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DYNAMICS OF A NON-AUTONOMOUS THREE-DIMENSIONAL POPULATION SYSTEM

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ABSTRACT. In this paper, we study a non-autonomous Lotka-Volterra model with two predators and one prey. The explorations involve the persistence, extinction and global asymptotic stability of a positive solution.

1. INTRODUCTION

The dynamics of Lotka-Volterra models and their permanence, stability, global attractiveness, coexistence, extinction have been studied by several authors. Takeuchi and Adachi [10] showed that some chaotic motions may occur in the model of three species. Krikorian [5] considered an autonomous system of three species and obtained some results on global boundedness and stability. Korobeinikov and Wake [6], Korman [7] investigated a model of two preys, one predator and another one of two predators, one prey with constant coefficients, where direct competition is absent. Ahmad [3] obtained necessary and sufficient conditions for survival of species which rely on the averages of the growth rates and the interaction of coefficients. Besides, we also refer to [1, 2, 8, 9].

In this paper, we consider the following Lotka-Volterra model of two predators and one prey

$$\begin{aligned} x_1'(t) &= x_1(t)[a_1(t) - b_{11}(t)x_1(t) - b_{12}(t)x_2(t) - b_{13}(t)x_3(t)], \\ x_2'(t) &= x_2(t)[-a_2(t) + b_{21}(t)x_1(t) - b_{22}(t)x_2(t) - b_{23}(t)x_3(t)], \\ x_3'(t) &= x_3(t)[-a_3(t) + b_{31}(t)x_1(t) - b_{32}(t)x_2(t) - b_{33}(t)x_3(t)], \end{aligned}$$
(1.1)

where $x_i(t)$ represents the population density of species X_i at time t $(i \ge 1)$, X_1 is the prey and X_2, X_3 are the predators and they interact with each other. $a_i(t), b_{ij}(t) (1 \le i, j \le 3)$ are continuous functions on \mathbb{R} that are bounded above and below by some positive constants. At time $t, a_1(t)$ is the intrinsic growth rate of X_1 , and $a_i(t)$ is the death rate of $X_i(i \ge 2)$; $\frac{b_{i1}(t)}{b_{1i}(t)}$ denotes the coefficient in conversion X_1 into new individual of the $X_i(i \ge 2)$; $b_{ij}(t)$ measures the amount of competition between X_i and X_j $(i \ne j, i, j \ge 2)$, and $b_{ii}(t)(i \ge 1)$ measures the inhibiting effect of environment on X_i .

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This article is organized as follows. Section 2 provides some definitions and notations. In Section 3, we state some results on invariant set and asymptotic stability for problem (1.1). In Section 4, we assume that the coefficients $b_{ij}(t)$ $(1 \le i, j \le 3)$ are constants, then we give some inequalities, involving the average of the coefficients, which guarantees persistence of the system. Section 5 is a special case of Section 4 in which the coefficients $a_i(t)$ $(i \ge 1)$ are constants. We also give some inequalities which imply non-persistence; more specifically, extinction of the third species with small positive initial values.

2. Definitions and notation

In this section we introduce some basic definitions and facts which will be used in next sections. Let $\mathbb{R}^3_+ = \{(x_1, x_2, x_3) \in \mathbb{R}^3 | x_i \ge 0, i \ge 1\}$. For a bounded continuous function g(t) on \mathbb{R} , we denote

$$g^u = \sup_{t \in \mathbb{R}} g(t), \quad g^l = \inf_{t \in \mathbb{R}} g(t).$$

The existence and uniqueness of the global solutions of system (1.1) can be found in [11]. From the uniqueness theorem, it is easy to prove the following result.

Lemma 2.1. Both the non-negative and positive cones of \mathbb{R}^3 are positively invariant for (1.1).

In the remainder of this paper, for biological reasons, we only consider the solutions $(x_1(t), x_2(t), x_3(t))$ with positive initial values; i.e., $x_i(t_0) > 0, i \ge 1$.

Definition 2.2. System (1.1) is said to be permanent if there exist positive constants δ, Δ with $0 < \delta < \Delta$ such that $\liminf_{t\to\infty} x_i(t) \ge \delta$, $\limsup_{t\to\infty} x_i(t) \le \Delta$ for all $i \ge 1$. System (1.1) is called persistent if $\limsup_{t\to\infty} x_i(t) > 0$, and strongly persistent if $\liminf_{t\to\infty} x_i(t) > 0$ for all $i \ge 1$.

Definition 2.3. A set A is called to be an ultimately bounded region of system (1.1) if for any solution $(x_1(t), x_2(t), x_3(t))$ of (1.1) with positive initial values, there exists $T_1 > 0$ such that $(x_1(t), x_2(t), x_3(t)) \in A$ for all $t \ge t_0 + T_1$.

Definition 2.4. A bounded non-negative solution $(x_1^*(t), x_2^*(t), x_3^*(t))$ of (1.1) is said to be global asymptotic stable solution (or global attractive solution) if any other solution $(x_1(t), x_2(t), x_3(t))$ of (1.1) with positive initial values satisfies

$$\lim_{t \to \infty} \sum_{i=1}^{3} |x_i(t) - x_i^*(t)| = 0.$$

Remark 2.5. It is easy to see that if the system (1.1) has a global asymptotic stable solution, then so are all solutions of (1.1).

3. The model with general coefficients

Let ϵ be a positive constant. We put

$$\begin{split} M_1^{\epsilon} &= \frac{a_1^u}{b_{11}^l} + \epsilon, \quad M_2^{\epsilon} = \frac{-a_2^l + b_{21}^u M_1^{\epsilon}}{b_{22}^l}, \\ M_3^{\epsilon} &= \frac{-a_3^l + b_{31}^u M_1^{\epsilon}}{b_{33}^l}, \quad m_1^{\epsilon} = \frac{a_1^l - b_{12}^u M_2^{\epsilon} - b_{13}^u M_3^{\epsilon}}{b_{11}^u}, \end{split}$$

EJDE-2009/157 A NON-AUTONOMOUS THREE-DIMENSIONAL POPULATION SYSTEM 3

$$m_2^{\epsilon} = \frac{-a_2^u + b_{21}^l m_1^{\epsilon} - b_{23}^u M_3^{\epsilon}}{b_{22}^u}, \quad m_3^{\epsilon} = \frac{-a_3^u + b_{31}^l m_1^{\epsilon} - b_{32}^u M_2^{\epsilon}}{b_{33}^u},$$

$$B_{1}^{\epsilon}(t) = a_{1}(t) - 2b_{11}(t)m_{1}^{\epsilon} - b_{12}(t)m_{2}^{\epsilon} - b_{13}(t)m_{3}^{\epsilon} + b_{21}(t)M_{2}^{\epsilon} + b_{31}(t)M_{3}^{\epsilon},$$

$$B_{2}^{\epsilon}(t) = -a_{2}(t) + b_{21}(t)M_{1}^{\epsilon} - 2b_{22}(t)m_{2}^{\epsilon} - b_{23}(t)m_{3}^{\epsilon} + b_{12}(t)M_{1}^{\epsilon} + b_{32}(t)M_{3}^{\epsilon}, \quad (3.1)$$

$$B_{3}^{\epsilon}(t) = -a_{3}(t) + b_{31}(t)M_{1}^{\epsilon} - 2b_{33}(t)m_{3}^{\epsilon} - b_{32}(t)m_{2}^{\epsilon} + b_{13}(t)M_{1}^{\epsilon} + b_{23}(t)M_{2}^{\epsilon}.$$

We have the following theorems.

Theorem 3.1. If $m_i^{\epsilon} > 0$ for all $i \ge 1$, then the set Γ_{ϵ} defined by

$$\Gamma_{\epsilon} = \{ (x_1, x_2, x_3) \in \mathbb{R}^3 | m_i^{\epsilon} \le x \le M_i^{\epsilon}, i \ge 1 \}$$

is positively invariant with respect to system (1.1).

Proof. We know that the logistic equation

$$X'(t) = AX(t)[B - X(t)] \quad (A, B \in \mathbb{R}, B \neq 0)$$

has a unique solution

$$X(t) = \frac{BX_0 \exp\{AB(t-t_0)\}}{X_0 \exp\{AB(t-t_0)\} + B - X_0},$$

where $X_0 = X(t_0)$.

We now consider the solution of system (1.1) with the initial values $(x_1^0, x_2^0, x_3^0) \in \Gamma_{\epsilon}$. By Lemma 2.1, we have $x_i(t) > 0$ for all $t \ge t_0$ and $i \ge 1$. We have

$$\begin{aligned} x_1'(t) &\leq x_1(t)[a_1(t) - b_{11}(t)x_1(t)] \\ &\leq x_1(t)[a_1^u - b_{11}^l x_1(t)] \\ &= b_{11}^l x_1(t)[M_1^0 - x_1(t)]. \end{aligned}$$

Using the comparison theorem, we obtain that

$$x_{1}(t) \leq \frac{x_{1}^{0}M_{1}^{0}\exp\{a_{1}^{u}(t-t_{0})\}}{x_{1}^{0}\left[\exp\{a_{1}^{u}(t-t_{0})\}-1\right]+M_{1}^{0}} \\ \leq \frac{x_{1}^{0}M_{1}^{\epsilon}\exp\{a_{1}^{u}(t-t_{0})\}}{x_{1}^{0}\left[\exp\{a_{1}^{u}(t-t_{0})\}-1\right]+M_{1}^{\epsilon}}.$$
(3.2)

Then, it follows from $x_1^0 \leq M_1^{\epsilon}$ that $x_1(t) \leq M_1^{\epsilon}$ for all $t \geq t_0$. On the other hand, from $x_2^0 \leq M_2^{\epsilon}$ and

$$x_2'(t) \le x_2(t)[-a_2^l + b_{21}^u M_1^{\epsilon} - b_{22}^l x_2(t)] = b_{22}^l x_3(t)[M_2^{\epsilon} - x_2(t)],$$

it implies that $x_2(t) \leq M_2^{\epsilon}$ for all $t \geq t_0$. Similarly, we can prove that $x_3(t) \leq M_3^{\epsilon}$ for all $t \geq t_0$. From the above results, we have

$$x_1'(t) \ge x_1(t)[a_1^l - b_{12}^u M_2^{\epsilon} - b_{13}^u M_3^{\epsilon} - b_{11}^u x_1(t)] = b_{11}^u x_1(t)[m_1^{\epsilon} - x_1(t)].$$

It follows from $x_1^0 \ge m_1^{\epsilon}$ that

$$x_1(t) \ge \frac{m_1^{\epsilon} x_1^0 \exp\{b_{11}^u m_1^{\epsilon}(t-t_0)\}}{x_1^0 \left[\exp\{b_{11}^u m_1^{\epsilon}(t-t_0)\} - 1\right] + m_1^{\epsilon}} \ge m_1^{\epsilon} \quad \text{for all } t \ge t_0.$$

Similarly, it is easy to see that $x_2(t) \ge m_2^{\epsilon}, x_3(t) \ge m_3^{\epsilon}$ for all $t \ge t_0$. The proof is complete.

Theorem 3.2. If $m_i^{\epsilon} > 0$ $(i \ge 1)$, then the set Γ_{ϵ} is an ultimately bounded region, *i.e.*, system (1.1) is permanent.

Proof. From (3.2) we have $\limsup_{t\to\infty} x_1(t) \leq M_1^{\epsilon}$. Thus, there exist $\epsilon > 0$ and $t_1 \geq t_0$ such that $x_1(t) \leq M_1^{\epsilon}$ for all $t \geq t_1$. By the same argument in Theorem 3.1, it can be shown that $\limsup_{t\to\infty} x_i(t) \leq M_i^{\epsilon}$ and $\liminf_{t\to\infty} x_i(t) \geq m_i^{\epsilon}(i \geq 2)$. Then Γ_{ϵ} is an ultimately bounded region with a sufficiently small $\epsilon > 0$. \Box

In the following theorem, we give some conditions which ensure the extinction of the predators

Theorem 3.3. If $M_i^0 < 0$ then $\lim_{t\to\infty} x_i(t) = 0, i \ge 2$.

Proof. We see that if $M_i^0 < 0$ then $M_i^{\epsilon} < 0$ with a sufficiently small ϵ . Similarly as in the proof of Theorem 3.1, we get

$$x'_{i}(t) \le b^{l}_{ii} x_{i}(t) [M^{\epsilon}_{i} - x_{i}(t)] < 0, i \ge 2.$$
(3.3)

Therefore, $0 < x_i(t) \le x_i(t_0)$ for $t \ge t_0$ and there exists $c \ge 0$ with $\lim_{t\to\infty} x_i(t) = c$. If c > 0 then $0 < c \le x_i(t) \le x_i(t_0), t \ge t_0$. From (3.3), there exists $\nu > 0$ such that $x'_i(t) < -\nu$ for all $t \ge t_0$. It follows $x_i(t) < -\nu(t-t_0) + x_i(t_0)$ and $\lim_{t\to\infty} x_i(t) = -\infty$ which contradicts the inequality $x_i(t) > 0$ for all $t \ge t_0$. Hence, $\lim_{t\to\infty} x_i(t) = 0$.

Now, to consider the global asymptotic stability of a solution, we need the following result, called Barbalat's lemma (see [4])

Lemma 3.4. Let h be a real number and f be a non-negative function defined on $[h, +\infty)$ such that f is integrable on $[h, +\infty)$ and uniformly continuous on $[h, +\infty)$. Then $\lim_{t\to\infty} f(t) = 0$.

Proof. We suppose that $f(t) \neq 0$ as $t \to \infty$. There exists a sequence $(t_n), t_n \geq h$ such that $t_n \to \infty$ as $n \to \infty$ and $f(t_n) \geq \varepsilon$ for all $n \in \mathbb{N}$. By the uniform continuity of f, there exists a $\delta > 0$ such that, for all $n \in \mathbb{N}$ and $t \in [t_n, t_n + \delta]$, $|f(t_n) - f(t)| \leq \frac{\varepsilon}{2}$. Thus, for all $t \in [t_n, t_n + \delta]$ and $n \in \mathbb{N}$ we have

$$f(t) = |f(t_n) - [f(t_n) - f(t)]| \ge |f(t_n)| - |f(t_n) - f(t)| \ge \varepsilon - \frac{\varepsilon}{2} = \frac{\varepsilon}{2}$$

Therefore,

$$\int_{t_n}^{t_n+\delta} f(t)dt = \int_{t_n}^{t_n+\delta} f(t)dt \ge \frac{\varepsilon\delta}{2} > 0$$

for each $n \in \mathbb{N}$. By the existence of the Riemann integral $\int_{h}^{\infty} f(t)dt$, the left hand side of the above inequality converges to 0 as $n \to \infty$ yielding a contradiction. \Box

Theorem 3.5. Let $(x_1^*(t), x_2^*(t), x_3^*(t))$ be a solution of system (1.1). If $m_i^{\epsilon} > 0$ and $\limsup_{t\to\infty} B_i^{\epsilon}(t) < 0$ for all $i \ge 1$, then $(x_1^*(t), x_2^*(t), x_3^*(t))$ is globally asymptotically stable.

Proof. From the assumptions, there exists $t_1 > t_0$ such that $\sup_{t \ge t_1} B_i^{\epsilon}(t) < 0$, $i \ge 1$. Let $(x_1(t), x_2(t), x_3(t))$ be any solution of positive initial value system (1.1). Since Γ_{ϵ} is an ultimately bounded region, there exists $T_1 > t_1$ such, that for all $t \ge T_1$,

$$(x_1(t), x_2(t), x_3(t)), (x_1^*(t), x_2^*(t), x_3^*(t)) \in \Gamma_{\epsilon}.$$

Now, we consider a Liapunov function defined by $V(t) = \sum_{i=1}^{3} |x_i(t) - x_i^*(t)|, t \ge T_1$. For brevity, we denote $x_i(t), x_i^*(t), a_i(t)$ and $b_{ij}(t)$ by x_i, x_i^*, a_i and b_{ij} , respectively.

EJDE-2009/157 A NON-AUTONOMOUS THREE-DIMENSIONAL POPULATION SYSTEM 5

A direct calculation of the right derivative $D^+V(t)$ of V(t) along the solution of system (1.1) gives

$$\begin{split} D^+V(t) &= \sum_{i=1}^3 \operatorname{sgn}(x_i - x_i^*) [x_i' - x_i^{*'}] \\ &= \operatorname{sgn}(x_1 - x_1^*) [x_1(a_1 - \sum_{j=1}^3 b_{1j}x_j) - x_1^*(a_1 - \sum_{j=1}^3 b_{1j}x_j^*)] \\ &+ \sum_{i=2}^3 \left[x_i(-a_i + b_{i1}x_1 - \sum_{j=2}^3 b_{ij}x_j) \right] \\ &- x_i^*(-a_i + b_{i1}x_1^* - \sum_{j=1}^3 b_{ij}x_j^*) \right] \operatorname{sgn}(x_i - x_i^*) \\ &= [a_1 - b_{11}(x_1 + x_1^*)] |x_1 - x_1^*| \\ &- \operatorname{sgn}(x_1 - x_1^*) \sum_{j=2}^3 b_{1j}(x_1x_j - x_1^*x_j^*) \\ &+ \sum_{i=2}^3 [-a_i - b_{ii}(x_i + x_i^*)] |x_i - x_i^*| \\ &+ \operatorname{sgn}(x_2 - x_2^*) [b_{21}(x_1x_2 - x_1^*x_2^*) - b_{23}(x_2x_3 - x_2^*x_3^*)] \\ &+ \operatorname{sgn}(x_3 - x_3^*) [b_{31}(x_1x_3 - x_1^*x_3^*) - b_{32}(x_2x_3 - x_2^*x_3^*)] \\ &= [a_1 - b_{11}(x_1 + x_1^*) - b_{12}x_2 - b_{13}x_3] |x_1 - x_1^*| \\ &+ [-a_2 + b_{21}x_1 - b_{22}(x_2 + x_2^*) - b_{23}x_1^*] |x_2 - x_2^*| \\ &+ [-a_3 + b_{31}x_1 - b_{33}(x_3 + x_3^*) - b_{32}x_2(x_3 - x_3^*)] \\ &+ \operatorname{sgn}(x_2 - x_2^*) [b_{21}x_2^*(x_1 - x_1^*) - b_{23}x_2(x_3 - x_3^*)] \\ &+ \operatorname{sgn}(x_2 - x_2^*) [b_{21}x_2^*(x_1 - x_1^*) - b_{23}x_2(x_3 - x_3^*)] \\ &+ \operatorname{sgn}(x_2 - x_2^*) [b_{21}x_2^*(x_1 - x_1^*) - b_{23}x_3(x_2 - x_2^*)] \\ &\leq [a_1 - b_{11}(x_1 + x_1^*) - b_{12}x_2 - b_{13}x_3 + b_{21}x_2^* + b_{31}x_3^*] |x_1 - x_1^*| \\ &+ [-a_2 + b_{21}x_1 - b_{22}(x_2 + x_2^*) - b_{23}x_3^* + b_{12}x_1^* + b_{23}x_3] |x_2 - x_2^*| \\ &+ [-a_3 + b_{31}x_1 - b_{33}(x_3 + x_3^*) - b_{32}x_2^* + b_{13}x_1^*] |x_1 - x_1^*| \\ &+ [-a_2 + b_{21}x_1 - b_{22}(x_2 + x_2^*) - b_{23}x_3^* + b_{23}x_3^*] |x_2 - x_2^*| \\ &+ [-a_3 + b_{31}x_1 - b_{33}(x_3 + x_3^*) - b_{32}x_2^* + b_{13}x_1^* + b_{23}x_2] |x_3 - x_3^*| \\ &\leq [a_1 - 2b_{11}m_1^\epsilon - b_{12}m_2^\epsilon - b_{13}m_3^\epsilon + b_{21}M_2^\epsilon + b_{31}M_3^\epsilon] |x_1 - x_1^*| \\ &+ [-a_2 + b_{21}M_1^\epsilon - 2b_{22}m_2^\epsilon - b_{23}m_3^\epsilon + b_{12}M_1^\epsilon + b_{23}M_2^\epsilon] |x_3 - x_3^*| \\ &\leq [a_1 - 2b_{11}m_1^\epsilon - b_{12}m_2^\epsilon - b_{13}m_3^\epsilon + b_{23}m_2^\epsilon + b_{13}M_1^\epsilon + b_{23}M_2^\epsilon] |x_3 - x_3^*| \\ &= \sum_{i=1}^3 B_i^\epsilon(t) |x_i - x_i^*|. \end{aligned}$$

From the above arguments, there exists a positive constant $\mu > 0$ such that

$$D^{+}V(t) \le -\mu \sum_{i=1}^{3} |x_{i}(t) - x_{i}^{*}(t)| \quad \text{for all } t \ge T_{1}.$$
(3.4)

Integrating both sides of (3.4) from T_1 to t, we obtain

$$V(t) + \mu \int_{T_1}^t \left[\sum_{i=1}^3 |x_i(t) - x_i^*(t)| \right] dt \le V(T_1) < +\infty, t \ge T_1.$$

Then

$$\int_{T_1}^t \left[\sum_{i=1}^3 |x_i(t) - x_i^*(t)| \right] dt \le \frac{1}{\mu} V(T_1) < +\infty, \quad t \ge T_1.$$

Hence, $\sum_{i=1}^{3} |x_i(t) - x_i^*(t)| \in L^1([T_1, +\infty))$. On the other hand, the ultimate boundedness of x_i and x_i^* imply that both x_i and $x_i^*(i \ge 1)$ have bounded derivatives for $t \ge T_1$. As a consequence $\sum_{i=1}^3 |x_i(t) - x_i^*(t)|$ is uniformly continuous on $[T_1, +\infty)$. By Lemma 3.4 we have

$$\lim_{t \to \infty} \sum_{i=1}^{3} |x_i(t) - x_i^*(t)| = 0$$

which completes the proof.

4. The model with constant interaction coefficients

In this section, we assume that the coefficients b_{ij} , $1 \le i, j \le 3$ in system (1.1) are positive constants and the limit

$$M[a_i] = \lim_{T \to \infty} \frac{1}{T} \int_{t_0}^{t_0 + T} a_i(t) dt$$

exists uniformly with respect to t_0 in $(-\infty, \infty)$. First, we consider a predator-prey system

$$x'_{1}(t) = x_{1}(t)[a_{1}(t) - b_{11}x_{1}(t) - b_{12}x_{2}(t)],$$

$$x'_{2}(t) = x_{2}(t)[-a_{2}(t) + b_{21}x_{1}(t) - b_{22}x_{2}(t)].$$
(4.1)

Put $Z_i(T) = \frac{1}{T} \int_{t_0}^{t_0+T} z_i(t) dt$. We have the following theorem.

Theorem 4.1. Assume that $b_{11}b_{12}a_2^l + b_{11}b_{22}a_1^l - b_{12}b_{21}a_1^u > 0$. Then $\inf_{t \ge t_0} x_1(t)$ > 0. Furthermore, (:) If $M[a] < b_{21} M[a]$ then inf m(t) > 0

(1) If
$$M[a_2] < \frac{b_{21}}{b_{11}} M[a_1]$$
 then $\inf_{t \ge t_0} x_2(t) > 0$ and

$$\lim_{T \to \infty} X_1(T) = \frac{b_{22}M[a_1] + b_{12}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}}, \quad \lim_{T \to \infty} X_2(T) = \frac{b_{21}M[a_1] - b_{11}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}}.$$
ii) If $M[a_2] > \frac{b_{21}}{b_{11}} M[a_1]$ then

$$M[a_1]$$

$$\lim_{T \to \infty} X_1(T) = \frac{M[a_1]}{b_{11}}, \quad \lim_{T \to \infty} X_2(T) = 0.$$

Proof. The proof for the first statement is similar to that of Theorem 3.1. Let $\epsilon>0$ be a sufficiently small constant. From the comparison theorem and $x_1'(t)\leq$ $x_1(t)[a_1^u - b_{11}x_1(t)]$, it is easy to see that $\limsup_{t\to\infty} x_1(t) \le \frac{a_1^u}{b_{11}}$. Then there exists $T_1 > t_0$ such that $x_1(t) < P_1^{\epsilon} = \frac{a_1^u}{b_{11}} + \epsilon$ for all $t \ge T_1$. Thus

$$x_2'(t) < x_2(t)[-a_2^l + b_{21}P_1^{\epsilon} - b_{22}x_2(t)] \quad \text{for } t \ge T_1.$$
(4.2)

Let us consider two cases:

Case 1. There exists $\epsilon > 0$ such that $-a_2^l + b_{21}P_1^{\epsilon} < 0$. From (4.2), it follows that $\lim_{t\to\infty} x_2(t) = 0$. Therefore, there exists $T_2 > T_1$ such that $a_1(t) - b_{12}x_2(t) > \frac{1}{2}a_1^l$. It follows from the first equation of the system (4.1) that

$$x'_1(t) \ge x_1(t) \left[\frac{1}{2} a_1^l - b_{11} x_1(t) \right] \text{ for } t \ge T_2.$$

Using the comparison theorem, we have $\liminf_{t\to\infty} x_1(t) \ge a_1^l/2b_{11}$.

Case 2. $-a_2^l + b_{21}P_1^0 \ge 0$. It follows from (4.2) that $\limsup_{t\to\infty} x_2(t) \le P_2^{\epsilon} = \frac{-a_2^l + b_{21}P_1^{\epsilon}}{b_{22}}$. Then, we can choose a sufficiently small positive ϵ and $T_3 > T_1$ such that $x_1(t) \le P_1^{\epsilon}, x_2(t) \le P_2^{\epsilon}$ for all $t \ge T_3$. From the first equation of the system (4.1), we have $x_1'(t) \ge x_1(t)[a_1^l - b_{12}P_2^{\epsilon} - b_{11}x_1(t)]$ for $t \ge T_3$. Because of our assumption $b_{11}b_{12}a_2^l + b_{11}b_{22}a_1^l - b_{12}b_{21}a_1^u \ge 0$, there exists a sufficiently small positive ϵ such that

$$a_1^l - b_{12}P_2^{\epsilon} = \frac{b_{11}b_{12}a_2^l + b_{11}b_{22}a_1^l - b_{12}b_{21}a_1^u}{b_{11}b_{22}} - \epsilon \frac{b_{12}b_{21}}{b_{22}} > 0.$$

Then $\liminf_{t\to\infty} x_1(t) > 0.$

The conclusions of two above cases implies that $\inf_{t \ge t_0} x_1(t) > 0$. Then there exists $c_1 > 0$ such that

$$c_1 < x_1(t) < d_1 \text{ for all } t \ge t_0.$$
 (4.3)

To prove Part i), first, we show that it is impossible to have

$$\lim_{t \to \infty} x_2(t) = 0. \tag{4.4}$$

Assuming the contrary, from (4.3) and (4.4) we get

$$\lim_{T \to \infty} \frac{1}{T} \ln \left[\frac{x_1(t_0 + T)}{x_1(t_0)} \right] = 0, \quad \lim_{T \to \infty} \frac{1}{T} \int_{t_0}^{t_0 + T} x_2(s) ds = 0$$

Then, from the first equation of (4.1) we have

$$\lim_{T \to \infty} \frac{1}{T} \int_{t_0}^{t_0 + T} b_{11} x_1(s) ds$$

= $\lim_{T \to \infty} \frac{1}{T} \Big[\int_{t_0}^{t_0 + T} a_1(s) ds - \int_{t_0}^{t_0 + T} b_{12} x_2(s) ds - \ln[\frac{x_1(t_0 + T)}{x_1(t_0)}] \Big]$ (4.5)
= $M[a_1].$

It follows from (4.4) that $\frac{1}{T} \ln[\frac{x_2(t_0+T)}{x_2(t_0)}] < 0$ for large values of T. By (4.5), we find

$$-M[a_2] + b_{21} \frac{M[a_1]}{b_{11}} = \lim_{T \to \infty} \frac{1}{T} \Big[-\int_{t_0}^{t_0+T} a_2(s) ds + b_{21} \int_{t_0}^{t_0+T} x_1(s) ds \Big]$$
$$= \lim_{T \to \infty} \frac{1}{T} \Big[\ln[\frac{x_2(t_0+T)}{x_2(t_0)}] + b_{22} \int_{t_0}^{t_0+T} x_2(s) ds \Big] \le 0,$$

which contradicts our assumption. This contradiction proves that

$$\limsup_{t \to \infty} x_2(t) = d > 0.$$

If, contrary to the assertion of the theorem, $\inf_{t \ge t_0} x_2(t) = 0$, then there exists a sequence of numbers $\{s_n\}_1^\infty$ such that $s_n \ge t_0, s_n \to \infty$ as $n \to \infty$ and $x_2(s_n) \to 0$ as $n \to \infty$. Put

$$c = \frac{1}{2} \liminf_{T \to \infty} \frac{1}{T} \int_{t_0}^{t_0 + T} x_2(t) dt$$

Since $x_2(t) > c$ for arbitrarily large values of t and since $s_n \to \infty$ and $x_2(s_n) \to 0$ as $n \to \infty$, there exist sequences $\{p_n\}_1^\infty, \{q_n\}_1^\infty$ and $\{\tau_n\}_1^\infty$ such that for all $n \ge 1, t_0 < p_n < \tau_n < q_n < p_{n+1}, x_2(p_n) = x_2(q_n) = c$ and $0 < x_2(\tau_n) < \frac{c}{n} \exp\{-b_{21}d_1n\}$. Further, there exist sequences $\{t_n\}_1^\infty$ and $\{t_n^*\}_1^\infty$ such that for $n \ge 1, t_n < \tau_n < t_n^*$,

$$x_2(t_n) = x_2(t_n^*) = \frac{c}{n}, \quad x_2(t) \le \frac{c}{n} \quad \text{for } t \in [t_n, t_n^*].$$
 (4.6)

Thus

$$0 < \frac{1}{t_n^* - t_n} \int_{t_n}^{t_n^*} x_2(t) dt \le \frac{c}{n} \to 0 \quad \text{as } n \to \infty.$$

$$(4.7)$$

We show that the following inequalities hold:

$$t_n^* - t_n > t_n^* - \tau_n \ge n \quad \text{for } n \ge 1.$$
 (4.8)

In fact, $x'_2(t) = x_2(t)[-a_2(t) + b_{21}x_1(t) - b_{22}x_2(t)] < b_{21}d_1x_2(t)$ for all $t \ge t_0$, then for $t \ge \tau_n$,

$$x_{2}(t) = x_{2}(\tau_{n}) \exp\{\int_{\tau_{n}}^{t} [-a_{2}(s) + b_{21}x_{1}(s) - b_{22}x_{2}(s)]ds\}$$

$$\leq \frac{c}{n} \exp\{-b_{21}d_{1}n\} \exp\{b_{21}d_{1}(t-\tau_{n})\}$$

$$= \frac{c}{n} \exp\{b_{21}d_{1}(t-\tau_{n}-n)\}.$$

(4.9)

From (4.9) and (4.6), we obtain $t_n^* - \tau_n \ge n$. It follows from (4.8) that

$$M[a_i] = \lim_{n \to \infty} \frac{1}{t_n^* - t_n} \int_{t_n}^{t_n^*} a_i(t) dt, \quad i = 1, 2.$$

Using the first equation of system (4.1) we get

$$\frac{1}{t_n^* - t_n} \ln\left[\frac{x_1(t_n^*)}{x_1(t_n)}\right] = \frac{1}{t_n^* - t_n} \left[\int_{t_n}^{t_n^*} a_1(t)dt - b_{11}\int_{t_n}^{t_n^*} x_1(t)dt - b_{12}\int_{t_n}^{t_n^*} x_2(t)dt\right].$$
Then, it follows from (4.3), (4.7) and (4.8) that

Then, it follows from (4.3), (4.7) and (4.8) that

$$\lim_{n \to \infty} \frac{1}{t_n^* - t_n} \int_{t_n}^{t_n^*} x_1(t) dt = \frac{M[a_1]}{b_{11}}.$$
(4.10)

Similarly, from the second equation of the system (4.1) we have

$$\frac{1}{t_n^* - t_n} \ln\left[\frac{x_2(t_n^*)}{x_2(t_n)}\right] = \frac{1}{t_n^* - t_n} \left[-\int_{t_n}^{t_n^*} a_2(t)dt + b_{21} \int_{t_n}^{t_n^*} x_1(t)dt - b_{22} \int_{t_n}^{t_n^*} x_2(t)dt \right].$$

Taking into account the above relations, (4.6), (4.7) and (4.10) we get

$$-M[a_2] + \frac{b_{21}}{b_{11}}M[a_1] = 0$$

Since this contradicts our assumption, we obtain $\inf_{t \ge t_0} x_2(t) > 0$. Therefore, there exists $c_2 > 0$ such that

$$c_2 < x_2(t) < d_2 \quad \text{for all } t \ge t_0.$$
 (4.11)

Now, by (4.1), for all T > 0, we have

$$\frac{1}{T}\ln\frac{x_1(t_0+T)}{x_1(t_0)} = A_1(T) - b_{11}X_1(T) - b_{12}X_2(T),$$

EJDE-2009/157

$$\frac{1}{T}\ln\frac{x_2(t_0+T)}{x_2(t_0)} = -A_2(T) + b_{21}X_1(T) - b_{22}X_2(T).$$

Then

$$X_{1}(T) = \frac{b_{22}[A_{1}(T) - \frac{1}{T}\ln\frac{x_{1}(t_{0}+T)}{x_{1}(t_{0})}] + b_{12}[\frac{1}{T}\ln\frac{x_{2}(t_{0}+T)}{x_{2}(t_{0})} + A_{2}(T)]}{b_{12}b_{21} + b_{11}b_{22}},$$

$$X_{2}(T) = \frac{b_{21}[A_{1}(T) - \frac{1}{T}\ln\frac{x_{1}(t_{0}+T)}{x_{1}(t_{0})}] - b_{11}[\frac{1}{T}\ln\frac{x_{2}(t_{0}+T)}{x_{2}(t_{0})} + A_{2}(T)]}{b_{12}b_{21} + b_{11}b_{22}}.$$
(4.12)

It follows from (4.3) and (4.11) that

$$\lim_{T \to \infty} \frac{1}{T} \ln \frac{x_i(t_0 + T)}{x_i(t_0)} = 0 \quad (i = 1, 2).$$

Then

$$\lim_{T \to \infty} X_1(T) = \frac{b_{22}M[a_1] + b_{12}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}},$$
$$\lim_{T \to \infty} X_2(T) = \frac{b_{21}M[a_1] - b_{11}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}}.$$

To prove Part (ii), first, we show that $\lim_{t\to\infty} x_2(t) = 0$. Assuming the contrary we can find $\delta > 0$ and a sequence of numbers $\{T_n\}_1^\infty, T_n > 0, T_n \to \infty(n \to \infty)$ such that $\delta < x_2(t_0 + T_n) < d_2$ for all n. Then, from the second equation of (4.12), we get

$$\lim_{n \to \infty} X_2(T_n) = \frac{b_{21}M[a_1] - b_{11}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}} < 0,$$

which contradicts $X_2(T) \ge 0$ for all T > 0. This implies that $\lim_{t\to\infty} x_2(t) = 0$ and then $\lim_{T\to\infty} X_2(T) = 0$. It follows from the first equation of (4.12) that $\lim_{T\to\infty} X_1(T) = \frac{M[a_1]}{b_{11}}$.

Now, we consider the system

$$x_{1}'(t) = x_{1}(t)[a_{1}(t) - b_{11}x_{1}(t) - b_{12}x_{2}(t) - b_{13}x_{3}(t)],$$

$$x_{2}'(t) = x_{2}(t)[-a_{2}(t) + b_{21}x_{1}(t) - b_{22}x_{2}(t) - b_{23}x_{3}(t)],$$

$$x_{3}'(t) = x_{3}(t)[-a_{3}(t) + b_{31}x_{1}(t) - b_{32}x_{2}(t) - b_{33}x_{3}(t)].$$

(4.13)

Proposition 4.2. If

$$M[a_{2}] < \frac{b_{21}}{b_{11}b_{22}} + b_{11}b_{22}a_{1}^{l} - b_{12}b_{21}a_{1}^{u} > 0,$$

$$M[a_{2}] < \frac{b_{21}}{b_{11}}M[a_{1}],$$

$$M[a_{3}] < \frac{(b_{31}b_{22} - b_{32}b_{21})M[a_{1}] + (b_{31}b_{12} + b_{11}b_{32})M[a_{2}]}{b_{12}b_{21} + b_{11}b_{22}},$$
(4.14)

then $\limsup_{t\to\infty} x_3(t) > 0.$

Proof. We assume that $\lim_{t\to\infty} x_3(t) = 0$. Then

$$\lim_{T \to \infty} X_3(T) = 0. \tag{4.15}$$

Replacing t_0 by a larger number, if necessary, we may assume that $a_1(t) - b_{13}x_3(t) > 0$ for $t \ge t_0 - 1$. We put,

$$a_{1}^{*}(t) = \begin{cases} a_{1}(t) - b_{13}x_{3}(t), & t \ge t_{0}, \\ a_{1}(t) - (t - t_{0} + 1)b_{13}x_{3}(t), & t_{0} - 1 \le t < t_{0}, \\ a_{1}(t), & t < t_{0} - 1, \end{cases}$$
$$a_{2}^{*}(t) = \begin{cases} a_{2}(t) + b_{23}x_{3}(t), & t \ge t_{0}, \\ a_{2}(t) + (t - t_{0} + 1)b_{23}x_{3}(t), & t_{0} - 1 \le t < t_{0}, \\ a_{2}(t), & t < t_{0} - 1. \end{cases}$$

Then a_i^* is continuous on $\mathbb{R}, a_i^{*l} > 0, a_i^{*u} < \infty$ for i = 1, 2. Moreover, since $\lim_{t\to\infty} x_3(t) = 0$, the limit

$$M[a_i^*] = \lim_{T \to \infty} \frac{1}{T} \int_{t_*}^{t_* + T} a_i^*(t) dt = \lim_{T \to \infty} \frac{1}{T} \int_{t_*}^{t_* + T} a_i(t) dt = M[a_i]$$

exists uniformly with respect to $t_* \in \mathbb{R}$ and i = 1, 2. Then for $t \ge t_0$, $(x_1(t), x_2(t))$ is a solution of the following competitive system

$$\begin{aligned} x_1'(t) &= x_1(t) \big[a_1^*(t) - b_{11} x_1(t) - b_{12} x_2(t) \big], \\ x_2'(t) &= x_2(t) \big[-a_2^*(t) - b_{21} x_1(t) - b_{22} x_2(t) \big]. \end{aligned}$$

By condition (4.14) and Theorem 4.1, we have

$$\lim_{T \to \infty} X_1(T) = \frac{b_{22}M[a_1] + b_{12}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}},$$

$$\lim_{T \to \infty} X_2(T) = \frac{b_{21}M[a_1] - b_{11}M[a_2]}{b_{12}b_{21} + b_{11}b_{22}}.$$
(4.16)

From the third equation of the system (4.13) we have

$$\frac{1}{T}\ln\left[\frac{x_3(t_0+T)}{x_3(t_0)}\right] = -A_3(T) + b_{31}X_1(T) - b_{32}X_2(T) - b_{33}X_3(T).$$

Then $-A_3(T)+b_{31}X_1(T)-b_{32}X_2(T)-b_{33}X_3(T) < 0$ for T sufficiently large. Letting $T \to \infty$ and using (4.15) and (4.16) we obtain

$$-M[a_3] + \frac{(b_{31}b_{22} - b_{32}b_{21})M[a_1] + (b_{12}b_{31} + b_{11}b_{32})M[a_2]}{b_{12}b_{21} + b_{11}b_{22}} \le 0,$$

which contradicts (4.14). This proves the proposition.

Proposition 4.3. If the following conditions hold

$$M[a_{3}] < \frac{b_{11}b_{13}a_{3}^{l} + b_{11}b_{33}a_{1}^{l} - b_{13}b_{31}a_{1}^{u} > 0,$$

$$M[a_{3}] < \frac{b_{31}}{b_{11}}M[a_{1}],$$

$$M[a_{3}] < \frac{(b_{31}b_{33} - b_{23}b_{31})M[a_{1}] + (b_{31}b_{13} + b_{11}b_{23})M[a_{3}]}{b_{13}b_{31} + b_{11}b_{33}}$$

$$(4.17)$$

then $\limsup_{t\to\infty} x_2(t) > 0.$

The proof of the above proposition is similar to that of Proposition 4.2, and it is omitted.

Theorem 4.4. If conditions (4.14) and (4.17) hold, then system (4.13) is persistent.

$$\square$$

Proof. From Propositions 4.2 and 4.3, we have

$$\limsup_{t \to \infty} x_i(t) > 0, \quad i = 2, 3.$$
(4.18)

Now, we show that $\limsup_{t\to\infty} x_1(t) > 0$. Assume the contrary, then there exist $t_1 > t_0$ and two positive numbers b_2, b_3 such that

 $-a_i + b_{i1}x_1(t) < -b_i$, for all $t \ge t_1, i = 2, 3$.

Then for i = 2, 3 and $t \ge t_1$, $x'_i(t) \le x_i(t)[-b_i - b_{ii}x_i(t)]$. By the comparison theorem, it follows that $\lim_{t\to\infty} x_i(t) = 0$ which contradicts (4.18). The proof is complete.

5. The model with the constant intrinsic growth rates

In this section, we consider system (1.1) under the condition $a_i, b_{ij}, 1 \le i, j \le 3$ are constants, then (1.1) becomes

$$\begin{aligned} x_1'(t) &= x_1(t)[a_1 - b_{11}x_1(t) - b_{12}x_2(t) - b_{13}x_3(t)], \\ x_2'(t) &= x_2(t)[-a_2 + b_{21}x_1(t) - b_{22}x_2(t) - b_{23}x_3(t)], \\ x_3'(t) &= x_3(t)[-a_3 + b_{31}x_1(t) - b_{32}x_2(t) - b_{33}x_3(t)]. \end{aligned}$$
(5.1)

Put

$$x_1^* = \frac{a_1b_{22} + a_2b_{12}}{b_{11}b_{22} + b_{12}b_{21}}, \quad x_2^* = \frac{a_1b_{21} - a_2b_{11}}{b_{11}b_{22} + b_{12}b_{21}}$$

Theorem 5.1. If

$$a_2 < \frac{b_{21}}{b_{11}}a_1$$
 and $-a_3 + b_{31}x_1^* - b_{32}x_2^* < 0$,

then the stationary solution $(x_1^*, x_2^*, 0)$ of (5.1) is locally asymptotically stable. It means that if $(x_1(t), x_2(t), x_3(t))$ is a solution of (5.1) such that $(x_1(t_0), x_2(t_0))$ is close to (x_1^*, x_2^*) and $x_3(t_0)$ is sufficiently small and positive, then $\lim_{t\to\infty} x_1(t) = x_1^*$, $\lim_{t\to\infty} x_2(t) = x_2^*$, $\lim_{t\to\infty} x_3(t) = 0$.

Proof. It is easy to see that $x_1^* > 0, x_2^* > 0$ and $(x_1^*, x_2^*, 0)$ is a stationary solution of system (5.1). Put

$$f_1(x_1, x_2, x_3) = x_1(a_1 - b_{11}x_1 - b_{12}x_2 - b_{13}x_3),$$

$$f_2(x_1, x_2, x_3) = x_2(-a_2 + b_{21}x_1 - b_{22}x_2 - b_{23}x_3),$$

$$f_3(x_1, x_2, x_3) = x_3(-a_3 + b_{31}x_1 - b_{32}x_2 - b_{33}x_3),$$

then system (5.1) becomes $x'_i = f_i(x_1, x_2, x_3)$ and $f_i(x_1^*, x_2^*, 0) = 0, i \ge 1$. Consider

$$A = \begin{bmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} & \frac{\partial f_1}{\partial x_3} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} & \frac{\partial f_2}{\partial x_3} \\ \frac{\partial f_3}{\partial x_1} & \frac{\partial f_3}{\partial x_2} & \frac{\partial f_3}{\partial x_3} \end{bmatrix} (x_1^*, x_2^*, 0) = \begin{bmatrix} -b_{11}x_1^* & -b_{12}x_1^* & -b_{13}x_1^* \\ b_{21}x_2^* & -b_{22}x_2^* & -b_{23}x_2^* \\ 0 & 0 & -a_3 + b_{31}x_1^* - b_{32}x_2^* \end{bmatrix}.$$

Since

$$\det(A - \lambda I) = (-a_3 + b_{31}x_1^* - b_{32}x_2^* - \lambda) [\lambda^2 + (b_{11}x_1^* + b_{22}x_2^*)\lambda + (b_{11}b_{22} + b_{12}b_{21})x_1^*x_2^*],$$

it follows that all eigenvalues of A are less than zero. Therefore, $(x_1^*, x_2^*, 0)$ is locally asymptotically stable.

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