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Asymptotic Stability of Solutions of Lotka-Volterra Predator-Prey Model for Four Species

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Abstract

In this paper, we consider Lotka-Volterra predator-prey model between one and three species. Two cases are distinguished. The first is Lotka-Volterra model of one prey-three predators and the second is Lotka-Volterra model of one predator-three preys. The existence conditions of nonnegative equilibrium points are established. The local stability analysis of the system is carried out.

1. Introduction

The Lotka-Volterra model provides a nice mathematical device to study and understand complex systems of mutually interacting species or agent [1]. In the past decades, Lotka-Volterra type systems have been extensively investigated, especially in biology and ecology [2]-[8]. A basic issue addressed in the studies concerns stability property of the systems because of its relevance to the coexistence of different species in a community [9]. It turns out that the stability of a Lotka-Volterra system relies crucially on the interaction matrix of the system.

A Lotka-Volterra system of n-dimensions is expressed by the ordinary differential equations [4] [10]:

$$\dot{x}_i(t) = x_i(t)\left(b_i - \sum_{j=1}^{n} a_{ij}x_j(t)\right), \quad i \in N. \tag{1.1}$$

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where $N = \{1, 2, \cdots, n\}$ and n is the species number. In (1.1), the function $x_i(t)$ represents the density of species i at time t, the constant b_i, is the carrying capacity of species i, and a_{ij} represents the effect of interspecific (if $i \neq j$) or intraspecific (if $i = j$) interaction. In vector form, System (1.1) is expressed as

$$\dot{x} = X(b - Ax),$$

where $x = col(x_1, x_2, \cdots, x_n)$ is an n-dimensional state vector, $X = diag(x_1, x_2, \cdots, x_n)$ is an $n \times n$ diagonal matrix, $b = col(b_1, b_2, \cdots, b_n)$ is an n-dimensional real vector, and $A = (a_{ij})$ is an $n \times n$ community matrix.

The existence and stability of a nonnegative equilibrium point of system (1.1) or subsystems of (1.1) has been investigated by many authors [9] [11] and [12]. The global stability of system (1.1) has been studied by many authors [9] [11] [13]-[16].

In this paper, we shall concentrate on Lotka-Volterra systems of the fourth dimension. A Lotka-Volterra two preys-two predators system is studied by Takeuchi and Adachi [15], and [16]. The first is Lotka-Volterra model of one prey-three predators and the second is Lotka-Volterra model of three prey-one predator.

This work is organized as follows: In Section 2, we describe our model. In Section 3, the existence conditions of nonnegative equilibrium points are established. The local stability analysis of the system is carried out in Section 4.

In Section 5, we present an example to clarify each case.

2. The Model

Lotka-Volterra Model

In this section we consider Lotka-Volterra predator-prey model between one and three species and assume that there is no interspicific competition between the three species x_2, x_3 and x_4. This is represented by the following system of differential equations:

$$\left.\begin{array}{l} x_1'(t) = x_1(t)\left[b_1 - a_{11}x_1(t) - a_{12}x_2(t) - a_{13}x_3(t) - a_{14}x_4(t)\right], \\ x_2'(t) = x_2(t)\left[b_2 - a_{21}x_1(t) - a_{22}x_2(t)\right], \\ x_3'(t) = x_3(t)\left[b_3 - a_{31}x_1(t) - a_{33}x_3(t)\right], \\ x_4'(t) = x_4(t)\left[b_4 - a_{41}x_1(t) - a_{44}x_4(t)\right]. \end{array}\right\} \tag{2.1}$$

where $x_i(t), (i = 1, 2, 3, 4)$ represents the density of species i at time t, the constant b_i is the carrying capacity of species i and a_{ij} represents the effect of interspecific (if $i \neq j$) or intraspecific (if $i = j$) interaction. In vector form, system (2.1) is expressed as:

$$\dot{x} = X(b - Ax),$$

where $x = col(x_1, x_2, x_3, x_4)$ is a 4-dimensional state vector, $X = diag(x_1, x_2, x_3, x_4)$ is a 4×4 diagonal matrix, $b = col(b_1, b_2, b_3, b_4)$ is a 4-dimnsional real vector, and

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & a_{33} & 0 \\ a_{41} & 0 & 0 & a_{44} \end{pmatrix}. \tag{2.2}$$

is a 4×4 community matrix.

The system (2.1) is a prey-predator system if the following assumption is satisfied.

(H1) $a_{ii} > 0, a_{1j}a_{j1} < 0, i = 1, 2, 3, 4, j = 1, 2, 3.$

Two cases of system (2.1) can be distinguished:

The first case describes a one prey-three predators system where x_1 represents the prey and x_2, x_3, x_4 represent the predators. In this case we assume that the following conditions are satisfied in addition to (H1):

(H2) $a_{1j} > 0, a_{j1} < 0, j = 2, 3, 4.$

(H3) $b_1 > 0, b_j < 0, j = 2, 3, 4.$

The second case describes a one predator-three preys system where x_1 represents the predator and x_2, x_3, x_4 represent the preys. In this case we assume that the following conditions are satisfied in addition to (H1).

(H2)' $a_{1j} < 0, a_{j1} > 0, j = 2,3,4,$

(H3)' $b_1 < 0, b_j > 0, j = 2,3,4.$

3. Equilibrium Analysis

3.1. Existence of the Quilibrium Points

In this section, the existence of the equilibrium points of system (2.1) in each case is investigated. At most there are nine possible non-negative equilibrium points for system (2.1) in the first case, the existence conditions of them are given as the following:

1) The equilibrium points $E_0 = (0,0,0,0)$ and $E_1 = \left(\dfrac{b_1}{a_{11}}, 0, 0, 0 \right)$ are always exist where E_1 is the equili-

brium point in the absence of predation and $\dfrac{b_1}{a_{11}} > 0$ according to conditions (H1) and (H3).

2) The positive equilibrium point $E_{1j} = \left(\tilde{x}_{1j}, \tilde{x}_j \right), j = 2,3,4$ exists in the first quadrant of the $x_1 x_j$ plane if and only if the following condition is satisfied

(H4): $\dfrac{b_1}{b_j} < \dfrac{a_{11}}{a_{j1}}, j = 2,3,4,$

where $\tilde{x}_{1j}$ and $\tilde{x}_j$ are given by

$$\left. \begin{aligned} \tilde{x}_{1j} &= \frac{a_{jj}b_1 - a_{1j}b_j}{a_{11}a_{jj} - a_{1j}a_{j1}}, \\ \tilde{x}_j &= \frac{a_{11}b_j - a_{j1}b_1}{a_{11}a_{jj} - a_{1j}a_{j1}}, j = 2,3,4. \end{aligned} \right\} \tag{3.1}$$

3) The positive equilibrium point $E_{1jk} = \left(\hat{x}_{1jk}, \hat{x}_{jk}, \hat{x}_{kj} \right), j = 2,3, k = 3,4, j \neq k$ exists in the first octant of $x_1 x_j x_k$ space if and only if the following conditions are satisfied:

(H5): $b_j > a_{j1} \left(\dfrac{a_{kk}b_1 - a_{1k}b_k}{a_{11}a_{kk} - a_{1k}a_{k1}} \right) = a_{j1}\tilde{x}_{1k},$

$b_k > a_{k1} \left(\dfrac{a_{jj}b_1 - a_{1j}b_j}{a_{11}a_{jj} - a_{1j}a_{j1}} \right) = a_{k1}\tilde{x}_{1j},$

$j = 2,3, \ k = 3,4, \ j \neq k.$

where $\hat{x}_{1jk}, \hat{x}_{jk}$ and $\hat{x}_{kj}$ are given by

$$\left. \begin{aligned} \hat{x}_{1jk} &= \frac{a_{jj}a_{kk}b_1 - a_{1j}a_{kk}b_j - a_{1k}a_{jj}b_k}{a_{11}a_{jj}a_{kk} - a_{1j}a_{j1}a_{kk} - a_{1k}a_{k1}a_{jj}}, \\ \hat{x}_{jk} &= \frac{-a_{j1}a_{kk}b_1 - a_{1k}a_{k1}b_j + a_{11}a_{kk}b_j + a_{1k}a_{j1}b_k}{a_{11}a_{jj}a_{kk} - a_{1j}a_{j1}a_{kk} - a_{1k}a_{k1}a_{jj}}, \\ \hat{x}_{kj} &= \frac{-a_{jj}a_{k1}b_1 + a_{1j}a_{k1}b_j - a_{1j}a_{j1}b_k + a_{11}a_{jj}b_k}{a_{11}a_{jj}a_{kk} - a_{1j}a_{j1}a_{kk} - a_{1k}a_{k1}a_{jj}}, \\ j &= 2,3, \ k = 3,4, \ j \neq k. \end{aligned} \right\} \tag{3.2}$$

4) The positive equilibrium point $E^* = \left(x_1^*, x_2^*, x_3^*, x_4^* \right)$ exists in the positive cone (nonnegative octant) $R_+^4 = \left\{ x = (x_1, x_2, x_3, x_4) \in R^4 \mid x_i \geq 0, i = 1,2,3,4 \right\}.$ if and only if the following conditions are satisfied

(H6) $\quad b_2 > a_{21}\left(\dfrac{a_{33}a_{44}b_1 - a_{13}a_{44}b_3 - a_{14}a_{33}b_4}{a_{11}a_{33}a_{44} - a_{13}a_{31}a_{44} - a_{14}a_{41}a_{33}}\right) = a_{21}\hat{x}_{134},$

$\quad\quad\quad b_3 > a_{31}\left(\dfrac{a_{22}a_{44}b_1 - a_{14}a_{22}b_4 - a_{12}a_{44}b_2}{a_{11}a_{22}a_{44} - a_{12}a_{21}a_{44} - a_{14}a_{41}a_{22}}\right) = a_{31}\hat{x}_{124},$

$\quad\quad\quad b_4 > a_{41}\left(\dfrac{a_{22}a_{33}b_1 - a_{12}a_{33}b_2 - a_{13}a_{22}b_3}{a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{13}a_{31}a_{22}}\right) = a_{41}\hat{x}_{123}.$

where $\;x_i^*, i = 1, 2, 3, 4\;$ are given by

$$x_i^* = \frac{\overline{x}_i}{|A|},\; i = 1, 2, 3, 4, \tag{3.3}$$

where

$$\overline{x}_1 = a_{22}a_{33}a_{44}b_1 - a_{12}a_{33}a_{44}b_2 - a_{13}a_{22}a_{44}b_3 - a_{14}a_{22}a_{33}b_4,$$

$$\overline{x}_2 = -a_{21}a_{33}a_{44}b_1 + \left(a_{11}a_{33}a_{44} - a_{14}a_{41}a_{33} - a_{13}a_{31}a_{44}\right)b_2 + a_{13}a_{21}a_{44}b_3 + a_{14}a_{21}a_{33}b_4,$$

$$\overline{x}_3 = -a_{22}a_{31}a_{44}b_1 + a_{12}a_{31}a_{44}b_2 + \left(a_{11}a_{22}a_{44} - a_{12}a_{21}a_{44} - a_{14}a_{41}a_{22}\right)b_3 + a_{14}a_{22}a_{31}b_4,$$

$$\overline{x}_4 = -a_{22}a_{33}a_{41}b_1 + a_{12}a_{33}a_{41}b_2 + a_{13}a_{22}a_{41}b_3 + \left(a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{13}a_{31}a_{22}\right)b_4,$$

$$|A| = a_{11}a_{22}a_{33}a_{44} - a_{12}a_{21}a_{33}a_{44} - a_{13}a_{31}a_{22}a_{44} - a_{14}a_{41}a_{22}a_{33}.$$

A is the interaction matrix defined in (2.2).

For the second case of system (2.1), at most there are fifteen possible nonnegative equilibrium points. The existence conditions of them are given as the following:

1) The equilibrium points

$$E_0 = (0,0,0,0),\quad E_2 = \left(0, \frac{b_2}{a_{22}}, 0, 0\right),\quad E_3 = \left(0, 0, \frac{b_3}{a_{33}}, 0\right)\;\text{and}\;E_4 = \left(0, 0, 0, \frac{b_4}{a_{44}}\right)$$

are always exist where E_2, E_3, E_4 are the equilibrium points in the absence of predation and $\dfrac{b_j}{a_{jj}} > 0, (j = 2, 3, 4)$

according to conditions (H1) and (H3)'.

2) The positive equilibrium point $E_{1j} = (\tilde{x}_{1j}, \tilde{x}_j), j = 2, 3, 4$ exists in the first quadrant of $x_1 x_j$ plane if and only if the following condition is satisfied

(H4)': $\quad \dfrac{b_1}{b_j} > \dfrac{a_{1j}}{a_{jj}},\; j = 2, 3, 4.$

where $\;\hat{x}_{1j}\;$ and $\;\hat{x}_j\;$ are given by (3.1).

3) In the absence of predator and one prey species, both the other two prey species grow. Thus, the equilibrium point $E_{jk} = \left(\dfrac{b_j}{a_{jj}}, \dfrac{b_k}{a_{kk}}\right), j = 2, 3, k = 3, 4, j \neq k$ always exists in the interior of $x_j x_k$ plane where $\dfrac{b_j}{a_{jj}} > 0$,

$\dfrac{b_k}{a_{kk}} > 0$ according to conditions (H1) and (H3)'.

4) The positive equilibrium point $E_{1jk} = \left(\hat{x}_{1jk}, \hat{x}_{jk}, \hat{x}_{kj}\right), j = 3, 4, k = 3, 4, j \neq k$ exists in the first octant of $x_1 x_j x_k$ space if and only if the following conditions are satisfied

(H5)' $\quad b_1 > \dfrac{a_{1j}}{a_{jj}}b_j + \dfrac{a_{1k}}{a_{kk}}b_k,$

$\quad\quad\quad b_j > a_{j1}\left(\dfrac{a_{kk}b_1 - a_{1k}b_k}{a_{11}a_{kk} - a_{1k}a_{k1}}\right) = a_{j1}\tilde{x}_{1k},$

$\quad\quad\quad b_k > a_{k1}\left(\dfrac{a_{jj}b_1 - a_{1j}b_j}{a_{11}a_{jj} - a_{1j}a_{j1}}\right) = a_{k1}\tilde{x}_{1j}.$

where $\hat{x}_{1jk}$, $\hat{x}_{jk}$ and $\hat{x}_{kj}$ are given by (3.2).

5) In the absence of predator, all three prey species grow. Thus, the positive equilibrium point

$$E_{234} = \left(\frac{b_2}{a_{22}}, \frac{b_3}{a_{33}}, \frac{b_4}{a_{44}} \right) \text{ always exists in the interior of } x_2 x_3 x_4 \text{ space.}$$

6) The positive equilibrium point $E^* = \left(x_1^*, x_2^*, x_3^*, x_4^* \right)$ exists in R_+^4 if and only if the following conditions are satisfied

(H6)': $b_1 > \dfrac{a_{12}}{a_{22}} b_2 + \dfrac{a_{13}}{a_{33}} b_3 + \dfrac{a_{14}}{a_{44}} b_4$,

$$b_2 > a_{21} \left(\frac{a_{33}a_{44}b_1 - a_{13}a_{44}b_3 - a_{14}a_{33}b_4}{a_{11}a_{33}a_{44} - a_{13}a_{31}a_{44} - a_{14}a_{41}a_{33}} \right) = a_{21}\hat{x}_{134},$$

$$b_3 > a_{31} \left(\frac{a_{22}a_{44}b_1 - a_{14}a_{22}b_4 - a_{12}a_{44}b_2}{a_{11}a_{22}a_{44} - a_{12}a_{21}a_{44} - a_{14}a_{41}a_{22}} \right) = a_{31}\hat{x}_{124},$$

$$b_4 > a_{41} \left(\frac{a_{22}a_{33}b_1 - a_{12}a_{33}b_2 - a_{13}a_{22}b_3}{a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{13}a_{31}a_{22}} \right) = a_{41}\hat{x}_{123}.$$

where $x_i^*, i = 1, 2, 3, 4$ are given by (3.3).

3.2. Remark

We will use the symbols E_{1200}, E_{1030} and E_{1004} to denote the nonnegative equilibrium points $(\tilde{x}_{12}, \tilde{x}_2, 0, 0)$, $(\tilde{x}_{13}, 0, \tilde{x}_3, 0)$ and $(\tilde{x}_{14}, 0, 0, \tilde{x}_4)$ respectively, where $\tilde{x}_{1j}$ and $\tilde{x}_j, j = 2, 3, 4$ are given by (3.1), the symbols E_{1230}, E_{1204} and E_{1034} to denote the nonnegative equilibrium points $(\hat{x}_{123}, \hat{x}_{23}, \hat{x}_{32}, 0)$, $(\hat{x}_{124}, \hat{x}_{24}, 0, \hat{x}_{42})$ and $(\hat{x}_{134}, 0, \hat{x}_{34}, \hat{x}_{43})$ respectively, where $\hat{x}_{1jk}, \hat{x}_{jk}, \hat{x}_{kj}, j = 1, 2, k = 3, 4, j \neq k$ are given by (3.2) and use the symbols E_{0230}, E_{0204} and E_{0034} to denote the nonnegative equilibrium points $\left(0, \dfrac{b_2}{a_{22}}, \dfrac{b_3}{a_{33}}, 0 \right)$, $\left(0, \dfrac{b_2}{a_{22}}, 0, \dfrac{b_4}{a_{44}} \right)$ and

$\left(0, 0, \dfrac{b_3}{a_{33}}, \dfrac{b_4}{a_{44}} \right)$ respectively.

4. Stability Analysis

4.1. Stability of Equilibrium Points

In this section, the local stability analysis of equilibrium points is investigated. Assuming that all previous equilibrium points existing.

The Jacobian matrix J of system (2.1) is given by:

$$J = \begin{bmatrix} b_1 - 2a_{11}x_1 - a_{12}x_2 \\ -a_{13}x_3 - a_{14}x_4 & -a_{12}x_1 & -a_{13}x_1 & -a_{14}x_1 \\ -a_{21}x_2 & \begin{matrix} b_2 - a_{21}x_1 \\ -2a_{22}x_2 \end{matrix} & 0 & 0 \\ -a_{31}x_3 & 0 & \begin{matrix} b_3 - a_{31}x_1 \\ -2a_{33}x_3 \end{matrix} & 0 \\ -a_{41}x_4 & 0 & 0 & \begin{matrix} b_4 - a_{41}x_1 \\ -2a_{44}x_4 \end{matrix} \end{bmatrix}. \tag{4.1}$$

Computing the variation matrixes corresponding to each equilibrium point and then using Routh-Hurwitz criteria [17], the following results can be observed:

1) Substituting by E_0 in the variation matrix (4.1), we get the eigenvalues $\lambda_i = b_i, i = 1, 2, 3, 4$.

So for the first case, E_0 is a saddle point with locally stable manifold in the $x_2 x_3 x_4$ space and with unstable

manifold in the x_1 direction. Near E_0 the prey's population x_1 grows while the predators' populations x_2, x_3 and x_4 decline.

For the second case, E_0 is a saddle point with locally stable manifold in the x_1 direction and with unstable manifold in the $x_2x_3x_4$ space. Near E_0 the predator population x_1 decline while the preys' populations x_2, x_3 and x_4 grow.

2) Substituting by E_1 in the variation matrix (4.1), we get the eigenvalues $\lambda_1 = -b_1 < 0$, $\lambda_j = b_j - \dfrac{a_{1j}}{a_{11}} b_1 > 0$,

$j = 2,3,4$.

(By using (H3) and (H4)).

So E_1 is a saddle point with locally stable manifold in the x_1 direction and with unstable manifold in the $x_2x_3x_4$ space. Near E_1 the prey species x_1 remains close to $\dfrac{b_1}{a_{11}}$.

Similarly, E_2 has three positive eigenvalues

$$\lambda_1 = b_1 - \frac{a_{12}}{a_{22}} b_2 > 0, \quad \lambda_2 = -b_2 < 0, \quad \lambda_3 = b_3 > 0, \quad \lambda_3 = b_3 > 0.$$

(By using (H3)' and (H4)')

So E_2 is a saddle point with locally stable manifold in the x_2 direction and with unstable manifold in the $x_1x_3x_4$ space. Near E_2 the prey species x_2 remains close to $\dfrac{b_2}{a_{22}}$.

E_3 and E_4 have the same stability behavior of E_2.

We now state the local stability behavior of other equilibrium points in the form of Theorems. The proofs of these theorems follow directly from the Routh-Hurwitz criteria [12].

Theorem 4.1

1) E_{12} is locally asymptotically stable in the x_1x_2 plane.

2) If E_{1230} and E_{1204} exist, then E_{1200} is a saddle point with locally stable manifold in the x_1x_2 plane and with unstable manifold in the x_3x_4 plane.

Proof

Consider the following subsystem from (2.1)

$$\left.\begin{array}{l} x_1'(t) = x_1(t)\left[b_1 - a_{11}x_1(t) - a_{12}x_2(t)\right], \\ x_2'(t) = x_2(t)\left[b_2 - a_{21}x_1(t) - a_{22}x_2(t)\right]. \end{array}\right\} \tag{4.2}$$

Evaluating the variation matrix of system (4.2) at E_{12}, we have

$$M_{12} = \begin{pmatrix} -a_{11}\tilde{x}_{12} & -a_{12}\tilde{x}_{12} \\ -a_{21}\tilde{x}_{12} & -a_{22}\tilde{x}_2 \end{pmatrix}.$$

The characteristic polynomial is

$$\lambda^2 + \left(a_{11}\tilde{x}_{12} + a_{22}\tilde{x}_2\right)\lambda + \left(a_{11}a_{22} - a_{12}a_{21}\right)\tilde{x}_{12}\tilde{x}_2. \tag{4.3}$$

Since

$$\text{trace}(M_{12}) = \lambda_1 + \lambda_2 = -\left(a_{11}\tilde{x}_{12} + a_{22}\tilde{x}_2\right) < 0,$$
$$\det(M_{12}) = \lambda_1\lambda_2 = \left(a_{11}a_{22} - a_{12}a_{21}\right)\tilde{x}_{12}\tilde{x}_2 > 0.$$

Then, λ_1 and λ_2 have negative real parts. Thus, E_{12} is locally asymptotically stable in the x_1x_2 plane.

Computing the variation matrix (4.1) at E_{1200}, we have

$$J_{12} = \begin{bmatrix} -a_{11}\tilde{x}_{12} & -a_{12}\tilde{x}_{12} & -a_{13}\tilde{x}_{12} & -a_{14}\tilde{x}_{12} \\ -a_{21}\tilde{x}_2 & -a_{22}\tilde{x}_2 & 0 & 0 \\ 0 & 0 & b_3 - a_{31}\tilde{x}_{12} & 0 \\ 0 & 0 & 0 & b_4 - a_{41}\tilde{x}_{12} \end{bmatrix}.$$

The characteristic equation of matrix V_{12} is

$$\left[\lambda^2 + \left(a_{11}\tilde{x}_{12} + a_{22}\tilde{x}_2\right)\lambda + \left(a_{11}a_{22} - a_{12}a_{21}\right)\tilde{x}_{12}\tilde{x}_2\right]\left(b_3 - a_{31}\tilde{x}_{12} - \lambda\right)\left(b_4 - a_{41}\tilde{x}_{12} - \lambda\right) = 0.$$

Comparing with (4.3) we get that λ_1 and λ_2 have negative real parts and

$$\lambda_3 = b_3 - a_{31}\tilde{x}_{12}, \quad \lambda_4 = b_4 - a_{41}\tilde{x}_{12}.$$

If E_{1230} and E_{1204} exist, then $\lambda_3 > 0$ and $\lambda_4 > 0$ (by using (H5) and (H5)').

Therefore, E_{1200} is a saddle point with locally stable manifold in the x_1x_2 plane and with unstable manifold in the x_3x_4 plane.

4.2. Remark

1) Behavior of solutions near the equilibrium points E_{13} and E_{14} are the same behavior of solutions near the equilibrium point E_{12}.

2) Behavior of solutions near E_{1030} and E_{1004} are the same behavior of solutions near E_{1200}.

Theorem 4.1

a) E_{23} is locally asymptotically stable in the x_2x_3 plane.

b) If E_{1230} exists, then E_{0230} is a saddle point with locally stable manifold in the x_2x_3 plane and with unstable manifold in the x_1x_4 plane.

Proof

Consider the following subsystem from (2.1)

$$\left.\begin{array}{l} x_2'(t) = x_2(t)\left[b_2 - a_{22}x_2(t)\right], \\ x_3'(t) = x_3(t)\left[b_3 - a_{33}x_3(t)\right]. \end{array}\right\} \tag{4.4}$$

Evaluating the variation matrix of system (4.4) at E_{23}, we have

$$M_{23} = \begin{pmatrix} -b_2 & 0 \\ 0 & -b_3 \end{pmatrix},$$

which have the eigenvalues $\lambda_1 = -b_2 < 0$ and $\lambda_2 = -b_3 < 0$ (by using (H3)').

Therefore, E_{23} is locally asymptotically stable in the x_2x_3 plane.

Substituting by E_{0230} in the variation matrix (4.1), we get the eigenvalues

$$\lambda_1 = b_1 - \frac{a_{12}}{a_{22}}b_2 - \frac{a_{13}}{a_{33}}b_3, \quad \lambda_2 = -b_2, \quad \lambda_3 = -b_3, \quad \lambda_4 = b_4.$$

If E_{1230} exists, then

$$\lambda_1 > 0, \quad \lambda_2 < 0, \quad \lambda_3 < 0, \quad \lambda_4 > 0.$$

(By using (H3)' and (H5)').

Hence E_{0230} is a saddle point with locally stable manifold in the x_2x_3 plane and with unstable manifold in the x_1x_4 plane.

Theorem 4.2

a) E_{123} is locally asymptotically stable in the $x_1x_2x_3$ space.

b) If E^* exists, then E_{1230} is a saddle point with locally stable manifold in the $x_1x_2x_3$ space and with unstable manifold in the x_4 direction.

Proof

Consider the following subsystem from (2.1)

$$\left.\begin{array}{l} x_1'(t) = x_1(t)\left[b_1 - a_{11}x_1(t) - a_{12}x_2(t) - a_{13}x_3(t)\right], \\ x_2'(t) = x_2(t)\left[b_2 - a_{21}x_1(t) - a_{22}x_2(t)\right], \\ x_3'(t) = x_3(t)\left[b_3 - a_{31}x_1(t) - a_{33}x_3(t)\right]. \end{array}\right\} \tag{4.5}$$

Evaluating the variation matrix of system (4.5) at E_{123}, we have

$$M_{123} = \begin{pmatrix} -a_{11}\hat{x}_{123} & -a_{12}\hat{x}_{123} & -a_{13}\hat{x}_{123} \\ -a_{21}\hat{x}_{23} & -a_{22}\hat{x}_{23} & 0 \\ -a_{31}\hat{x}_{32} & 0 & -a_{33}\hat{x}_{32} \end{pmatrix},$$

which has the characteristic polynomial

$$\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3, \tag{4.6}$$

where

$$c_1 = a_{11}\hat{x}_{123} + a_{22}\hat{x}_{23} + a_{33}\hat{x}_{32},$$
$$c_2 = a_{11}a_{22}\hat{x}_{123}\hat{x}_{23} + a_{11}a_{33}\hat{x}_{123}\hat{x}_{32} + a_{22}a_{33}\hat{x}_{23}\hat{x}_{32} - a_{12}a_{21}\hat{x}_{123}\hat{x}_{23} - a_{13}a_{31}\hat{x}_{123}\hat{x}_{32},$$
$$c_3 = \left[a_{11}a_{22}a_{33} - a_{12}a_{21}a_{33} - a_{13}a_{31}a_{22}\right]\hat{x}_{123}\hat{x}_{23}\hat{x}_{32}.$$

From Routh-Hurwitz criterion, E_{123} is locally asymptotically stable if and only if $c_1 > 0$, $c_3 > 0$ and $c_1c_2 > c_3$.

It is clear that all the coefficients c_1, c_2 and c_3 are positive and

$$c_1c_2 - c_3 = a_{11}\hat{x}_{123}\left[a_{11}a_{22}\hat{x}_{123}\hat{x}_{23} + a_{11}a_{33}\hat{x}_{123}\hat{x}_{32} - a_{12}a_{21}\hat{x}_{123}\hat{x}_{23} - a_{13}a_{31}\hat{x}_{123}\hat{x}_{32}\right]$$
$$+ a_{22}\hat{x}_{23}\left[a_{11}a_{22}\hat{x}_{123}\hat{x}_{23} + a_{11}a_{33}\hat{x}_{123}\hat{x}_{32} + a_{22}a_{33}\hat{x}_{23}\hat{x}_{32} - a_{12}a_{21}\hat{x}_{123}\hat{x}_{23}\right]$$
$$+ a_{33}\hat{x}_{32}\left[a_{11}a_{22}\hat{x}_{123}\hat{x}_{23} + a_{11}a_{33}\hat{x}_{123}\hat{x}_{32} + a_{22}a_{33}\hat{x}_{23}\hat{x}_{32} - a_{13}a_{31}\hat{x}_{123}\hat{x}_{32}\right] > 0$$

Therefore E_{123} is locally asymptotically stable in the $x_1x_2x_3$ space.

Substituting by E_{1230} in the variation matrix (4.1), we get the characteristic equation

$$\left[\lambda^3 + c_1\lambda^2 + c_2\lambda + c_3\right]\left(b_4 - a_{41}\hat{x}_{123} - \lambda\right) = 0.$$

Comparing with (4.6), we obtain that λ_1, λ_2 and λ_3 have negative real parts while $\lambda_4 = b_4 - a_{41}\hat{x}_{123} > 0$ (by using (H6) and (H6)')

Therefore, E_{1230} is a saddle point with locally stable manifold in the $x_1x_2x_3$ space and with unstable manifold in the x_4 direction.

Remark 4.1

1) Behavior of solutions near E_{124} and E_{134} are the same behavior of solutions near the equilibrium point E_{123}.

2) Behavior of solutions near E_{1204} and E_{1034} are the same behavior of solutions near E_{1230}.

Theorem 4.3

a) E_{234} is locally asymptotically stable in the $x_2x_3x_4$ space.

b) If E^* exists, then E_{0234} is a saddle point with locally stable manifold in the $x_2x_3x_4$ space and with unstable manifold in the x_4 direction.

Proof

Proof of this theorem follows directly as proof of Theorem 4.2

Now, we study asymptotic stability of the positive equilibrium E^*.

Substituting by E^* in the variation matrix (4.1), we get the characteristic equation

$$\lambda^4 + c_1\lambda^3 + c_2\lambda^2 + c_3\lambda + c_4 = 0,$$

where

$$c_1 = a_{11}x_1^* + a_{22}x_2^* + a_{33}x_3^* + a_{44}x_4^*,$$
$$c_2 = a_{11}a_{22}x_1^*x_2^* + a_{11}a_{33}x_1^*x_3^* + a_{11}a_{44}x_1^*x_4^* + a_{22}a_{33}x_2^*x_3^* + a_{22}a_{44}x_2^*x_4^*$$
$$+ a_{33}a_{44}x_3^*x_4^* - a_{12}a_{21}x_1^*x_2^* - a_{13}a_{31}x_1^*x_3^* - a_{14}a_{41}x_1^*x_4^*,$$
$$c_3 = a_{11}a_{22}a_{33}x_1^*x_2^*x_3^* + a_{11}a_{22}a_{44}x_1^*x_2^*x_4^* + a_{11}a_{33}a_{44}x_1^*x_3^*x_4^* + a_{22}a_{33}a_{44}x_2^*x_3^*x_4^*$$
$$- a_{12}a_{21}a_{33}x_1^*x_2^*x_3^* - a_{12}a_{21}a_{44}x_1^*x_2^*x_4^* - a_{13}a_{31}a_{22}x_1^*x_2^*x_3^* - a_{13}a_{31}a_{44}x_1^*x_3^*x_4^*$$
$$- a_{14}a_{41}a_{22}x_1^*x_2^*x_4^* - a_{14}a_{41}a_{33}x_1^*x_3^*x_4^*,$$
$$c_4 = \left(a_{11}a_{22}a_{33}a_{44} - a_{12}a_{21}a_{33}a_{44} - a_{13}a_{31}a_{22}a_{44} - a_{14}a_{41}a_{22}a_{33}\right)x_1^*x_2^*x_3^*x_4^*.$$

From Routh-Hurwitz criterion [12], E^* is locally asymptotically stable if and only if $c_1 > 0, c_3 > 0, c_4 > 0$ and $c_1 c_2 c_3 > c_3^2 + c_1^2 c_4$.

It is clear that all the coefficients c_1, c_2, c_3 and c_3 are positive and if

$$c_1 c_2 c_3 - c_3^2 - c_1^2 c_4 > 0.$$

Then E^* is locally asymptotically stable in R_+^4.

Theorem 4.4

E^* is globally asymptotically stable in R_+^4 for every carrying capacity $b \in R^4$.

Proof.

We define the Liapunov function $V(x)$ by

$$V(x) = \sum_{i=1}^{4} w_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*} \right),$$

where $x = (x_1, x_2, x_3, x_4)$, $w_i > 0, i = 1, 2, 3, 4$.

In the region

$$G = \{(x_1, x_2, x_3, x_4) | x_i > 0, i = 1, 2, 3, 4\}.$$

It is clear that

$$V(x) \in C^1(G, R),$$
$$V(x) = 0 \Leftrightarrow x = E^*,$$
$$V(x) > 0 \text{ for } x \in G - \{E^*\}.$$

Then calculating the time derivative of V along the positive solutions of system (2.1), we have

$$\dot{V} = -w_1 a_{11} (x_1 - x_1^*)^2 - (w_1 a_{12} + w_2 a_{21})(x_1 - x_1^*)(x_2 - x_2^*)$$
$$- (w_1 a_{13} + w_3 a_{31})(x_1 - x_1^*)(x_3 - x_3^*) - (w_1 a_{14} + w_4 a_{41})(x_1 - x_1^*)(x_4 - x_4^*)$$
$$- w_2 a_{22}(x_2 - x_2^*)^2 - w_3 a_{33}(x_3 - x_3^*)^2 - w_4 a_{44}(x_4 - x_4^*)^2.$$

Then, we can choose

$$w_1 = 1, \quad w_j = -\frac{a_{1j}}{a_{j1}}, \quad j = 2, 3, 4.$$

Hence, we obtain

$$\dot{V} = -a_{11}(x_1 - x_1^*)^2 + \frac{a_{12}}{a_{21}} a_{22}(x_2 - x_2^*)^2 + \frac{a_{13}}{a_{31}} a_{33}(x_3 - x_3^*)^2 + \frac{a_{14}}{a_{41}} a_{44}(x_4 - x_4^*)^2 < 0.$$

Therefore, it follows from well-known Liapunov-LaSalle theorem that the positive equilibrium E^* is globally asymptotically stable in R_+^4.

5. Numerical Simulations

The reader can be check local asymptotic stability of the system 2.1 for:

Example 5.1

$$b_1 = a_{12} = a_{22} = 1, \quad a_{11} = a_{13} = a_{44} = 0.5, \quad a_{33} = a_{14} = 0.25$$
$$a_{21} = -1, \quad a_{31} = b_2 = -0.75, \quad a_{41} = b_3 = -0.5$$

Example 5.2

$$b_1 = -1, \quad a_{11} = 1, \quad a_{22} = a_{41} = a_{44} = b_3 = 0.5, \quad a_{21} = a_{33} = b_4 = 0.25,$$
$$a_{31} = b_2 = 0.75, \quad a_{12} = -0.75, \quad a_{13} = -0.5, \quad a_{14} = -0.25$$

Acknowledgements

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