade the resident population.

THEOREM 4.6. *Suppose that $\mathcal{R}_0 > 1$ holds. If $a_{00} > a_{10}$ and $a_{11} > a_{01}$ hold, then S is a repeller of the system $f : X \rightarrow X$, 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 $t \geq T$.*

The inequalities $a_{00} > a_{10}$ and $a_{11} > a_{01}$ imply that competition is more severe within than between year-classes. Fig. 4.2 is a numerical example of this theorem. In this figure, two year-classes coexist at a stable equilibrium point. If we further increase \mathcal{R}_0 , then the dynamics becomes unstable (see Fig. 4.3). However, as ensured by Theorem 4.6, two year-classes coexist even if the population dynamics is oscillatory.

The above two theorems can be proved by using the average Liapunov function $P : X \rightarrow \mathbb{R}_+$ defined by $P(\mathbf{x}) = x_0x_1$ (see [11, 12, 13, 14] for the theorem of average Liapunov functions). The complete proof is given in [17].

Acknowledgements. This research was partially supported by the 21st Century COE Program “Development of Dynamic Mathematics with High Functionality (Kyushu University)” and the Grant-in-Aid for Young Scientists (B), 17740060, 2005, the Ministry of Education, Culture, Sports, Science and Technology, Japan.

REFERENCES

- [1] M. G. Bulmer, Periodical insects, *Amer. Natur.*, **111**, 1099–1117 (1977).
- [2] H. Caswell, *Matrix Population Models*, 2nd Ed., Sinauer Associates, Sunderland, MA, (2001).
- [3] J. M. Cushing, An introduction to structured population dynamics. CBMS-NSF Regional Conference Series in Applied Mathematics, 71, Society for Industrial and Applied Mathematics (SIAM), Philadelphia, PA, (1998).
- [4] J. M. Cushing, Cycle chains and the LPA model, *J. Difference Equ. Appl.*, **9**, 655–670 (2003).
- [5] J. M. Cushing and J. Li, Intra-specific competition and density dependent juvenile growth, *Bull. Math. Biol.*, **54**, 503–519 (1992).
- [6] J. M. Cushing and J. Li, The dynamics of a size-structured intraspecific competition model with density dependent juvenile growth rates, Chapter 6 in *Individual-based models and approaches in ecology: populations, communities and ecosystems* (D. L. DeAngelis and L. J. Gross, eds.), Routledge, Chapman, and Hall, New York, (1992).
- [7] N. V. Davydova, O. Diekmann and S. A. van Gils, Year class coexistence or competitive exclusion for strict biennials?, *J. Math. Biol.*, **46**, 95–131 (2003).
- [8] N. V. Davydova, Dynamics and bifurcations in families of single year class maps, (preprint).
- [9] O. Diekmann, N. V. Davydova and S. A. van Gils, On a boom and bust year class cycle, *J. Difference Equ. Appl.*, **11**, 327–335 (2005).
- [10] K. Heliövaara, R. Väisänen and C. Simon, Evolutionary ecology of periodical insects, *Trends in Ecology & Evolution*, **9**, 475–480 (1994).
- [11] J. Hofbauer, V. Hutson and W. Jansen, Coexistence for systems governed by difference equations of Lotka-Volterra type. *J. Math. Biol.*, **25**, 553–570 (1987).
- [12] J. Hofbauer and J. W.-H. So, Uniform persistence and repellers for maps, *Proc. Amer. Math. Soc.*, **107**, 1137–1142 (1989).
- [13] V. Hutson, A theorem on average Liapunov functions, *Monatsh. Math.*, **98**, 267–275 (1984).
- [14] V. Hutson and K. Schmitt, Permanence and the dynamics of biological systems, *Math. Biosci.*, **111**, 1–71 (1992).
- [15] R. Kon, Permanence of discrete-time Kolmogorov systems for two species and saturated fixed points, *J. Math. Biol.*, **48**, 57–81 (2004).
- [16] R. Kon, Non-existence of synchronous orbits and class coexistence in matrix population models, *SIAM J. Appl. Math.*, **66**, 616–626 (2005).
- [17] R. Kon, Competitive exclusion between year-classes in a semelparous biennial population, (submitted).
- [18] R. Kon, Y. Saito and Y. Takeuchi, Permanence of single-species stage-structured models, *J. Math. Biol.*, **48**, 515–528 (2004).
- [19] M. Lloyd and H. S. Dybas, The periodical cicada problem. I. population ecology, *Evolution*, **20**, 133–149 (1966).
- [20] M. Lloyd and H. S. Dybas, The periodical cicada problem. II. evolution, *Evolution*, **20**, 466–505 (1966).
- [21] R. M. May, Periodical cicadas, *Nature*, **277**, 347–349 (1979).
- [22] E. Mjølhus, A. Wikan and T. Solberg, On synchronization in semelparous populations, *J. Math. Biol.*, **50**, 1–21 (2005).
- [23] T. M. Powledge, The 17-year itch. *Sci. Amer.*, **290**, 32–33 (2004).
- [24] A. Wikan and E. Mjølhus, Overcompensatory recruitment and generation delay in discrete age-structured population models, *J. Math. Biol.*, **35**, 195–239 (1996).