International Journal of Differential Equations and Applications
Volume 17 No. 1 2018, 45-59
ISSN: 1311-2872
url: http://www.ijpam.eu
doi: http://dx.doi.org/10.12732/ijdea.v17i1.5727

acadpubl.eu

PREY-PREDATOR TRIDIAGONAL LOTKA-VOLTERRA MODELS

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Abstract: The prey-predator Lotka-Volterra models are some of the most popular mathematical models in biology and chemistry. Usually, these models are the first tool used to analyze cooperativity, oscillatory behavior, and spaces synchronization at large scale of biochemistry, bio-molecular, and medical interaction models. These properties are in relationship with existence of first integrals and stability behavior of the systems. Especially, and maybe the most essential results are related to existence (or non-existence) of bounded and periodic orbits.

In this paper we determine a family of independent first integrals, criteria for existence of bounded orbits, and stability criteria for a family of n-dimensional Lotka-Volterra systems, generated by periodic tridiagonal matrices.

AMS Subject Classification: 34C07, 34C05, 34C40
Key Words: prey-predator Lotka-Volterra system, tridiagonal matrix, first integral, stability, limit sets, invariance principle

1. Introduction and Statement

In 1926 V. Volterra and in 1956 A.J. Lotka independently derived a simple system of ordinary differential equations in two-dimensional space to describe

Received: April 12, 2018

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different mathematical models: predator-prey relationship and dynamics in chemical reactions, see [20] and [17]. We consider the simplest form of such a system in d-dimensional space

$$\dot{\boldsymbol{x}} = \boldsymbol{D}(\boldsymbol{x})\left(\boldsymbol{A}\boldsymbol{x} + \boldsymbol{b}\right), \tag{1}$$

where: $\boldsymbol{x} = \begin{pmatrix} x_1 & x_2 & \dots & x_d \end{pmatrix}^t \in \mathbb{R}^d$; $\boldsymbol{D}(\boldsymbol{x}) = \begin{pmatrix} x_1 & 0 & \dots & 0 \\ 0 & x_2 & \dots & 0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & x_d \end{pmatrix}$; $\boldsymbol{A} = \begin{pmatrix} a_{ij} \end{pmatrix}$ is a real $(d\times d)$-matrix; $\boldsymbol{b} = \begin{pmatrix} b_1 & b_2 & \dots & b_d \end{pmatrix}^t \in \mathbb{R}^d$. Usually, the natural additional conditions are

$$\begin{aligned} a_{ij} &\neq 0 \text{ – effects between } i\text{-th and } j\text{-th species, } i \neq j, \\ b_i &\neq 0 \text{ – natural growth or death rate of } i\text{-th species.} \end{aligned} \tag{2}$$

These conditions leads to mathematical models in which each species or agent depends on a finite set of resources. For more information see [7], [4], and [3], also the references therein.

In 1976 Smale in [18] showed that any asymptotic behavior of solutions is possible if $d \geq 5$. In additional (and as a contrast) Hirsh in [9]-[14] demonstrated that there exists a closed invariant set which is a global attractor, if $d \leq 4$.

There are also many results, establishing the cases of the existence of first integrals of Lotka-Volterra system. Here, we refer to [5], where all cases of integrability of the 3-dimensional Lotka-Volterra system are listed.

In the present article, we will assume that the matrix $\boldsymbol{A}$ is periodic tridiagonal, i.e.

$$\boldsymbol{A} = \begin{pmatrix} a_{11} & a_{12} & \cdots & 0 & a_{1d} \\ a_{21} & a_{22} & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & a_{d-1\,d-1} & a_{d-1\,d} \\ a_{d1} & 0 & \cdots & a_{d\,d-1} & a_{dd} \end{pmatrix}.$$

In this case, we will say *the system* (1) *is periodic tridiagonal system.*

The main result in the article is the existence result of first integral(s) of periodic tridiagonal Lotka-Volterra system, see Section 2.

Also, let us note that the periodic tridiagonal system is a natural generalization of the classical Lotka-Volterra 2-dimensional and 3-dimensional systems.

In Section 3 we prove a result establishing the behavior of ω-limit set of any bounded orbits. More precisely, a set of conditions is established such that the system (1) has not any periodic orbits or any different (including chaotic) attractors in first orthant $\mathbb{R}_+^d$.

The following remark includes well-known results (they have been added only for completeness).

Remark 1 (Invariant sets of Lotka-Volterra system)**.** 1. Each coordinate plane is invariant with respect to the system (1).

To prove this fact, we refer to following well known result (in general case see [1]): Let Ω be a smooth closed surface in $\mathbb{R}^d$ without boundary, $\boldsymbol{n}$ be the normal vector to Ω, and let moreover

$$\langle \boldsymbol{n}, \boldsymbol{D}(\boldsymbol{x})\,(\boldsymbol{A}\boldsymbol{x}+\boldsymbol{b})\rangle = 0.$$

Then Ω is invariant with respect to the system (1).

Now, to prove for example, that the coordinate plane $x_n = 0$ is invariant, it is sufficient to note that $\boldsymbol{n} = \begin{pmatrix}0 & 0 & \dots & 1\end{pmatrix}^t$ is normal to plane $x_n = 0$. Hence at the point $(x_1, x_2, \dots, 0)^t$, we have

$$\langle \boldsymbol{n}, \boldsymbol{D}(\boldsymbol{x})\,(\boldsymbol{A}\boldsymbol{x}+\boldsymbol{b})\rangle = \left\langle \begin{pmatrix}0\\0\\\vdots\\1\end{pmatrix}, \begin{pmatrix} x_1(a_{11}x_1 + a_{12}x_2 + a_{1d}x_d + b_1)\\ x_2(x_{21}x_1 + a_{22}x_2 + a_{23}x_3 + b_2)\\ \vdots\\ 0\end{pmatrix}\right\rangle = 0.$$

Therefore (using the Uniqueness Theorem), the first orthant $\mathbb{R}_+^d$ is also an invariant set.

2. Equilibria. Obviously, $(0, 0, \dots, 0)^t$ is one stationary point of the system (1).

If $\det(\boldsymbol{A}) = 0$, then the system (1) has infinitely many stationary points. If $\det(\boldsymbol{A}) \neq 0$, then the system (1) has only one more stationary point $\boldsymbol{A}^{-1}\boldsymbol{b}$.

2. First Integrals of Periodic Tridiagonal Lotka-Volterra System

In this section we consider periodic tridiagonal Lotka-Volterra system, supposing in addition: $a_{ii} = 0$, $i = 1, \dots, d$.

We introduce the following semi-periodic tridiagonal matrix

$$\boldsymbol{B} = \begin{pmatrix} a_{12} & a_{21} & \cdots & 0 & 0 \\ 0 & a_{23} & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & a_{d-1\,d} & a_{d\,d-1} \\ a_{1d} & 0 & \cdots & 0 & a_{d1} \end{pmatrix}$$

Theorem 2. *Let (1) be a periodic tridiagonal system. Moreover, let:*

1. $a_{i\,i+1} \neq 0 \neq a_{i+1\,i}$, $i = 1, \ldots, d-1$; $a_{1d} \neq 0 \neq a_{d1}$; $a_{ii} = 0$, $i = 1, \ldots, d$.
2. $\operatorname{rank}(\boldsymbol{B}) = d - 1$. *Let* $\boldsymbol{\lambda}^* = \begin{pmatrix} \lambda_1^* & \lambda_2^* & \ldots & \lambda_d^* \end{pmatrix}^t$ *be a non-trivial solution of the system* $\boldsymbol{B\lambda} = \boldsymbol{0}$ *such that* $\operatorname{rank}(\boldsymbol{A}^t) = \operatorname{rank}(\boldsymbol{A}^t|\boldsymbol{c}) = d-1$, *where* $\boldsymbol{c} = -\begin{pmatrix} b_1\lambda_1^* & b_2\lambda_2^* & \ldots & b_d\lambda_d^* \end{pmatrix}^t$.
3. *There exists a solution* $\boldsymbol{\mu}^*$ *of the system* $\boldsymbol{A}^t\boldsymbol{\mu} = \boldsymbol{c}$ *such that* $\langle \boldsymbol{\mu}^*, \boldsymbol{b} \rangle = 0$.

Then

$$\Psi(\boldsymbol{x}) = \langle \boldsymbol{\lambda}^*, \boldsymbol{x} \rangle + \langle \boldsymbol{\mu}^*, \ln(\boldsymbol{x}) \rangle ,$$

is a first integral of periodic Lotka-Volterra system, where $\ln(\boldsymbol{x}) = \begin{pmatrix} \ln x_1 & \ln x_2 & \ldots & \ln x_d \end{pmatrix}^t$.

Remark 3. The condition $\operatorname{rank}(\boldsymbol{B}) = d-1$ (and condition (1) of Theorem 2) is equivalent to

$$\det(\boldsymbol{B}) = 0, \quad \text{here } \det(\boldsymbol{B}) = a_{d\,1} \prod_{i=1}^{d-1} a_{i\,i+1} + (-1)^{d+1} a_{1\,d} \prod_{i=1}^{d-1} a_{i+1\,i}.$$

Indeed $\det(\boldsymbol{B}) = 0$ implies $\operatorname{rank}(\boldsymbol{B}) \leq d-1$ and condition (1) of the theorem implies $\operatorname{rank}(\boldsymbol{B}) \geq d-1$, because the U matrix $\boldsymbol{U_B}$ in PLU-decomposition of the matrix $\boldsymbol{B}$ is

$$\boldsymbol{U_B} = \begin{pmatrix} a_{12} & a_{21} & \cdots & 0 & 0 \\ 0 & a_{23} & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & a_{d-1\,d} & a_{d\,d-1} \\ 0 & 0 & \cdots & 0 & \det(\boldsymbol{B}) \left(\prod_{i=1}^{d-1} a_{i\,i+1} \right)^{-1} \end{pmatrix}$$

In such a case all solutions of the system $\boldsymbol{B\lambda} = \boldsymbol{0}$ depend on one free parameter, for example, λ_d.

Proof. Let

$$\Psi(\boldsymbol{x}) = \langle \boldsymbol{\lambda}, \boldsymbol{x} \rangle + \langle \boldsymbol{\mu}, \ln(\boldsymbol{x}) \rangle ,$$

where $\lambda = \begin{pmatrix} \lambda_1 & \lambda_2 & \dots & \lambda_d \end{pmatrix}^t$ and $\mu = \begin{pmatrix} \mu_1 & \mu_2 & \dots & \mu_d \end{pmatrix}^t$.

Obviously

$$\begin{aligned} \dot{\Psi}(\boldsymbol{x}) &= \langle \boldsymbol{\lambda}, (\boldsymbol{D}(\boldsymbol{x})(\boldsymbol{A}\boldsymbol{x} + \boldsymbol{b})) \rangle + \langle \boldsymbol{\mu}, (\boldsymbol{A}\boldsymbol{x} + \boldsymbol{b}) \rangle \\ &= \langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{A}\boldsymbol{x} \rangle + \langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{b} \rangle + \langle \boldsymbol{\mu}, \boldsymbol{A}\boldsymbol{x} \rangle + \langle \boldsymbol{\mu}, \boldsymbol{b} \rangle , \end{aligned}$$

i.e. the total derivative of $\Psi(\boldsymbol{x})$ is a sum of quadratic and linear forms. Hence, $\Psi(\boldsymbol{x})$ is a first integral of the tridiagonal system, i.e. $\dot{\Psi}(\boldsymbol{x}) = 0$, if and only if

$$\begin{aligned} \langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{A}\boldsymbol{x} \rangle &= 0, \\ \langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{b} \rangle + \langle \boldsymbol{\mu}, \boldsymbol{A}\boldsymbol{x} \rangle &= 0, \\ \langle \boldsymbol{\mu}, \boldsymbol{b} \rangle &= 0. \end{aligned} \tag{3}$$

Step 1: Nullifying the quadratic form $\langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{A}\boldsymbol{x} \rangle$.

From the first equation in (3):

$$\begin{aligned} &\langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{A}\boldsymbol{x} \rangle \\ &= \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \vdots \\ \lambda_{d-1} \\ \lambda_d \end{pmatrix}^t \begin{pmatrix} 0 & a_{12}x_1 & \cdots & 0 & a_{1d}x_1 \\ a_{21}x_2 & 0 & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & 0 & a_{d-1\,d}x_{d-1} \\ a_{d\,1}x_d & 0 & \cdots & a_{d\,d-1}x_d & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_{d-1} \\ x_d \end{pmatrix} \\ &= (\lambda_2 x_2 a_{21} + \lambda_d x_d a_{d1})\, x_1 + \cdots + (\lambda_1 x_1 a_{1d} + \lambda_{d-1} x_{d-1} a_{d-1\,d})\, x_d \\ &= \sum_{i=1}^{d-1} (a_{i\,i+1}\lambda_i + a_{i+1\,i}\lambda_{i+1})\, x_i x_{i+1} + (a_{1d}\lambda_1 + a_{d1}\lambda_d)\, x_1 x_d. \end{aligned}$$

Hence, if the following semi-periodic tridiagonal system

$$\begin{pmatrix} a_{12} & a_{21} & 0 & \cdots & 0 & 0 \\ 0 & a_{23} & a_{32} & \cdots & 0 & 0 \\ \vdots & & \ddots & \ddots & 0 & 0 \\ 0 & 0 & 0 & \cdots & a_{d-1\,d} & a_{d\,d-1} \\ a_{1d} & 0 & 0 & \cdots & 0 & a_{d1} \end{pmatrix} \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \vdots \\ \lambda_{d-1} \\ \lambda_d \end{pmatrix} = \boldsymbol{B}\boldsymbol{\lambda} = \boldsymbol{0}. \tag{4}$$

has non-trivial solution, then the first equation in (3) has a solution. Therefore, the first equation in (3) has a non-trivial solution if and only if $a_{d1} \prod_{i=1}^{d-1} a_{i\,i+1} =$

$(-1)^d a_{1d} \prod_{i=2}^{d} a_{i\,i-1}$. Moreover, let us mark that we may write the solution in the form

$$\lambda_j = (-1)^{d-j} \lambda_d \prod_{i=j}^{d-1} a_{i+1\,i}\, a_{i\,i+1}^{-1},\ j = 1, \ldots, d-1; \quad \lambda_d \in \mathbb{R}.$$

Below, for simplification of notations, let $\boldsymbol{\lambda}$ be the non-trivial solution of the first equation in (3).

Step 2: Nullifying the linear form $\langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{b} \rangle + \langle \boldsymbol{\mu}, \boldsymbol{A}\boldsymbol{x} \rangle$.

The left-hand side second equation in (3) has the following coordinate form

$$\begin{aligned}
&\langle \boldsymbol{\lambda}, \boldsymbol{D}(\boldsymbol{x})\boldsymbol{b} \rangle + \langle \boldsymbol{\mu}, \boldsymbol{A}\boldsymbol{x} \rangle \\
&= \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \vdots \\ \lambda_{d-1} \\ \lambda_d \end{pmatrix}^t \begin{pmatrix} b_1 x_1 \\ b_2 x_2 \\ \vdots \\ b_{d-1} x_{d-1} \\ b_d x_d \end{pmatrix} + \begin{pmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_{d-1} \\ \mu_d \end{pmatrix}^t \begin{pmatrix} a_{12}x_2 + a_{1d}x_d + b_1 \\ a_{21}x_1 + a_{23}x_3 + b_2 \\ \vdots \\ a_{d-1\,d-2}x_{d-2} + a_{d-1\,d}x_d + b_d \\ a_{d1}x_1 + a_{d\,d-1}x_{d-1} + b_d \end{pmatrix} \\
&= \sum_{i=1}^{d} \lambda_i b_i x_i + \mu_1 \left(a_{12}x_2 + a_{1d}x_d + b_1\right) \\
&\quad + \sum_{i=2}^{d-1} \mu_i \left(a_{i\,i-1}x_{i-1} + a_{i\,i+1}x_{i+1} + b_i\right) + \mu_d \left(a_{d1}x_1 + a_{d\,d-1}x_{d-1} + b_d\right) \\
&= \left(a_{21}\mu_2 + a_{d1}\mu_d + \lambda_1 b_1\right) x_1 + \sum_{i=2}^{d-1} \left(a_{i-1\,i}\mu_{i-1} + a_{i+1\,i1}\mu_{i+1} + \lambda_i b_i\right) x_i \\
&\quad + \left(a_{1d}\mu_1 + a_{d-1\,d}\mu_{d-1} + \lambda_d b_d\right) x_d + \sum_{i=1}^{d} b_i \mu_i.
\end{aligned}$$

Nullifying the linear form, $\boldsymbol{\mu}$ have to be a solution of the following system

$$\boldsymbol{A}^t \boldsymbol{\mu} = \begin{pmatrix} 0 & a_{21} & \cdots & 0 & a_{d1} \\ a_{12} & 0 & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & 0 & a_{d\,d-1} \\ a_{1d} & 0 & \cdots & a_{d-1\,d} & 0 \end{pmatrix} \begin{pmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_{d-1} \\ \mu_d \end{pmatrix} = - \begin{pmatrix} b_1 \lambda_1 \\ b_2 \lambda_2 \\ \vdots \\ b_{d-1} \lambda_{d-1} \\ b_d \lambda_d \end{pmatrix} = \boldsymbol{c}. \quad (5)$$

It follows from the second assumption of the theorem that the system has a solution $\boldsymbol{\mu}^*$.

Step 3: The equality $\langle \boldsymbol{\mu}^*, \boldsymbol{b} \rangle = 0$ follows directly from the assumption (3) of theorem.

Using the results in previous steps, we obtain $\dot{\Psi}(\boldsymbol{x}) = 0$, i.e. $\Psi(\boldsymbol{x})$ is a first integral of the periodic tridiagonal Lotka-Volterra system (1). □

Example 4 (Three-dimensional Lotka-Volterra system)**.** Consider the system

$$\begin{aligned} \dot{x}_1 &= x_1(\qquad\quad a_{12} x_2 + x_3 + b_1), \\ \dot{x}_2 &= x_2(x_1 \qquad\quad + a_{23} x_3 + b_2), \\ \dot{x}_3 &= x_3(a_{31} x_1 + x_2 \qquad\quad + b_3). \end{aligned} \tag{6}$$

In this case, the quadratic form is

$$\begin{aligned} &\boldsymbol{\lambda}^t \boldsymbol{D}(\boldsymbol{x}) \boldsymbol{A} \boldsymbol{x} \\ &= \begin{pmatrix} \lambda_1 & \lambda_2 & \lambda_3 \end{pmatrix} \begin{pmatrix} x_1 & 0 & 0 \\ 0 & x_2 & 0 \\ 0 & 0 & x_3 \end{pmatrix} \begin{pmatrix} 0 & a_{12} & 1 \\ 1 & 0 & a_{23} \\ a_{31} & 1 & 0 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} \\ &= (\lambda_2 a_{21} + \lambda_1 a_{12})\, x_2 x_1 + (\lambda_3 a_{31} + \lambda_1 a_{13})\, x_3 x_1 + (\lambda_2 a_{23} + \lambda_3 a_{32})\, x_2 x_3. \end{aligned}$$

or (the system corresponding to (4)):

$$\begin{pmatrix} a_{12} & 1 & 0 \\ 0 & a_{23} & 1 \\ 1 & 0 & a_{31} \end{pmatrix} \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \lambda_3 \end{pmatrix} = \mathbf{0}. \tag{7}$$

Obviously, the system (7) has non-trivial solutions if $a_{12} a_{23} a_{31} = -1$.

The linear term is

$$\begin{aligned} &\boldsymbol{\lambda}^t \boldsymbol{D}(\boldsymbol{x}) \boldsymbol{b} + \boldsymbol{\mu}^t (\boldsymbol{A} \boldsymbol{x} + \boldsymbol{b}) \\ &= \begin{pmatrix} \lambda_1 \\ \lambda_2 \\ \lambda_3 \end{pmatrix}^t \begin{pmatrix} b_1 x_1 \\ b_2 x_2 \\ b_3 x_3 \end{pmatrix} + \begin{pmatrix} \mu_1 \\ \mu_2 \\ \mu_3 \end{pmatrix}^t \begin{pmatrix} a_{12} x_2 + x_3 + b_1 \\ x_1 + a_{23} x_3 + b_2 \\ a_{31} x_1 + x_2 + b_3 \end{pmatrix} \\ &= \sum_{i=1}^{3} \lambda_i b_i x_i \\ &\quad + \mu_1 (a_{12} x_2 + x_3 + b_1) + \mu_2 (x_1 + a_{23} x_3 + b_2) + \mu_3 (a_{31} x_1 + x_2 + b_3) \\ &= (a_{31} \mu_3 + \lambda_1 b_1 + \mu_2)\, x_1 + (a_{12} \mu_1 + \lambda_2 b_2 + \mu_3)\, x_2 \\ &\quad + (a_{23} \mu_2 + \lambda_3 b_3 + \mu_1)\, x_3 + \mu_1 b_1 + \mu_2 b_2 + \mu_3 b_3. \end{aligned}$$

The system

$$
\begin{aligned}
a_{31}\mu_3 + \mu_2 &= -\lambda_1 b_1, \\
a_{12}\mu_1 + \mu_3 &= -\lambda_2 b_2, \\
a_{23}\mu_2 + \mu_1 &= -\lambda_3 b_3
\end{aligned}
\tag{8}
$$

has solutions if and only if

$$b_2 = a_{23}b_1 - a_{12}a_{23}b_3.$$

Let us also mark that all the solutions of (7) and (8) are

$$
\begin{aligned}
\lambda_1 &\in \mathbb{R}, & \mu_1 &= a_{12}a_{23}b_3\lambda_1 - a_{23}\mu_2, \\
\lambda_2 &= -a_{12}\lambda_1, & \mu_2 &\in \mathbb{R}, \\
\lambda_3 &= a_{12}a_{23}\lambda_1; & \mu_3 &= a_{12}a_{23}\mu_2 - a_{12}a_{23}b_1\lambda_1.
\end{aligned}
$$

In this case, by direct calculations, we have $\mu_1 b_1 + \mu_2 b_2 + \mu_3 b_3 = 0$.

Here, we received two parametric family of first integrals:

$$
\begin{aligned}
\Psi(\boldsymbol{x}) = \lambda_1 x_1 - a_{12}\lambda_1 x_2 + \lambda_1 a_{12}a_{23}x_3 - (a_{12}a_{23}b_3\lambda_1 + a_{23}\mu_2)\ln(x_1) \\
+ \mu_2 \ln(x_2) + (a_{12}a_{23}b_1\lambda_1 + a_{12}a_{23}\mu_2)\ln(x_3).
\end{aligned}
$$

In particular:

$$
\begin{aligned}
\Psi(\boldsymbol{x}) &= -a_{23}\ln(x_1) + \ln(x_2) + a_{12}a_{23}\ln(x_3), \\
\Psi(\boldsymbol{x}) &= x_1 - a_{12}x_2 + a_{12}a_{23}x_3 - a_{12}a_{23}b_3\ln(x_1) + a_{12}a_{23}b_1\ln(x_3),
\end{aligned}
$$

where $\lambda_1 = 0$, $\mu_2 = 1$ and $\lambda_1 = 1$, $\mu_2 = 0$, respectively. This result has been published for the first time in [5].

As numerical example, let

$$a_{12} = -0.5, \quad a_{23} = -1, \quad a_{31} = -2, \quad b_1 = b_3 = 3, \quad b_2 = -4.5.$$

Then all conditions of Theorem 2 hold true. Therefore a first integral of Lotka-Volterra system is (for example, let $\lambda_1 = 2$, $\mu_2 = -7$)

$$\Psi(\boldsymbol{x}) = 2x_1 + x_2 + x_3 - 10\ln(x_1) - 7\ln(x_2) - 0.5\ln(x_3).$$

The orbits of the system lie in the level surfaces of $\Psi(\boldsymbol{x})$: $\Psi(\boldsymbol{x}) = C > -11.869... = C_{\min} = \min\left\{\Psi(\boldsymbol{x}) : \boldsymbol{x} \in \mathbb{R}^d_+\right\}$, see Figure 1. Hence any trajectory lies in a bounded regions. Since $C > C_{\min}$, a fixed trajectory cannot tends

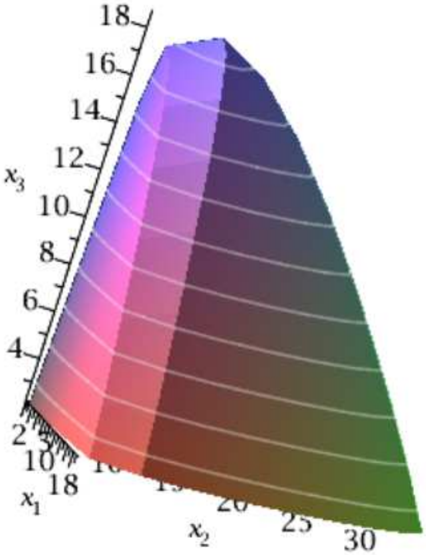

Figure 1: Level surfaces of $\Psi(\boldsymbol{x})$

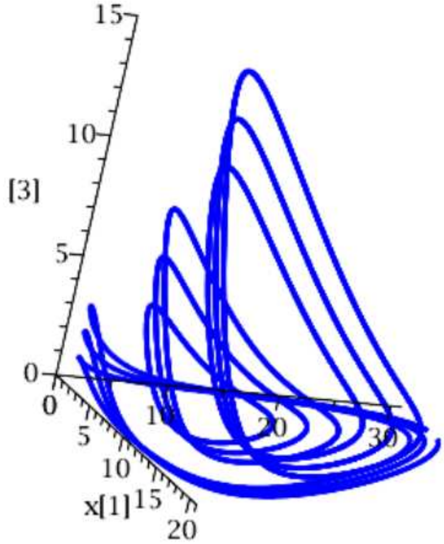

Figure 2: The graphs of some orbits of system (6)

to stationary point of the system. Therefore (using Poincaré-Bendixon Theorem) any trajectory is a periodic or tends to periodic orbit. But for any fixed x_i and x_j the equation $\Psi(\boldsymbol{x}) = C$ has two solutions for x_k, where the indices $i, j, k \in \{1, 2, 3\}$ are different. Hence, it is possible to be periodic orbit only. So, the second statement in Poincaré-Bendixon Theorem is impossible.

Hence, all orbits in the first octant are periodic. Some orbits of the system are plotted on Figure 2.

3. Tridiagonal system with non-zero elements on main diagonal

Contrary to Example 4, in this subsection, we will prove that if $a_{ii} < 0$ for some i, then it is impossible to exist periodic orbits of tridiagonal Lotka-Volterra system in general case.

Let

$$\boldsymbol{A} = \begin{pmatrix} a_{11} & a_{12} & \cdots & 0 & a_{1d} \\ a_{21} & a_{22} & \ddots & 0 & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & 0 & \ddots & a_{d-1\,d-1} & a_{d-1\,d} \\ a_{d1} & 0 & \cdots & a_{d\,d-1} & a_{d\,d} \end{pmatrix}.$$

Theorem 5. *Let the following conditions hold true:*

1. *The Lotka-Volterra system* (1) *has unique equilibrium point*

$$\boldsymbol{x}^* = \begin{pmatrix} x_1^* & x_2^* & \dots & x_d^* \end{pmatrix}^t, \text{ with } x_i^* > 0 \text{ for all } i = 1, 2, \dots, d.$$

2. *For all* $i = 1, 2, \dots, d$, *we have* $a_{ii} \leq 0$.
3. *There exists an index* i_0 *such that* $a_{i_0\,i_0} < 0$ *and* $a_{i_0\,i_0+1} < 0$.
4. *The following implications hold true*

$$a_{i\,i+1}a_{i+1\,i} \leq 0, \; a_{i+1\,i} \neq 0 \quad i = 1, \dots, d-1;$$

$$a_{d1} \prod_{i=1}^{d-1} a_{i\,i+1} = (-1)^d a_{1d} \prod_{i=1}^{d-1} a_{i+1i}.$$

Then for any $\boldsymbol{x}_0 \in \mathbb{R}_+^d$, *the* ω*-limit set of any bounded orbit of system* (1) *through* $\boldsymbol{x}_0$ *is* $\boldsymbol{x}^*$. *Therefore, the system* (1) *has not periodic orbits in* $\mathbb{R}_+^d$.

Proof. Let us consider the following function

$$\Psi(\boldsymbol{x}) = \sum_{i=1}^{d} A_i \left(x_i - x_i^* \ln x_i\right),$$

where A_i are constants, $i = 1, 2, \dots, d$.

Our goal is to prove that we may choose the constants $A_i > 0$ such that $\Psi(\boldsymbol{x})$ is a global Lyapunov type function for system (1) in $\mathbb{R}_+^d$. Let us mark that this type of function are widely used, see for example the lecture notes [8], Subsection 6.2 and [19] (also the references in [19]).

Indeed, we have

$$\dot{\Psi}(\boldsymbol{x}) = \sum_{i=1}^{d} A_i \left(1 - x_i^* \frac{1}{x_i}\right) \dot{x}_i = \sum_{i=1}^{d} A_i \frac{\dot{x}_i}{x_i} \left(x_i - x_i^*\right).$$

Obviously ($\boldsymbol{x}^*$ is equilibrium point):

$$
\begin{aligned}
b_1 =& - a_{11}x_1^* - a_{12}x_2^* - a_{1d}x_d^*,\\
b_i =& - a_{i\,i-1}x_{i-1}^* - a_{ii}x_i^* - a_{ii+1}x_{i+1}^*,\\
b_d =& - a_{d1}x_1^* - a_{d\,d-1}x_{d-1}^* - a_{dd}x_d^*,
\end{aligned}
$$

or

$$
\begin{aligned}
\frac{\dot{x}_1}{x_1} =& a_{11}x_1 + a_{12}x_2 + a_{1d}x_d + b_1\\
=& a_{11}(x_1 - x_1^*) + a_{12}(x_2 - x_2^*) + a_{1d}(x_d - x_d^*),\\
\frac{\dot{x}_i}{x_i} =& a_{i\,i-1}x_{i-1} + a_{ii}x_i + a_{ii+1}x_{i+1} + b_i\\
=& a_{i\,i-1}(x_{i-1} - x_{i-1}^*) + a_{ii}(x_i - x_i^*) + a_{ii+1}(x_{i+1} - x_{i+1}^*),\\
\frac{\dot{x}_d}{x_d} =& a_{d1}x_1 + a_{d\,d-1}x_{d-1} + a_{dd}x_d + b_d\\
=& a_{d1}(x_1 - x_1^*) + a_{d\,d-1}(x_{d-1} - x_{d-1}^*) + a_{dd}(x_d - x_d^*),
\end{aligned}
$$

where $i = 2, \dots, d-1$.

Therefore

$$
\begin{aligned}
\dot{\Psi}(\boldsymbol{x}) =& \sum_{i=1}^{d} A_i \frac{\dot{x}_i}{x_i}\,(x_i - x_i^*)\\
=& A_1\left(a_{11}(x_1 - x_1^*) + a_{12}(x_2 - x_2^*) + a_{1d}(x_d - x_d^*)\right)(x_1 - x_1^*)\\
&+ \sum_{i=2}^{d-1} A_i \left(a_{i\,i-1}(x_{i-1} - x_{i-1}^*) + a_{ii}(x_i - x_i^*) + a_{ii+1}(x_{i+1} - x_{i+1}^*)\right)\\
&\times (x_i - x_i^*)\\
&+ A_d\left(a_{d1}(x_1 - x_1^*) + a_{d\,d-1}(x_{d-1} - x_{d-1}^*) + a_{dd}(x_d - x_d^*)\right)\\
&\times (x_d - x_d^*)\\
=& \sum_{i=1}^{d} A_i a_{i\,i}(x_i - x_i^*)^2\\
&+ \sum_{i=1}^{d-1} \left(A_i a_{i\,i+1} + A_{i+1}a_{i+1\,i}\right)(x_{i+1} - x_{i+1}^*)(x_i - x_i^*)\\
&+ \left(A_1 a_{1d} + A_d a_{d1}\right)(x_d - x_d^*)(x_1 - x_1^*).
\end{aligned}
$$

Let $A_1 = 1$ and

$$
A_{i+1} = -A_i \frac{a_{i\,i+1}}{a_{i+1\,i}},\ \ i = 1, \dots, d-1.
$$

Obviously: $A_1 > 0$, $A_2 = -\dfrac{a_{12}}{a_{21}} > 0$, $A_3 = \dfrac{a_{12}}{a_{21}}\dfrac{a_{23}}{a_{32}} > 0$, ..., and moreover $A_1 a_{1d} + A_d a_{d1} = 0$, because

$$A_d = (-1)^d \left(\prod_{i=1}^{d-1} a_{i\,i+1}\right)\left(\prod_{i=1}^{d-1} a_{i+1\,i}\right)^{-1}.$$

and condition (4) of the theorem.

Then the total derivative of $\Psi(\boldsymbol{x})$ simplifies to

$$\dot{\Psi}(\boldsymbol{x}) = -\sum_{i=1}^{d} A_i\,|a_{i\,i}|\,(x_{i-1} - x_{i-1}^*)^2.$$

In general for the function $\Psi(\boldsymbol{x})$ we have:

1. The function $\Psi(\boldsymbol{x})$ is smooth and bounded below (because it is a sum of bounded below functions).
2. The total derivative $\dot{\Psi}(\boldsymbol{x})$ is not a positive function.
3. $\dot{\Psi}(\boldsymbol{x}) = 0$ if and only if $\boldsymbol{x} = \boldsymbol{x}^*$.

Therefore, the proof of Theorem 5 follows from LaSalle's Invariance Principle (see [15], [16], also Section 14 and Section 34 in [22], [2], [21]). □

Example 6. Consider the system

$$\begin{aligned}\dot{x}_1 &= x_1(-x_1 + x_2 - 8x_3 + 8),\\ \dot{x}_2 &= x_2(-x_1 - 2x_2 + 4x_3 - 1),\\ \dot{x}_3 &= x_3(2x_1 - x_2 - 1).\end{aligned} \tag{9}$$

The stationary points are $(0,0,0)$ and $(1,1,1)$.

It is not hard to calculate:

$$\begin{aligned} A_1 &= A_2 = A_3 = 1,\\ \Psi(\boldsymbol{x}) &= \sum_{i=1}^{3}(x_i - \ln x_i),\\ \dot{\Psi}(\boldsymbol{x}) &= -(x_1 - 1)^2 - 2(x_2 - 1)^2.\end{aligned}$$

Then all conditions of the previous theorem hold true. Hence the system has not any closed orbits in $\mathbb{R}^d_+$. Moreover the ω-limit set of all bounded orbits is the non-trivial stationary point (see Figure 3).

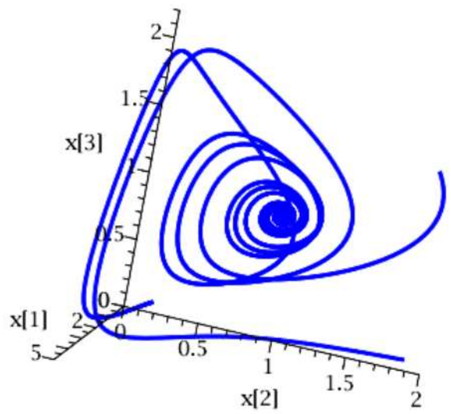

Figure 3: Some orbits of the system (9)

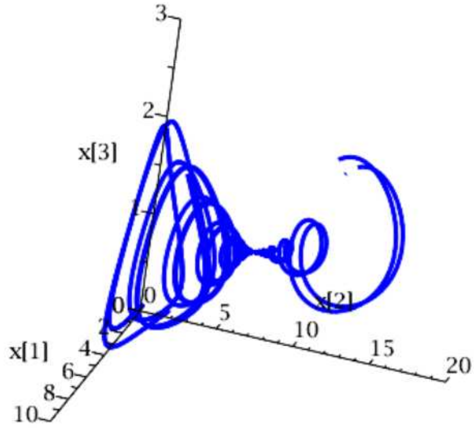

Figure 4: Some orbits of the system (10)

Of course the situation in the case $a_{11} < 0$ but $a_{22} = a_{33} = 0$ is similar, see Figure 4, where some orbits of the system

$$\begin{aligned} \dot{x}_1 &= x_1(-x_1 + x_2 - 8x_3 + 8), \\ \dot{x}_2 &= x_2(-x_1 + 4x_3 - 1), \\ \dot{x}_3 &= x_3(2x_1 - x_2 - 1). \end{aligned} \tag{10}$$

are plotted.

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