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Asymptotic behaviour in periodic three species predator–prey systems

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Abstract For a three-dimensional periodic Lotka–Volterra system, the asymptotic behaviour of its positive solutions is investigated. More specifically, we give suitable average conditions which lead to extinction of the competitively inferior species and global stable coexistence of the two remaining predator and prey species.

Keywords Predator–prey model · Three species community · Periodic systems · Extinction

Mathematics Subject Classification (2000) 34D25, 34D23, 34C25, 92D25

1 Introduction

The dynamics of Lotka–Volterra predator–prey models have been investigated by several authors in order to study permanence, stability, global attractivity, coexistence and extinction.

In the case of autonomous systems, Krikorian [5] classifies three species models obtaining results regarding global boundedness and stability. Using Lyapunov’s method and Hopf’s bifurcation theory, stability of two-prey, one-predator communities is investigated by Takeuchi and Adachi in [9]. They give conditions for stable coexistence, for extinction and they show that a chaotic motion may occur. Korobeinikov and Wake [4], Korman [3] analyse both two-prey, one-predator and two-predator, one-prey models with constant coefficients in which direct competition is absent. Their three-dimensional systems, such as

$$\begin{cases} x_1' = x_1(a_1 - b_1y) \\ x_2' = x_2(a_2 - b_2y) \\ y' = y(-c + d_1x_1 + d_2x_2) \end{cases}, \quad (1.1)$$

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consist of the classical Lotka–Volterra model of the predator–prey interaction by adding the presence of a third species. They show that either the prey more susceptible to predation or the less voracious predator is always driven to extinction and the system behaves asymptotically as a two-dimensional predator–prey system. Recently a nonautonomous Lotka–Volterra system with m -predators and n -preys is studied in [10, 11]. Yang and Xu [10] suppose periodic coefficients and obtain sufficient conditions for existence, uniqueness and global attractivity of the positive periodic solution. Using the notion of lower and upper average introduced by Ahmad and Lazer [1], Zhao and Jiang [11] find conditions for permanence and global attractivity.

Our purpose in this paper is to consider both two-predator, one-prey and two-prey, one-predator models with periodic coefficients in which competition is present, too. We introduce average conditions which lead to extinction of the competitively inferior species and global stable coexistence of the two remaining predator and prey species. Consequently our conditions lead to the same conclusions of [3, 4] for the periodic case, avoiding any chaotic phenomenon.

To our knowledge, the results of this article seems to be new even in the autonomous case. Indeed this special case, cannot be derived by autonomous model (1.1), which is simpler and less realistic than our analogous system (3.1). Extinction in three species periodic competitive systems has recently been studied in [8] by the same author.

2 Two-predator competing for one-prey

The first model discussed in this paper is described by the following system of differential equations:

$$\begin{cases} x_1' = x_1(a_1(t) - b_{11}(t)x_1 - b_{12}(t)x_2 - b_{13}(t)x_3) \\ x_2' = x_2(-a_2(t) + b_{21}(t)x_1 - b_{22}(t)x_2 - b_{23}(t)x_3) \\ x_3' = x_3(-a_3(t) + b_{31}(t)x_1 - b_{32}(t)x_2 - b_{33}(t)x_3) \end{cases} \quad (2.1)$$

where $x_1(t)$ denotes the density of prey species at time t , $x_2(t)$, $x_3(t)$ denote the density of predator species at time t , all coefficients are continuous, T -periodic, $b_{ij}(t)$ are positive ($i, j = 1, 2, 3$) and

$$m[a_i] = \frac{1}{T} \int_0^T a_i(s) ds > 0, \quad i = 1, 2, 3.$$

In (2.1), $b_{23}(t)$, $b_{32}(t)$ measure the competitive effect between the predator species $x_2(t)$, $x_3(t)$, $b_{12}(t)$, $b_{13}(t)$, $b_{21}(t)$, $b_{31}(t)$ are the coefficients due to predation.

Lemma 2.1 *Let $(x_1(t), x_2(t), x_3(t))$ be a solution of (2.1) with positive initial value. Then it is positive for all $t > 0$.*

Proof By assumption $x_1(0), x_2(0), x_3(0) > 0$. Since

$$\frac{x_1'}{x_1} = a_1(t) - b_{11}(t)x_1 - b_{12}(t)x_2 - b_{13}(t)x_3$$

therefore

$$x_1(t) = x_1(0) \exp \left\{ \int_0^t (a_1(s) - b_{11}(s)x_1(s) - b_{12}(s)x_2(s) - b_{13}(s)x_3(s)) ds \right\}.$$

It follows that

$$x_1(t) > 0, \quad t > 0.$$

The same holds for $x_2(t)$ and $x_3(t)$. \square

Lemma 2.2 *All positive solution of (2.1) are bounded for $t \geq 0$.*

Proof First recall some properties regarding the logistic equation

$$u' = u(a(t) - b(t)u) \quad (2.2)$$

where $a(t)$, $b(t)$ are continuous, T-periodic, $b(t) > 0$.

If $m[a] > 0$, it is well-known that (2.2) has a unique positive, T-periodic solution $U(t)$. Any positive solution $u(t)$ of (2.2) is bounded above and below by positive reals on $[0, +\infty)$ and

$$\lim_{t \rightarrow \infty} (u(t) - U(t)) = 0. \quad (2.3)$$

If $m[a] \leq 0$ and $u(t)$ is any positive solution of (2.2), then $\lim_{t \rightarrow \infty} u(t) = 0$. Now consider $(x_1(t), x_2(t), x_3(t))$ positive solution of (2.1) (for $t \geq 0$). If $u(t)$ denotes the solution of $u' = u(a_1(t) - b_{11}(t)u)$ with initial condition $x_1(0)$, then by a known comparison theorem

$$x_1(t) < u(t) \quad \text{for } t > 0$$

so that

$$x_1(t) \leq k \quad \text{for some } k > 0.$$

About $x_2(t)$ we get

$$x_2(t) < v(t), \quad t > 0$$

where $v(t)$ is the solution of the logistic equation

$$v' = v(-a_2(t) + k - b_{22}(t)v)$$

with initial condition $v(0) = x_2(0)$.

Hence $x_2(t)$ is bounded above. Similar argument holds for $x_3(t)$. \square

The following result concerning the two-species system

$$\begin{cases} u_1' = u_1(a_1(t) - b_{11}(t)u_1 - b_{12}(t)u_2) \\ u_2' = u_2(-a_2(t) + b_{21}(t)u_1 - b_{22}(t)u_2) \end{cases} \quad (2.4)$$

is proved in [2].

Theorem 2.1 Let $U_1(t)$ denote the positive T -periodic solution of the logistic equation

$$u' = u(a_1(t) - b_{11}(t)u).$$

If

$$m[a_2] < m[b_{21}U_1], \quad (2.5)$$

then a periodic positive solution $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ of (2.4) exists such that

$$0 < \overset{\circ}{u}_1(t) < U_1(t) \quad \text{for all } t > 0.$$

Remark 2.1 It is also known (see [11]) that

$$0 < \overset{\circ}{u}_2(t) < V_2(t), \quad t > 0$$

where $V_2(t)$ is the positive, T -periodic solution of the logistic equation

$$v' = v((-a_2 + b_{21}U_1)(t) - b_{22}(t)v).$$

In [7] a global stability result concerning $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ is proved. Its statement needs the notations below.

Let

$$\begin{aligned} a_{ij}(t) &= (b_{ij}\overset{\circ}{u}_j)(t), \quad i, j = 1, 2 \\ \beta_{\pm}(t) &= \frac{a_{21}}{a_{12}} \left[\left(1 + \frac{2b_{11}b_{22}}{b_{21}b_{12}} \right) \pm \sqrt{\left(1 + \frac{2b_{11}b_{22}}{b_{21}b_{12}} \right)^2 - 1} \right], \\ \alpha &= \max_{t>0} \beta_-(t) \end{aligned} \quad (2.6)$$

$$\Delta_{\alpha}(t) = (\alpha a_{12}(t) - a_{21}(t))^2 - 4\alpha (a_{11}a_{22})(t)$$

$$B_{\alpha}(t) = \max \left\{ \frac{\Delta_{\alpha}(t)}{4\alpha a_{11}(t)}, \frac{\Delta_{\alpha}(t)}{4a_{22}(t)} \right\},$$

and let $\lambda_{\alpha}(t)$ be the greatest eigenvalue of the symmetric matrix

$$\begin{pmatrix} -\alpha a_{11}(t) & -\frac{(\alpha a_{12} - a_{21})(t)}{2} \\ -\frac{(\alpha a_{12} - a_{21})(t)}{2} & -a_{22}(t) \end{pmatrix}.$$

Theorem 2.2 Suppose inequality (2.5) holds. Let $M_{\alpha}(t)$ be the T -periodic function defined by

$$M_{\alpha}(t) = \begin{cases} \frac{\lambda_{\alpha}(t)}{\alpha} & \text{if } \beta_-(t) \leq \alpha < \frac{a_{21}(t)}{a_{12}(t)} \\ \frac{B_{\alpha}(t)}{\alpha} & \text{if } \frac{a_{21}(t)}{a_{12}(t)} \leq \alpha < \beta_+(t) \\ B_{\alpha}(t) & \text{if } \beta_+(t) \leq \alpha \end{cases} \quad (2.7)$$

in the case $\alpha \geq 1$, whereas

$$M_\alpha(t) = \begin{cases} \lambda_\alpha(t) & \text{if } \beta_-(t) \leq \alpha < \frac{a_{21}(t)}{a_{12}(t)} \\ B_\alpha(t) & \text{if } \frac{a_{21}(t)}{a_{12}(t)} \leq \alpha < \beta_+(t) \\ \alpha B_\alpha(t) & \text{if } \beta_+(t) \leq \alpha \end{cases} \quad (2.8)$$

in the case $0 < \alpha \leq 1$. If

$$m[M_\alpha(t)] < 0, \quad (2.9)$$

then the solution (\hat{u}_1, \hat{u}_2) of system (2.4), whose existence is ensured by Theorem 2.1, is a global attractor in the first quadrant .

Theorem 2.3 Suppose average condition (2.5) holds. Let $(x_1(t), x_2(t), x_3(t))$ be a positive solution of (2.1), then there exists $t_0 > 0$ such that

$$x_1(t) < U_1(t), \quad \text{for any } t > t_0 .$$

Proof If, for some $t_0 \geq 0$, $x_1(t_0) \leq U_1(t_0)$, then, by known comparison results,

$$x_1(t) < U_1(t), \quad \text{for any } t > t_0 .$$

Now assume

$$x_1(t) > U_1(t) \quad \text{for all } t \geq 0 . \quad (2.10)$$

Let $u(t)$ be the solution of

$$u' = (a_1(t) - b_{11}(t)u), \quad u(0) = x_1(0) .$$

By (2.3)

$$\lim_{t \rightarrow \infty} u(t) = U_1(t)$$

hence the inequalities

$$U_1(t) < x_1(t) < u(t)$$

lead to

$$\lim_{t \rightarrow \infty} x_1(t) = U_1(t) .$$

As a consequence

$$\lim_{t \rightarrow \infty} (x_1(t), x_2(t), x_3(t)) = (U_1(t), 0, 0) .$$

Take $\epsilon > 0$ such that

$$m[a_2] < m[b_{21}U_1] - \epsilon m[b_{21} + b_{22} + b_{23}] \quad (2.11)$$

and, for some $t_0 > 0$,

$$(x_1(t), x_2(t), x_3(t)) \in]U_1(t) - \epsilon, U_1(t) + \epsilon[\times]0, \epsilon[\times]0, \epsilon[, \quad t > t_0 .$$

We deduce

$$x_2'(t) > x_2(t) (-a_2 + b_{21}(U_1 - \epsilon) - b_{22}\epsilon - b_{23}\epsilon), \quad t > t_0 .$$

Since by (2.11)

$$m[-a_2 + b_{21}(U_1 - \epsilon) - b_{22}\epsilon - b_{23}\epsilon] > 0 ,$$

it follows

$$\lim_{t \rightarrow \infty} x_2(t) = +\infty$$

which contradicts Lemma 2.2 .

We conclude that (2.10) cannot occur and the proof is complete. \square

Theorem 2.4 Consider $(x_1(t), x_2(t), x_3(t))$, positive solution of (2.1), and assume that

$$m[a_2] < m[b_{21}U_1], \quad m[a_3] > m[b_{31}U_1] .$$

Then

$$\lim_{t \rightarrow \infty} x_3(t) = 0 . \quad (2.12)$$

Proof By Theorem 2.3, for some $t_0 > 0$,

$$x_1(t) < U_1(t), \quad t > t_0 .$$

Let $w(t)$ the solution of the following initial value problem

$$\begin{cases} w' = (-a_3 + b_{31}U_1)(t) w \\ w(t_0) = x_3(t_0) > 0. \end{cases}$$

From the inequality

$$-a_3(t) + b_{31}(t)U_1(t) > -a_3(t) + b_{31}(t)x_1(t) - b_{32}(t)x_2(t) - b_{33}(t)x_3(t), \quad t > t_0,$$

it follows

$$x_3(t) < w(t), \quad t > t_0 . \quad (2.13)$$

On the other hand, since $m[-a_3 + b_{31}U_1] < 0$, $w(t)$ vanishes exponentially as $t \rightarrow \infty$. Using (2.13) and positiveness of $x_3(t)$, we obtain (2.12). \square

Lemma 2.3 Let $p(t), g(t)$ be continuous functions for $t > t_0$, satisfying

$$(i) \quad \int_s^t p(\tau) d\tau \leq -k(t-s)$$

for some fixed $k > 0$ and $t \geq s \geq t_0$, t great enough,

$$(ii) \quad \lim_{t \rightarrow \infty} g(t) = 0 .$$

Then the solution $z(t)$ of the following initial value problem

$$\begin{cases} z' = p(t)z + g(t) \\ z(t_0) = z_0 > 0 \end{cases}$$

vanishes as $t \rightarrow \infty$.

Proof By the variation of constants formula

$$z(t) = z_0 e^{\int_{t_0}^t p(\tau) d\tau} + \int_{t_0}^t g(s) e^{\int_s^t p(\tau) d\tau} ds . \quad (2.14)$$

Fix t great enough. By hypothesis (i)

$$e^{\int_{t_0}^t p(\tau) d\tau} \leq e^{k t_0} e^{-k t} .$$

Furthermore

$$\left| \int_{t_0}^t g(s) e^{\int_s^t p(\tau) d\tau} ds \right| \leq e^{-k t} \int_{t_0}^t |g(s)| e^{k s} ds .$$

If $\int_{t_0}^{+\infty} |g(s)| e^{k s} ds < +\infty$, from (2.14) we obviously get $\lim_{t \rightarrow \infty} z(t) = 0$.
Otherwise, using (ii)

$$\lim_{t \rightarrow \infty} \frac{\int_{t_0}^t |g(s)| e^{k s} ds}{e^{k t}} = \lim_{t \rightarrow \infty} \frac{|g(t)|}{k} = 0$$

hence again $z(t)$, defined by (2.14), vanishes as $t \rightarrow \infty$. \square

Now we can give the following main result about system (2.1).

Theorem 2.5 *Assume that*

$$m[a_2] < m[b_{21}U_1], \quad m[a_3] > m[b_{31}U_1]$$

and

$$m[M_\alpha] < 0$$

where $M_\alpha(t)$ is defined by either (2.7) or (2.8).

If $(x_1(t), x_2(t), x_3(t))$ is any positive solution of (2.1) and $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ is the unique positive, T -periodic solution of (2.4), then

$$x_1(t) \rightarrow \overset{\circ}{u}_1(t), \quad x_2(t) \rightarrow \overset{\circ}{u}_2(t), \quad x_3(t) \rightarrow 0, \quad \text{as } t \rightarrow \infty .$$

Proof Under our assumptions, by Theorem 2.2, the two-species prey-predator system (2.4) has a unique solution $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ which is globally attractive in the first quadrant. Moreover system (2.1) cannot admit any positive, T -periodic solution. Indeed, by contradiction, suppose that $(\bar{x}_1(t), \bar{x}_2(t), \bar{x}_3(t))$ is a T -periodic solution of (2.1) such that

$$0 < \bar{x}_i(t), \quad t \geq 0, \quad i = 1, 2, 3 .$$

It follows from the third equation of system (2.1)

$$m[a_3] = m[b_{31}\bar{x}_1] - m[b_{32}\bar{x}_2] - m[b_{33}\bar{x}_3] < m[b_{31}\bar{x}_1] .$$

By Theorem 2.3 and the periodicity of both $U_1(t)$ and $\bar{x}_1(t)$,

$$\bar{x}_1(t) < U_1(t), \quad t \geq 0$$

hence

$$m[a_3] < m[b_{31}\bar{x}_1] < m[b_{31}U_1]$$

which contradicts our assumption about $m[a_3]$.

Now take $(x_1(t), x_2(t), x_3(t))$ positive solution of (2.1). From Theorem 2.4 we get

$$\lim_{t \rightarrow \infty} x_3(t) = 0.$$

Consider the two-dimensional system

$$\begin{cases} x_1' = x_1 (a_1 - b_{11} x_1 - b_{12} x_2) - b_{13} x_1 x_3 \\ x_2' = x_2 (-a_2 + b_{21} x_1 - b_{22} x_2) - b_{23} x_2 x_3. \end{cases} \quad (2.15)$$

Introducing the functions

$$x(t) = \frac{x_1(t)}{\overset{\circ}{u}_1(t)} - 1, \quad y(t) = \frac{x_2(t)}{\overset{\circ}{u}_2(t)} - 1, \quad (2.16)$$

system (2.15) turns into

$$\begin{cases} x' = (1+x)(-a_{11}(t)x - a_{12}(t)y - b_{13}(t)x_3) \\ y' = (1+y)(a_{21}(t)x - a_{22}(t)y - b_{23}(t)x_3) \end{cases} \quad (2.17)$$

where $a_{ij}(t) = b_{ij}(t)\overset{\circ}{u}_j(t)$, $i, j = 1, 2$.

At this point, arguing as in [7], define the function

$$V(x, y) = \alpha (x - \log(1+x)) + (y - \log(1+y)) \quad (2.18)$$

where α is chosen as in (2.6).

We have the following computation

$$\begin{aligned} \frac{d}{dt}(V(x(t), y(t))) &= \alpha \frac{x'(t)}{1+x(t)} x(t) + \frac{y'(t)}{1+y(t)} y(t) \\ &= (-\alpha a_{11}) x^2 - \alpha a_{12} x y + a_{21} x y - a_{22} y^2 - \alpha b_{13} x x_3 - b_{23} y x_3(t) \\ &= (-\alpha a_{11}) x^2 - (\alpha a_{12} - a_{21}) x y - a_{22} y^2(t) + g(t) \end{aligned}$$

where

$$g(t) = (-\alpha b_{13} x - b_{23} y)(t) x_3(t).$$

Using Theorem 3.1 [7], we deduce

$$\frac{dV}{dt} \leq M_\alpha(t) (1 - e^{-V}) + g(t). \quad (2.19)$$

Introducing the further function

$$Z(t) = e^{V(x(t), y(t))} - 1 \quad (2.20)$$

we get from (2.19)

$$Z'(t) \leq M_\alpha(t) Z(t) + g(t) (Z(t) + 1)$$

that is

$$Z' \leq (M_\alpha(t) + g(t))Z + g(t). \quad (2.21)$$

We claim that

$$\lim_{t \rightarrow \infty} Z(t) = 0. \quad (2.22)$$

Note that $x(t)$ and $y(t)$ are bounded, hence

$$\lim_{t \rightarrow \infty} g(t) = 0.$$

Define

$$p(t) = M_\alpha(t) + g(t)$$

and observe that for $t \geq s$

$$\lim_{t \rightarrow \infty} \frac{1}{t-s} \int_s^t p(\tau) d\tau = \lim_{\omega \rightarrow \infty} \frac{1}{\omega} \int_s^{s+\omega} (M_\alpha(\tau) + g(\tau)) d\tau = m[M_\alpha] < 0.$$

Therefore there exist $t_0 > 0$, $k > 0$ such that

$$\int_s^t p(\tau) d\tau > -k(t-s), \quad t \geq s \geq t_0.$$

By Lemma 2.3, denoting by $z(t)$ the solution of

$$\begin{cases} z' = (M_\alpha(t) + g(t))z + g(t) \\ z(t_0) = Z(t_0) \end{cases}$$

we get

$$\lim_{t \rightarrow \infty} z(t) = 0.$$

From (2.21), claim (2.22) is proved.

Using Theorem 2.4, (2.20), (2.18) and (2.16) the proof is complete. \square

Remark. The average inequalities of the type

$$m[a_i] \leq m[b_{ij}U_j], \quad i, j = 1, 2, 3$$

can be verified by numerical valuations, as done in [6], since an explicit formula is available for the positive, periodic solution of the logistic equation.

If the coefficients b_{ij} are positive constants, we have

$$m[U_j] = \frac{m[a_j]}{b_{jj}}, \quad j = 1, 2, 3,$$

so that the average conditions provided for Theorem 2.4 are easy to be verified. About the further inequality

$$m[M_\alpha] < 0$$

appearing in the statement of Theorem 2.5, we discussed the autonomous case in [7].

3 One predator acting on two competing prey species

In this section we will investigate the following one-predator, two-prey system

$$\begin{cases} x_1' = x_1(-a_1(t) - b_{11}(t)x_1 + b_{12}(t)x_2 + b_{13}(t)x_3) \\ x_2' = x_2(a_2(t) - b_{21}(t)x_1 - b_{22}(t)x_2 - b_{23}(t)x_3) \\ x_3' = x_3(a_3(t) - b_{31}(t)x_1 - b_{32}(t)x_2 - b_{33}(t)x_3). \end{cases} \quad (3.1)$$

where $x_1(t)$ denotes the density of predator species at time t , $x_2(t)$, $x_3(t)$ the density of prey species at time t . The coefficients $a_i(t)$, $b_{ij}(t)$, $i, j = 1, 2, 3$ are continuous, T -periodic, $b_{ij}(t) > 0$ and $m[a_i] > 0$. In our model $b_{23}(t)$ and $b_{32}(t)$ measure the amount of competition between the prey species.

Let $U_i(t)$ be the T -periodic, positive solution of the logistic equation

$$y' = y(a_i(t) - b_{ii}(t)y) \quad i = 2, 3.$$

Arguing as in Lemma 2.1 and Theorem 2.3, we can state the following result.

Theorem 3.1 *Let $(x_1(t), x_2(t), x_3(t))$ a solution of (3.1) with positive initial value. Then it is positive for all $t > 0$. Moreover there exists $t_0 > 0$ such that*

$$x_2(t) < U_2(t), \quad x_3(t) < U_3(t), \quad t > t_0.$$

Theorem 3.2 *Let $(x_1(t), x_2(t), x_3(t))$ be a positive solution of (3.1). If*

$$m[a_1] < m[b_{12}U_2]$$

and $V_1(t)$ denotes the positive, T -periodic solution of the logistic equation

$$x' = x((-a_1 + b_{12}U_2 + b_{13}U_3)(t) - b_{11}(t)x)$$

then, for an appropriate $\bar{t} > 0$

$$x_1(t) < V_1(t), \quad t > \bar{t}. \quad (3.2)$$

Proof Note that

$$m[-a_1 + b_{12}U_2 + b_{13}U_3] > m[-a_1 + b_{12}U_2] > 0$$

so that we can consider $V_1(t)$.

By Theorem 3.1, for all $t > t_0$,

$$(-a_1 + b_{12}U_2 + b_{13}U_3)(t) > (-a_1 + b_{12}x_2 + b_{13}x_3)(t)$$

therefore, if $x_1(\bar{t}) \leq V_1(\bar{t})$, for some $\bar{t} > t_0$, we deduce

$$x_1(t) < V_1(t), \quad t > \bar{t}.$$

It remains to consider the case

$$x_1(t) > V_1(t) \quad \text{for all } t > t_0.$$

Arguing as in the proof of Theorem 2.3, we obtain

$$\lim_{t \rightarrow +\infty} x_1(t) = V_1(t)$$

so that $x_1(t)$ has upper and lower positive bounds, from which

$$\lim_{\omega \rightarrow +\infty} \frac{1}{\omega} \int_{t_0}^{t_0+\omega} \frac{x_1'(s)}{x_1(s)} ds = \lim_{\omega \rightarrow +\infty} \frac{1}{\omega} \ln \left(\frac{x_1(t_0 + \omega)}{x_1(t_0)} \right) = 0.$$

For a bounded function $a(t)$, continuous for $t > t_0$, assume

$$M[a(t)] = \lim_{\omega \rightarrow +\infty} \frac{1}{\omega} \int_{t_0}^{t_0+\omega} a(s) ds .$$

Using the first equation in system (3.1)

$$M[-a_1 - b_{11} x_1 + b_{12} x_2 + b_{13} x_3] = 0$$

which yields

$$M[b_{11} x_1] = M[-a_1 + b_{12} x_2 + b_{13} x_3] < m[-a_1 + b_{12} U_2 + b_{13} U_3] = m[b_{11} V_1] .$$

The above inequality excludes the occurrence that $x_1(t) > V_1(t)$ for all $t > t_0$. \square

It follows from Theorem 3.1 and Theorem 3.2 that any solution of (3.1) which has positive initial value remains bounded for $t > 0$.

The statement of next theorem needs some preliminary notations.

For fixed $t \geq 0$, $\beta, \gamma > 0$, we define by $A(t)$ the maximum of the function

$$f_t(x_1, x_2, x_3) = (-\beta a_2(t) + \gamma a_3(t)) + (\beta b_{21}(t) - \gamma b_{31}(t))x_1 \\ + (\beta b_{22}(t) - \gamma b_{32}(t))x_2 + (\beta b_{23}(t) - \gamma b_{33}(t))x_3$$

on the three-dimensional rectangle $Q_t = [0, V_1(t)] \times [0, U_2(t)] \times [0, U_3(t)]$, that is

$$A(t) = \max_{(x_1, x_2, x_3) \in Q_t} f_t(x_1, x_2, x_3) \quad (3.3)$$

Theorem 3.3 *If*

$$m[a_1] < m[b_{12} U_2], \quad m[a_2] > m[b_{21} V_1], \quad m[a_2] > m[b_{23} U_3],$$

$$m[a_3] < m[b_{31} V_1], \quad m[a_3] < m[b_{32} U_2]$$

and

$$m[A(t)] < 0 \quad (3.4)$$

where $A(t)$ is defined by (3.3), then

$$\lim_{t \rightarrow \infty} x_3(t) = 0$$

for any positive solution of (3.1).

Proof Thanks to our average conditions on coefficients of differential system (3.1), we can find two positive real numbers β, γ such that

$$\frac{m[a_3]}{m[a_2]} < \frac{\beta}{\gamma} < \min \left\{ \frac{m[b_{32}U_2]}{m[a_2]}, \frac{m[a_3]}{m[b_{23}U_3]}, \frac{m[b_{31}V_1]}{m[b_{21}V_1]} \right\}. \quad (3.5)$$

Using Theorem 3.1 and Theorem 3.2, take $t_0 > 0$ so that

$$x_1(t) < V_1(t), \quad x_2(t) < U_2(t), \quad x_3(t) < U_3(t), \quad t > t_0 \quad (3.6)$$

hence

$$(x_1(t), x_2(t), x_3(t)) \in Q_t \quad t > t_0.$$

For $t > t_0$, define

$$\Phi(t) = (x_2(t))^{-\beta} (x_3(t))^\gamma.$$

Easy computations give

$$\begin{aligned} \Phi'(t) = & [(-\beta a_2 + \gamma a_3) + (\beta b_{21} - \gamma b_{31})x_1 \\ & + (\beta b_{22} - \gamma b_{32})x_2 + (\beta b_{23} - \gamma b_{33})x_3] \Phi(t) \end{aligned}$$

therefore

$$\Phi'(t) = f_t(x_1(t), x_2(t), x_3(t)) \Phi(t). \quad (3.7)$$

We claim that our average assumptions ensure that $f_t(x_1(t), x_2(t), x_3(t))$ is a periodic function with negative mean value in each vertex of Q_t . Indeed

$$f_t(0, 0, 0) = -\beta a_2 + \gamma a_3$$

and from the first inequality in (3.5), we get

$$\begin{aligned} m[-\beta a_2 + \gamma a_3] & < 0. \\ f_t(V_1, 0, 0) & = (-\beta a_2 + \gamma a_3) + (\beta b_{21}V_1 - \gamma b_{31}V_1) \end{aligned}$$

and, by (3.5) $\beta m[b_{21}V_1] - \gamma m[b_{31}V_1]$ is negative.

Analogously

$$f_t(0, U_2, 0) = (-\beta a_2 + \gamma a_3) + (\beta b_{22}U_2 - \gamma b_{32}U_2)$$

and

$$\beta m[b_{22}U_2] - \gamma m[b_{32}U_2] = \beta m[a_2] - \gamma m[b_{32}U_2] < 0.$$

Finally

$$f_t(0, 0, U_3) = (-\beta a_2 + \gamma a_3) + (\beta b_{23}U_3 - \gamma b_{33}U_3)$$

and our choice of β and γ yields

$$\beta m[b_{23}U_3] - \gamma m[b_{33}U_3] = \beta m[b_{23}U_3] - \gamma m[a_3] < 0.$$

The previous calculations prove the claim.

From (3.7) and (3.3), we deduce

$$\Phi'(t) \leq A(t) \Phi(t). \quad (3.8)$$

Note that, for fixed $t > t_0$, $f_t(x_1, x_2, x_3)$ is linear hence its maximum value, $A(t)$, on the three-dimensional rectangle Q_t , is achieved in one of the vertices. Assumption (3.4), which is stronger than the above claim, and (3.8) imply

$$\lim_{t \rightarrow \infty} \Phi(t) = 0.$$

Therefore the theorem follows from the inequality

$$(x_3(t))^\gamma = \Phi(t) (x_2(t))^\beta$$

and the boundedness of $x_2(t)$. \square

Corollary 3.1 *If the coefficients b_{ij} , $i, j = 1, 2, 3$, are positive constants and the follow inequalities*

$$\begin{aligned} m[a_1] &< \frac{b_{12}}{b_{22}} m[a_2], & m[a_2] &> \frac{b_{23}}{b_{33}} m[a_3], \\ m[a_3] &< \frac{b_{32}}{b_{22}} m[a_2], & m[a_3] &< \frac{b_{31}}{b_{21}} m[a_2] \end{aligned}$$

are satisfied, then the same conclusion of Theorem 3.3 holds.

Proof Arguing as in the previous theorem and in Theorem 3.3 [8], we see that, for each fixed t , great enough

$$f_t(x_1, x_2, x_3) \leq -\beta a_2(t) + \gamma a_3(t) \quad \text{on } Q_t,$$

where $m[-\beta a_2(t) + \gamma a_3(t)] < 0$. This estimate, together with (3.7), proves our assertion. \square

Remark. In absence of the third species $x_3(t)$, system (3.1) becomes

$$\begin{cases} u'_1 = u_1(-a_1(t) - b_{11}(t)u_1 + b_{12}(t)u_2) \\ u'_2 = u_2(a_2(t) - b_{21}(t)u_1 - b_{22}(t)u_2) \end{cases} \quad (3.9)$$

Comparing it to (2.4), we observe an exchange of index 1 with index 2. Indeed (2.4) is a prey–predator model whereas (3.9) is a predator–prey system.

Using the above Remark, we are ready to prove the final result concerning the asymptotic behaviour of the positive solutions of our one-predator, two-prey system (3.1).

Theorem 3.4 *Suppose all hypothesis of the previous theorem are satisfied. If the T -periodic function $N_\alpha(t)$, defined by either (2.7) or (2.8), after exchanging indices 1 and 2, has negative mean value, then for any positive solution of (3.1)*

$$\lim_{t \rightarrow \infty} x_3(t) = 0, \quad \lim_{t \rightarrow \infty} (x_1(t) - \overset{\circ}{u}_1(t)) = 0, \quad \lim_{t \rightarrow \infty} (x_2(t) - \overset{\circ}{u}_2(t)) = 0$$

where $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ is the unique positive, T -periodic solution of predator–prey system (3.9).

Proof By Theorem 3.3, we know that $x_3(t)$ vanishes as $t \rightarrow \infty$. The remaining part of our statement can be proved as in Theorem 2.5. Hence we only sketch the main steps of the proof.

Since

$$m[a_1] < m[b_{12}U_2]$$

and

$$m[N_\alpha] < 0$$

existence and uniqueness of $(\overset{\circ}{u}_1, \overset{\circ}{u}_2)$ follows from Theorem 2.2. In the first two equations of system (3.1) we put

$$x(t) = \frac{x_1(t)}{\overset{\circ}{u}_1(t)} - 1, \quad y(t) = \frac{x_2(t)}{\overset{\circ}{u}_2(t)} - 1$$

so we obtain

$$\begin{cases} x' = (1+x)(-a_{11}(t)x + a_{12}(t)y + b_{13}(t)x_3) \\ y' = (1+y)(-a_{21}(t)x - a_{22}(t)y - b_{23}(t)x_3) \end{cases} \quad (3.10)$$

where $a_{ij}(t) = b_{ij}(t)\overset{\circ}{u}_j(t)$, $i, j = 1, 2$. Note that system (3.10) can be treated as system (2.17). Hence the proof proceeds using the same arguments of Theorem 2.5 \square

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