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Modelling and Analysis of a Competitive Model with Stage Structure

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Abstract—A two-species Lotka-Volterra type competition model with stage structures for both species is proposed and investigated. In our model, the individuals of each species are classified as belonging either to the immature or the mature. First, we consider the stage-structured model with constant coefficients. By constructing suitable Lyapunov functions, sufficient conditions are derived for the global stability of nonnegative equilibria of the proposed model. It is shown that three typical dynamical behaviors (coexistence, bistability, dominance) are possible in stage-structured competition model. Next, we consider the stage-structured competitive model in which the coefficients are assumed to be positively continuous periodic functions. By using Gaines and Mawhin's continuation theorem of coincidence degree theory, a set of easily verifiable sufficient conditions are obtained for the existence of positive periodic solutions to the model. Numerical simulations are also presented to illustrate the feasibility of our main results. © 2005 Elsevier Ltd. All rights reserved.

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1. INTRODUCTION

The classical Lotka-Volterra type competitive system is an important population model and has been studied by many authors (see, for example, [1-9]). The two-species autonomous competitive system is of the form,

$$\frac{dx_i(t)}{dt} = x_i(t) \left( b_i - \sum_{j=1}^{2} a_{ij} x_j(t) \right), \quad i = 1, 2, \quad (1.1)$$

where $x_i(t)$ denotes the density of the $i^{th}$ species at time $t$, respectively. $b_i$ and $a_{ij}$ are positive constants, $i, j = 1, 2$. $b_i$ is the intrinsic growth rate of the $i^{th}$ species, $a_{ii}$ is the intra-specific
competition rate of the $i^{th}$ species, $a_{12}$ and $a_{21}$ are interspecific competition rates of two species. In system (1.1), it is assumed that during the whole life histories each individual admits the same ability to compete with other species. This assumption is obviously unrealistic for many animals. In the real world, almost all animals have stage structure of immature and mature. In the natural world, for many animals whose babies are raised by their parents, or are dependent on the nutrition from the eggs they stay in, the babies are much weaker than the mature. Competition with other individuals of the community and the ability to reproduce babies can be ignored. Therefore, it is important and practical to introduce the stage structure into the competition model. In this paper, we intend to consider the stage structure of two species. We classify individuals of prey as belonging either the immature or the mature and suppose that only adult individuals can compete with other individuals of the community.

Stage-structured models have received much attention in recent years (see for example [10–19]). The pioneering work of Aiello and Freedman (1990) on a single species growth model with stage structure represents a mathematically more careful and biologically meaningful formulation approach. In [10], a model of single-species population growth incorporating stage structure as a reasonable generalization of the classical logistic model was derived and investigated. This model assumes an average age to maturity which appears as a constant time delay reflecting a delayed birth of immatures and a reduced survival of immatures to their maturity. Recently, Magnusson [11], Wang and Chen [12], Zhang et al. [13] proposed and investigated predator-prey models with stage structure for prey or predator to analyze the influence of a stage structure for the prey or the predator on the dynamics of predator-prey models. We note that little attention has been paid to the study on stage-structured competition models.

In the present paper, we first discuss the effect of stage structure on the dynamics of Lotka-Volterra type competition systems with constant coefficients. To do so, we consider the following differential system,

$$
\begin{align*}
\dot{x}_1(t) &= b_1 x_2(t) - r_1 x_1(t) - s_1 x_1(t), \\
\dot{x}_2(t) &= a_1 x_1(t) - a_{12} x_2(t) y_2(t), \\
\dot{y}_1(t) &= b_2 y_2(t) - r_2 y_1(t) - a_{21} y_1(t), \\
\dot{y}_2(t) &= a_{22} y_2(t) - a_{12} x_2(t) y_2(t),
\end{align*}
$$

where $x_1(t)$ and $x_2(t)$ represent the densities of immature and mature individuals of the first species $X$ at time $t$, respectively; $y_1(t)$ and $y_2(t)$ denote the densities of immature and mature individuals of the second species $Y$ at time $t$, respectively. In system (1.2), it is assumed that $a_{11}, a_{12}, a_{21}, a_{22}, b_1, b_2, r_1, r_2$ are positive constants.

The model is derived under the following assumptions.

(A1) The Immature Population. The birth rate into the immature population is proportional to the existing mature population with a proportionality $b_i$ ($i = 1, 2$); the death rate of the immature population is proportional to the existing immature population with proportionality $r_i$ ($i = 1, 2$).

(A2) The Mature Population. $s_i$ denotes the rate of immature population becoming mature population, $i = 1, 2$. It is assumed that this rate is proportional to the density of the existing immature population. $a_{11}$ and $a_{22}$ are death and intra-specific competition rates of species $X$ and $Y$, respectively. $a_{12}$ and $a_{21}$ are interspecific competition rates between species $X$ and species $Y$, respectively.

We note that any biological or environmental parameters are naturally subject to fluctuation in time. As Cushing [20] pointed out, that it is necessary and important to consider models with periodic ecological parameters or perturbations which might be quite naturally exposed (for example, those due to seasonal effects of weather, food supply, mating habits, hunting, or harvesting seasons, etc.). Thus, the assumption of periodicity of the parameters is a way of incorporating the periodicity of the environment. Therefore, in this paper, we will also consider
the combined effects of periodicity of the ecological and environmental parameters and stage structure for each species on the dynamics of Lotka-Volterra type competition systems. To this end, we will consider the following differential system,

\[
\begin{align*}
\dot{x}_1(t) &= b_1(t) x_2(t) - r_1(t) x_1(t) - \alpha_1(t) x_1(t), \\
\dot{x}_2(t) &= \alpha_1(t) x_1(t) - \alpha_{11}(t) x_1^2(t) - \alpha_{12}(t) x_2(t) y_2(t), \\
\dot{y}_1(t) &= b_2(t) y_2(t) - r_2(t) y_1(t) - \alpha_2(t) y_1(t), \\
\dot{y}_2(t) &= \alpha_2(t) y_1(t) - \alpha_{22}(t) y_2^2(t) - \alpha_{21}(t) x_2(t) y_2(t),
\end{align*}
\]

where \(\alpha_{ij}(t), \alpha_{12}(t), \alpha_{21}(t), \alpha_{22}(t), b_1(t), b_2(t), r_1(t), r_2(t)\) are assumed to be continuously positive periodic functions with common period \(\omega\).

The initial conditions for system (1.2) and (1.3) take the form of

\[
\begin{align*}
x_1(0) > 0, & \quad x_2(0) > 0, & \quad y_1(0) > 0, & \quad y_2(0) > 0.
\end{align*}
\]

In this paper, we discuss system (1.2) and (1.3) only in \(R^4_{+0} = \{(x_1, x_2, x_3, x_4) : x_i > 0, i = 1, 2, 3, 4\}\).

It is well known by the fundamental theory of ordinary differential equations that system (1.2), (1.3)) has a unique solution \(s(t) = (x_1(t), x_2(t), y_1(t), y_2(t))\) satisfying initial conditions (1.4). It is easy to show that all solutions of system (1.2) (1.3)) corresponding to initial conditions (1.4) are defined on \([0, +\infty)\) and remain positive for all \(t \geq 0\). In this paper, the solution of system (1.2) (1.3)) satisfying initial conditions (1.4) is said to be positive.

This paper is organized as follows. In the next section, we first discuss system (1.2). By constructing suitable Lyapunov functions, sufficient conditions are derived for the global stability of nonnegative equilibria of system (1.2) with initial conditions (1.4). We show that three typical dynamical behaviors (coexistence, bistability, and dominance) are possible in two-species stage-structured competition model. In Section 3, we consider system (1.3). By using Gaines and Mawhin's continuation theorem of coincidence degree theory, we show the existence of positive periodic solutions to system (1.3) with initial conditions (1.4). Some examples are given respectively in Sections 2 and 3 to illustrate the feasibility of our main results. The paper ends with several discussions in Section 4 to show the effects of stage structure on the global dynamics of competition system.

## 2. GLOBAL STABILITY

In this section, we are concerned with the global asymptotic stability of nonnegative equilibria of system (1.2) by means of suitable Lyapunov functions.

System (1.2) has three boundary equilibria: \(E_0(0, 0, 0, 0), E_1(\bar{x}_1, \bar{x}_2, 0, 0), E_2(0, 0, \bar{y}_1, \bar{y}_2)\), where

\[
\begin{align*}
\bar{x}_1 &= \frac{\alpha_1 b_1^2}{a_{11}(r_1 + \alpha_1)^2}, & \bar{x}_2 &= \frac{\alpha_1 b_1}{a_{11}(r_1 + \alpha_1)}, \\
\bar{y}_1 &= \frac{\alpha_2 b_2^2}{a_{22}(r_2 + \alpha_2)^2}, & \bar{y}_2 &= \frac{\alpha_2 b_2}{a_{22}(r_2 + \alpha_2)}. 
\end{align*}
\]

Let

\[
\begin{align*}
A &= a_{11}a_{22} - a_{12}a_{21}, \\
A_1 &= \alpha_1 b_1 a_{22} (r_2 + \alpha_2) - \alpha_{12} a_2 b_2 (r_1 + \alpha_1), \\
A_2 &= \alpha_2 b_2 a_{11} (r_1 + \alpha_1) - \alpha_{21} a_1 b_1 (r_2 + \alpha_2).
\end{align*}
\]

If \(A_1A_2 > 0\), then, system (1.2) has a unique positive equilibrium \(E^* (x_1^*, x_2^*, y_1^*, y_2^*)\), where

\[
\begin{align*}
x_1^* &= \frac{b_1 x_2^*}{r_1 + \alpha_1}, & x_2^* &= \frac{A_1}{A (r_1 + \alpha_1)(r_2 + \alpha_2)}, \\
y_1^* &= \frac{b_2 y_2^*}{r_2 + \alpha_2}, & y_2^* &= \frac{A_2}{A (r_1 + \alpha_1)(r_2 + \alpha_2)}.
\end{align*}
\]
It is easy to prove that $E_0$ is a saddle; if $A_2 < 0$, then, the nonnegative equilibrium $E_1$ is locally stable, if $A_2 > 0$, then, $E_1$ is locally unstable; if $A_1 < 0$, then, $E_2$ is locally stable, if $A_1 > 0$, then, $E_2$ is locally unstable; if $A > 0$, then, the positive equilibrium $E^*$ is locally stable, if $A < 0$, then $E^*$ is locally unstable.

We first give a result on the boundedness of solutions to system (1.2) with initial conditions (1.4).

**Lemma 2.1.** Positive solutions of system (1.2) with initial conditions (1.4), are ultimately bounded.

**Proof.** Suppose $z(t) = (x_1(t), x_2(t), y_1(t), y_2(t))$ is any positive solution of system (1.2) with initial conditions (1.4).

Define

$$\rho(t) = x_1(t) + x_2(t) + y_1(t) + y_2(t).$$

Calculating the derivative of $\rho(t)$ along positive solutions of (1.2), it follows,

$$\dot{\rho}(t) \leq -A_0 \rho(t) + \left(\frac{b_1 + A_0}{4a_{11}} \right)^2 \rho(t) + \left(\frac{b_2 + A_0}{4a_{22}} \right)^2,$$

where $A_0 = \min\{r_1, r_2\}$. It follows from (2.4) that

$$\lim\sup_{t \to \infty} \rho(t) \leq \left(\frac{b_1 + A_0}{4A_0a_{11}} + \frac{b_2 + A_0}{4A_0a_{22}} \right) := M^*_1.$$

Therefore, there exists a $T > 0$ and an $M_1 > M^*_1$, such that, if $t > T$, $\rho(t) \leq M_1$. This completes the proof.

We are now in a position to formulate our result on the global stability of three nonnegative equilibria of system (1.2).

**Theorem 2.1.** If $A_1 > 0, A_2 > 0$, then, the positive equilibrium $E^*(x_1^*, x_2^*, y_1^*, y_2^*)$ of system (1.2) is globally asymptotically stable.

**Proof.** Let $z(t) = (x_1(t), x_2(t), y_1(t), y_2(t))$ be any positive solution of system (1.2) with initial conditions (1.4).

System (1.2) can be rewritten as

$$\begin{align*}
\dot{x}_1(t) &= \frac{b_1}{x_1^*} [-x_2(t)(x_1(t) - x_1^*) + x_1(t)(x_2(t) - x_2^*)], \\
\dot{x}_2(t) &= \frac{a_1}{x_2^*} [-x_1(t)(x_2(t) - x_2^*) + x_2(t)(x_1(t) - x_1^*)] + x_2(t)[-a_{11}(x_2(t) - x_2^*) - a_{12}(y_2(t) - y_2^*)], \\
\dot{y}_1(t) &= \frac{b_2}{y_1^*} [-y_2(t)(y_1(t) - y_1^*) + y_1(t)(y_2(t) - y_2^*)], \\
\dot{y}_2(t) &= \frac{a_2}{y_2^*} [-y_1(t)(y_2(t) - y_2^*) + y_2(t)(y_1(t) - y_1^*)] + y_2(t)[-a_{22}(y_2(t) - y_2^*) - a_{21}(x_2(t) - x_2^*)].
\end{align*}$$

(2.5)

Define a Lyapunov function,

$$V_1(t) = \sum_{i=1}^{2} c_i \left( x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right) + \sum_{i=1}^{2} c_{i+2} \left( y_i - y_i^* - y_i^* \ln \frac{y_i}{y_i^*} \right),$$

(2.6)

where $c_i$ ($i = 1, 2, 3, 4$) are positive constants to be determined.
Calculating the derivative of $V_1(t)$ along solutions of system (2.5), it follows that,

$$
\frac{dV_1(t)}{dt} = \sum_{i=1}^{2} c_i \left( x_i(t) - x_i^* \right) \frac{\dot{x}_i(t)}{x_i(t)} + \sum_{i=1}^{2} c_{i+2} \left( y_i(t) - y_i^* \right) \frac{\dot{y}_i(t)}{y_i(t)}
$$

$$
= \frac{c_1 b_1 (x_1(t) - x_1^*)}{x_1(t)} \left[ -x_2(t) (x_1(t) - x_1^*) + x_1(t) (x_2(t) - x_2^*) \right] + \frac{c_2 a_1 (x_2(t) - x_2^*)}{x_2(t)x_2(t)} \left[ -x_1(t) (x_2(t) - x_2^*) + x_2(t) (x_1(t) - x_1^*) \right] + c_4 (x_2(t) - x_2^*) \left[ -a_{11} (x_2(t) - x_2^*) - a_{12} (y_2(t) - y_2^*) \right] + c_2 b_2 (y_1(t) - y_1^*) \left[ -y_2(t) (y_1(t) - y_1^*) + y_1(t) (y_2(t) - y_2^*) \right] + c_4 (y_2(t) - y_2^*) \left[ -a_{22} (y_2(t) - y_2^*) - a_{21} (x_2(t) - x_2^*) \right].
$$

(2.7)

Set $c_1 = \alpha_1 x_1^*/(b_1 x_1^*)$, $c_2 = 1$, $c_3 = \alpha_2 y_1^*/(b_2 y_2^*)$, $c_4 = 1$. We derive from (2.7) that

$$
\frac{dV_1(t)}{dt} = -\frac{c_1}{x_2^*} \left[ \sqrt{x_2(t)} \left( x_1(t) - x_1^* \right) - \sqrt{x_2(t)} \left( x_2(t) - x_2^* \right) \right]^2 - \frac{\alpha_2}{y_2^*} \left[ \sqrt{y_2(t)} \left( y_1(t) - y_1^* \right) - \sqrt{y_2(t)} \left( y_2(t) - y_2^* \right) \right]^2 - a_{11} (x_2(t) - x_2^*)^2 - a_{12} (x_2(t) - x_2^*) (y_2(t) - y_2^*) - a_{21} (x_2(t) - x_2^*) (y_2(t) - y_2^*) - a_{22} (y_2(t) - y_2^*)^2 \leq -X^T M X,
$$

(2.8)

where

$$
X^T = (x_2(t) - x_2^*, y_2(t) - y_2^*)^T, \quad M = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}.
$$

Noting that $A_1 > 0$, $A_2 > 0$, imply $A > 0$, we see that the matrix $M$ is positive definite. Therefore, we have

$$
\frac{dV_1(t)}{dt} \leq -\lambda \|X\| = -\lambda (x_2(t) - x_2^*)^2 - \lambda (y_2(t) - y_2^*)^2,
$$

(2.10)

where $\lambda$ is the smallest positive eigenvalue of $M$.

We have from (2.10) that

$$
V_1(t) + \lambda \int_0^t (x_2(s) - x_2^*)^2 ds + \lambda \int_0^t (y_2(s) - y_2^*)^2 ds \leq V_1(0),
$$

which implies $(x_2(t) - x_2^*)^2$, $(y_2(t) - y_2^*)^2 \in L^1[0, \infty)$. In addition, by Lemma 2.1, $x_2(t), y_2(t)$ are bounded. This, together with (1.2), implies that $x_2(t) - x_2^*$, $y_2(t) - y_2^*$, $\dot{x}_2(t)$, and $\dot{y}_2(t)$ are uniformly continuous. Applying Barbalat's lemmas [21, Lemmas 1.2.2, 1.2.3], we conclude that,

$$
\lim_{t \to \infty} (x_2(t) - x_2^*)^2 = 0, \quad \lim_{t \to \infty} \dot{x}_2(t) = 0,
$$

$$
\lim_{t \to \infty} (y_2(t) - y_2^*)^2 = 0, \quad \lim_{t \to \infty} \dot{y}_2(t) = 0,
$$

which imply that,

$$
\lim_{t \to \infty} x_2(t) = x_2^*, \quad \lim_{t \to \infty} y_2(t) = y_2^*,
$$

$$
\lim_{t \to \infty} x_1(t) = x_1^*, \quad \lim_{t \to \infty} y_1(t) = y_1^*.
$$

This completes the proof.
THEOREM 2.2. If \( A_2 < 0, A > 0 \), then the nonnegative equilibrium \( E_1(\bar{x}_1, \bar{x}_2, 0, 0) \) of system (1.2) is globally asymptotically stable.

PROOF. Let \( z(t) = (x_1(t), x_2(t), y_1(t), y_2(t)) \) be any positive solution of system (1.2) with initial conditions (1.4).

System (1.2) can be rewritten as

\[
\begin{align*}
\dot{x}_1(t) &= \frac{b_1}{\bar{x}_1} \left[-x_2(t)(x_1(t) - \bar{x}_1) + x_1(t)(x_2(t) - \bar{x}_2)\right], \\
\dot{x}_2(t) &= \frac{a_1}{\bar{x}_2} \left[-x_1(t)(x_2(t) - \bar{x}_2) + x_2(t)(x_1(t) - \bar{x}_1)\right] \\
&\quad + x_2(t)\left[-a_{11}(x_2(t) - \bar{x}_2) - a_{12}y_2(t)\right], \\
\dot{y}_1(t) &= b_2y_2(t) - (\alpha_1 + \alpha_2)y_1(t), \\
y_2(t) &= \alpha_2y_1(t) - a_22y_2(t) - a_21(x_2(t) - \bar{x}_2)y_2(t) - a_21x_2y_2(t).
\end{align*}
\]

Define a Lyapunov function,

\[
V_2(t) = \sum_{i=1}^{2} c_i \left( x_i - \bar{x}_i - \bar{x}_i \ln \frac{x_i}{\bar{x}_i} \right) + c_3y_1(t) + c_4y_2(t),
\]

where \( c_i \) (\( i = 1, 2, 3, 4 \)) are positive constants to be determined.

Calculating the derivative of \( V_2(t) \) along solutions of system (2.11), it follows that,

\[
\frac{dV_2(t)}{dt} = \sum_{i=1}^{2} c_i (x_i(t) - \bar{x}_i) \frac{\dot{x}_i(t)}{x_i(t)} + c_3y_1(t) + c_4y_2(t)
\]

\[
= \frac{c_1b_1}{\bar{x}_1x_1(t)} \left[-x_2(t)(x_1(t) - \bar{x}_1) + x_1(t)(x_2(t) - \bar{x}_2)\right] \\
+ \frac{c_2a_1}{\bar{x}_2x_2(t)} \left[-x_1(t)(x_2(t) - \bar{x}_2) + x_2(t)(x_1(t) - \bar{x}_1)\right] \\
+ c_2(x_2(t) - \bar{x}_2)\left[-a_{11}(x_2(t) - \bar{x}_2) - a_{12}y_2(t)\right] \\
+ c_3[b_2y_2(t) - (\alpha_2 + \alpha_1)y_1(t)] \\
+ c_4 \left[a_2y_1(t) - a_22y_2(t) - a_21(x_2(t) - \bar{x}_2)y_2(t) - a_21x_2y_2(t)\right].
\]

Set \( c_1 = a_1\bar{x}_1/(b_1\bar{x}_2) \), \( c_2 = 1 \), \( c_3 = a_21\bar{x}_2/b_2 \), \( c_4 = 1 \). We derive from (2.13) that

\[
\frac{dV_2(t)}{dt} = \frac{-\alpha_1}{\bar{x}_2} \left[\sqrt{x_2(t)}(x_1(t) - \bar{x}_1) - \sqrt{x_1(t)}(x_2(t) - \bar{x}_2)\right]^2 \\
- a_{11}(x_2(t) - \bar{x}_2)^2 - (a_{12} + a_{21})y_2(t)(x_2(t) - \bar{x}_2) \\
- a_{22}y_2^2(t) + \frac{A_2}{(r_1 + \alpha_1)(r_2 + \alpha_2)}y_1(t) \\
\leq -X_T^T M X_1,
\]

since \( A_2 < 0 \), where \( X_T^T = (x_2(t) - \bar{x}_2, y_2(t)) \), \( M \) is defined in (2.9).

Noting that \( A > 0 \), we see that the matrix \( M \) is positive definite. Therefore, we have

\[
\frac{dV_2(t)}{dt} \leq -\lambda \|X_1\| = -\lambda (x_2(t) - \bar{x}_2)^2 - \lambda y_2^2(t),
\]

where \( \lambda \) is the smallest positive eigenvalue of \( M \).

By using a similar argument in the proof of Theorem 2.1, one can show that,

\[
\lim_{t\to\infty} x_2(t) = \bar{x}_2, \quad \lim_{t\to\infty} y_2(t) = 0, \\
\lim_{t\to\infty} x_1(t) = \bar{x}_1, \quad \lim_{t\to\infty} y_1(t) = 0.
\]

This completes the proof.

Similarly, one can prove the following result.
**Theorem 2.3.** If $A_1 < 0$, $A > 0$, then the nonnegative equilibrium $E_2(0, 0, \bar{y}_1, \bar{y}_2)$ is globally asymptotically stable.

**Remark 1.** In this section, we have discussed the effect of stage structure on the dynamics of a two-species Lotka-Volterra type competitive system with constant coefficients. By constructing suitable Lyapunov functions, sufficient conditions are derived for the global asymptotic stability of nonnegative equilibria of system (1.2). By Theorems 2.1–2.3, we have shown the following three typical dynamical behaviors are possible.

(i) Coexistence. If $A_1 > 0$, $A_2 > 0$ (i.e., $a_{12}/a_{22} < a_1b_1(r_2 + \alpha_2)/a_2b_2(r_1 + \alpha_1) < a_{11}/a_{21}$), then, there exists a positive and globally stable equilibrium point. This case is realized if the interspecific competition is weaker than the intra-specific competition.

(ii) Bistability. If $A_1 < 0$, $A_2 < 0$ (i.e., $a_{11}/a_{21} < a_1b_1(r_2 + \alpha_2)/a_2b_2(r_1 + \alpha_1) < a_{12}/a_{22}$), then, a positive equilibrium exists, but it is a saddle point: For this case, only one species can survive and the survivor is determined by initial population densities of two species. This is the case if interspecific competition is stronger than intra-specific competition.

(iii) Dominance. If $A_1 < 0$, $A > 0$ or $A_2 < 0$, $A > 0$ (i.e., $a_{11}/a_{21} < a_1b_1(r_2 + \alpha_2)/a_2b_2(r_1 + \alpha_1) < a_1b_1(r_2 + \alpha_2)/a_2b_2(r_1 + \alpha_1)$), then, no positive equilibria exist, and one of the one-species equilibria is globally asymptotically stable. For this case, the survivor does not depend on the initial population densities. This holds if one of the competitors has the superior ability to compete with the other.

From what has been discussed above we see that if $A_1 > 0$, $A_2 > 0$ (therefore, $A > 0$) or $A_1 < 0$, $A > 0$, or $A_2 < 0$, $A > 0$, system (1.2) has no interior periodic orbit. We would like to mention here that if $A_1 < 0$, $A_2 < 0$, then, $A < 0$. In this case, the equilibrium $E^*$ is still feasible. We cannot rule out the possibility of coexistence via interior periodic orbits.

We now give two examples to illustrate the feasibility of Theorems 2.1 and 2.2.

**Example 1.** Consider the following stage-structured competition system,

\[
\begin{align*}
\dot{x}_1(t) &= 5x_2(t) - 0.1x_1(t) - 3x_1(t), \\
\dot{x}_2(t) &= 3x_1(t) - 8x_2(t) - 0.3x_2(t)y_2(t), \\
\dot{y}_1(t) &= 4y_2(t) - 0.2y_1(t) - 2y_1(t), \\
\dot{y}_2(t) &= 2y_1(t) - 10y_2(t) - 0.5x_2(t)y_2(t).
\end{align*}
\]

(2.16)

Figure 1. The temporal solution found by numerical integration of system (2.16) with initial conditions $x_1(0) = x_2(0) = y_1(0) = y_2(0) = 0.5$. 
It is easy to show that $A_1 = 322.56$, $A_2 = 181.9$. Thus, by Theorem 2.1, the positive equilibrium $E^* (16128000/16881887, 32560/544577, 363800/5990347, 181900/544577)$ of system (2.16) is globally asymptotically stable. Numerical integration of system (2.16) is carried out using standard algorithms ode45 in MATLAB. As shown in Figure 1, numerical simulation illustrates the result above.

EXAMPLE 2. Consider another stage-structured competition system,

$$
\begin{align*}
\dot{x}_1 (t) &= 10x_2 (t) - 0.1x_1 (t) - 2x_1 (t), \\
\dot{x}_2 (t) &= 2x_1 (t) - 2x_2 (t) - x_2 (t) y_2 (t), \\
\dot{y}_1 (t) &= 2y_2 (t) - 0.2y_1 (t) - y_1 (t), \\
\dot{y}_2 (t) &= y_1 (t) - 5y_2 (t) - 5x_2 (t) y_2 (t).
\end{align*}
$$

(2.17)

It is easy to show that $A_2 = -111.6$, $A = 5$. By Theorem 2.2, we see that the nonnegative equilibrium $E_1 (10000/441, 100/21, 0, 0)$ of system (2.17) is globally asymptotically stable. Numerical simulation is in agreement with the above result (see Figure 2).

3. EXISTENCE OF PERIODIC SOLUTIONS TO SYSTEM (1.3)

In this section, we show the existence of positive periodic solutions to system (1.3) with initial conditions (1.4) by using Gaines and Mawhin’s continuation theorem of coincidence degree theory. For convenience, we shall summarize in the following a few concepts and results from [22] that will be used in this section.

Let $X, Y$ be real Banach spaces, $L : \text{Dom} L \subset X \to Y$ a linear mapping, and $N : X \to Y$, a continuous mapping. The mapping $L$ is called a Fredholm mapping of index zero if $\dim \text{Ker} L = \text{codim} \text{Im} L < +\infty$ and $\text{Im} L$ is closed in $Y$. If $L$ is a Fredholm mapping of index zero and there exist continuous projectors $P : X \to X$, and $Q : Y \to Y$ such that $\text{Im} P = \text{Ker} L$, $\text{Ker} Q = \text{Im} L = \text{Im} (I - Q)$, then, the restriction $L_P$ of $L$ to $\text{Dom} L \cap \text{Ker} P : (I - P)X \to \text{Im} L$ is invertible. Denote the inverse of $L_P$ by $K_P$. If $\Omega$ is an open bounded subset of $X$, the mapping $N$ will be called $L$ - compact on $\Omega$ if $QN(\Omega)$ is bounded and $K_P (I - Q)N : \Omega \to X$ is compact. Since $\text{Im} Q$ is isomorphic to $\text{Ker} L$, there exists an isomorphism $J : \text{Im} Q \to \text{Ker} L$. 

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{The temporal solution of system (2.17) with initial conditions $x_1 (0) = x_2 (0) = y_1 (0) = y_2 (0) = 25$.}
\end{figure}
LEMMA 3.1. Let $\Omega \subset X$ be an open bounded set. Let $L$ be a Fredholm mapping of index zero and $N$ be $L$-compact on $\Omega$. Assume

(a) for each $\lambda \in (0, 1), x \in \partial \Omega \cap \text{Dom} L$, $Lx \neq \lambda Nx$;
(b) for each $x \in \partial \Omega \cap \text{Ker} L$, $QN x \neq 0$;
(c) $\text{deg}\{JQN, \Omega \cap \text{Ker} L, 0\} \neq 0$.

Then, $Lx = Nx$ has at least one solution in $\Omega \cap \text{Dom} L$.

The following notations will also be needed in the following discussion,

$$ f = \frac{1}{\omega} \int_{0}^{\omega} f(t) \, dt, \quad f^L = \min_{t \in [0, \omega]} f(t), \quad f^M = \max_{t \in [0, \omega]} f(t), $$

where $f$ is a continuous $\omega$-periodic function.

We are now able to state and prove our main result on the existence of positive periodic solutions to system (1.3) with initial conditions (1.4).

**THEOREM 3.1.** System (1.3) has at least one strictly positive $\omega$-periodic solution provided that

(H1) $\alpha_1^L b_1^L \left( r_2^L + \alpha_2^L \right) > a_{12}^L M b_2^L \left( r_1^L + \alpha_1^L \right)$,

(H2) $\alpha_2^L b_2^L \left( r_1^L + \alpha_1^L \right) > a_{21}^L M b_1^L \left( r_2^L + \alpha_2^L \right)$.

**PROOF.** Let

$$ u_i (t) = \ln x_i (t), \quad u_{i+2} (t) = \ln y_i (t) \quad (i = 1, 2). \quad (3.1) $$

On substituting (3.1) into (1.3), we derive

$$ \frac{du_1 (t)}{dt} = b_1 (t) e^{u_2 (t) - u_1 (t)} - r_1 (t) - \alpha_1 (t), $$
$$ \frac{du_2 (t)}{dt} = a_1 (t) e^{u_1 (t) - u_2 (t)} - a_{11} (t) e^{u_2 (t)} - a_{12} (t) e^{u_4 (t)}, $$
$$ \frac{du_3 (t)}{dt} = b_2 (t) e^{u_4 (t) - u_3 (t)} - r_2 (t) - \alpha_2 (t), $$
$$ \frac{du_4 (t)}{dt} = a_2 (t) e^{u_3 (t) - u_4 (t)} - a_{21} (t) e^{u_2 (t)} - a_{22} (t) e^{u_1 (t)}. \quad (3.2) $$

It is easy to see that if system (3.2) admits one $\omega$-periodic solution $(u_1^*(t), u_2^*(t), u_3^*(t), u_4^*(t))^T$, then, $(x_1^*(t), x_2^*(t), y_1^*(t), y_2^*(t))^T = (\exp[u_1^*(t)], \exp[u_2^*(t)], \exp[u_3^*(t)], \exp[u_4^*(t)])^T$ is a positive $\omega$-periodic solution of system (1.3). Thus, to complete the proof, it suffices to show that system (3.2) has at least one $\omega$-periodic solution.

Set

$$ X = Y = \{ (u_1 (t), u_2 (t), u_3 (t), u_4 (t))^T \in C (R, R^4) : u_i (t + \omega) = u_i (t), \ i = 1, 2, 3, 4 \} $$

and

$$ \left\| (u_1 (t), u_2 (t), u_3 (t), u_4 (t))^T \right\| = \sum_{i=1}^{4} \max_{t \in [0, \omega]} |u_i (t)|, $$

here $\| \cdot \|$ denotes the Euclidean norm. It is easy to see that $X$ and $Y$ are Banach spaces with the norm $\| \cdot \|$. Let

$$ L : \text{Dom} L \cap X \to X, \quad L (u_1 (t), u_2 (t), u_3 (t), u_4 (t))^T = \left( \frac{du_1 (t)}{dt}, \frac{du_2 (t)}{dt}, \frac{du_3 (t)}{dt}, \frac{du_4 (t)}{dt} \right)^T, $$
where \( \text{Dom}L = \{(u_1(t), u_2(t), u_3(t), u_4(t))^\top \in C^1([0, T]) \) and \( N : X \to X \),

\[
N = \begin{bmatrix}
  b_1(t) e^{u_2(t)-u_1(t)} - r_1(t) - \alpha_1(t) \\
  \alpha_1(t) e^{u_1(t)-u_2(t)} - a_{11}(t) e^{u_2(t)} - a_{12}(t) e^{u_4(t)} \\
  b_2(t) e^{u_4(t)-u_2(t)} - r_2(t) - \alpha_2(t) \\
  \alpha_2(t) e^{u_3(t)-u_4(t)} - a_{22}(t) e^{u_4(t)} - a_{21}(t) e^{u_1(t)}
\end{bmatrix}.
\]

Define

\[
P \begin{bmatrix}
  u_1 \\
  u_2 \\
  u_3 \\
  u_4
\end{bmatrix} = Q \begin{bmatrix}
  u_1 \\
  u_2 \\
  u_3 \\
  u_4
\end{bmatrix} = \begin{bmatrix}
  \frac{1}{\omega} \int_0^\omega u_1(t) \, dt \\
  \frac{1}{\omega} \int_0^\omega u_2(t) \, dt \\
  \frac{1}{\omega} \int_0^\omega u_3(t) \, dt \\
  \frac{1}{\omega} \int_0^\omega u_4(t) \, dt
\end{bmatrix},
\]

\[
\in X = Y.
\]

It is clear that

\[
\ker L = \{ x \mid x \in X, \ x = h, \ h \in \mathbb{R}^4 \},
\]

\[
\text{Im} L = \left\{ y \mid y \in Y, \int_0^\omega y(t) \, dt = 0 \right\}
\]

is closed in \( \mathbb{R}^4 \),

\[
\dim \ker L = \text{codim } \text{Im} L = 4.
\]

Therefore, \( L \) is a Fredholm mapping of index zero. Obviously, \( P \) and \( Q \) are continuous projectors such that

\[
\text{Im} P = \ker L, \quad \ker Q = \text{Im} L = \text{Im} (I - Q).
\]

Furthermore, it is easy to prove that the inverse \( K_P \) of \( L_P \) exists and is defined by \( \text{Im} L \to \text{Dom} L \cap \ker P \),

\[
K_P(y) = \int_0^t y(s) \, ds - \frac{1}{\omega} \int_0^\omega \int_0^t y(s) \, ds \, dt.
\]

Then, \( QN : X \to Y \) and \( K_P(I - Q)N : X \to X \) are given by

\[
QN x = \begin{bmatrix}
  \frac{1}{\omega} \int_0^\omega \left[ b_1(t) e^{u_2(t)-u_1(t)} - r_1(t) - \alpha_1(t) \right] \, dt \\
  \frac{1}{\omega} \int_0^\omega \left[ \alpha_1(t) e^{u_1(t)-u_2(t)} - a_{11}(t) e^{u_2(t)} - a_{12}(t) e^{u_4(t)} \right] \, dt \\
  \frac{1}{\omega} \int_0^\omega \left[ b_2(t) e^{u_4(t)-u_2(t)} - r_2(t) - \alpha_2(t) \right] \, dt \\
  \frac{1}{\omega} \int_0^\omega \left[ \alpha_2(t) e^{u_3(t)-u_4(t)} - a_{22}(t) e^{u_4(t)} - a_{21}(t) e^{u_1(t)} \right] \, dt
\end{bmatrix}
\]

\[
K_P(I - Q) x = \int_0^t N x(s) \, ds - \frac{1}{\omega} \int_0^\omega \int_0^t N x(s) \, ds \, dt - \left( \frac{t}{\omega} - \frac{1}{2} \right) \int_0^\omega N x(s) \, ds.
\]

It is easy to see that \( QN \) and \( K_P(I - Q)N \) are continuous.

In order to apply Lemma 3.1, we need to search for an appropriate open, bounded subset \( \Omega \).

Corresponding to the operator equation \( Lx = \lambda Nx \), \( \lambda \in (0, 1) \), it follows

\[
\begin{align*}
\frac{du_1(t)}{dt} &= \lambda \left[ b_1(t) e^{u_2(t)-u_1(t)} - r_1(t) - \alpha_1(t) \right], \\
\frac{du_2(t)}{dt} &= \lambda \left[ \alpha_1(t) e^{u_1(t)-u_2(t)} - a_{11}(t) e^{u_2(t)} - a_{12}(t) e^{u_4(t)} \right], \\
\frac{du_3(t)}{dt} &= \lambda \left[ b_2(t) e^{u_4(t)-u_2(t)} - r_2(t) - \alpha_2(t) \right], \\
\frac{du_4(t)}{dt} &= \lambda \left[ \alpha_2(t) e^{u_3(t)-u_4(t)} - a_{22}(t) e^{u_4(t)} - a_{21}(t) e^{u_1(t)} \right].
\end{align*}
\]

(3.3)

Suppose that \((u_1(t), u_2(t), u_3(t), u_4(t))^\top \in X\) is a solution of (3.3) for a certain \( \lambda \in (0, 1) \).
Since \((u_1(t), u_2(t), u_3(t), u_4(t))^T \in X\), there exist \(\xi_i, \eta_i \in [0, \omega]\), such that

\[
u_i (\xi_i) = \max_{t \in [0, \omega]} u_i (t) \quad (i = 1, 2, 3, 4) \tag{3.4}
\]

and

\[
u_i (\eta_i) = \min_{t \in [0, \omega]} u_i (t) \quad (i = 1, 2, 3, 4). \tag{3.5}
\]

It follows from (3.4) that,

\[u_i' (\xi_i) = 0 \quad (i = 1, 2, 3, 4),\]

that is,

\[a_{11} (\xi_2) e^{u_2 (\xi_2)} - a_{11} (\xi_1) e^{u_1 (\xi_1)} = 0, \tag{3.6}\]

\[a_1 (\xi_2) e^{u_1 (\xi_2)} - a_{11} (\xi_2) e^{u_2 (\xi_2)} - a_{12} (\xi_2) e^{u_3 (\xi_2) + u_4 (\xi_2)} = 0, \]

\[b_2 (\xi_3) e^{u_4 (\xi_3)} - (r_2 (\xi_3) + a_2 (\xi_3)) e^{u_3 (\xi_3)} = 0, \]

\[a_2 (\xi_4) e^{u_3 (\xi_4) + u_4 (\xi_4)} = 0. \]

We derive from the first equation of system (3.6) that

\[e^{u_2 (\xi_2)} \leq \frac{b_{12} e^{u_1 (\xi_1)}}{r_1^2 + \alpha_1^2}. \tag{3.7}\]

It follows from the second equation of (3.6) that

\[a_{11} (\xi_2) e^{u_2 (\xi_2)} \leq a_1^M e^{u_1 (\xi_2)} \leq a_1^M e^{u_1 (\xi_1)}, \]

which, together with (3.7), yields

\[u_2 (\xi_2) \leq \ln \frac{a_1^M b_{12}^M}{a_{11} (r_1^2 + \alpha_1^2)}. \tag{3.8}\]

Therefore, we obtain from (3.7) and (3.8) that

\[u_1 (\xi_1) \leq \ln \frac{a_1^M (b_1^M)^2}{a_{11} (r_1^2 + \alpha_1^2)^2}. \tag{3.9}\]

Similarly, we derive from the third and the fourth equations of (3.6) that

\[u_4 (\xi_4) \leq \ln \frac{a_2^M b_2^M}{a_{22} (r_2^2 + \alpha_2^2)}, \quad u_3 (\xi_3) \leq \ln \frac{a_2^M (b_2^M)^2}{a_{22} (r_2^2 + \alpha_2^2)^2}. \tag{3.10}\]

It follows from (3.5) that

\[u_i' (\eta_i) = 0 \quad (i = 1, 2, 3, 4),\]

that is

\[b_1 (\eta_1) e^{u_2 (\eta_1)} - (r_1 (\eta_1) + a_1 (\eta_1)) e^{u_1 (\eta_1)} = 0, \tag{3.11}\]

\[a_1 (\eta_2) e^{u_1 (\eta_2)} - a_{11} (\eta_2) e^{u_2 (\eta_2)} - a_{12} (\eta_2) e^{u_3 (\eta_2) + u_4 (\eta_2)} = 0, \]

\[b_2 (\eta_3) e^{u_4 (\eta_3)} - (r_2 (\eta_3) + a_2 (\eta_3)) e^{u_3 (\eta_3)} = 0, \]

\[a_2 (\eta_4) e^{u_3 (\eta_4) + u_4 (\eta_4)} - a_{22} (\eta_4) e^{u_2 (\eta_4) + u_4 (\eta_4)} = 0. \]

We obtain from the first equation of (3.11) that

\[e^{u_2 (\eta_1)} \geq \frac{b_1^L}{r_1^L + \alpha_1^L} e^{u_2 (\eta_1)}. \tag{3.12}\]
It follows from the second equation of (3.11) and (3.12) that
\[
\begin{align*}
    a_{11} (\eta_2) e^{2u_2(\eta_2)} &= a_1 (\eta_2) e^{u_1(\eta_2)} - a_{12} (\eta_2) e^{u_2(\eta_2)+u_4(\eta_2)} \\
    &\geq a_1^2 e^{u_1(\eta_1)} - a_{12}^2 e^{u_2(\eta_2)+u_4(\eta_2)} \\
    &\geq \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} e^{u_2(\eta_1)} - a_{12}^2 e^{u_2(\eta_2)+u_4(\eta_2)} \\
    &\geq \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} e^{u_2(\eta_1)} - a_{12}^2 e^{u_2(\eta_2)+u_4(\xi_4)},
\end{align*}
\]
which, together with (3.10), yields
\[
a_{11} (\eta_2) e^{u_2(\eta_2)} \geq \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} - a_{12}^2 e^{u_4(\xi_4)} \tag{3.13}
\]
Therefore, we have
\[
u_2 (\eta_2) \geq \ln \left\{ \frac{1}{a_{11}} \left( \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} - a_{12}^2 \right) \right\} := \ln \rho_2. \tag{3.14}
\]
It follows from (3.12) and (3.14) that
\[
u_1 (\eta_1) \geq \ln \left\{ \frac{b_1^L}{a_{11}} \left( \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} - a_{12}^2 \right) \right\} := \ln \rho_1. \tag{3.15}
\]
Similarly, we derive from the third and the fourth equations of (3.11) and (3.8) that
\[
u_4 (\eta_4) \geq \ln \left\{ \frac{1}{a_{22}} \left( \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} - a_{21}^2 \alpha_1^M b_2^M \right) \right\} := \ln \rho_4 \tag{3.16}
\]
and
\[
u_3 (\eta_3) \geq \ln \left\{ \frac{b_2^L}{a_{22}} \left( \frac{a_1^2 b_1^L}{r_M + \alpha_4^M} - a_{21}^2 \alpha_1^M b_2^M \right) \right\} := \ln \rho_3. \tag{3.17}
\]
It therefore follows from (3.8)--(3.10) and (3.14)--(3.17) that
\[
\begin{align*}
    \max_{t \in [0,\omega]} |u_1(t)| &< \max \left\{ \ln \frac{\alpha_1^M b_1^L}{a_{11}^2 (r_M^2 + \alpha_4^M)} \left\| \ln \rho_1 \right\| : = R_1, \\
    \max_{t \in [0,\omega]} |u_2(t)| &< \max \left\{ \ln \frac{\alpha_1^M b_1^L}{a_{11}^2 (r_M^2 + \alpha_4^M)} \left\| \ln \rho_2 \right\| : = R_2, \\
    \max_{t \in [0,\omega]} |u_3(t)| &< \max \left\{ \ln \frac{\alpha_1^M b_1^L}{a_{22}^2 (r_M^2 + \alpha_4^M)} \left\| \ln \rho_3 \right\| : = R_3, \\
    \max_{t \in [0,\omega]} |u_4(t)| &< \max \left\{ \ln \frac{\alpha_1^M b_1^L}{a_{22}^2 (r_M^2 + \alpha_4^M)} \left\| \ln \rho_4 \right\| : = R_4.
\end{align*}
\]
We note that $R_1$, $R_2$, $R_3$, and $R_4$ in (3.18) are independent of $\lambda$. Denote $M = R_1 + R_2 + R_3 + R_4 + R_0$, where $R_0$ is taken sufficiently large such that the unique solution $(u_1^*, u_2^*, u_3^*, u_4^*)^T$ of the following system of algebraic equations,
\[
\begin{align*}
    \bar{b}_1 e^{u_2-u_1} - \bar{r}_1 - \bar{\alpha}_1 &= 0, \\
    \bar{\alpha}_1 e^{u_1-u_2} - \bar{a}_{11} e^{u_2} - \bar{a}_{12} e^{u_4} &= 0, \\
    \bar{b}_2 e^{u_4-u_3} - \bar{r}_2 - \bar{\alpha}_2 &= 0, \\
    \bar{\alpha}_2 e^{u_3-u_4} - \bar{a}_{22} e^{u_4} - \bar{a}_{21} e^{u_2} &= 0, \tag{3.19}
\end{align*}
\]
satisfies $\| (u_1^*, u_2^*, u_3^*, u_4^*)^T \| = |u_1^*| + |u_2^*| + |u_3^*| + |u_4^*| < M$.\]
We now take \( \Omega = \{(u_1(t), u_2(t), u_3(t), u_4(t))^T \in X : \|(u_1, u_2, u_3, u_4)^T\| < M\} \). This satisfies Condition (a) in Lemma 3.1. When \((u_1(t), u_2(t), u_3(t), u_4(t))^T \in \partial \Omega \cap \text{Ker}L = \partial \Omega \cap R^4\), \((u_1, u_2, u_3, u_4)^T\) is a constant vector in \(R^4\) with \(|u_1| + |u_2| + |u_3| + |u_4| = M\). Thus, we have

\[
QN = \begin{bmatrix}
  (u_1) \\
  (u_2) \\
  (u_3) \\
  (u_4)
\end{bmatrix}
= \begin{bmatrix}
  \tilde{b}_1 e^{u_2-u_1} - \tilde{r}_1 - \tilde{a}_1 \\
  \tilde{a}_1 e^{u_1-u_2} - \tilde{a}_{11} e^{u_2} - \tilde{a}_{12} e^{u_4} \\
  \tilde{b}_2 e^{u_4-u_3} - \tilde{r}_2 - \tilde{a}_2 \\
  \tilde{a}_2 e^{u_3-u_4} - \tilde{a}_{22} e^{u_4} - \tilde{a}_{21} e^{u_2}
\end{bmatrix} \neq \begin{bmatrix}
  0 \\
  0 \\
  0 \\
  0
\end{bmatrix}.
\]

This proves that Condition (b) in Lemma 3.1 is satisfied.

We now prove that Condition (c) in Lemma 3.1 holds. Taking \( J = I : \text{Im}Q \rightarrow \text{Ker}L \), \((u_1, u_2, u_3, u_4)^T \rightarrow (u_1, u_2, u_3, u_4)^T\) and by a direct calculation, we can derive

\[
\deg\left(JQN (u_1, u_2, u_3, u_4)^T, \Omega \cap \text{Ker}L, (0, 0, 0, 0)^T\right)
= \deg\left(\tilde{b}_1 e^{u_2-u_1} - \tilde{r}_1 - \tilde{a}_1, \tilde{a}_1 e^{u_1-u_2} - \tilde{a}_{11} e^{u_2} - \tilde{a}_{12} e^{u_4}, \tilde{b}_2 e^{u_4-u_3} - \tilde{r}_2 - \tilde{a}_2, \tilde{a}_2 e^{u_3-u_4} - \tilde{a}_{22} e^{u_4} - \tilde{a}_{21} e^{u_2}\right),
\]

\[
= \text{sgn}\left(\tilde{b}_1 \tilde{b}_2 (\tilde{a}_{11} \tilde{a}_{22} - \tilde{a}_{12} \tilde{a}_{21}) e^{2u_2^*+2u_4^*-u_1^*-u_3^*}\right)
= 1,
\]

since (H1),(H2) imply that \(\tilde{a}_{11} \tilde{a}_{22} - \tilde{a}_{12} \tilde{a}_{21} > 0\), where \((u_1^*, u_2^*, u_3^*, u_4^*)\) is the unique solution of (3.19).

Finally, it is easy to show that the set \(\{K_P(I - Q)Nx \mid x \in \Omega\}\) is equicontinuous and uniformly bounded. By using the Arzela-Ascoli Theorem, we see that \(K_P(I - Q)N : \Omega \rightarrow X\) is compact. Consequently, \(N\) is \(L\)-compact.

By now, we have proved that \(\Omega\) satisfies all the requirements in Lemma 3.1. Hence, (3.2) has at least one \(\omega\)-periodic solution. Accordingly, system (1.3) has at least one positive \(\omega\)-periodic solution. This completes the proof.

In order to illustrate the feasibility of Theorem 3.1, we give two examples.

\[
\text{Figure 3. The periodic solution found by numerical integration of system (3.20), with initial conditions } x_1(0) = x_2(0) = y_1(0) = y_2(0) = 0.5.
\]
EXAMPLE 3. Consider the following competition system,

\begin{align*}
\dot{x}_1(t) &= (5 + \sin t) x_2(t) - 0.1x_1(t) - (3 + \sin t) x_1(t), \\
\dot{x}_2(t) &= (3 + \sin t) x_1(t) - 8x_2(t) - 0.3x_2(t) y_2(t), \\
y_1(t) &= (4 + \cos t) y_2(t) - 0.2y_1(t) - (2 + \cos t) y_1(t), \\
y_2(t) &= (2 + \cos t) y_1(t) - 10y_2(t) - 0.5x_2(t) y_2(t).
\end{align*}

(3.20)

It is easy to prove that the coefficients of system (3.20) satisfy (H1),(H2). Thus, by Theorem 3.1, system (3.20) with initial conditions (1.4) has at least one positive $2\pi$-periodic solution. As shown in Figure 3, numerical simulation illustrates the result above.

EXAMPLE 4. Consider the following model,

\begin{align*}
\dot{x}_1(t) &= (5 + \sin t) x_2(t) - 0.1x_1(t) - (3 + \sin t) x_1(t), \\
\dot{x}_2(t) &= (3 + \sin t) x_1(t) - 6x_2(t) - x_2(t) y_2(t), \\
y_1(t) &= (4 + \sin t) y_2(t) - 0.2y_1(t) - (2 + \cos t) y_1(t), \\
y_2(t) &= (2 + \cos t) y_1(t) - 5y_2(t) - x_2(t) y_2(t).
\end{align*}

(3.21)

It is easy to show that (H1),(H2) don’t hold for system (3.21). In this case, we cannot get any information for system (3.21) by Theorem 3.1. However, numerical simulation shows that system (3.21) still has at least one strictly positive periodic solution (see Figure 4).

![Figure 4](image-url)  

Figure 4. The periodic solution found by numerical integration of system (3.21), with initial conditions $x_1(0) = x_2(0) = y_1(0) = y_2(0) = 0.5$.

REMARK 2. In this section, we have discussed the combined effects of periodicity of the ecological and environmental parameters and stage structure on the dynamics of competitive model. By using Gaines and Mawhin's continuation theorem of coincidence degree theory, we have shown the existence of positive periodic solutions to a two-species periodic Lotka-Volterra type competition model with stage structure for both species. By Theorem 3.1, we see that higher intra-specific competition rates and lower interspecific competition rates will benefit the existence of positive periodic solutions to system (1.3) with initial conditions (1.4).

We would like to mention here that Example 4 shows that our result in Theorem 3.1 has room for improvement. Another interesting problem associated with the study of model (1.3) should be the uniqueness and global stability of positive periodic solutions. We leave these for future work.
4. DISCUSSION

Now, we discuss how the stage structure affects the global dynamics of a two-species Lotka-Volterra type competition system with constant or periodic coefficients. To this end, we first recall some well-known results for system (1.1).

**THEOREM 4.1.** Assume that,

\[
\frac{a_{12}}{a_{22}} < \frac{b_1}{b_2} < \frac{a_{11}}{a_{21}},
\]

then, system (1.1) has a unique positive equilibrium which is globally asymptotically stable.

**THEOREM 4.2.** Assume that,

\[
\frac{a_{11}}{a_{21}} < \frac{b_1}{b_2} \quad \text{and} \quad \frac{a_{12}}{a_{22}} < \frac{b_1}{b_2},
\]

then, the nonnegative equilibrium \((b_1/a_{11}, 0)\) of system (1.1) is globally asymptotically stable.

**THEOREM 4.3.** Assume that,

\[
\frac{b_1}{b_2} < \frac{a_{11}}{a_{21}} \quad \text{and} \quad \frac{b_1}{b_2} < \frac{a_{12}}{a_{22}},
\]

then, the nonnegative equilibrium \((0, b_2/a_{22})\) of system (1.1) is globally asymptotically stable.

In system (1.2), let \(b_1 = \alpha_1\), i.e., we study the following competition model with stage structure for species \(Y\), but without stage structure for species \(X\),

\[
\begin{align*}
\dot{x}(t) &= x(t) \left( b_1 - a_{11} x(t) - a_{12} y_2(t) \right), \\
\dot{y}_1(t) &= b_2 y_2(t) - r_2 y_1(t) - a_{21} y_1(t), \\
\dot{y}_2(t) &= a_2 y_1(t) - a_{22} y_2^2(t) - a_{21} x(t) y_2(t),
\end{align*}
\]

(4.1)

with initial conditions \(x(0) > 0, y_1(0) > 0, y_2(0) > 0\). Using several similar arguments in the proof of Theorems 2.1–2.3, we can derive the following results for system (4.1).

**THEOREM 4.4.** Assume that,

\[
\frac{a_{12}}{a_{22}} < \frac{b_1 (r_2 + \alpha_2)}{\alpha_2 b_2} < \frac{a_{11}}{a_{21}},
\]

then, system (4.1) has a unique positive equilibrium which is globally asymptotically stable.

**THEOREM 4.5.** Assume that,

\[
\frac{a_{12}}{a_{22}} < \frac{a_{11}}{a_{21}} < \frac{b_1 (r_2 + \alpha_2)}{\alpha_2 b_2},
\]

then, the nonnegative equilibrium \((b_1/a_{11}, 0, 0)\) of system (4.1) is globally asymptotically stable.

**THEOREM 4.6.** Assume that,

\[
\frac{b_1 (r_2 + \alpha_2)}{\alpha_2 b_2} < \frac{a_{12}}{a_{22}} < \frac{a_{11}}{a_{21}},
\]

then, the nonnegative equilibrium \((0, b_2 a_1/(a_{22} (r_2 + \alpha_2)), a_2/a_{22})\) of system (4.1) is globally asymptotically stable.

Now, we compare the conditions in (H4) and (H7). Noting that \(r_2 + \alpha_2 > \alpha_2\), we see that for species \(X\) smaller birth rate is required to make (H7) hold than that in (H4), this means that
with the introduction of stage structure of its competitor \( Y \), it is easier for species \( X \) to drive the species \( Y \) into extinction. Therefore, in the stage-structured competition system, stage structure of one species may have negative effect on its permanence and may lead the species to extinction if the death rate of the immature species is large enough.

Similarly, we consider the following nonautonomous system,

\[
\dot{x}_i(t) = x_i(t)(b_i(t) - \sum_{j=1}^{2} a_{ij}(t)x_j(t)), \quad i = 1, 2, \tag{4.2}
\]

where \( b_i(t), a_{ij}(t) \ (i, j = 1, 2) \) are continuously positive periodic functions with common period \( \omega \). Using a similar argument in the proof of Theorem 3.1 we obtain the following result.

**Theorem 4.7.** Assume that,

\[
\begin{align*}
&\frac{a_{12}^L}{a_{22}^L} < \frac{b_1^L}{b_2^L} < \frac{b_1^M}{b_2^M} < \frac{a_{11}^L}{a_{21}^L}, \\
&\frac{a_{12}^L}{a_{22}^L} < \frac{b_1^L}{b_2^M} < \frac{b_1^M}{b_2^M} < \frac{a_{11}^L}{a_{21}^L},
\end{align*}
\]

then, system (4.2) admits at least one positive periodic solution.

**Theorem 4.8.** In system (4.2), let

\[
\frac{a_{11}^L}{a_{21}^L} < \frac{b_1^M}{b_2^L} \quad \text{and} \quad \frac{a_{12}^L}{a_{22}^L} < \frac{b_1^M}{b_2^M},
\]

then, \( \lim_{t \to +\infty} x_2(t) = 0. \)

**Theorem 4.9.** In system (4.2), let

\[
\frac{b_1^M}{b_2^L} < \frac{a_{11}^L}{a_{21}^L} \quad \text{and} \quad \frac{b_1^M}{b_2^M} < \frac{a_{12}^L}{a_{22}^L},
\]

then, \( \lim_{t \to +\infty} x_1(t) = 0. \)

In system (1.3) letting \( b_1(t) = \alpha_1(t) \), we study the following system,

\[
\begin{align*}
\dot{x}(t) &= x(t)(b_1(t) - a_{11}(t)x(t) - a_{12}(t)y_2(t)), \\
y_1(t) &= b_2(t)y_2(t) - r_2(t)y_1(t) - \alpha_2(t)y_1(t), \\
y_2(t) &= \alpha_2(t)y_1(t) - a_{22}(t)y_2^2(t) - a_{21}(t)x(t)y_2(t),
\end{align*}
\]

with initial conditions \( x(0) > 0, \ y_1(0) > 0, \ y_2(0) > 0 \). It is easy to derive the following results for system (4.3).

**Theorem 4.10.** Assume that,

\[
\begin{align*}
&\frac{a_{12}^L}{a_{22}^L} < \frac{b_1^L}{b_2^M} < \frac{b_1^M}{b_2^M} < \frac{a_{11}^L}{a_{21}^L}, \\
&\frac{a_{12}^L}{a_{22}^L} < \frac{b_1^L}{b_2^M} < \frac{b_1^M}{b_2^M} < \frac{a_{11}^L}{a_{21}^L},
\end{align*}
\]

then, system (4.3) admits at least one positive periodic solution.

**Theorem 4.11.** In system (4.3), let

\[
\frac{a_{12}^L}{a_{22}^L} < \frac{a_{12}^L}{a_{22}^L} < \frac{b_1^L}{b_2^M} < \frac{\alpha_1^L}{\alpha_2^L},
\]

then, \( \lim_{t \to +\infty} y_1(t) = \lim_{t \to +\infty} y_2(t) = 0. \)
THEOREM 4.12. In system (4.3), let

\[
\frac{b^M(r^2 + a^M_2)}{a^M_2a^M_2} < \frac{a^M_{22}}{a^M_{21}} < \frac{a^M_{11}}{a^M_{21}},
\]

then, \(\lim_{t \to +\infty} x(t) = 0\).

Now, we compare the conditions in (H10) and (H13). If \(a_2\) is a positive constant, we have \(r_2(t) + a_2 > a_2\). Therefore, we know that for species \(X\) smaller birth rate is required to make (H13) hold than that in (H10), this means that with the introduction of stage structure of its competitor \(Y\), it is easier for species \(X\) to drive the species \(Y\) into extinction. Therefore, in the periodic time-dependent stage-structured competition system, stage structure of one species may have negative effect on the existence of positive periodic solutions and may lead the species to extinction if the death rate of the immature species is large enough.

REFERENCES